

# Effects of Potassium Deficiency on the Photosynthesis and Respiration of Leaves of Sugar Beet under Conditions of Low Sodium Supply<sup>1</sup>

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## ABSTRACT

Sugar beet plants (*Beta vulgaris* L. cv. F58-554H1) were germinated and cultured under standardized environmental conditions. The effects of K deficiency on photosynthetic and respiratory CO<sub>2</sub> exchange rates of attached leaves were studied under conditions of low Na supply by withholding both Na and K from the culture medium at cut-off (28 days after planting). Potassium and Na concentrations in the leaf blade and petiole decreased rapidly during the 8 days after cut-off, then more slowly.

Photosynthetic CO<sub>2</sub> uptake per unit leaf area decreased rapidly with time after cut-off to 23% of the control rate in 17 days. Mesophyll resistance to CO<sub>2</sub> ( $r_m$ ) increased sharply after cut-off,  $r_m$  eventually attaining 8.3 sec cm<sup>-1</sup>. Leaf (mainly stomatal) diffusion resistance,  $r_l'$ , also increased rapidly from 4 days after cut-off, reaching 1.9 sec cm<sup>-1</sup> 13 days later. The photorespiratory evolution of CO<sub>2</sub> into CO<sub>2</sub>-free air decreased progressively after cut-off, but the rate of dark respiratory CO<sub>2</sub> evolution increased. It was concluded that withholding Na as well as K at cut-off increased the deleterious effects of K deficiency on photosynthesis and stomatal opening.

In an earlier paper (10), we explored the effects of potassium deficiency on the photosynthetic and respiratory CO<sub>2</sub> exchange rates of attached sugar beet leaves. Sodium was found to be taken up by the plant in response to K deficiency, and it was suggested that Na may have substituted for K in stomatal opening, either directly, as an alternative cation to K, or indirectly by conserving K supply. The addition of Na to the culture medium in that study (10) may also have lessened the effects of K deficiency on other aspects of photosynthetic or respiratory CO<sub>2</sub> exchange. To explore this possibility we have studied the effects of K deficiency in the absence of added Na by withholding both Na and K from the culture medium at cut-off. We found that low Na did increase the K deficiency damage to the photosynthetic but not the respiratory systems of sugar beet leaves, and we have attempted to ascertain which physiological roles may be mediated by K or Na or both.

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## MATERIALS AND METHODS

Details of the procedures followed in the culture of plants, in the determination of gas exchange parameters of individual attached leaves, and in the estimation of the contents of leaf mineral elements, are as outlined in an earlier paper on the effects of K deficiency in the presence of added Na (10). K and Na were withheld from the culture medium at the 10-leaf stage, 28 days after planting. The composition of the culture

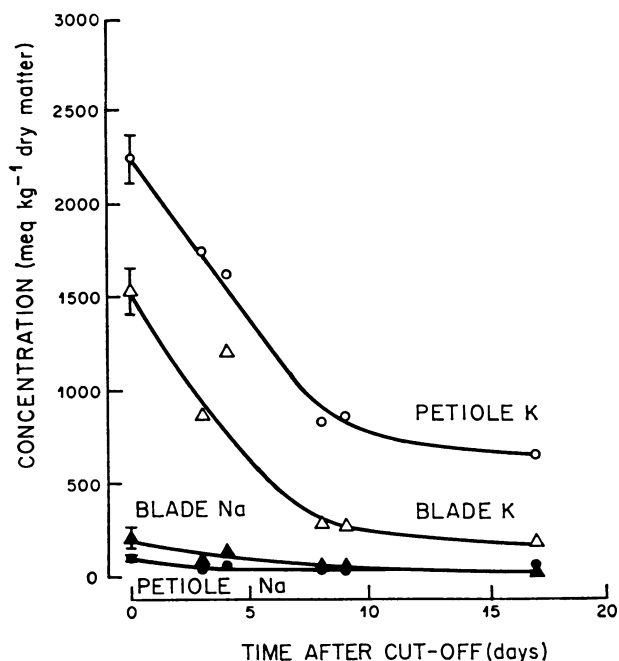


FIG. 1. Effects of withholding K and Na from the culture solution on the concentrations of K and Na in the leaf blade and petiole with time after cut-off. Vertical lines through points represent twice the standard errors.

solution used from K-Na cut-off to the termination of the experiment (45 days from planting) expressed in millimoles per liter was: 3.75 Ca(NO<sub>3</sub>)<sub>2</sub>·4 H<sub>2</sub>O, 0.5 H<sub>3</sub>PO<sub>4</sub>, 1.0 MgSO<sub>4</sub>·7 H<sub>2</sub>O, 0.25 CaCl<sub>2</sub>·2 H<sub>2</sub>O; and in mg l<sup>-1</sup>: 0.25 B, 0.25 Mn, 0.025 Zn, 0.01 Cu, 0.005 Mo, and 2.5 Fe supplied as ferric-sodium ethylenediaminetetraacetate complex.

