

Review

The anomaly of silicon in plant biology

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ABSTRACT Silicon is the second most abundant element in soils, the mineral substrate for most of the world's plant life. The soil water, or the "soil solution," contains silicon, mainly as silicic acid, H_4SiO_4 , at 0.1–0.6 mM—concentrations on the order of those of potassium, calcium, and other major plant nutrients, and well in excess of those of phosphate. Silicon is readily absorbed so that terrestrial plants contain it in appreciable concentrations, ranging from a fraction of 1% of the dry matter to several percent, and in some plants to 10% or even higher. In spite of this prominence of silicon as a mineral constituent of plants, it is not counted among the elements defined as "essential," or nutrients, for any terrestrial higher plants except members of the Equisetaceae. For that reason it is not included in the formulation of any of the commonly used nutrient solutions. The plant physiologist's solution-cultured plants are thus anomalous, containing only what silicon is derived as a contaminant of their environment. Ample evidence is presented that silicon, when readily available to plants, plays a large role in their growth, mineral nutrition, mechanical strength, and resistance to fungal diseases, herbivory, and adverse chemical conditions of the medium. Plants grown in conventional nutrient solutions are thus to an extent experimental artifacts. Omission of silicon from solution cultures may lead to distorted results in experiments on inorganic plant nutrition, growth and development, and responses to environmental stress.

"It is to be observed that a definition is, strictly speaking, no part of the subject in which it occurs." (Alfred North Whitehead and Bertrand Russell, *Principia Mathematica*)

Soil, dominated for the most part by aluminosilicate minerals, is the source of the majority of the chemical elements that go into the make-up of terrestrial

plants and, hence, of their consumers. It is the solid phase of the soil that is the reservoir of the mineral elements, both nutrient and non-nutrient, that the roots of plants ultimately draw upon. The immediate source of most of these elements, however, is the soil water, or more accurately, the soil solution, supplied by the solid phase through the processes of weathering: solution, ion exchange, desorption—in fact, the whole gamut of processes whereby the solid, liquid, and gaseous phases of the soil ceaselessly interact with one another and with the part of the biosphere that resides there (1–7). The roots of plants through their interplay with soil minerals play a major role in the solubilization of Si and, hence, the supply of it in the soil solution available for absorption (6, 8–10).

As a result of these processes, Si, mainly in the form of silicic acid, H_4SiO_4 , is prominent in the soil solution. Actual concentrations vary widely in space and time, depending on the particular soil minerals present and many other factors, both abiotic and biotic (11). Concentrations on the order of 0.1–0.6 mM may be considered in the normal range (1, 11, 129). Concentrations of this magnitude are common for a number of the major inorganic nutrients such as K^+ , Ca^{2+} , and SO_4^{2-} and are far in excess of phosphate concentrations in the soil solution (12, 13). Si therefore looms large as one of the major constituents of the soil solution in contact with plant roots.

In the form of H_4SiO_4 , Si is readily absorbed by plants (14), and all soil-grown plants contain it as an appreciable fraction of the dry matter (Table 1). The table lists all the essential (nutrient) mineral elements, as well as several others not known to be generally essential for higher green plants but essential for some species or important for various reasons. (The concept of essentiality is discussed below, under that heading.) As is customary, concentrations are given on a dry weight basis and expressed as percentages for the macronutrient and ppm (mg/kg) for the micronutrient elements. For each element a range of concentrations is given because, depending on soil conditions, genotypes, and many other factors, the content of any one mineral

element in plant matter varies greatly. The table is based on analyses of crop species, and leaf material for the most part, because that is the provenance of most published values. For any one species, the range of concentrations would be much narrower. (Values below and above those listed may be encountered, but most would fall within the ranges indicated.)

As for Si, the table reveals a remarkable feature. Of all the mineral elements listed that are not known to be generally essential for green plants, Si alone is consistently present at concentrations corresponding to those of the macronutrient elements. At the low end of the range, 0.1%, Si corresponds in amount per unit of dry plant matter to such macronutrients as P, S, Ca, and Mg. Its upper values, 10% or even higher, exceed the tissue concentrations of even the most abundant mineral nutrients such as K and N. Si thus figures as a major mineral constituent of plants.

