Sodium Helps Overcome Potassium Deficiency Effects on Water Relations of Cauliflower

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Abstract. When grown in refined sand with one-twentieth normal K supply, cauliflower (*Brassica oleracea* L. var. botrytis L. cv. Pusi) had lower dry matter and tissue concentration of K than the controls and developed visible symptoms characteristic of K deficiency. In K-deficient plants, the specific leaf weight, diffusive resistance, and proline concentration in leaves were significantly higher and relative water content (RWC), leaf water potential (ψ), stomatal aperture, stomatal density, and transpiration rate were significantly lower than in control plants. When K-deficient plants were supplied additional Na to the extent K was deficient, Na concentration in the plants increased and the plants recovered from the K deficiency effect on free proline concentration, RWC, leaf water potential, stomatal aperture, stomatal density, specific leaf weight, diffusive resistance, and transpiration.

In an earlier study we have shown that cauliflower requires 4 mM K supply for normal growth (Singh and Sharma, 1988a). Plants grown at suboptimal K showed retarded growth and increased water stress (Sharma et al., 1985; Singh and Sharma, 1988b). Beneficial effects of Na and the substitution of Na for K in growth and metabolism in several species have been documented (Flower and Läuchli, 1983). Our study was undertaken to determine whether the disturbance in water relations caused by low supply of K can be overcome by supplying Na.

Cauliflower was grown in refined sand (Hewitt, 1966) with normal (4 mM) and low (0.2 mM) K, supplied as sulfate, in white plastic pots of 8-liter capacity. Plants receiving low K were grown in two lots, one was supplied 3.8 mM Na as sodium sulfate, the other lot was maintained without any additional Na. Nitrogen was supplied as a combination of 4 mM nitrate and 2 mM ammonium. The composition of the basal nutrient solution was, in mM: 4 $\text{Ca}(\text{NO}_3)_2$; 2 MgSO_4 ; 1.33 $(\text{NH}_4)_2\text{HPO}_4$; 0.1 NaCl; 0.1 Fe-EDTA; in μM : 10 MnSO_4 ; 1 CuSO_4 ; 1 ZnSO_4 ; 33 H_3BO_3 ; 0.2 Na_2MoO_4 ; 0.1 CoSO_4 and 0.1 NiSO_4 . Plants were maintained under glasshouse conditions for 123 days. Each pot was supplied 500 ml of nutrient solution

daily around 10 AM. The effect of supplying Na to K-deficient plants was examined in comparable leaves (4 to 5 from the top) of 57-day-old plants.

Potassium and Na were determined by flame photometry after digesting the oven-dried material in a mixture of 10 nitric acid : 1 perchloric acid (Piper, 1942). Proline was measured calorimetrically as ninhydrin complex in toluene by the method of Bates et al. (1973). Leaf water potential and RWC were measured about 10 AM, when the sand in the pots was saturated with nutrient solution. Leaf water potential was determined by Sharda-kov technique (Kozłowski, 1964). Leaf disks were immersed in small volumes of test solutions of various concentrations of sucrose lightly colored with methylene blue. After exposure, drops of the colored solutions were transferred with a micropipette to colorless solutions of the same initial concentration of sucrose and the movement of the colored drop

in the solution was observed. The test solution in which the colored drop became stationary corresponded to the water potential of the leaf disks. Relative water content (RWC) was measured according to Barrs and Weatherly (1962). The 30 leaf disks 7.5 mm in diameter used for RWC measurements were also used for determining specific leaf weight. Dry weight was determined after drying the tissue disks at 105°C for 24 hr. Diffusive resistance and rate of transpiration were measured in intact leaves using a LI-COR model LI-1600 (LI-COR, Lincoln, Neb.) steady-state porometer about 10 AM under glasshouse conditions [24°C, 57% RH, and light intensity (PAR) ranging from 400 to 700 $\mu\text{mol}\cdot\text{s}^{-1}\cdot\text{m}^{-2}$]. Stomatal density and stomatal width were measured microscopically using microrelief impression of leaf surfaces (Sharma et al., 1982). Transpiration and diffusive resistance were measured on nine replicates. All other measurements were made on three replicates. The results have been tested for significance using Duncan's multiple range test.

Low supply of K retarded the growth of cauliflower. Leaves of the low-K plants developed mild chlorosis and their lamina appeared undulated. The severity of the visible symptoms was lessened by additional supply of Na. Compared to plants grown at 4 mM K, plants grown at 0.2 mM K contained less total dry matter (Table 1). Additional Na partially (not significantly) ameliorated the K-deficiency effect on dry matter. Leaf tissue concentrations of K in low-K plants were significantly less than in normal-K plants. Additional supply of Na to low-K plants did not make any significant change in the leaf tissue concentration of K. Deficiency of K caused a significant increase in Na concentration (Table 1). The effect became still more marked when the K-deficient plants were supplied Na to the extent K was omitted from the nutrient medium.

