REVIEW PAPER

Impact of silicon in managing important rice diseases: blast, sheath blight, brown spot and grain discoloration

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Abstract

In the Asia regions, the most important staple food consumed by nearly one-half of the world's population is the rice. However, important diseases of rice namely blast, brown spot, sheath blight and grain discoloration are major limitations on rice production and are becoming more severe on rice grown in silicon (Si) depleted soils, with blast being the most devastating disease. This review presents the research findings on the role of Si in plant protection against diseases, focusing on rice. Absorption of Si in plants takes place in the form of monosilicic acid and rice is known for its capability to actively absorb Si in high amounts. The possible mechanisms of Si mediated alleviation of disease infection are also being explored in this paper.

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Introduction

Disease that occurs to plant may reduce the ability for the plant to survive and in more severe cases could eventually lead to plant death. Lucas *et al.* (1997) define plant disease as a disturbance that averts normal development and brings down the economic or aesthetic value of a plant. Diseases are caused by microorganisms which are usually regarded as pathogens, which include bacteria, fungi and viruses. A plant challenged by pathogenic microorganisms typically responds to changes of physical properties and composition of the cell walls and also, biosynthesis of secondary metabolites that function to restrain disperse of invading pathogens and necrotic lesions at the invasion region. These responses which are known as hypersensitive reaction are very complex and vary based on the nature of the causal agent (Hopkins and Hüner, 2004). Disease affects all parts of plants by reducing the growth and quality of plant, minimizing the absorption, distribution and use of nutrients by the plant, thus may lead to economic loss. Strategies to control diseases are limited and mainly centered on the usage of chemical treatments such as application of fungicides which are environmental concern. Thus, the potential role of mineral nutrition may provide a feasible and significant alternative for disease management. The article's purpose is to review the research findings of beneficial role of silicon (Si) in protecting plants against diseases, mainly emphasizing on rice. The possible mechanisms involved in Si-mediated plant resistance towards disease are also being discussed in this paper.

The element silicon: Since the last decade, Si has become a major subject of interest due to its relevancy to various branches of fields including global change biogeochemistry, agronomy and biotechnology (Guntzer *et al.,* 2010; Neethirajan *et al.,* 2009; Laruelle *et al.,* 2009). After oxygen, Si is the next most plentiful element on the surface of the earth (Matichenkov and Calvert, 2002). Silicon infrequently exists as an integral part of biological matter although it is 146 times more ample than carbon. Silicon shares many properties with carbon

which forms the backbone of many organic molecules. The Si-Si bonds are weaker than C-C bonds, thus formation of the integral component of Si in biomolecules is very rare (Vasanthi *et al.,* 2012). Soil mass consists of about 50-70% of silicon dioxide (SiO_2). About 28% of the earth's surface is formed by Si (Ashtiani *et al.,* 2012; Singer and Munns, 2005; Epstein, 1994). Due to the abundance of Si, all soil-rooted plants hold if not much, little amount of Si in their tissues (Ma and Yamaji, 2006). In the shoot, concentration of Si may exhibit a scale from 0.1-10% Si on dry weight basis and the presence of Si in plants is equivalent to or even exceeding certain amount of other macronutrients such as P, Mg and Ca (Vasanthi *et al.,* 2012; Epstein, 1994). Up to now, essentiality of Si has not been verified thus, Si is considered as a beneficial element. Silicon is not considered as an essential element because it does not play role as a fundamental constituent of the plant structure or metabolism, hence its absence does not affect the completion of plant's life cycle (Epstein and Bloom, 2003). As for this reason, Si is excluded from any formulations of nutrient solutions such as Hoagland nutrient solution (Hossain *et al.,* 2002). Silicon is absorbed by plants from the soil solution as monosilicic acid, or also known as orthosilicic acid [H_4SiO_4] (Meena *et al.,* 2013; Matichenkov *et al.,* 1999; Yoshida, 1975). Once Si is absorbed by plants, it is deposited between the plant cells and regarded as phytolith. The word phytolith derives from the Greek word which means stone of plants. Phytolith ($SiO_2.nH_2O$) is also regarded as plant opal, siliceous plant remains, biogenic silica, amorphous silica gel or silica bodies (Piperno, 2006). Savant *et al.* (1997) reported that crops in the families Poaceae and Cyperaceae absorb Si at concentration levels equal to or larger than some of the essential nutrients like N and K. Plants from the Poaceae plants contain the highest levels of Si with the largest uptake of Si by rice (*Oryza sativa* L.) (Hossain *et al.,* 2007). The difference in Si accumulation level between species is dependent on the different ability of their roots to uptake Si. In the leaf blades of rice, Si is deposited as a 2.5 μm layer right beneath the 0.1 μm cuticle layer, thus forming a fine cuticle-Si double layer (Ma and

