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# Silicon accumulation and water uptake by wheat

H.F. MAYLAND, J.L. WRIGHT and R.E. SOJKA
*U.S.D.A., Agricultural Research Service, Kimberly, ID 83341, USA*

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## Abstract

Silicon (Si) content in cereal plants and soil-Si solubility may be used to estimate transpiration, assuming passive Si uptake. The hypothesis for passive-Si uptake by the transpiration stream was tested in wheat (*Triticum aestivum* cv. Stephens) grown on the irrigated Portneuf silt loam soil (Durixerollic calciorthid) near Twin Falls, Idaho. Treatments consisted of 5 levels of plant-available soil water ranging from 244 to 776 mm provided primarily by a line-source sprinkler irrigation system. Evapotranspiration was determined by the water-balance method and water uptake was calculated from evapotranspiration, shading, and duration of wet-surface soil. Water extraction occurred from the 0 to 150-cm zone in which equilibrium Si solubility (20°C) was 15 mg Si $L^{-1}$ in the $A_p$ and $B_k$ (0–58 cm depth) and 23 mg Si $L^{-1}$ in the $B_{kq}$ (58–165 cm depth).

At plant maturity, total Si uptake ranged from 10 to 32 g $m^{-2}$, above-ground dry matter from 1200 to 2100 g $m^{-2}$ and transpiration from 227 to 546 kg $m^{-2}$. Silicon uptake was correlated with transpiration ($Si_{up} = -0.7 + .06T$, $r^2 = 0.85$) and dry matter yield with evapotranspiration ($Y = 119 + 3.3ET$, $r^2 = 0.96$). Actual Si uptake was 2.4 to 4.7 times that accounted for by passive uptake, supporting designation of wheat as a Si accumulator. The ratio of Si uptake to water uptake increased with soil moisture. The confirmation of active Si uptake precludes using Si uptake to estimate water use by wheat.

## Introduction

Grasses, unlike most dicotyledonous plants, tend to accumulate high concentrations of silicon (Si). Pot studies of Si uptake by oat plants (*Avena sativa* L.) documented the concomitant uptake of Si with the transpiration stream (Jones and Handreck, 1965). The amount of Si in the oat plants could be calculated from the concentration of Si in the soil solution and the amount of water transpired, suggesting that Si was likely taken up passively by oat and other graminaceous species.

Paltridge and De Vries (1973) and Hutton and Norrish (1974) suggested, conversely, that the amount of water used by the plant could be calculated from the Si solubility in soil and the amount accumulated in the plant. For field-grown wheat (*Triticum aestivum* L.), they reported a significant, empirical linear relationship ($r^2 = 0.94$, $n = 8$) between evapotranspiration (ET) and Si concentration in the husk (head minus grain). They were unable to explain why ET was not correlated to Si content in the head ($r^2 = 0.58$, ns, $n = 6$). Both groups worked with the same or similar data, but did not measure soil-solution Si concentrations. Because of the high correlation between Si concentration in wheat husk and water use, they concluded that Si solubility in soil solutions was constant. Paltridge and De Vries (1973) further noted that 'Silicon percentage in the soil solution would

appear to have little effect on a limited range of normal wheat soils'. McKeague and Cline (1963), however, showed that there was considerable range in soil-solution Si concentrations.

Van der Vorm (1980) measured Si uptake of five plant species grown in nutrient solutions varying in Si concentration. He found in monocots a preferential absorption at low concentrations of Si (0.35 mg Si $L^{-1}$) and some exclusion at high concentrations (75 mg Si $L^{-1}$). Using 10- and 20 mg Si $L^{-1}$ concentrations, Jarvis (1987) reported active Si uptake by perennial ryegrass (*Lolium perenne* L.) and wheat growing in flowing-nutrient culture. Barber and Shone (1966) concluded that Si was taken up actively in barley (*Hordeum vulgare* L.) since the process was sensitive to metabolic inhibitors. Therefore the existence of active Si uptake under field conditions would reduce the validity of water use or ET estimations being made from the Si content of plants or plant parts as proposed by Hutton and Norrish (1974).

