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Effects of Potassium Deficiency on the Photosynthesis and Respiration of Leaves of Sugar Beet[1]

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ABSTRACT

Sugar beet plants (*Beta vulgaris* L. var. F5855441) were germinated and cultured under standardized environmental conditions for 28 days. Potassium deficiency was then induced by withholding K from the culture solution. Changes in CO_2 and water vapor exchange rates and surface temperatures of individual attached leaves were measured with time after K cut-off, along with changes in the concentrations of the leaf minerals K, Na, Ca, Mg, Fe, Mn, Cu, and Zn. During the 1st week after K cut-off the concentration of Na in the leaf blade increased from 200 to 1000 milliequivalents per kilogram dry matter while K decreased from 1500 to 300 milliequivalents per kilogram. During the subsequent 2 weeks, both Na and K concentrations decreased. The concentrations of other leaf minerals, except Mn, were little affected by K cut-off. Photosynthetic CO_2 uptake per unit area decreased linearly with time after cut-off and attained one-third of the control rate after 21 days. Low K apparently decreased photosynthesis through an increase in mesophyll resistance to CO_2 (r_m) from 2.8 to 5.3 seconds per centimeter in 21 days. Leaf (mainly stomatal) diffusion resistance (r'_1) increased only slowly during the first 15 days from 0.3 to 0.5 second per centimeter, eventually reaching 1.6 seconds per centimeter at 21 days. Low K progressively decreased the photorespiratory evolution of CO_2 into CO_2-free air, but steadily increased the rate of CO_2 evolution in dark.

Potassium has been implicated functionally in numerous roles within the plant (7, 17, 25, 26), and effects of its deficiency are manifested in many ways (4, 12, 13, 24, 25). Rates of photosynthetic CO_2 uptake have been shown to be diminished by K deficiency (2, 4, 12, 20, 23). Peaslee and Moss (21) examined the effects of low K on the gas diffusion resistances of leaves and concluded that low K primarily affected photosynthetic CO_2 uptake by increasing stomatal diffusion resistance, although mesophyll resistance to CO_2 also increased. Respiration rates have been shown to increase with K deficiency in some instances (2, 11, 12) and to decrease in others (18, 23). The present investigation seeks to determine how K deficiency affects photosynthetic and respiratory activity of sugar beets grown in controlled environments under standardized conditions, paying particular attention to the effects of low K in the presence of Na on the diffusion resistances of leaves.

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MATERIALS AND METHODS

Details of the procedures and materials used in this study of potassium deficiency on leaf gas exchange are essentially the same as those given for phosphorus deficiency in a previous paper (28). Only the main features of the present work and the differences from the phosphorus study are presented below.

Plant Culture. Sugar beet plants (*Beta vulgaris* L. var. F5855441) were cultured in growth chambers at 25 C and irradiated at 15.6 mw visible radiation per cm^2. The composition of the culture solution supplied to the control plants expressed in millimoles per liter was: 2.5 $Ca(NO_3)_2 \cdot 4\ H_2O$, 0.5 KH_2PO_4, 2.5 KNO_3, 1.0 $MgSO_4 \cdot 7\ H_2O$, 0.5 NaCl; and in milligrams per liter: 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. The culture solution for the K-deficient plants contained (in millimoles per liter) 3.75 $Ca(NO_3)_2 \cdot 4\ H_2O$ and 0.5 $NaH_2PO_4 \cdot H_2O$ in place of the 2.5 $Ca(NO_3)_2 \cdot 4\ H_2O$, 0.5 KH_2PO_4, and 2.5 KNO_3, of the control culture solution.

The seeds were planted on day 0, and the germinated seedlings were transplanted at the two-leaf stage on day 14. Potassium deficiency was induced on day 28 (cut-off) by rinsing the plant roots with distilled water and transferring the plants individually to pots containing the K-deficient culture solution. Comparable plants serving as controls were transferred to solutions containing K. Culture solutions were replenished by the addition of stock solutions on day 35 and were replaced on day 42. The experiment terminated on day 49.