## RESULTS

The effect of withholding K and Na from the culture solution was to decrease the concentrations of both of these ele-

ments in the leaf (Fig. 1). The concentrations of K in the blade and in the petiole decreased rapidly by about  $1200 \text{ meq kg}^{-1}$  or more during the first 8 days after cut-off; subsequently K concentrations diminished very slowly with time. Na concentration decreased from  $200 \text{ meq kg}^{-1}$  in the blade and  $110 \text{ meq kg}^{-1}$  in the petiole to about  $30 \text{ meq kg}^{-1}$  in both instances during the first 8 days and remained at that level for the duration of the experiment. The withholding of Na, as well as K after cut-off, resulted in increases in the concentration of other cations, e.g., blade Ca increased from 400 to  $1000 \text{ meq kg}^{-1}$  and blade Mg from 400 to  $600 \text{ meq kg}^{-1}$ , which may have helped to offset the decrease in cation concentration due to the drop in K and Na concentrations. The concentrations of Fe, Mn, Cu, and Zn in the leaf blade did not change significantly after K cut-off.

Rates of photosynthetic  $\text{CO}_2$  uptake, F and  $F^*$ , of individual attached leaves were determined at saturating irradiance ( $50 \text{ mw visible radiation cm}^{-2}$ ),  $25 \text{ C}$ , and at an ambient  $\text{CO}_2$  concentration of  $300 \text{ ng CO}_2 \text{ cm}^{-3}$  air.  $F^*$ , the  $\text{CO}_2$  exchange rate

in oxygen-free air, and F, the rate in normal air ( $21\% \text{ O}_2$ ), decreased rapidly after K and Na were withheld from the culture solution, eventually attaining 23% of the control rate 17 days after cut-off (Fig. 2A). Initially, the decreases in  $F^*$  and F are attributable to increased mesophyll resistance to  $\text{CO}_2$ ,  $r_m^*$ , the mesophyll resistance in  $\text{O}_2$ -free air, and  $r_m$ , the mesophyll resistance in normal air containing  $21\% \text{ O}_2$ , increased during the first 4 days after cut-off to 1.8 and  $3.2 \text{ sec cm}^{-1}$  (Fig. 2D), respectively, while leaf diffusion resistance,  $r_1'$ , (mainly the resistance due to stomata) remained unchanged (Fig. 2C). Subsequently, however,  $r_1'$  increased rapidly so that the decreases in  $F^*$  and F after the first 4 days are attributable to both increased stomatal diffusion resistance and to increased mesophyll resistance.

The rate of respiratory evolution of  $\text{CO}_2$  into  $\text{CO}_2$ -free air in the light,  $R_L$ , was determined by extrapolation of the linear relation between F and  $C_w$ , the concentration of  $\text{CO}_2$  at the surfaces of the mesophyll cell walls, i.e.,  $R_L = F$  when  $C_w = 0$ .

