AGENCY FOR INTERNATIONAL DEVELOPMENT
WASHINGTON, D. C. 20523

BIBLIOGRAPHIC INPUT SHEET

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1. SUBJECT CLASSIFICATION

A. PRIMARY: Agriculture

B. SECONDARY: Fertilizers

2. TITLE AND SUBTITLE

Possible mechanisms for crop response to silicate applications

3. AUTHOR(S)

Silva, J.A.

4. DOCUMENT DATE	5. NUMBER OF PAGES	6. ARC NUMBER
1971	11 p.	ARC

7. REFERENCE ORGANIZATION NAME AND ADDRESS

University of Hawaii, Department of Agronomy and Soil Science, College of Tropical Agriculture, Honolulu, Hawaii 98622

8. SUPPLEMENTARY NOTES *(Sponsoring Organization, Publishers, Availability)*

(In Proceedings of the International Symposium on Soil Fertility Evaluation, New Delhi, v. 1. p. 805-814) (In Hawaii Agricultural Experiment Station Journal, Series k228)

9. ABSTRACT

To promote a better understanding of mechanisms of plant response to silicate applications, this paper reviews earlier studies and relates them to more recent findings. The effects of silicate on plant growth appear to be related to reactions of this element with phosphorus in the soil and in the plant. This is largely because of the chemical similarity of the two elements. Evidence also suggests that silicate has a role in phosphorus metabolism. Crop response to silicate applications in Hawaii may also arise from Ca, the major cation associated with the silicate carrier. Soil mechanisms for increased growth involving silicate include these four: increased solubility of sorbed soil phosphorus, decreased phosphorus fixation, increased cation exchange capacity, and decreased Al activity. The Ca also contributes to increased pH, which decreases phosphorus fixation, increases cation exchange capacity, and decreases concentrations of Al, Mn, and Fe. Increased pH also contributes to increased Ca supply. Plant mechanisms for increased growth which involve silicate include these four mechanisms: increased phosphorus adsorption by roots, increased phosphorus transport from roots to tops, increased efficiency of phosphorus utilization by the plant, and correction of nutrient imbalances. Carrier Ca also contributes to plant growth by increasing Ca levels and correcting nutrient imbalances in the plant.

10. CONTROL NUMBER

PN-AAC-370

11. PRICE OF DOCUMENT

12. DESCRIPTORS

Calcium silicates
Exchange reactions
Hawaii
Phosphorus
Yield

13. PROJECT NUMBER

14. CONTRACT NUMBER

CSD-2833 211(d)

15. TYPE OF DOCUMENT

AID 590-1 (4-74)

CSQ-2833 211(d)
PN-AAC-370

Reprinted from

Proceedings of the International Symposium on Soil Fertility Evaluation, New Delhi
Volume 1, 1971

Possible Mechanisms for Crop Response to Silicate Applications

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(Proc. Int. Symp. Soil Fert. Evaln., New Delhi, 1, 1971)

Possible Mechanisms for Crop Response to Silicate Applications*

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ABSTRACT

The effects of Si on plant growth appear to be related to reactions of this element with P in the soil and in the plant. Chemical similarity of the two elements is largely responsible for this. In addition, evidence has been presented which strongly suggests that Si has a role in P metabolism. Crop response to Si applications in Hawaii may also arise from Ca, the major cation associated with the silicate carrier. Soil mechanisms for increased growth which involve Si are increased solubility of sorbed soil P, decreased P fixation, increased cation exchange capacity and decreased Al activity. In addition, Ca contributes to increased pH which decreases P fixation, increases cation exchange capacity, and decreases concentrations of Al, Mn and Fe, as well as to increased Ca supply. Plant mechanisms for increased growth which involve Si are increased P absorption by roots, increased P transport from roots to tops, increased efficiency of P utilization by the plant, and correction of nutrient imbalances. Carrier Ca also contributes to plant growth by increasing Ca levels and correcting nutrient imbalances in the plant.

Numerous plant yield responses to Si applications have been obtained in Hawaii since the first response to sodium silicate was reported by Sherman *et al.* (1955) in a pot study. Silicon, applied in the form of various silicate salts, produced yield responses in grass, legume, vegetable and fruit crops. Most of these experiments have been reviewed by Plucknett (1970). A number of possible mechanisms for plant response to Si were suggested in some of these studies, but these are scattered throughout the theses and literature from Hawaii. It is the objective of the present paper to review these early studies and relate them to more recent findings so that a clearer understanding of mechanisms of plant response to Si applications is possible.