Determination of Gas Exchange Parameters. The main parameters of leaf gas exchange considered below are: (*a*) the net rates of CO_2 exchange in oxygen-free air, F^*, and in normal air, *i.e.*, containing about 21% oxygen, F; (*b*) the rate of respiratory CO_2 evolution in the dark, R_D; (*c*) the rate of respiratory evolution of CO_2 in the light into CO_2-free air, R_L, determined by extrapolation of the linear relation between F and C_w, the concentration of CO_2 at the surfaces of the mesophyll cell walls, *i.e.*, $R_L = F$ when $C_w = 0$; (*d*) the resistance to the diffusion of water vapor from the surfaces of the mesophyll cell walls to the external leaf surface, r_1'; (*e*) the resistances to CO_2 movement from the surfaces of the mesophyll cell walls to the intracellular site of photosynthesis determined in normal air, r_m, and in oxygen-free air, r_m^*. These parameters were obtained from measurements of CO_2 and water vapor exchange and surface leaf temperature of attached leaves mounted in a leaf chamber in an open flow gas circuit (for details of the apparatus see Terry *et al.* [29] and for the procedure followed

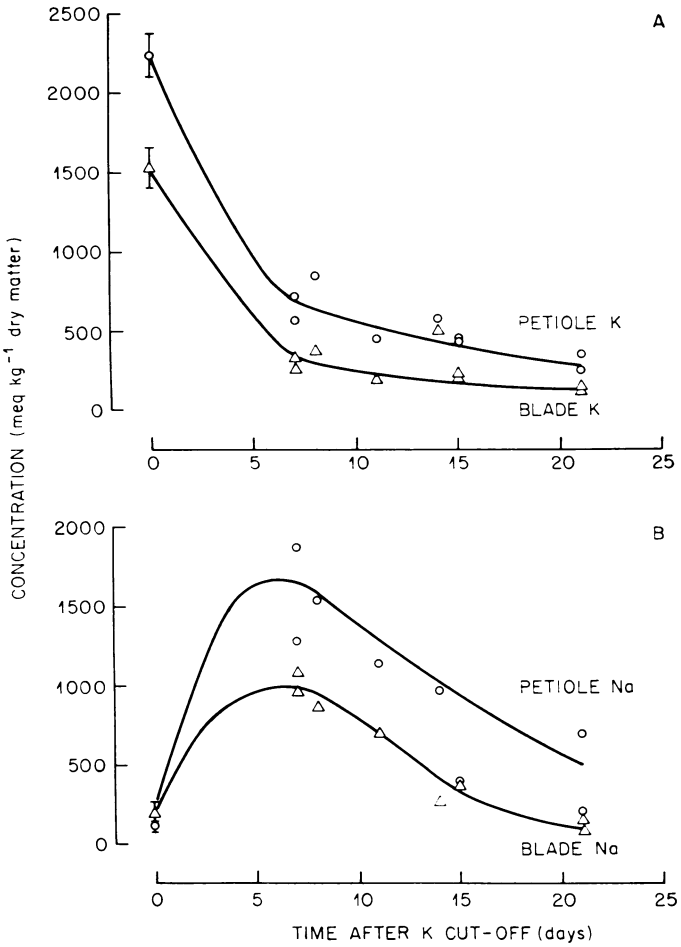

FIG. 1. Effects of withholding K from the culture solution on the concentrations of K (A) and Na (B) in the leaf blade (△) and petiole (○) with time after cut-off. Vertical lines through points represent twice the standard errors.

in deriving the gas exchange parameters see Terry and Ulrich [28]).

Estimation of Leaf Minerals. The concentrations of each of the cations, K, Na, Ca, Mg, Fe, Mn, Cu, and Zn, were obtained by wet oxidation of dried leaf tissue with nitric and perchloric acids by an adaptation of the method of Johnson and Ulrich (16). The digest was diluted to 0.1 N perchloric acid, and the concentrations of Cu, Fe, Mn, and Zn were determined by atomic absorption spectrophotometry. An aliquot was diluted with $SrCl_2$ in perchloric acid so that the solution used for the spectrophotometric determination of K, Na, Ca, and Mg contained Sr at a concentration of 500 mg liter^{-1} (1, 6).