Essentiality

Its quantitative importance as a plant constituent notwithstanding, Si is not usually listed among the generally essential elements, or nutrients, of plants (12, 17–20). Plant physiologists consider an element essential by two criteria. The first, and classical, definition was laid down by Arnon and Stout (21): an element is essential if a deficiency of it makes it impossible for the plant to complete its life cycle and if that effect is not merely due to the amelioration by the element of some unfavorable chemical or microbiological condition of the substrate; i.e., the element must be directly involved in the inorganic nutrition of the plant. A second criterion of essentiality (12) is that the element is part of the molecule of an essential plant constituent or metabolite. It is by the first criterion that the essentiality of the elements now known to be essential has been established. Conceptually, it is a simple, operational definition. In practice, it is not necessarily easy to apply if, as is the case with Si, it is difficult to create and maintain an environment adequately purged of the element.

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Table 1. Mineral elements in crop plants

Element	Range of concentrations (dry weight basis)	Remarks
Nitrogen, %	0.5–6	Essential macronutrients
Phosphorus, %	0.15–0.5	
Sulfur, %	0.1–1.5	
Potassium, %	0.8–8	
Calcium, %	0.1–6	
Magnesium, %	0.05–1	
Iron, ppm	20–600	Essential micronutrients
Manganese, ppm	10–600	
Zinc, ppm	10–250	
Copper, ppm	2–50	
Nickel, ppm	0.05–5	
Boron, ppm	0.2–800	
Chlorine, ppm	10–80,000	
Molybdenum, ppm	0.1–10	
Cobalt, ppm	0.05–10	Essential in all nitrogen-fixing systems
Sodium, %	0.001–8	Essential for some plants; often beneficial
Silicon, %	0.1–10	
Aluminum, ppm	0.1–500	Not known to be essential; often toxic to plants on acid soils

Modified after Epstein (15, 16).

Si is a ubiquitous contaminant. It is present as an impurity in the macronutrient salts used in making up nutrient solutions, in the water even if distilled or demineralized, in containers (glass, of course, must be avoided), and as dust (22). Woolley (23) went to considerable lengths to exclude Si from the environment to determine whether it is an essential element for the tomato, *Lycopersicon esculentum*. The Si-deprived plants grew as well as those deliberately supplied with the element. The Si content of the shoots of the Si-deprived plants was 4.2 ppm, and that of the roots, 2.8 ppm. These values are on the order of levels of Cu generally considered adequate (12). If, then, Si is essential for the tomato plant, its requirement for the element would be met by the concentrations found in Woolley's Si-deprived plants. Perhaps Si is a micronutrient the requirement for which by solution-cultured plants is generally met by the inadvertent supply of it usually present as an environmental contaminant.

In a number of publications Miyake and Takahashi have concluded on the basis of the responses of plants grown in nutrient solutions with and without the addition of Si that omission of the element causes deficiency symptoms in the tomato (24) and cucumber, *Cucumis sativus* (25), and marked adverse effects as well on the growth of the soybean, *Glycine max* (26), and strawberry, *Fragaria × ananassa* (27). These and other such findings have led to an implication of Si as an essential

element for higher plants (22, 28). The claim needs to be viewed with reserve, for a number of reasons. Cl, an essential micronutrient (12, 18), was not included in the nutrient solutions used by the Japanese investigators, except for occasional additions of HCl for pH adjustment. In the experiments with cucumber (25), the SiO₂ content of the leaves in the Si-deprived plants was "extremely low at about 0.1% SiO₂" (or about 0.05% Si), or 2 orders of magnitude higher than the Si content of the tomato plants that were deprived of Si in Woolley's experiments (23). It is possible that the observed effects were due to interactions between Si and P or Si and Ca; such effects have been noted in rice by Ma and Takahashi (29, 30). In regard to the experiments with cucumber (25), Marschner *et al.* (31) concluded that the results were due to an interplay between Zn, P, and Si: in the experiments of Miyake and Takahashi (25), the concentrations of Zn were low (0.1 μM or less) and those of P were high (0.23–2.3 mM). Addition of Si rectified a combination of Zn deficiency and excessive P accumulation. Marschner *et al.* (31) could achieve the same rectification by lowering the concentration of P in the solution culture or raising that of Zn. Thus the observation by Miyake and Takahashi (25) is an instance of an element, Si in this case, correcting an unfavorable chemical condition in the medium, and that, according to the classical definition for essentiality laid down by Arnon and Stout (21), does not qualify

the element for "essential" status. Adata and Besford (32), also working with cucumber but using a balanced, recirculating nutrient solution, found no extreme abnormalities but made a number of interesting observations (discussed below, under *Silicon and Growth*) indicating positive effects of Si on the growth of the plants.

