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Uptake of silica by grapevines from soil and recirculating nutrient solutions

by

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S u m m a r y : The uptake of silica by grapevines was investigated both in the field and in hydroponic cultures. In aqueous soil suspensions (14 d at 20 °C) of 6 different locations (clay/loam) an equilibrium of 55-71 ppm of soluble silica (expressed as SiO_2) was measured; the content of grapevine leaves at harvest time was between 0.44 and 0.73 % of the dry matter, the concentrations being correlated with the silica solubility of the relative soil. Before budburst xylem exudates contained only about 1-4 ppm SiO_2 (rising with soil temperature), whereas during summer up to 68 ppm were measured.

Six different grapevine cultivars were grown in recirculating nutrient solutions supplied with different amounts (112, 10 and 0 ppm) of SiO_2; the solutions were changed weekly. The average SiO_2 content of leaf dry matter at harvest time (0.1-2 %) was correlated with leaf age and the SiO_2 concentration of the nutrient solution whereas in stems and petioles it was always less than 0.1 %. Significant varietal differences could be found only for cv. Regent which accumulated about 20 % more SiO_2 than the other varieties from the 112 ppm solutions. By the end of the vegetation period fresh leaves from plants grown on 112 ppm contained always around 0.1 % of water soluble SiO_2, irrespective of the leaves' age whereas the total amount of SiO_2 was up to 2 % in old leaves from the basis of the shoots and less than 0.5 % in the apical region. In the leaf center the silica concentration was always around 50 % lower than in the leaf periphery.

K e y w o r d s : Vitis, silica uptake.

Introduction

It is long known that silica enhances the fungus resistance of plants (GERMAR 1934; WAGNER 1940; reviews may be found in KAUFMAN *et al.* 1981; RAVEN 1983; SANGSTER and HODSON 1986; BÉLANGER *et al.* 1995). These effects were long thought to be restricted to 'Si accumulators' like grasses (KUNOH and ISHIZAKI 1975). To our knowledge the first to point to the role of Si in 'non-accumulators' were STAVELY *et al.* (1969) for *Trifolium*. HEATH (1981) and HEATH and STUMPF (1986) demonstrated the induction of insoluble silica in cell walls of mildew-infected leguminoses. MIYAKE and TAKAHASHI (1983) and ADATIA and BESFORD (1986) found that Si was an important factor of *Sphaerotheca* resistance of cucumber and MENZIES *et al.* (1991) associated this resistance with Si accumulation at the infection site. BÉLANGER *et al.* (1991) described similar effects with *Pythium* infections of cucumbers but according to CHÉRIF *et al.* (1992) the effect of Si was not due to concentrations at the infection sites. In *Vitis vinifera*, powdery mildew resistance in the field seems to be associated with Si supply (SCHALLER *et al.* 1990; BOWEN *et al.* 1992; GRUNDHÖFER 1994; LAFOS 1995; REYNOLDS *et al.* 1996) and large silica endoskeletons are formed if one cell is attacked by powdery mildew (BLAICH and WIND 1989; HEINTZ and BLAICH 1991; GRUNDHÖFER 1994). This paper deals with the uptake of silica under controlled conditions by mildew resistant grapevines (*Vitis* hybrids) and susceptible cultivars (*Vitis vinifera*) and its distribution in the plant as a basis for studies on its possible role in disease resistance.

Material and methods

E q u i p m e n t : All plants were grown in plastic containers; distilled deionized water from a copper still was used for silicate free cultures. For analyses all glassware was replaced by plastic devices.

G r a p e v i n e c u l t i v a r s : Riesling, Müller-Thurgau (*Vitis* vinifera – susceptible to powdery mildew); Regent, Phoenix, Gf.Ga-54-14 (now named Staufer), Orion and Sirius (interspecific varieties – more or less resistant).

H y d r o p o n i c c u l t u r e i n t h e g r e e n h o u s e : Two-bud cuttings were rooted in mid-March, grafted plants two weeks later. In mid-May 1989 they were transferred into 8 l plastic pots with forced aeration covered by a lid where the stem was fixed. In the following years (1990, 1991) the nutrient solution was pumped from catchment tanks to the top ends of gullies, where it flowed past the grapevine roots. Each gully was 3 x 0.15 m, with a slope of one in 10 and contained 10 plants. The flow was interrupted every 15 min for a 15 min root aeration. The temperature in these years was 1-2.8 °C above the long term average. Leaves were sampled after 3-4 months of growth.

