Plant and Soil XXIX, no. 3 December 1968

STUDIES OF SILICA IN THE OAT PLANT

IV. SILICA CONTENT OF PLANT PARTS IN RELATION TO STAGE OF GROWTH, SUPPLY OF SILICA, AND TRANSPIRATION

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INTRODUCTION

It was discovered long ago by plant analysts that the concentration of silica varies widely among the parts of the one plant and the earliest work drew attention to the contrasting silica content of the grain and 'straw' of cereals [13]. More recent analyses show that the 'husks' of cereals contain much higher concentrations of silica than vegetative parts [2 8 11]. This information is derived from analyses of plants at one stage of growth only or of plants grown on only one soil. Comprehensive information on the effects of both soil and stage of growth on the distribution of silica among the parts of the cereal plant is lacking.

In the present work a study has been made of the changes in the content and distribution of silica in oat plants during the growing period. The influence of the soil on these changes was also studied by growing the plants on soils in which the level of supply of silica in solution ranged from 7 to 67 ppm SiO_2.

MATERIALS AND METHODS

The soils selected for these experiments were: a black clay from a reclaimed swamp at Penola in the south-east of South Australia; a

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sandy loam from the experimental area of the School of Agriculture, University of Melbourne; and a krasnozem from Wollongbar near Lismore in New South Wales. They are hereafter referred to by their place names; data on their mechanical, chemical and mineralogical composition are given in the previous paper in this series [7]. The pH's of the soils were adjusted to 5.6 ± 0.1. The levels of monosilicic acid in the soil solutions were: Penola, 67; University, 54; and Wollongbar, 7 ppm expressed as SiO_2. In the previous paper in this series it was shown that these levels remain constant despite repeated withdrawals of solution [7].

The culture pots were of polyethylene and held 7.00 kg of the University soil and 4.75 kg of the Penola and Wollongbar soils. Each pot of soil had mixed into it the following: KH_2PO_4, 0.52 g; $Ca(NO_3)_2.4H_2O$, 1.62 g; NH_4NO_3, 0.55 g. During the growing period each pot received two surface applications of N, each containing 1.62 g $Ca(NO_3)_2.4H_2O$ and 0.55 g NH_4NO_3.

The soils were watered to pF 2.0 and forty seeds of *Avena sterilis* L. (var. Algerian) were sown in each pot in mid-June. There were four pots of University soil and two pots of each of the Penola and Wollongbar soils. All pots were mulched with polyethylene pellets at the rate of 700 g per pot and housed in a glass-house. Throughout the growing period the pots were weighed daily at about 5 p.m. and adjusted to pF 2.0 with distilled water. Cumulative water losses from each pot were computed from these weighings.

At the three-leaf stage plants were thinned to twenty-four per pot. Plants removed from the one soil were bulked and divided into individual leaves. The blades of the first leaf, designated I, were dissected at intervals to give transverse segments which were dried at 105°C and analysed for silica. The blades of leaves II and III were similarly dissected into segments and these were also analysed for silica.

Six harvests were made after thinning; these were at 30, 72, 90, 111, 132, and 170 days after sowing. At harvest 6 the plants were at full maturity. The numbers of plants removed from each pot at the successive harvests were: six, five, three, three, three and four. At each harvest the plants were divided into individual parts which were dried, ground, and analysed for silica. A small proportion of the plant material at each harvest was classified as 'miscellaneous'. This comprised material which was immature and could not be included with any particular part; at harvests 5 and 6 the miscellaneous material also included occasional small, sterile tillers.

From the time of harvest 4 (111 days after sowing), two pots of oats on the University soil were reserved to provide material for frequent determinations of silica and dry matter in the developing spikelet.

In the present experiments the plant material was analysed for total silica. The methods employed were those described in the previous paper in this series [7].

RESULTS

A feature of the results is that the general trends of the changes in the silica content with growth, and the distribution of silica among the parts of the plant, were much the same on all three soils. The level of silica in the soil solution, that is the level of supply to the plant, affected only the concentration and amount of silica present in the whole tops or parts (Tables 1 and 2) but not the general trends in its distribution during the growing period.