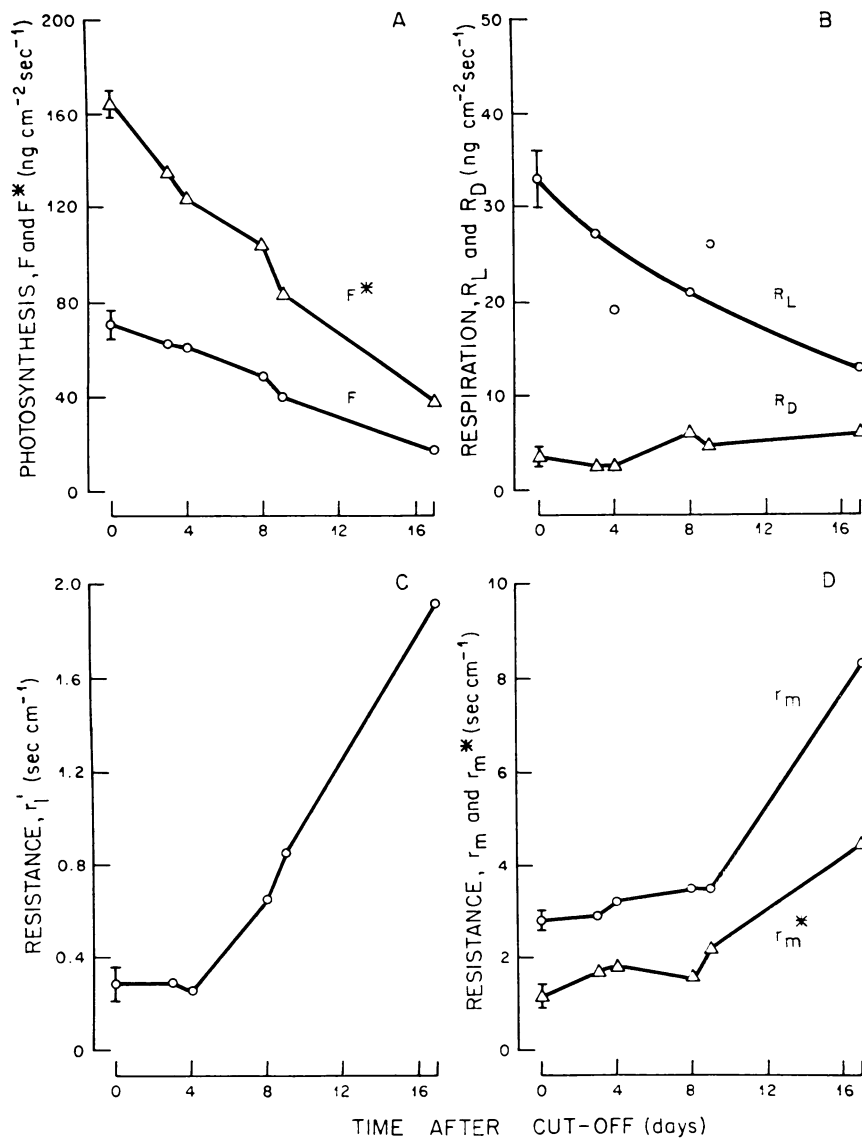


FIG. 2. Effects of withholding K and Na on various leaf gas exchange parameters with time after cut-off. The data were determined at saturating irradiance,  $25 \text{ C}$ , and at an ambient  $\text{CO}_2$  concentration of  $300 \text{ ng cm}^{-3}$  air. A: Changes in rate of photosynthetic  $\text{CO}_2$  uptake in  $\text{O}_2$ -free air,  $F^*$  ( $\Delta$ ), and in normal air ( $21\% \text{ O}_2$ ), F ( $\circ$ ); B: changes in rates of respiratory  $\text{CO}_2$  evolution in the light,  $R_L$  ( $\circ$ ), and dark,  $R_D$  ( $\Delta$ ); C: changes in leaf diffusion resistance for water vapor,  $r_1'$ ; D: changes in  $\text{CO}_2$  mesophyll resistance in  $\text{O}_2$ -free air,  $r_m^*$  ( $\Delta$ ), and in normal air,  $r_m$  ( $\circ$ ). Vertical lines through points represent twice the standard errors.

Values of  $R_L$  fluctuated somewhat with time but we believe that the effect of K-Na cut-off was to progressively decrease  $R_L$  in the manner suggested by the curve shown in Fig. 2B. Respiratory evolution in the dark,  $R_D$ , however, increased slightly with time after K cut-off (Fig. 2B).

### DISCUSSION

The effect of withholding K and Na from the culture medium was to decrease immediately the concentrations of these elements in the leaf blade and petiole; this rapid decrease was maintained for about 1 week and then slowed considerably. The experiment was terminated before any visible effects of K-Na deficiency on the sample leaves became apparent, although there were visible symptoms on the older leaves. In the earlier experiment on K deficiency in which Na was supplied (10), low K plants absorbed Na<sup>+</sup> as a substitute cation for K<sup>+</sup> and as a result did not take up other metallic cations in appreciable quantities. When Na was not supplied, as in the present work, low K leaves acquired higher concentrations of Ca<sup>2+</sup> and Mg<sup>2+</sup> than did the control leaves. Tullin (13) similarly found that decreased Na supply increased Ca<sup>2+</sup> uptake by beets.

Rates of photosynthetic CO<sub>2</sub> uptake,  $F^*$  and  $F$ , decreased more rapidly when Na was withheld along with K; low K-low Na leaves attained one-third of the control rates in only 14 days, whereas the low K-high Na leaves (10) did not drop to such low rates until 21 days had elapsed. Withholding Na as well as K caused a more rapid increase in the mesophyll resistance to CO<sub>2</sub>;  $r_m^*$  and  $r_m$  for low K-low Na leaves each increased almost 2-fold over a comparable period compared to the values of  $r_m^*$  and  $r_m$  for the low K-high Na leaves (10). The additional increase in mesophyll resistance upon withholding Na may have been due to a diminished supply of a common pool of Na and K ions, with each ion being able to substitute at least partly for the other. However, an alternative explanation is that Na may have had a unique role, independent of K, either in the transfer of CO<sub>2</sub> from the mesophyll cell walls to the chloroplast or in carboxylation itself. There is indirect evidence of a unique role for Na from growth studies which show that Na addition increased yields even when K was in ample supply and when the plant K status was high (1-3, 6, 12), *i.e.* in situations when K was presumed not to be limiting growth. Much of the leaf Na is probably concentrated in the chloroplast (9), so that Na may well have been involved in photosynthesis, especially since the sucrose synthesis of flax leaves has been shown to be increased on the addition of Na (8).