N u t r i e n t s o l u t i o n : 38 g KNO_3, 16 g NH_4NO_3, 9 g $Ca(NO_3)_2 \cdot 4\,H_2O$, 5 g KH_2PO_4, 10.8 g $MgSO_4 \cdot 7\,H_2O$, 0.5 g $MnSO_4 \cdot 4H_2O$, 0.3 g H_3BO_3, 0.1 g $ZnSO_4 \cdot 7H_2O$, 2 mg KJ, 6 mg $Na_2MoO_4 \cdot 2H_2O$, 0.5 mg $CuSO_4 \cdot 5H_2O$, 0.5 mg $Co(NO_3)2 \cdot 6H_2O$ are dissolved in 1000 ml water. The hydroponic medium contained 15 ml of this solution and 80.2 $mg \cdot l^{-1}$ Folicin-DP (iron chelate) and was adjusted to pH 6.9 by HNO_3. Silica was added as potassium silicate (8.41 % K_2O,

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28 % SiO_2, Thompson-Siegel GmbH, Düsseldorf, Germany), the surplus of potassium was compensated by reduction of KNO_3. Three SiO_2 concentrations were used: no silica, 0.024 g = 5 mg $SiO_2 \cdot l^{-1}$, 0.470 g = 100 mg $SiO_2 \cdot l^{-1}$. Since in the last two cases tap water was used, the real concentration of SiO_2 was 10 and 112 mg$\cdot l^{-1}$, respectively. Some supplementary experiments were carried out with concentrations of 200 and 400 ppm forming an oversaturated solution which can, however, be considered stable over some days because, according to RAVEN (1983), it takes weeks to equilibrate $Si(OH)_4$ solutions and all solutions were replaced weekly by fresh ones.

Extraction of water soluble silica from soil: Soil samples were collected at 6 locations in the fields of the Institut für Rebenzüchtung Geilweilerhof from depths of 0-30 and 30-60 cm. 20 g of soil were suspended in 200 ml water and extracted for two weeks at 20 °C and 5 °C, respectively, under frequent shaking. After centrifugation the supernatant was analyzed for SiO_2; this procedure was repeated 5 times on the same samples. Xylem exudates were collected according to ALLEWELDT and MERKT (1992).

Leaf extracts: 50 g of fresh leaves were wetted with water, homogenized in a Pollähne press, centrifuged at 10 °C and filtered.

Preparation of biological samples: The plant material was washed with distilled water, oven-dried at 105 °C and ground. According to the expected SiO_2 content 200-500 mg were dry-ashed in a nickel crucible (600 °C: red hot bottom). After cooling 6 ml of a solution of 100 g NaOH in 178 ml water was added, the crucible was heated again and kept at 600 °C for 15 min. The fused bead was then dissolved in a few ml of water.

Determination of SiO_2 by atomic absorption spectrometry (AAS): The solution prepared as described above was adjusted to pH 5.0 with hydrochloric acid, made up to 100 ml with water and filtrated. SiO_2 from exudates or extracs of fresh leaves was analyzed without prior treatment. The atomic absorption spectrometer (Perkin Elmer Model 3030) was equipped with a Si lamp and a nitrous oxide/acetylene burner (reducing flame) and adjusted as follows: 251.1 nm wave length, 15 A lamp current, 0.2 mm slot width, 0.45x50 mm burner slot, 2.6 ml$\cdot$min^{-1} sample flow, 11 s measuring time. A Si AAS standard (Aldrich Chemical Company, Inc.) was used for calibration.

Determination of SiO_2 by spectrophotometry: This method bases on forming molybdosilicates in solution and reducing them to molybdenium blue; it is rather susceptible to variations of the test parameters (modified after NAYAR 1975). The following substances were made up to 100 ml with water: (A) 18.4 ml concentrated HCl, (B) 2.5 ml concentrated HCl and 0.5 ml ammonium molybdate, (C) 2 g citric acid, (D) 12 ml concentrated HCl and 0.84 g ascorbic acid. The contents of the crucible (in this case prepared from 100 mg dry substance) were dissolved in 20 ml (A) and made up to 100 ml with water. In a 22 °C thermostate 1 ml of this solution was transferred into a 10 ml plastic tube, after 30 min 4 ml of (B) was added, after 20 min 1 ml of (C) and after 4 min 4 ml of (D). After another 20 min the absorbance at 810 nm was compared with water and a reagent blank. Lambert-Beer law was obeyed over the range 0.75-2.5 µg $SiO_2 \cdot ml^{-1}$. A calibration curve was established with Titrisol® Silicium Standard 9947 (Merck).

