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Effect of Moisture Supply upon Translocation and Storage of ^{14}C in Sugarcane[1]

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Summary. Low moisture supply, controlled by 3 methods (adding NaCl to a complete nutrient solution, allowing a cut stalk to wilt, or withholding irrigation in the field), decreased the velocity and percentage rate of translocation of ^{14}C-photosynthate. The surplus sucrose not used in growth moved more slowly in the phloem and was stored in the stalk.

Low moisture supply depressed translocation of ^{14}C-photosynthate more severely than it curtailed formation of ^{14}C-photosynthate in the same leaf; therefore, the effect of moisture supply upon translocation was primary.

Low moisture supply retarded profile development in the stem, and a loss in moisture gradient was associated with a steepened slope of the profile. These results indicate a flow mechanism of translocation rather than diffusion.

Results reported now and previously point to the operation of a slow pressure-flow mechanism particularly during the night but also during the day; superimposed upon this general mass transport is the more rapid process of phototranslocation which is independent of sugar gradients and which can cause the accumulation of sucrose at the storage-sink.

During ripening, storage of sucrose in the stalk may be increased by withholding water because less sucrose is hydrolyzed in transit, less is used in growth, and the slowly moving sucrose has more time for transfer from the phloem to the storage parenchyma.

The effect of moisture supply upon translocation of photosynthate has interested several investigators. Some studies indicated a beneficial effect of moisture stress upon translocation (4, 5, 24, 29), whereas other results have suggested a deleterious effect (28, 34, 36, 37, 38). The dissimilarity of effects may be explained partly by interpretation. Because they found a greater accumulation of carbohydrates in the roots of the plants under moisture stress, Eaton and Ergle (4) and Ehara and Sekioka (5, 29) concluded that increased translocation of carbohydrates to roots was stimulated by drought, low relative humidity or low soil moisture. On the other hand, Zholkevich and Koretskaya (39) considered the accumulation of sugars in pumpkin roots during drought to be a consequence of the retardation of translocation.

Workers studying translocation of ^{14}C photosynthate from the leaf have found that moisture stress decreased translocation (28, 36, 37, 38). Roberts (28), in his investigation concerning translocation from the leaves of 3-year-old potted seedlings of yellow poplar, reported that moisture stress decreased the total percentage of ^{14}C translocated, the distance translocated downward and the velocity of translocation; but increased the percentage translocated upward in the stem. Wiebe and Wihrheim (36, 37) reported that total translocation of ^{14}C from the treated leaf of sunflower plants decreased with increasing diffusion pressure deficit between 1 and 8 atm above which it leveled off; moisture stress decreased downward and generally upward translocation. Zholkevich (38) reported that irrigation increased translocation from the leaf and into the ear of wheat plants.

Plaut and Reinhold (27) applied ^{14}C-sucrose to the lower epidermis of bean leaves and studied its translocation in plants supplied with or deprived of water. The control plants generally translocated better than the stressed plants out of the treated leaf, up and down the stalk. At 15 hours, the roots of the stressed plants had more radioactivity, both total and percentage, in the ethanol extract than the roots of the controls. However, the ethanol-insoluble fractions were all considerably higher in

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the controls. Since all the ^{14}C in the roots reached its destination by translocation, translocation to the roots was improved by adequate moisture supply. The logarithmic profile at 2 hours was much steeper in the stressed than in the control plants.

The results presented now may assist in resolving these differences. Results of this investigation show that a low moisture supply not only decreases the velocity and percentage of translocation of ^{14}C but also increases storage of ^{14}C in the sugarcane plant.