In view of this and other evidence, claims for the general essentiality of Si for higher plants cannot presently be supported. Because of the difficulty of depriving plants of access to Si, the likelihood of obtaining adequately Si-purged media is low. One has to agree with Volcani's assessment as quoted in Sangster and Hodson (33): "The answer is most probably, not right now."

While for plants in general Si cannot be considered essential, it is so for certain groups of plants. Among the algae, Si is essential for diatoms and other members of the yellow-brown or golden algae (34, 35). The beautiful "frustules" of diatoms consist of silica, SiO₂·nH₂O (36–38). For a discussion of these and other silicified algae see Round (39). The significance of diatom Si in the chemical economy of nature is impressive (40–43).

The only terrestrial plants for which Si is unquestionably essential are members of the Equisetaceae, or "scouring rushes," so called because in bygone days their ash, containing abundant gritty silica, was used to scour pots and pans. Chen and Lewin (44) showed that plants of the species *Equisetum arvense* died in solution cultures to which Si had not been added.

In concluding this section let it be noted that Si is an essential element for higher animals (45).

Silicon in Plants

As already mentioned, Si as H₄SiO₄ is readily absorbed by plants, but as indicated in Table 1, the Si content of plants varies widely. Jones and Handreck (17), in their classic review, distinguished three groups of crop plants on the basis of the Si content of their tissues. Dicotyledons have tissue concentrations at the low end of the range given in Table 1, on the order of 0.1% (dry weight basis); dryland grasses such as oats and rye have about 1%; and the "wetland" grass, paddy-grown rice, has levels on the order of 5% or higher. Going beyond crop plants, Takahashi and Miyake (46) have broadly sketched the characteristics of Si distribution in the plant kingdom. They did this on the basis of analyses of 175 species grown in the same soil. Of nine elements analyzed for (Si, Ca, Mg, K, P, Fe, Mn, B, and Al), Si was the most variable. Plants with more than 1% Si in dry leaf matter were considered as Si accumulators, and 34 species, or about 19% of

those in the study, fell in that category, with an average Si content of 1.96%. The corresponding value for the nonaccumulators (81% of the species) was 0.25%. Leaf matter of herbaceous legumes has low Si values as a rule. Even genotypes within a species may have Si tissue concentrations that vary by as much as a factor of 3, as shown for barley, *Hordeum vulgare*, grown in nutrient solutions (47).

There is a large literature on the distribution and eventual deposition of Si in plants. For a discussion of mechanistic aspects of its transport, which are beyond the scope of this paper, the review by Raven (14) is unexcelled. Because the uptake of undissociated H_4SiO_4 may be nonselective and energetically passive, and its transport from root to shoot is in the transpiration stream in the xylem, the assumption has sometimes been made that the movement of Si follows that of water (48). The evidence for that correlation was held to be best for dryland grasses (14). On the basis of nonselective, passive uptake of Si, the Si content of plants might serve as a convenient tracer for water uptake (48), but recent evidence lends little support to a directly proportional relationship between water and Si uptake, even for dryland grasses (49–51). During its passage through the xylem Si has to remain in solution—i.e., it must remain unpolymerized. The mechanisms preventing polymerization are not well understood; they may involve association with organic compounds (52, 53).

The form in which Si is ultimately deposited is mainly amorphous $SiO_2 \cdot nH_2O$, or “opal.” Once deposited in this form, Si is immobile and not redistributed (14, 54). The hydrated, amorphous silica may be deposited in cell lumens, cell walls, and intercellular spaces or external layers (31). It is present in roots (55–61), leaves (62–70), and inflorescence bracts of cereals (71–75).

