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The Absorption of Silica from Aqueous Solutions by Plants

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WITH ONE FIGURE IN THE TEXT

Received 14 October 1965

ABSTRACT

Silica dissolves in water to a small extent and below pH7 exists in solution essentially in a non-polar form. In this respect it contrasts with nutrient cations and anions and a study of its uptake by plants was thought to be of interest. It was found that in common with the absorption of ionized solutes the entry of silica into plants appears to require the expenditure of metabolic energy since the process is sensitive to both metabolic inhibitors and variations in temperature. Furthermore, except under conditions of very low humidity, silica enters barley plants at a relatively greater rate than the water lost in transpiration, and its concentration in the xylem sap of bean plants may be greater than that in the external solution.

INTRODUCTION

AMORPHOUS silica is slightly soluble (0·01 to 0·015 per cent) in water at room temperature under neutral or acid conditions. There is evidence from diffusion measurements that soluble silica consists largely of monosilicic acid, $Si(OH)_4$ (Iler, 1955) and it is considered to be in this form in the soil solution (McKeague and Cline, 1963). This compound behaves as a very weak acid so that at pH7 only 0·2 per cent is ionized in the negatively charged form, but both the solubility and the degree of ionization increase with rising pH. Under neutral or acid conditions, however, silica can be regarded as an essentially non-polar solute.

It is usually assumed that the mechanisms whereby ions are absorbed by plants are linked with the electrical charges carried by cations and anions. It was considered therefore that an examination of the factors influencing the uptake of uncharged silica might throw further light on the absorption of ions or at least indicate whether a non-polar solute could be metabolically accumulated. The initial entry of silica into the free space of roots appeared to conform to the passive diffusion of a non-polar solute (Shone, 1964). The experiments described in this paper were therefore carried out to ascertain whether its movement across the root into the transpiration stream could also be explained by passive diffusion and mass flow in water. If this were so, silica and water would be expected to pass concomitantly into the shoots of

plants, a process which would be favoured by the small size of the monosilicic acid molecule.

MATERIALS AND METHODS

Barley (*Hordeum vulgare* var. Proctor) and dwarf bean (*Phaseolus vulgaris* var. 'The Prince') plants were grown for one and three weeks respectively in water culture in a controlled-environment chamber (20° C, 16-hour day of 1,400 f.c.). The standard culture solution employed for beans contained, in m.equiv/l: K 6·0; Ca 3·0; Mg 3·0; Na 2·0; NO_3 10·0; SO_4 3·0; H_2PO_4 1·0; and minor nutrients. For barley plants this solution was diluted to one-fifth. The effects on the uptake of silica of variations of transpiration and temperature, metabolic inhibitors, and of different concentrations of ions and silica in the culture solutions were then investigated. In all experiments the pH of the culture solutions was below 7.

In preliminary studies the uptake of silica by some other species of plants was also examined. It was noted that pea plants absorbed little silica relative to beans and that nettle (*Urtica dioica*) plants grown in nominally silica-free culture solutions showed little capacity to sting. When, however, a solution of silica was added to the culture solution stinging ability developed within two weeks; this was assumed to be due to hardening of the stinging hairs through deposition in them of silica.

Solutions of silica were prepared by passing dilute (less than 0·4 per cent) sodium metasilicate pentahydrate solution through a column containing the cation exchange resin 'Zeo-Karb' 225 in the hydrogen form. The eluate from the column was usually at pH4 to 4·5 and was essentially supersaturated monosilicic acid containing less than 2 ppm sodium. For studying the uptake of silica by plants this solution was added in varying amounts to the distilled water used in making up the culture media; the resulting solutions were adjusted to pH5-6 and were usually unsaturated with respect to silica.

