CHAPTER 1
LITERATURE REVIEW

1.1 Introduction

Silicon (Si) is the second most abundant element in the earth's crust and all plants rooting in soil contain significant amounts of Si (Ma and Takahashi, 2002). However, Si has not been recognized as an essential element for plant growth. The major reason is that there is no evidence to show that Si is involved in the metabolism of plant, which is one of the three criteria required for being essential element as established by Arnon and Stout (1939). The reason for this marked discrepancy is the conclusion that Si is not an essential element because most plants can grow in nutrient solutions which lack Si in their formulations (Epstein, 2001). Recently, Epstein and Bloom (2003) have reconsidered the definition of essential element and proposed a new definition of elements that are essential for plant growth: An element is essential if it fulfills either one or both of two criteria, viz., (1) the element is part of a molecule which is an intrinsic component of the structure of metabolism of the plant, and (2) the plant can be so severely deficient in the element that it exhibits abnormalities in growth, development or reproduction, i.e., "performance", compared to plants with a lower deficiency.

According to this new definition, Si is an essential element for higher plants because Si deficiency causes various abnormalities in the plant (Ma, 2004). Although Si has not been recognized as an essential element for plant growth, the beneficial effects of Si have been observed in a wide variety of plant species. The beneficial effects of Si are usually expressed more clearly in Si-accumulating plants under various abiotic and biotic stress conditions. Si is effective in controlling various pests and diseases caused by both fungi and bacteria in different plant species. Si also exerts alleviative effects on various abiotic stresses including salt stress, metal toxicity, drought stress, radiation damage, nutrient imbalance, high temperature, freezing and

so on. These beneficial effects are mainly attributed to the high accumulation of silica on the tissue surface although other mechanisms have also been proposed (Ma, 2003).

Although Si is not considered as an essential element for growth and development, addition of this element can increase growth and yield of rice (Yoshida, 1981; Takahashi *et al*., 1990; Takahashi, 1995; Savant *et al*., 1997). The beneficial effects of Si on the rice growth are mostly attributable to the characteristics of the silica gel accumulated on the epidermal tissues. This accumulation helps alleviate water stress by decreasing transpiration, to improve light interception characteristics by keeping leaf blade erect, to increase resistance to diseases, pests and lodging, to improve reproductive fertility and to increase final yield (Yoshida *et al*., 1969; Idris *et al*., 1975; Marwat and Baloch, 1985; Snyder *et al*., 1986; Takahashi, 1995; Savant *et al*., 1997; Ma and Takahashi, 2002).

1.2 Silicon in Rice

Higher plants differ characteristically in their capacities to take up Si. Depending on their Si contents (SiO_2, expressed as a percentage of shoot dry weight), plants can be divided into three major groups: firstly, high-level group, is a members of Cyperaceae (*Equisetum arvense*) and wetland species of Poaceae (Gramineae), such as rice, 10-15%; secondly, medium-level group, is dryland species of Poaceae, such as sugarcane and most of the cereal species, and thirdly, low-level group, is a few dicotyledons, 1-3%; and most dicotyledons, especially legumes, <0.5%. In a survey of 175 plant species which were grown in the same soil, Takahashi and Miyake (1977) distinguished between two types: (a) accumulators, plants in which Si uptake largely exceeds water uptake and (b) nonaccumulators, plants in which Si uptake is similar to or less than water uptake (Marscher, 1995). Rice is a known Si accumulator (Takahashi *et al*., 1990), and the plant benefits from Si nutrition (Yoshida, 1975; Takahashi, 1995). Si at up to 10% of dry weight is accumulated in shoot, and more than 90% of Si is present in the form of silica gel (also referred to as opal or phytoliths in higher plants) (Ma and Takahashi, 2002). Consequently, there is a definitive need to consider Si as an agronomically-essential element for increasing

and/or sustaining rice production (Takahashi and Miyake, 1977; Yoshida, 1981; Ma, 2004).

