

Review Article

Effect of Silicon on Rice Blast Disease

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ABSTRACT

Silicon is the second most plentiful element in soil and is beneficial for a large variety of plants. It is concentrated in plant tissues in quantities similar to that of macronutrients. Considerable damages to plants caused by abiotic stresses such as drought stress, salinity stress, heavy metal stress and nutrient imbalance, as well as biotic stresses like insect pests and pathogens and even herbivorous attacks, have been reported to be reduced significantly by silicon application. Among rice diseases, blast is recognized as the most devastating one. Silicon fertilization has been reported to be efficacious in controlling and mitigating rice blast severity. Two different hypotheses are proposed for the ability of silicon to lessen disease severity. The first hypothesis emphasizes on silicon function as a mechanical barrier against appressorial penetration, while the second hypothesis is based upon the belief that silicon has some physiological roles in disease resistance.

Keywords: Silicon, rice, *Pyricularia oryzae*, blast

WHAT IS SILICON?

Silicon (Si) is the second most abundant element in soil and it is considered as an absolutely useful element for a large variety of plants (Nakata *et al.*, 2008). In fact, silicon forms 28% of the earth's surface (Rodrigues & Datnoff, 2005; Elawad & Green, 1979; Singer & Munns, 2005; Epstein, 1994). Although it is usually not classified as an essential element for higher plants (Hayasaka *et al.*, 2008; Marschner, 1995; Epstein, 1994), silicon is concentrated at levels equivalent

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to those of macro nutrients (Kamenidou *et al.*, 2009; Epstein, 1994). The positive impacts of silicon in improving plant growth and yield are significant, and these include increasing resistance against environmental stresses such as cold and salinity stress, insect attacks and penetration of pathogens (Jones & Handreck, 1967; Elawad & Green, 1979; Belanger *et al.*, 1995; Savant *et al.*, 1996). In addition to what has been mentioned above, using appropriate amount of silicon has been found to reduce the probability of plants being grazed by herbivores (Rodrigues & Datnoff, 2005; Belanger *et al.*, 1995; Datnoff *et al.*, 1997; Savant *et al.*, 1996). Meanwhile, a large number of valuable investigations have been conducted on the positive effects of silicon in plants. Many plant species, especially those from the family of *Poaceae*, are able to accumulate silicon in their tissues (Hayasaka *et al.*, 2008; Ma *et al.*, 2006). Typically in soils with low amounts of silicon, silicon fertilization has been applied to increase both the quality and quantity of agricultural crops such as rice and sugar cane (Korndorfer & Lepsch, 2001). In addition, foliar applications of silicon have been confirmed to increase the resistance against pathogens in plant species that do not absorb silicon efficiently (Epstein, 1994; Bowen *et al.*, 1992). Much of the research on silicon has been focused on rice, although its benefits to other crops such as wheat and corn have also been proven (Wang *et al.*, 2001). The goal of this article is to review the research findings in relation to silicon and rice blast disease.

Rice is considered as one of the major crops in view of its vast consumption as a source of energy throughout the world (Hayasaka *et al.*, 2008; Greenland, 1997) and its capability to actively absorb silicon in high amounts. Under silicon deficient conditions, some diseases such as blast, brown spot and sheath blight can be extremely threatening to rice cultivation (Rodrigues & Datnoff, 2005). Accumulated silicon in rice tissues enhances resistance against insects and diseases, increases erectness of leaves resulting in increased photosynthesis, improves water usage, and decreases toxicity of heavy metals and cuticular transpiration (Nakata *et al.*, 2008; Epstein, 1994). Accumulation rates of silicon in different plants vary between 1-10 % (Elawad & Green, 1979; Epstein, 1994) and monocots store more silicon in comparison to dicots (Rodrigues & Datnoff, 2005; Jones & Handreck, 1967; Epstein, 1999; Rodrigues *et al.*, 2001). The amounts of silicon accumulated in rice plants can be as much as 10% of plant dry weight. It is often several times higher than the rate of accumulation of other essential macro nutrients such as nitrogen, phosphorus and potassium (Nakata *et al.*, 2008; Ma *et al.*, 2006). In the tropics (where the soils are classified as Ultisols and Oxisols), high levels of weathering may result in nutrient deficiencies in soils, particularly silicon (Rodrigues & Datnoff, 2005; Juo & Sanchez, 1986). Silicon deficiency has also been observed in highly organic soils, as these soil types contain low amounts of minerals (Rodrigues & Datnoff, 2005; Savant *et al.*, 1996).