Silica was analysed by the method of Morrison and Wilson (1963) which involves the formation of a blue complex with molybdic acid; the method is only sensitive to the mono- and disilicic acids which comprise soluble silica and eliminates interference by phosphates. The blue colour was compared with standard solutions of silica in a 'Unicam' S.P. 600 spectrophotometer at a wavelength of 800 mμ; no interference by phosphate was apparent at the levels of phosphate and silica employed. Culture solutions and xylem exudate of bean plants were analysed directly; plant tissues were dried and digested with nitric acid. The solids which remained were fused with anhydrous sodium carbonate and the melt brought into solution for analysis. This procedure necessarily gives the total silica content of the plant material and would include silica which had polymerized after entry into the plant. However, a comparison of the analytical results obtained on samples of the culture solutions and of xylem exudate before and after fusion with sodium carbonate gave no indication that silica was present in these samples in a polymeric form.

In all experiments determinations were made on plants grown under the same conditions but in solutions to which no silica had been added. Where silica was found to be present in these control samples the appropriate correction was made.

RESULTS

1. *Effect of rate of transpiration on the uptake of silica*

One-week-old barley plants were grown for three days in nutrient solution containing 0·066 mg soluble silica per ml. There were four plants in each culture vessel. To correct for the seed-borne silica, control plants were grown in nominally silica-free culture solution and harvested at the end of the experiment. On average the leaves contained 0·4 and the roots 1·0 mg silica/g dry weight which represented respectively 5 to 13 and 25 to 40 per cent of that taken up during the experiment. The values obtained for roots must therefore be interpreted with caution.

The plants were sealed at the base of the shoot into the lids of the culture vessels, thus enabling transpiration to be measured directly from the loss in weight of the vessels. The rate of transpiration was varied by growing the plants under PVC hoods, one of which contained moist sand and the other dehydrated silica gel. A comparison was made under these conditions between plants with living roots and plants with roots killed by immersion for two minutes in boiling water. Plants were harvested daily, and the dried material and external solutions were analysed for silica; there was no evidence of any changes in the external concentration of silica over the experimental period, nor was any increase discernible in the content of silica in the controls. The relative uptake of silica and transpiration of water is illustrated in Fig. 1, the axes denoting these quantities have been adjusted to 0·066 mg SiO_2 = 1 ml H_2O, this being the concentration of the external solution. Although the rate of transpiration of the plants subjected to low humidity was some 2½ to 3 times that of those in a moist atmosphere, there was no significant difference in the quantity of silica entering the shoots of the plants with living roots. However, for plants with killed roots the uptake of silica was significantly higher at low humidity than in a moist atmosphere ($P < 0{\cdot}001$); this difference was similar to that found for the amount of water transpired.

The relative rates of entry of water and a solute into a plant may be conveniently expressed as a Transpiration Stream Concentration Factor or T.S.C.F. (Russell and Shorrocks, 1959). This is defined for silica as:

$$\text{T.S.C.F.} = \frac{\text{concentration of silica in transpiration stream}}{\text{concentration of silica in external solution}}$$

Table 1 shows the quantities of water transpired and of silica taken up by the leaves and roots together with the values of the T.S.C.F. These indicate that at high humidity the rate of entry of silica was relatively greater than that of water by a factor of from two to three for plants with live roots and in

