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Effect of Potassium Deficiency upon Translocation of ^{14}C in Detached Blades of Sugarcane[1]

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ABSTRACT

The translocation of radioactive photosynthate was studied in blades detached from plants which had been grown in nutrient solution with and without potassium. Basipetal translocation decreased in the blades of plants deprived of potassium, even when deficiency symptoms were not visible. In such slightly potassium-deficient leaves, translocation was decreased in the light but not in the dark. More severe potassium deficiency decreased translocation both in darkness and in light. Potassium deficiency decreased translocation at light intensities giving no difference in rate of photosynthesis between plus and minus potassium leaves and even at light intensities at which there was no net fixation of carbon dioxide. At all levels of deficiency, the relative decrease in translocation was greater than the relative decrease in photosynthesis. Translocation was affected at potassium deficiency levels which had no effect upon photosynthesis.

Potassium deficiency decreased translocation relatively more than it decreased moisture content. There was a much better correlation between the decrease in potassium and translocation than between the decrease in moisture and translocation.

An experiment with radioactive phosphorus indicated an upset in phosphorylation in the stems of potassium-deficient plants.

Experiments reported in the preceding paper (9) led to the conclusion that K may exert a direct effect upon translocation of photosynthate. This conclusion was confirmed and strengthened by studies with detached blades reported herein.

K is not the only nutrient required for translocation, since deficiencies in N and P also decrease the transport of sugar in the sugarcane plant (6, 11).

MATERIALS AND METHODS

The varieties of sugarcane studied in these experiments were previously described (9).

Shoots grown from stem cuttings cultured in volcanic black sand for 2.5 months were transplanted to tap water culture, two plants per 16-liter pot or one per 8-liter pot. After about 1 month in tap water, the plants were supplied with nutrient solutions prepared with distilled or deionized water. The complete solution contained K; the −K solution contained no K (9).

All of the methods of application of $^{14}CO_2$, sampling, analysis, and radioactivity counting were the same as with attached blades, the only difference being that the system under investigation was a detached blade rather than an entire plant, a system with several advantages (12).

Blades were cut from the plant at about 8 AM, recut twice under water, and taken to the air-conditioned room. The cut end of the blade remained in water during the entire test. After preillumination, measured doses of $^{14}CO_2$ were supplied to portions of the blades for 5 min in artificial light. The feeding chamber (6, 15) was quickly removed, and the blade was placed under the illumination desired for translocation. The portion of the blade above the fed part is called the apex; that below the fed part, the base.

Translocation took place for 6 or 24 hr, after which each blade was cut into measured sections, and the sections were weighed, dried, and reweighed for moisture determination. The dried sections were milled, and the milled powder was counted at infinite thickness with the Geiger counter. Results are expressed as relative specific activity, which is the net count per minute at infinite thickness; as relative total counts, which is the relative specific activity times the total dry weight in milligrams; and as percentage of total in the blade, obtained by adding the relative total counts in all parts of the blade.

$^{14}CO_2$ was applied under 2000 or 3000 ft-c incandescent illumination. Translocation took place under 2000 ft-c incandescent, 0.1 g-cal/cm^2 per min, or 250 ft-c or 100 ft-c fluorescent illumination, or in total darkness. All experiments were conducted in duplicate, except one on December 9 (Table III).

In one experiment the P fractions were labeled with ^{32}P.

RESULTS

Translocation in the Light. Blades which exhibited no visible symptoms of K deficiency were selected for the measurement of translocation, photosynthesis, and analysis of K, moisture, and sugars (Table I). The level of K in the blades deprived of K was not low enough to decrease the rate of photosynthesis. Basipetal translocation was less in the blades deprived of K than in the control blades. An increase in percentage of reducing sugars, with no significant change in sucrose, was evident in the blades deprived of K.