In the roots, silica is deposited to a marked extent in the cell walls, but there are phylogenetically associated differences in the particulars (57, 59). In young wheat (*Triticum aestivum*) leaves the abaxial (lower) epidermal cells are important sites of silica deposition, but in older leaves silica is also deposited in the adaxial (upper) epidermis (68). In inflorescence bracts of wheat (lemma and glume) it is the outer epidermal walls that are most heavily silicified (75). Hairs or trichomes are often sites of prominent silicification (52, 59). Cotton (*Gossypium hirsutum*) fibers (technically trichomes) contain Si, which has been postulated to play a role in their development (76). There are fairly distinct differences in the distribution and characteristics of silica depositions between C_3 and C_4 plants (69, 77).

It is the distribution, formation, and form of silica depositions that have attracted the attention of most researchers who have concerned themselves with Si in plants. In the papers discussed above it is shown that amorphous silica, or opal, can assume an enormous range of highly characteristic morphological configurations (“opal phytoliths”). Inasmuch as amorphous silica has no intrinsic morphological forms, the multitude of observed morphologies must be due to extrinsic factors—namely, the organic matrices where the silica depositions are formed (78). This is an aspect of biomineralization and should be viewed in that context (53, 79–81).

Silicon and Mineral Nutrition

In regard to this and the following sections, an important note is in order concerning terminology and rationale. In keeping with virtually universal usage, reference will frequently be made to the “effects of Si” on this or that feature or process. The reason for that terminology is the usual omission of Si from formulations of nutrient solutions, that being considered the “control” or “standard” condition. Addition of Si is then an “experimental treatment” the effects of which are examined. The point of view embodied in the present review is the opposite. The presence of Si in the medium, and consequently in the plant, is considered the “control” or “normal” condition, being the one that applies to soil-grown plants. It is the omission of Si from the medium, and the growth of plants with abnormally low Si content, that should be looked upon as an experimental treatment—a treatment that causes a variety of abnormalities in mineral nutrition, growth and development, and resistance to abiotic and biotic stresses.

An early and striking demonstration of the significance of Si in plant nutrition was given by Williams and Vlamis in 1957 (82). They found that a concentration of Mn in barley leaf tissue of 300–400 ppm on a dry weight basis was toxic when no Si had been added to the nutrient solution but harmless when the solution contained Si at 0.36 mM. Adding Si to the solution did not diminish the Mn content of the leaves. Rather, in the absence of Si, Mn was concentrated in necrotic spots, whereas in the presence of Si, the distribution of Mn was more nearly even and no necrotic spots appeared. Other Gramineae showed similar responses (83).

In view of their chemical affinities, interaction between silicate and phosphate would be expected. Reference has already been made above, under *Essentiality*, to the effect on the growth of cucumber plants of Si when added to solutions with a low (0.1 μM) concentration of Zn and high concentrations of P

(0.23–2.3 mM). Although the original authors had concluded that the omission of Si resulted in Si deficiency, it was shown subsequently that the positive effect on the growth of the plants of adding Si resulted from its rectifying an imbalance in Zn and P supply (31).

Ma and Takahashi (29) compared phosphorus uptake by rice plants from nutrient solutions without and with addition of Si (1.66 mM H_4SiO_4), adjusted to pH 5.5. There were three levels of KH_2PO_4 : 0.014, 0.21, and 0.70 mM. In the treatment with Si, the shoots had a content of inorganic P (expressed as percent dry weight) on the order of half that of the Si-deprived plants. The shoot concentrations of Fe and Mn were also much lower in the Si-treated plants. A confounding factor in these experiments may have been the use of a nutrient solution whose basic formulation did not include Cl, and partial substitution of KCl for KH_2PO_4 to maintain K concentrations in the two lower P treatments identical with that having the top (0.70 mM) P concentration. The same authors (30) found addition of Si to the nutrient solution to diminish the uptake of Ca by rice plants. The reverse was not the case: different Ca concentrations in the solution did not cause differences in Si uptake and deposition.