The objective of this study was to test the hypothesis, under field conditions, that Si is taken up passively by wheat, i.e. by mass flow in the transpiration stream. The outcome of this test has a direct bearing on the usefulness of Si measurements to assess water uptake by wheat.

## Methods

### *Site*

The experimental site was located 10 km east of Twin Falls, Idaho USA (42°30′ N and 114°8′ W, altitude 1200 m). The area has a semiarid, continental climate with 290 mm annual precipitation. Precipitation from April through October averages 130 mm, whereas, pan evaporation over this same period averages 1400 mm. The study was conducted on the Portneuf silt loam loess soil (*Durixerollic calciorthid*). The water holding capacity at the drained upper limit (above field capacity) is 32%, and the drained lower limit (below field capacity) is 28% volumetric water content.

The Portneuf soil at this site has an $A_p$ (0–28 cm), $B_k$ (28–58 cm), $B_{kq1}$ (58–102 cm) and a $B_{kq2}$ (102–165 cm) horizon (Ritchie et al. 1987). The fertile $A_p$ contains 10 g $kg^{-1}$ organic matter, the 1:1 soil:water pH is 8.0 and the 1:2 soil:0.01 *M* $CaCl_2$ pH is 7.5. The electrical conductivity (EC) of saturated soil-paste extract is 65 mS $m^{-1}$. The $A_p$ horizon contains 20 g $kg^{-1}$ of $CaCO_3$ equivalent, but subsoils contain 120 to 240 g $kg^{-1}$. The $B_{kq}$ horizons is a nearly continuous, calcium carbonate, silicate cemented durapan. The hardpan does not restrict infiltration and when moist, it is penetrated by wheat roots to about 100 cm depth. Soil in the upper 58 cm of the profile contains approximately 20% clay, 68% silt, and 12% sand. Below the 58-cm depth, the proportion of clay decreases, and that of sand increases. Clays in the $A_p$ contain 100 to 210 g $kg^{-1}$ montmorillonite, 0 to 100 g $kg^{-1}$ vermiculite, 500 to 600 g $kg^{-1}$ illite, 110 to 160 g $kg^{-1}$ kaolinite and 110 to 170 g $kg^{-1}$ quartz.

### *Experimental*

A soft-white winter wheat (*Triticum aestivum* L., cv. Stephens) was sown on 25 September 1987 after incorporating 112 kg N $ha^{-1}$ as granular urea. Plants emerged by 8 October 1987 and overwintered in fair condition. About 125-mm precipitation was received between planting and 27 April 1988 when irrigation began.

Variable irrigation levels were provided during the 1988 experimental year with a line-source sprinkler system similar to the design of Hanks et al. (1976). Irrigation followed at about 10-day intervals with the last irrigation on 6 July 1988. The application rate varied linearly with distance from the line source, being about 7.2 mm $h^{-1}$ at 4.6 m and 0 mm $h^{-1}$ at 18.3 m from the line source. Soil moisture treatments W1 (driest) through W5 (wettest) were positioned perpendicular to the line source. Subplots were 3.05 m × 18.3 m and replicated 4 times.

Canal irrigation water originated from the Snake River. Periodic water quality analyses had shown this water to contain (in mg $L^{-1}$) about 220 $HCO_3$, 50 Ca, 20 Cl, 18 Na, 15 Mg, 12 $SO_4$-S, 4 K, and 0.1 $PO_4$-P. The EC is about 46 mS $m^{-1}$ and pH about 8.2 (McDole and Maxwell, 1987).

Liquid-nitrogen fertilizer, as urea-ammonium nitrate, was applied twice through the line-source sprinkler system (27 April and 9 June)

providing an additional 46.0, 34.5, 23.0, 11.5, and 0 kg N $ha^{-1}$ at distances of 4.6, 7.6, 10.7, 13.7 and 16.8 m from the line source, respectively.