Takahashi, 2002). This double-cuticular layer protects plant from multiple biotic and abiotic stresses. Expanding number of studies reveal that Si has a beneficial role in yield increment and promotes growth for many crop species (Sattar *et al.*, 2013; Epstein and Bloom, 2005; Ma, 2009).

Effect of Si in managing rice blast disease: Rice is known to be the most effective Si-accumulator crop with the Si accumulation may exceed 10% of the shoot dry weight which is few-fold greater than the essential macronutrients particularly N, P and K (Ma and Takahashi, 2002). Rice is regarded as the major staple food in many countries as well as primary source of energy and protein (Zhang *et al.*, 2008; Lee and Rush, 1983). In Malaysia, million tones of biomass are being generated each year and one of the contributors to the biomass residues is the rice. About 100 million tons of rice husks are produced annually and 90% of the residues generated come from the emergent countries such as Malaysia (Rebitanim *et al.*, 2013; Islam and Ani, 2000). However like any other crops, rice is subjected to diseases that led to major limitations on the production. Important diseases of rice are blast, sheath blight, brown spot and grain discoloration which can be extremely threatening to cultivation of rice (Datnoff *et al.*, 1992 and 2005).

Rice blast disease caused by the pathogenic fungus called *Pyricularia oryzae* (Cooke) Sacc.) (telemorph *Magnaporthe oryzae* (T.T. Hebert) Yaegashi & Udagawa) Barr is the most devastated and common rice disease specifically occurring in irrigated and tropical upland rice, as well as temperate zone (Ou, 1985; Wattanapayapkul *et al.*, 2011). Outbreaks of blast disease are considered as immensely severe situation as every year enough of rice plant is damaged by this disease alone (Zeigler *et al.*, 1994; Pooja and Katoch, 2014). Rice blast is an airborne disease and infection prevails at the attachment of fungal spores on the surface of leaves using a special adhesive discharged from the tip of the spores. The spores then germinate and develop a specialized infection cell, namely appressorium which create vast

turgor pressure (up to 8MPa) that break into the leaf cuticle, thus invading the underlying leaf tissues (Dean, 1997; Hamer *et al.*, 1988). In organic rice industry, the usage of fungicides to control this disease is not permitted, thus alternate control measures which are environmentally friendly are needed. Silicon application may provide a viable procedure to enhance resistance against blast disease. Positive effects of Si application in controlling blast disease have been reported in many studies (Wattanapayapkul *et al.*, 2011; Seebold, 1988; Seebold *et al.*, 2000; Prabhu *et al.*, 2001).

In Malaysia, Ashtiani *et al.* (2012) investigated the effects of different rates and sources of Si on rice variety MR219 towards controlling the blast disease. Silicon was applied to the soil prior to planting using two different Si sources which were silica gel (0, 60, 120, 180 g/5kg soil) and liquid sodium silicate (0, 1, 2, 3 mL/l), respectively. Results revealed that there was a significant decline on disease severity and incidence for all rice plants that were treated with Si compared to the non-treated rice plants. The Si depositions were more intensive on the dumbbell-shaped cells in the Si-treated plants compared to the non-treated plants. Highest reduction (75%) of disease severity was observed for plants receiving silica gel application at the rate of 120 g. This result confirmed that Si displays a significant role in controlling rice blast fungus.