TABLE 1

Concentration of silica in a leaf (number VII) in relation to age (% SiO_2 in dry matter)

Soil	SiO_2 in soil solution ppm	Days after sowing *				
		72	90	111	132	170
Penola	67	0.50	1.65	2.68	3.00	3.49
University	54	0.14	0.41	1.02	1.37	1.66
Wollongbar	7	0.10	0.18	0.22	0.33	0.39

* Harvests 2, 3, 4, 5 and 6 respectively.

The silica content of the plants increased during the growing period. Table 3, which is based on analyses of plants grown on Penola soil, shows the typical increases in both the concentration and amount of silica in the various parts of the tops. The silica content of individual leaf blades and sheaths also increased with increasing age and this trend is shown by data in Table 1 for the blade of leaf VII.

The distribution of silica can be compared with that of dry matter when the amounts of these in the parts are expressed as proportions of the totals in the tops (Fig. 1). At each of harvests 5 and 6 the inflorescence contained similar proportions of the total silica and dry matter. This relationship did not hold for any of the other parts (Fig. 1) because the silica content per unit dry weight was always lower in the stems than in the leaves (Table 3).

Besides the data on the distribution of silica among the parts of a plant some data were obtained on the distribution among the leaves. The silica content of leaf XII, *i.e.* the flag leaf, was always higher than that of lower leaves, both in terms of the concentration of

TABLE 2

Silica content of the parts of oat plants grown on three soils *
and sampled at maturity (harvest 6)
(Silica expressed as SiO_2)

Plant part	Penola soil		University soil		Wollongbar soil	
	% d.m.	mg/plant	% d.m.	mg/plant	% d.m.	mg/plant
Leaf blade	5.30	70.3	2.15	44.6	0.46	6.42
Leaf sheath	4.07	42.6	2.32	30.3	0.39	4.54
Stem	1.03	27.2	0.71	17.7	0.08	2.00
Rachis	2.44	3.7	0.83	1.3	0.15	0.17
Palea	10.72	13.5	7.28	11.7	1.76	2.01
Lemma	7.76	56.8	5.39	44.0	0.98	6.11
Empty glumes	9.24	25.0	4.40	13.7	0.79	1.85
Awn	6.86	3.3	3.64	2.3	0.75	0.33
Caryopsis	0.06	1.2	0.06	1.3	0.01	0.21
Miscellaneous	4.12	7.0	2.11	9.6	0.51	2.09
Whole tops	2.94	250.6	1.82	176.5	0.30	25.73

* SiO_2 in soil solutions: Penola, 67; University, 54; Wollongbar, 7 ppm.

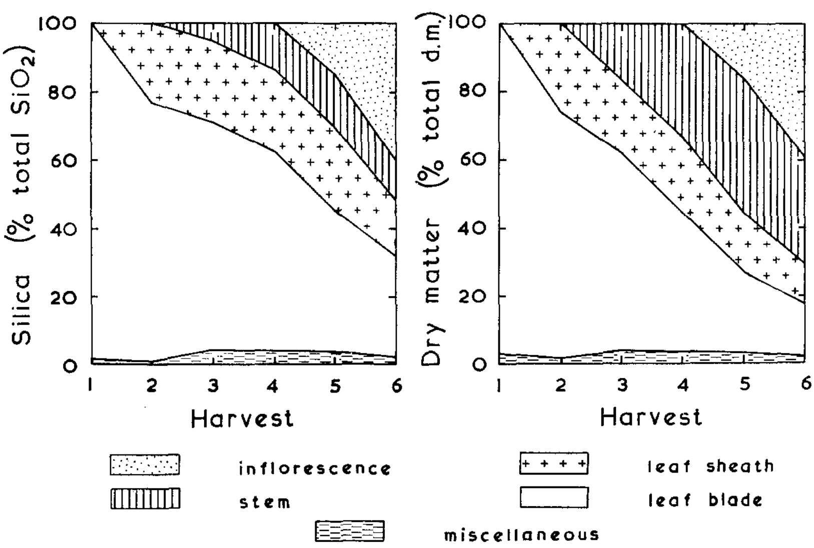

Fig. 1. Distribution of silica and dry matter among parts of the oat plant grown on Penola soil. Amounts of silica and dry matter are shown as percentages of the total in the plant at each harvest.