*Measurement*

Soil-water content was measured throughout the growing season (8 April to 24 July) with a neutron moisture meter using access tubes installed in each subplot to a depth of 1.5 m. Potential leaching losses were monitored in three 3.6-m deep neutron access tubes positioned in the wettest treatment. Soil water depletion was calculated from changes in soil-water content as measured with the neutron meter. Evapotranspiration (ET) for each access-tube site was calculated from the soil-water balance by:

$$ET = D + I + R - L$$

where D is soil water depletion, I is irrigation, R is rainfall and L is leaching loss or drainage below the root zone. Irrigation and rainfall were measured at each access tube with rain gages. Leaching below 1.5 m was never detected, therefore L was considered to be zero.

Wheat ET was referenced to that of clipped-grass ET measured with a nearby weighing lysimeter (Wright, 1982, 1988). Grass ET data verified the accuracy of the wheat ET for adequately watered treatments using previously developed ET crop coefficients for winter wheat (Wright, 1981, 1982).

In the absence of deep leaching, transpiration (T) for the wheat plots was estimated from measured ET by:

$$T = (1 - K_s)ET$$

where $K_s$ is a dimensionless coefficient, $0 \leq K_s \leq 1$, relating soil-water evaporation to ET. The value of $K_s$ is dependent upon the moisture content of the soil surface and the degree of soil shading. For bare ground, $K_s = 1$, but for full cover $K_s \approx 0.05$, meaning that 100% and 5% of ET, respectively, is then due to soil evaporation (Wright, 1981). The value of $K_s$ was empirically estimated from information on crop canopy conditions and the recency of wetting the soil surface, using the partitioning concepts of Hanks (1983) and Wright (1981). Thus:

$$K_s = (1 - F_s)\,[1 - (t/t_d)^{0.5}]$$

where $F_s$ is a dimensionless shading factor, $0 \leq F_s \leq 1$, t is the number of days since rain or irrigation and $t_d$ is the number of days after rain or irrigation until the soil surface appears visually dry. For periods when t exceeded $t_d$, t was set equal to $t_d$. To facilitate estimating $K_s$, it was assumed that $F_s = 0$ in the absence of plants and that for maximum canopy conditions $F_s = 0.95$. Linear interpolation based on canopy height was used to scale $F_s$ from the beginning of growth until full cover. Since canopy height and surface moisture conditions were generally the same across replications at the same irrigation level, transpiration was estimated using the above procedures from the mean ET values for each irrigation level. A linear equation relating transpiration to ET was fitted to these data and used to estimate transpiration for each subplot of the experiment.

The single-line sprinkler source provided 5 soil-moisture treatments ranging from 244 to 776 mm available water for the period 10 April to 25 July. This range included the difference between the beginning and ending available soil water in the 1.5-m profile, plus the addition of rain and irrigation water.

Minimum-maximum soil temperatures were measured using thermocouples placed at 30-cm depth. Growing degree days (GDD-0°C base) were calculated as [((daily maximum + minimum air temperature)/2) − base air temperature], where base temperature is 0°C for wheat.

Silicon equilibrium-solubility data were determined for the Portneuf silt loam soil using two approaches. First, soil samples were taken from the $A_p$ (0 to 28 cm) and $B_k$ (28 to 58 cm) horizons, 30 hour after irrigation. The field-drained soil was immediately centrifuged for 30 minutes at 1000 *g* (Adams et al., 1980) and the solution passing through the soil was retained for Si analysis. In the second approach, field samples from the $A_p$ (0 to 28 cm), $B_k$ (28 to 58 cm) and the $B_{kq1}$ (58 to 102 cm) plus the upper 20 cm of the $B_{kq2}$ (102 to 165 cm) were air dried, passed through 2-mm sieve and then shaken with

0.02 *M* $CaCl_2$. Subsamples were continuously shaken with 0.02 *M* $CaCl_2$ (40:80, soil:solution) for 1, 72, and 144 hour each at 5, 24, and 35°C (Elgawhary and Lindsay, 1972). The soil solutions were filtered through 0.22-$\mu$m filter and retained for Si analysis. Silicon was also determined in irrigation water sampled at ten weekly intervals and filtered through 0.22-$\mu$m membrane.