RESULTS

Potassium concentrations in the leaf blade and petiole decreased rapidly with time after K cut-off, from 1500 to 300 meq kg^{-1} in the blade and from 2250 to 750 meq kg^{-1} in the petiole, in the 1st week (Fig. 1A). During the same period Na concentrations increased from 200 to about 1000 meq kg^{-1} in the blade and from 100 to about 1700 meq kg^{-1} in the petiole (Fig. 1B), strongly suggesting that Na was taken up by the plant as an alternative cation to K. After the 1st week K concentrations decreased slowly in the petioles and very slowly in the blades. There were no obvious visible symptoms of K deficiency on the low K blades. Sodium concentrations also decreased in the blades and in the petioles after the 1st week. The concentrations of several other cations (Fig. 2) changed much less with time; Ca and Mg increased to a small extent, but Fe, Cu, and Zn changed very little. Manganese, however, decreased from 7 to about 2 meq kg^{-1} over the 3 weeks from K cut-off.

The effects of K deficiency on leaf gas exchange are shown in Figure 3. Rates of photosynthetic CO_2 uptake in normal and O_2-free air, F and F^*, respectively, decreased rapidly with time after K cut-off, so that by 21 days they were about one-third of the control rate (Fig. 3A). Most of the decrease in photosynthetic rates was attributable to an increase in mesophyll resistance, r_m (Fig. 3D); leaf diffusion resistance r_1', which was mainly attributable to the resistance to diffusion through the stomata, increased only slowly during the first 15 days, and, although it increased sharply thereafter, it still only accounted for 31% of the total diffusion resistance to CO_2 at the end of 21 days (Fig. 3C). Since K concentrations in the leaf blade decreased over the 2-week period from 1500 to 200 meq kg^{-1}, before r_1' was appreciably increased, stomatal opening was initially very little affected by a large drop in leaf K. Mesophyll resistance, r_m, however, increased progressively from the 1st week, r_m and r_m^* increasing by factors of 2 and 2.5, respectively.

The changes in F^*, F, and r_1', with increase in irradiance, were followed for a leaf of a plant cultured for 10 days with-

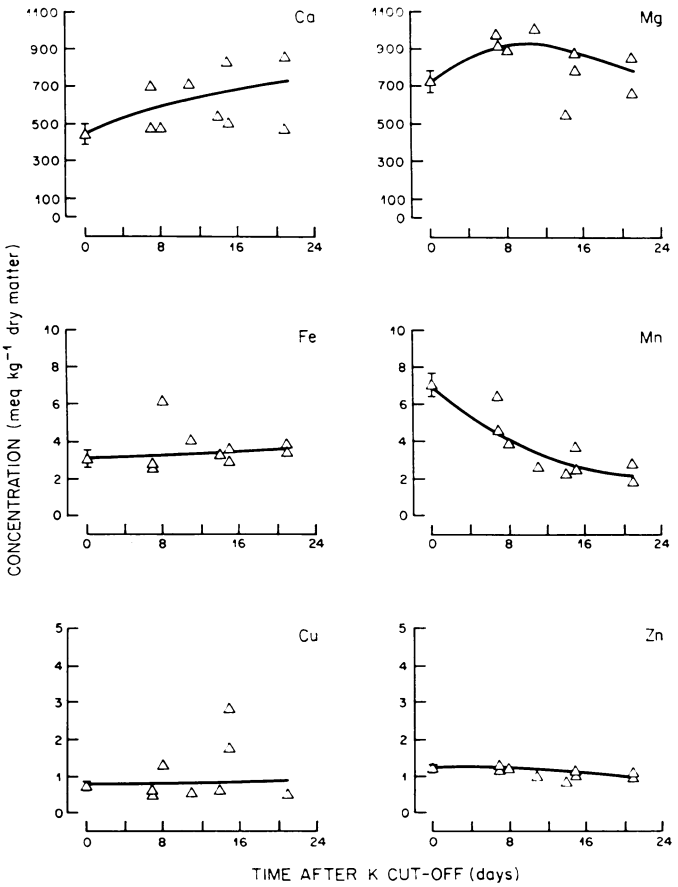

FIG. 2. Effects of K deficiency on the concentrations of various cations in the leaf blade with time after cut-off. (For convenience the concentrations of Fe, Cu, and Mn are expressed in terms of the element in its divalent form.) Vertical lines through points represent twice the standard errors.