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*Published with the approval of the Director of the Hawaii Agricultural Experiment Station as Journal Series No. 1228. Some of the work reported was supported by grants from the Tennessee Valley Authority and the National Science Foundation.

In Hawaii, crop responses to Si application are generally obtained on the highly weathered, Si depleted soils of the high rainfall regions. Under the new U.S. Comprehensive Soil Classification system, they belong to the Hydrandept, Gibbsihumox, and Tropohumult great groups (Fox *et al.* 1967a). The P fixing capacities of these soils are extremely high and essentially all (99.5%) of the added P can be immobilized in one hour in some soils (Mahilum 1966). These soils also have a variable charge which increases with addition of specifically adsorbed ions such as sulfate, phosphate and silicate. The positive change in pH (Delta pH) determined in K_2SO_4 compared to that in water is a result of displacement by sulfate of OH coordinated to the metal ion of the colloid and serves to identify soils likely to respond to Si applications.

Historically, Si has not been considered an essential element for plant growth and many of the early responses obtained from Si application were explained as indirect effect of Si or its carrier. Since these effects may occur in both soil and plant, they will be discussed separately.

Effects in the Soil

The literature and current unpublished research suggest the following possible soil effects for applied calcium silicate.

1. Increased availability of soil P
2. Increased soil Ca levels
3. Increased soil pH
4. Decreased concentrations of potentially "toxic" elements such as Al, Fe, Mn, etc.
5. Increased net negative charge, thus less leaching of nutrient cations.

Availability of soil P : Increased P uptake following Si applications has been reported in much of the earlier research and has been interpreted as indicating increased availability of soil P. Explanations offered for increased P availablity following calcium silicate applications have included P release in soils with high oxide content (Sherman *et al.* 1955), reduced P fixing capacity (King 1961 ; Suehisa *et al.* 1963), reduced Al concentration due to increased pH and Ca (Monteith & Sherman 1963 ; Suehisa et al. 1963), substitution of Si for soil P (Suehisa *et al.* 1963) and improved conditions for P absorption by plants (Clements 1965b). Several studies have reported increased extractable soil P following Si applications, but only a few permit an evaluation of the effect of Si (Ibrahim 1968 ; Teranishi 1968 ; Adlan 1969 ; Rosenau 1969 ; Roy 1969). In most of these studies the modified Truog method of Ayres and Hagihara (1952),

0.02N H_2SO_4 + $(NH_4)_2SO_4$, was used to extract "available" P. Teranishi (1968) analyzed samples of Kapaa soil (Typic Gibbsihumox) from a field experiment with a factorial combination of three levels each of Si, P, and pH. Extractable P, measured after a nine-month crop of sugarcane, was highest at the highest level of applied Si. Since the experiment was designed to separate Si effects from pH effects, the results can be attributed to Si alone. Roy (1969) studied P sorption from solutions containing varying amounts of P, in soil samples with and without Si treatment. This was followed by successive desorption of these samples with distilled water. Phosphorus concentrations in equilibrium solutions decreased with repeated desorption, but P concentration was higher in the samples treated with Si. Similar results were obtained with a Hydrandept and it was demonstrated quite conclusively that Si increases the solubility of sorbed soil P. Elsewhere, Jones and Handreck (1967) suggested that the release of P by Si was not due to anion exchange, but possibly due to increased pH or decreased Al activity which prevent P precipitation.

Decreased P fixing capacity of soil as a result of Si additions was demonstrated by Roy (1969) using soil samples collected from the Si × P × pH experiment of Teranishi (1968). The P sorption technique of Fox and Kamprath (1970) was used in which graded amounts of P as $Ca(H_2PO_4)_2$ in 0.01 M $CaCl_2$ were equilibrated with soil samples for six days and the P concentration in the supernatant determined. Applied Si (TVA slag) reduced P sorption (fixation) markedly and to a greater extent at pH 5.5 than 6.2 with 110 kg P/ha applied as shown by P sorbed at 0.2 ppm P in solution below.

pH	Si applied (kg/ha)	P sorbed (μg/g)
5.5	0	910
6.2	0	800
5.5	1660	580
6.2	1660	675

The overall effect of silicate applications on P sorption may be explained by (1) the interaction of Si compounds with sorption sites and/or (2) the inactivation of Fe and Al by the formation of insoluble compounds with Si (Roy 1969). Hingston *et al.* (1968) in Australia also demonstrated decreased P absorption by Goethite in the presence of added Si which they attributed to the ability of Si to increase the negative charge of the surface. The data above indicate quite clearly that Si applications increase P availability by increasing solubility of sorbed P and by decreasing the P fixing capacity of

soils. Raupach and Piper (1959) in Australia, and Okuda and Takahashi (1965) in Japan, have reached similar conclusions.