Si is required for healthy and productive development of rice plant (Lewin and Reimann, 1969; Yoshida, 1975). This element is absorbed by rice from the soil in large amounts that are several-fold greater than those of other macronutrients. For example, Si accumulation is about 108% greater than that of nitrogen. It is estimated that a rice crop producing a total grain yield of 5,000 kg ha^{-1} will remove Si at 230 to 470 kg ha^{-1} from the soil (Savant *et al*., 1997). However, its deficiency has been reported to be associated with the following symptoms in the rice plant: (a) lower leaves becoming yellow or brown and nacrotic, (b) poor tillering and retarded growth, (c) leaf tips wilting (probably due to impaired transpiration) and drying out, and (d) smaller panicles with increasing sterility (Savant *et al*., 1997).

1.2.1 Chemical form and accumulation process of silicon in rice

Si in soil solution is mainly present in the form of an uncharged monomeric molecule, silicic acid [Si(OH)$_4$] at a pH below 9.0. At a higher pH (> 9.0), silicic acid will dissociates into silicate ion [(OH)$_3$SiO^{-1}] (Ma *et al*., 2001; Ma and Takahashi, 2002). The solubility of silicic acid in water is 2 mM (equivalent to 56 mg Si L^{-1}) at 25°C and polymerization of silicic acid into silica gel, SiO$_2$.H$_2$O, occurs when the concentration of silicic acid exceeds 2 mM (Marscher, 1995; Ma *et al*., 2001; Ma and Takahashi, 2002). The form of Si absorbed by plant roots is silicic acid. After silicic acid is transported to the shoot with transpiration stream, it is concentrated due to loss of water and is polymerized to colloidal silicic acid and finally to silica gel with increasing silicic acid concentration. More than 90% of Si in the rice plant is present in the form of silica gel and the concentration of colloidal plus monomeric Si is kept below 0.3 to 0.5 mg SiO$_2$ g^{-1} fresh weight. Si is deposited as a 2.5 μ-thick layer in the space immediately below the thin (0.1 μ) cuticle layer, forming a cuticle-Si double layer in the leaf blade of rice. These layers play an important role in controlling transpiration, maintain erect leaves, and resistance to diseases and pests.

There are two types of silicified cell; silica cell and silica body or silica motor cell. Silica cells are located on vascular bundles, showing a dumbbell-shape, while silica bodies are in bulliform cells of rice leaves. When the Si content in the rice shoot is below 5% SiO_2, only silica cells are formed. Silica bodies are formed when the Si content is above 5% SiO_2 and the number of silica bodies increases with increasing Si content in the shoot. The silicification process of cells in rice leaves starts from silica cells to silica bodies. In addition to leaf blades, silicified cells are also observed in the epidermis and vascular tissues of stem, leaf sheath and hull (Ma *et al*., 2001; Ma and Takahashi, 2002). These deposition functions of Si are to protect plants from multiple abiotic and biotic stresses. The silicified cells also provide useful palaeoecological and archaeological informations which have been known as plant opal or phytoliths (Ma and Yamaji, 2006).

Si also accumulates on the bulliform cells, dumbbell cells, long and short cells on the surface of leaves and hulls, where the end of transpiration stream lies; and is distributed uniformly in root. The distribution of Si in rice is closely related with transpiration, therefore, the high Si content in rice shoot can be an indicator to evaluate uptake ability of Si, easy translocation of Si together with the transpiration stream, concentration at the end of the stream, and automatical polymerization property at a high concentration of silicic acid (Ma and Takahashi, 2002). However, Si accumulation in the shoot varies considerably with the plant species and varieties. The difference in Si accumulation was attributed mainly to the ability of the roots to uptake Si (Ma, 2004).

1.2.2 Silicon uptake in rice plant and the mechanism of uptake

All plants were grown in soil containing Si (Takahashi *et al*., 1990; Epstein, 1999), but the Si concentration of plant shoots varied greatly among plant species; ranging from 0.1% to 10% (w/w) Si on a dry weight basis (Takahashi *et al*., 1990; Eptein, 1994). This large variation was largely due to different capacities for Si uptake by plant roots. The uptake modes had been suggested: active, passive and rejective uptake (Takahashi *et al*., 1990). The mode of uptake employed was dependent on the particular plant species (Takahashi *et al*., 1990; Ma *et al*., 2001).

Rice (*Oryza sativa*) is a typical plant that shows active uptake of Si. Rice roots take up Si in form of silicic acid, an uncharged molecule (Takahashi and Hino, 1978).