out K addition. At light saturation, 25 C, and with an ambient CO_2 concentration of 500 ng cm^{-2}, the maximal rates of F^* and F for the K-deficient plant were 166 and 105 ng CO_2 cm^{-2} sec^{-1}, respectively, compared to 190 and 125 ng CO_2 cm^{-2} sec^{-1} for F^* and F obtained with leaves of control plants. Leaf diffusion resistance, r_1', was greater in the K-deficient plant than in the control plants but followed the same relationship to irradiance as in K-sufficient leaves. With an increase in visible radiation from 2 to 35 mw cm^{-2}, r_1' decreased from 1.8 to 0.6 sec cm^{-1} in the K-deficient leaf compared to 1.3 to 0.3 sec cm^{-1} in control leaves.

Potassium deficiency increased respiratory evolution of CO_2 in the dark, R_D, with time after cut-off (Fig. 3B). Respiratory CO_2 evolution into CO_2-free air in the light, R_L, however, decreased significantly with time to about one-half of the rates of control leaves in the 21-day period (Fig. 3B).

DISCUSSION

The effect of withholding K from the culture solution was to diminish rapidly the K concentration of the blade tissue and the rate of photosynthetic CO_2 uptake per unit area of leaf. No visible effects of K deficiency were apparent. The effects of low K on photosynthesis were apparently more severe than those of low P (24) in that the rates of CO_2 uptake were reduced to one-third in only 21 days after K cut-off, whereas a similar reduction in rate was attained 30 days after P cut-off. The initial effect of low leaf K on photosynthesis was to increase the mesophyll resistance to CO_2, r_m, and not stomatal diffusion resistance, which increased only slowly for the first 15 days.

There are a variety of ways that low K may have increased mesophyll resistance. Low K has been shown to diminish Hill reaction activity (27), and to diminish the rate of production of ATP and reduced NADP in beet chloroplasts (31) so that low K may have increased the carboxylation resistance through an effect on the photochemical reactions of photosynthesis. Lack of K also causes chlorosis (22), and, although chlorosis was not observed in the present experiments, low K may nevertheless have resulted in diminished amounts of chlorophyll.

Several investigators (8, 9, 15, 30) have suggested that stomata may open as a result of the uptake of ions, particularly K^+, into the guard cells. If this were so, then one might expect stomatal opening to be impeded in low K leaves. However, in the present experiments it appeared that not until the leaf K content had decreased to below 200 meq kg^{-1} (roughly 1% dry matter) did there appear to be any appreciable increase in leaf (mainly stomatal) diffusion resistance, r_1'. Desai (5) also found little effect of low K on stomatal aperture unless K deficiency was severe enough for visible damage. Also, there was no large increase in stomatal resistance at limiting light levels in low K leaves such as we found in low P leaves (28); r_1' attained values of 9 sec cm^{-1} at 2 mw visible radiation cm^{-2} in low P leaves compared to only 1.8 sec cm^{-1} with low K leaves, so that low K appeared to affect stomata much less than did low P. Assuming that stomata do require univalent cations in osmotic amounts for opening, this suggests that in the sugar beet K may not be specifically required for stomatal opening as proposed (14).

Sodium was absorbed in amounts roughly equivalent to the decrease in leaf K after K cut-off. During the 1st week the Na concentration increased 5-fold in the blade and 7-fold in the petiole. None of the other six cations determined increased in concentration to such a marked extent. Thus Na could have been present in sufficient amounts to have acted as an alternative cation to K for stomatal opening. Addition of Na has been