Mass-flow of Si from the Portneuf silt loam soil to the wheat plant was calculated as the sum of the monthly products of millimeters transpiration (1 mm equivalent to 1 kg $m^{-2}$) for given month and Si solubility in soil water at mean-monthly soil temperature measured at the 30-cm depth.

Harvested wheat plants were cut at 2-cm stubble height from 1 $m^2$ (early harvests) and later in the season from 0.5 $m^2$ areas. The plant samples were washed for 1 to 2 minutes in distilled water containing 1 mL $L^{-1}$ detergent, thoroughly rinsed in a running stream of distilled water for another 1 to 2 minutes, dried at 60°C for 24 hours and ground to pass a 1-mm stainless steel screen. In this study, the term 'above-ground dry matter' (DM) includes stem or tiller (above 2-cm stubble height), plus all attached leaves and rachis, glumes (lemma and palea), awns and kernels, when present.

Silicon in plant ash, irrigation water, and soil-water extracts was determined spectrophotometrically using the blue silicomolybdous method of Fox et al. (1969). Other elements were determined by atomic absorption spectroscopy on tissue samples digested in 3:1 $HNO_3$:$HClO_4$, and diluted to appropriate volumes with deionized water. National Institute of Standards and Technology samples, SRM-3150 silicon solution and SRM-1572 citrus leaves, were used throughout the study to monitor analytical quality. All plant-tissue Si data are reported on a dry matter basis.

## Results

### *Wheat growth and water relations*

Spring weather favored tillering and good growth. June and July were warmer (1707 vs. 1527 GDD) and drier than normal, hastening maturity by 10 to 14 days. These conditions increased the already high-transpiration by wheat in this area. Seasonal ET on treatments W1 through W4 was limited by available soil water (Table 1). Water applied to the wettest treatment (W5), exceeded ET. Dry matter yield ranged from 1210 g $m^{-2}$ on the driest plots to nearly 2070 g $m^{-2}$ on the adequately watered plots (Table 1). Total dry matter yield was linearly related to ET ($Y_{g/m2} = 119 + 3.3\,ET_{mm}$, $r^2 = 0.96$). Hanks (1983) also reported that the dry-matter yield of wheat was linearly related to ET.

### *Silicon*

Washed-plant samples contained only 91 ± 28 $\mu$g Fe $g^{-1}$, well below the 200 $\mu$g Fe $g^{-1}$ threshold above which soil and Si contamination might be expected (Mayland and Sneva, 1983; Wallace, 1989). Measured Si values were, therefore, considered as endogenous Si which was absorbed

*Table 1.* Mean data for water use, wheat yield, and Si uptake for the period corresponding to Feekes scale 2 through 11.4

| Treatment | Available soil $H_2O$ | ET | T | Wheat yield | | Si uptake (mg $m^{-2}$) | Si uptake per unit[a] | |
|---|---|---|---|---|---|---|---|---|
| | | | | Total DM | Grain | | T (mg $kg^{-1}$) | DM (mg $g^{-1}$) |
| | (mm) | | | (g $m^{-2}$) | | | | |
| W1 | 244 | 256 | 212 | 1210 | 424 | 10300 | 48.5 | 8.6 |
| W2 | 319 | 328 | 259 | 1340 | 469 | 13800 | 49.3 | 10.3 |
| W3 | 488 | 479 | 390 | 1560 | 538 | 19300 | 53.1 | 12.4 |
| W4 | 636 | 609 | 526 | 1950 | 823 | 29500 | 55.7 | 14.9 |
| W5 | 776 | 638 | 550 | 2070 | 867 | 32100 | 58.2 | 15.5 |
| $LSD_{.05}$ | 29 | 26 | 21 | 300 | 157 | 7350 | 14.2 | 2.3 |

[a] Calculated as mg Si $m^{-2}$ absorbed during season divided by 1) kg $H_2O$ $m^{-2}$ transpired, 2) grain yield, or 3) dry matter yield.

and translocated to the plant shoots. The weekly applied irrigation-water contained $3.5 \pm 1.0$ mg Si $L^{-1}$. Some water was retained on the plants following each irrigation, but the amount of Si on the leaf surface after evaporation, was considered insignificant. There is no evidence that the sprinkler applied irrigation water or even the sample rinse water leached any of the endogenous Si from the plants.