The uptake rate of Si by rice roots is much faster than that of water, resulting in a quick decrease in Si concentration of external solution (Okuda and Takahashi, 1962a). The Si uptake is not affected by the transpiration, but is inhibited by a respiratory inhibitor such as sodium cyanide (NaCN) (Okuda and Takahashi, 1962a) and metabolic inhibitors such as 2,4-dinitrophenol, iodoacetate and dichlorophenoxy acetate (2,4-D) (Okuda and Takahashi, 1962b). The Si uptake was mediated by a type of proteinaceous transporter on plasma membrane. From kinetic studies, the K_m value for Si uptake was estimated to be 0.32 mM, suggesting that the transporter had a low affinity for silicic acid. The uptake of Si by rice roots is a transporter-mediated process and this transporter contains cysteine (Cys) residues but not lysine (Lys) residues (Tamai and Ma, 2003). The Si uptake system in rice roots was investigated by using two mutants of rice, one defective in the formation of root hairs (RH2) and another in that of lateral roots (RM109). These results clearly indicated that lateral roots contributed to the Si uptake in rice plant, whereas root hairs did not.

1.3 Beneficial effects of silicon on rice growth and yield

The beneficial effects of Si on rice growth are mostly attributable to the characteristics of the silica gel accumulated on the epidermal tissues. Si application can increase the dry matter and yield production of rice by increasing the photosynthetic rate of individual leaf and by improving the canopy structure (Ando *et al*., 2002). Si deposited in the leaf blade of rice keeps the leaf erect. Therefore, Si may stimulate canopy photosynthesis by improving light interception. This is of particular importance since it helps minimize mutual shading in dense plant stands when nitrogen fertilizers are heavily applied (Ma and Takahashi, 2002). Under conditions without mutual shading, the effect of Si for increasing the photosynthesis in rice was investigated by Takahashi *et al*. (1966). The amount of assimilation per individual plant was higher in the plant with a high Si content than those with a low Si content (Ma and Takahashi, 2002). Furthermore, under water-stress conditions, the

photosynthetic rate was reported to be higher in +Si (Si supplied) plants than in the –Si plants (Matoh *et al*., 1991) which was probably due to the Si-induced decrease of transpiration rate.

According to Agarie *et al*. (1992), the maintenance of photosynthetic activity due to Si fertilization could be one of the reasons for the increasing dry matter production. They also observed an increase in water use efficiency in Si-amended rice plant which was probably due to prevention of excessive transpiration (Savant *et al*., 1997). Poor tillering and wilting of leaf tips due to an impaired transpiration in Si-deficient rice plants have been reported by Bergmann (1992) (Savant *et al*., 1997). The effects of Si supply on the growth of rice plant seem to be most remarkable during the reproductive growth stage (Ma *et al*., 1989). Si also has a positive effect on the number of spikelets on secondary branches of panicles and the ripening of grains (Seo and Ota, 1983; Lee *et al*., 1990; Savant *et al*., 1997). While Si deficiency increased the number of empty grains, inhibited rice growth and promoted dying-off of leaf blades after heading, it resulted in the difference in dry weight or yields between the rice with and without Si supply (Ma and Takahashi, 2002).

1.4 Beneficial effects of silicon in rice under stress conditions

Rice is exposed to various biotic and abiotic stresses in the field. Numerous studies have shown that beneficial effects of Si are slight under optimized growth conditions, but obvious under stress conditions (Epstein, 1994).

1.4.1 Silicon and biotic stress

The economic, social and political implications of losses in grain yield and quality are caused by biotic stress. Several studies have shown that Si is effective in enhancing the resistance to diseases and pests in rice.

1) Silicon and rice diseases

Rice blast, caused by *Magnaporthe grisea* (Hebert) Barr, is the most destructive fungal disease of rice, particularly in temperate, irrigated rice and tropical upland rice. The pathogen can infect all the above-ground parts of the rice

plant, but occurs most commonly on leaves causing leaf blast during the vegetative stage of growth or on neck nodes and panicle branches during the reproductive stage, causing neck blast (Bonman *et al*., 1989). Si reduces the epidemics of both leaf and panicle blast at different growth stages. In Florida, where soil is deficient in Si, application of silicate fertilizer is as effective as fungicide application in controlling rice blast (Datnoff *et al*., 1997). Si fertilization has been shown to induce resistance to blast in rice by several investigators (Volk *et al*., 1958; Kozaka, 1965; Silva, 1971; Kim and Lee, 1982; Kim *et al*., 1986; Yamauchi and Winslow, 1987; Datnoff *et al*., 1992; Winslow, 1992; Seedblod *et al*., 1995; Maekawa *et al*., 2001; Prabhu *et al*., 2001; Seebold *et al*., 2001).