It is clear that pests and diseases cause significant losses to rice plantings (Nakata *et al.*, 2008; Ou, 1985). Rice blast disease, caused by the fungus *Pyricularia oryzae* (Couch & Kohn, 2002), is particularly prevalent in all areas under rice cultivation and it also causes heavy yield losses (Nakata *et al.*, 2008; Ou, 1985). Development of efficient and cost-effective methods to manage the disease is one of the priority issues in rice production (Hayasaka *et al.*, 2008). There are many management methods that are being evaluated for rice blast disease management and these include, among others, breeding of resistant varieties (time consuming) and management methods to improve soil nutrients (Hayasaka *et al.*, 2008).

Rice productivity has been reported to be higher in temperate regions as compared to the tropics (Rodrigues & Datnoff, 2005; Savant *et al.*, 1997) because the amount of silicon in the tropical soils is about 5 to 10 times lower than its amount in the temperate region soils (Rodrigues & Datnoff, 2005; Foy, 1992).

The minimum amount of silicon needed to control blast disease in rice is 3-5% (Datnoff *et al.*, 1997). Positive effects and importance of silicon as a nutrient element in rice plants have been reported in several studies (Hayasaka *et al.*, 2008; Ando *et al.*, 2002; Ma *et al.*, 2006; Kamenidou *et al.*, 2009; Deren *et al.*, 1992; Ma & Takahashi, 2002; Gao *et al.*, 2004) and a gene which plays a role in the transport of silicon has also been detected (Hayasaka *et al.*, 2008; Ma *et al.*, 2006).

Silicon is an important element which is applied to paddy farms in the form of fertilizers (Ohta *et al.*, 1953; Snyder *et al.*, 1986). Plants absorb silicon in the form of mono silicic acid $\text{Si}(\text{OH})_4$ (Rodrigues & Datnoff, 2005; Elawad & Green, 1979), which is accumulated in cell walls as silica gel. $\text{SiO}_2\text{-nH}_2\text{O}$ is also referred to as 'Opals' or 'Phytoliths' in leaves (Rodrigues & Datnoff, 2005; Yoshida *et al.*, 1962; Lanning, 1963). The highest rate of silicon accumulation in leaves can be observed in epidermal cells (Rodrigues & Datnoff, 2005; Elawad & Green, 1979). Besides the positive effects which have been mentioned for silicon, its presence in plant tissue at high concentrations does not cause any toxicity or damage to the plant (Ma *et al.*, 2006).

BLAST SUPPRESSION BY SILICON APPLICATION

In the early twentieth century, many Japanese researchers stated that the use of various sources of silicon would increase resistance of rice to blast disease (Ishiguro, 2001). Similarly, subsequent studies have also confirmed that the application of silicon is an effective method to reduce and control rice blast disease (Datnoff *et al.*, 1991; Hayasaka *et al.*, 2005; Seebold *et al.*, 2000; Seebold *et al.*, 2001).

In retrospect, the authors found beneficial effects of silicon on growth of rice, as demonstrated by Sommer (1926). The usefulness of silicon application to confer resistance in rice plants against blast was demonstrated by Kawashima in 1927 as well. The amount of silicon applied to

soil and the concentration of silicon in rice husks and straw had a linear relationship and both were inversely proportional with blast severity. Similar findings were reported by Inokari and Kubota (1930), Ito and Hayashi (1931) and Miyake and Ikeda (1932), who confirmed the beneficial effects of silicon application in conferring resistance against blast. A significant reduction of blast severity due to various silicon sources applied to paddy fields was demonstrated in Japan (Suzuki, 1935; Kozaka, 1965). In 1997, a study was conducted at the Rice Research Institute of Iran (RRII) to assess the effects of application of silica on the growth and yield of a local rice variety. Silicon was applied as calcium silicate at 0, 400, 800 and 1600 kg/ha. The highest increase in dry matter and grain yield was observed with the application of 400 kg/ha of calcium silicate (Kumleh & Kavossi, 2003). Meanwhile, the application of calcinated serpentinit as a silicon source prior to rice planting has also been reported to be effective in reducing leaf blast severity and this reduction has a linear relationship with tissue sugar content. This indicates that the reduction of blast severity in leaves with increased rates of calcinated serpentinite is linear and can therefore be ascribed to decreased sugar levels (Prabhu *et al.*, 2007).

In the late 1950s, the first attempt to assess the possible uses of industrial by-products containing silicon as fertilizers was conducted in China. Subsequently, silicon application as fertilizers has increased steadily since 1970, and Si fertilizers have been applied repeatedly to improve rice

production by enhancing resistance to diseases (Wang *et al.*, 2001) and increasing yields (Zhu & Chen, 1963).