Investigations of the effect of moisture conditions upon translocation of photosynthate in sugarcane were undertaken for the following reasons. A) Several conditions found to decrease translocation may also decrease the percentage of moisture in the plant: e.g., low root temperatures, nutritional deficiencies (12). B) An explanation was sought of the often quoted statement (23) that dry weather raises the sugar content in cane. C) Another reason, of considerable economic importance to the sugar industry, was to establish the validity of the practice of withholding water on irrigated plantations for several months before harvesting. D) Previous results also showed that low moisture supply decreased photosynthesis in sugarcane (1, 7, 8, 9, 15). Does low moisture decrease translocation as a result of its effect upon photosynthesis, or in addition to this effect?

Experiments reported herein and in part reported elsewhere (2, 11, 16) as well as in the Annual Reports of this Station for 1960 and 1961, indicate that a low moisture supply has a deleterious effect upon translocation. Because translocation was affected more severely than photosynthesis in the same leaf, the author believes that the effect of low moisture upon translocation does not result from its effect upon photosynthesis but is an additional, direct effect.

The effects of temperature (12) and of light (13, 14, 17) have recently been reported. The experiments on moisture were conducted in 1959 to 1960, before those on light, and are reported now to study the role of moisture, in view of the important role of light, in the mechanism of translocation.

Materials and Methods

The variety of sugarcane used in these experiments was H37-1933, previously described (21).

Moisture supply was controlled by 3 methods: 1) by adding NaCl to complete nutrient solutions, 2) by cutting the stalk and allowing it to wilt, and 3) by withholding irrigation in the field.

The methods of preparing and applying $^{14}CO_2$, harvesting, sampling, and counting were the same as previously reported (21). Briefly, equal portions of $^{14}CO_2$ were supplied to a 20-cm length of a single blade for 5 or 10 minutes in bright sun, using the chamber described elsewhere (11). After removal of the chamber, translocation (with the plant maintained under the experimental conditions) proceeded for 90 minutes, 5 hours, 24 hours, or 6 weeks. At harvest the plants were measured, subdivided, weighed, and sampled. Dried, milled samples were counted at infinite thickness. Samples of extracts were counted at infinite thinness. Samples for sugar analyses were boiled and extracted with ethanol. Sugars were analyzed by the method described by Tanimoto and Burr (30), and chromatographed by the methods mentioned previously (21). Chromatograms were counted on the paper.

Results are expressed as: relative specific activity, which is the net cpm at infinite thickness: relative total counts, which is the relative specific activity times the total dry weight in milligrams: and percentage of relative total counts in the plant,

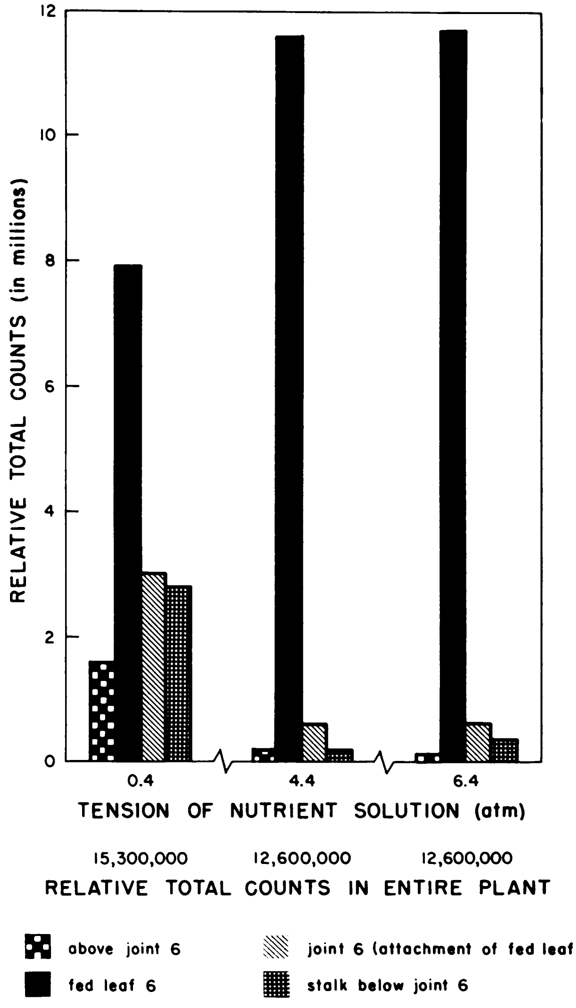

FIG. 1. Effect of moisture supply upon translocation for 90 minutes. Plants were placed in their respective solutions (±NaCl) at 10 AM and harvested 48 hours later. Ninety minutes before harvest, $^{14}CO_2$ was administered to a portion of blade 6 for 5 minutes in sunlight.