Solution-cultured young orange trees, *Citrus sinensis*, on rough lemon, *Citrus limon*, rootstock, grown without and with added Si (2.4 mM) differed in the Si content of their leaves and feeder roots, and these differences were correlated with differences in the concentrations of several other elements in these and other organs and tissues (84).

Silicon and Growth

Si plays a major role in the intimate interplay between the solid phase of the soil and the soil solution. For this reason the present review is largely confined to work with nutrient solutions. They are the only means by which roots can be exposed to a medium amenable to accurate control and monitoring (85). In this section on growth, however, some experiments with soil-grown plants will be included because they dramatically illustrate the importance of Si for the growth of at least some species under field conditions.

Plants for which Si has been shown to be essential fail to grow normally when the element is deficient, that being part of the very definition of essentiality formulated by Arnon and Stout (21). Many species, however, for which Si has not been shown to be essential may grow better in media containing ample Si than in media, whether solution cultures or soil, with low concentrations of Si in readily absorbable form. Such instances have been encountered in several of the investigations referred to above, under

the headings *Essentiality* and *Silicon and Mineral Nutrition*. Thus, the barley plants in which addition of Si to the culture solution prevented Mn toxicity, in the early experiments of Williams and Vlamis (82), also grew better; after 6 weeks, the roots of the Si-treated plants had nearly twice the weight of the Si-deprived ones; the weight of the Si-treated shoots also exceeded that of those in the Si-deficient cultures. The alleviation of Mn toxicity in rice by addition of Si to the nutrient solution also improved the growth of the shoots, but not that of the roots (86). In other instances also in which Si enhanced growth the effect was due to an alleviation by Si of nutrient imbalances. Thus the positive effect of Si on the growth of cucumber plants already referred to (31) was shown to be due to the mitigation, by Si, of an imbalance in the supply of P and Zn. In the experiments of Ma and Takahashi (30), the growth of rice was enhanced by the addition of Si to the nutrient solution at 1.66 mM, an effect possibly related to the Ca concentration of the shoot tissue, which was much diminished by the Si treatment.

However, not all instances in which Si promoted growth can be attributed to its effect in moderating or alleviating nutrient imbalances. Addition of Si at 0.39 mM to cultures in which loblolly pine, *Pinus taeda*, grew for 40 weeks enhanced the growth of the seedlings; there was no evidence of nutrient imbalance in the Si-deprived plants (87). (The plants were grown in sand and fritted clay media so that, even the Si-deprived plants had some Si available, more so than would be the case in pure solution culture without any/solid substrate.)

In well-controlled experiments in which cucumber plants were grown in recirculating nutrient solutions containing Si at a low (0.17 mM) or high (1.84 mM) concentration, Adatia and Besford (32) observed a number of positive effects of the high-Si treatment on the growth of the plants: greater leaf thickness than that of the low-Si plants, greater dry weight per unit area of leaf, a small but significant added increment in root fresh and dry weight, and less propensity of the leaves to wilt. The lower leaves of the high-Si plants were darker green and positioned better for light interception, and their senescence was retarded compared with that of the leaves of low-Si plants. The high-Si leaves had 50% more total chlorophyll and, on a unit area basis, 50% more ribulose-1,5-bisphosphate carboxylase.

Even when there is no effect of Si on the overall growth of plants, specific aspects of growth or development may be positively affected when the Si supply is ample. For a recent instance, the weight at the late flowering stage of roots, stems, leaves, and inflorescences of cheat, *Bro-*

mus secalinus, was the same whether the nutrient solution contained Si at 0.00036 mM (the “-Si” control), or at 1.07 or 3.57 mM (88). Si added at the two high levels, however, increased the reproductive output of the plant by markedly enlarging the number of filled, viable seeds.

In respect to plant growth, however, it is field experiments that provide the most impressive evidence for a role of Si. From a plant physiological point of view that evidence is not as clearcut as that from experiments with solution culture, because of indirect effects of Si on the plants brought about by interactions of Si with various soil constituents. Nevertheless, evidence suggests direct effects of Si as well. When for at least two major crops, rice and sugarcane, fertilization with silicate has become commercial practice, experiments with soil-grown plants cannot be overlooked. Early observations are cited in the review by Jones and Handreck (17). Shkolnik (89) has summarized a good deal of literature, including material not readily available in the West. A few recent examples will drive home the impact that Si applications can have on the growth of crops.