Soil Ca levels: The most usual carrier for Si is calcium silicate and this material can supply Ca to a Ca-deficient soil. In several studies no attempt was made to maintain constant Ca levels with increasing calcium silicate applications and thus there is no way to separate Si from Ca effects. Monteith and Sherman (1963) and Ayres (1966) reasoned that since both calcium silicate and calcium carbonate treatments had increased plant Ca levels, but only calcium silicate treatments had increased yields, that calcium supply probably was not the factor causing higher yields in their studies. According to Teranishi (1968), yield increases from calcium silicate applications could not be attributed to Ca supply in his experiment since plant Ca values were above established critical levels for sugarcane and also since calcium carbonate had been added to the zero Si plots to maintain pH and supply adequate Ca. Increased soil Ca can increase retention of cations such as K against leaching due to the complementary ion effect (Ayres 1966 ; Rosenau 1969 ; Mahilum *et al.* 1970). Rosenau (1969) presented data to show exchangeable K increased with increasing pH and Ca level and was highest at pH 6.2. These studies suggest that yield increases from non-silicon effects are not entirely due to Ca supply, but may be related to decreased leaching of nutrient cations.

Soil pH : Calcium silicate is reported to have about 80 per cent of the liming potential of calcium carbonate. In many Si studies, increased pH and associated reduction in "soluble" soil Al were considered responsible for yield increases. Suehisa *et al.* (1963) suggested that Si may also be responsible for reduction in soil Al. This was demonstrated by Teranishi (1968) and Rosenau (1969) who showed that applied Si decreased KCl-extractable Al when pH was held constant, but the decrease was small compared with the effect of increased pH. These authors suggest that decreased Al activity following calcium silicate applications may be due to Ca and pH effects as well as Si effects. Ayres (1966) stated that increased pH may reduce the concentration of soil Mn as well as Al and also stimulate the activity of soil microorganisms which, in turn, results in more rapid breakdown of organic matter and release of organically bound N, P and S. However, he concluded from the experiments discussed that apparently neutralization of soil acidity by calcium silicate (slag) was not a factor in the improved growth of cane. Response to calcium silicate applications were obtained with rice under flooded conditions in which pH of all treatments was about 7.0 in both pot and field experiments by Ibrahim (1968).

Yield effects of Si and pH were clearly separated by Teranishi (1968) who showed that increasing amounts of calcium silicate resulted in cane yield increases even when pH was held constant. Soil pH affected the shape of the yield response curves due to decreasing Si solubility with increasing pH, i.e., at low pH with high Si solubility, highest yield (141 T/ha) was obtained with the first Si rate, but at high pH with low Si solubility, maximum yield (162 T/ha) was attained only with the highest rate of Si. Soil pH alone also increased yields markedly, possibly due to increased availability of other nutrients and/or decreased activity of Al, Mn, etc. Increased pH resulting from calcium silicate applications is apparently not the sole cause of the yield response obtained since Si increased yields when pH was held constant.

"Toxic" elements in soil : Clements *et al.* (1967) presented evidence that the function of calcium silicate as well as calcium carbonate in improving cane growth is to eliminate, through precipitation, soil solutes which are injurious to sugarcane. They stated that wheat seeds failed to germinate in soil extracts containing ferrous iron and that Al and Mn may also be toxic in certain soils. Yields of sudan grass grown in pots containing toxic levels of Mo, B, Cu, Fe^{++}, Mn^{++}, Zn, and Al were increased when either calcium silicate or calcium carbonate were added. Calcium silicate and calcium carbonate were equally effective in reducing toxicities in this pot test. Ayres (1966) commenting on soil toxicities, stated that there was no reason to believe that any of the soils growing sugarcane in Hawaii contained toxic amounts of Mn or Al. Since both calcium silicate and carbonate applications reduce effects of "toxic" elements (if they are present) in soils, this reduction is not a unique effect of Si.