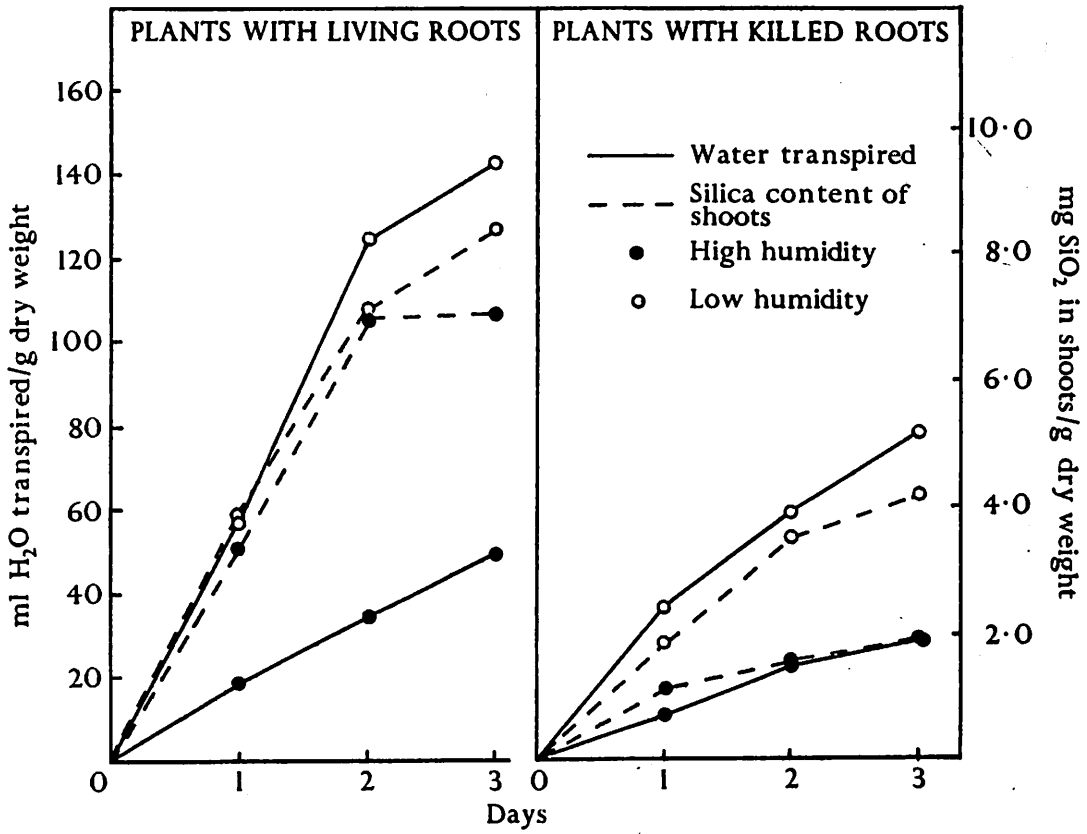

FIG. 1. Quantities of water transpired and silica taken up by barley shoots.

Axes indicating quantities of water and silica are adjusted to the concentration of silica in the culture solution (0·066 mg SiO_2 per ml).

TABLE 1

Quantities of water transpired and silica taken up by the roots and shoots of barley plants

The concentration of silica in culture solutions was 0·066 mg SiO_2/ml.

Mean values are quoted for three replicates in each treatment

	High Humidity				Low Humidity			
	Shoots			Roots	Shoots			Roots
Time days	H_2O transpired ml/g dry wt	Silica taken up mg SiO_2/g dry wt	T.S.C.F.*	Silica taken up, mg SiO_2/g dry wt	H_2O transpired ml/g dry wt	Silica taken up mg SiO_2/g dry wt	T.S.C.F.*	Silica taken up mg SiO_2/g dry wt
Plants with live roots								
1	19·1	3·38	2·66	1·43	56·9	3·85	1·02	1·82
2	34·9	6·97	3·11	1·86	124·4	7·36	0·89	2·52
3	49·6	7·03	2·21	2·70	143·0	8·85	0·94	2·91
Plants with killed roots								
1	10·2	1·16	1·72	0·26	37·5	2·01	0·81	0·39
2	22·2	1·56	1·06	0·08	59·8	3·60	0·91	0·00
3	28·3	1·82	0·97	0·00	79·2	3·85	0·74	0·24

* Transpiration stream concentration factor (T.S.C.F.) $= \frac{\text{concentration of silica in transpiration stream}}{\text{concentration of silica in external solution}}$.

contrast, for the plants with killed roots, except in the 24-hour sample the T.S.C.F. was close to unity both at high and at low humidities. While the amount of silica absorbed from solution by the living roots increased daily, the silica content of the killed roots remained close to that of the controls.