The other main effect of withholding Na, as well as K on photosynthetic CO<sub>2</sub> uptake, was to increase leaf (mainly stomatal) diffusion resistance,  $r_1'$ , sooner and more rapidly than when Na was supplied to low K leaves (10). It was suggested (10) that if stomata do require monovalent cations in osmotic amounts for opening as proposed (4, 5, 7, 11), Na may have acted as an alternative cation to K, especially since Na was

found to be taken up by leaves in amounts roughly equivalent to the decrease in leaf K. Further support for this hypothesis comes from the observation that when Na was supplied (10), the leaf blade K concentration dropped from 1500 to 200 meq kg<sup>-1</sup> before stomatal opening was affected, while in the present work, when Na was not supplied, stomata began to close rapidly when the K concentration was still a relatively high 750 meq kg<sup>-1</sup>; this suggests that when Na was not available as an alternative cation to K, the stomata were affected more rapidly by the decrease in K supply.

The effect of withholding K and Na on the respiratory evolution of CO<sub>2</sub> in the light,  $R_L$ , and in the dark,  $R_D$ , paralleled the results of the earlier investigation in that, after K cut-off,  $R_D$  increased and  $R_L$  diminished progressively. Decreasing the supply of Na to the leaf may have increased the effect of low K on  $R_L$  to a small extent, but not on  $R_D$ .

In conclusion, we found that the detrimental effects of K deficiency on photosynthetic CO<sub>2</sub> exchange were considerably increased when Na was not supplied in the culture medium. It is suggested that Na may be able to substitute at least partly for the apparent K requirement in stomatal opening. It is not clear, however, whether Na substitutes for K in some unidentified role in photosynthetic CO<sub>2</sub> uptake within the mesophyll or whether Na has a unique function in this respect independent of K.

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### LITERATURE CITED

- ADAMS, S. N. 1961. The effect of sodium and potassium fertilizer on the mineral composition of sugar beet. *J. Agr. Sci.* 56: 383-388.
- EL-SHEIKH, A. M., A. ULRICH, AND T. C. BROYER. 1967. Sodium and rubidium as possible nutrients for sugar beet plants. *Plant Physiol.* 42: 1202-1208.
- EL-SHEIKH, A. M. AND A. ULRICH. 1970. Interactions of rubidium, sodium, and potassium on the nutrition of sugar beet plants. *Plant Physiol.* 46: 645-649.
- FISCHER, R. A. 1971. Role of potassium in stomatal opening in the leaf of *Vicia faba*. *Plant Physiol.* 47: 555-558.
- FUJINO, M. 1967. Role of adenosine triphosphate and adenosine triphosphatase in stomatal movement. *Sci. Bull. Fac. Educ. Nagasaki Univ.* 18: 1-47.
- HARMER, P. M., E. J. BENNE, W. M. LAUGHLIN, AND C. KEY. 1953. Factors affecting crop response to Na applied as common salt on Michigan muck soil. *Soil Sci.* 76: 1-17.
- HUMBLE, G. D. AND T. C. HSIAO. 1970. Light-dependent influx and efflux of potassium of guard cells during stomatal opening and closing. *Plant Physiol.* 46: 483-487.
- MOSCOLOV, J. V. AND V. A. ALEKSANDROVSKAYA. 1962. Physiological role of sodium in plants. *Chem. Abstr.* 56(2): 1784h.
- STOCKING, C. R. AND A. ONGUN. 1962. The intracellular distribution of some metallic elements in leaves. *Amer. J. Bot.* 49: 284-289.
- TERRY, N. AND A. ULRICH. 1973. Effects of potassium deficiency on the photosynthesis and respiration of leaves of sugar beet. *Plant Physiol.* 51: 43-47.
- THOMAS, D. A. 1970. The regulation of stomatal aperture in tobacco leaf epidermal strips. I. The effect of ions. *Aust. J. Biol. Sci.* 23: 961-979.
- TRUOG, E., K. C. BERGER, AND O. J. ATTOE. 1953. Response of nine economic plants to fertilization with Na. *Soil Sci.* 76: 41-50.
- TULLIN, V. 1954. Response of sugar beet to common salt. *Physiol. Plant.* 7: 810-834.