Cation exchange capacity : An increase in cation exchange capacity following calcium silicate or carbonate applications has been reported by Monteith and Sherman, 1963 ; Mahilum, 1966 ; and Rosenau, 1969. Mahilum (1966) suggested that this increase following Si applications may be due to both pH and silicate effects. Rosenau (1969) noted that exchangeable soil K increased with increasing Si applications with pH held constant at 6.2 which he suggests may be partly due to increased cation exchange capacity. Mekaru (1969) demonstrated that adsorption of phosphate by a Hydrandept soil increased the cation exchange capacity by 0.8 me for every millemole of adsorbed phosphate. Silicate adsorption would also increase cation exchange capacity, but to a lesser extent.

Effects of calcium silicate applications on soils can be attributed to mechanisms involving Si and/or Ca. Suggested mechanisms involving Si include increasing solubility of sorbed soil P, decreasing P

fixation, increasing cation exchange capacity and decreasing Al activity. Mechanisms involving this form of Ca are largely due to increased P fixation, increased cation exchange capacity in some soils and decreased activity of Al, Mn, Fe, etc. The increased Ca level also increased retention of nutrient cations against leaching.

Effects in Plants

The literature and current unpublished research suggest the following possible plant effects for calcium silicate applications.

1. Increased level of P
2. Increased root absorption of P
3. More effective utilization of plant P
4. Decreased levels of toxic elements such as Fe, Al, Mn, etc.
5. Increased levels of Ca, K, etc.
6. Increased level of Si

Level of P : Increased P uptake following Si applications has been reported in graminaceous plants by many investigators. Some have also reported increased P uptake in non-graminaceous plants (Manuelpillai 1967 ; Silva *et al.* 1968 ; Adlan 1969 ; Thiagalingam 1970). These increases usually have been attributed to effects of Si on soil P availability as discussed in the previous section. However, one may question the conclusion that yield increases following calcium silicate applications are due to increased P uptake. Ayres (1966) stated that the increased P content of sugarcane with slag applications, appeared to be commensurate with the larger yields resulting from the use of this material. Therefore, increased P uptake resulted from increased yields rather than increased yields being the result of greater P uptake. Fox *et al.* (1967a) reported that the observed silicate response did not result from improved P nutrition because a fourfold increase in P fertilizer had little effect on yield. Teranishi (1968) concluded that increased P uptake may account for the yield increase from the first Si increment, but not for the increase from the second Si increment in his sugarcane experiment. The pattern of P uptake at these two levels of Si differed markedly from the yield pattern. In addition, Si applications resulted in increased yields even at the 1,120 kg P/ha level. It appears that increased P uptake following Si applications is an effect rather than a cause of increased yields.

Root absorption of P : Increased P absorption by roots of some plants in the presence of Si was demonstrated in nutrient solution cultures by Roy (1969). He studied the effect of Si-P interactions in several plant species using a split-root technique. He found that Si

applied with P increased P absorption by roots of plants which accumulate little Si and decreased P absorption by roots of species that accumulate large amounts of Si. He concluded the effect of this Si-P interaction was either inherent in the species or involved in P metabolism in the plant rather than being a simple absorption phenomenon. Another explanation for this effect is suggested by Akhromeiko's (1934) finding that a SiO_2 sol increased the rate of diffusion of P_2O_5 through a collodian membrane. He suggested that SiO_2 is deposited on plant roots thereby increasing root surface and ability to absorb P_2O_5. Thus, part of the increased P uptake may be the result of absorption. Roy (1969) also found that supplying Si and P together in the same solution increased P transport from roots to tops in species which accumulate little Si, and generally decreased P transport to tops in species which accumulate large amounts of Si. Apparently both P absorption by roots and P transport are enhanced by Si in some plant species.

Utilization of plant P: Evidence was first obtained by Ali (1966) which suggested that Si in some way increased the efficiency of P utilization by the plant. Since then, Silva *et al.* (1968), Teranishi (1968), and Rosenau (1969) have reported similar effects in lettuce and sugarcane. Teranishi (1968) showed that higher yields were obtained with the same concentration of sheath P with Si than without Si applications, i.e., with 800 ppm P in the plant, cane yield was 141 tons per hectare with zero Si, but with 830 kg Si per hectare, 800 ppm P was associated with a yield of 157 tons per hectare. This suggests that Si in some way decreased the internal P requirement by some efficient utilization of plant P. Alexander's finding (1968) that reactions involving leaf phosphatase, amylase, peroxidase, and phenol oxidase in sugarcane can be suppressed by Si also suggests a role for Si in P metabolism.