TABLE 2

Effect of temperature and inhibitors on transpiration and silica transport in barley seedlings

Mean values are quoted for three replicates in each treatment

Experiment	H_2O transpired ml/g dry wt		Silica content of shoots mg SiO_2/g dry wt		T.S.C.F. (*b*)	
	24 hr	48 hr	24 hr	48 hr	24 hr	48 hr
1. Effect of temperature						
25° C	24·2 (*a*)	42·3	4·65	6·90	2·24	1·90
5° C	20·5	42·4	2·10	3·40	1·21	0·97
2. Effect of inhibitors at 25° C						
Control	58·7 (*a*)	..	5·30	..	1·27	..
10^{-4} M dinitrophenol	26·9	..	1·41	..	0·73	..
10^{-3} M sodium azide	31·8	..	0·64	..	0·28	..

(*a*) In studying the effect of temperature, the plants were covered with a PVC hood. This was absent in the experiment on the effect of inhibitors, which accounts for the higher rate of transpiration at 25° C.

(*b*) Transpiration stream concentration factor (T.S.C.F.)

$$= \frac{\text{concentration of silica in transpiration stream}}{\text{concentration of silica in external solution}}.$$

The concentrations of silica in the culture solutions in Experiments 1 and 2 were 0·086 and 0·071 mg SiO_2/ml respectively.

These results suggested that the relative rates at which silica and water entered the shoots were largely controlled by metabolic processes in the root. They also indicated that under conditions of high humidity, silica appeared to be entering the shoots against a concentration gradient in plants with living roots.

2. *Effect of temperature and inhibitors on the uptake of silica*

To study the effect of temperature two-week-old barley plants were transferred to culture solution containing 0·086 mg SiO_2/ml. The culture vessels were placed in adjacent constant-temperature baths at 25° C and 5° C respectively; the water in the baths was thermally insulated from the leaves by a sheet of expanded polyurethane. A common PVC hood was placed over both sets of plants so that the shoots were under the same conditions of temperature and humidity. Leaves were harvested after 24 or 48 hours and analysed for silica, and the rate of transpiration was measured from the loss in weight of the culture vessels. The effect of 2,4-dinitrophenol (10^{-4}M) and sodium azide (10^{-3}M) on the uptake of silica from a culture solution containing 0·071 mg SiO_2/ml was studied at 25° C over a 24-hour period. Table 2 shows

that while reduction of the temperature had no significant effect on the amount of water transpired, the quantity of silica transported to the shoot and therefore the T.S.C.F. were markedly lowered ($P < 0.001$). Table 2 also shows that although the inhibitors reduced both transpiration ($P < 0.01$) and the content of silica ($P < 0.001$) in barley leaves, the effect on the uptake of silica was greater and resulted in a marked lowering of the T.S.C.F.

3. *Effect of varying the concentration of silica in the culture solution*

The experiments on barley plants had indicated that silica appeared under certain conditions to enter the plant against a concentration gradient. In order to confirm this, and to establish that silica in the vascular sap was still in the monomeric form, experiments were carried out on beans to determine the effect of varying the concentration of silica in the culture solution on that of soluble silica in the xylem exudate.

TABLE 3

Effect of varying the concentration of silica in the culture solution on its concentration in the xylem sap of bean plants

Exudate collected 3 hours after removal of the tops was rejected and samples were taken after 6 and 24 hours

Replication was four- or fivefold except for the two highest concentrations of silica (two or three replicates)

Concentration in culture solution mg SiO_2/ml	Concentration in xylem sap mg SiO_2/ml				Ratio of concentration in xylem sap to that in culture solution	
	6 hr	S.E. of means	24 hr	S.E. of means	6 hr	24 hr
0·0042	0·044±0·004		0·067±0·009		10·5	15·9
0·015	..		0·109±0·024		..	7·3
0·049	0·254±0·025		0·226±0·017		5·2	4·6
0·103	0·248±0·032		0·232±0·021		2·4	2·3
0·141	0·304±0·032		0·278±0·034		2·2	2·0
0·209	0·338±0·019		0·372±0·009		1·6	1·8
0·360	0·295±0·027		0·265±0·028		0·8	0·7

Soluble silica was added in varying amounts to the culture solution immediately before the shoots were removed. The exudate was sampled and analysed after varying periods up to 24 hours; after three hours low values were obtained presumably owing to dilution by the silica-free sap originally present in the xylem vessels. The values obtained from three to six and from six to 24 hours were higher and usually of comparable magnitude; thereafter, both the rate of exudation and the concentration of silica fell markedly. Table 3 shows that, except at the highest level, the concentration of silica in the exudate was greater than that in the culture solution. No difference was found between xylem exudate and aqueous solutions of silica in the rate of development of the coloured complex formed with ammonium molybdate, and it was therefore concluded that if silica were complexed in the exudate, the compound present must be very labile. The solutions at the two highest

levels were supersaturated with respect to silica but an examination of a number of samples of culture solution and exudate showed that the silica was in the soluble form, indicating that little polymerization had occurred over the experimental period.