The organic soils (Histosols) of the Florida Everglades, like many such soils, are low in Si available to crops. Applications of calcium silicate slag raised the yield of sugar from sugarcane, *Saccharum* spp. (90–92). The yield increases (sugar) were large, on the order of 50% to over 100%. Although many soil properties are affected by the application of Si materials, these and other such field experiments nevertheless suggest that the growth-promoting effects of these applications were in large measure due to the increased Si content of the plants. Indications were that for maximal yields, leaf Si concentrations had to be in excess of 1% (dry weight basis).

The highly leached upland soils (Ultisols) of the humid tropics tend to have low levels of nutrients—i.e., they are infertile—and their Si content is often low. Applications of Si increased the yield of rice on such a soil (93). The effect was apparently direct and not due to the increase in soil pH caused by the Si application. Different rice genotypes responded differentially to Si applications (94). The indica group of genotypes was more responsive to Si applications than were the japonicas, both in terms of yield and in terms of the total amount of Si in the shoot. The Si application nearly doubled the yield of rice over a 2-year period (mean for all eight genotypes in the study). The higher yields due to Si application were correlated with higher flag-leaf Si concentrations. Although marked improvement of yields due to Si applications have been noted mainly for rice and sugarcane, other Gramineae such as bar-

ley may also benefit from such applications (95).

In experiments with both solution-cultured and soil-grown plants, a recurring observation has been that plants supplied amply with Si resist lodging (drooping, leaning, or even becoming prostrate). The mechanical strength of plants enabling them to achieve and maintain an erect habit conducive to light interception resides in the cell wall. Reviews on the role of Si in plants therefore stress the association of Si with cell walls and discuss the increased rigidity of cell walls of plants grown with ample available Si in terms of that association (14, 17).

The incorporation of silica into cell walls has at least two energetically positive effects. First, the role of silica is analogous to that of lignin in that it is a compression-resistant structural component of cell walls. Raven (14) has calculated that on a unit weight basis, the energetic cost of incorporating silica is only 3.7% that of incorporating lignin. For incorporation of silica compared with that of cell-wall carbohydrate, the corresponding value is 6.7%. Silica is thus an energetically inexpensive structural component of cell walls. Second, the erect habit and the disposition of the leaves of plants amply supplied with Si favor light interception and, hence, photosynthesis. Thus in the experiment with cucumber plants grown in a recirculating nutrient solution already referred to (32), the authors found that the responses of the leaves of the high-Si plants resembled those elicited by high levels of solar radiation. Although no systematic comparisons have been made, it is likely that many of the positive effects of Si on plant growth that have been recorded were due to increased total energy capture via the features discussed by Adatia and Besford (32). At the very least, then, Si plays an important supporting role in plant energetics and growth. The impregnation of root cell walls with silica may also assist in the growth of roots through a medium dominated by a solid phase.

Silicon and Abiotic and Biotic Stresses

The effect on Mn toxicity of inclusion of Si in solution cultures of barley plants, discussed under the heading *Silicon and Mineral Nutrition*, may be looked upon as the reversal of a heavy-metal stress by Si. Other such instances have been noted in which inclusion of Si in the medium of plants (usually crop species) has mitigated or reversed mineral stress conditions. Thus inclusion of Si in solution cultures of bean plants, *Phaseolus vulgaris*, mitigated Mn toxicity, not by diminishing its absorption or translocation to the shoot but by increasing the ability of leaf tissue to tolerate the Mn absorbed

(96). In rice, also, inclusion of Si in the solution culture alleviated Mn toxicity (86). Effects of Si on the toxicity of other heavy metals such as Al are likely (97), but information on the subject is scant.

Another mineral stress, salinity, unlike heavy-metal stress, manifests itself only at high concentrations of (mainly) Na⁺ salts. In experiments with rice (98) and wheat (99), addition of Si to the solution cultures enhanced the resistance of the plants to salinity stress. In both cases the addition of Si diminished the Na concentration in the plants. Soil-grown mesquite, *Prosopis juliflora*, irrigated with saline water (260 mM NaCl) responded much less to the stress in the presence of Si (0.46 mM Na₂SiO₃) than in the absence of this amendment (100).

