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Silicon: A New Macronutrient Deficiency in Upland Rice



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PREFACE

"Everything should be made as simple as possible, but not more so."

- Albert Einstein

In an attempt to make the results of this research more meaningful and relevant, I have drawn upon and synthesized from a wide range of scientific disciplines, such as geology, inorganic and organic chemistry, soil science, ecology, evolution, genetics, pathology, plant physiology and agronomy. In so doing, I run the risk of oversimplification, as well as exceeding the limits of my own expertise.

Nevertheless, I hope these risks are compensated by placing the present research into a broader, more interesting and more relevant context.

In presenting this work as a CIAT Working Document, I am seeking to preserve it in a useful and readily available format, not to imply that the views represented here necessarily have the official endorsement of the Institution or of my colleagues. It has not been internally reviewed in a formal sense by CIAT, although the broad outlines were presented as a CIAT Internal Seminar on June 14, 1995 and it reflects the interactions I have had with a number of knowledgeable colleagues over recent years, both within and outside the Institute. I hope to publish aspects of it in refereed journal form in the near future.

Mark D. Winslow
CIAT, Cali, Colombia
June 30, 1995

ACKNOWLEDGEMENTS

The work described here is a product of inter-disciplinary, as well as both intra- and inter-institutional collaboration. Dr. Kensuke Okada, a JIRCAS physiologist seconded to CIAT, made it possible for us to diagnose the silicon status of rice agro-ecosystems by introducing and adapting published Si analysis methods for soil, water and plant samples. The most difficult of these, the plant analysis, is based on work by Drs. C. Elliot and G. Snyder of the University of Florida which produced valuable simplifications of previous methods. I am grateful for Dr. Snyder's continuing interest and support of our efforts to acquire and utilize this method, and in a number of other areas such as in providing the silicon fertilizers used in our studies, as well as valuable research ideas and advice.

The University of Florida also made substantial contributions in the area of field pathology. Dr. Lawrence Datnoff of that institution and Dr. Fernando Correa of CIAT, both pathologists, established collaborative trials in 1992 at CIAT's Santa Rosa station on the effects of silicon in ameliorating blast disease. After I joined CIAT late that year, I sought to expand the work to sites broadly representative of the South American savannas. To achieve this, two soil scientists from the then-Savannas Program, Drs. Dennis Friesen and Jose Sanz, kindly agreed to contribute by identifying appropriate sites and designing and conducting the field response trials during 1993. Results demonstrated large yield increases, and when I examined the effects on grain quality, it was clear that even more significant benefits were attained, which could have large economic consequences.

Dr. Correa's data confirmed that a major basis of the response appeared to be through rice blast disease control, so my subsequent efforts focused on the mechanisms of this effect, and possibilities of genetic differences that could be exploited in breeding. Again, I have been fortunate to be able to draw upon the expertise of others, in particular Dr. Richard Howard, a physiologist at DuPont Company in Wilmington, Delaware who is contributing microscopic analyses of the process by which the fungus penetrates into rice tissue to begin the infection based on samples grown by myself, Dr. Okada and Dr. Correa at CIAT. Dr. Elcio Guimaraes of CIAT provided the upland rice germplasm which was the starting point for the field studies of genotypic differences.

Finally, as in all research, the contributions of any one individual are but the tip of an iceberg, underpinned by contributions from the global scientific literature. That information resource, acknowledged by citations throughout this monograph, has been essential in providing the knowledge base and perspectives from which I developed a number of interpretations, inferences, hypotheses, conclusions and even speculations, for which of course I am solely responsible.

SILICON, A NEW MACRONUTRIENT DEFICIENCY IN UPLAND RICE

Executive Summary

Silicon (Si) is the second-most abundant element in the earth's crust, yet paradoxically, appears to be massively deficient in upland rice. This new finding from CIAT research could account for over a half billion dollars in lost rice production annually, equivalent to about 15% of the region's total rice farm-gate value.

The basis of silicon deficiency lies in the low Si-supplying capacity of the highly weathered Oxisol and Ultisol soils which dominate the savannas; and in the absence of Si in rainwater, the only source of water for upland rice. Irrigated rice, in contrast obtains ample Si from the typically less-weathered alluvial soils and Si-rich groundwater used to flood the crop.

A healthy rice crop contains several-fold more Si than N, P or K, yet those more conventional macronutrients have received far greater research effort. The rarity of Si deficiency in irrigated rice globally may account for the astonishingly little research attention that has been paid to this "mega-nutrient". Since upland rice is proportionally and strategically more important in Latin America than elsewhere in the world, however, Si would seem to deserve special research attention here.

Collaborative research between the Rice and Tropical Lowland Programs of CIAT, with important inputs from the University of Florida and DuPont Company are shedding light on this knowledge gap. Correcting Si deficiency experimentally by applying calcium silicate to typical savanna soils (Matazul and La Florida, 1993) increased the yield of marketable whole rice grains by 61%. Most of the effect appears to be caused by a reduction in neck blast disease, a fungus which not only reduces the quantity of grain production, but also reduces the quality of those grains which are produced. Grain discoloration, another widespread cause of low grain quality in upland rice, is also greatly alleviated. Upland rice farmers in the savanna view low grain quality as the major constraint in further development of the industry; so indirectly, low quality could also slow the adoption of upland rice-based agropastoral systems, viewed as key to increasing the sustainability of tropical savanna agriculture in South America.

The identification and quantification of Si deficiency, and the installation of diagnostic tools and skills at CIAT are the major outputs of this research so far. These can help the region identify and manage the problem to an important extent. Rapid tests for soil, water and plant tissue are now in place, and critical level ranges have become evident. Perhaps the easiest and most powerful indicator is the analysis of rice husk tissue, which is readily available in stored

grain samples all over the continent. A mapping of the region's Si status could be quickly achieved in this way. Values of <3% Si on a dry weight basis suggest deficiency; 3-5%, borderline; and >5%, probable adequacy.

Besides diagnosis, of course we would also like to find practical solutions for Si deficiency. Si fertilizers are technically feasible but their economics will probably be location-specific, and require more detailed investigation by local and private sector institutions, as well as IFDC. Iron-ore slag, a waste byproduct of steel manufacture, is the most promising, and there are numerous steel mills in the savannas of Brazil. Rice husk ash, if solubilized could also have interesting possibilities. To be practical, it appears that materials and methods must be found to deliver 500 kg soluble Si/ha to the field for about US\$100 or less per hectare, to achieve a 2:1 benefit/cost ratio. Finding solutions to the low efficiency of recovery of applied Si, a result of strong adsorption of silicic acid by soil sesquioxides, would be a major advance in making Si fertilizers economically attractive by reducing application rates and transport costs.

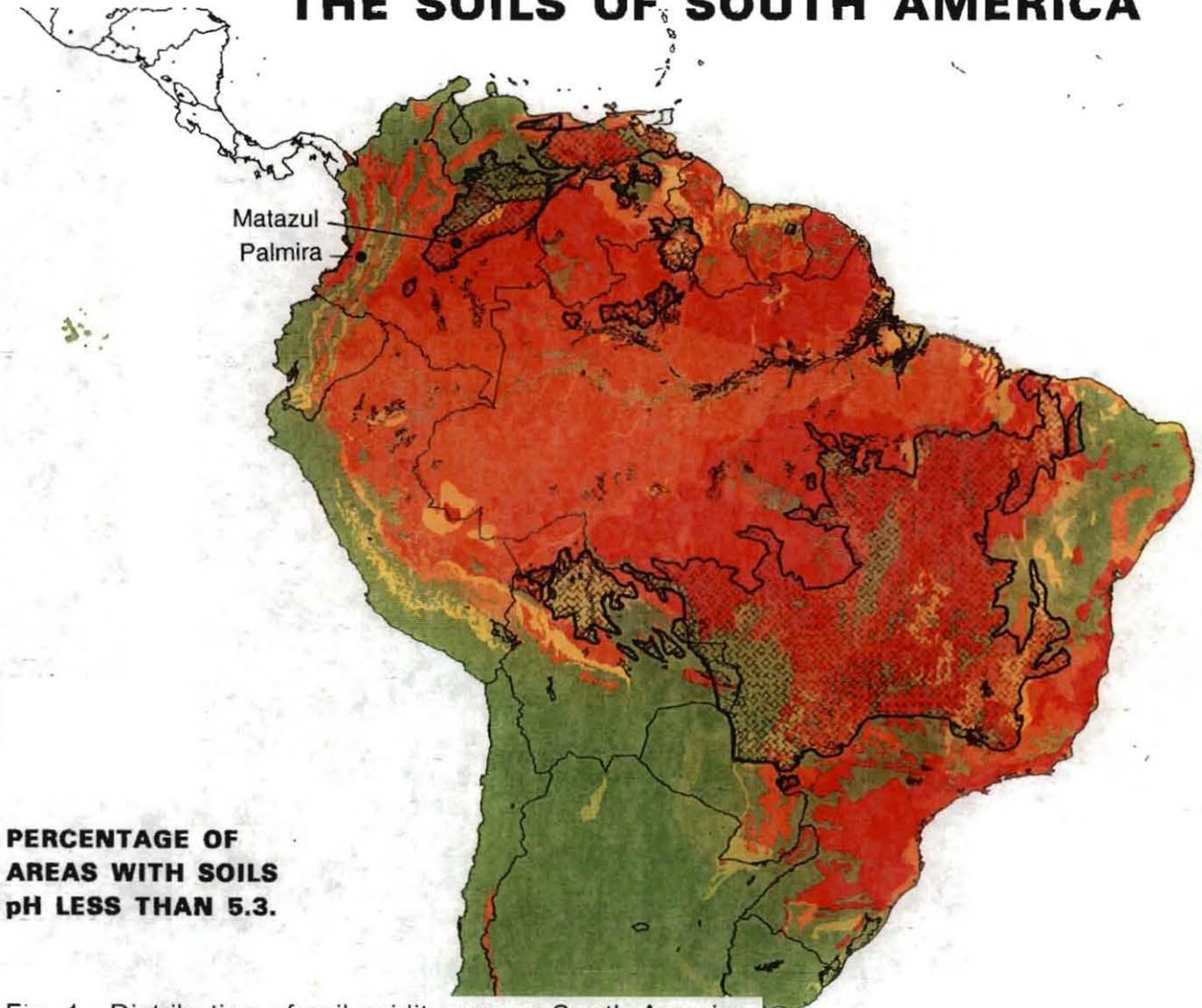
Another part of the solution may be genetic. The important role of Si in blast resistance provides an opportunity to identify new gene-based mechanisms against the disease. However, this has also received little study. Silicon was hypothesized to block fungal penetration over thirty years ago, yet the hypothesis has still not been tested (though often quoted!) Penetration defense mechanisms in general have received a fraction of the research attention accorded to post-penetration defenses, despite possessing many attractive potentialities.

Penetration appears to be a weak link in the fungal attack strategy. Penetrating fungi are exposed to a number of environmental hazards as well as host defense challenges, and as a result, most die in the attempt. Si plays a key defensive role, presumably including a "constitutive" physical barrier presented by the Si layer under the cuticle, and possibly also an "inducible" reinforcement by new Si deposition as penetration is initiated. However, neither mechanism has been experimentally demonstrated to date. Data we are currently collecting appears to be confirming the penetration-blockage hypothesis. Such evidence could lead to the identification of valuable new resistance genes which could be highly durable and complementary to the more familiar post-penetration, race-specific genes. The literature suggests that similar genes are at work in other crops such as beans.

Present evidence leads to the conclusion, however that genes alone are not likely to overcome the huge shortfall in Si supplying capacity in the savanna, which is just one-tenth of the amount provided to irrigated rice in the CIAT-Palmira environment. An integrated strategy is clearly called for, to be developed through a continued multi-disciplinary and multi-institutional research effort.

FIGURES

THE SOILS OF SOUTH AMERICA



**PERCENTAGE OF
AREAS WITH SOILS
pH LESS THAN 5.3.**

Fig. 1. Distribution of soil acidity across South America, and location of key field testing sites used in this study. Soil acidity is a good proxy for soil weathering, and hence low Si supply, across most of the tropics. Hatched-outlined areas are ecologically defined as savannas, where upland rice has great potential.

 **Savannas area**



LEGEND

	0 - 10 %
	10 - 20 %
	20 - 30 %
	30 - 40 %
	40 - 50 %
	50 - 60 %
	60 - 70 %
	70 - 80 %
	80 - 90 %
	90 - 100 %

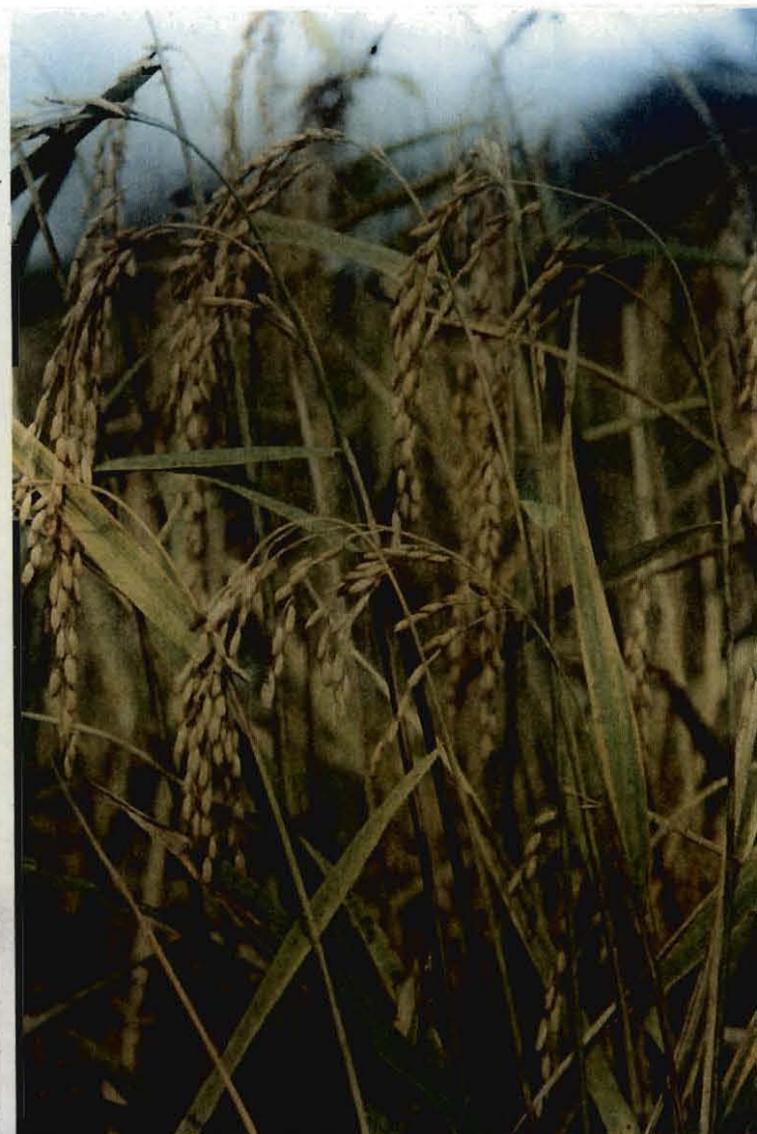


FIG. 2

Si deficiency results in neck blast (left), a fungal disease which reduces yield and quality and causes the panicle to die and break over (left). Addition of 500 kg Si/ha corrects the problem (right).