The results of several similar experiments may be compared, in which the blades studied did, or did not, display visible symptoms of deficiency (Table II). The results are grouped in the order of increasing severity of symptoms in the K-deficient blades. Blades at the levels of 0.5 to 0.8% K, with no or mild visible

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Table I. *Effect of Mild K Deficiency upon Translocation of ^{14}C in the Light or Dark, and Related Measurements*

$^{14}CO_2$ (10 μc) was fed to a 20-cm length of blade 5[1] (with no visible symptoms) with the chamber placed 50 cm above the cut base, for 5 min at 3000 ft-c. Translocation took place for 24 hr under cool, white fluorescent lamps (0.1 g-cal/cm^2 per min) or in the dark. Photosynthesis was measured with the infrared analyzer, on other blades, and sugar analyses on a third set, all in duplicate. Variety H 37-1933.

Series	Distribution of ^{14}C in Blade			Relative Total Counts, Millions, in the Blade	K	Moisture
	Apex	Fed	Base			
	%	%	%		% dry wt	%
+K (light)	0.4, 0.3	21.6, 25.5	78.0, 74.2	8.9, 8.9	1.64, 1.60	69.9, 68.9
−K (light)	0.3, 0.3	28.5, 28.7	71.2, 71.0	10.1, 9.1	0.79, 0.60	67.6, 66.9
+K (dark)	26.8, 21.9	64.9, 73.8	8.4, 4.3	4.2, 4.5	2.35, 2.09	77.6, 76.5
−K (dark)	29.7, 22.5	65.7, 72.7	4.6, 4.8	3.8, 4.1	0.79, 0.91	74.0, 74.6

	Rate of Photosynthesis	K	Moisture
	ml CO_2/dm^2 per hr	% dry wt	%
+K	18.9, 18.4	2.02, 2.02	71.5, 71.3
−K	18.7, 16.1	0.94, 1.05	71.0, 71.2

	Sugars		
	Total	Reducing	Sucrose
	% dry wt		
+K	3.6, 5.3	0.4, 0.4	3.1, 4.7
−K	5.5, 5.4	2.1, 1.9	3.2, 3.3

[1] Blades are numbered from the top downward, with the spindle called blade 1.

Table II. *Effect of Severity of K Deficiency upon Translocation and Photosynthesis*

$^{14}CO_2$ (10μc) was fed to a 20-cm central length of blade for 5 min. Light intensity during feeding was 2000 or 3000 ft-c and during translocation, 2000 ft-c or 0.1 g-cal/cm^2 per min.

Visible Symptoms in Fed Blade	Percentage of K in −K[1] Fed Blade	Decrease (−) or Increase (+) in − K		
		Photosynthesis	Translocation	
			Basipetal	Acropetal
		%	%	%
None	0.5–0.8	No[2]	−7 to −39	No
Mild	0.6	No	−40	No
Intermediate	0.2–0.4	−6 to −42	−34 to −81	No to +(slight)
Severe	0.11–0.19	−65 to −96	−84 to −99	+(slight) to +(definite)

[1] The percentage of K in control blades ranged from 1.4 to 2.0%, dry weight.

[2] No = no effect.

symptoms, did not differ from controls in their rate of photosynthesis, which is in agreement with previous results (10). All of the blades with intermediate or severe symptoms of K deficiency decreased in total fixation of $^{14}CO_2$, the decrease being greater at a K percentage ranging from 0.11 to 0.19%, dry weight, than at a K percentage of 0.22 to 0.4%. Basipetal translocation decreased at all levels of K deprivation. Acropetal translocation was not affected by mild deficiency, but with more severe deficiency there was a slight increase. At all levels of K deficiency the decrease in basipetal translocation was greater than the decrease in total fixation. These results indicate that in excised blades as in intact plants (9), basipetal translocation was more sensitive to K deficiency than photosynthesis was, and that acropetal translocation was affected by only the severest deficiency, if at all.

Translocation in the Dark. Although translocation for 24 hr in the light was less in blades deprived of K but showing no deficiency symptoms, translocation in the dark was not affected by a similar level of deficiency (Table I). In another test conducted 1 week earlier, blade 5, free of symptoms, also showed no effect of K deficiency on translocation in the dark. With more severe deficiency and visible symptoms, basipetal translocation in blade 7 decreased in the deficient blade both in the dark and in the light (Table III). Apparently basipetal translocation was more sensitive to K deficiency in the light than in the dark.