TABLE 3

Silica content of the parts of oat plants grown on Penola soil * and sampled at intervals during the growing period (silica expressed as SiO_2)

Plant part	Harvest number (days after sowing in parentheses)											
	1 (29)		2 (72)		3 (90)		4 (111)		5 (132)		6 (170)	
	% d.m.	mg/ plant	% d.m.	mg/ plant	% d.m.	mg/ plant	% d.m.	mg/ plant	% d.m.	mg/ plant	% d.m.	mg/ plant
Leaf blade	1.88	1.1	1.94	12.8	3.42	27.0	3.49	49.8	4.48	69.6	5.30	70.3
Leaf sheath			1.70	4.0	2.32	9.8	2.77	20.4	3.71	42.8	4.07	42.6
Stem					0.62	2.3	1.07	11.7	1.03	26.8	1.03	27.2
Inflorescence									2.43	27.8	3.10	103.5
Miscellaneous			3.35	0.1	1.71	1.5	2.19	3.2	4.08	7.6	4.12	7.0
Whole tops	1.88	1.1	1.88	16.9	1.94	40.6	2.56	85.1	2.61	174.6	2.94	250.6

* 67 ppm SiO_2 in soil solution.

silica in the dry matter and the total amount of silica per leaf (Table 4).

The distribution of silica along the individual blades at the three-leaf stage is shown in Fig. 2. At the apex, or tip, the concentration of silica was four to twelve times greater than that at the base of the leaf. The pattern of distribution was unaffected by the position of the leaf or the level of supply of silica. In the mature leaf blade the pattern of distribution was similar to that in immature leaves. The distribution of silica along the oat leaf resembles the distribution of silicified bulliform cells along the leaf blades of rice [16] and two other grasses, namely *Molinia caerulea* and *Sieglingia decumbens* [12]. The silicified bulliform cells are most frequent in the apical regions and

TABLE 4

Silica content of flag (number XII) and lower leaves of oats grown on Penola soil and sampled at maturity (silica expressed as SiO_2)

Plant part	% d.m.	mg/plant	% of total in tops
Leaf blade			
XII	9.78	11.5	4.6
I to XI combined	4.87	58.8	23.5
Leaf sheath			
XII	4.22	11.1	4.4
I to XI combined	4.02	31.5	12.5

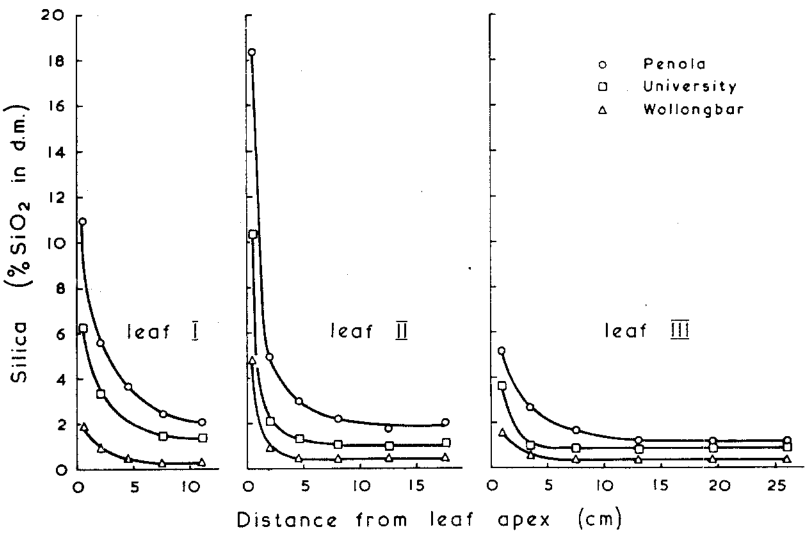

Fig. 2. Concentration pattern of silica in individual leaf blades of oat plants harvested at the three-leaf stage. Plants grown on soils containing silica in solution as follows: Penola, 67; University, 54; Wollongbar, 7 ppm SiO_2.