Potassium affected stomatal opening (Table 1). A large proportion of the stomata in leaves of K-deficient plants remained closed

Table 1. Effect of supplying Na to low-K plants on dry matter, tissue concentration of K and Na, stomatal aperture and stomatal density in leaves of cauliflower.*

K and Na supply (mM)	Dry matter (g/plant)	K (mmol·g ⁻¹ dry wt)	Na (mmol·g ⁻¹ dry wt)	Stomatal aperture (μm)	Stomatal density (number/cm ²)	
					Abaxial surface	Adaxial surface
4.00 K ⁺	0.658 a	1.06 a	0.17 c	5.56 a	4.27 a	2.07 a
0.20 K ⁺	0.524 b	0.16 b	0.56 b	2.16 c	2.55 c	1.45 b
0.20 K ⁺ + 3.80 Na ⁺	0.581 b	0.17 b	1.25 a	4.23 b	3.00 b	2.07 a

*Mean separation within columns by Duncan's multiple range test, $P = 0.05$. Data are means of three replicates.

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Table 2. Effect of supplying Na to low-K plants on transpiration, diffusive resistance, specific leaf weight, RWC, and free proline in leaves of cauliflower.*

K and Na supply	Transpiration ^y (g·s ⁻¹ ·cm ⁻²)	Diffusive ^y resistance (s·cm ⁻¹)	Specific leaf wt ^x (g·cm ⁻²)	RWC ^x (%)	ψ ^x (kPa)	Proline ^x (μmol/100 g fresh wt)
4.00 K ⁺	5.30 b	2.72 b	0.074 c	91.71 a	-267 b	92 b
0.20 K ⁺	4.13 c	4.02 a	0.090 a	88.21 b	-308 a	163 a
0.20 K ⁺ + 3.80 Na ⁺	7.55 a	2.14 b	0.081 b	92.14 a	-107 c	153 a

*Mean separation within columns by Duncan's multiple range test, $P = 0.05$.

^yData are means of nine replicates.

^xData are means of three replicates.

at all times of the day. In the few stomata that were open, the width of aperture was less than half that in control plants. Supplying Na to low-K plants caused a significant increase in stomatal opening, but stomatal aperture of plants supplied additional Na still remained significantly less than in normal plants.

Potassium deficiency caused a significant decrease in stomatal density on both leaf surfaces (Table 1). Supplying Na to K-deficient plants ameliorated this effect. There was no significant difference in the stomatal density on the adaxial surface of leaves of plants supplied additional Na or the corresponding surface of normal plants, but stomatal density on the abaxial surface of leaves of plants supplied additional Na still remained significantly lower than the corresponding surface of normal plants.

Deficiency of K significantly decreased the rate of transpiration (Table 2). When K-deficient plants were supplied Na to the extent K was deficient, the transpiration rate showed an increase that was not only significantly higher than of leaves of K-deficient plants but also higher than leaves of normal plants. The leaves of low-K plants had significantly higher diffusive resistance and specific leaf weight and lower RWC and ψ than in control plants (Table 2). Potassium-deficient leaves also accumulated significantly more proline than leaves of K-sufficient plants and the supply of Na did not make any significant difference in its accumulation (Table 2). Supplying Na to K-deficient plants reduced

all these effects. There was no significant difference in RWC and diffusive resistance between low-K plants supplied Na and normal K plants.

The ψ of the plants supplemented with Na became significantly less negative than control plants, but specific leaf weight of low-K plants supplied Na still remained significantly higher than specific leaf weight of normal plants.

Observed changes in stomatal aperture, RWC, transpiration, diffusive resistance, and proline accumulation in cauliflower plants subjected to K deficiency are in accord with our earlier observations (Sharma et al., 1985; Singh and Sharma, 1988b). High specific leaf weight, low RWC, low ψ , and increased accumulation of proline in leaves of cauliflower plants supplied low K indicate a state of water stress that seems to result from poor absorption or restricted transport of water, thus leading to increased stomatal resistance and decreased transpiration. Changes in RWC, ψ , transpiration, and stomatal resistance by supplying Na in place of K suggest a beneficial effect of Na in overcoming K deficiency on water balance of cauliflower. In fact, the Na effect on transpiration seems to be more marked than the K effect. Beneficial response to Na is known to occur in salt-tolerant species, such as sugarbeet, where Na replaces K and contributes to the solute potential and consequent generation of turgor (Marschner and Possingham, 1975), thus affecting growth and water balance of the plants (Durrant et al., 1978; Lawlor and Mil-

ford, 1973; Milford et al., 1977). In any case, Na effectively compensates for K deficiency.

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