Intensity of Light. Basipetal translocation was greater in the control than in the −K blades at 100, 250, and 2000 ft-c (Table III). K deficiency did not affect the rate of photosynthetic fixation of CO_2 in similar blades at 100 or 2000 ft-c. Translocation was greater in both + and −K leaves at all intensities of light than in the dark. Thus light intensities giving no differences in fixation of CO_2 between + and −K leaves and even those giving no net uptake of CO_2, increased basipetal translocation compared with darkness. The increase in the light was not entirely due to a net fixation of CO_2 but to some other factor.

K Content. The percentages of K in the leaves deprived of K were considerably lower than in the control blades (Tables I, II, and III). Furthermore, the control blades exhibited a steep gradient in percentage of K calculated as percentage in the leaf water, increasing from the apex toward the base (Fig. 1). The percentage of K in the blades deprived of K not only was much lower than the controls but also decreased from the apex toward the base. The correlation coefficient between decreases in K content of the entire blade and basipetal translocation in the same blades was 0.93.

Table III. *Effect of Light Intensity upon Translocation of ^{14}C in + and −K Blades*

$^{14}CO_2$ (10 μc) was fed to a 20-cm length of blade 7 or 8 (the −K blade having typical symptoms of deficiency) with the chamber placed 40 cm above the cut base for 5 min at 2000 ft-c. Translocation took place for 6 hr in darkness or under cool, white fluorescent lamps at 100 or 250 ft-c, or under incandescent lamps at 2000 ft-c. Rate of photosynthesis was measured on blade 7. Variety H 37-1933.

Series	Distribution of ^{14}C in Blade			Relative Total Counts, Millions in the Blade	K	Moisture
	Apex	Fed	Base			
	%	%	%		%, *dry wt*	%
+K(dark)[1]	1.3	85.4	13.4	6.2	1.18	68.2
−K(dark)[1]	0.5	90.6	8.9	5.4	0.25	66.1
+K(100 ft-c)[2]	4.3, 5.8	68.3, 69.0	27.4, 25.2	8.6, 7.4	1.73, 1.68	71.4, 72.0
−K(100 ft-c)[2]	0.2, 3.6	77.4, 83.3	22.4, 13.1	7.1, 7.2	0.65, 0.43	69.8, 69.3
+K(250 ft-c)[1]	0.5	55.8	43.7	9.8	1.15	67.7
−K(250 ft-c)[1]	0.1	60.3	39.7	5.8	0.35	65.3
+K(2,000 ft-c)[2]	0.2, 0.5	41.4, 44.0	58.3, 55.5	8.9, 8.6	1.68, 1.58	70.9, 70.1
−K(2,000 ft-c)[2]	1.0, 0.1	64.9, 58.3	34.1, 41.6	8.0, 8.4	0.43, 0.55	68.4, 67.3

Series	Date	Rate of Photosynthesis		
		ml CO_2/dm^2 per hr		
+K	10–23	9.9(2,000 ft-c); 0(100 ft-c)	1.64	70.5
−K	10–23	9.9(2,000 ft-c); 0(100 ft-c)	0.74	70.4
+K	12–20	15.9(8,000 ft-c)	1.57	66.0
−K	12–20	11.2(8,000 ft-c)	0.23	64.5

[1] Date of test, 12-9; blade 8.
[2] Date of test, 10-23; blade 7.