Silicon fertilization was reported to have significantly reduced the occurrence of blast in rice plants (Qin, 1979; Zang, 1989). The degree of resistance increased in proportion to the amount of silicon accumulated in the plants (Chen *et al.*, 1985; Chen, 1989). Shui *et al.* (1995) determined the efficacy of silicon fertilization on rice disease resistance to leaf and neck blast in silicon deficient soil. The results revealed that the resistance of rice to blast was enhanced by silicon application, and that disease index for leaf and neck blast was reduced by 50.5 and 26.8%, respectively. Maekawa *et al.* (2001) evaluated two sources of silicon on the blast occurrence in rice seedlings; one as silica gel and the other as potassium silicate. The silica gel application at 200 or 250 g per nursery bed (2.5 kg soil) significantly limited the blast occurrence to 10% of the control (without application). Potassium silicate application at 12 g per nursery bed was also effective in controlling the occurrence of blast. It was reported that silicon addition to soils increased rice yields by up to 10% and these increased yields could exceed 30% where leaf blast was severe (Yoshida, 1981; Korndorfer & Lepsch, 2001).

It has also been reported that rice blast severity is directly related with silicon deficiency in soils (Kim *et al.*, 2002; Rodrigues *et al.*, 2003; Ranganathan *et al.*, 2006). In Colombia, experiments were conducted in soils classified as Oxisols (with

silicon deficiency) to assess the effects of silicon deficiency on favouring rice blast. Different levels and sources of silicon including Calcium Meta Silicate, as well as slag, were tested, and it was reported that silicon fertilization significantly reduced the severity of leaf (26%) and neck blast (53%) in non-treated plots to 15% in silicon-treated ones. It was also revealed that disease development could be further controlled due to the residual effect after years of silicon applications and this could be an efficient control method in rice production (Correa-Victoria *et al.*, 2001).

Several researchers have demonstrated that silicon application has a suppressive effect on fungal diseases such as rice blast (*Magnaporthe grisea*, teleomorph, *Pyricularia oryzae*, anamorph), brown spot (*Cochliobolus miyabeanus*, teleomorph; *Bipolaris oryzae*, anamorph), leaf scald (*Gerlachia oryzae*), sheath blight (*Rhizoctonia solani*, teleomorph) and stem rot (*Sclerotium oryzae*, teleomorph) (Datnoff *et al.*, 1991, 1992, 1997; Savant *et al.*, 1997; Seebold, 1998; Winslow, 1992). Datnoff *et al.* (1991, 1992) reported decreases in blast severity ranging from 17 to 30% in the rice planting regions of Colombia on Histosols where silicon was applied. Disease severity tended to be reduced by increasing the concentration of silicon in tissues.

On the other hand, Okamoto (1957a, 1957b) observed that under silicon deficiency, the growth of rice was inhibited and this caused dying-off of leaf blades after heading, resulting in differences in

the dry weights between the silicon-treated rice and non-treated ones. Moreover, dark brown spots were also observed on the stems and head of rice of the untreated plants. *Pyricularia oryzae* was isolated from the dark brown spots. It was concluded that silicon might not be an essential element for the growth of rice plants, since rice could ripen even without silicon, but silicon was considered as an agronomically essential element for rice production, since silicon deficiency causes significant reductions in grain yield.

In 2001, Ishiguro announced that silicon could alleviate rice blast. During cold summers, the occurrence of disease is usually serious. According to Ohyama (1985), silicon supplied to soil as compost (36 tonnes per hectare) and calcium silicate (1.8 tonnes per hectare) resulted in meaningful increases in the silicon content of leaf blades and a significant decrease in the severity of leaf blast as well as ear blast. Calcium silicate application caused an increase in the Si to N ratio, and resulted in the control of blast. In the year with a cold summer, the N content of rice plants was high, while the silicon content was low since silicon uptake decreased at low temperature. This resulted in a favourable silicon to N ratio, and thus explained why in a cold summer year, silicon application was more capable of reducing blast severity and damage.

Hayasaka *et al.* (2005) investigated the content of SiO₂ which was necessary for rice plants to be resistant against rice blast disease. Nine rice cultivars with different

complete resistance genes, as well as various degrees of partial resistance, were planted in nursery soils with different rates of silica gel amendment. At 28 days after planting, seedlings were inoculated with rice blast fungus (*Pyricularia oryzae*) to evaluate resistance of seedlings to blast. The results confirmed that the number of infections in all the cultivars was decreased significantly by increasing the silicon content of rice seedlings. The results showed that by increasing the SiO₂ content of the seedlings to 5%, a significant decrease could be observed in the number of blast lesions. Based on these findings, a 5% SiO₂ content in rice seedlings would be effective in controlling blast disease under a range of conditions.