According to Maekawa *et al*. (2001), rice seedling blast is significantly suppressed by the application of Si fertilizers in the nursery. Recently, Seebold *et al*. (2001) have tested the effects of Si on several components of resistance to blast using susceptible, partially-resistant, and completely-resistant rice cultivars. They reported that, regardless of the cultivar resistance, incubation period was lengthened, and the number of sporulating lesions, lesion size, rate of lesion expansion and the number of spores per lesion were significantly reduced by Si application. In addition, Volk *et al*. (1958) also reported that the number of blast lesions on leaves decreased linearly as the Si content in leaf blades increased. Rabindra *et al*. (1981) showed that the content of Si leaf and neck tissues varied among four rice cultivars when grown under similar climatic conditions; and that those cultivars accumulating more Si in shoots showed less incidence of leaf and neck blast. Interestingly, the susceptibility to blast of some rice cultivars grown with different rates of Si was negatively correlated with the content of Si in the shoots (Savant *et al*., 1997). The penetration rate of the rice blast pathogen is lower in plants with a higher level of silica, due to mechanical barrier created by an accumulation of silica in the epidermis. Electron microscopic studies revealed the presence of a cuticle and silica double layer in the epidermal cell wall.

Varieties resistant to rice blast contain a higher amount of silica than susceptible varieties and the degree of resistance increases in proportion to the amount of silica applied. Heavy nitrogen application decreases silicate accumulation in plants, resulting in a decrease in number of silicified cells in the uppermost leaves.

The percentage of neck blast closely correlates with the number of silicified cells in the uppermost leaves at the heading stage or at the five-day stage before heading. The number of silicated cells per unit area is largest in the lower leaves, decreasing towards the upper leaves during the vegetative growth stage. At heading, the number of silicated cells in the upper leaves increases. The mediated resistance of the rice plant and leaves seem to be related to silicification of epidermal cells with age (Volk *et al*., 1958; Prabhu and Filippi, 1993; Prabhu *et al*., 2001).

In addition to blast, the occurrence of brown spot, stem rot, sheath brown rot on rice decreased by increasing the Si supply (Ma, 2004). Rice bacterial blight caused by *Xanthomonas oryzae* pv. Oryzae (Xoo) is a serious disease worldwide. Chang *et al*. (2002) reported that the cultivar TN1 which is susceptible to this disease, the Si content in leaves was lower than that of the resistant breeding line, TSWY7, under the adopted nutrient cultural system. The degree of resistance to this disease increased in parallel with the increased amount of applied Si. Si-induced decreases soluble sugar content in the leaves seems to contribute to the field resistance of the disease.

Grain discoloration, caused by a complex of fungal species such as *Bipolaris oryzae*, *Curvularia* spp., *Phoma* spp., *Microdochium* spp., *Nigrospora* spp. and *Fusarium* spp., 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 decreased linearly as the rates of SiO_2 in the soil increased. The severity of grain discoloration was reduced by 17.5%, on average, at the rate of 200 kg ha^{-1} application of SiO_2, while grain weight increased 20%.

Stem rot (*Magnaporthe salvinii* Cattaneo), leaf scald and sheath blight also have been efficiently suppressed by Si application (Elawad and Green, 1979). Regarding bacterial diseases, Chang *et al*. (2002), recently reported a significant reduction in lesion length of bacterial leaf blight (*Xanthomonas oryzae* pv. *oryzae*) of 5 to 22% among four rice cultivars following Si application. 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 levels of

Si in roots also showed increased resistance to the root-knot nematode *Meloidogyne* spp. (Swain and Prasad, 1988).