Si deficiency results in neck blast (left), a fungal disease which reduces yield and quality and causes the panicle to die and break over (left). Addition of 500 kg Silva corrects the problem (right).

Fig. 3. Effect of Si on neck blast *in vitro*. Plants were grown in pots receiving different levels of Si, then excised and inoculated with droplets of blast spore suspension in petri dishes. Areas showing damage (blackening) are locations where droplets were applied. Photo taken one week after inoculation.

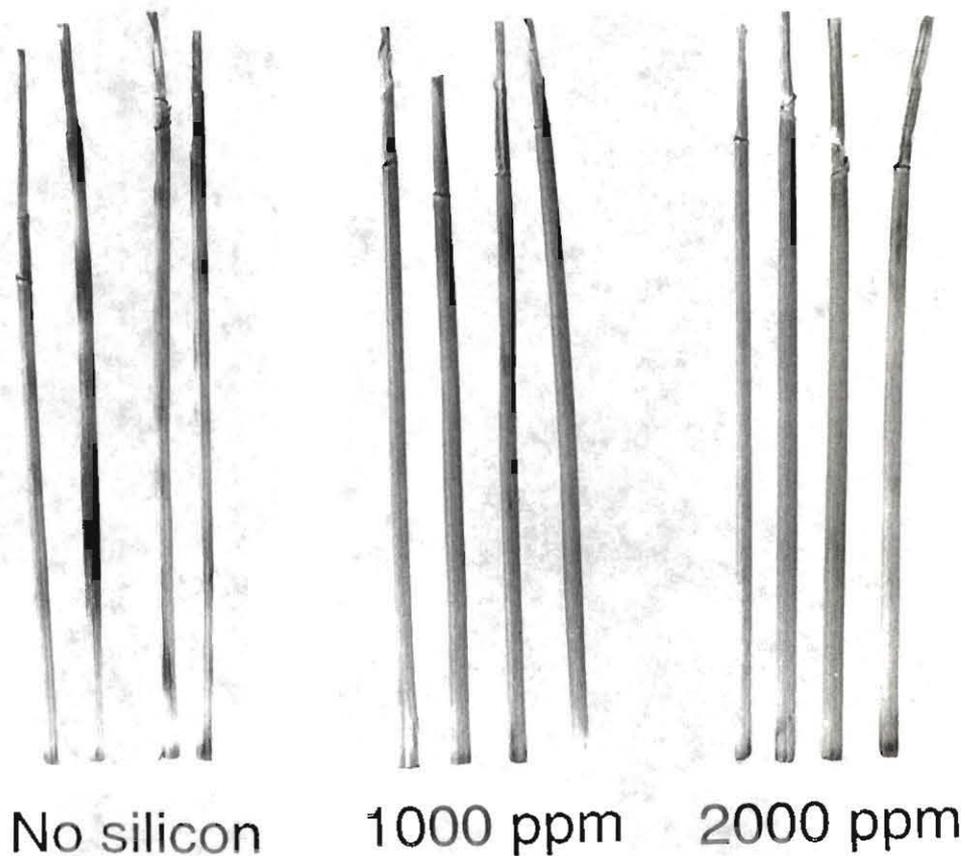


Fig. 4. Effect of Si applied to soil on grain (husk) discoloration under upland conditions. Lowland-adapted, indica-type rices are more susceptible, and show a greater response to supplemental Si.

<u>Matazul, 1994</u>	Varietal Type: J=japonica I=indica	Husk Si, %	
<u>Variety</u>			
Colombia 1	J	2.68	
Moroberekan	J	2.67	
Ngovie	J	2.64	
Tox 1785-19-18	J	2.30	
IRAT 13	J	2.09	
Oryzica Sabana 6	J	1.98	
Oryzica Turipana 7	J	1.91	
TOx 1859-102-6M-3	I	1.60	
Oryzica Llanos 5	I	1.18	
Nam Segui 19	I	1.10	
Makalioka	I	0.92	

Fig. 5

The BottleNECK: Weak Link in the Line of Defense against Blast?

- Neck blast causes the major economic damage
- **Location:** Neck is the direct pipeline for grain filling
- Grain **quality**, as well as quantity is affected
- **Timing:** No chance to recover before crop matures
- **Physiology:** Si content in neck is strikingly low.



INTRODUCTION

The Silicon Knowledge Gap

Silicon (Si) is a major nutrient for rice. This monograph describes recent (1993-95) research convened by CIAT towards identifying and understanding Si deficiency in upland rice cultivation in the South American tropical savannas.

Research is only necessary, of course in areas where knowledge is presently lacking. Over the past century, there has been an enormous amount of research on the mineral nutrition of crop plants, including the world's most important food crop, rice. Silicon is the nutrient in highest concentration and content in the rice crop, found at levels seven times greater than nitrogen, for example (Table 1).

From these simple precepts, it would seem that silicon should have received substantial research attention by now, at least in comparison to the quantitatively-lesser macronutrients. Remarkably, this is not the case, however (Tables 2,3).

Why is this so? My impressions, gained through reviewing the literature and discussing with scientists over the years, are the following:

1. Silicon is usually not deficient in irrigated rice

The majority of rice research to date has been focused on irrigated rice, and rightly so considering that it is the most important form of rice cultivation both in economic and total production volume terms. Since irrigated rice is rarely silicon-deficient, why should importance be attached to this element?

However, upon further reflection this explanation is found wanting. Deficiencies in more "conventional" macroelements, such as nitrogen, phosphorus and potassium, were identified long ago and practical, economic solutions devised and implemented to an extent such that large deficiencies are rare in conscientiously-managed irrigated fields. Nevertheless, research on these non-deficient elements (in a practical sense) continues apace (Tables 2,3).

Continued research on conventional macronutrients is reasonable, of course even if they are non-deficient, because a better understanding of the agro-ecological processes, physiological roles and gene-based mechanisms that involve them could lead to valuable and cost-saving management innovations, and other benefits. But if this rationale is valid for the "effectively non-deficient" elements N, P, K, is it not also for silicon?

2. Limited research on upland rice, in which Si deficiency may be widespread

Research on crop constraints in marginal environments has been increasing since socio-economic studies in the early 1970's began to point out that the benefits of "Green Revolution" research breakthroughs had largely bypassed the poorer farmers and rural communities occupying less-favored production environments. Within the rice research community, this shift in emphasis was reflected in increased effort on upland rice, as reflected in the publication of four major global analyses of upland rice research (IRRI, 1975; IRRI, 1985; IRRI, 1986; and Gupta and O'Toole, 1986). Two of them represent global conferences on the subject, with hundreds of participants.

Perhaps within these tomes one might expect to find the issue of silicon deficiency raised as a constraint characteristic of this neglected agro-ecosystem. However, a reading of them provides only a single suggestion concerning the possibility and significance of silicon deficiency, and that from two soil scientists not part of the core rice research community:

"The strongly weathered soils in tropical regions have reached a high degree of desilication. Research is needed to determine the effect of Si... on upland rice in the highly desilicated Oxisols and Ultisols."

- Juo and Sanchez (1986), Jakarta Conference, page 89

To give proper recognition, it should be noted that Juo had raised the issue a decade earlier, although perhaps in a forum that is less widely read by the rice research community:

"The low soluble silica content in the well-weathered kaolinitic Ultisols and Oxisols may become an important limiting factor in upland rice cultivation..."

- Juo (1978), IITA 1976 Annual Report, pages 58-59

Subsequent to the global conferences, funding constraints have precluded further major assemblies with this under-researched agro-ecosystem as a central theme, and the momentum to accelerate progress in the uplands has inevitably suffered in like manner.

Nevertheless, an excellent and comprehensive analysis of upland rice was published in 1986 by Gupta and O'Toole, which made an indirect reference to another (unfortunately remote) citation of an important effect of silicon deficiency in upland rice by J. M. Bonman, formerly a rice pathologist at IRRI :

" Bonman ... suggested ... reasons for increased blast severity in upland

environments ... [including] upland rice plants have relatively low silicon content".

- Gupta and O'Toole, 1986, citing IRRI 1983 training course lecture notes

Despite Bonman's hint, however the conventional explanation of the upland blast phenomenon continues to be that water deficits themselves (the most obvious difference between upland and irrigated environments) are the cause. The lack of general awareness or acceptance of Bonman's reminder, which itself derives from much earlier knowledge from Japan (described in Suzuki, 1963) appears to be reflected elsewhere in this same treatise, albeit with evident dissatisfaction concerning the state of current knowledge.

"Water deficits seem to increase blast... Unfortunately we must base this... on synthesis of indirect observations because neither the mineral nutrition nor microclimatic aspects of blast epidemiology... [in upland rice] have been studied."

- Gupta and O'Toole, 1986, p. 36-37

Shifting from a global to a regional focus, it is clear that upland rice commands a substantially greater proportion of the total rice area in Latin America and West Africa than in Asia (Table 4), and even takes on important commercial dimension in the former. Accordingly, even in the face of dwindling resources research institutions in these regions have found it necessary to continue to accord high priority to upland rice research. It would be logical to suspect that silicon may have received more direct attention in these regions. However, there are very few mentions of silicon in regional information databases (Table 3), and only recently has the magnitude of the deficiency been demonstrated (Yamauchi and Winslow, 1989; Winslow, 1992; and present document). Of course, it must be kept in mind that together these two regions account for just 8% of global rice production, and their research contributions are a proportionally small fraction of the global rice research effort.

In conclusion, while it is true that upland rice has received much lower and less steady funding than for irrigated rice, it seems that even so the research effort on silicon has been extraordinarily limited in relation to its importance in this agro-ecosystem.

3. Silicon is not an "essential element"

The norm in plant nutrition research has been to categorize elements found in plants into those which are "essential", i.e. without which the plant cannot survive,

and those which are nonessential. In a recent, incisive review, Epstein (1994) has pointed out that, because of the hidden implication that nonessential means unimportant, this paradigm may have influenced plant nutrition researchers to neglect silicon, considered non-essential even though it is acknowledged to be extremely important for field agronomic performance in a range of crops. This analysis is all the more compelling in that Epstein is one of the most experienced and respected voices in plant nutrition research. He further points out that the "essentiality" mindset may limit the relevance of much past solution-culture work to real field production situations.

4. Silicon research is not traditional

Closely related and probably deriving in part from the third reason above, is the relative absence of mention of silicon in the advanced-degree training which many rice scientists receive in universities of the western world. Rice is not a major crop in most of those countries, and where it is, it is irrigated and thus rarely silicon-deficient. The other major crops of the temperate zone do not have high silicon requirements, and temperate soils are probably less likely to be silicon deficient, although the available information is so limited that even this basic point is speculative. An education in such institutions produces students more confident in studying the more traditional, well-explored macronutrients such as N, P, K, Mg and Ca.

Two important exceptions to this generalization should be made, however. First, the most advanced knowledge of the mechanisms through which silicon ameliorates plant diseases comes from advanced institutions in the developed world, albeit on crops other than rice (namely sugarcane, beans, cowpeas, and cucumber). It is somewhat ironic that the future rice research community may find itself seeking to catch up by learning from research on these far less important and less silicon-dependent crops.

Second, the largest volume of silicon research on rice by far comes from Japan, the only developed country with a long rice-growing tradition. That this experience has had limited transfer to or impact in the Western developed world, or even to the tropical developing world, may be a testimony to the importance of language and cultural barriers in limiting the effective global interchange and application of scientific knowledge. While the Japanese research findings are increasingly finding their way westward, they do not include much mention of upland rice, since this form of cultivation is extremely limited there. Nevertheless, the Japanese literature forms the most substantial starting point for expanding the knowledge base into the upland rice situation.

- - - - -
In considering these last two reasons for the limited research on silicon, one is reminded of an observation of John Maynard Keynes:

"The difficulty lies not in the new ideas, but in escaping the old ones."

- - - - -
The main purpose of this monograph is to contribute to shrinking this knowledge gap, and to bring the gap to greater awareness in the rice research community so that a better understanding of the role of silicon can be developed in the future. This in turn should lead to more productive and stable rice production in the important but relatively neglected upland agro-ecosystem. It may be particularly appropriate that such a missive emanates from CIAT, an institution with a rice research mandate for the region that has the world's highest proportion of rice (Latin America and the Caribbean); and which views upland rice as a crucial strategic leverage point which can trigger the adoption of more sustainable agricultural systems across the tropics.

BACKGROUND AND LITERATURE REVIEW

Si in the Environment

The dilemma of silicon deficiency, as with nitrogen can be described as "starvation in the midst of plenty". Just as nitrogen is the dominant component of the atmosphere while agricultural systems are often N-deficient, silicon is the second most common constituent of the earth's crust, yet upland rice grown on acid soils (the most common substrate for the crop) faces a severe shortage of this element, as detailed later. The reasons for these dilemmæ are also analogous: N_2 gas in the atmosphere cannot be metabolized by higher plants (except indirectly through symbiotic associations), and in most common chemical forms in which Si occurs, the element has extremely low solubility in water and is therefore not available for uptake by rice roots.

Silicon in the geo-biosphere is found in a number of major chemical forms:

- Silicon, the element (Si, mw=28)
- Silicic acid: $Si(OH)_4$ major form in aqueous solutions; tetrahedral
 - Silicate ion: SiO_4^{4-} forms salts with calcium, sodium, aluminum, etc.
- Silica: SiO_2
 - Crystalline silica (regular lattices; quartz and other rock minerals)
 - Amorphous silica (disorganized polymers; many rock minerals, & glass)
 - - Amorphous hydrated silica: $SiO_2 \cdot nH_2O$ (silica gel), or opal (denser, less hydrated, less reactive form; common in plants)

Si in Soils

Si mineralogy

Plant-available Si originates from the mineral substrate of the earth's crust. The simplest mineral silicates are networks of silica (SiO_2) units, ranging from highly organized crystals such as quartz to disordered amorphous "opal".

Of interest to plant scientists are forms which can contribute soluble Si, which is almost entirely in the form of monomeric silicic acid, $Si(OH)_4$ (McKeague and

Cline, 1963a). This is a tetrahedral molecule, consisting of a central Si surrounded by four OH groups. The silica molecule is chemically active; the OH groups can bond with other entities through condensation to form polymers or crystal lattices, hydrogen bonds, and polar attractions leading to adsorption (McKeague and Cline, 1963c).

An important source of silicic acid in agricultural soils are the clay minerals called "phyllosilicates", layered silica sheets with three of the hydroxyl groups of a silica tetrahedron forming one plane, and the fourth group perpendicular to that plane, bonding with an Mg or Al atom. Two-layer phyllosilicates, with the silica plane considered as one layer and the metal cations as the other, form clays such as kaolinite, while three-layer phyllosilicates, consisting of two silica sheets linked by a central layer of metal ions, form clays such as mica, montmorillonite, and vermiculite.

Si does not appear to leach rapidly. It is an active solute that is mostly adsorbed before being lost by leaching (Khalid et. al. 1978; McKeague and Cline, 1963b).