Hayasaka *et al.* (2005) studied the amount of SiO_2 content in rice seedlings that would be effective in controlling blast. Rice cultivars with dissimilar true resistance genes, as well as partial resistance with different degrees were grown in nursery and given several different rates of silica gel amendment. Rice seedlings at third leaf stage were inoculated with rice blast fungus (*P. grisea*) 28 days after sowing. The results showed that rice seedlings shall contain 5% of SiO_2 content to control blast disease effectively. Even though the number of lesions of rice plant differs depending on the supremacy of particular partial resistance, it was evident that lesions number was significantly reduced when content of SiO_2 increased

in seedlings of all rice cultivars. This was in line with study by Sun *et al.* (2010) who observed that rice plants which were given a single dose of Si (1.7 mM $NaSiO_3$) promptly after inoculation (-/+Si) of rice blast (*M. grisea*) displayed similar high level of suppression against rice blast as the plants that were constantly treated with Si (+/+Si) throughout the whole experiment, with 20.8 and 19.6% of disease severity indices, respectively. These resistance was significantly higher than in the +/- Si plants in which at first they were provided with Si but the Si application was discontinued prior to blast inoculation. It was recorded that the severity index of +/- Si was 33.3%, while -/- Si (control; Si was not given) was 63.7%. The results suggest that available Si present in cell at the time of infection is more significant than that the already deposited Si which is immobile.

Rodrigues *et al.* (2004) planted rice seedlings cv. M201 in plastic pots filled with peat amended with calcium silicate slag (0 and 10 g/pot). At the appearance of the seventh leaf from the main tiller, the rice plants were inoculated with *M. grisea*. Ninety-six hours after inoculation, impact of Si on progression of leaf blast lesions were observed. The leaves of −Si plants exhibited severe chlorosis compared to the +Si plants. Immense and coalescing lesions enclosed by a chlorotic halo were observed on −Si plants, while smaller and more distinct lesions were found developed on +Si plants. In another study, Datnoff *et al.* (2007) demonstrated that deposition of Si was more effective in combating fungal infection when Si is being uptake by the roots. This was confirmed by (Cacique *et al.,* 2013) who studied the impact of root and leaf applications of soluble Si in enhancing rice resistance against blast infection. The result indicated that Si treatment was able to reduce the number and size of lesions and the reduction of blast were best attained when Si was taken up by the roots. Foliar application by spraying the soluble Si or potassium silicate was observed to also decrease the blast severity. However, this method did not lead to deposition of Si on the adaxial leaf epidermis because the Si concentration was not found to increase in the leaf tissues, regardless if the leaves were washed or not before analysis.

Kim *et al.* (2002) grown two rice cultivars namely, i) Jinmi (blast-susceptible cultivar) and ii) Hwaseong (partially resistant cultivar) in a hydroponic culture system containing modified Yoshida's nutrient solution with 0, 50, 100 and 200 ppm of Si treatment. The plants were then subjected to inoculation with two isolates of *M. grisea* (KI-197 and KI-409). The averages disease severity of control and Si-treated plants of cv. Jinmi challenged with KI-409 were 4.96% and less than 1.60%, respectively. For cv. Hwaseong challenged with both isolates, the disease severity was lower compared to cv. Jinmi. Partial resistance rice cultivars are greatly potent in managing blast disease, particularly in regions of tropical lowland (Bonman *et al.,* 1991). Partial resistance is a kind of incomplete resistance designated by decreased formation of spores in spite of the vulnerable response by the host to the pathogen (Parlevliet, 1979). From this study, it was concluded that Si treatments enhanced resistance against blast development regardless of fungal isolates.