Silicon accumulated in the plants as soil water was assimilated during growth (Fig. 1A, 1B). Measurable amounts of dry matter ($100\,g\,m^{-2}$) and accumulated Si ($1.0\,g\,m^{-2}$) were present on 9 April 1988, when growth and water monitoring began i.e., approximately 8, 7, 6, 5 and 5% of the final dry matter and 10, 7, 5, 3 and 3% of final Si for the driest through wettest moisture treatments, respectively. These initial values were offset by later leaf loss (Fig. 1A), thus no corrections were attempted when calculating the total Si/water flux, Si/DM and water/DM data (Table 1).

Silicon solubility in the Portneuf soil was not different between the 72 and 144 hour ($p < 0.01$) extractions and was assumed to be at equilibrium. As shown in Figure 2, the solubility was linearly related to extraction temperature. The solubility data for the $A_p$ and the $B_k$ were not different ($p = 0.01$) and these values, for both the 72- and 144-hour extraction, were combined. Silicon solubility of the $B_{kq}$ was higher than that of the overlying $A_p$ and $B_k$ horizons, reflecting the increased concentrations of silicate and calcium carbonate in the cemented hard pan or durapan.

A Si-solubility value of 16 mg Si $L^{-1}$ was measured in the 19°C solution extracted from the $A_p$ soil horizon, 30 hours after irrigation. This value was not different ($p < 0.05$) from that of 14.8 mg Si $L^{-1}$ calculated at 19°C for the $A_p$ and $B_k$ soils equilibrated with 0.02 *M* $CaCl_2$ for 72 to 144 hours (Fig. 2). The Si-solubility equations shown in Figure 2 were used to calculate Si solubility and uptake by the wheat plant. The mean-monthly-soil temperatures at 30-cm depth were selected as representative of solution temperatures in the rooting zone.

Wheat dry matter was linearly related to ET (Fig. 3A) and Si uptake was linearly related to T (Fig. 3B). The regression equation for Si uptake

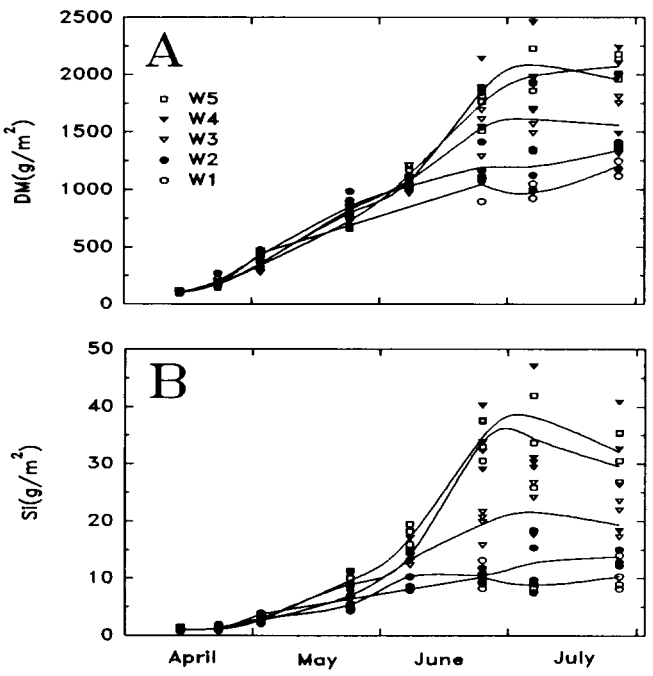


*Fig. 1.* (**A**) Dry matter accumulation and (**B**) silicon uptake by wheat grown with five soil water levels over 9 April through 26 July.