which is obtained by adding the relative total counts of each part. Results counted at infinite thinness are expressed as total counts.

Results

Distribution of ^{14}C Photosynthate in the Plant. Translocation for 90 minutes decreased in the plants at the higher tensions (fig 1): from the fed blade, up the stalk, and down the stalk. Although nearly 50 % of the radioactive carbon had been translocated from the fed leaf of the control plant, less than 10 % of ^{14}C in the plants at higher tension had been translocated.

Translocation for 24 hours (fig 2) resulted in less relative total counts up the stalk above the node of the fed leaf, and less in the roots, of the plants at the higher tensions than of the control. The detrimental effect of tension upon translocation into joints 1 to 7 was particularly evident (fig 3). On the other hand, more ^{14}C accumulated in the joint to which the fed leaf was attached (#8) and the stalk below joint 8 in the plants at the higher tensions (fig 2). Moisture percentages were higher in the control plant at 0.4 atm than in the plants at 2.4 and 4.4 atm, particularly in the young, growing joints, 1 to 7 (fig 4). A low moisture supply decreased the total consumption of water (from 825 ml in 46 hours in the plant at 0.4 atm to 125 ml at 6.4 atm); decreased elongation of the young joints 1 to 4 (from 4.5 cm in the plant at 0.4 atm to 1.5 cm at 4.4 atm); decreased elongation of a young sheath at an index position (from 1.2 cm in 41 hours in the plant at 0.4 atm to 0.2 cm at 4.4 atm); and caused incipient wilting as shown by rolling of the young leaves in the plants at 6.4 atm.

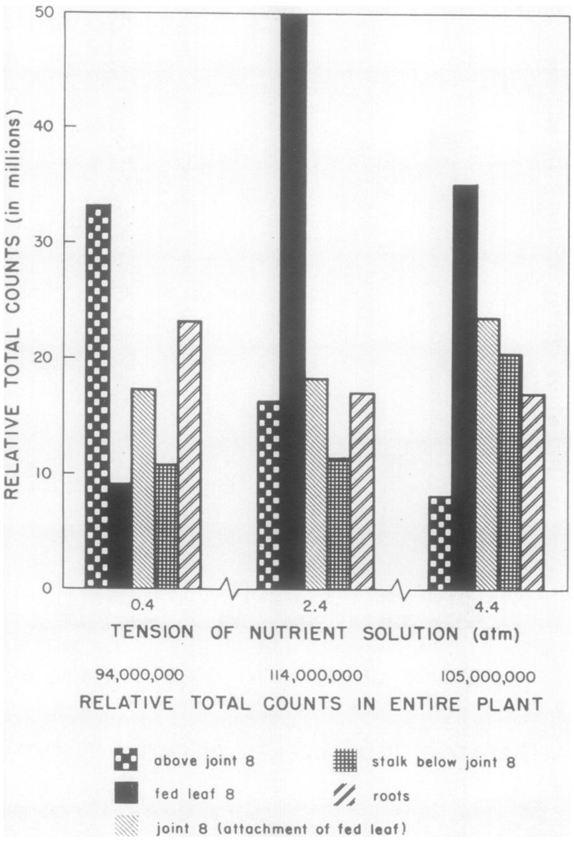

FIG. 2. Effect of moisture supply upon translocation for 24 hours. Plants were placed in their respective solutions (±NaCl) at 2:45 PM and harvested 43 hours later. Twenty-four hours before harvest, $^{14}CO_2$ (200 μc) was administered to a portion of blade 8 for 5 minutes in sunlight. See figure 4 for moisture percentages.