Effect of Si in suppressing other diseases of rice: Sheath blight is a fungal disease caused by *Rhizoctonia solani* Kühn and occurs mainly in the temperate and tropical rice-production areas (Zuo *et al.,* 2006). The symptoms of this disease include lesions on sheaths of lower leaves near the water line. These lesions are usually oval to elliptical-shaped and greenish-gray with yellow margins (Gangopadhyay and Chakrabarti, 1982). Control management of sheath blight is limited since there are no strong genetic sources of resistance known yet. Currently, the cultivable varieties in the Southern US range from very susceptible to moderately resistant (Kumar *et al.,* 2009). Therefore, biological and cultural management are being practiced to reduce the severity of sheath blight (Willocquet *et al.,* 2000; Rodrigues *et al.,*2003). Silicon fertilization may proffer a practical remedy to restrain sheath blight, primarily where Si in soil is limited. Zhang *et al.* (2013) studied the effect of Si on two rice cultivars

with different resistancy to *R. solani* namely i) Ningjing 1 (susceptible cultivar) and ii) Teqing (resistant cultivar). The rice cultivars were inoculated with *R. solani* using the colonized match-stick procedure and treated with two levels of Si, 0 (-Si) and 1.5 mM (+Si), respectively. The results revealed that Si treatment decreased the disease ratings (rated from 0 to 9) of sheath blight by 2.96 and 0.65, for Ningjing 1 and Teqing. For +Si Ningjing 1, there was a significant reduced in disease ratings compared with −Si treatment and this showed that Si engaged actively in improving the basal resistance towards sheath blight. However for +Si Teqing, the disease rating was slightly lower than −Si Teqing, but it was not statistically different due to the intrinsic resistance of this cultivar to sheath blight.

A study by Rodrigues *et al.* (2003) investigated the influence of Si amendment on *R. solani* in six Brazilian rice cultivars. The rice was grown in pots containing soil that was Si-deficient and Si treatment was applied at several different rates. At occurrence of maximum tillering level, plants were inoculated with *R. solani*. The concentration of Si in the straw was raised above 60% when the Si treatment increased from 0 to 1.92 g/pot for all rice cultivars. This result showed that the Si content in straw was directly related to the quantity of Si applied to the soil. The sheath blight potency was largely decreased for the rice cultivars given the highest rate of Si compared to the rice grown without Si. As the application rate of Si elevated, the total amount of sheath blight lesions and sheath blight severity reduced by 37 and 52%, respectively. This confirmed that Si is capable to complement inherent host resistance and enhance resistance of plants against sheath blight disease. According to Winslow (1992), Si treatment only decreased the sheath blight intensity in irrigated *indica* rice but not in *japonica* upland rice and intermediate genotypes. Meanwhile, the application of Si has also been reported to enhance resistant of rice towards sheath blight although there was no significant difference between high and low levels of Si (Mathai *et al.*, 1977).

Rodrigues *et al.* (2003) grew rice plants (cv. Rio Formoso) in pots fertilized with five rates of Si and then inoculated with *R. solani* at five rice development levels which were at four-leaf, eight-leaf, tillering, booting and panicle exsertion stage. Silicon content was highest at the four-leaf stage as a result of the decreased dry matter accumulation due to high intensity of sheath blight. At booting and panicle exsertion stages when plants grew older, the Si concentration was reduced intensely. The number of lesions and total AURLEC reduced at all rice growth stages when the application of Si was raised. As the rates of Si were increased, severity of sheath blight was lower at booting and panicle exsertion stages. Meanwhile, study by Rodrigues *et al.* (2001) on the application of calcium silicate slag as a Si source has also been reported to be effective in reducing sheath blight severity and the total AUVLEPC for susceptible and moderately susceptible US rice cultivars compared to those cultivars high in partial resistance but not amended with Si. Dry matter production was significantly higher when Si was applied. Rodrigues *et al.* (1998) investigated the effects of Si on three different rice cultivars (high level of partial resistance, moderately susceptible and susceptible) towards their resistance to sheath blight. The results showed that for all rice cultivars, the Si significantly decreased the AUDPC for development of lesion and final disease severity for sheath blight. Both moderately susceptible and susceptible cultivars had more severe sheath blight development compared to high level of partial resistance cultivar. The AUDPC and final disease severity values were not significantly different for partial resistance cultivars grown in non-amended soil and moderately susceptible cultivars amended with Si.