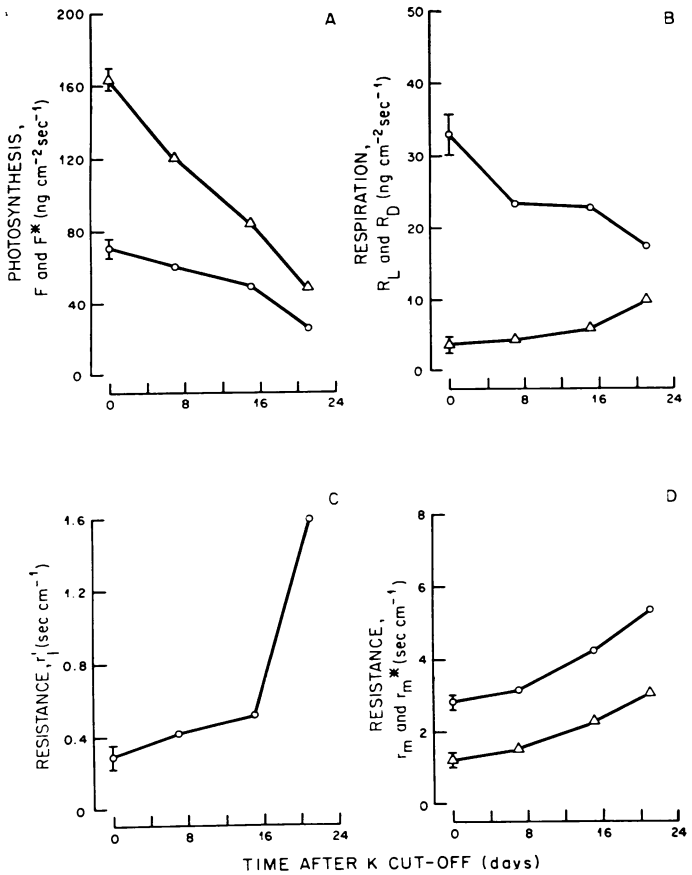

FIG. 3. Effects of K deficiency on various leaf gas exchange parameters with time after cut-off. The data were determined at saturating irradiance, 25 C, and at an ambient CO_2 concentration of 300 ng cm^{-3} air. A: Changes in rate of photosynthetic CO_2 uptake in O_2-free air, F^* (△), and in normal air (21% O_2), F (○); B: changes in rates of respiratory CO_2 evolution in the light, R_L (○), and dark, R_D (△); C: changes in leaf diffusion resistance for water vapor, r_1'; D: changes in CO_2 mesophyll resistance in O_2-free air, r^*_m (△), and in normal air, r_m (○). Vertical lines through points represent twice the standard errors.

shown to effect changes in stomatal aperture (3, 32) and may have substituted for K directly as the cation taken up by the guard cells. It could also have acted by conserving the supply of leaf K: the addition of Na to K-limited plants might have caused K^+ ions to move from the vascular tissue into the mesophyll cells through a cation exchange mechanism, thus releasing K^+ ions for specific functions such as stomatal opening.

The increase in stomatal diffusion resistance in the 3rd week may have occurred through any one of several mechanisms: for example, low K is known to diminish leaf water content and water potential (10, 18), which may in turn increase stomatal resistance. Also, if we assume that Na or K ions are required to effect stomatal opening, then these ions may not have been present in the later stages of K deficiency to bring about normal stomatal opening, since by 21 days both Na and K concentrations in the leaf blade had declined to the low level of 100 to 150 meq kg^{-1}. Finally, since the energy for light-activated stomatal opening may come from photophosphorylation (15, 19), which is diminished by low K (31), stomatal opening may have been affected by K deficiency directly through the energy supply.

Low K increasingly depressed the rate of CO_2 evolution into CO_2-free air in the light but steadily increased the rate of CO_2

evolution in the dark. Other workers have found that K deficiency initially increased respiration in the dark but ultimately, with increasing severity of K deficiency, respiration rates decreased (18, 23). Okamoto (18) found that low K increased the activity of the tricarboxylic acid cycle and of mitochondrial respiration, and he suggested that respiration of low K leaves may be uncoupled from oxidative phosphorylation. It is also possible that low K increased dark respiration by increasing the amount of available substrate since carbohydrate concentrations in the leaf blades increase under K deficiency conditions (7). Correspondingly, low rates of respiratory CO_2 evolution in the light with low K may have been due to depressed levels of substrates, since the rate of production of photorespiratory substrates such as glycolate is probably dependent on the rate of photosynthetic CO_2 fixation.

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