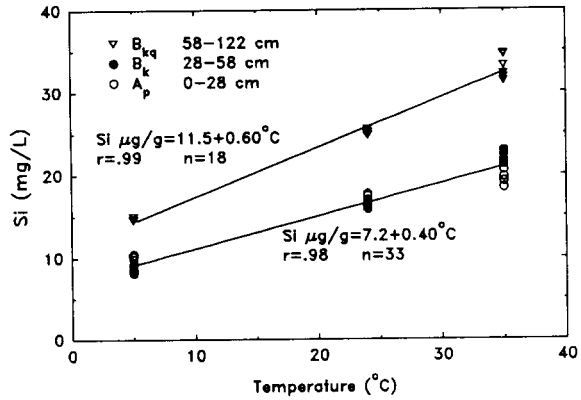


*Fig. 2.* Silicon solubility in 0.02 *M* $CaCl_2$ suspensions of $A_p$, $B_k$ and $B_{kq}$ horizons of Portneuf silt loam soil as a function of temperature. Silicon solubilities of $A_p$ and $B_k$ soil were not different ($p < 0.10$).

was $Si_{up} = 0.71 + 0.06\,T_{mm}$, where $r^2 = 0.85$. Some available soil water remained in the subsoil depths between 58 and 150 cm. At these depths, Si solubility was 64% greater than for the 0 to 58 cm depth (Fig. 2). Thus, there was potentially more Si per unit of water absorbed from the subsoil than from the surface soil.

At harvest, plants had accumulated 10,300 to 32,100 mg Si $m^{-2}$ (Table 1). The ratio of Si uptake to water transpired increased with increasing soil-water availability whether the quantity of Si was expressed as a ratio of mass of water transpired or total dry matter produced (Table 1).

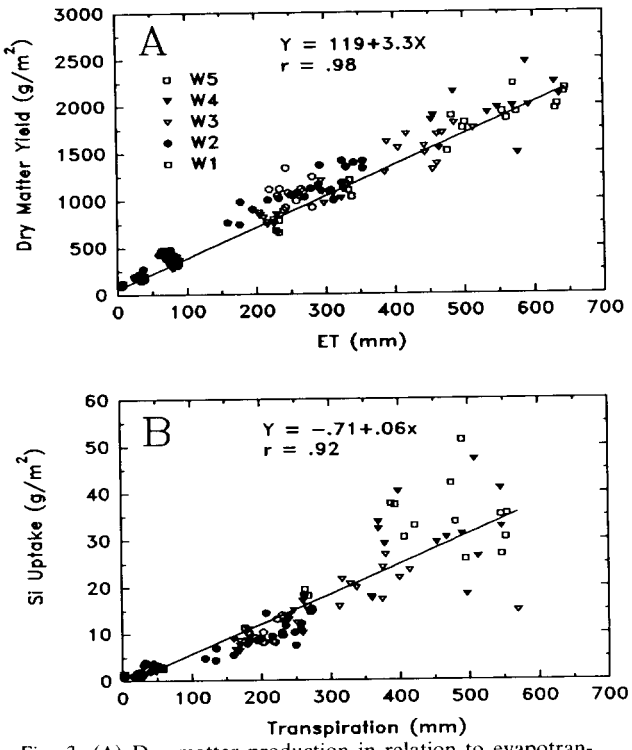


*Fig. 3.* (**A**) Dry matter production in relation to evapotranspiration (ET) and (**B**) silicon uptake in relation to transpiration (T).

## Discussion

Silicon solubility in the Portneuf soil was dependent upon sampling depth and temperature. The Portneuf has a calcium and silica cemented hardpan or durapan at 58 to 165 cm depth. In the 0 to 58 cm depth, $H_4SiO_4$ has an equilibrium solubility of 15 mg Si $L^{-1}$ at 20°C whereas this solubility averages 23 mg $L^{-1}$ in the durapan. Silicon solubility of the Portneuf soil, when shaken with 0.02 *M* $CaCl_2$ for 72 to 144 hours was not different when adjusted for soil temperature, from the solubility determined in soil water extracts obtained by centrifugation 30 hours after irrigation. This similarity confirms the use of the equilibrium-solubility equations given in Figure 2.