Estimation of molecular weights: 0.5 ml of leaf extract or xylem exudate were put on top of a separation column (450x16 mm) filled with Fraktogel (TSK-HW 55F, Merck) and eluted with a 0.1 % solution of NaCl. Collected fractions (2 ml) were analyzed for their SiO_2 content by spectrophotometry. $Si(OH)_4$, glucose and oxalic acid were used as standards.

Isolation of cell walls: According to BAUMANN (1991, pers. communication), the 15th leaf (counted from top) of some shoots was crushed in liquid nitrogen, eluted 2 times with 100 mM phosphate buffer pH 6.0 (PB), two times with 500 mM PB and 4 times with water, then rinsed with methanol and acetone and dried at 105 °C.

Statistical analysis: Data were evaluated with the SAS software program. If the F-test revealed significant differences the average values were compared with the Tukey test. The data from xylem exudates and soil samples were too few to warrant statistical treatment. In this case enlargening of the database was not considered worthwile due to the following reasons: The data from the soil samples were only intended to give indications for the SiO_2 concentrations to be used in the nutrient solutions. The collection of xylem exudades involved the defoliation of the plants, thus the SiO_2 contents in the exudates cannot be considered to represent the true conditions in the xylem vessels of complete plants and hence are used only as supplementary data for discussion.

Results

SiO_2 content of soil suspensions: Soils were extracted 5 times at 20 °C which took nearly 3 months. As expected the SiO_2 content of the last extraction was still more than 90 % of the first one: there is an equlibrium between soluble and insoluble silica. The solubility at 5 °C was reduced to about 50 % as compared to 20 °C. The SiO_2 content of leaves from grapevines grown near the sites of soil sampling seem to reflect the solubility at this location. Interestingly, this is less in samples taken from the depth of 30-60 cm (Tab. 1).

SiO_2 content in xylem exudates: Prior to budbreak in xylem exudates from field plants only small amounts of SiO_2 were found which seem to be correlated with soil temperature (Fig. 1). Differences between cultivars or between grafted and ungrafted plants were not significant. In summer, all canes were removed from some plants grown at the locations mentioned in Tab. 1 and xylem sap was collected. The SiO_2 content was 66 ppm and 69 ppm in Müller-Thurgau and Riesling, respectively (both grafted on Kober 5 BB). Sap from grafted Orion contained 40 ppm, but

Table 1

Silica content in the leaf dry mass of some grapevine cultivars grown at different locations in the field; single measurements as a basis for concentrations to be expected in hydroponic cultures. Water soluble silica in soil of these locations taken at two different depths, results of the first extraction of the soil samples, the concentrations in subsequent analyses of the same samples (0-30 cm) decreased to 80-90 % after the 5th extraction

	Regent	Sirius	Orion	Phoenix	Riesling	Müller-Thurgau
Leaf SiO_2, %	0.44	0.50	0.53	0.40	0.70	0.73
Soil SiO_2 in 0-30 cm, ppm	55.0	64.0	64.5	66.0	70.5	71.0
Soil SiO_2 in 30-60 cm, ppm	19.5	35.5	25.5	-	40.5	52.5

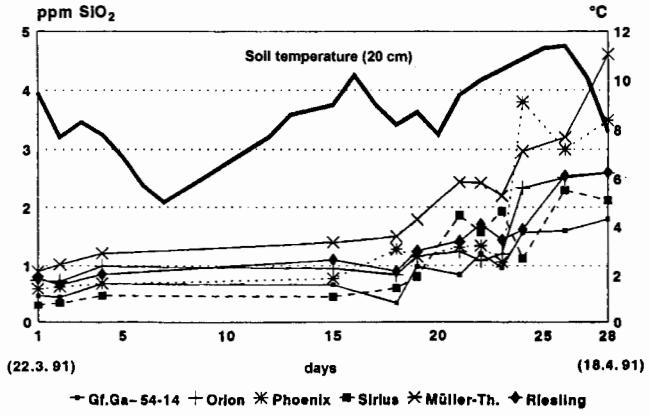

Fig. 1: SiO_2 concentrations in xylem exudates of some grapevine cultivars grafted on Kober 5 BB, measured in the field during 3 weeks prior to budbreak. There are no significant varietal differences and the SiO_2 content seems to follow soil temperature with some delay.

only 20 ppm in ungrafted plants. These values were identical for 4 different shoots analyzed separately; they remained constant during 5 d and then decreased to 50 %, probably due to the onset of a drought period.