Two mechanisms for Si-enhanced resistance to diseases have been proposed. One is that Si acts as a physical barrier. Si is deposited beneath the cuticle to form a cuticle-Si double layer. This layer can mechanically impede penetration by fungi and, thereby, disrupt the infection process. Another mechanism proposed recently is that soluble Si acts as a modulator of host resistance to pathogens. The study in rice has shown that plants supplied with Si could produce phenolics and phytoalexins in response to fungal infection such as those causing rice blast. Si is also able to activate some defence mechanisms. In rice, differential accumulation of glucanase, peroxidase and PR-1 transcipts were associated with limited colonization by fugus *M. grisea* in epidermal cells of a susceptible rice cultivar which was supplied with Si. These biochemical responses are only induced by soluble Si, suggesting that soluble Si might play an active role in enhancing host resistance to diseases by stimulating some mechanisms of the defense reaction. However, the exact nature of interaction between the soluble Si and the biochemical pathways of the plants which leads to disease resistance remains unknown, although several possible mechanisms have been proposed (Ma and Yamaji, 2006).

2) Silicon and rice pests

Silicon suppresses insect pests such as stem borer, brown planthopper, rice green leafhopper and white-backed planthopper, and noninsect pests such as leaf spider and mites (Savant *et al.*, 1997). Stems damaged by the rice stem borer were found to contain a lower amount of Si (Sasamoto, 1961). In a field study, apposite relationship between the Si content of rice and resistance to the brown planthopper has been observed (Savant *et al.*, 1997). This Si-enhanced effect is attributed to Si deposition in plant tissues which provides a mechanical barrier against sticking and chewing by insects (Ma and Yamaji, 2006).

1.4.2 Silicon and abiotic stress

1) Silicon and water stress

Water deficiency (drought stress) leads to the closure of stomata and subsequent decrease in the photosynthetic rate. Si can alleviate water stress by decreasing transpiration. Transpiration from the leaves occurs mainly through the stomata and partly through the cuticle. As Si is deposited beneath the cuticle of the leaves forming a Si-cuticle double layer, the transpiration through the cuticle may decrease by Si deposition. Si can reduce the transpiration rate by 30% in rice, which has a thin cuticle. Under water-stressed condition (low humidity), the effect of Si on rice growth was more pronounced than on rice that is cultivated under non-stressed conditions (high humidity) (Ma *et al*., 2001).

When rice leaves were exposed to a solution containing polyethylene glycol (PEG), electrolyte leakage (an indicator of membrane lesion) from the leaf tissues decreased with the increase in the level of Si in the leaves (Agarie *et al*., 1998). The level of polysaccharides in the cell wall was higher in the leaves containing Si than in those lacking Si. These results suggest that Si in rice leaves is involved in the water relations of cells, such as mechanical properties and water permeability.

Among the yield components, the percentage of ripened grains is most affected by Si in rice (Ma and Takahashi, 2002). This function of Si may be attributed to the alleviative effect of Si on water stress. One important factor for the normal development of the spikelets is to keep a high moisture condition within the hull (Seo and Ohta, 1982). The Si content in the hull of the rice grain becomes as high as 7% Si. Si in the hull is also deposited between the epidermal cell wall and the cuticle, forming a cuticle-Si double layer as in the leaf blades. However, in contrast to the leaves, transpiration occurs only through the cuticle because the hull does not have a stoma. Si is effective in decreasing the transpiration from the hull. The rate of water loss from Si-free spikelets was about 20% higher than that from spikelets containing Si (7% Si) at both the milky and maturity stages (Ma *et al*., 2001). Therefore, Si plays an important role in keeping a high moisture condition within the

hull by decreasing the transpiration rate from the hull. This is an extraordinary role of Si under both water deficiency stress and stress associated with climatic conditions.

2) Silicon and radiation damage

Radiant rays cause injury of rice, but degree of damage is related to physiological status. Si seems to protect rice from radiation injury. When rice seedlings (30 days old) were irradiated with different doses of γ-rays, decreasing in the dry weight was less appreciable in the Si-supplied plants than in the Si plants that had not been treated with Si, suggesting that Si increases the resistance of rice to radiation stress. Furthermore, when the plant was supplied with Si after radiation treatments, the growth recovery was faster compared to the plants without Si supplied (Ma and Takahashi, 2002; Ma, 2004).