TABLE 5

Distribution of silica and dry matter between the caryopsis and husks * of the spikelet from oats grown on University soil **. Spikelets sampled at various stages of development up to maturity

Stage of ear development	Caryopsis		Husks		Whole spikelet	
	mg d.m.	% SiO_2 in d.m.	mg d.m.	% SiO_2 in d.m.	mg d.m.	% SiO_2 in d.m.
Pre-emergence	—	—	3.1	0.18	3.1	0.18
Emergence	—	—	5.6	0.32	5.6	0.32
	—	—	9.2	0.69	9.2	0.69
Anthesis	—	—	12.8	1.11	12.8	1.11
	—	—	13.7	1.47	13.7	1.47
	1.7	0.13	16.2	2.00	17.9	1.82
'Milk'	5.8	0.12	15.8	2.71	21.6	2.01
	10.8	0.08	17.8	4.20	28.6	2.64
'Dough'	14.7	0.16	18.2	4.58	32.9	2.60
Mature	26.3	0.06	16.9	5.29	45.2	2.05

* Husks: empty glumes, palea, lemma and awn.

** 54 ppm SiO_2 in soil solution.

become progressively less frequent in moving towards the base of the leaf.

The distribution of silica and dry matter between the caryopsis and the other parts of the developing spikelet is shown in Table 5. From pre-emergence to maturity there was a continuous and rapid increase in the concentration of silica in the husks (*i.e.* empty glumes, palea, lemma and awn). The concentration of silica in the whole spikelet increased rapidly until the 'milk' stage, but then levelled off. This levelling off is due to the rapid increase in the dry weight of the caryopsis combined with its characteristically low silica content.

DISCUSSION

A summary of our knowledge of silica in the oat plant will provide background for a discussion of the results of the present studies.

Silica is present in soil and culture solutions [7] as the undissociated molecule monosilicic acid (H_4SiO_4) and two lines of evidence indicate that the uptake of monosilicic acid is a passive, non-selective process. First, the total silica in the tops can be accounted for in terms of the level of monosilicic acid in the external (soil) solution and the amount of water transpired [7]. Second, the concentration of monosilicic acid in xylem sap sampled at the base of the stem is similar to that in the external solution [6]. As water is lost by transpiration the liquid phase of the tops becomes more concentrated with respect to monosilicic acid. Analyses of expressed sap, which give an average concentration of monosilicic acid in the total liquid phase, show that this generally exceeds that of a saturated solution of amorphous silica (120 ppm SiO_2 at 25°C) and may reach 222 ppm SiO_2 [7]. The concentration depends on the soil but for a given soil it varies little during the life of the plant [7]. The characteristic increases in the total silica content of the tops as a whole, and of individual parts, must therefore be attributed to a continuous deposition of solid silica. This silica, which is amorphous opal [8 9], accumulates in the walls of all types of epidermal cells in all plant parts [10]. In some parts the walls of the mesophyll cells and the thickened tissues of the xylem are also impregnated with solid silica [10]. The deposition of solid silica within the cell walls is consistent with the hypothesis that water moves from the xylem to the transpiring cell by mass flow in the cell walls rather than from vacuole to vacuole [4 15].

The foregoing indicates that monosilicic acid and water move concomitantly from the root to the evaporating surfaces, and that solid silica is deposited in greatest quantities in the terminal regions of the transpiration stream. The distribution of silica within the plant tops may therefore reflect the pattern of water loss from the various parts. It may be noted that once silica is deposited it cannot dissolve and be retranslocated because it is in contact with a supersaturated solution of monosilicic acid.

At maturity the inflorescence contained 41.4 to 42.0 per cent of the total silica in the tops (Table 2). An estimate of the amount of water transpired by the inflorescence may be obtained from data on the cumulative losses of water by the plants at various stages during the growing period. At ear emergence (circ. 125 days after sowing) the plants had transpired 45 to 50 per cent of the water used during the entire growing period and had accumulated a similar proportion of the total silica. From ear emergence to maturity, the leaves and stems accumulated a further 10 to 15 per cent of the total silica, which suggests that they transpired a further 10 to 15 per cent of the total water. On this basis it may be concluded that the inflorescence accounted for 35 to 45 per cent of the total water lost by the plant during the growing period. The literature contains no direct evidence in support of this conclusion but it is recognized that the awns are structures carrying out intensive transpiration [5]. The other parts of the husks are also likely to carry out intensive transpiration because the radiation incident on them would be high and they have a high photosynthetic activity [14].