It is interesting, if somewhat of a digression to mention a completely different basis for Si deficiency found in the Histosols. Histosols, such as in the Florida Everglades region, also show Si deficiency when cropped to irrigated rice (Snyder et. al.1986). These soils have only a relatively small mineral fraction, about 20%; and a correspondingly low bulk density. Hence, total Si supply is limited.

Biogenetic opal

A particularly interesting type of amorphous silica is biogenetic opal. In rice, as in most plants, Si is mainly found in this form. Biogenetic opal a denser, less hydrated, less reactive form of silica than silica gel (Lanning, 1963). Plants take up Si in its soluble form (silicic acid), and concentrate and precipitate it as opal within the plant structure; this material is deposited on the soil after plant death. Biogenetic opal is resistant to weathering, so it accumulates in the soil over time. For example, it biogenetic opal residues have been dated at 1000 years of age in Australian surface soils (Baker, 1959a).

McKeague and Cline (1963) note that "biological deposition of silica proceeds on a grand scale in soils." Lovering (1958) argued that the extraction and re-deposition of biogenetic opal in tropical jungles is so massive that it could substantially change the soil type over several thousand years, a very short time period in geological terms. Biogenetic opal sometimes makes up as much as 1-2% of the weight of the surface soil in grasslands, particularly in soils of the Mollisol order (Baker, 1959b). A soil layer up to 30 cm thick consisting purely of phytoliths was reported on the Reunion Islands in East Africa (Riquer,1960).

Much of the biogenetic opal originates from specialized "silica cells", which have shapes characteristic of the plant species that produced them. Once deposited in soils, these are termed "phytoliths", and their presence can be used as a pedologic indicator of the type of vegetation that was growing in the past. For example, phytoliths of grasses can be distinguished from those of other plant communities, such as deciduous forests, and even different types of grasses can be identified (Twiss et. al. 1969; Verna and Rust, 1969; Wilding and Drees, 1971).

Solubility of Si

Silica units in quartz are closely packed and stable, and as a consequence contribute little Si to solution (3 ppm at 25 °C). This is why sandy soils, which may be almost 100% silica and appropriately referred to as "siliceous", are nevertheless very low in available Si. Amorphous silica is less dense and more soluble, ranging between 60-80 ppm (McKeague and Cline, 1963a).

While these figures provide a useful benchmark, actual solubility in tropical soils and waters is substantially lower, due to a variety of factors which are described below. On the other hand, concentrations within plant tissues may be substantially higher, due to biochemical mechanisms.

It is somewhat of an oversimplification, however, to quote solubilities for Si materials, because these are highly dependent on particle size, pH, temperature, solution volume, time of equilibration method of equilibration (i.e. shaking vs. perfusion vs. settling), and the presence of other solutes or adsorbents.

Particle size, surface area and solubility

As an example, grinding quartz particles to a size below 5 microns in diameter increases Si solubility from the 6 ppm mentioned above to 120 ppm or more. Apparently there is a "disturbed layer" of high solubility at the surface of quartz, and hence increasing its surface area increases solubility (McKeague and Cline, 1963).

This principle could be used to advantage in developing more effective Si fertilizers (Datnoff et. al. 1992). A particular case of note is biogenic opal such as that found in rice husk. Since these particles of organic origin are of cellular or sub-cellular size, they would present a large surface area to the soil solution, which would increase solubilization.

Weathering: making Si available to plants

Weathering of soils is an "aging" process characterized by the breakdown of "young" clays into simpler forms, with the concomitant release of soluble Si, a process known as "desilication" (McKeague and Cline, 1963c). Substitution of other atoms such as Mg, Al, Ca, K, Na, etc. into silica lattices weakens silicate minerals, making them weather more easily. Two-layer phyllosilicates split readily along the layers, releasing the metal ions into the soil solution, providing other important plant nutrients in addition to Si.

As less-tightly bound Si is removed, only the more weathering-resistant mineral structures remain. Mineral segments containing Al in the substitution positions, for example are more stable than those with Mg, and hence release less Si and weather more slowly. The types of clay found in a particular soil are thus indicators of degree of weathering, with those containing 1:1 phyllosilicates rich in aluminum and iron oxides (sesquioxides) occupying the most-weathered end of the spectrum. Some important clays along this spectrum include, in order of less- to more-weathered: illite, interstratified mica intermediates, montmorillonite, kaolinite, and gibbsite. Hence, soils rich in gibbsite are likely to be low in soluble Si content (Fox et. al. 1967). The linkage between weathering and Si availability is strong enough that Gallez et. al. (1977) argued that Si solubility could be used as a quantitative measure of soil weathering in the tropics.

Since extreme weathering is characteristic of Ultisol and Oxisol soils, and these are the most important upland rice soils worldwide (and particularly in the South American tropical savannas, it is reasonable to suspect that silicon deficiency may be widespread in upland rice (Juo, 1977; Juo and Sanchez, 1986). However, experimental confirmation of this hypothesis is to date only available for West Africa (Yamauchi and Winslow, 1989; Winslow, 1992).

The soil nutritional basis for silicon deficiency in sugarcane in Hawaii has been particularly well documented (Fox et. al. 1967; Fox et. al. 1969). Soils in which Si responses of sugarcane are frequent are typically the highly weathered, leached tropical soils with low pH, low extractable Si, low base saturation, and low silica-sesquioxide ratios (Silva, 1973). Their clay minerals are predominantly hydrated aluminum and iron oxides (gibbsite and goethite or hematite) and kaolinite, which have high phosphorus sorption (fixation).

Adsorption of silicic acid

Adsorbed amorphous Si is the main immediate insoluble source of soil solution Si, governing its solubility dynamics in that medium (McKeague and Cline, 1963c).

The 1:1 phyllosilicate clay mineral gibbsite is of special interest because it is rich in aluminum sesquioxides. Sesquioxides of aluminum adsorb considerable amounts of silicic acid, removing it from solution. Indeed, precipitates of aluminum, iron, and magnesium oxides are used commercially to remove silica from industrial waters (McKeague and Cline, 1963c). The mechanisms of adsorption are not well understood, but Alvarez, Fadley, Silva and Uehara (1976) concluded that Si adsorption was weak on gibbsite in the absence of Ca. Alvarez, Cramer and Silva (1976) further concluded that there are specific interactions of Ca, silicate and phosphate ions with the surface hydroxyls of gibbsite.

The adsorption of Si onto aluminum and iron hydroxides in highly weathered soils leads to questions about the efficiency with which plants can recover available Si. Investigating this question, Khalid et. al. (1978) applied calcium silicate at rates of 830 and 1660 kg Si/ha to plots on a highly weathered tropical Gibbsite soil in Hawaii. They found that after five years of continuous cropping with sugarcane, maize, and kikuyugrass (*Pennisetum clandestinum* H.), a total of only 12-21% of the applied Si had been recovered by the crops. At the end of the experiment, they performed repeated extractions of soil samples with acetic acid-phosphate solution but were only able to recover an additional 14-28% of the applied Si. Soil analysis during the course of the experiment had revealed that virtually no Si had moved below 30 cm depth, and therefore leaching losses could be ruled out. This means that 57-72% of the applied Si was held in fixed form not readily available to plants or displaceable by acid or phosphate.

In a sequel experiment (Khalid and Silva, 1978) they attempted "biological extraction" of the remaining Si by growing rice in pots containing soil from the field plots for a 20-week period (including a ratoon crop). On soil from control plots (where no Si had been added), more Si was extracted by rice plants than by the repeated acid-phosphate extractions that followed the first experiment. This was attributed to the longer period of soil contact experienced by the rice plants, or possibly due to some unknown mechanism of greater efficiency of extraction of native soil Si by rice. In contrast, the acid-phosphate solution was more effective than rice in extraction of Si from plots where Si had been applied. These findings imply some difference between the ways in which "native" and "applied" Si are retained by the soil.

The role of aluminum sesquioxides in adsorbing Si has led to the hypothesis that substances which could reduce the activity of sesquioxides would accordingly release soluble Si (Low and Black, 1947). Chelating substances from organic matter might have such an effect. If so, the cropping system effects on quantity and quality of organic matter, as well as crop genetic capacity to produce organic substances at the root-soil interface, could affect Si availability and uptake.

Si-P interaction

An important specific case of adsorption dynamics concerns the postulated competition between Si and P for adsorption sites in weathered soils: there is evidence that Si may displace P from adsorption sites, and vice-versa, depending on their relative concentrations (Silva, 1971, 1973; Smyth and Sanchez, 1980). The adsorption of Si to the aluminum hydroxide surfaces of gibbsite appears to be weaker than the adsorption of phosphate (Alvarez et. al. 1976b). Nevertheless, heavy applications of silicate would still shift the equilibrium towards a release of phosphate. Silicate fertilizer applications can thus reduce the rate of P application needed to reach a given yield level in P-adsorbing soils (Thiagalingam, 1971), a potentially remunerative practice since Si fertilizers may be less costly than P fertilizers.

Si and pH

Acidifying a particular soil sample increases soluble Si concentration, presumably because H⁺ ions compete with silicic acid hydroxyl units for hydrogen bond sites at sesquioxide surfaces, displacing some silicic acid molecules into solution (Khalid et. al. 1978). Conversely, when bases such as lime are added to increase soil pH, H⁺ ions are removed from the sesquioxides and silicic acid molecules move onto their adsorption sites. Therefore, liming reduces soluble Si concentration.

Although Si solubility is affected by solution acidity, pH does not reflect all the factors distinguishing acid soils from their less-acid counterparts. Neutral-pH soils, in fact often have more available Si than do acid soils. This is because neutral-pH soils are usually less weathered than acid soils and are therefore richer in easily-weatherable clays that can release Si into the soil solution. Neutral soils also tend to be lower in sesquioxide content. Thus, highly weathered and acidic tropical soils often assay at less than 1 ppm soluble silicon, while neutral black clay vertisols and other young alluvial valley bottom soils may have 13-35 ppm (Elawad and Green, 1979; Fox et. al. 1967; Fox et. al. 1969).

Availability of biogenic opal

Si cycling is rarely measured, however, so little quantitative data are available. The classical work of Nye and Greenland (1960) examined in detail nutrient cycling in shifting cultivation, in which rice played a predominant role; but the authors made no mention of Si. Some tropical trees have high Si contents; the hollow stem of bamboo is reported to contain masses of almost pure silica gel (Iler, 1955). It is likely that more soil Si is extracted by the biomass of a tropical rain forest per year

than in a temperate forest. No references are available which compare biomass uptake of Si between forests and grasslands or cultivated lands.

Because of its inertness, biogenic opal may not supply much soluble Si to crops. Considering such dynamic factors, McKeague and Cline (1963c) conclude that the processes of biological insolubilization of Si combined with soil adsorption together contribute towards maintaining the generally low concentrations of Si found in soil solutions.

The slow breakdown of biogenic opal unfortunately renders ineffective the use of rice hulls, which may be 15-20% silica, or rice hull ash, which is almost entirely silica, as a cheap local source of Si fertilizer. No response was obtained from heavy rates of application of these materials to upland rice on a tropical Ultisol (M.D. Winslow, unpublished data). However, chemical modification or grinding of rice hull ash to reduce particle size and hence increase solubility, might be worth considering. Rice hull is currently a waste byproduct of little value.

The effect of soil moisture regime on soil Si availability

Drying a soil reduces the total amount of soluble Si, presumably by enhancing adsorption as the solution becomes more concentrated. The ready adsorption of Si to sesquioxides raise questions about availability of Si in soils undergoing intermittent wet-dry cycles due to rainfall variation. McKeague and Cline (1963a) found that, when sufficient water was added to just saturate soil samples, soluble Si concentration rose rapidly and then levelled off, such that by five minutes after wetting the concentration reached 50% of that achieved in ten days. This suggests that Si rapidly re-enters soil solution upon rewetting of dry soil.

Effect of flooding soil for irrigated rice culture

The reduced solubility of Si with increasing pH, described earlier for aerobic soils, is in apparent contradiction to what is found when soils are flooded for rice cultivation. Flooding raises the pH to around 7.0 but also increases soluble Si. This is attributed to the reducing conditions created by flooding, which deactivate the aluminum and iron oxides that adsorb Si (De Datta, 1981). It could also be caused by CO₂ and organic acids which build up in flooded rice paddies. Acids release Si from adsorption sites, as described above. Following the initial rise in Si concentration after flooding, a slow decline ensues which over a period of months can result in values lower than the original aerobic level (Ponnamperuma, 1972). This may be due to recombination with aluminosilicates following the decline in CO₂ concentration. However, the exact mechanisms involved are unclear.

Plant-available (dissolved) Si in soils

The outcome of the numerous interactions among the above factors are soluble Si in the soil solution, available for plant uptake. Si in actual soil solutions are hard to measure except with sophisticated techniques such as lysimeters or pressure plates. Extracts provide a relative indicator, but do not reflect the actual content to which the plant root is exposed (McKeague and Cline, 1963c).

Silicon concentrations in aqueous extracts of soils generally range from less than 1 to as much as 80 ppm (Jones and Handreck, 1967). The range of 1-2 ppm appears to be most common for tropical upland Oxisols and Ultisols (Fox et al. 1969; Winslow, 1992; and Table 5).

Si in Water Sources

An additional factor comes in to play in irrigated agriculture as well: irrigation water, especially well water or any source exposed to a period of equilibration with mineral substrates rich in available Si, eg. easily-weatherable clays), is often high in Si (circa 30 ppm). Rice irrigated with such water is seldom Si deficient. Runoff from recent rainfall, such as mountain streamwater, however, may have had insufficient opportunity to equilibrate with soil particles and pick up soluble Si, leading to Si deficiency despite irrigation (Fox et al. 1967).

Rainwater, the only source of water for true upland rice, is a product of distillation and as such contains essentially no silicon. Thus, upland rice is absent a major component of the Si sources of irrigated and rainfed lowland rice culture (which are fed by lateral movement of groundwater).

Si Variation Across Rice Agro-Ecosystems

Rice occupies a range of positions along toposequences, corresponding to the terms "upland" and "lowland" (the latter often irrigated) rice. This perspective can provide a number of insights in rice cultivation (Moorman et al. 1977)

In regards to Si, however the first toposequence analysis was with sugarcane. Fox et al. (1967) measured soil Si levels in sugar cane soils in several fields along a transect going down the slope of the volcanic island of Oahu, Hawaii. At higher elevations (above 300 m) rainfall was greatest (2300 mm), and soils (Humic Latosols) were weathered, acidic, and high in gibbsite containing active aluminum. Soil water-extractable Si levels were very low, about 0.6 ppm. Severe deficiency symptoms ("leaf freckling", a physiological brown-spotting), and poor growth were seen. In the intermediate position of the transect (150 m), rainfall was lower, about

1500 mm, and supplementary irrigation was done using mountain drainage water, which contained 2.5 ppm Si. Soil water extractable Si measured 1-1.6 ppm. Freckling was minor and plant growth much improved. At the lowest level of the toposequence, soils were alluvial, containing montmorillonite, and rainfall was low (650 mm), and the crop was irrigated with well water, which contained 30 ppm Si. Soil Si measured 6-13 ppm. Freckling symptoms were absent and growth was vigorous. The authors concluded that the soil soluble Si corresponded in a general way with soil mineralogy, a point also emphasized by Gallez et. al. (1977), but was also greatly influenced by the composition of irrigation water.