Brown spot caused by the fungus (*Bipolaris oryzae*) is one of the most important and devastating disease of rice. The symptoms of this disease comprised of appearance of circular to oval lesions with a gray center surrounded by a reddish brown margin (Ou, 1985). Currently, the major strategies to control this disease are through fungicide application and manipulation of nutrients. Rice plants are known to

be more susceptible to brown spot if they were grown in soil with low K, Mn, Si, Fe, Ca or Mg (Dallagnol et al., 2009; Lee, 1992). Faria and Prabhu (1983) reported that soils amended with both high and low N rates may elevate rice susceptibility to brown spot under upland conditions. Ning et al. (2014) demonstrated the effect of steel and iron slag fertilizers towards growth and brown spot development in rice. The steel and iron slag consisted of HCl-soluble Si content of 7.61 and 9.35%, respectively. Rice leaves were naturally infected with brown spot disease at the jointing stage. Results indicated that both Si fertilizers enhanced the growth and yield of rice with higher grain weight for plants applied with steel slag fertilizers. Higher grain weight for steel fertilizer was probably attributed to the influence of cooling process towards Si dissolution and the presence of other nutrients supplied by the slag. Rice leaf lesion was most severe for plants that were not treated by Si (-Si) with an incidence and disease index of 39.6 and 56.0%, respectively. The -Si plants exhibited symptoms of brown spot disease five days earlier than those plants applied with slags. As the application rate of Si slag was increased, the lesion areas of leaves decreased. This indicate that both steel and iron slag were effective in suppressing brown spot disease.

Dallagnol et al. (2009) grew rice from cv. Oochikara and lsi1 (low silicon 1) mutant applied with two rates of Si which were 0 and 2 mM. Lsi1 is a rice mutant defective in active uptake of Si. At the emergence of eighth leaf from the main tiller, the plants were inoculated with B. oryzae. The -Si leaves of Oochikara exhibited a severe chlorosis and higher number of coalesced necrotic lesions. For +Si Oochikara, the severity of chlorosis with the number and size of necrotic lesions were greatly decreased. In the case of -Si treatment of lsi1, the lesions that appeared on the leaves were larger and higher in number, enclosed by well-developed chlorotic halo compared to +Si treatment. This shows that employing a mutant deficient in the active Si uptake leads to low concentration of Si in the leaf tissues thus, affecting the resistance of plants towards brown spot.

Dallagnol et al. (2103) extended his study using the same seed material and Si rate applications with additional application of fungicide treatment and the rice panicles were inoculated with B. oryzae. Results showed that application of fungicides to the seeds and amendment of Si to the rice plants decreased the transmission of B. oryzae from seed to seedling. Rice plants which were amended with Si, particularly from the cv. Oochikara exhibited rice seeds that have lower brown spot severity in grains, in which the Si content in the husks was greater than in the lsi1 mutant. Plants of cv. Oochikara treated with Si revealed a high proportion of seeds with a brown spot severity lower than 10%. The lsi1 gene which was present in the cv. Oochikara plays a vital role in increasing the Si concentration of the husks with greater percentage of emerged seedlings, lower percentage of infected seedlings and greater seedlings dry matter. Zanão Júnior et al. (2009) examined the incidence of brown spot after application of Si and Mn on rice. Rice plants that were grown with Si treatment showed significant reduction of number of brown spot lesions, real disease severity and AUBSPC regardless of manganese rates. With application of Si, the incubation period of rice leaves were observed to significantly rise, showing that there is a time delay for fungus to penetrate the epidermal cell. Without addition of Si to rice plants, size and number of necrotic lesions were greater and coalesced, with intense chlorosis compared to the plants that were added with Si. The results indicated that Si has the ability to control the progress of brown spot disease effectively, despite the states of low or high Mn. Other studies have also reported the effectiveness of Si application towards suppressing brown spot disease (Takahashi, 1967; Gangopadhyay and Chatopadhyay, 1974; Lee et al., 1981).