Seebold *et al.* (2000) also studied the effects of different rates of silicon application as well as host resistance on the severity of blast in upland rice, and concluded that in soils with insufficient amounts of silicon, the application of silicon could reduce the severity of leaf and neck blast in partially resistant and susceptible cultivars. The reduction was dependent on the rates of silicon applied as well as disease pressure. Meanwhile, in areas where disease pressure is not very high, lower rates of silicon application can be sufficiently effective for disease control.

Providing appropriate amounts of silicon to the plants cultivated in silicon deficient soils could considerably improve the rate of plant growth as well as its resistance against biotic and abiotic stresses (Kamenidou *et al.*, 2009; Menzies *et al.*, 1991; Ma *et al.*,

2001; Savvas *et al.* 2002). Among the most controversial impacts and benefits of silicon is its ability to reduce transpiration and to increase photosynthesis rates in some plants such as rice (*Oryza sativa* L.), corn (*Zea mays* L.), soybeans (*Glycine max* L.), and wheat (*Triticum aestivum* L.) (Kamenidou *et al.*, 2009; Kupfer & Kahnt, 1992; Pandley & Yadav, 1999; Gao *et al.*, 2004). These effects may be related to the distribution of silicon in the cell wall as a double silicon-cuticle layer (Kamenidou *et al.*, 2009; Ma & Takahashi, 2002), and also its role as a mechanical barrier against pathogens and pests (Kamenidou *et al.*, 2009; Belanger *et al.*, 1995). Under drought stress condition, silicon can further stimulate and increase photosynthesis (Kamenidou *et al.*, 2009; Matoh *et al.*, 1991; Trenholm *et al.*, 2004). This may be caused by lower transpiration rates due to silicon accumulation in the leaves (Kamenidou *et al.*, 2009).

POSSIBLE MECHANISMS FOR SILICON MEDIATED RISE RESISTANCE

There are different hypotheses on how silicon confers and induces resistance to some plants specially rice against diseases such as blast (Ishiguro, 2001). These hypotheses can be classified into two groups (Hayasaka *et al.*, 2008).

One hypothesis is based on the belief that silicon acts as a mechanical barrier against fungal penetration (Hayasaka *et al.*, 2008) which is also known as physical resistance, while the second hypothesis is based upon physiological resistance. The

first suggests that resistance induced by silicon is the result of increased number of silicified bulliform cells in the epidermis of leaves that act as a physical barrier to impede penetration by *M. grisea* (Ishiguro, 2001; Snyder *et al.*, 1986). This physical barrier hypothesis is further strengthened by the findings of Yoshida *et al.* (1962) who reported the existence of a layer of silica beneath the cuticle of rice leaves and sheath. These cuticles inhibit the penetration of *M. grisea*, and consequently decrease the number of infections on the leaves. Volk *et al.* (1958) suggested the formation of complexes with organic compounds with silicon in cell walls of epidermis cells, thereby conferring resistance to degradation by the enzymes released by *M. grisea*. In fact, silicon can be associated with lignin-carbohydrates complexes in the cell wall of rice epidermal cells (Inanaga *et al.*, 1995).

The second suggests that the induced resistance is the result of silicon cuticle double-layer formation (Hayasaka *et al.*, 2008; Sakamoto, 1968). This kind of resistance could be related to the conservative action of Si-cuticle layer against $\text{NH}_4\text{-N}$ volatilization loss from the surface of leaves (Park, 1982), since dissolving volatilized $\text{NH}_4\text{-N}$ in dew drops or rain water can act as a nutrition source for the spores of pathogens.