In plants from hydroponic cultures supplied with 10 ppm SiO_2, the SiO_2 content of the xylem sap was nearly identical to that of the nutrient solution, at higher concentrations it was less (Tab. 2). It could be further enhanced by nutrient solutions with 200 and 400 ppm SiO_2, although $Si(OH)_4$ saturates at 150 ppm at 20 °C. However, the temperatures in the greenhouse were often much higher than 20 °C and $Si(OH)_4$ solutions take weeks to equilibrate (RAVEN 1983).

Total contents of grapevines: As to be expected from the analyses in the field the silica content of hydroponic plants depended on the nutrient solution (Fig. 2). The average content in dried leaves from plants grown in 112 ppm was 1 % SiO_2. In 1989 among the ungrafted plants only Regent accumulated significantly more silicon, differences between the other cultivars were not significant but

Table 2

SiO_2 contents (ppm) in xylem exudates of different grapevine varieties grafted on rootstock Kober 5 BB and grown in different SiO_2 concentrations in recirculation nutrient solution (gully culture); tentatively two oversaturated concentrations were tested in pots. Single measurements (joined exudates of 5 one-shooted, defoliated plants) at the end of the vegetation period

Nutrient solution	Regent	Sirius	Orion	Staufer	Müller-Thurgau
Si 0 (gully)	1.0	1.0	2.0	2.1	1.1
Si 10 (gully)	10.0	9.5	9.2	9.6	10.0
Si 112 (gully)	85.3	86.0	82.0	87.0	85.5
Si 200 (pot)	139.0	-	-	-	-
Si 400 (pot)	145.0	-	-	-	-

seemed to be correlated with the development of the root system. This could be shown in 1990 and 1991, when grafted plants were used which had more roots and gathered more SiO_2 than ungrafted ones in 1989. Varietal differences in these years were not significant although Regent and Müller-Thurgau always had the highest content. Leaves from 10 ppm SiO_2 solutions had always less than 0.1 % SiO_2.

Different leaf ages: In all cultivars older leaves contained around 2 % SiO_2 whereas young leaves had less than 0.5 % (Fig. 2).

Different leaf regions: In 1992 different parts of the leaves of plants grown on 112 ppm SiO_2 were analyzed separately after removal of the larger veins. The center of all leaves contained only 40-50 % of that of the periphery.

Shoots and petioles: The concentration in petioles as well as in shoots was always less than 10 % of that of the leaves. In grapes grown in 10 ppm SiO_2 between 0.01 and 0.02 % were found, in 112 ppm between 0.03 and 0.08 %. Roots could not be analyzed because they were consistently contaminated with diatoms whose shells were identified by scanning electron microscopy.

Isolated cell walls: After the isolation according to BAUMANN (personal communication) it was evident that the bulk of leaf dry matter consisted of cell wall material although exact analyses were not carried out in view of the fact that the effects of this isolation procedure are not well defined. Cell wall preparations from Müller-Thurgau and Regent grown in 10 and 112 ppm SiO_2 had concentrations of 0.6 % and 2.2 % SiO_2, respectively.

Different forms of plant silica: From plants cultivated in 112 ppm the soluble silica of fresh leaves, along with their total content, was analyzed (Tab. 3, see p. 165). Irrespective of the leaves' age always about 0.1 % of the dry matter was soluble silica which made up about 30 % of the total silica in young leaves (5th from the top), 15 % in medium (10th) and less than 7 % in older leaves. The proportion of "soluble silica" could be doubled if dried leaves were extracted with boiling water: In this case from lower leaves 9-13 % were dissolved, from middle leaves 22-24 %, from upper leaves more than 60 %. As related to the total