Grain discoloration is an economically important disease of rice which is caused by various fungal and bacterial pathogens. The major pathogenic fungi causing grain discoloration are B. oryzae, Phoma sorghina and Gerlachia oryzae (Ou, 1985). Grain discoloration may decrease the weight of grain, seed germination and market value of the grain (Tanaka,

1986). Prabhu *et al.* (2012) studied the effects of Si towards reduction of brown spot disease using eight genotypes under a greenhouse condition. The result revealed the relationship between Si rates and brown spot severity was linear negative. Additionally, the author studied the response of Si rates and decrease of grain discoloration using forty-eight rice genotypes which were grown in upland conditions. The relationship between rates of Si and grain discoloration was quadratic negative. Thus this suggests that Si plays a successful role in enhancing the resistance of rice to brown spot and grain discoloration disease for a number of rice genotypes. This was supported by Korndörfer *et al.* (1999) who

investigated the effects of five rates of Si on four Si-deficient savanna soils from Brazil. Silicon application increased total grain weight and decreased grain discoloration independent of the soil class. Grain discoloration was reduced as the Si application levels were raised, with reduction from 46% for the control to 29% for the highest Si rate. When Si concentration in the tissues increases, rice diseases were found reduced (Datnoff *et al.,* 1997). Positive effect of Si in enhancing plant resistance towards pathogens infection was not only reported in the rice, but numerous studies have also demonstrated that Si plays role in suppressing diseases in many other plants (Table 1).

Table 1. Disease Resistance and Suppression by Si Application.

Host	Pathogen	Disease	References
Rose	*Diplocarpon rosae*	Black spot	Gillman *et al.* (2003)
Wheat	*Blumeria graminis;* *Erysiphe graminis*	Powdery mildew	Guével *et al.* (2007), Leusch and Buchenauer (1989)
Cucumber	*Sphaerotheca fuliginea*	Powdery mildew	Liang *et al.* (2005), Menzies *et al.* (1992), Adatia and Besford (1986)
	Phythium spp.	Root disease	Chérif *et al.* (1994)
Muskmelon	*Sphaerotheca fuliginea*	Powdery mildew	Menzies *et al.* (1992)
Barley	*Erysiphe graminis*	Powdery mildew	Jiang *et al.* (1989)
Zucchini squash	*Erysiphe cichoracearum*	Powdery mildew	Menzies *et al.* (1992)
Grape	*Uncinula necator*	Powdery mildew	Bowen *et al.* (1992)
Banana	*Cylindrocladium spathiphylli*	Root disease	Vermeire *et al.* (2011)
	Fusarium oxysporum	Fusarium wilt	Fortunato *et al.* (2012)
Sugarcane	*Leptosphaeria sacchari*	Ring spot	Raid *et al.* (1992)
	Puccinia melanocephala	Sugar rust	Dean and Todd (1979)
Bell pepper	*Phytophthora capsici*	Phytophthora blight	French-Monar *et al.* (2010)
Corn	*Fusarium moniliforme*	Fusarium stalk rot	Sun *et al.* (1994)
St. Augustine grass	*Magnaporthe grisea*	Gray leaf spot	Brecht *et al.* (2004)
Pea	*Mycosphaerella pinodes*	Leaf spot	Dann and Muir (2002)
Avocado	*Colletotrichum gloeosporioides*	Anthracnose	Anderson *et al.* (2005)
Perennial Ryegrass Turf	*Magnaporthe oryzae*	Gray leaf spot	Nanayakkara *et al.* (2008)
Pumpkin	*Podosphaera xanthii*	Powdery mildew	Heckman *et al.* (2003)