By comparison, Elgawhary and Lindsay (1972) showed soil-Si solubility ranging between 2.8 mg $L^{-1}$ (quartz) and 51 mg $L^{-1}$ (amorphous silica). Jones and Handreck (1967) and McKeague and Cline (1963), reported Si solubility from various soils and soil minerals between 1 and 37 mg Si $L^{-1}$. Elgawhary and Lindsay (1972) reported equilibrium concentrations of 25 and 19 mg Si $L^{-1}$ for the calcareous Ulysses and the acid Paxton soil, respectively. These solubility values are for 20°C and are expected to be proportional to temperature.

Irrigation water contained $3.5 \pm 1$ mg Si $L^{-1}$. Upon contact with the Portneuf soil, the Si concentration in the solution phase would increase. As solution passed into the durapan zone it would have Si concentrations approaching 23 mg $L^{-1}$. In this study, only the wetter treatments had wet subsoils during the later portion of the growing season. Water in the durapan had a higher soluble-Si concentration than the upper horizons. Therefore, plants extracting water from the durapan encountered higher concen-

*Table 2.* Actual Si uptake by wheat plant versus mass-flow supply of Si calculated for several Si sources

| Treatment | Actual Si uptake (A) | Mass-flow supply of Si uptake[a] by wheat plants calculated for | | | | Actual Si uptake/Si uptake calculated as mass flow | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | Portneuf soil | | Theoretical estimates | | Portneuf soil | | Theoretical estimates | |
| | | $A_p + B_k$[b] | $B_{kq1} + B_{kq2}$[c] | Amorphous Si | Quartz | $A_p + B_k$[b] | $B_{kq1} + B_{kq2}$[c] | Amorphous Si | Quartz |
| | | (mg m$^{-2}$) | | | | | | | |
| W1 | 10300 | 2810 | 4400 | 9030 | 448 | 3.68 | 2.35 | 1.15 | 23 |
| W2 | 13800 | 3400 | 5330 | 11000 | 543 | 4.04 | 2.58 | 1.26 | 25 |
| W3 | 19300 | 5140 | 8050 | 16500 | 820 | 3.76 | 2.40 | 1.17 | 24 |
| W4 | 29500 | 6840 | 10700 | 21900 | 1090 | 4.32 | 2.76 | 1.35 | 27 |
| W5 | 32100 | 6870 | 10800 | 22000 | 1100 | 4.66 | 2.98 | 1.46 | 29 |

[a] Mass-flow supply of Si calculated as Si solubility of given source times transpired water. See text for details.

[b] Assumes all transpired water originated in the $A_p$ (0 to 28 cm) and $B_k$ (38 to 58 cm) horizons where soluble mg Si $L^{-1}$ = 7.17 + 0.395 mean monthly soil temperature (°C) at 30 cm depth.

[c] Assumes all transpired water originated in the $B_{kq1}$ (58 to 102 cm) and 20 cm portion of $B_{kq2}$ (102 to 165 cm) horizons where soluble mg Si $L^{-1}$ = 11.54 + 0.595 mean monthly soil temperature (°C) at 30 cm depth.

trations of Si than those extracting water from the surface 28 cm.

The mass-flow of Si to wheat plants was calculated for several situations (Table 2). In each case, the solubility of Si (Fig. 4) was adjusted for mean-monthly soil temperature at the 30-cm depth. First, computations were made assuming that all of the Si uptake occurred from the $A_p + B_k$ horizons or second, that all occurred from the $B_{kq}$ horizon where Si solubility was higher. For comparison, computations were made also for soil solutions assumed to be at equilibrium with amorphous silica, the most soluble form, or with quartz, the least soluble form of Si in soils. Silicon uptake by wheat greatly exceeded that accounted for by passive uptake of solution Si in equilibrium with quartz or even amorphous Si (Table 2). Solution Si in equilibrium with other clays in this soil would be intermediate to quartz and amorphous Si.