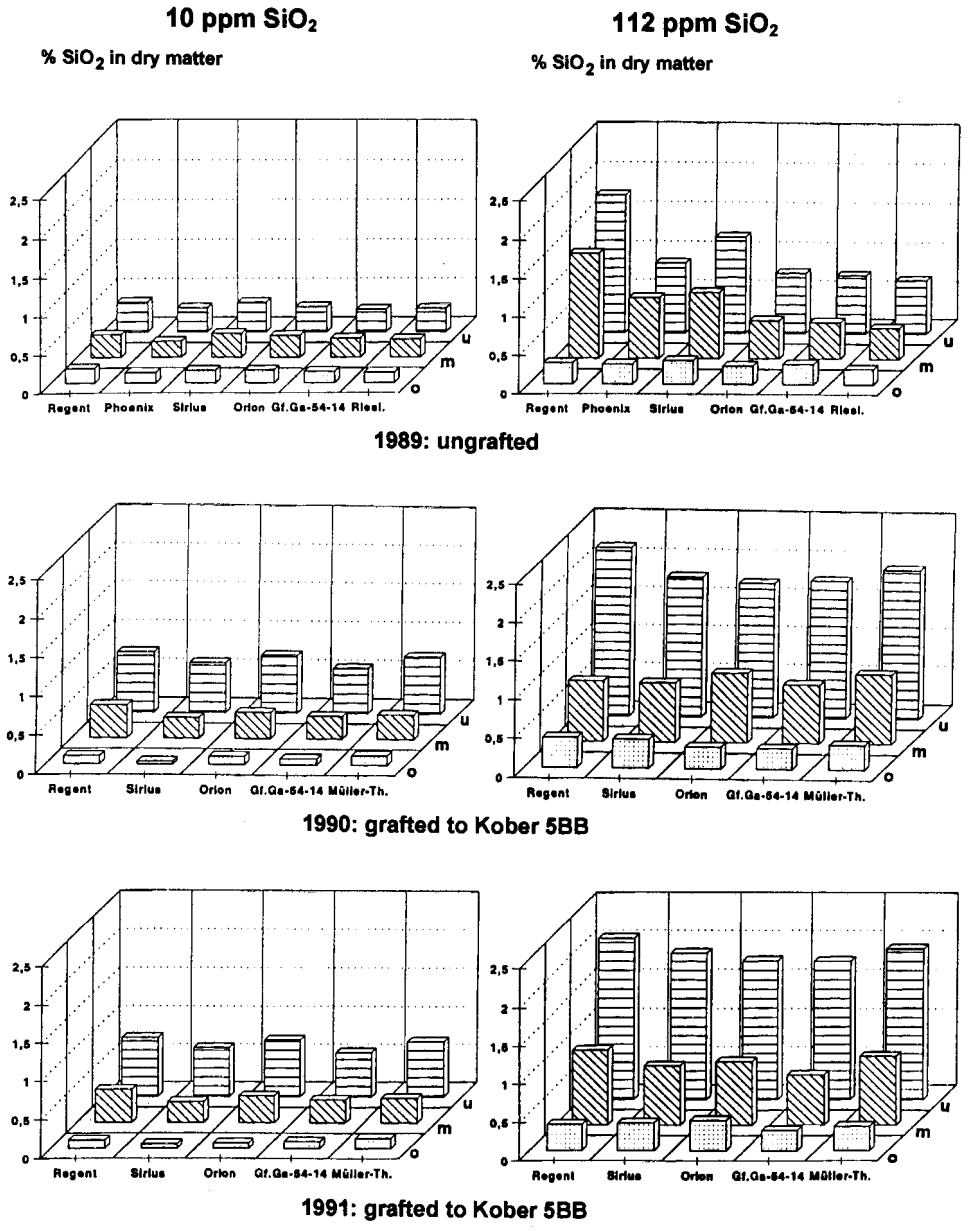

Fig. 2: SiO_2 contents of leaves (% of dry matter) of different grapevine cultivars grown in recirculating nutrient solutions containing 10 and 112 ppm SiO_2, respectively. Leaves were separated into three age classes: o = 1st to 10th leaf from top, m = 11th to 20th leaf, u = 21st leaf and older. Whithin each cultivar differences were significant between all leaf classes and between both nutrient solutions. Between cultivars differences are not significant except for Regent cultivated in 112 ppm, which in 1989 differed from all other cultivars.

content this was always the same amount: about 0.20 % of the dry matter.