There is much interest, and deservedly so, in the development of plants resistant to the adverse effects of mineral toxicities and salinity (101). When genetic screening and physiological experimentation with selected genotypes are done by the solution culture technique, Si is not as a rule included in the formulation of these solutions. However, the results referred to above suggest that Si should be included in solution cultures used in research on mineral stress. The eventual medium in which the selected plants are to be grown is soil, and the plants exposed to mineral stress will therefore have Si available and will absorb it. Their responses to the stress may then differ from those elicited by the Si-deficient media used in the earlier screening and experimentation.

Evidence that Si affords protection against the abiotic stresses discussed above is surpassed by the evidence of its importance for resistance to biotic stresses—mainly, the depredations inflicted by fungi and insects. As long ago as 1940 Wagner (102) demonstrated the efficacy of Si applications in protecting crops against fungal attack (cited in ref. 103).

Several positive effects of Si on the growth of solution-cultured cucumber plants (32) have already been noted, but in addition there was increased resistance of those plants to the powdery mildew fungus, *Sphaerotheca fuliginea*. Even when fungicide was applied repeatedly, outbreaks of the fungal disease occurred in the low-Si plants, whereas the Si-treated plants were virtually free of the disease. Similar results had been shown for both solution-cultured (25) and soil-grown (104) cucumber plants. Still more recent evidence of the protection from fungal disease bestowed on cucumber plants by Si has been provided (103, 105, 106). In the last paper (106) the evidence was extended to other vegetable crops, and Si was applied as a foliar spray; it was effective in reducing the severity of infection by powdery mildew. The same method proved successful with grape-

vines (107). The mechanisms whereby Si affects the ability of pathogenic fungi to colonize plant tissues are not well understood (108–111).

The dicotyledonous crops discussed above are notorious for their sensitivity to pathogens. But as long ago as 1967 Jones and Handreck (17) were able to cite a number of papers in which rice and other cereals were shown to resist fungal attack when amply supplied with Si. This is not surprising in view of the normally high Si content of Gramineae. In contrast to the situation with vegetable crops, research on this topic with cereals has mostly been done in the field, with impressive and economically valuable results, especially with rice.

Yamauchi and Winslow (93), in their paper on the growth of rice in Si-poor tropical soils, noted not only an increase in yield when Si was applied, as already discussed, but in addition, a marked reduction in the incidence of grain discoloration. This discoloration is the result of infection of the husks by several fungi. In a subsequent investigation (94), a number of rice disease organisms were identified. Applications of Si to the soil reduced the severity of all diseases identified; different rice genotypes responded to various degrees.

Rice is not only grown on heavily leached mineral soils low in available Si but on largely organic low-Si soils as well. On such soils, also, applications of Si dramatically reduced the severity of fungal diseases (112). The authors commented on the scrutiny being bestowed on the use of fungicides on environmental grounds, and the desirability of exploring alternatives such as Si applications. As is the case for the dicotyledonous vegetable species discussed earlier, the mechanisms whereby Si impedes fungal infections of cereals need further study. Interesting observations in experiments with barley are recorded by Carver *et al.* (113), who also mentioned the possibility of breeding crops that absorb Si to high levels and effectively mobilize it to resist fungal penetration.

Not all plant parasites are fungi, nor are plant shoots the only organs attacked. *Striga* spp. (Scrophulariaceae), known as witch weed, is a parasitic flowering plant that attacks the roots of important crops such as rice, sorghum, millet, corn, sugarcane, and small grains. According to Slife (114), it is the most widespread and serious of all seed plants that are crop parasites. Its haustoria penetrate into the host roots; the degree to which this takes place varies depending on the host genotype and the thickness of the host root endodermis and pericycle due to the degree of their lignification, silicification, and possibly other factors (115, 116). No clear-cut correlation has been shown,

however, between the degree of resistance and silicification.

Fungal hyphae and parasite haustoria successfully infecting plant cells must breach the cell wall, and they do so by chemical means. Herbivores, including phytophagous insects, have to penetrate the cell wall mechanically. The physical properties of the wall are factors affecting the severity of herbivory, as, of course, are the cell contents once the wall has been pierced or macerated. There is evidence that plants with a high Si content are thereby afforded a measure of protection against herbivory (117, 118), an important effect in view of the huge role of herbivory in the economy of nature (119).