Soil fertility scientists at IITA studied soluble soil Si in the mid-1970's as an indicator of soil weathering (Gallez et. al. 1977). In the 1977 Annual Report (IITA, 1978) they noted that acidic Ultisols and Oxisols were lowest in soluble Si. They suggested that such low values might be inadequate for upland rice. However, it was not followed up with response trials. The idea was repeated in 1985 (Juo and Sanchez, 1986).

A study of rice performance along a toposequence at IITA (Moormann et. al. 1977) noted sharply higher incidence of blast disease on the drought-affected, upper part of the landscape as compared to the hydromorphic mid-zone or flooded valley bottom. It was also noted that toxic levels of iron and manganese were coming from spring water midway down the toposequence. It is interesting to note that blast, iron toxicity, and manganese toxicity have been reported to be ameliorated by Si (see later discussion), and that flooded soils and those receiving drainage water are normally higher in Si than are free-draining upland soils, as discussed previously. It would be interesting to know if Si played any role in the variation in stress damage along this toposequence. Soil Si levels, however, were not considered in that trial.

Some typical Si values from these studies, and from the present study for comparison, are shown in Table 5.

In summary, it appears that lower positions on toposequences have access to less-weathered clays and groundwater sources higher in Si. This could largely explain why upland rice, occupying the higher positions in toposequences, has much less available Si than lowland rice, found in the lower positions. Intermediate between these is "rainfed lowland" rice, which likewise may vary from Si-deficient to adequate.

It is possible, however to find irrigated rice on upper terraces irrigated by low-Si water sources and/or grown on highly weathered soil substrates. This appears to be the case in Japan, where Si responses in irrigated rice are common, and are corrected by fertilizer use.

Si in Plants

The role of Si in plants has been reviewed by Elawad and Green (1979), Jones and Handreck (1967), Lewin and Reimann (1969), and Werner and Roth (1983).

Briefly, silicon is found as a major component of a diverse array of living organisms:

- Protozoans, flagellates, sponges
- Diatoms
- Higher plant families which accumulate silicon:
 - Graminae
 - Cyperaceae
 - Pinaceae
 - Urticaceae

Higher plants can be divided into three groups, according to their Si content on a dry weight basis: marshland Gramineae, such as rice and horsetails, 5%; dryland Gramineae, such as sugarcane and most of the cereal species, 1%; and most dicots, particularly legumes, <0.1% (Marschner, 1986; Takahashi and Miyake, 1977).

The presence of large amounts of Si in a wide array of plants does not necessarily demonstrate that it is biologically essential for plant life, in the sense that, say N, P and K are. In fact, most plants can survive in the absence of Si, albeit under artificial, highly-protected conditions. As a result, silicon is not considered formally essential for terrestrial plants (except for the Equisitaceae, or "scouring rushes") by the definition of essentiality of Arnon and Stout (1939). Whether or not Si is strictly essential for plant life may be a moot point for agriculturalists, however as it has been shown to be very beneficial towards achieving high and stable yields of economical products, especially in rice and sugarcane.

Despite this practical importance, the non-essential status of Si appears to have exerted a psychological influence which has restrained research efforts on this element in comparison to "essential" nutrients found in much lower quantities. An interesting recent discussion of the anomalous status of Si in plant physiology, and its implications for academic versus practical research is provided by Epstein (1994), one of the recognized authorities in the field.

Crop responses to applied Si

Commercial Si fertilizer use on irrigated rice is well established in Japan. Yield increases of 10-20% in response to calcium silicate applications are common in crops grown on old (Ultisol) alluvial terraces there (Silva, 1973). Nearly one third of Japan's rice hectareage falls into this category. Si fertilizers are also used in Korea.

In the Asian humid tropics, responses to Si in irrigated rice were observed in Sri Lanka where leaf Si fell below 5%, and straw Si was below 2% for indica varieties (Taakijima and Gunawardena, 1969) or 2.5% for japonicas (Yoshida et. al. 1969). Irrigated rice yield responses have also been observed in Taiwan and India, according to Silva (1973).

Sugar cane responses have also been reported in diverse locations spanning the tropics, such as Mauritius (Wong You Cheong and Halais, 1970), Puerto Rico and Hawaii. Yields of sugar cane have increased by 10-50% on deficient soils in Hawaii from Si application. Cane production on the more weathered soils of higher altitudes there would not be economical without these applications (J. Silva, personal communication). Responses can be expected when leaf Si content falls below 1.5%.

In the Florida Everglades region of North America, application of 1 t/ha electric furnace calcium silicate slag (a byproduct of elemental P production that contains about about 20% Si) to irrigated rice grown on the typical organic Histosol soils increased yields by over 30%, and greatly reduced incidence of grain discoloration (Snyder et. al.1986). Si fertilization on commercial production fields is now an established practice, as much for the sugarcane crop as for rice. Sugar yields were increased by 25% in response to 2 t/ha electric furnace slag (Anderson et. al. 1987). Responses were also seen on muck soils in Florida; yields were increased by 79% in the first cane crop, and 129% in the ratoon crop in response to application of 15 t/ha electric furnace slag (Elawad et. al. 1982). Application of Portland cement gave a similar yield increase.

In South America, most studies on rice (until the present research) have examined Si responses under irrigated, rather than upland conditions. Significant yield increases were observed in Venezuela under irrigated culture (Adams, M. and A.D. Rivillo. 1991) to the application of both cement (at a rate of 520 kg Si/ha) and "silica sand" (720 kg Si/ha). However, a study on irrigated rice at the La Libertad station of ICA in Colombia (Rodriguez and Ponce, 1983) reported no response to rice husk, rice husk ash and sodium metasilicate applied three rice varieties during the second semester cropping cycle (a drier, cooler period when blast disease is less favored). Rates of the Si materials were 0, 30 and 80 ppm; the basis for these numbers (dry weight of soil? wet weight? to what depth?) was not provided,

so it is not possible to compare them with other published rates. No yield or blast-control responses to any of the Si materials was observed; nor was there any significant change in Si concentration in the leaf.

However, large increases in yield and excellent blast control have been repeatedly observed under hydromorphic and/or upland conditions at CIAT's Santa Rosa station from 1991 to present (F. Correa and L. Datnoff, unpublished data). The Santa Rosa soil is of alluvial piedmont origin, in contrast to the poorer, acid soil at La Libertad; however, the Si response trials at Santa Rosa were placed in an area with less groundwater access (presumably reducing contact with Si-bearing interflow water).

Responses to silicon in upland rice

In comparison to lowland culture, little is known about the Si responses of upland rice. This is surprising, since upland rice is cultivated on highly weathered soils where Si deficiencies are most likely to occur (Juo, 1976; Juo and Sanchez, 1986). The first reports of such a response appears to be those of Yamauchi and Winslow (1988), and Winslow (1992) in West Africa. Si sharply reduced all fungal diseases, particularly neck blast and grain discoloration, which are the most serious problems in the humid forest zone; and clear differences in Si response among rice varieties were observed.

As of yet, there are no published reports of Si responses in upland rice in Asia or Latin America. Neither the La Libertad nor the Santa Rosa soils of Colombia, tested for irrigated and hydromorphic rice cultures as described earlier, can be considered representative of the typical upland rice-growing soils of the South American savannas. Furthermore, irrigated and hydromorphic culture (as practiced in the studies at those sites) present substantially different conditions of Si supply from water sources as compared to the well-drained uplands, so extrapolation of results from the former to the latter would not be advisable.

Over 1 million tons of calcium silicate are used each year to fertilize rice in Japan. It is applied in the form of steel furnace slag, a waste byproduct of steel manufacture, at a rate of 1.5-2.0 tons of slag per hectare (De Datta, 1981).

In Korea, a mined source of calcium metasilicate is used, called wollastonite. Compost is also reported to be a good source of Si (Hemmi, 1946; Akai, 1953).

Some forms of applied silicate have been found to be more effective than others. In Hawaii, Hawaiian Cement Corporation and Tennessee Valley Authority calcium silicates were found more effective than technical grade calcium silicate, and had longer residual effects (Thiagalingam, 1971). Plants grown on the more efficient

materials had higher Si content, suggesting these materials to be more available to plant uptake. This would imply a lower rate of soil adsorption for these materials. Further investigations in this area might lead to ways of increasing the efficiency of silicate applications (eg. Datnoff et. al. 1992).

The interaction between Si and P, mentioned earlier can be used to advantage on soils which are high in P fixation capacity. In these cases it may be cheaper to apply silicate to release fixed P than to apply heavy rates of P. Application of 1666 kg Si/ha in addition to 280 kg P/ha was less costly but gave the same maize yield as 1120 kg P/ha in a Hawaiian soil (Thiagalingam, 1971).

Si absorption by rice in solution cultures is increased in the presence of magnesium (Ishizuka and Hayakawa, 1951). Application of Mg along with Si enhanced disease resistance and yield response of upland rice to Si in field trials on Si and Mg-deficient soils (IITA, 1987; Yamauchi and Winslow, 1988).

In Hawaii, fertilizer Si as calcium silicate was formerly produced by a cement factory through special agreement with the sugar cane growers association (Plucknett, 1971; J. Silva, personal communication). The binding agent in cement, known as tobermorite, is a form of hydrated calcium silicate, and it was therefore convenient for these factories to also produce calcium silicate. The basic ingredients are coral limestone and quartz sand.

Plant uptake of Si

Plants and microbes have evolved mechanisms to extract insoluble forms of Si from the soil. Keller (1957) indicated that the acidic environment adjacent to plant roots is favorable for the dissolution of silicates. Indeed, acetic acid extracts are sometimes used in soil analyses to measure potentially available Si (Gallez et. al. 1977). Some plants can weather fresh rock, due to strong acidity at the root surface or release of chelating agents (McKeague and Cline, 1963c). In the microbiological sphere, there is a bacterium (*Bacillus siliceus*) reported to be able to decompose aluminosilicates as an energy source. This bacterium is said to be used as a fertilizer in the Soviet Union (Cooper, 1959). A *Pseudomonas* species from soil was reported to produce 2-ketogluconic acid that dissolved powdered silicates, presumably by chelation (Webley et. al. 1960). Khalid and Silva (1978) found rice to be more efficient in extracting soil Si than repeated chemical extractions with acetic acid- phosphate solution.

In taking up silicic acid, rice concentrates it to levels many times higher than those in the soil solution. Uptake of silicic acid is an active process in rice, closely dependent on root metabolism (Elawad and Green, 1969).

Transport up the shoot

Transport of Si up the shoot appears to be passive, via the transpiration stream (Yoshida et. al. 1962d) although this principle has been questioned in sugar cane, where translocation seems to be energy-dependent (Fox et. al. 1969; Thiagalingam, 1971). It moves in the apoplast, being deposited at the termini of the transpiration stream, mainly in the outer walls of the epidermis on both surfaces of the leaves (Handreck and Jones, 1968; Yoshida et. al. 1962b). Because of this terminal accumulation, Si contents are higher in leaves and hulls than in the stem or roots. Silva (1969) noted that soluble Si concentrations are highest in young tissues of sugar cane, whereas total Si was highest in recently matured tissue. Once a leaf is mature, there is little subsequent change in Si content.

Fate of Si In the plant

Upon reaching the end of the transpiration stream, most (90-95%) of the silicic acid condenses to form insoluble, hydrated, amorphous silica, often called "silica gel" ($\text{SiO}_2 \cdot n\text{H}_2\text{O}$). When dehydrated, this is called biogenetic opal, which Lanning (1963) argued is the real form present (not gel) within rice tissues. Monomeric silicic acid constitutes just 0.5 to 8% of plant silica, and colloidal silicic acid forms the remaining 0 to 3.3% (Yoshida et. al. 1962d). No enzyme appears to participate in the condensation that converts soluble Si to the insoluble form in rice (Yoshida et. al. 1962), although it does seem to be an active process in sugar cane (Silva, 1969). Much of the insoluble Si is strongly bound to cellulose and occurs in layers within the epidermis and cell wall. In addition specialized cells, called "silica" cells, seem to fill up entirely with silica gel. After plant death these formations are identifiable in soils and are called "phytoliths" (see earlier discussion). Amorphous silica is also deposited in the walls of xylem cells and root epidermal cells.

Effects of Si on plants

Si was also reported to reduce grain discoloration in lowland irrigated rice grown on organic soils (Datnoff et. al. 1992; Snyder et. al. 1986), and on upland rice in highly weathered tropical soils (IITA, 1987; Yamauchi and Winslow, 1988). This is apparently a new finding as it is not mentioned as a control measure in the encyclopedic work of Ou (1985). Previous concepts of control centered around fungicides and avoiding contact of the grain with moisture.

Si in the root aerenchyma may stiffen the wall structure, increasing the volume and thereby increasing oxidizing power. Si in leaves and stems causes a more

erect growth habit, thereby improving distribution of light within the canopy (Yoshida et. al. 1969).

Plants grown in Si-free media have considerably higher rates of transpiration. Hence, a thick Si layer in the cuticle has been suggested as a mechanism of drought resistance (Yoshida et. al. 1962c), although one attempt to demonstrate this in the field could not find a significant correlation (Garrity et. al.1984).

In a number of crops, Si also seems to reduce the activity of toxic elements in the soil such as manganese, iron and possibly aluminum (Silva, 1973; Vlamis and Williams, 1967). It is reported to reduce accumulation of Mn and Fe from the soil (Lewin and Reimann, 1969). Silica strengthens aerenchyma walls, which increases the volume of these air conduits and improves oxygen movement to the roots. When grown in flooded (reducing) conditions, this enables rice to oxidize and thereby precipitate out greater amounts of toxic elements like iron and manganese (Horiguchi, 1988; Okuda and Takahashi, 1964). It also has an ameliorating effect within rice tissues, and disperse Mn within the leaf in beans (Marschner, 1986) These effects prevent brown spotting in bean plants, and perhaps also the "freckling" of sugar cane and physiological brown spot of rice and barley.

On a biochemical level, silicic acid may form complexes with enzymes which act as protectors or regulators of photosynthesis (Silva, 1973). In-vitro studies found that silicic acid can suppress the activities of invertase, peroxidase, polyphenol oxidase, phosphatase, and ATP. Suppression of invertase results in increased sucrose production, while reduced phosphatase activity is believed to provide a greater supply of essential high-energy precursors needed for optimum cane growth and sugar production.

Silicon and disease resistance under upland conditions

The effectiveness of Si applications in reducing damage from rice blast fungus has been thoroughly demonstrated under irrigated conditions, particularly in Japan. Water deficits such as those caused by non-flooding under field or pot-trial conditions have also been shown many times to reduce Si content and increase blast damage. For example, several groups have noted that the number of silicified cells is greater in rice grown on flooded soil as opposed to well-drained soil (Hemmi, 1926, 1933; H. Suzuki, 1935). This has been extended by the observation that the Si supply in valley-bottom soils and in floodwater is usually much greater than in upland soils and rainwater, resulting in greater disease damage in the uplands (Winslow, 1992).