On the other hand, the other group believes that the induction of resistance to plants by silicon is as a result of phenolics and phytoalexins accumulation and is related to the activity of P-R genes (Rodrigues & Datnoff, 2005). Rodrigues *et al.*, (2003)

investigated the ultrastructural changes of the rice-*M. grisea* interaction upon silicon application, which provided the first cytological evidence that silicon-mediated resistant to *M. grisea* was related with the deposition of the osmophilic material that occluded the epidermal cells. These amorphous materials contain phenolic compounds which play a crucial role in rice defence response against infection by *M. grisea*. Therefore, silicon could be acting as a modulator to positively amplified rice defence responses, i.e. by influencing the synthesis of antifungal compounds after the penetration peg of *M. grisea* into the epidermal cell. Rodrigues *et al.* (2004) further hypothesized that the alteration of the development of *M. grisea* in leaf tissue of rice plant amended with silicon could be associated with an enhanced production of phytoalexins. The evidence obtained from their research indicated that antifungal compounds (phytoalexins) were present 2 to 3 times more in the leaf extract from the plants amended with silicon and inoculated with *M. grisea* as compared to the lower levels observed in the leaf extract from non-inoculated plants amended with or without silicon. The rice plants that were not amended with silicon and inoculated with *M. grisea* were not protected against fungal colonization, in spite of releasing antifungal compounds. By contrast, the rice plants amended with silicon and inoculated with *M. grisea* released higher amounts of antifungal compounds, probably earlier in the infection process, benefited from a lower level of blast severity.

While little is known about the mechanism(s) of the resistance of rice plants amended with silicon 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 silicon deposition, delayed fungal ingress and colonization provide the rice plant enough time for synthesizing the antifungal compounds in response to infection by *M. grisea* to accumulate considerable levels and to express their fungitoxicity within the zone of the infection site. On the other hand, as proposed, the soluble silicon present in the plant cells may mediate some defense responses that are functionally similar to systemic acquired resistance. Evidence put forth by several researchers strongly suggest that silicon plays an active role in the resistance of rice plant to blast rather than simply forming physical barrier in leaf epidermis to impede fungal penetration.

FUTURE OUTLOOK

Although the function of silicon in rice plant is not wholly recognized, the application of this element would be an encouraging method to improve rice production in areas with soils poor in silicon, since it has been known to have the ability to lessen vulnerability of rice against different kinds of diseases, specifically those caused by fungal pathogens such as *Pyricularia oryzae*.

An important fact about silicon in addition of the aforementioned points is that it is an environmentally friendly

element in relation to soils, fertilizers and plant nutrition. Hence, it can be beneficial in IPM programmes for those crops where silicon has been proven to have a positive impact. However, silicate slags are not only expensive sources of silicon to be applied as fertilizers, many of these are also high in heavy metals which may discourage their use due to environmental concern. Therefore, it is necessary to find more cost effective silicon sources especially in the tropics where soils are poor in silicon. Recycling rice straw and husks can be considered as alternatives that provide cheaper silicon sources. Meanwhile, the positive effects of silicon in plant nutrition and resistance against diseases have been well established. Thus, providing the knowledge about silicon to farmers and rice growers will help the agriculture industry to manage and control rice diseases effectively. Such efforts will ensure the production of safe food and provide for adequate environmental protection.

REFERENCES

- Ando, H., Kakuda, K., Fujii, H., Suzuki, K., & Ajiki, T. (2002). Growth and canopy structure of rice plants grown under field conditions as affected by Si application. *Soil science and plant nutrition*, 48(3), 429-432.
- Belanger, R. R., Bowen, P. A., Ehret, D. L., & Menzies, J. G. (1995). Soluble silicon: its role in crop and disease management of greenhouse crops. *Plant Disease*, 79(4), 329-336.
- Bowen, P., Menzies, J., Ehret, D., Samuels, L., & Glass, A. D. M. (1992). Soluble silicon sprays inhibit powdery mildew development on grape leaves. *Journal of the American Society for Horticultural Science*, 117(6), 906-912.