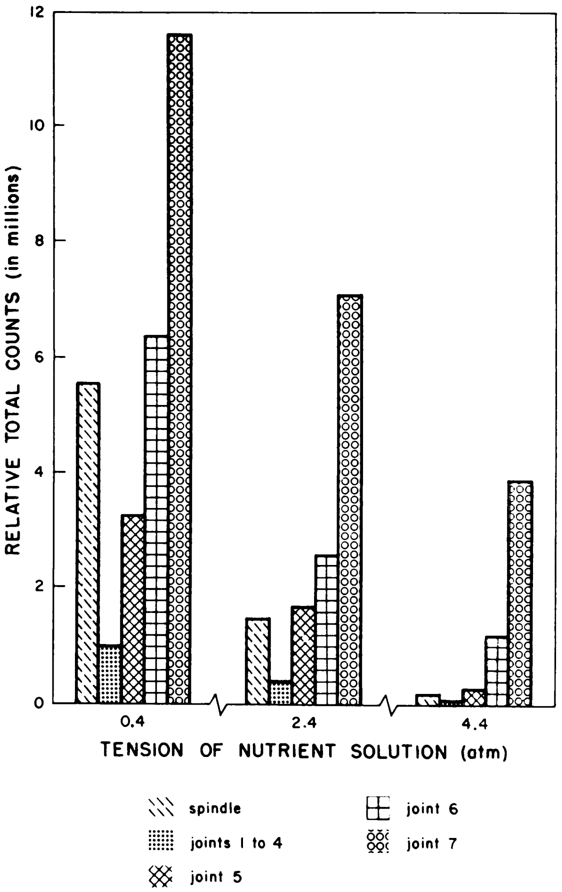

FIG. 3. Effect of moisture supply upon upward translocation for 24 hours. Total results above joint 8 (fig 2) are presented for spindle and individual joints. See figure 4 for moisture percentages.

Velocity. The distance translocated in 90 minutes was determined by locating the advancing front of translocation. The velocities were as follows: 0.4 atm (osmotic concentration of the nutrient solution), 1.3 cm per min: 4.4 atm, 1.0 cm per min: 6.4 atm, 1.1 cm per min. Velocities of transport were also compared in cut and attached stalks. When translocation terminated at 90 min-

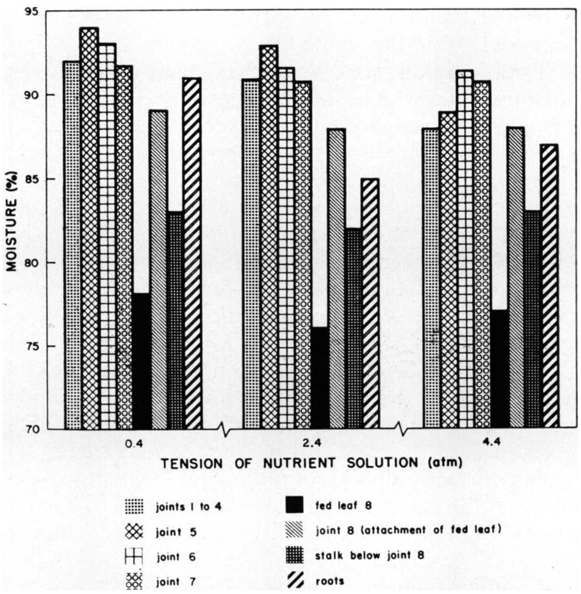

FIG. 4. Effect of moisture supply upon moisture percentages in the plants. After 43 hours in complete nutrient solutions (±NaCl), plants were harvested. See figures 2 and 3 for translocation results.

utes, the velocity of downward transport in an attached stalk was 1.2 cm per min and the velocity in a cut (but not wilted) stalk was 1.1 cm per min, a difference not considered significant. Translocation for 5 hours showed the velocity in the control stalk (attached, not wilted) was at least 1.3 cm per min (the radioactive sugar having reached the bottom of the stalk). The velocity in the cut and wilted stalk was only 0.5 cm per min, which may be considered an overall average value for the 5-hour period.