One might logically infer from these established facts that Si deficiency could be a major reason why blast and other fungal disease damage is much less in flooded

rice culture than in upland. Curiously, though this conclusion and its implications do not appear to be widely recognized for upland rice, as reflected by the paucity of publications or common knowledge on the subject within the rice research community.

Mechanisms of the disease-reducing effect of Si

As noted above, most Si is deposited at the end of the transpiration stream as insoluble silica gel, in association with organic substances such as cellulose or others. The working hypothesis that this material might form a barrier (whether physical or chemical) to penetration was put forward by Volk et. al. (1958) to explain their observed positive correlation between leaf age, silicon content and blast resistance.

Further circumstantial evidence in support of the penetration-blockage hypothesis was provided by Yoshida et. al. (1962c), who studied the anatomical distribution of the siliceous materials in the leaf and husk, and discovered a thick layer of deposition over the epidermal cells, between the cuticle and cell wall. Cellulose layers appeared to be interspersed within the silica, leading the authors to coin the phrase "cuticle-silica double layer". They suggested that this layer might be relatively resistant to penetration by fungi. However, a direct observation of the effect on blast spore penetration of different silicon applications has never been published.

In contrast, a publication by Kim (1987) concluded that greater blast susceptibility in non-flooded rice was not attributable to increased penetration. However, that pot trial did not control or measure silicon content in either the soil or water component, so it is quite likely that the silicon deficiency normally found in the field was not attained, leading to an incorrect conclusion.

Sherwood and Vance (1980) challenged a diverse set of grass species with fungi to which they were not normally host (i.e. the grasses were nonsuscept), to learn why infections fail. Consistently, infection attempts were unsuccessful due to failure of the pathogen to penetrate the nonsuscept leaf. Failed penetration attempts were associated with the formation of cell wall thickenings, or "appositions". They concluded that there appear to be two types of penetration resistance mechanism, one attributable to "constitutive" defenses (i.e. those which are present with or without the presence of fungal attack) and the other due to "inducible" defenses (ones which materialize only in response to fungal attack). Appositions represent an inducible defense, since they only form once the plant is attacked.

Heath (1981), using energy-dispersive X-ray analysis (EDX) found an

accumulation of Si in areas encasing the cowpea rust (*Uromyces vignae*) fungus attacking cowpea (*Vigna sinensis*), and subsequently Heath and Stumpf (1986) observed increased blockage of penetration pegs of the same pathogen attacking common bean (*Phaseolus vulgaris*) when grown in solution cultures with Si added. These observations could suggest Si accumulation as a defensive reaction to block penetrating hyphae in this normally low-Si plant.

In a study of the anatomical events taking place during rice blast fungus penetration into goosegrass (*Elusine indica*), a common weed of rice fields, Heath et. al. (1992) noted that successful penetration was rare, and that cessation of fungal growth was most commonly associated with the deposition of a material that appeared to contain Si.

Carver et. al. (1987) observed the micro-anatomical process of penetration of powdery mildew fungus, *Erysiphe graminis* into barley leaves. Using energy-dispersive X-ray microanalysis, they observed accumulation of Si in host cells in parasite contact regions, and even Si uptake by fungal germlings at the attack points. Higher levels of Si were noted at sites where penetration failed. They concluded this was a defensive response in the host.

Examining the Si effect in cucumber from an epidemiological point of view, Menzies et. al. (1991) found that Si application in solution cultures reduced the numbers and sizes of powdery mildew (*Sphaerotheca fuliginea*) colonies on cucumber leaves, and even reduced the germination of conidia collected from those leaves.

Samuels et. al. (1991a) examined the mechanisms involved in this disease system. They determined that areas of the host cell wall next to germinating hyphae exhibited a modified surface morphology and high Si concentrations, and found high Si concentrations to correlate with low fungal growth, inducible Si deposition apparently constituting a rapid response defense mechanism against pathogen attack. They also studied the timing of Si supply in relation to this inducible effect (Samuels et. al. 1991b), by transferring cucumber plants in and out of Si-containing solution cultures before inoculation. They found that plants had to be bathed in Si-containing solution during the time of fungal attack to exhibit the Si defense response. Prior growth in Si-containing media was not beneficial if Si was absent at the time of infection. This suggests that earlier-deposited Si cannot be remobilized to perform this rapid response blockage; current soluble Si is required. In a third study (1994), they used energy dispersive X-ray analysis to localize the Si, and found it located in the papillae, host cell walls, around the haustorial neck and in deposits between the host cell wall and plasma membrane.

Varietal differences in silicon content, and their effects

Miyake and Adachi (1922) were the first to link varietal differences in blast resistance to inherent differences in Si content in irrigated rice varieties. They found that a resistant variety, 'Bozu', contained a higher amount of Si than the susceptible 'Akage.' Other cell constituents such as soluble carbohydrates, phosphate, magnesium, and other microelements did not correlate well with resistance. Subsequent reports from other areas corroborated their findings (Adyanthaya and Rangaswami, 1952; Suzuki, 1963). However, some reports have indicated no correlation between blast resistance and varietal differences in Si content (Ou, 1985; Yoshii, 1946).

Varietal differences in resistance to stem borer, Chilo suppressalis (Walker), were found to correlate with differences Si content (Djamin and Pathak, 1967). Mandibles of borer larvae sampled from high-Si varieties showed excessive wear, which indicates low feeding efficiency.

Garrity et. al. (1984) found fourfold differences in the thickness of the husk cuticle silica layer among a set of 16 lowland rice cultivars. Their hypothesis was that cultivars with thicker silica layers would be more drought resistant due to reduced transpiration. However, the differences found did not correlate with known differences in field drought resistance among the cultivars. More factors are apparently involved.

Majumder et. al. (1985) studied the inheritance of silica uptake in lowland rice in a seven-parent diallel cross. They reported that mainly additive but also non-additive effects were present. Therefore progress in breeding for higher Si content seemed possible. They noted that genotypic differences were already expressed 60 days after sowing. With a rapid Si analysis procedure, selection could be made before flowering (commonly about 95 DAS) and superior individuals could be recombined which could make for rapid breeding progress in a recurrent crossing scheme.

In an irrigated but Si-deficient environment of the Everglades Histosols of Florida, Deren et. al. (1992) found that genotypic differences among 18 cultivars were significant, and consistent across three sites. This suggests that Si content is a heritable trait which could be genetically manipulated.

Recently, Winslow (1992) found varietal differences in Si content which were associated with differences in resistance to neck blast and grain discoloration diseases in West Africa. Furthermore, the varietal differences were greatest between the two major genetic sub-groups of cultivated rice, the indica and japonica types. Japonica types, which are the traditional upland rices of the tropics, had substantially higher levels of Si in plant tissues, and were more resistant to these important upland diseases. While this is circumstantial

evidence, it is significant in light of the known effect of applied Si in reducing those same diseases. When Si was applied in that same study, the indica types showed a greater response in terms of increased Si content, yield and disease control, than did japonicas, as might be expected given the greater "inherent deficiency" characteristic of indicas.

Interpreting these observations, that paper noted that indicas, the common irrigated rices of the tropics, evolved in high-Si environments; this may have obviated the need to evolve mechanisms for high Si-efficiency, resulting in the low Si contents expressed in Si-deficient upland conditions.

While generally associated with blast resistance, there were some cases where high-Si varieties fell susceptible, apparently to specifically compatible blast races (Winslow, 1992). This led to the conclusion that, although it is an important resistance factor, Si is not the only determinant of blast resistance.

MATERIALS AND METHODS

Field Trials

Four field sites in Colombia were used over the two years of this study:

Matazul, a typical acid upland rice soil in the savanna of Colombia:

Oxisol, pH 4.7 in H₂O, ECEC 1.99, Al Saturation 79%

Presumed low in available Si

La Florida, an even more stressful upland savanna site due to high sand content

Oxisol, pH 5.9 in H₂O, ECEC 0.76, Al Saturation 67%

Presumed low in available Si

Santa Rosa, a medium-productivity hydromorphic piedmont soil

Inceptisol, pH 4.7, ECEC 3.11, Al Saturation 18.3%

Presumed intermediate in available Si

Palmira, a high-productivity valley bottom black clay soil, irrigated rice

Neutral pH, irrigated by well water.

Presumed high in available Si

Field trials, 1993

To determine whether Si deficiency existed in the savannas, collaborative trials between members of the Rice (F. Correa, M. Winslow, K. Okada, F. Correa) and then-Savannas (D. Friesen, J.I. Sanz) Programs were established at two acid upland research sites, Matazul and La Florida. Three Si levels were created: 0, 250 and 500 kg Si/ha as wollastonite (calcium metasilicate, CaSiO₃). Due to this material's basifying effect, chemically-equivalent amounts of calcite lime were applied to the 0 and 250 kg Si plots to create a total lime value on all plots equivalent to 2400 kg CaCO₃/ha. All other nutrients were supplied at adequate levels. Plots were drilled, 4.25 m wide x 12 m long. The design was an RCBD with four replications. Plots were harvested for yield, and evaluated for disease, grain quality and tissue Si content.

Leaf blast pressure was moderate, and neck blast was serious during 1993.

Searching for genotypic differences in inherent Si content, a diverse sample of 60 breeding parents, including both indica and japonica sub-types, in use by CIAT's upland rice improvement project were provided by Dr. E. Guimaraes. The lines were sown in two-row, 5 m long plots with three reps/location at three locations:

Matazul, Santa Rosa, and Palmira. Unfortunately, the Matazul site was lost that year due to grazing by cattle. At Santa Rosa, flag leaf and grain samples were collected for Si analysis; at Palmira, samples for Si analysis of flag leaf at flowering and flag leaf, husk and neck at maturity were collected.

Field trials, 1994

In 1994, a selected group of 11 varieties out of the 60 which had shown consistently high or low Si content across plant organs and sites was identified based on analyses of the 1993 tissue samples, and sown in larger plots to see if the differences were repeatable. The varieties were:

TOx 1785-19-18
Ngovie
Colombia 1
TOx 1859-102-6M-3
Oryzica Turipana 7
IAC 165
Oryzica Llanos 5
Nam Segui
Makalioka
Oryzica Sabana 6
IRAT 13

The trial was sown at Matazul, a presumed low-Si site, and Palmira (Si-rich, irrigated). No supplemental Si was supplied. Other nutrients were provided to the level needed. At Palmira, plots were transplanted (29-day old seedlings) at 30 x 30 cm spacing, in 12 rows (3.6 m) wide x 16 rows (4.8 m) long; the outer rows were eliminated from harvest. Due to some stand establishment problems, parts of some plots were avoided; care was taken not to harvest any hills near gap areas. For yield components and some tissue samples for Si analysis, 10 random hills not adjacent to a gap were collected and dried. At Matazul, plots were drilled, 12 rows spaced 20 cm; the central 8 m² was harvested for yield. For yield components and some Si tissue samples, three randomly-selected samples were collected per plot, each consisting of 3 adjacent rows 50 cm long. There was negligible rice blast fungus pressure on these trials in 1994.

Laboratory Analyses

Methods of Si analysis

Soil, water and plant tissue samples were analyzed for total Si content using the following methods:

- Soil: 10 parts water:1 part soil shaken for 4 hours (after Fox et. al. 1967), followed by molybdate blue method for colorimetric Si analysis (Kilmer, 1965).
- Water: Molybdate blue method described in Elliot and Snyder, 1991.
- Plant: Autoclave-induced digestion followed by molybdate blue method: Elliot and Snyder, 1991.

Collaborative experiments with DuPont Co., USA

To investigate the mechanisms of Si-mediated blast resistance, collaboration was established with Dr. Richard Howard, a plant physiologist at DuPont Co., Wilmington, Delaware. Plant tissue samples (cv. 'Orizica 1, an indica-type irrigated rice variety widely grown in Colombia) were sown in 10-inch (25 cm) diameter pots filled with 6 kg Matazul soil, and treated with three different levels of Si (calcium silicate): none, 1000 ppm, and 2000 ppm (soil dry weight basis). There were five replications. Pots were irrigated with de-ionized water only to prevent contamination from Si in the tap water source. At 20 and 40 days after sowing, leaf samples approx 5 cm long were excised from the center of the most recent fully-expanded leaf and taped onto glass microscopic slides, adaxial surface up which were placed into petri dishes for inoculation with blast. A piece of filter paper was kept on the bottom of the dish and moistened as needed over the course of the experiment to maintain the high humidity favorable for blast germination and infection.

Neck samples were also collected by harvesting at the neck emergence stage (approx. 85 days after sowing). They were suspended horizontally in the petri dishes by placing them onto a bent glass rod which encircled the dish.

For both types of tissue, the blast isolate Oryzica 1-237 was used to attempt infection. The rice variety Oryzica 1 is highly susceptible to this isolate. It was diluted to a spore concentration 500,000/ml. Inoculation was carried out by placing 4-5 droplets of about 10 ul. each spaced about 1 cm apart onto the leaf

surface. For necks, droplets of spore suspension were applied to the cylindrical neck surface; due to gravity they hung from the bottom side of these horizontally-placed necks holding on by water tension and due to addition of gelatin as a sticking agent to the spore solution before inoculation.

Spores were incubated for 36 hours, the approximate time needed for appressorial attachment and penetration, at room temperature. Then samples were immediately placed into test tubes containing boiled, 70% ethanol and sent to Dr. Richard Howard of DuPont Co., Wilmington, Delaware. That laboratory microscopically examined the samples for appressoria, which were scored for presence or absence of a penetration peg, after Howard et. al. (1991). Fifty appressoria were counted per replication, and there were five replications.

RESULTS AND DISCUSSION

Causes, and Evidence of Si Deficiency

Soil minerology and water source: the determinants of Si supply in rice

Our results show that an understanding of soil and water sources in a particular field can provide a good idea of the Si supply to the rice crop. I assembled a generalized model of typical Si concentrations in soil extracts and water sources for upland vs. irrigated rice (Table 8) to illustrate the enormous magnitude of differences encountered. The values in this table are representative of published data (Tables 6,7) and are a good fit to our own measurements in Colombia.

Corresponding to these agro-ecosystem characteristics, upland rice Si content dropped drastically when the crop was grown in a typical savanna upland rice site (Matazol, Colombia) as compared to a favorable irrigated site (Palmira, Colombia) (Table 9). It is noteworthy that Si harvested per unit area, and also Si concentration in plant tissue, fell much more precipitously than total biomass, which indicates that, although there may be a variety of stresses reducing crop productivity in such harsh upland environments, Si deficiency considerably exceeded those other constraints. This could only be observable if Si itself did not strictly limit biomass production, for if it had, biomass would have fallen to the same proportion as Si, leaving tissue concentration unchanged. Ironically, the sensitivity of Si tissue concentration as a deficiency indicator (see diagnostics section later) seems to be a product of its non-essentiality for plant growth (see literature review).