Mechanisms for Si-mediated plant resistance towards disease: There have been various debates to explain the mechanisms involved in silicon-mediated plant resistance. Up to date, two types of mechanism for Si to confer and induce resistance have been classified (Hayasaka *et al.,* 2008). The first mechanism of enhanced resistance can be associated with accumulation and polymerization of silicic acid in leaf epidermal cells which play a passive role as a physical or mechanical barrier against fungal

penetration (Hayasaka *et al.,* 2008; Cai *et al.,* 2008; Ashtiani *et al.,* 2012). Such polymerization has resulted in increased density of silicified bulliform cells present in the leaf epidermis of rice which act as a barrier to physically block penetration by *M. grisea* (Ito and Hayashi, 1931; Ishiguro, 2001; Datnoff *et al.,* 2007). In addition, Si deposition beneath the cuticle forms a cuticle-Si double layer that contributes to enhance resistance (Fauteux *et al.,* 2005). This layer mechanically prevent fungi penetration, thus

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interrupt the infection process. This is supported by Yoshida *et al.* (1962) who revealed the presence of a silica layer about 2.5 mm thick beneath the cuticle of rice leaves and sheath, and this layer restrain penetration of *M. grisea* and reduce the number of infections on the leaves.

Ning *et al.* (2014) showed that application of Si to rice resulted in more pronounced cell silicification in the leaves and the papillae were more extended and larger. Silicon layers were formed in the epidermal cell walls of rice and increasing Si treatment increases the thickness of the layer resulting in improved levels of resistance to brown spot. Extended papillae might improve resistance of plants to fungal infestation (Cai *et al.*, 2008; Zhang *et al.*, 2006). This was supported by Kim *et al.* (2002) through their study of electron microscopy and X-ray microanalysis which revealed that deposition of Si takes place in the epidermal cell walls, middle lamellae and intercellular spaces of Si-treated rice leaves despite the leaf growth stages. The epidermal cell wall was consisted of two evident layers which were an outer electron-dense Si layer about 1-3.5 μm thick and an inner electron translucent layer that were usually composed of thin electron-dense Si layers fixed in the cellulose microfibrils. No appearance of Si was detected in the cytoplasm of plants treated with Si. In another study by Savvas *et al.* (2002), Si deposition increased the stem diameter of gerbera flowers with increasing Si concentration in nutrient solution thus providing mechanical strength to the stems and increases the quality of gerbera flower.

Volk et al. (1958) reported the formation of complexes of Si with organic compounds in the cell walls of epidermal cells, thus increasing the resistance to degradation by enzymes discharged by *M. grisea*. Inanaga *et al.* (1995) suggested that it is likely Si was deposited into cell walls as Si-aromatic ring which can be associated with lignin-carbohydrate complexes in the rice leaves. These organo-Si complexes in the cell walls may limit the expansion of lesions, thus decreasing the infection efficiency (Volk *et al.*, 1958). Kawamura and Ono (1948) claimed that a blast-

resistant rice cultivar had a reduced number of lesions on the leaves and higher quantity of silicified epidermal cells than rice of susceptible cultivar. This was in term with Kwon *et al.* (1974) who reported that rice resistant to blast has more silicified cells compared to susceptible crop, although (Hashioka, 1942) reported that the density of silicified cells in the epidermis of rice leaves is not always proportional to the level of resistance to blast attack. It is well known that Si layers and silica bodies are usually not uniformly distributed along the epidermis cell wall. Thus, this mechanical barrier mechanism cannot solely explain the role of Si in enhancing plant resistance and resulted in many speculations that the defend mechanism must be more than just a physical barrier.