Since there was no evidence that silica was present in the sap in a combined or polymerized form, these results indicated that in bean plants, and by inference in barley, soluble silica can move into the xylem sap against a concentration gradient.

TABLE 4

Effect of varying concentrations of culture solutions on concentrations of silica, potassium, and caesium in xylem exudate of bean plants

The concentrations of silica in the culture solutions in Experiments 1 and 2 were 0·1 and 0·066 mg SiO_2/ml respectively.

The concentration of caesium in Experiment 1 was 0·1 m.equiv/l. Replication was fourfold in most treatments.

Composition and concentration of culture solution, m.equiv/l as nitrates		Concentration of xylem exudate: SiO_2 as mg SiO_2/ml. K and Cs as m.equiv/l. Standard errors of means are also given		
Experiment 1				
Ca	K	SiO_2	K	Cs
0·2	1·0	0·25±0·03	8·7±0·7	0·49±0·12
	4·6	0·31±0·04	13·5±1·2	0·14±0·02
	9·7	0·28±0·02	17·5±0·9	0·09±0·01
	10·0	0·37±0·04	21·2±1·8	0·20±0·03
2·0	1·0	0·33±0·05	6·6±0·7	0·19±0·02
	4·6	0·24±0·02	9·7±1·0	0·08±0·02
	10·0	0·32±0·04	22·0±1·9	0·09±0·01
20·0	1·0	0·30±0·03	6·4±0·7	0·07±0·01
	4·6	0·28±0·04	12·9±3·0	0·06±0·01
	9·7	0·23±0·06	Not determined	0·08±0·01
	10·0	0·34±0·03	16·2±0·9	0·09±0·01
Experiment 2				
Full culture solution		0·23±0·03	Not determined	..
One-fifth strength culture solution		0·21±0·01	Not determined	..

4. *Effect of variations in composition of culture solution*

Three-week-old bean plants were transferred to solutions containing varying quantities of potassium and calcium nitrates together with 0·1 m.equiv/l labelled caesium chloride and 0·1 mg/ml SiO_2. In one experiment silica was added to a complete culture solution at full or one-fifth strength to bring the concentration of silica in both cases to 0·066 mg/ml SiO_2. The exudate was sampled after six hours. Table 4 shows that although variations in the composition of the solutions had considerable effects on the concentrations of potassium and caesium in the exudate, there was no significant difference in the concentration of silica for a given concentration in the external solution.

The possibility that over a longer period of time the composition of the nutrient solution might affect the silica content of the exudate was examined

by transferring the plants to full-strength or one-fifth-strength nutrient solutions containing the same concentration of silica for five days before removal of the tops. Up to the time of transference the plants had been grown on full-strength nutrient. It was found that the concentration of silica in the exudate was over four times greater in the plants grown in the diluted culture solution. Comparable effects on the silica content of the exudate were observed when plants were grown on for five days in culture solutions of varying composition containing the same quantity of silica, but it was not possible to ascribe these effects to interaction with any particular solute: they may rather reflect a general physiological change occasioned by altering the balance of nutrients.

DISCUSSION

The results indicate that the entry of silica into plants has certain characteristics in common with that of nutrient ions. Thus the mechanisms by which both silica and nutrients are absorbed appear to be largely independent of the rate of transpiration and both are affected by temperature and metabolic inhibitors. Similarly, Mitsui and Takatoh (1963) found that sodium fluoride inhibited the uptake and translocation of silica and phosphate by rice plants, whereas iodoacetate, 2,4-dinitrophenol, sodium cyanide, and antimycin A depressed the rate of translocation of silica by the roots. This observation led these authors to conclude that absorption of silica by the roots was effected by metabolic energy arising from respiration.