Profile Development. At 90 minutes the profile of radioactivity in the stem was further developed in the control plant at 0.4 atm than in the other plants at 4.4 and 6.4 atm (fig 5). At 5 hours the profile in the cut stalk was much steeper and less developed compared with the attached stalk (fig 6). The moisture percentage of the cut and wilted stalk was considerably lower than that of the attached stalk (fig 6 legend). Furthermore, the cut stalk apparently had lost its gradient in moisture.

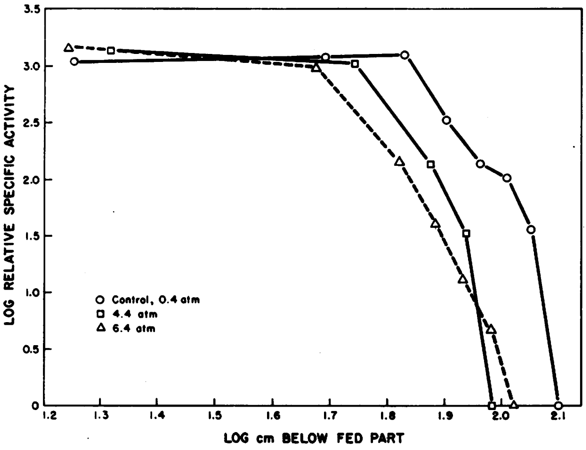

FIG. 5. Effect of moisture supply upon profile development in 90 minutes. Treatment of plants, as in legend to figure 1.

Effect of Translocation upon Storage. The results of each of 4 experiments were calculated as percentage of activity in the experimental series compared with the control which was plotted as 100% (fig 7). Although the moisture supply of the plants was varied by different methods, the following trend with time was apparent. At 90 minutes, the plant with low moisture supply (4.4 atm) had greater radioactivity than the control in the fed blade only. This difference indicates poor translocation from the fed blade into the sheath and stalk. At 5 hours, the plant with low moisture supply (stalk cut and wilted) had greater activity than the control not only in the fed blade, but also in the sheath and joint of the fed blade and 1 joint below it. However, in the older joints the plant with low moisture supply had considerably less ^{14}C than the control. At 24 hours, the plant with low moisture supply (4.4 atm) had more radioactivity than the control in the fed leaf and its joint and even in the older joints. At 6 weeks, the plant with low moisture supply (not irrigated) had the same percentage of activity remaining in

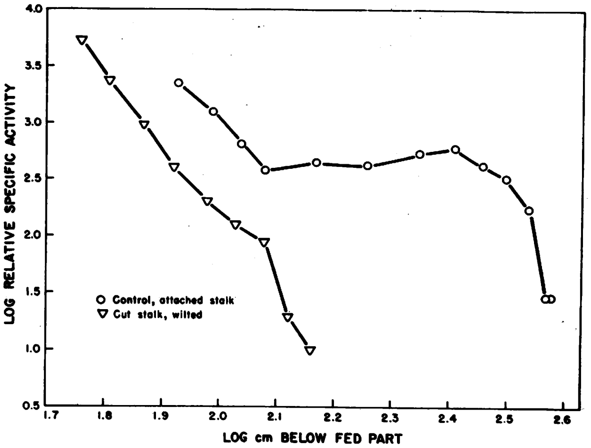

FIG. 6. Effect of moisture supply upon profile development in 5 hours. $^{14}CO_2$ (400 μc) was administered to a portion of blade 8 of a long stalk for 10 minutes in bright sun. Immediately after removing the chamber, one stalk was cut at the base, under water, and the cut end remained under water the entire translocation period of 5 hours: the leaves of the cut stalk wilted at about 2 hours, probably because of a strong wind. Attached stalks did not wilt. Control, attached stalk: fed at 8:27 AM November 10. Cut stalk: fed at 8:54 AM December 18. Moisture percentage of joint 7: control, 87.6; cut, 76.8; joint 8: control, 83.8; cut, 76.8; joint 9: control, 80.7; cut, 76.8.