Estimation of the molecular weight: Xylem exudate and plant sap were separated on a Fraktogel column. In all samples the SiO_2 seemed to be present as $Si(OH)_4$. This was confirmed by treatment of these solutions with heat or NaOH which should have caused changes of the SiO_2 concentration if silica gel would have been present.

Discussion

In view of the differences between years, soils, cultural techniques and analytical methods it is quite surprising that most of our data (for more details see GRUNDHÖFER 1994) are in good accordance with the results presented in the work of LAFOS (1995). Measurements of silica uptake by and distribution within the grapevine are certainly not sufficient to explain the molecular basis of the mechanisms involved, but there is no doubt that the amounts of silica found in specific organs of the grapevine depend (1) on their age, (2) on the local intensity of transpiration and (3) on the contents of the nutrient solution. The bulk of silica was found in old leaves – mainly in their periphery. This is in accordance with observations in grasses, where silica is concentrated in leaf tips and margins (PARRY and SMITHSON 1964; LEUSCH and BUCHENAUER 1988). Thus it is tempting

Table 3

SiO_2 contents (% of dry matter) in fresh leaves of different cultivars grown in 112 ppm SiO_2 solution; water soluble SiO_2 and total amount of SiO_2 analyzed separately in the 5th, 10th and 15th leaves from the top of the shoot at harvest time. Each value is the average of 6 leaves; no significant differences between the cultivars

		Regent	Sirius	Orion	Staufer	Müller-Thurgau
5th leaf	soluble	0.08	0.06	0.07	0.07	0.08
	total	0.25	0.18	0.19	0.17	0.21
10th leaf	soluble	0.11	0.09	0.12	0.13	0.10
	total	0.81	0.74	0.85	0.73	0.85
15th leaf	soluble	0.07	0.11	0.18	0.19	0.08
	total	1.17	1.55	1.48	1.25	1.50

to use a simple "wick mechanism" to explain the SiO_2 distribution in the grapevine: A wick (the xylem), protected by a glass tube (the cuticle), whose lower end (the roots) dips into a $Si(OH)_4$ solution, accumulates silica gel at its unprotected upper end (the leaves). Actually, as to be expected from such a model, "transport regions" (petioles, stem) contain more or less constant amounts of soluble SiO_2.

There are, however, a number of observations which cannot be explained by so simple a mechanism and grapevine roots and stems are much more complicated than a cotton wick. Lafos (1995) found that SiO_2 concentrated in the nutrient solution and he furthermore calculated that a passive "wick mechanism" would have accumulated much more SiO_2 than actually could be found in the plants. This could not be tested in our experiments because the nutrient solution was changed weekly. The $Si(OH)_4$ concentration we found in xylem exudates during summer was not, or only slightly, below that of our nutrient solution. However, since all shoots of the test plants were used to collect exudates, no leaves remained and xylem flow rate was considerably reduced as compared to transpirating plants. In this context "xylem exudate" can certainly not be considered identical to the content of xylem vessels of intact plants which actually might have contained considerably less $Si(OH)_4$ than the nutrient solution.

Assuming that most SiO_2 is taken up via the apoplast (Jones and Handreck 1965; Samuels *et al.* 1991) and this being restricted to young root tips without Casparian strip, a dilution would result since the bulk of water penetrates via the symplast. This model seems to be supported by our analyses of xylem exudates in field grapevines in March which contained only 1-4 ppm SiO_2 at soil temperatures between 5 and 10 °C where the concentration of the "soil solution" should be above 30 ppm: In early spring there exist no fresh root tips but a relatively high water flow, root growth starting only about two months later. However, there might be no uptake at all during this time (the silica being supplied by the root), or the uptake might depend on the activity of the root metabolism (providing root pressure) which would explain the influence of the soil temperature on the SiO_2 content of the exsudate. According to Lafos (1995) high summer temperatures seem to have similar effects, in addition his more detailed root analyses showed that the SiO_2 uptake seems to be cultivar specific rather than influenced by the development of the root system as could have been presumed from our observations.

Lafos (1995) found the concentration of silica in the roots to be always correlated with but considerably higher than the SiO_2 content of the nutrient solution. Hence there must be a concentrating mechanism unlike the evaporation in the leaf. As calculated by Raven (1983) $Si(OH)_4$ molecules can penetrate plasma membranes sufficiently fast to allow an equilibration within 24 h between a plant cell and the surrounding apoplast. Thus the $Si(OH)_4$ might be concentrated in the symplasts around the xylem from where it could diffuse slowly into the transpiration stream. This would lead to a dilution according to the speed of the water flow which could explain the high concentrations in "slow" xylem exudates.