Visual symptoms of Si deficiency

Visual observation of the effects of Si on the upland rice crop may not impress the casual observer. Indeed, this may be a basic reason why the rice research community has been slow to recognize the significance of Si deficiency. Si deficiency does not greatly restrict total biomass production, so the crop may appear quite normal. The absence of "essential" nutrients such as N, P and K on the other hand is readily visible in terms of restricted foliar growth, obvious leaf coloration changes etc. An Si-deficient crop may show only subtle symptoms prior to maturity, such as less erect growth, which is not striking upon visual observation in the absence of a control plot provided with adequate Si. Leaf blast incidence may be erratic over years due to climatic and epidemiological variation, and neck blast is only observable upon close inspection prior to maturity. Grain discoloration (another disease enhanced by Si deficiency- see later) likewise is only clear near harvest time.

Extrapolation of results based on soil-water principles

Clearly, the difference in Si supply between irrigated and weathered true (rainwater-fed only) upland rice are not gradative- they are "night and day". Table 7 indicates differences of several orders of magnitude for soils, and all vs. nothing for water sources. These enormous differences, found in typical sites in Colombia which are reasonably representative of the South American tropical savannas, give me confidence to extrapolate to the conclusion that savanna upland rice, covering some 3 million hectares on the continent, faces a large and widespread degree of Si deficiency.

The genesis of the present research was, in fact an extrapolation made based on similarities between West African and South American soils. Si deficiency had been previously shown in the former (Winslow, 1992; Yamauchi and Winslow, 1989). As in West Africa, the savannas of tropical Latin America are weathered, acidic Oxisols and Ultisols; and rainwater, the only moisture source for true upland rice, is always absent Si, regardless of location.

Based on such simple and well-known parameters, I believe that the extrapolation process can be taken even farther. The hill rice (true upland rice) areas of southeast Asia are likewise solely rainwater dependent, and weathered Oxisols and Ultisols account for the largest proportion of the area occupied by the crop (Gupta and O'Toole, 1986). These soils are particularly predominant in northeastern Thailand, Myanmar, Vietnam, Indonesia, and neighboring countries. This leads me to venture another inter-continental prediction: on these soils, Asian upland rice probably suffers from widespread and severe Si deficiency.

This prediction, if validated has even larger consequences than for the previous two continents. Despite the minor fraction of all Asian rice which is upland (Table 4), the actual area grown on weathered soils greatly exceeds that of Latin America and West Africa combined (Gupta and O'Toole, 1986, p. 45). Yet, to date there is no report testing the possibility of Si deficiency in Asian upland rice. Given the large economic impact calculated earlier for South America alone, the significance of this constraint to Asia, and the dependence of Asian people on rice as a staple food source, a research investigation to test this prediction would seem well justified.

Economic implications of Si deficiency

Nevertheless, this illusion masks large economic damage due to deficiency. In terms of the economically important products of rice cultivation, rice itself, the responses to applied Si were also impressive (Table 10). Viewed in reverse,

these responses of course also constitute an estimate of the magnitude of rice production currently foregone due to uncorrected Si deficiency. In economic terms, they appear to have a value exceeding a half billion US dollars per year in South America (Table 11). This is approximately equivalent to over 10 percent of the entire continent's current rice crop! Clearly, Si deficiency in upland rice has major economic consequences, which have until now not been recognized by the agricultural science and technology community in South America, as evidenced by the absence of any publication describing the phenomenon nor any diagnostic method, extension advice, commercial fertilizer or other tool to address it.

Diagnostic Tools to identify Si Deficiency

Soil, water and plant sampling

A fairly simple understanding of the effects of soil mineralogy and water source on Si supply has led to powerful diagnostic tools which can identify Si deficiency. These tools, adapted from the literature, are now in place at CIAT (see Materials and Methods). Large numbers of soil, water and tissue samples can now be analyzed with good precision. The plant tissue tests are the most difficult, since Si first has to be separated from the organic matrix and other minerals, and then dissolved; however, even with this difficulty the method in place can analyze 40-80 samples per day with a single technician.

These diagnostic tools could be extremely useful in identifying Si deficiency. Once informed of the problem, farmers could consider a number of management options, as discussed later. Diagnostics are well known to have enormous value for other crop nutrients, diseases and environmental constraints; so is the case for Si. Old sayings such as "forewarned is forearmed" and "identifying the problem is half the solution" are certainly valid in these cases.

Based on our data over sites and years, I would suggest the critical diagnostic levels for soil, water and plant samples shown in Table 8. These values agree well with the observations of Fox et. al. (1967) and Fox et. al. (1969) for soils grown to sugarcane, and Winslow (1992) for upland rice in West Africa, as well as the other Si data presented in Tables 5,6. The consistency in data collected from geographically diverse sites and cropping situations suggests that these critical levels might be reasonably robust and thus useful in practical terms for rice scientists around the world.

Which plant tissue to sample?

Plant tissue diagnosis bears special discussion. The plant, as an integrator of the two sources of Si supply (soil, water) and as the direct determinant of crop performance, is at least in concept the most informative and relevant sampling material for obtaining an overall measure of effective Si supplying capacity of a particular growing environment. What parts of, and how should the plant be sampled, though?

Most of the literature reports tissue Si contents in terms of straw Si concentration (percent). Straw, however would appear to have a number of drawbacks as a sampling source. It is an ill-defined material that it may or may not include leaves, culm, sheaths, and panicle, depending on one's understanding of the term and the time of harvest (leaves rapidly senesce, decay and break off the culm); it is a bulky substance to harvest, transport and process; its collection must be done at or very shortly following crop harvest to avoid deterioration; it requires careful and laborious sampling procedures to achieve representativeness; it is easily contaminated with the underlying soil, which contains large amounts of Si; and stored samples which could be tested are not readily available on a wide geographic scale for comparative analysis.

My experience indicates that these drawbacks could be avoided by measuring another organ instead, the husk material encasing the rice grains. This material is readily available in large quantities- it constitutes over 20% of the dry weight of the harvested crop, so-called "paddy" rice. Our results show that this material is a sensitive reflector of Si supply across environments (Table 9). This is presumably because a) Si is not "essential" for rice growth, so its shortage, for example does not restrain growth, which would otherwise prevent concentration from declining proportionately- a drawback which complicates the tissue testing of the "essential" nutrients; and b) this organ develops and matures during the time period of maximum crop growth rate, when crop demand for nutrients is maximal, so that deficiencies, as reflected in husk concentrations, would be most pronounced during that period (eg., as is the well-known case for nitrogen).

Furthermore, rice husk samples can be taken from grain bags which are easily and thoroughly mixed, achieving a representativeness that results in greater experimental precision than for other types of plant samples. This is reflected in the lower coefficients of variation measured for husks over diverse environments and years in our experiments (Table 12).

In addition to providing sensitivity, accuracy and precision, sampling of rice husk is eminently practical and economical. Paddy rice is stored every year from yield trials by breeders and agronomists all over the world, representing rice crops grown in a wide range of important agro-ecosystems. Since stored material is

available for long periods of time after harvest, and plant opal (the Si-bearing material in tissue) does not deteriorate in storage, obtaining these samples on a wide geographic scale would be practical and inexpensive, and would not require specific field collections by the analyst. The husks can be easily stripped off the grain with laboratory de-husker machines, and then ground for Si analysis. Once done, interpretation of the results can be powerfully enhanced by association with the other data routinely collected in these trials, such as site topography, cropping history and hydrology, soil type, climatic conditions, yield, lodging, diseases etc. The advantages of rice husk as a sampling material are summarized in Table 13.

Indeed, it would appear practical to design a survey on a continental and even global scale that could, at relatively low cost quickly survey the extent and magnitude of Si deficiency in major rice-growing areas. Given the economic implications of Si deficiency, such a survey would appear to have considerable merit.

One potential source of error in plant tissue sampling is the effect of rice genotype. Significant differences were observed among different rice varieties (Tables 18, Fig. 4). This error source holds for all plant organs, including the husk. A substantial part of this error can be adjusted for by noting whether the variety sampled is of the indica or japonica plant type; the latter are widely used in the uplands, and they generally contain 50-100% more Si than the former in Si-deficient environments (Fig. 4, and Winslow, 1992), although the difference diminishes as Si supply increases. Another error-reducing consideration is that the differences between Si-rich and Si-poor environments, often 10-fold (Table 9), are sufficient to "swamp out" even the large genotypic effect for most purposes. Nevertheless, it is helpful to sample the same or similar varieties whenever possible.

Potential Si Fertilizers

Economics: benefits and costs

Large responses to applied Si observed in this research suggest that Si fertilizers could largely correct the deficiency of the element in upland rice. However, these may be costly. Si fertilizers are currently used on rice in Japan and Florida, and on sugarcane in Hawaii and Florida. The high rates of application used in those places must involve significant costs, particularly for transportation of the material to the field and machinery costs for application. Such costs may be affordable in developed nations with good infrastructure and crop subsidies, but could be more problematic in the developing world.

much greater plant biomass found in a crop grown to maturity (as opposed to seedlings). Trials using high rates of husk ash at IITA in Nigeria observed no yield or disease control response (M. Winslow, unpublished data). Lopez (1991; see Fig. 1) could not detect elevated contents of soluble Si in field soils treated with rates of husk ash as high as 16 t/ha in Colombia. Recent CIAT trials (K. Okada, unpublished data) at an upland savanna site similarly found no yield response to high rates of rice husk ash, although seedling-stage vigor benefits were observed.

However, it would be wise not to ignore the potential of this Si source if it could be solubilized. Since the raw material is relatively pure and finely graded, and located close to industrial scale operations (mills) as well as end-users, such a process would not need to entail expensive pre-treatment operations characteristic of other fertilizer manufactures such as mining, crushing, transport of ore from remote locations to industrial installations, purification, disposal of byproducts, etc. Linkages should be established with industrial and commercial enterprises to explore this option in more detail.

Effect of Si Deficiency on Blast Disease in Upland Rice

Recognition of the phenomenon

Despite the well-known effect of Si in controlling blast, the role of Si deficiency as a causal factor for blast disease in upland rice is not generally recognized within the rice research community. Upland, high-nitrogen conditions have long been known to be blast-promotive, and have been advocated and intensively used for blast resistance screening for many years. The explanation for this phenomenon, however has long rested on the apparently more limiting water status of the plant. However, some have noted that this explanation appears to be superficial and unsubstantiated:

"Water deficits seem to increase blast... Unfortunately we must base this... on synthesis of indirect observations because neither the mineral nutrition nor microclimatic aspects of blast epidemiology... [in upland rice] have been studied."
Gupta and O'Toole, 1986, p. 36-37

Furthermore, the water-deficit hypothesis would seem to run contrary to epidemiological principles. Wet, humid conditions are required for blast germination and infection, and these are less likely under water-deficit conditions. Ou (1985, p.140-41), however provided an insightful resolution of this apparent contradiction by pointing out that the duration of the nightly dew period, a key blast-promotive factor, is actually lengthened when rice is cultivated under upland

conditions. Dew periods commence when the crop canopy cools down sufficiently to induce condensation of atmospheric water onto leaf surfaces. The upland canopy cools faster than for irrigated rice since the latter is insulated by the flood water which moderates temperature changes. While this may be completely correct, it is a different and additional factor to Si deficiency which is also prevalent under upland conditions, yet is still not widely recognized as a causative factor in upland blast.

Mechanisms of Si-mediated resistance to blast

The penetration-blockage hypothesis, and alternatives

Physical blockage of entry into the host, caused by the toughening of the leaf surface due to the presence of the cuticle-silica double layer over the epidermis, has been the dominant hypothesis for the mechanism of Si-mediated blast resistance for the past 35 years, as discussed in the literature review. Despite the importance of this hypothesis in rice cultivation and productivity, it has never been experimentally confirmed.

Indeed, other plausible explanations for the Si-mediated blast control effect could be proffered. Si might, for example prevent the attachment of the spores to the leaf surface, a necessary prerequisite for attempted penetration. Chemically, Si deposited as plant opal is similar to glass, and it has been reported that blast spores do not attach to glass (Howard et. al. 1991).

Another possibility is that the Si effect might occur post-penetration, i.e. by restricting development of the fungus within the leaf tissue. This fits preliminary observations by the present author, in which leaf sections inoculated at high doses under ideal conditions *in vitro* showed delayed symptom development, suggesting post-penetration interference by Si (while not ruling out the possibility of penetration-stage interference as well). Another report found that Si in solution cultures did not reduce the total number of blast lesions; rather, it reduced the spread of those lesions, suggesting a post-penetration defensive action, rather than penetration inhibition (Canizalez, 1990). Both penetration and post penetration effects are suggested from field epidemiological studies currently underway in University of Florida-CIAT collaborative trials (K. Seebold, unpublished data).

In view of these different possibilities, which have important implications in searching for resistance gene action, the long-held assumption that Si functions solely by blocking penetration should be experimentally tested and verified.

Penetration: the weak link in the fungal offense?

While these other possible mechanisms of Si-mediated blast resistance could be important, the physical blockage of penetration has not been ruled in or out; and it remains an attractive hypothesis. Penetration could be a weak link in the fungus' attack strategy, a weakness which the rice plant may have exploited during the evolution of defense mechanisms. To use a medieval analogy, attackers are most vulnerable when scaling the castle wall. It is easier to keep them out (eg., by pushing the ladder away from the wall, pouring boiling oil, raining down arrows and spears, etc.) than to battle them once inside.

Applying these allegories to the case of rice blast, the rationale for weakness at penetration is threefold. Firstly, germinating fungi require liquid water and moderate temperatures to survive and carry out the penetration process, but microclimatic conditions can rapidly change over short time intervals, leaving the fungus "high and dry". Secondly, the germinating spore is entirely dependent on its own nutrient reserves, so events which might slow down penetration could extend the demand on those finite reserves to exhaustion. Thirdly, before penetration is completed, the physical blockage of access to host cytoplasm means that the fungus has no opportunity to employ its additional offensive capacities which are in storage- its post-penetration anti-biotic mechanisms of attack and parasitism. Thus, the fungal germling truly appears to be at a disadvantage at the penetration stage.

Penetration as a weak link in the fungal offense has experimental support from broad analyses of host-pathogen interactions. Sherwood and Vance (1980) inoculated a wide range of grass species with fungi that do not normally attack those species, and found that in nearly all cases the failure occurred during penetration. They suggested that the first line of penetration defenses (which they labeled "constitutive" resistance, i.e. an inbuilt feature which is present whether the pathogen attacks or not) may be due to cell wall thickness, roughness, waxiness or other structural features, and noted that rice was one of three species displaying exceptional resistance of this type.

Another, albeit circumstantial piece of evidence in support of the "penetration-as-weak-link" postulate is the fact that the most effective and widely used rice blast fungicides are those which interfere with penetration, such as tricyclazole, pyroquilon, fthalide, and possibly IBP (Sisler, 1986). While some of the reasons these have been widely used are unrelated to their effectiveness *per se*, such as their high specificity to rice blast and relatively low toxicity to non-target organisms, effectiveness is an equally important pre-requisite for their commercial success. The effectiveness of these chemicals could be at least in part a result of the exposed state of rice blast germlings on the plant surface - a state which renders them particularly vulnerable to the micro-biocidal equivalents of boiling oil, spears

and arrows flung down from the castle wall.