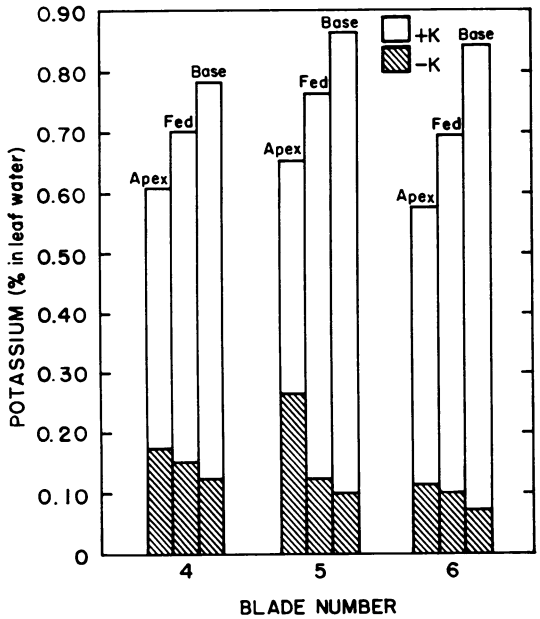

FIG. 1. Effect of K deficiency upon percentage of K in the leaf water, in various parts of the blade. Age: 7 months, 3 weeks. Differential K treatment: 4 months, 10 days. Variety H 44-3098. Length of base, 23 cm; fed part, 20 cm; apex, rest of blade. Typical deficiency symptoms on each −K blade. Basipetal translocation in 6 hr at 2000 ft-c, expressed as percentage of relative total counts in the blade:

Blade Number	Control	−K
4	44	9
5	50	4
6	44	7

Moisture Content. A previous paper reported that small differences in percentage of moisture were associated with considerable differences in translocation of ^{14}C in entire plants (8).

The blades deprived of K had slightly lower percentages of moisture than the controls in several of the experiments, but the correlation coefficient between decreases in K content and overall moisture percentage in the same blades was only 0.30. As previously shown (9), changes in moisture content may or may not be evident when translocation is affected by K deficiency.

Phosphorus. No P determinations were performed in these translocation tests. Previous reports have indicated an accumulation of inorganic P in plants deficient in K, presumably due to a decreased ability to convert inorganic to organic P and to transfer P from outer to inner space (3–5, 13). Since phosphorylation may be essential for the transfer of sucrose from the phloem to

Table IV. *Effect of K Deficiency upon P and Sugar Fractions in Stem*

Joints 6 to 10 were sampled after 62 days ± K, the last 20 days in ^{32}P (1 mc of ^{32}P per pot of two plants). Variety H 37-1933.

Constituent	P Fractions of Total ^{32}P		Control	−K
	Control	−K		
	%	%	%, *dry wt*	
Soluble inorganic P	3.1	49.5		
Glycerate 3-P	53.0	1.8		
Lipid P	7.6	6.2		
Insoluble P in residue	20.4	23.4		
Other organic P (by dif.)	15.9	19.1		
K			2.03	0.21
Reducing sugars			5.34	14.18
Sucrose			12.61	5.29

storage parenchyma, an experiment mentioned in the Annual Report of this Station for 1961 may be of interest (Table IV). Stems of the plants deficient in K were very high in inorganic ^{32}P, low in ^{32}P phosphoglyceric acid, high in reducing sugars, and low in sucrose. These data suggest that a deficiency in K resulted in less storage of sucrose because of an upset in phosphorylation, but they do not indicate whether these differences occurred in the phloem or in the parenchyma cells or both.

DISCUSSION

The results in this paper confirm those previously reported (9) in showing that a high percentage of K in the plant is associated with good translocation of ^{14}C and a low percentage of K with poor translocation. Not only the percentage of K but also the distribution of K within the blade may be related to translocation. According to Figure 1, the percentage of K, on the leaf water basis, increased from apex to base of the control blades but decreased from apex to base of the −K blades. These gradients, of course, are for the total tissues. Bowen (unpublished data)[2] reported that B decreases from apex to base of a sugarcane leaf, probably owing to accumulation at the apex resulting from transpiration, hence a xylem gradient. The K gradient in the −K blades thus resembled a xylem gradient, while the K gradient in the control blades resembled a phloem gradient. Richardson (23) stated that there appears to be a gross transport of K down the sieve tube. If the K gradient in the control blades is a phloem gradient, the increase in percentages of K from apex to base of the blade might indicate that K had in fact moved down the phloem. The author does not know whether K moved into the water in which the cut ends of the blades were standing, because the water was not tested for K. Only a trace of ^{14}C was found in the water (14). K is known to be withdrawn from attached leaves and reutilized in younger leaves (3). The K gradient in the −K blades may suggest a difficulty in withdrawal of K, in which case there was a difficulty in translocation of both K and ^{14}C in the −K blades.