The reconcentration of silica in the leaves due to evaporation certainly would afford no specific molecular mechanisms, but there are still many problems: While in the epidermis of grapevine leaves and berries endoskeletons are formed upon external triggering (Blaich and Wind 1989; Reynolds *et al.* 1996), in unchallenged leaves no such structures could be found although the bulk of leaf silica seems to be insoluble and our analyses of "cell wall fractions" indicated its association with the cell walls. According to the analysis of fresh leaf sap, the soluble silica in leaves of all ages seemed to be saturated (around 150 ppm as related to fresh weight). The formation of endoskeletons would then dilute the silica solution and thus attract more SiO_2 into the infected leaf - actually Lafos (1995) has shown that mildew-infected leaves contained more silica than healthy ones.

If in our experiments and those of Lafos (1995) dried leaves were extracted with hot water much higher amounts of "soluble" silica were obtained (both by us and Lafos 1995), but this will not be discussed here since they cannot be considered to represent true *in vivo* values. Nevertheless oversaturation might be possible since weeks are required to establish an equilibrium between monosilicic acid and solid phases (Raven 1983), in addition the oversaturation might be stabilized by other colloids. In this case the formation of endoskeletons could be understood as a polymerization from an oversaturated solution involving a nucleating mechanism. On the other hand, it is reasonable to assume that plants can prevent uncontrolled polymerization to silica gel, probably by the formation of organic complexes (Laroche and Robert 1976). In this case endoskeletons could be induced via the activation of esterases and changes of the pH which actually have been observed around fungus attacked cells (Heintz and Blaich 1990). In contrast to rye with large amounts of Si galactosides (Engel 1953), the grapevine contains only traces of galactose (Lafos 1995). If any, there should exist other complexes and this is where future research has to start.

Acknowledgements

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References

ADATIA, M. H.; BESFORD, R. T.; 1986: The Effects of Silicon on Cucumber Plants Grown in Recirculating Nutrient Solution. Ann. Bot. **58**, 343-351.

ALLEWELDT, G.; MERKT, N.; 1992: Der Stickstoffexport der Wurzel und die Zusammensetzung des Xylemexudats. Teil 1: Der Einfluß einer zunehmenden Stickstoffdüngung. Vitis **31**, 121-130.

BÉLANGER, R. R.; BOWEN, P. A.; EHRET, D. L.; MENZIES, J. G.; 1995: Soluble silicon: its role in crop and disease management of greenhouse crops. Plant Dis. **79**, 329-336.

- -; CHÉRIF, M.; TREMBLAY, J.; 1991: Control of pythium root rot in greenhouse grown cucumbers with soluble silicon amendments. Phytopathology **81**, 120.

BLAICH, R.; WIND, R.; 1989: Inducible silica incrusts in cell wall of *Vitis* leaves. Vitis **28**, 73-80.

BOWEN, P., MENZIES, J.; EHRET, D.; 1992: Soluble silicon sprays inibit powdery mildew development on grape leaves. J. Amer. Soc. Hort. Sci. **117**, 906-912.

CHÉRIF, M.; BENHAMOU, N.; MENZIES, J. G.; BÉLANGER, R. R.; 1992: Studies of silicon distribution in wounded and Pythium ultimum infected cucumber plants. Physiological and Molecular Plant Pathol. **41**, 371-385.

ENGEL, W.; 1953: Untersuchungen über die Kieselsäureverbindungen im Roggenhalm. Planta **41**, 5385-5390.

GERMAR, B.; 1934: Über einige Wirkungen der Kieselsäure in Getreidepflanzen, insbesondere auf deren Resistenz gegenüber Mehltau. Z. Pflanzenern., Düngung, Bodenk. **35**, 102-115.

GRUNDHÖFER, H.; 1994: Einfluß von Silikataufnahme und -einlagerung auf den Befall der Rebe mit Echtem Mehltau, 114 pp. Diss. Univ. Hohenheim.

HEATH, M. C.; 1981: Insoluble silicon in necrotic cowpea cells following infection with an incompatible isolate of the cowpea rust fungus. Physiol. Plant Pathol. **19**, 173-276.