Testing the penetration-blockage hypothesis

To counter the host's defenses against penetration, rice blast has apparently evolved the capacity to exert very large physical pressures to push the infection peg through the leaf surface barrier. Measurements of that pressure registered 80 bars, by far the largest pressure ever reported for any biological system (Howard et. al. 1991). The fungus can even penetrate the plastic coverslips commonly used for microscopic slides! Possibly, the need to evolve the capacity to generate such enormous force would be in response to the rice plant's defensive system, particularly an extremely tough physical barrier, such as the cuticle-silica layer observed by Yoshida et. al. (1962c).

Despite the impressive force generated by the blast appressorium, penetration usually fails. For example, Peng et. al. (1986) found a maximum of 30% successful penetration under ideal conditions in growth chambers, using the most susceptible young rice leaves. Others have obtained similar data. Presumably, the frequency of success under the harsher conditions of natural infection is considerably lower. It would appear that the host plant's penetration defenses, long hypothesized to involve Si, are indeed formidable.

A particularly key constraint for the fungus during penetration is moisture supply. Ou (1985) points out that the length of the dew period is a key determining factor in the success of blast infections, since the fungal spore requires free water and high humidity to germinate and infect. This factor might well interact with Si status. Apparently, Si increases leaf hardness (Ito and Sakamoto, 1939 cited in IRRI, 1963 p. 281-282), and harder surfaces slow penetration by blast (Howard et. al. 1991). Under natural conditions of short and undependable dew periods, penetration would appear to be largely a race against time; it must be completed before the dew and humidity dry off the leaf surface in the morning. By extending the time required for penetration beyond the length of the dew period, Si may increase the number of penetration failures and thereby reduce blast damage.

To summarize, it would appear that rice plants may have evolved the capacity to use the unique chemical and physical properties of Si (inertness, hardness) to provide an imposing defense against penetration into the plant by the blast fungus. While intuitively attractive, however this long-offered hypothesis has never been directly tested.

In this document, however we present the first evidence of its validation (Table 16). Rice was sown in pots on soil from an Si-deficient upland rice site (Matazol, Colombia) treated with different amounts of Si (including a no-Si control).

Following inoculation of detached leaves of the 20-day old seedlings and a 36-hour incubation period in petri dishes under high humidity, the samples were fixed in alcohol and appressoria were examined under the microscope. Successful vs. failed penetrations could be assessed by counting those with or without a penetration peg (after Howard et. al., 1991). As the Table shows, Si application almost completely blocked penetration, while the fungus achieved approximately 20% successful penetration in the no-Si controls.

This is the first direct evidence that Si reduces rice blast damage by blocking penetration. It does not distinguish whether that blockage was achieved by reinforcing the "constitutive" barrier to penetration, i.e. the normal silica-cuticle double layer which develops regardless of the presence or absence of a pathogenic assault; or by strengthening a possible "inducible" barrier that is triggered by fungal attack (Sherwood and Vance, 1980) such as found associated with Si in barley (Carver et. al. 1987), cowpea (Heath, 1981), bean (Heath, 1979) and cucumber (Samuels et. al. 1991a); or both. Nor do these results rule out the possibility that Si has additional functions as well, such as interference with fungal hyphae proliferation within host tissue, interfering with fungal development and/or reproduction, etc. Further studies would be needed to determine the possible significance of these additional mechanisms.

Penetration resistance: genetic advantages

Penetration resistance mechanisms are worth researching for a number of reasons, such as their distinctiveness from, and probable complementarity to, the more conventionally-studied gene-for-gene antibiosis resistance systems widely utilized in modern plant breeding and studied by researchers (Table 15). Penetration defenses act at a different time and site within the host tissue, and operate by fundamentally different means such as physical blockage (as opposed to biochemical antibiosis).

Because of these differences, it is reasonable to suspect that penetration defenses are under different genetic control from post-penetration mechanisms. This has important implications for resistance breeding, because it implies that it might be possible to "pyramid" these different genetic systems into a single genotype, to derive a double benefit and possibly even extra resistance derived from synergy between them. For instance, a fungus weakened by having to force its way through stronger physical barriers might have fewer reserves and grow more slowly once inside the host, making it more susceptible to the antibiotic compounds or other post-penetration defenses.

As would be expected for a mechanistically-distinct defense system, varietal differences in penetration resistance usually do not correspond to those for post-

penetration resistance in rice (Peng and Shishiyama, 1989). Also, the "induced" deposition of Si, a penetration defense mechanism, was not triggered by biochemical compounds known to elicit post-penetration defenses in bean (Ryerson and Heath, 1992).

Not only could penetration resistance be complementary to known resistance mechanisms, there is reason to suspect it may be more broad-based against pathogen strains, i.e. race non-specific. Evidence in support of this conjecture can be found from the work of Sherwood and Vance (1980), who found that appositions (an induced form of penetration blockage) are widely utilized by plants as a generalized (pathogen non-specific) defensive mechanism. Additionally, Heath et. al. (1990) examined different host species/blast race combinations, and found that even in the the most susceptible combinations, many appressoria did not form infection hyphae, i.e. were blocked during penetration. These observations suggest that penetration defenses operate to at least some degree against a wide range of pathogen types, the opposite of what one would expect if this defense system were to be highly race-specific. Nevertheless, a direct test of any possible race specificity of penetration resistance appears to be lacking in the literature, for any crop.

If indeed Si-mediated resistance to blast is less race specific than conventional defense mechanisms, it would be even more attractive for study and use in genetic improvement. Race-nonspecific resistance is expected to be more durable and dependable over time, and to provide a more ecologically and evolutionarily-sound basis for blast resistance breeding.

Significance of upland Si deficiency in blast resistance screening

An awareness of the role of Si-deficiency in breeders' upland resistance screening nurseries could lead to more efficient identification of field sites for those nurseries, more effective *ex-situ* blast resistance screening (i.e. through the use of Si-deficient soil in greenhouse pot blast screening experiments), and a clearer interpretation of the results of such trials. It could also have important consequences for breeding strategy.

Current screening methodology, which unknowingly advocates the use of Si-deficient upland sites, strips away the penetration defenses of the rice plant provided by Si, which apparently enables breeders to more reliably observe the race-related antibiosis responses which are expressed subsequent to penetration. While these internal reactions are extremely important and have served as the major basis for resistance gene manipulations in rice breeding to date, it would appear that this screening method may largely bypass another set of useful genetic mechanisms, those which might be Si-dependent and operative during the

penetration phase. Especially for irrigated rice, which can be expected to have access to ample Si under real cultivation conditions, the use of a screening system which seems to de-habilitate a whole class of resistance mechanisms that could be expected to be important under commercial cultivation of the crop, might represent an opportunity missed.

On the other hand, the current screening system may be quite appropriate for upland rice, which is likely to face Si-deficient conditions under typical cultivation conditions.

Neck blast, and Si

The neck: weak link in the host plant's defense against blast?

Whereas penetration may be the weak link in fungal attack, the rice host plant also has a weakness: a particularly vulnerable organ, the neck, or uppermost stem internode connecting the leaf canopy to the grain (Figs. 2, 5).

Neck blast is a more serious problem than leaf blast for upland rice, particularly when yield-enhancing technologies are employed, such as higher nitrogen applications and more responsive varieties containing indica genetic heritage (Winslow, 1992). It is not uncommon to find 50% or more of the necks in an upland rice field affected by blast (eg., Table 10). A neck blast epidemic in the Colombian savanna in 1993 caused major losses in commercial production of the newly-released, high yield-potential variety 'Oryzica Sabana 6', necessitating an urgent search for replacement genotypes. Most agronomists familiar with upland rice in South America view neck blast as the most important unresolved constraint facing the crop.

However, leaf blast has recieved far more study. One reason is that the latter is a much easier system to work with. Leaves are ready for inoculation shortly after planting, and are easy to handle and prepare for microscopic observation. Seedling rice plants (the source of leaf samples) are much easier to inoculate and manipulate, both under field and greenhouse conditions.

By interfering with grain production, neck blast has major economic consequences for farmers. The neck is the direct pipeline for grain filling. It matters little how large and vigorous a foliar photosynthetic capacity has been established prior to grain fill, if the starch flow from leaves to panicle is reduced or cut off due to "neck rot" (neck blast). Whereas leaf area lost to blast can, in most situations be compensated or replaced, the neck is the only pathway to the grain; alternative routes do not exist. Furthermore, it plays its critical role just prior to crop maturation; if damaged, there is no time left for recovery (assuming that recovery

mechanisms even existed; I am unaware of any).

Reduced grain fill means lower grain quality, specifically less-dense grains which break during milling. Broken grains are not marketable for table rice, and must be sold very cheaply for chickenfeed or other secondary uses. Millers recognize the implications of poorly-filled grains, and test incoming rice for this quality factor, discounting the price paid accordingly.

Analyses of the effects of neck blast control treatments should therefore take into consideration not only effects on gross yield of paddy rice, but also on grain quality, specifically the yield of marketable whole grains (Tables 10,11). This gives a truer picture of the economic significance of the treatments.

Si in the neck

The neck is inherently much lower in Si content than the leaves, which may predispose it to blast damage (Winslow, 1992; also see Table 18). This is supported by the striking disease control achieved by Si application (Fig. 2). These facts alone would seem to provide an ample justification for increased research activity on the mechanisms of the Si effect in this organ.

It is interesting to note that, at the time the neck emerges from the boot, it is highly susceptible to blast (when Si-deficient), whereas the adjacent flag leaf is essentially immune at the same time. Curiously, there appears to be no analysis in the literature of why this is the case. The several-fold difference in Si concentration between these genotypically-identical organs, located in close proximity, would seem a plausible starting point for such an investigation.

Neck samples treated with different Si levels were gathered and preserved in the present study; more time will be needed to observe them for the presence or absence of penetration blockage. When completed, this will be the first evidence I am aware of concerning the mechanism of Si-mediated neck blast control, a phenomenon with major economic consequences in rice production.

Grain, or Husk Discoloration

The disease complex commonly referred to as grain discoloration (more appropriately termed husk discoloration, since that is the organ which is actually affected) is also much more common in upland rice than in irrigated systems. Like neck blast, it is usually associated with low-density, breakage-prone grains, and thus is of considerable concern to farmers and millers.

One has to be careful in distinguishing cause and effect with this disease, however. Husk discoloration is common in stressful environments; good growing conditions rarely result in the occurrence of this disease. These fungi appear to be non-aggressive, opportunistic parasites which only attack husk tissue weakened by other factors, such as low nutritional supply, cold temperatures, severe diseases in other organs which weaken the entire plant, etc. Thus, husk discoloration may be a useful visual symptom of plant stress, but other factors are usually the cause of that stress.

Husk discoloration is one characteristic of Si-deficient upland rice (Winslow, 1992). In many cases it is probably a secondary result of the weakening effect of leaf and neck blast which are also common in Si-deficient situations. However this is not always the case. In the present research, trials at Si-deficient Matazul in 1994 escaped blast, yet some varieties showed considerable husk discoloration (Fig. x).

Interestingly, the discolored varieties were substantially lower in husk Si content (Table 17; Fig. 4), and were of indica genetic origin (see Materials and Methods). These observations parallel those of Winslow (1992) in West Africa (see literature review). Additionally, Si application is known to correct husk discoloration (Datnoff et. al. 1991; Winslow, 1992). These observations form strong circumstantial evidence that Si plays an important role in protecting rice from husk discoloration fungi. To date, however there have been no investigations into the mechanisms behind this effect.

Genetic Variation, and the Potential for Breeding Higher-Si Varieties

Significant genotypic differences in inherent Si content, observed in 1993 in small plots with 2-3 replications, were confirmed in 1994 on larger plots with five replications at the Si-deficient site, Matazul (Table 18). That these differences were repeatable, on a different site in a different year, even given the high coefficients of variation engendered by these stress environments, lends support to the impression that the differences are real and heritable. Furthermore, these observations are in agreement with others in the literature (see literature review).

If the differences are real, the question arises as to whether breeding for higher Si content is desirable, feasible, and how it should be done.

I believe that enough evidence has been gathered, as discussed so far in this paper, to conclude that elevating Si content would indeed be desirable. It should significantly improve agronomic performance, disease resistance and grain quality in upland rice. Specifically, if Si-mediated blast resistance is truly an independent, durable resistance mechanism (as argued in the earlier section on "genetic considerations"), then selection for high Si content would be one means of

increasing the durability (non race-specificity) of blast resistance, a major objective in upland rice improvement. The merits of a pyramiding strategy, and synergy among different mechanisms (also described earlier) would lead to the conclusion that this approach should complement, not replace ongoing selection activity for race-related resistance.

Is it feasible, though? This would mainly depend on the magnitude of genetic diversity for Si content, its heritability, and whether methodologies exist to implement a practical breeding strategy to select for the trait. Sufficient genetic differences do seem to exist between the indica and japonica groups, on the order of 50-100% in husk tissue (Fig. 4), to expect selection response. This situation is quite relevant, since much current rice breeding effort focuses on introgressing desirable indica traits (such as high yield responsiveness) into the stress and disease-resistant japonica background. Thus, selection for the japonica-type high inherent Si content in indica x japonica crosses should help upgrade the disease resistance of this material. Within the japonicas themselves, there is also some modest room for improvement, as seen in the several varieties in Fig. 4 which have higher Si content than the widely-grown upland variety *Oryza Sabana 6*.

The heritability (narrow-sense) of Si differences has not been examined in the present study. Majumder et. al. (1985), however concluded that heritability for Si content was reasonably high and additive in a set of irrigated rice germplasm in India. The identification of diversity for Si content in the set of 11 varieties used in the present research (Fig. 4), which required two years, could serve as a valuable starting point for crosses (high x low-Si) to determine heritability.

What, in practical terms would be the key procedural elements of a project to elevate the Si content of upland rice? First, screening sites would need to be chosen. In my trials, expressed Si differences have been largest and most consistent in crops grown on Si-deficient soils such as Matazul, rather in Si-rich irrigated environments like Palmira. Since the Si-deficient conditions are the ones intended for the ultimate product anyway (new upland rice varieties), I would recommend that screening be done on such soils, despite the higher coefficients of variation encountered there. Such selection might be aided and enhanced by pot screening at Palmira using Si-deficient soil (eg. collected inexpensively from Matazul); this could increase uniformity and enable year-round selection, as well as dry-season confirmation of selections made during the growing season in the field at Matazul.

It is important to note that pot trials at Palmira (using Si-deficient soil from Matazul or similar upland locations) must be irrigated with de-ionized water, not with tap or well water. The latter are rich in Si and would thus eliminate the deficiency condition.

Tissue analyses for Si concentration (% of dry weight) should serve as the basis for selection, since this appears to be the determining factor in plant performance. Since Si contents are relatively high compared to other nutrients, very small amounts of tissue (less than 1 g, dry weight- see Appendix) are sufficient for analysis (if collected carefully to ensure representativeness). Sampling can be done pre-flowering (Majumder et. al. 1985), to enhance selection efficiency, but may be more convenient and even more accurate at maturity. We could easily perform 40 such analyses per day per technician, assuming the tissues had been previously ground in a Wiley mill. This rate could probably be increased manyfold if the analysis were transferred to automated systems (autoanalyzer) available in the Analytical Services Lab. At the moment, that Lab does not offer the Si analysis, due to low volume of demand.