- Chen, C. Q., Xu, Y. L., Qin, S. C., Zheng, W. Z., Lin, Z. S., & Wu, Z. J. (1985). Investigation of the relationship between rice blast and silicon contents in rice and paddy soil analyzed by fast neutron activation. *Application of Atomic Energy in Agriculture*, 3, 13-16.
- Chen, Z. Q. (1989). Investigations on tile mechanism of resistance to rice blast disease. *Journal of South China Agricultural University* 10, 82-91.
- Correa-Victoria, F., Datnoff, L. E., Okada, K., Friesen, D. K., Sanz, J. I., & Snyder, G. H. (2001). Effects of silicon fertilization on disease development and yields of rice in Colombia. *Studies in Plant Science*, 8, 313-322.
- Couch, B. C., & Kohn, L. M. (2002). A multilocus gene genealogy concordant with host preference indicates segregation of a new species, *Magnaporthe oryzae*, from *M. grisea*. *Mycologia*, 94(4), 683-693.
- Datnoff, L. E., Raid, R. N., Snyder, G. H., & Jones, D. B. (1991). Effect of calcium silicate on blast and brown spot intensities and yields of rice. *Plant Disease*, 75(7), 729-732.
- Datnoff, L. E., Snyder, G. H., & Deren, C. W. (1992). Influence of silicon fertilizer grades on blast and brown spot development and on rice yields. *Plant Disease*, 76(10), 1011-1013.
- Datnoff, L. E., Deren, C. W., & Snyder, G. H. (1997). Silicon fertilization for disease management of rice in Florida. *Crop Protection*, 16(6), 525-531.
- Deren, C., Datnoff, L., & Snyder, G. (1992). Variable silicon content of rice cultivars grown on everglades histosols. *Journal of plant nutrition*, 15(11), 2363-2368.
- Elawad, S. H., & Green, V. E. (1979). Silicon and the rice plant environment: A review of recent research. *Il Riso*, 28, 235-253.
- Epstein, E. (1994). The anomaly of silicon in plant biology. *Proceedings of the National Academy of Sciences*, 91(1), 11-17.
- Epstein, E. (1999). Silicon. *Annual review of plant physiology and plant molecular biology*, 50(1), 641-664.
- Foy, C. D. (1992). Soil chemical factors limiting plant root growth. *Advances in soil science*, 19, 97-149.
- Gao, X., Zou, C., Wang, L., & Zhang, F. (2004). Silicon improves water use efficiency in maize plants. *Journal of plant nutrition*, 27(8), 1457-1470.
- Greenland, D. J. (1997). *The sustainability of rice farming*: CABI.
- Hayasaka, T., Fujii, H., & Namai, T. (2005). Silicon content in rice seedlings to protect rice blast fungus at the nursery stage. *Journal of General Plant Pathology*, 71(3), 169-173.
- Hayasaka, T., Fujii, H., & Ishiguro, K. (2008). The role of silicon in preventing appressorial penetration by the rice blast fungus. *Phytopathology*, 98(9), 1038-1044.
- Inanaga, S., Okasaka, A., & Tanaka, S. (1995). Does silicon exist in association with organic compounds in rice Plant? *Japan Journal of Soil Science. Plant Nutrition*, 11, 111-117.
- Inokari, G., & Kubota, T. (1930). On the effect of soil dressing and silica application to peatland paddy fields. *Journal of Sapporo Society of Agriculture Science*, 98, 484-485.
- Ishiguro, K. (2001). Review of research in Japan on the roles of silicon in conferring resistance against rice blast. *Studies in Plant Science*, 8, 277-291.
- Ito, S., & Hayashi, H. (1931). On the relation of silica supply to rice blast. *Journal of Sapporo Society of Agriculture Science*, 103, 460-461.
- Jones, L., & Handreck, K. (1967). Silica in soils, plants, and animals. *Advances in Agronomy*, 19(2), 107-149.

