Silicon accumulation and water uptake by wheat

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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_{ka} (58–165 cm depth).

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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 fieldgrown 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* CaCl₂ 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 CaCO₃ 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 $3.05 \text{ m} \times 18.3 \text{ m}$ 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 HCO₃, 50 Ca, 20 Cl, 18 Na, 15 Mg, 12 SO₄-S, 4 K, and 0.1 PO₄-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 linesource 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:

$$\mathbf{ET} = \mathbf{D} + \mathbf{I} + \mathbf{R} - \mathbf{L}$$

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 clippedgrass 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, $0 \le K_s \le 1$, 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 sur-

face, 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, $0 \le$ $F_s \leq 1$, 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 fielddrained 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 $0.02 M \text{ CaCl}_2$. Subsamples were continuously shaken with $0.02 M \text{ CaCl}_2$ (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 $0.22 - \mu \text{m}$ filter and retained for Si analysis. Silicon was also determined in irrigation water sampled at ten weekly intervals and filtered through $0.22 - \mu \text{m}$ 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 meanmonthly 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 soilwater 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 HNO₃:HClO₄, 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 planttissue 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 ($Y_{g/m2} = 119 + 3.3 \text{ ET}_{mm}$, $r^2 = 0.96$). Hanks (1983) also reported that the dry-matter yield of wheat was linearly related to ET.

Silicon

Washed-plant samples contained only $91 \pm 28 \ \mu g$ Fe g⁻¹, well below the 200 μg 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

Treatment	Available	ET	T	Wheat yield		Si uptake	Si uptake per unit ^a	
				Total DM	Grain	(mg m)	T	DM
	(mm)			$(g m^{-2})$			$(mg kg^{-1})$	(mg g ^{- ,})
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

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

^a Calculated as mg Si m⁻² absorbed during season divided by 1) kg H_2Om^{-2} transpired, 2) grain yield, or 3) dry matter yield.

and translocated to the plant shoots. The weekly applied irrigation-water contained 3.5 ± 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 gm^{-2}) and accumulated Si (1.0 gm^{-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 equilib-

rium. 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* CaCl₂ 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 meanmonthly-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* CaCl₂ 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



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

more Si per unit of water absorbed from the subsoil than from the surface soil.

At harvest, plants had accumulated 10,300 to $32,100 \text{ mg Si m}^{-2}$ (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).

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 CaCl₂ 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 McK-eague 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 $3.5 \pm 1 \text{ mg Si L}^{-1}$. 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-

Treatment	Actual Si	Mass-flow sup	ply of Si uptake ^a by	wheat plants calcu	lated for	Actual Si upt	ake/Si uptake calcı	ulated as mass flow	
	uptake (A)	Portneuf soil		Theoretical estin	nates	Portneuf soil		Theoretical esti	mates
		$A_p + B_k^b$	$\mathbf{B_{kq1}}+\mathbf{B_{kq2}}^{c}$	Amorphous Si	Quartz	$\mathbf{A}_{\mathbf{p}} + \mathbf{B}_{\mathbf{k}}^{\mathbf{b}}$	$\mathbf{B}_{kqi}+\mathbf{B}_{kq2}^{c}$	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
WS	32100	6870	10800	22000	1100	4.66	2.98	1.46	29
^a Mass-flow su	pply of Si calculated	as Si solubility e	of given source time	s transpired water.	See text for c	letails.			
^b Assumes all	transpired water orig	inated in the \mathbf{A}_{p}	(0 to 28 cm) and B_k	(38 to 58 cm) horize	ons where solu	ble mg Si L ^{-1} = 7	.17 + 0.395 mean m	onthly soil temperat	ure (°C) at
30 cm depth.							-		
^c Assumes all	transpired water orig	inated in the B _{kq1}	(58 to 102 cm) and	20 cm portion of B_k	₁₄₂ (102 to 165 d	cm) horizons whe	re soluble mg Si L ⁻¹	= 11.54 + 0.595 me	an monthly

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

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_{ka} 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 guartz 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, \leq 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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