3) Silicon and heat stress

Si also increases the tolerance to heat stress in rice plant. Agarie *et al.* (1998) observed that electrolyte leakage caused by high temperature (42.5°C) was less pronounced in the leaves grown with Si than in those grown without Si. These results suggested that Si may be involved in the thermal stability of lipids in cell membranes although the mechanism has not been elucidated (Ma, 2004).

4) Silicon and stress associated with climatic conditions.

Si application in rice is effective in alleviating the damage caused by climatic stress such as typhoons, low temperature and insufficient sunshine during the summer season. A typhoon attack usually causes lodging and sterility in rice, resulting in a considerable reduction of the rice yield. Deposition of Si in rice enhances the strength of the stem by increasing the thickness of culm wall and the size of vascular bundles, thereby preventing lodging. Strong winds also cause excess water loss from the spikelets, resulting in sterility. Si deposited in the hull is effective in preventing excess water loss. In addition, the effect of Si on the rice yield is also obvious under stress due to low temperatures and insufficient sunshine (Ma *et al.*, 2001; Ma and Takahashi, 2002; Ma, 2004).

5) Silicon and deficiency in Phosphorus

Deficiency in phosphorus (P) in soil is a worldwide problem. The beneficial effects of Si under P-deficiency stress have been observed in rice. In

an experiment using a nutrient solution, Si supply resulted in a larger increase of the dry weight of rice shoot at a low P level (14 μM P) than at a medium level (210 μM P) (Ma and Takahashi, 1990a; Ma, 2004). Such beneficial effects of Si were previously attributed to a partial substitution of Si for P or to the enhancement of P availability in soil. However, subsequent experiments showed that Si was unable to affect P availability in soil. In a P-deficient soil, previous addition of silicic acid at various concentrations did not affect the P fixation capacity of soil (Ma and Takahashi, 1990b; Ma, 2004). Phosphorus fixation was absorbed by various concentrations of silicic acid (Ma and Takahashi, 1991). Si is present in the form of silicic acid in the soil solution, which does not undergo dissociation at a pH below 9. Therefore, it is unlikely that interaction between silicic acid and phosphate (anionic form) occurs in soil (Ma, 2004).

The uptake of P was also not affected by the Si supply at a low P level in both soil and solution culture (Ma and Takahashi, 1990a, b, 1991). However, the uptake of Fe and Mn significantly decreased in the Si-treated plants. Phosphorus is translocated and redistributed in plants in an inorganic form. Since P shows a high affinity with metals such as Fe and Mn, internal availability of P could be controlled by the level of Mn, Fe, and other metals when the P concentration is low. Therefore, the larger beneficial effect of Si on plant growth under P-deficiency stress may be attributed to the enhanced availability of internal P through the decrease of excess Fe and Mn uptake. This is supported by the fact that Si supply increased the rate of P translocation to the panicles in rice (Nagaoka, 1998; Ma, 2004).

6) Silicon and N excess

Application of nitrogen (N) fertilizers is an important practice for increasing yield. However, excess N causes lodging, mutual shading, susceptibility to diseases and so on. Si deposited on the stems and leaf blades prevents lodging and mutual shading. The occurrence of blast disease is significantly inhibited by Si application in the field, especially when N application is heavy (Ohyama, 1985). These functions of Si are especially important in the cultivation systems with dense planting and high N application (Ma, 2004).

7) Silicon and heavy metal toxicity

An alleviative function of Si on Mn toxicity has been observed in hydroponically-cultured rice. Si reduced Mn uptake by promoting the Mn oxidizing power of the roots. Si was also effective in alleviating Fe-excess toxicity in rice. Si enhanced the oxidative power of rice roots, resulting in enhanced oxidation of Fe from ferrous iron to insoluble ferric iron. Therefore, excess Fe uptake was indirectly prevented by Si application (Okuda and Takahashi, 1962; Ma, 2004).

8) Silicon and salinity

The beneficial effect of Si under salt stress has been observed in rice. Shoot and root growth of rice was inhibited by 60% in presence of 100 mM NaCl for three weeks, but Si addition significantly alleviated salt-induced injury. The Na concentration in the shoot decreased to about half by Si addition. This function of Si may be ascribed to the Si-induced decrease of transpiration and to the partial blockage of the transpirational bypass flow, the pathway by which a large proportion of the uptake of Na in rice occurs (Ma, 2004).