Most of the remaining silica was found in the leaf blades and sheaths and only about 10 per cent of the total silica in the tops was found in the stems (Table 2, Fig. 1). The small water loss suggested by this figure is consistent with the low transpiration activity of the stem. This is mostly attributable to its epidermis having few stomata [1] and to it being enclosed by the leaf sheaths during much of the growing period.

Among the leaves, the flag leaf had the highest silica content and its blade and sheath accounted for one-fifth of the total silica in the twelve leaves (Table 4). The literature contains no information on the relative amounts of water transpired by the flag and lower leaves. However, the flag leaf probably has a higher transpiration rate than lower leaves because it has a high photosynthetic capacity [14], and being unshaded it would receive more radiation than the lower leaves.

The pattern of distribution of silica in a leaf blade (Fig. 2) may also be explained by the concomitant movement of monosilicic acid and water in the transpiration stream. The greater age of the apical region would by itself produce a gradient in water loss along a blade; this effect would apply especially to the developing leaf. Additional effects may subsequently become important. As water is lost to the atmosphere, monosilicic acid would become more concentrated in the remaining solution and the bulk of the silica would be immobilized in epidermal and mesophyll cell walls. Some monosilicic acid may, however, diffuse back into the xylem and in so far as this occurs the transpiration stream would become more concentrated with respect to monosilicic acid in moving from the base to the apex of the blade. Finally, it is possible that the transpiration rate in the apical region is higher than in other regions because of some structural variation such as a greater evaporating surface per unit weight.

The figures for the distribution of silica among the various parts of the plant, among the leaves on the one plant, and along the one leaf, all support the thesis that monosilicic acid and water move concomitantly in the transpiration stream and that silica is deposited in greatest quantities in those parts and regions from which water is known or is likely to be lost in greatest quantities. Accordingly, the idea deserves to be entertained that the silica content of an individual part would provide a basis for estimating the water transpired by that part. This is an extension of our previous suggestion [7] that it should be possible to estimate the total water used by an oat plant from determinations of the amount of silica in the tops and the level of monosilicic acid in the soil solution. The additional step which is now suggested simply involves determining the amount of silica in a given part.

So far this discussion has dealt with the oat plant. In unpublished work the present authors have found that the pattern of distribution of silica was repeated rather closely in wheat, rye and barley. It is possible that in these and other grasses the distribution of silica within the tops might also reflect the pattern of water loss.

SUMMARY

Oat plants, *Avena sterilis* L., were grown on soils in which the concentration of monosilicic acid in the soil solution, that is the level of supply of silica, ranged from 7 to 67 ppm SiO_2. Analyses at intervals throughout the growing period showed that the level of supply affected the amount and concentration of silica in the plant but not the pattern of its distribution among the parts.

At maturity the caryopsis contained only 0.5 to 0.8 per cent of the total silica in the tops while the other parts of the inflorescence contained 40.7 to 41.3 per cent. The leaves (blade and sheath) contained 42.5 to 45.0 per cent of the total silica and the stems contained 7.8 to 10.9 per cent; the remainder was present in small sterile tillers.

The concentration of silica in the dry matter was highest in the palea, lemma glumes, awn, and leaves. Among the leaves, the flag leaf had the highest silica content, both in terms of concentration in the dry matter and amount per leaf. The distribution of silica along a leaf followed a hyperbolic curve, the concentration being highest at the apex and lowest at the base of the blade.

The chemistry of silica and the pattern of its distribution in the tops suggest that monosilicic acid and water move concomitantly in the transpiration stream and that solid silica is deposited in greatest quantities in those parts and regions from which water is lost in greatest quantities.

ACKNOWLEDGEMENTS

We are grateful to G. W. Leeper for helpful discussions and to H. C. Forster for providing laboratory and glass-house facilities.

Received June 27, 1967

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