- -; Stumpf, M.A.; 1986: Ultrastructural observations of penetration sites of the cowpea rust fungus in untreated and silicon-depleted French bean cells. Physiol. Mol. Plant Pathol. **29**, 27-39.

HEINTZ, C.; BLAICH, R.; 1990: Ultrastructural and histochemical studies on interactions between *Vitis vinifera* L. and *Uncinula necator* (SCHW.) BURR. New Phytol. 115, 107-117.

JONES, L. H. P.; HANDRECK, K. A.; 1965: Studies of silica in the oat plant. III. Uptake of silica from soils by the plant. Plant Soil **23**, 79-96.

KAUFMAN, P. B.; DAYANADAN, P.; TAKEOKA, Y.; BIGELOW, W. C.; JONES, J. D.; ILER, R.; 1981: Silica in shoots of higher plants. In: SIMPSON, T. L.; VOLCANI, B. E.; (Eds.).Silicon and Silicieous Structures in Biological Systems, 409-449. Springer-Verlag, New York.

KUNOH, H.; ISHIZAKI, H.; 1975: Silicon levels near penetration sites of fungi on wheat, barley, cucumber and morning glory. Physiol. Plant Pathol. **5**, 283-287.

LAFOS, K.; 1995: Die Aufnahme und Verteilung von Silicium in Reben (*Vitis* spp.). Diss. Geisenheimer Berichte No. 22. Veröffentlichungen der Forschungsanstalt Geisenheim.

LAROCHE, J.; ROBERT, D.; 1976: Mise en évidence en microscopie électronique, du transit de silice à la faveur des parois dans les feuilles d'*Equisetum arvense*. Compt. Rend. Acad. Sci. **282**, 1721-1723.

LEUSCH, H. J.; BUCHENAUER, H.; 1988: Si-Gehalte und Si-Lokalisation im Weizenblatt und deren Bedeutung für die Abwehr einer Mehltauinfektion. Kali-Briefe (Büntehof) **19**, 13-24.

MENZIES. J. G.; EHRET, D. L.; GLASS, A. D.M.; SAMUELS, A. L.; 1991: The influence of silicon on cytological interactions between *Spaerotheca fuliginea* and *Cucumis sativus*. Physiol. Mol. Plant Pathol. **39**, 403-414.

MIYAKE, Y.; TAKAHASHI, S. E.; 1983: Effects of silicon on the growth of cucumber plant in soil culture. Soil Sci. Plant Nutr. **29**, 463-471.

NAYAR, P. K.; MISRA, A. K.; PATNAIK, S.; 1975: Rapid microdetermination of silicon in rice plant. Plant Soil **42**, 491-494.

PARRY, D. W.; SMITHSON, F.; 1964: Types of opaline silica in leaves of British grasses. Ann. Bot. **28**, 169-185.

RAVEN, J. A.; 1983: The transport and function of silicon in plants. Biol. Rev. **58**, 179-207.

REYNOLDS, A. G.; VETO, L. J.; SHOLBERG, P. L., WARDLE, D. A.; HAAG, P.; 1996: Use of potassium silicate for the control of powdery mildew (*Uncinula necator* [SCHWEIN.] BURRILL) in *Vitis vinifera* L. cultivar Bacchus. Amer. J. Enol. Viticult. **47**, 421-428.

Sangster, A. G.; Hodson, M. J.; 1986: Silica in higher plant. In: EVERED, D.; O'CONNOR, M.; (Eds.): Silicon Biochemistry, 90-107. John Wiley & Sons Ltd., Sussex, UK.

SCHALLER, K.; LÖHNERTZ, O.; MUSKAT, S.; 1990: Anreicherung von Silizium in den Blättern von Müller-Thurgau und Silvaner im Verlaufe zweier Vegetationsperioden in Abhängigkeit von der Silikatdüngung. Wein-Wissenschaft **45**, 128-134.

STAVELY, J. R.; AMUJA, P.; HANSON, W. W.; 1969: Electron microscopy of the development of erysiphe polygoni in resistant and susceptible *Trifolium pratense*. Phytopathology **59**, 1688-1693.

WAGNER, F.; 1940: Die Bedeutung der Kieselsäure für das Wachstum einiger Kulturpflanzen, ihren Nährstoffhaushalt und ihre Anfälligkeit gegen echte Mehltaupilze. Phytopathol. Z. **12**, 427-479.

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