"Toxic" elements in plants: Applications of calcium silicate have generally been found to decrease concentrations of Mn, Al and Fe in various species of plants. Clements (1965a, 1965b), and Clements *et al.* (1967) reported marked decreases in Mn content and in the Mn/SiO_2 ratio of sugarcane leaf sheaths and decreased leaf freckle following calcium silicate applications. Calcium carbonate also decreased Mn content, but was less effective than calcium silicate in reducing the Mn/SiO_2 ratio. Leaf freckle in cane may not be related to high Mn or Mn/SiO_2 ratio in all cases since Fox *et al.* (1967a, b; 1970) observed severe leaf freckling at a Mn/SiO_2 ratio considered favourable by Clements. Clements suggested that since Si applications prevent freckling and bronzing of leaves, Si must also have a physiological role in preventing localized accumulations of ions

which cause necrotic spotting as proposed by Williams and Vlamis (1957) for Mn. Clements (1965b) concluded that while some of the effects of slag, as with coral, are due to chemical changes in soil, the substantial effects for silica are from within the plant—particularly within the leaf.

Other research showing decreased concentrations of certain elements following Si applications are Dias' (1965) work with Mn, Al, and Mg in Sudan grass ; Teranishi's (1968) with Mn/Si ratio in sugarcane ; Rosenau's (1969) with Mn, Al and Mg in sugarcane ; Silva's *et al.* (1968) and Thiagalingam's (1970) with Mn, Al and Mg in 22 species including grasses, legumes, vegetables and fruits. Ayres (1966) believed that the Mn uptake values obtained with sugarcane did not suggest Mn toxicity. Researchers elsewhere (Vlamis & Williams 1967 ; Okuda & Takahashi 1965) have also reported correction of Mn as well as Fe toxicity symptoms by Si in grasses. Although Si decreases concentrations of Al, Mn and Fe, yield increases resulting directly from this effect have not been demonstrated in Hawaii.

Levels of other nutrients : Increased Ca levels in plants have been reported by many researchers following calcium silicate applications. It is conceivable that correction of a Ca deficiency would result in increased yields. However, in many studies precautions were not taken to allow Ca response to be evaluated. Increased plant K following calcium silicate applications have been reported by Spillner (1965), Mahilum (1966), Rosenau (1969), Silva *et al.* (1968), and Thiagalingam (1970), but increased K was not shown to increase yields. Ayres (1966) stated that although larger amounts of N and K were taken up when slag was applied, these increases were in line with the larger yields resulting from the treatment. Spillner (1965) reported increases in N, Mg, and Zn while Ali (1966) noted little effect or a slight increase in Mn, Al and Fe in sugarcane from calcium silicate applications, but did not relate these increases to yield.

Level of Si : Plant Si consistently increases with calcium silicate applications. Clements (1965a) concluded that in test areas where plant Si is very low, Si shows itself to be irreplaceable and therefore perhaps essential to the plant. He also suggested in another paper (1965b) that since other elements can correct nutrient imbalances in the plant, as does Si, a firm conclusion that silicon is an element essential to plant growth cannot be drawn. He reasoned that silica may increase sugar yield simply by keeping the leaves green through correction of nutrient imbalances which cause freckling and bronzing of leaves.

Ayres (1966) studied the possible factors causing stimulating effects on cane and sugar yields following slag applications, and con-

cluded that the high content of Si in slag was responsible for this effect. He noted that it can be stated with certainty that Si is in some manner, directly or indirectly, beneficial to the growth and development of the cane plant under the conditions studied. Ali (1966), on the other hand, concluded from his pot study with sugarcane that the yield responses from silicate applications probably did not result from Si *per se* since check plants were not deficient in Si according to plant Si levels. Teranishi (1968) reasoned that since P applications resulted in higher yields with than without Si, then Si *per se* may be responsible for yield increases by increasing P efficiency or by some other direct or indirect means. Elsewhere, Vlamis and Williams (1967) postulated a function for Si beyond preventing Mn toxicity in grasses and Lewin and Reimann (1969) cite other research suggesting Si might be considered an essential element to plants with high Si contents.

One other effect of increased plant Si content which has been reported in literature elsewhere is the increased mechanical strength of plant tissues which results in reduced lodging, and reduced insect and disease damage. No quantitative data have been obtained on this effect in Hawaii.

The preceding data suggest quite strongly that Si *per se* is at least partly responsible for yield increases from calcium silicate applications. Suggested mechanisms in the plant include increased efficiency of P utilization and correction of nutrient imbalances in the plant. Clear demonstration of these mechanisms can be attained only through careful research in solution cultures to avoid confusion with soil effects of Si.

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