Thus, the second type of mechanism is based upon physiological resistance in which Si mediate some physiological changes in order to enhance plant resistance against pathogens (Hayasaka *et al.,* 2008). Increasing studies have suggested that Si plays a biochemical role in enhancing resistance to pathogens and that Si is associated with host defense responses (Liang *et al.,* 2005; Sun *et al.*, 2010). Study by Rodrigues *et al.* (2004) proved that development alteration of *M. grisea* in leaf tissue of rice amended with Si was strongly related with the formation of phytoalexins. Ethyl ether fraction (FII) analysis acquired from leaf extracts of plants treated without Si (-Si) and with Si (+Si) infected with *M. grisea* showed that from all the subfractions (SF), only SF5 exhibited antifungal action against *M. grisea*. This SF5 was further analyzed by HPLC which then allowed separation of two common rice phytoalexins, momilactones A and B that act as potential defense compounds which alter growth of fungal in the leaf cells. This is in term with Fawe *et al.* (1998) who reported that application of Si to cucumber induced resistance to powdery mildew due to the production of a novel flavonol phytoalexin.

Cai *et al.* (2008) studied the physiological mechanisms when Si was applied to two near-isogenic lines of rice with different resistance to blast,

which were susceptible line CO39 and resistant line C101LAC(*Pi-1*). Results indicated that for *M. grisea* infected plants, application of Si raised the lignin content for CO39 by 36%, while there were no obvious effects on C101LAC(*Pi-1*). However, there were no changes of lignin content for non-infected *M. grisea* plants whether it was treated with Si or non-treated with Si. Lignin which is the product of phenolic metabolism plays vital role in disease resistance. Defense-related enzymes such as POD, PPO and PAL play role in regulating the production of soluble phenolics (Cai *et al.*, 2008; Thypyapong *et al.*, 1995; Rösler *et al.*, 1997). After inoculation with *M. grisea*, Si application significantly reduced disease severity in both isogenic lines which was in line with increased activities of POD, PPO, PAL and higher lignin content (Cai *et al.*, 2008). This was in term with study by Chérif *et al.* (1994) who reported that Si activates defense responses to *Pythium* infection in cucumber which led to phenolic compounds accumulation and higher activities of chitinases, POD and PPO. Fawe *et al.* (2001) stated that presence of soluble Si in plant cells may induce defense responses that are functionally similar to systemic acquired resistance. Based on the evidence from the previous studies, it is suggested that Si actively take part in inducing defense towards plants disease and rather than simply acting as mechanical barrier, it is a more complex process.

Conclusion

Rice is one of the world's most important food crops especially in the Asia, where rice is highly consumed as staple food by the Asians. Important rice diseases such as the rice blast, sheath blight, brown spot and grain discoloration have become a problem in almost all rice cultivating areas of the world. The appropriate control measurements which are efficient, cost-effective and environmentally friendly are very much demanded in suppressing the diseases. Thus, Si application which does not cause harm to the environment is a convenient strategy for plant diseases management. The positive effects of Si in plant nutrition and suppression of diseases have been well established. Mechanisms of Si mediated

alleviation of disease infection have been centered into two different hypotheses which are i) deposition of Si act as mechanical barrier against fungal penetration and ii) Si mediate some physiological changes in order to enhance resistance. Since little is known about the exact defense mechanism of plants treated with Si in response to disease infection, the two mutually agreeable hypotheses must be considered. From the gathered evidences, Si is involved in a more complex defense mechanism rather than simply acting as a mechanical barrier to impede penetration of pathogens. Further researches must be carried out to evaluate whether these two mechanisms are mutually dependent or not. In the future, delivering information about Si to farmers and crop growers will assist the agriculture field to effectively manage and control plant diseases.

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