Depending on the assumed alternatives, there was 2.4 to 4.7 times as much Si taken up by the wheat plant as could have been delivered by mass flow (Table 2). Jarvis (1987) also showed that Si was taken up by wheat at concentrations exceeding that in nutrient culture. Van der Vorm (1980) reported data for wheat grown in nutrient culture in which the actual Si uptake/mass flow uptake (A/M) was 2.2 and 1.8 (computed) for Si uptake from the 15 and 23 mg Si $L^{-1}$ equilibrium (20°C) values determined in this field study. The A/M values for the field study are higher than those computed for the solution study of van der Vorm (1980). Results of the solution cultures and supporting field data on Si accumulation place wheat in a category with other Si accumulators like rice (*Oryza sativa* L.).

Raven (1983) noted that in vascular land plants the entry of Si from the soil water into the xylem can involve a flux ratio (mg Si $kg^{-1}$ water) that is less than (e.g. Leguminoseae), equal to (e.g. some gramineae like oat) or greater than (e.g. rice, and *Equisetum* sp.) the concentration in the soil solution. Lewin and Reimann (1969), Parry et al. (1984), Sangster and Hodson (1986) and Werner and Roth (1983), classified plants by their Si uptake; either as excluders, passive absorbers, or accumulators. Other terminology describes them as plants having exclusionary, passive, or active Si uptake mechanisms.

The oat plant was shown to passively accumulate Si (Jones and Handreck, 1967). Hence, Si uptake by oat can be used as an indirect measure of water uptake. This was not the case with wheat, as noted in this study and another reported by Jarvis (1987). Lewin and Reimann (1969) noted that the Si/water flux ratio was 200, 2 to 3, 1, ≤1, and 0.2 for rice, barley, oat, tomato (*Lycopersicon esculentum* L.) and Crimson clover (*Trifolium incarnatum* L.), respectively. The accumulation rate of Si by wheat in this field study was similar to that previously shown for barley. In addition, the Si/water flux ratio for wheat increased (r = 0.90) as soil moisture increased (Fig. 4). The explanation for this relationship is not obvious. Plants in the wetter

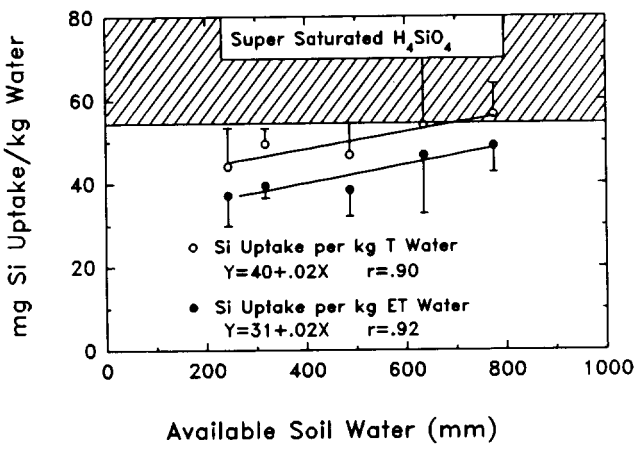


*Fig. 4.* Expected saturation range of soluble Si ($H_4SiO_4$) in contact with amorphous silica and Si/kg water uptake by the wheat plant as ET or transpiration (T) related to available soil water.

treatments may have derived more of their water and Si from the Si-rich durapan. In either case, the wheat plants actively absorbed much more Si than if it was absorbed passively.

Jones and Handreck (1967) noted that the uptake of silica by rice increased with soil water content. The Si in leaf blades of rice increased from 77 to 100 g $kg^{-1}$ when soil water content increased from 50% of moisture holding capacity to saturation. They suggested that this was not related to changes in pH, but might be related to organic acids released from organic matter as a result of reducing conditions. McKeague and Cline (1963) showed that poor drainage and low Eh were associated with relatively high concentrations of Si in solutions. None of these explanations would seem to apply in the present study.

Our data support the classification of wheat as a Si accumulator. Variations in Si solubility in specific soil horizons, plus the active accumulation of Si by the wheat plant precludes quantitative inferences of transpiration from measurements of accumulated Si in the wheat plant.

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