A direct effect of K upon translocation is an attractive idea because K is known to be one of the three largest constituents in sieve tube sap (20). Evans and Sorger (2) thought the capacity of K^+ to activate a wide variety of enzymes explains its requirement for growth. K-activated enzymes might be involved in translocation. Spanner (24) proposed that a circulation of K around the sieve plate might result in electrical forces which could speed up translocation. The results in this paper neither prove nor disprove the enzyme theory or electrical theory, but they do suggest that K exerts a direct effect upon translocation, for the following reasons. (*a*) K deficiency decreased basipetal translocation in blades showing no visible symptoms of K deficiency. (*b*) Basipetal translocation decreased at levels of K deficiency which had no effect upon photosynthesis. (*c*) The severity of the effect upon translocation increased with the severity of K deficiency. The correlation between decrease in K content and basipetal translocation was 0.93. (*d*) K deficiency decreased translocation at light intensities giving no difference in rate of photosynthesis between + and −K leaves and even at intensities at which there was no net fixation of CO_2.

K deficiency decreased basipetal translocation even in total darkness. However, the decrease in the dark apparently occurred only after K deficiency symptoms became visible. Therefore, translocation in the light was more sensitive to K deprivation than translocation in the dark. So the primary effect of K may be upon phototranslocation.

According to Table III, basipetal translocation in blades 7 or 8 of both + and −K plants, when tested for 6 hr, increased with light intensity, reaching saturation at an intensity closer to 250 ft-c than to 100 ft-c, the figure obtained for 24-hr tests (7). The number of 6-hr tests was inadequate for a comparable study.

Rains (21, 22) reported that the absorption of K^+ by corn leaf tissue was enhanced by light. Compared with absorption in darkness, the rate increased 50% at a light intensity of 500 lumen m^{-2}. Light saturation for the absorption of K^+ by corn leaf tissue was reached at low intensities: about 1100 lumen m^{-2} (21), or less than 5000 lumen m^{-2} (22). The curve illustrating the effect of light intensity upon K^+ absorption (Fig. 1 in Reference 22) strongly resembles my curve illustrating the effect of light intensity upon basipetal translocation of sucrose (Fig. 6 in Reference 7). Saturation at similar low intensities of light has also been reported for the absorption of chloride by leaves of *Vallisneria* (19) and for photoassimilation of glucose by *Chlorella* (16, 24).

Light-enhanced absorption of K^+ and of chloride, photoassimilation of glucose, and phototranslocation of sucrose are all saturated at approximately the compensation point, at light intensities considerably below saturation of photosynthesis whether measured as assimilation of CO_2 or as evolution of O_2. Perhaps these processes are activated by a similar mechanism. That the mechanism involves chlorophyll was shown by van Lookeren Campagne (19) and by Kylin (17, 18). Studies with inhibitors and anaerobic conditions indicated that light-stimulated transport derived its energy from cyclic photosynthetic phosphorylation (16, 19, 22, 25). Kylin (17), however, concluded that although many data on the effects of inhibitors fit the phosphorylation theory, some effects fit a cytochrome theory better, and both mechanisms may be involved. A role for some mechanism other than photophosphorylation is suggested by the low intensity light saturation of the transport processes, because photophosphorylations saturate at about 20,000 lux or even 200,000 lux for cyclic photophosphorylation with phenazonium methosulphate or pyocyanine (1). There may be another low intensity photo-process which is affected by certain inhibitors in a manner similar to photosynthetic phosphorylation, which supplies the energy not only for the transport across membranes of ions such as K^+ and of molecules such as glucose, but also for translocation of sucrose down the phloem of leaves. Possibly phosphorylation does not need to proceed at maximal rates in order to activate the transport processes.

Because of phosphorylation, the development of electrical forces, enzyme activation, or for some other reason, K is directly essential for the translocation of sucrose.

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