- Juo, A. S. R., & Sanchez, P. A. (1986). *Soil nutritional aspects with a view to characterize upland rice environments*. Paper presented at the 2nd International Upland Rice Conference.
- Kamenidou, S., Cavins, T. J. & Marek, S. (2009). Evaluation of silicon as a nutritional supplement for greenhouse zinnia production. *Scientia Horticulturae*, 119(3), 297-301.
- Kawashima, R. (1927). Influence of silica on rice blast disease. *Japanese Journal of Soil Science and Plant Nutrition*, 1, 86-91.
- Kim, S. G., Kim, K. W., Park, E. W., & Choi, D. (2002). Silicon-induced cell wall fortification of rice leaves: a possible cellular mechanism of enhanced host resistance to blast. *Phytopathology*, 92(10), 1095-1103.
- Korndorfer, G., & Lepsch, I. (2001). Effect of silicon on plant growth and crop yield. *Studies in Plant Science*, 8, 133-147.
- Kozaka, T. (1965). *Control of rice blast by cultural practices in Japan*. The Rice Blast Disease. Proceedings of a symposium at The International Rice Research Institute. Baltimore: Johns Hopkins University Press.
- Kumleh, S. A., & Kavossi, M. (2003). Evaluation of Interaction of Silica and Phosphorous on the Growth and Grain Yield of Rice (*Oryza sativa* L.). *Iranian Journal of Agricultural Science* 35(3), 581-586.
- Kupfer, C., & Kahnt, G. (1992). Effects of application of amorphous silica on transpiration and photosynthesis of soybean plants under varied soil and relative air humidity conditions. *Journal of Agronomy and Crop Science*, 168(5), 318-325.
- Lanning, F. C. (1963). Silicon in rice. *Journal of Agriculture and Food Chemistry*, 11, 435-437.
- Ma, J., Miyake, Y., & Takahashi, E. (2001). Silicon as a beneficial element for crop plants. *Studies in Plant Science*, 8, 17-39.
- Ma, J. F., & Takahashi, E. (2002). *Soil, fertilizer, and plant silicon research in Japan*: Elsevier Science.
- Ma, J. F., Tamai, K., Yamaji, N., Mitani, N., Konishi, S., Katsuhara, M., Ishiguro, M., Murata, Y., & Yano, M. (2006). A silicon transporter in rice. *Nature*, 440, 688-691.
- Maekawa, K., Watanabe, K., Aino, M., & Iwamoto, Y. (2001). Suppression of rice seedling blast with some silicic acid materials in nursery box. *Japanese Journal of Soil Science and Plant Nutrition*, 72(1), 56-62.
- Marschner, H. (1995). *Mineral Nutrition of Higher Plants*. San Diego: Academic Press.
- Matoh, T., Murata, S., & Takahashi, E. (1991). Effect of silicate application on photosynthesis of rice (*Oryza sativa*) plants. *Japanese Journal of Soil Science and Plant Nutrition*, 62(3), 248-251.
- Menzies, J. G., Ehret, D. L., Glass, A. D. M., Helmer, T., Koch, C., & Seywerd, F. (1991). Effects of soluble silicon on the parasitic fitness of *Sphaerotheca fuliginea* on *Cucumis sativus*. *Phytopathology*, 81, 84-88.
- Miyake, K., & Ikeda, M. (1932). Influence of silica application on rice blast. *Japanese Journal of Soil Science and Plant Nutrition*, 6, 53-76.
- Nakata, Y., Ueno, M., Kihara, J., Ichii, M., Taketa, S., & Arase, S. (2008). Rice blast disease and susceptibility to pests in a silicon uptake-deficient mutant. *Crop Protection*, 27, 865-868.
- Ohta, M., Kobayashi, K., & Kawaguchi, U. (1953). Studies on silicates for fertilizer use. *Memoirs of the Faculty of Liberal Arts and Education*, 4, 351-358.
- Ohyama, N. (1985). Effect of improvement in fertilization on the alleviation of cool-summer damage to rice. *Agriculture and Horticulture* 11, 1385-1389.
- Okamoto, Y. (1957a). Physiological studies of the effects of silicic acid upon rice plant n.

- Memoirs of the Faculty Liberal Arts Education*, 8, 172-175.
- Okamoto, Y. (1957b). Physiological studies of the effects of silicic acid upon rice plant in. *Proceedings of the Crop Science Society of Japan*, 25, 219-221.
- Ou, S. H. (1985). *Rice diseases* (Second ed.). Commonwealth Mycological Institute, Kew, England.
- Pandley, A. K., & Yadav, R. S. (1999). Effect of antitranspirants on physiological traits and yield of wheat under water deficit conditions. *Indian Journal of Agriculture Research*, 33(3), 159-164.
- Park, C. S. (1982). Conservation and management of soil resources as a basis of agricultural production. *The Association of Korean Agricultural Science Societies*, 128.
- Prabhu, A. S., Santos, A. B., & Didonet, A. D. (2007). Soluble tissue sugar content and leaf blast severity in response to the application of calcinated serpentinite as a silicon source in irrigated rice. *Summa Phytopathologica*, 33(4), 402-404.
- Qin, S. C. (1979). Effects of Si fertilizer on the enhancement of resistance of against fungal diseases and yield. *Journal of Zhejiang Agricultural Science*, 1, 12-15.
- Ranganathan, S., Suvarchala, V., Rajesh, Y. B. R. D., Prasad, M. S., Padmakumari, A. P., & Voleti, S. R. (2006). Effect of silicon sources on its deposition, chlorophyll content, and disease and pest resistance in rice. *Biologia Plantarum*, 50(4), 713-716.
- Rodrigues, F. A., Korndorfer, G. H., Correa, G. F., Buki, G. B., Silva, O. A., & Datnoff, L. E. (2001). Response of six gramineae species to application of calcium metasilicate. In L. E. Datnoff, G. H. Snyder, & G. H. Korndorfer (Eds.), *Silicon in Agriculture. Studies in Plant Science* (Vol. 8, pp. 378). Amsterdam, The Netherlands: Elsevier Science, BV.
- Rodrigues, F. A., Benhamou, N., Datnoff, L. E., Jones, J. B., & Belanger, R. R. (2003). Ultrastructural and cytochemical aspects of silicon-mediated rice blast resistance. *Phytopathology*, 93(5), 535-546.
- Rodrigues, F. A., McNally, D. J., Datnoff, L. E., Jones, J. B., Labbe, C., Benhamou, N., Menzies, J. G., & Belanger, R. R. (2004). Silicon enhances the accumulation of diterpenoid phytoalexins in rice: a potential mechanism for blast resistance. *Phytopathology*, 94(2), 177-183.
- Rodrigues, F. A., & Datnoff, L. E. (2005). Silicon and rice disease management. *Fitopatologia Brasileira*, 30(5), 457-469.
- Sakamoto, M. (1968). *Studies on resistance of rice to rice blast disease*. Sapporo, Jubilee Publication.
- Savant, N., Snyder, G., & Datnoff, L. (1996). Silicon management and sustainable rice production. *Advances in Agronomy*, 58, 151-199.
- Savant, N. K., Datnoff, L. E., & Snyder, G. H. (1997). Depletion of plant available silicon in soils: A possible cause of declining rice yields. *Communications in Soil Science and Plant Analysis*, 28, 1245-1252.
- Savvas, D., Manos, G., Kotsiras, A., & Souvaliotis, S. (2002). Effects of silicon and nutrient- induced salinity on yield, flower quality and nutrient uptake of gerbera grown in a closed hydroponic system. *Journal of Applied Botany*, 76, 153-158.
- Seebold, K. W. (1998). *The Influence of Silicon Fertilization on the Development and Control of Blast, Caused by Magnaporthe Grisea (Herbert) Barr; in Upland Rice* (Doctoral Thesis dissertation). University of Florida.
- Seebold, K., Datnoff, L., Correa-Victoria, F., Kucharek, T., & Snyder, G. (2000). Effect of silicon rate and host resistance on blast, scald, and yield of upland rice. *Plant Disease*, 84(8), 871-876.