Solution Culture

Solution culture is the only technique permitting exposure of plant roots to a mineral substrate whose composition is determined by the investigator and capable of being monitored and controlled (85). Of necessity, therefore, solution culture plays, and must continue to play, a prominent role in plant biological research including investigations in mineral plant nutrition, ion transport, mineral metabolism, water relations, and genotypic responses to environmental stresses—indeed, whenever the mineral milieu that the roots are exposed to must be known and under control.

This review has summarized ample evidence of several important roles that Si plays in plant biology. First, when Si is amply available, as in most soils and in solution cultures to which it has been added, plants contain Si in their tissues at levels comparable to those of several macronutrient elements such as K, Ca, Mg, S, and P. Second, most of the Si absorbed is deposited in the form of amorphous silica, SiO₂·nH₂O, or opal, which is most prominently associated with the cell wall, the particulars of its morphology and pattern of deposition depending on both the genotype and environmental conditions. Third, Si has major effects on the absorption and translocation of several macronutrient and micronutrient elements. Fourth, Si positively affects the growth and development of many plants, most particularly by contributing to the mechanical strength of cell walls and their function of keeping plants erect and their leaves well positioned for light interception. Fifth, Si often mitigates and sometimes abolishes the adverse effects of excess P or heavy metals or salinity in the medium. Sixth, the impregnation of cell walls with silica contributes to the resistance of plants to attacks by fungi, parasitic higher plants, and herbivores, including phytophagous insects.

Together, this evidence amounts to a powerful case for the importance of Si in

plant biology. Because of the conventional wisdom, however, to the effect that Si is not generally essential for plants, the element is not normally included in the formulation of nutrient solutions used in research in experimental plant biology. Hoagland and Arnon (120) listed the composition of four nutrient solutions used by early investigators, from 1860 to 1902. In none of them was Si included. The most comprehensive listing by far of the composition of nutrient solutions formulated over a period of more than a century is that by Hewitt (121). In the tabulation of about 150 of such formulations, Si is mentioned but a few times. Clearly, on the evidence briefly summarized in this review, the omission of Si from experimental solution cultures needs to be reexamined. The presence, at appreciable concentrations, of Si in the medium to which plant roots are normally exposed has such a plethora of diverse effects that its omission amounts to the imposition of an atypical environmental stress. Plants grown under these conditions are in important aspects experimental artifacts (122, 123). The definition of essentiality and the evaluation of Si in that framework provide no logical basis for omitting the element from the formulation of nutrient solutions. The actualities of plant biology prompt its inclusion. In this laboratory, 1 mM Na₂SiO₃ is included in a modified Hoagland solution (12). Most commonly, that solution is used at 0.25 times its full concentration, thus containing 0.25 mM Na₂SiO₃ (123). The recommendation that Si be included in the formulation of solution cultures (122, 123) is reiterated. Commercial hydroponicists should also take notice.

Conclusion: Silicon in Plant Biology and Beyond

The role of Si in experimental plant biology has implications beyond this field itself. Hodson and Sangster (74) discussed possible taxonomic, anatomical, archaeological, and medical implications. The taxonomical value of Si lies in the characteristic morphology of opal "phytoliths," which may serve as a diagnostic character. The common association of silica with cell walls and intercellular spaces represents a link to plant anatomy. Silica phytoliths found at archaeological sites may serve to identify crops grown by their inhabitants. The archaeological use of plant silica phytoliths has been advocated by Piperno (124). Phytoliths bonded to the teeth of an extinct ape that lived a million years ago have given indications of its diet (125). Dust from wheat and rice containing silicious fibers poses a health hazard similar to that due to nonbiogenic silicious fibrous materials such as asbestos (74).

The deposition of siliceous structures in conjunction with an organic matrix has implications for materials science and biomimetic syntheses (126–128). A greater awareness of the importance of Si in plants, especially on the part of experimental plant biologists, is bound to have beneficial synergistic effects beyond plant biology *per se*.

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