the fed blade as the control; and had stored considerably more ^{14}C photosynthate in the older joints than the control. Apparently increased time effected a progressive downward movement of the surplus ^{14}C in the series with low moisture supply compared with the controls.

Translocation was slower in plants with low moisture supply than in the controls, as shown by comparative velocity, percentage of distribution, translocation into roots, and profile development. The surplus ^{14}C not used in growth of roots, stem apex, etc., eventually was translocated from the leaf and was stored in the older joints of the stalk. The slower velocity of transport presumably provided more time for transfer of sucrose into storage. Thus, slow translocation improved storage.

Ripening. The accumulation of photosynthate in the stalk of the plants with low moisture supply is an economic benefit only if the photosynthate is sucrose at harvest. Ripening in sugarcane is concerned with decreasing the water content, increasing the sucrose, and decreasing the reducing sugars resulting in higher ratios of sucrose-reducing sugars. The higher the ratio the better the quality of the juice.

The sucrose-reducing sugar ratios of the newly formed radioactive sugars in the plants with low moisture supply were increased below the fed part of the leaf and in the sheath after translocation for 90 minutes (table I). No effect was apparent in the fed part of the blade; thus, the effect oc-

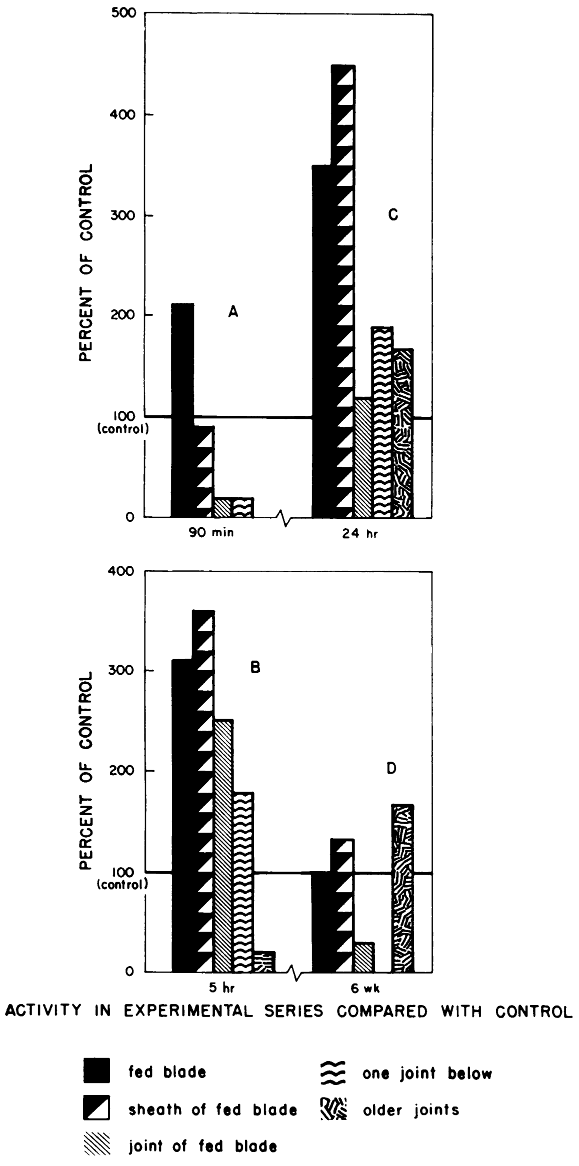

FIG. 7. Trend with time of effect of moisture supply upon translocation and storage of photosynthate. Total ^{14}C in each experimental series is expressed as percentage of activity in its control (plotted as 100 %). Treatments: A) 90 minutes: NaCl was added to a complete solution