- Seebold, K., Kucharek, T., Datnoff, L., Correa-Victoria, F., & Marchetti, M. (2001). The influence of silicon on components of resistance to blast in susceptible, partially resistant, and resistant cultivars of rice. *Phytopathology*, *91*(1), 63-69.
- Shui, M. X., Du, X. F., Chen, D. F., Ye, C., & Li, Q. (1995). Effect of soluble silicon fertilizer on rice resistance to blast. *Acta Agriculturae Zhejiangensis*, *7*, 289-292.
- Singer, M. J., & Munns, D. N. (2005). *Soils: An Introduction*. Prentice Hall.
- Snyder, G., Jones, D., & Gascho, G. (1986). Silicon fertilization of rice on Everglades Histosols. *Soil Science Society of America Journal*, *50*(5), 1259-1263.
- Sommer, A. L. (1926). *Studies concerning the essential nature of aluminum and silicon for plant growth*. University of California press.
- Suzuki, H. (1935). The influence of some environmental factors on the susceptibility of the rice plant to blast and Helminthosporium diseases and on the anatomical characters of the plant III. Influence of differences in soil moisture and in amounts of fertilizer and silica given. *Journal of the College of Agriculture*, *13*, 277-331.
- Trenholm, L. E., Datnoff, L. E., & Nagata, R. T. (2004). Influence of silicon on drought and shade tolerance of St. Augustine grass. *Hort. Technology*, *14*(4), 487-490.
- Volk, R. J., Kahn, R. P., & Weintraub, R. L. (1958). Silicon content of the rice plant as a factor influencing its resistance to infection by the blast fungus, *Piricularia oryzae*. *Phytopathology*, *48*, 121-178.
- Wang, H., Li, C., & Liang, Y. (2001). Agricultural utilization of silicon in China. *Studies in Plant Science*, *8*, 343-358.
- Winslow, M. D. (1992). Silicon, disease resistance, and yield of rice genotypes under upland cultural conditions. *Crop science*, *32*(5), 1208-1213.
- Yoshida, S., Ohnishi, Y., & Kitagishi, K. (1962). Chemical forms, mobility and deposition of silicon in rice plant. *Soil Science and Plant Nutrition*, *8*, 107-113.
- Yoshida, S. (1981). *Fundamentals of rice crop science*: Los Baños, Laguna, Philippines, International Rice Research Institute (IRRI).
- Zang, H. L. (1989). Effect of Si fertilizer on rice and the source of Si fertilizer. *Chemical Industry*, *16*, 12-14.
- Zhu, Q., & Chen, E. F. (1963). Properties of slag and their effects on crops grown in various soils. *Acta Pedologia Sinica*, *11*, 70-82.