The husk would be the easiest tissue to assess, as explained previously in the section on diagnostics. The husk is probably a good indicator of other tissues in the genotype as well (Table 17), although further confirmatory studies on this issue would be worthwhile. Selection for neck blast resistance, for example might benefit from specific measurement of Si in neck tissue rather than in the husk, although this requires more labor (to carry out a special harvest of neck tissue) and care in sampling. More data is needed from an actual breeding project to increase confidence in using one tissue to represent another.

The association of high inherent Si content with husk discoloration resistance, as found by Winslow (1992) and confirmed in the present study (Fig. 4 and Table 17), suggests that breeders could increase resistance to this disease by selecting high-Si varieties. In reality, the process can be enacted in reverse- breeders can easily perform a visual selection for clean grains in the field, which, unknowingly appears to elevate Si content. Nevertheless, additional progress appears to be attainable; varieties such as 'Ngovie' (Fig. 4) contain substantially more Si, and are cleaner than the modern upland rice variety dominant in the savanna of Colombia, *Oryzica* Sabana 6. This observation would seem to indicate that there may be merit in analyzing the Si content of advanced lines in addition to visually scoring grain discoloration, to help guide the breeder towards the selection of lines likely to be most resistant to this troublesome disease.

CONCLUSIONS

Silicon and Rice Evolution (a hypothesis)

The following hypothesis represents a synthesis and interpretation of the two broad conclusions of the present study and analysis, namely that:

- i) Upland rice environments are predominantly Si-deficient; and
- ii) Upland genotypes appear to have adapted to this deficiency, whereas lowland genotypes exhibit severe deficiency symptoms.

The hypothesis, then can be stated as follows:

1. Rice evolved in lowland aquatic environments, which are Si-rich
2. Rice evolved dependency on that ample Si resource
3. When farmers moved the crop to the uplands, which are Si-poor, dependency on Si became a flaw
4. Upland rices are evolving to become more efficient at Si use, and less Si-dependent

Evidence in support of the hypothesis

While the origin of cultivated rice is a source of much speculation, it is generally believed that it evolved as a swamp-adapted crop, and that upland rice was a derivative of the cultivated swamp varieties (Gupta and O'Toole, 1986, p. 104). Perhaps the strongest bit of evidence in support of this theory is that the wild relatives of rice are all swamp species. Nevertheless, it must be admitted that there is scanty evidence for these events which may have occurred over 10,000 years ago. *Oryza sativa* appears to have a diffuse origin, being distributed over a large area from the Himalayas to the Mekong Delta in Asia, and there may have been several centers of diversification as different human cultures in different agro-ecosystems adapted the crop to these different environments.

Most of the acid soils in Asia are in the south and southeastern portion of that continent, with major distributions in countries such as Thailand, Vietnam, Laos, Myanmar, and Indonesia (Gupta and O'Toole, 1986). This appears to correspond well with the center of diversity of a special genetic type of rice, the hardy "tropical

japonica" upland rices, often called "bulu" for their special plant type: tall with large, bold grains (Glaszmann, 1988). These plant type characters fit the types widely grown in traditional cultivation on acid soils in West Africa (de Kochko, 1987) and South America.

The distribution of the tropical upland japonicas, then seems to correlate with acid, weathered soils, not only in the center of diversity of these rice types but also in areas where rice cultivation is fairly recent (the last 500 years or so), i.e. Africa and South America. One can speculate that a process of farmer and natural selection took place for adaptation to these soils in all three locations, and the tropical japonica type apparently surfaced as the best-adapted among a number of genotypic options. (Other options which were presumably available probably included indica irrigated rices; they were probably tried and did not do well, judging by the lack of cultivation of these types in these areas today).

What characteristics might explain the superior adaptation of these tropical upland japonicas to the weathered, acid soils in these three geographically-distant regions? There may be many traits, but the focus of the present study of course is on Si. And here the circumstantial evidence is compelling. First, it is well established that Si is important for rice crop performance; second, it is now established that the weathered acid upland soils are Si-deficient (this paper; Winslow, 1992; and Yamauchi and Winslow, 1989); third, it is well known that tropical japonica upland varieties perform best in these environments; and fourth, there is now good evidence that upland tropical japonicas maintain higher inherent Si concentrations in their tissues (this paper, and Winslow, 1992).

These well-established facts would seem to strongly support that evolution for Si-efficiency has indeed taken place, in the living form of the tropical japonica upland varieties. This efficiency has apparently improved the performance of *Oryza sativa* in such environments, particularly for disease resistance and hence yield stability.

Genetics, however have not completely solved the problem. The tropical japonicas do suffer from neck blast and grain discoloration (albeit to a lesser extent than indicas when grown in those upland environments), and their plant type has low yield potential and other agronomic flaws (tall, bold grain type). Whether Si efficiency could be separated from those other flaws through plant breeding remains an open question. For example, higher yields in new varieties would require higher nitrogen responsiveness, but increased biomass growth due to nitrogen has a "diluting" effect on Si concentration when Si is in short supply. "Breeding out" the non-responsiveness of tropical upland japonicas might well affect the Si efficiency mechanism, which could be dependent on restricted total biomass. However this is only speculative at the present time.

Breeding efforts to enhance Si efficiency would be well worthwhile if only to clarify

what can, and cannot be done regarding this trait. Most likely, some progress can be made, and the rest will require amelioration of the deficiency by fertilizer application, irrigation or only cultivating high yield-target upland rice on less-weathered soils. Still, an understanding of the problem is essential to deal with it effectively. Raising our recognition of the problem is the main aim of the present monograph.

What follows are a few suggestions on promising research topics for the future:

Future Research Opportunities: Soil/Crop Management

- Si balances and cycles in upland conditions
- Chemistry of adsorbed Si; ways to reduce soil adsorption
- Forms, rates, timing and mode of application of Si fertilizers
- Si fertilizer industry development in major LAC upland rice areas
- Ancillary effects of Si on other crops/forages in savanna farming systems
- Test findings in Asia

Future Research Opportunities: Germplasm

- Mechanisms of Si-based resistance in rice
- Genes to desorb Si from clay surfaces (synergy with CIAT P project)
- Genes to preferentially deploy silicon to the neck
- Genes to more rapidly blockade penetrating hyphae
- Blast risk forecasting for upland rice, based on mechanistic models incl. Si

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TABLES

Table 1. Macronutrient composition of a healthy irrigated rice crop in the Philippines, 84 days after seeding.

<u>Nutrient</u>	<u>% of dry weight</u>
Si	7.3
K	2.4
N	1.1
Ca	0.5
Mg	0.3
P	0.1

* 84 day-old crop (heading stage). Source: IRRl, 1975, p. 65.

Table 2. Research on macronutrients in rice, according to global databases. Number of articles found in a computer search of the Commonwealth Agricultural Bureaux International (CABI) database using the keywords indicated.

	<u>Number of articles:</u>	
	<u>Rice</u>	<u>Upland Rice</u>
Nitrogen	2775	115
Phosphorus	960	60
Potassium	620	45
Silicon	198	6
Total	4553	226

Table 3. Research on macronutrients in rice as reflected in databases of rice research institutions in Latin America and Asia. Number of articles found in a computer search of the CIAT-Catal and IRRI library databases, using the keywords indicated.

	<u>CIAT Catal (Latin Amer.)</u>	<u>IRRI Library (Asia)</u>
Nitrogen	125	6213
Phosphorus	89	1583
Potassium	60	905
Silicon	14	173
Silicon, upland rice	2	1

Table 4. Regional proportions of upland rice.

Region	% of region's total rice area which is upland:
Developing Asia	9
Africa	50
Latin America	74

Source: Gupta and O'Toole, 1986

Table 5. Soluble Si concentrations in water extracts* of selected soils.

<u>Sampling site</u>	<u>Extract. Si. ppm</u>
I. Mountain slope transect, sugarcane fields, Hawaii ¹ (weathered upper slope »»»»» young bottomlands):	
Upper slope, Humic Latosol, rainfed	0.6
Mid-slope, Low Humic Latosol:	
irrig. with surface runoff water	1.2
irrig. with well water	5.8
Bottom land, irrig. with well water	
gray hydromorphic and recent alluvium	9.0
dark magnesium clay	12.9
II. West African upland rice soil, Ultisol ²	
No Si added (control)	0.7
Si added (187 kg/ha)	1.2
III. South American rice soils ³	
Ultisol, Matazul, upland rice testing site	1.3
Black valley bottom soil, Palmira (CIAT), irrig. rice	6.9

* Method: 10 parts water:1 part soil (dry weight), shaken for four hours.

Sources:

¹ Fox et. al. 1969.

² Winslow, 1992.

³ Present study, M. Winslow and K. Okada, CIAT.

Table 6. Soluble Si concentrations in various water sources.

<u>Water source</u>	<u>Si content, ppm</u>
Saturated water solution of pure amorphous silica ¹	61
Lowland irrigation water, Hawaii ²	30
Mean of 225 rivers in Japan ¹ :	
flowing through volcanic rock	21
flowing through sedimentary rock	5
Mouth of the Amazon river ¹	5
CIAT-Palmira (Colombia) ³ :	
canal water	7
rice paddy water	8
Rainwater (only water source for upland rice) ³	zero

Sources:

¹McKeague and Cline, 1963c.

²Fox et. al. (1969).

³Present study, M. Winslow and K. Okada, CIAT.

Table 7. Summary table illustrating typical values of the Si-supplying capacity of typical rice environments.

<u>Type of rice culture</u>	<u>Typical values (ppm):</u>	
	<u>Soil</u>	<u>Water</u>
Bottomland irrigated rice	10	7
Upland rice on weathered soils	1	zero

Table 8. Suggested critical values for diagnosis of Si status for rice in soil, water and plant samples.

<u>Material</u>	<u>Deficient</u>	<u>Borderline</u>	<u>Sufficient</u>
Soil	< 2 ppm	2-6 ppm	> 6 ppm
Water	< 1 ppm	1-4 ppm	>4 ppm
Plant (husk tissue):	< 3%	3-6%	> 6%

Table 9. Differences in Si content and biomass between an Si-rich and an Si-poor environment.

Location	Soil extract Si, ppm ¹	Si in water, ppm ²	Total Si in crop, kg/ha	Husk Si, % of dry weight	Total dry matter, kg/ha
Palmira: young soil, irrigated	6.88±1.5	7.42±0.39	483	9.3	9970
Matazul: weathered soil, upland (rain-fed)	0.98±0.2	zero detectable	42	1.9	4380
% change	-85	-100	-91	-79	-56

¹ Aqueous extract, 10 parts water: 1 part dry soil, shaken 4 hours (Fox et. al. 1967)

² Measured directly from appropriate water source for each location (irrigation canal water at Palmira; rain water at Matazul).

Table 10. Agronomic effects of Si deficiency in upland rice in the South American savannas.

Matazol, 1993:

Treatment	Yield, t/ha	Neck blast incidence, %	Milling recovery, %
No Si (control)	2.6	51	41
500 kg Si/ha	3.5	18	49

- Percent farm gate yield increase "rough rice" = 35%
- Percent real yield increase (marketable whole grains) = **61%**
- Similar results obtained in La Florida (savanna) and Santa Rosa (piedmont)

Table 11. Economic significance (estimated losses in farm-gate revenue) due to Si deficiency across the South American tropical savannas.

If we assume our results are representative of the region's savanna:

- Approximate area of savanna upland rice: 3 million ha
- Mean yield: 1.9 t/ha
- Farm-gate value of 1 ton rough rice: US\$175
- Farm gate revenues:
 - Current: $3,000,000 \times 1.9 \times 175 = \text{US\$}0.997 \text{ billion/year}$
 - With 61% real yield gain due to Si: $\text{US\$} 1.605 \text{ billion/year}$
- ∴ Farm gate revenues foregone due to Si deficiency: **US\$ 608 million/year**

Comparison: Total current LAC rice farm gate value: approx. \$3.3 billion

Table 12. Coefficients of variation of Si concentration in different plant parts over a range of trial sites and years.

Trial	Crop	Husk	Straw	Flag leaf at:		
				Flowering	Mature	Neck
High-Si sites:				----- % -----		
Palmira, '93		6.1		16.1	11.6	12.1
Palmira, '94	11.6	6.5	7.0		8.7	9.7
Intermediate-Si site:						
Santa Rosa, '93		16.4		18.6	20.5	
Low-Si site:						
Matazul, '94	40.2	17.0	19.5		18.7	28.7

Table 13. Advantages of the husk as a sampling material for the diagnosis of Si deficiency.

- Accuracy
 - Integrator over soil and water components
 - Integrator over crop growth cycle
 - Integrator over harvested area

- Precision
 - Low coefficient of variation

- Sensitivity
 - Strongly responds to environment
 - High levels of expression, i.e. ease of detection

- Convenience
 - Don't need fresh or bulky tissue
 - Use stored grain yield samples
 - Can convert to per unit area basis

Table 14. Economics of an hypothetical Si fertilizer.

- Additional revenues generated:
 - Real yield gain: $(1.9 \text{ t/ha} \times 1.61) - 1.9 = 1.16 \text{ t/ha gain}$
 - Value of gain @ US\$175/ton = \$203

- Additional costs incurred:
 - Manufacturing, mining and/or or proprietary costs
 - Transport/applic. costs: Need to apply one-two tons material per hectare (25% Si)

- Benefit-cost analysis:
 - Benefits should be double costs, for adoption to occur
 - ∴ A practical fertilizer should cost within \$100/ha, incl. tnspt & applic.

Table 15. Current global research emphasis, rice blast disease resistance mechanisms.

	<u>Articles*</u>
Penetration defenses	3
Post-penetration defenses	30

*Number of articles in recent major rice blast workshop (Ziegler et. al.1994)

Table 16. Effect of Si on penetration by blast appressoria.

Soil treatment	% Si in plant	No. of appressoria:	
		Counted	Penetrated
No Si added	1.50	250	51
1000 ppm Si	4.33	250	4

¹ 20-day old plants grown in pots containing Matazul soil. Excised leaves inoculated with blast in petri dishes.

Table 17. Inter-correlations of Si concentration among different plant organs, with grain discoloration symptoms. Data from an Si-deficient site (Matazul, 1' Eleven varieties x 5 reps (n=55).

Correlation with % Si in:

	Husk	Neck	Flag leaf	Straw
Grain discolor. score	-0.78***	-0.38**	-0.39**	-0.47*
Husk Si %		0.52***	0.54***	0.47**
Neck Si %			0.60***	0.53*
Flag lf. Si %				0.51*

*, **, *** significant at $p < 0.05$, 0.01 , and 0.001 , respectively.

Table 18. Significance of varietal differences for selected parameters, at an Si-deficient site (Matazul, 1994).

Parameter	F statistic	Coeff. variation, %	Range
Grain yield, kg/ha	5.2***	29	763-1745
Total dry matter, kg/ha	3.4*	32	3307-7469
Total crop Si, kg/ha	1.87 n.s.	40	29-64
Straw Si, %	4.88***	20	0.68-1.37
Husk Si, %	19.4***	19	0.92-2.68
Flag leaf Si, %	4.7***	19	0.87-1.75
Neck Si, %	12.8***	29	0.36-1.47