The marked effect of inhibitors on the uptake of silica and the fact that it can enter the transpiration stream against a concentration gradient are suggestive of active transport. For an ion, movement against a concentration gradient does not necessarily imply transport of that ion; it is well established (Dainty, 1962) that the active accumulation or exclusion of one or more ions may bring about a difference in electrical potential which may cause other ions to move passively up a concentration gradient.

Measurements of the electrical potential difference between xylem exudate of bean plants and the culture solution indicated that the exudate was negative with respect to the culture solution by a potential of about 50 mV. Passive movement of positively charged ions or complexes into the xylem against a concentration gradient is therefore possible. However, it is unlikely that the non-polar molecule of monosilicic acid could acquire a positive charge. If silica were present in the plant in cationic form, variations in the ionic concentration of the culture solutions should affect both its entry and that of other cations in the same manner; this, however, did not occur in short-term experiments (Table 4).

These results therefore suggest that soluble silica is actively transported across the roots of plants. In view of the uncharged and chemically unreactive nature of monosilicic acid, it is difficult to envisage that the accumulation of silica is due to a carrier mechanism similar to those which have been proposed to explain the transport of ions. The observation that its uptake has many

features in common with that of ions may encourage speculation as to whether the active transport of ions is wholly dependent on their electrical charge.

ACKNOWLEDGEMENTS

The authors thank Dr. Scott Russell for helpful discussions, Mr. B. O. Bartlett for his analysis of statistical data, and Mrs. W. A. Brooks for assistance in the experimental work.

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Enzymes of the Embden–Meyerhof and Pentose Phosphate Pathways in *Polyporus brumalis* Extracts

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WITH EIGHT FIGURES IN THE TEXT

Received 1 November 1965

ABSTRACT

The paper describes the detection of enzymes of the Embden–Meyerhof and pentose phosphate pathways by spectrophotometric and fluorimetric assays of cell-free extracts of the Basidiomycete *Polyporus brumalis*.

INTRODUCTION

BIOCHEMICAL investigations of fungi are now being made with a view to elucidating the metabolic changes associated with morphogenesis (e.g. Cantino, 1961; Hill and Sussman, 1964; Turian, 1961; Wessels, 1965). Other biochemical investigations deal with isolation from fungi of enzymes concerned with glucose oxidation. For example, all the enzymes necessary for the operation of the Embden–Meyerhof and pentose phosphate pathways (Beevers, 1961) were found in the spores of *Puccinia graminis tritici*, *Uromyces phaseoli* (Uredinales), and *Ustilago maydis* (Ustilaginales) by Caltrider and Gottlieb (1963). McKinsey (1959, 1964) isolated some of the enzymes of both pathways from the mycelium of *Ustilago maydis* and Newburgh *et al.* (1955) implicated the latter pathway in the metabolism of another smut fungus, *Tilletia caries*. On the other hand, Meloche (1962) has reported that in a monokaryon of the Hymenomycete *Lactarius torminosus* two of the necessary enzymes of the Embden–Meyerhof pathway, namely triosephosphate isomerase and phosphofructokinase, are absent. This paper reports the enzymatic evidence for the view that the metabolism of glucose by the dikaryotic mycelium of the Hymenomycete *Polyporus brumalis*, studied notably by Plunkett (1956, 1961), involves both the Embden–Meyerhof and pentose phosphate pathways at least when the fungus is grown in a carbohydrate-based medium (Difco malt).

Note. The following abbreviations are used: NAD^+ oxidized nicotinamide adenine dinucleotide; NADH reduced nicotinamide adenine dinucleotide; $NADP^+$ oxidized nicotinamide adenine dinucleotide phosphate; NADPH reduced nicotinamide adenine dinucleotide phosphate; ATP adenosine triphosphate; ADP adenosine diphosphate; TPP thiamine pyrophosphate;