1.5 Genotypic variability for silicon concentration in rice

Because Si is associated with such a broad array of plant responses, genotypic variation for Si concentration has been evaluated in crop cultivars without being specifically related to a particular trait (disease, nutrient concentration, etc.). Yuan and Cheng (1977) grew *indica* and *japonica* rice cultivars in nutrient solution containing a fixed (100 ppm) Si concentration. Total plant Si concentrations ranged from 117 mg g^{-1} to 171 mg g^{-1}, demonstrating that some genotypes are better at accumulating Si than others. Studies of the actual genetics of Si concentration are few (Deren, 2001). Majumder *et al.* (1985) created a 7-parent diallel cross to investigate the inheritance of Si uptake in rice. Genotype ranged in leaf Si concentration from 11 to 70 mg g^{-1} at 60 days and 32 to 85 mg g^{-1} at harvest. Variation was largely additive and some heterosis was observed.

As mentioned above, disease resistance is a major component of most crop breeding programs that include rice. Genetic variability of Si concentration and its relationship to disease reaction have been the subjects of several studies. Deren (2001)

frequently found that genotype with greater disease resistance did, in fact, have greater Si concentration. Blast [*Magnaporthe grisea* (Hebert) Barr] is a severe rice disease world-wide, and has been the subject of studies of the interaction of disease and Si. In Russia, Alesin *et al*. (1987) found that the blast resistance of cultivars was related to the silicon dioxide content in the leaves. In India, Rabindra *et al*. (1981) also found that irrigated rice varieties with greater Si content were lower in both leaf and neck blast. Upland rice, which is grown in a non-flooded aerobic environment, is also responsive to Si. Further research on a diverse array of upland rice genotypes in Colombia by Winslow *et al*. (1997) found a high negative correlation (r = -0.91) between Si concentration and husk discoloration (*Bipolaris orzae* and other organisms). Genotypic differences in Si concentration were associated with ecotype (subspecies). Tropical *japonica* rice types had 93% greater Si concentration than *indica* type. It was hypothesized that the *japonica* evolved in the Si-deficient upland and had developed mechanisms to attain greater Si concentration, whereas *indica* evolved in lowlands where Si was more available. Under African upland conditions, Winslow (1992) reported that there was a significant negative linear correlation between husk discoloration and Si concentration (Deren, 2001).

In addition, Deren *et al*. (1994) was to investigate the relationship between plant responses associated with yield and plant tissue Si concentration under both Si-limiting and Si-enriched environments. Seed weight and panicles were little changed by Si fertility, but brown spot decreased by about 40% and grains per panicle increased by about 15% with Si. Obviously, disease affects yield, so the increased seed set logically is a consequence of lowered brown spot severity. Genotypes varies for Si concentration in both Si environments, with concentration increasing up to 150% with Si fertilization. At both locations, there was a significant (P < 0.01) negative linear correlation between severity of brown spot and Si concentration in the Si-deficient control plots. This was similar to what Winslow (1992) found for husk discoloration in African upland rice. Increased Si concentration in some rice genotypes has been correlated with disease and/or insect resistance (Kozaka, 1965; Datnoff *et al*., 1991, 1992; Savant *et al*., 1997). It is possible that certain genotypes are more efficient than others in their accumulation of Si, thus making them more resistant (Deren *et al*., 1992, 1994; Winslow, 1992). Evidently, this is genetic factor

that seems to influence disease and possibly insect resistance in addition to Si level in plant tissue (Savant *et al*., 1997).

1.6 Conclusion and objective

From the literature review, a number of papers have concluded that the most beneficial effects of Si were expressed through Si deposition on the rice shoots. High accumulation of Si in rice has been demonstrated to be necessary for healthy growth and high and stable production. Si accumulation in the shoot varies considerably with the plant species and varieties. The difference in Si accumulation was attributed to the ability of the roots to take up Si. One approach to enhance the resistance of plants to multiple stresses is to genetically modify the Si uptake ability. Therefore, the proposed study is aimed to investigate genotypic variation and estimate genetical components for Si uptake in upland rice under drought condition. An understanding will be useful for developing and selecting drought-resistant genotypes.