raising the osmotic pressure from 0.4 atm in the control to 4.4 atm. Translocation was measured the last 90 minutes of a 48-hour period ±NaCl. B) 5 Hours: a cut and wilted stalk compared with an attached, turgid stalk. C) 24 Hours: as in A, with translocation measured the last 24 hours of a 43-hour period ±NaCl. D) 6 Weeks: irrigation withheld compared with the irrigated control, in field plots.

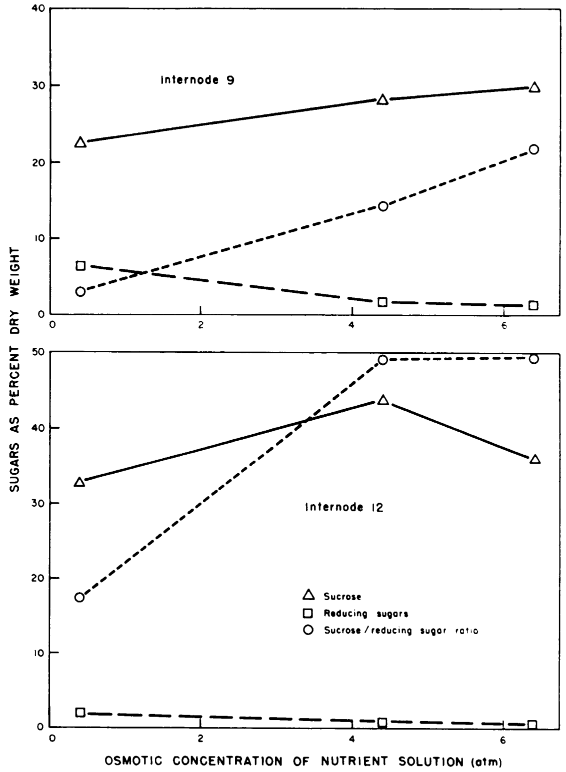

FIG. 8. Effect of moisture supply upon sugar percentages and ratios in the stalk. Treatment as in legend to figure 1.

Table I. *Effect of Moisture Supply upon Hydrolysis of Sucrose*

Plants were placed in their respective solutions (±NaCl) at 10 AM June 6, and harvested 48 hours later. Ninety minutes before harvest, $^{14}CO_2$ was administered to a portion of blade 6 for 5 minutes.

	Entire part			cpm/mg Dry wt		
Series*	Dry wt	Total counts			Glucose+	S-RS
atm	mgs	Sucrose	Glucose+fructose	Sucrose	fructose	Ratio**
		Fed blade 6, fed part				
0.4	600	65,900	9700	109.8	16.2	6.8
4.4	600	103,300	17,500	172.2	29.2	5.9
6.4	500	150,300	21,600	300.6	43.2	7.0
		Fed blade 6, below fed part				
0.4	1400	34,300	3500	24.5	2.5	9.8
4.4	1600	60,200	5700	37.7	3.6	10.5
6.4	900	48,100	4700	53.4	5.2	10.3
		Sheath 6				
0.4	1600	38,200	10,800	23.9	6.8	3.5
4.4	1700	38,700	3300	22.8	1.9	12.5
6.4	1200	27,600	2700	31.3	2.3	13.6

* Osmotic concentration of nutrient solutions.
** Sucrose-reducing sugar ratio.

curred in transit. Since ^{14}C photosynthate in sugarcane is translocated in the form of sucrose (11, 21), once the sugar is hydrolyzed it is no longer translocated. The relatively higher activity in the reducing sugars in the sheath of the control (0.4 atm) than of the series at 4.4 and 6.4 atm indicates greater hydrolysis in transit in the plants with high moisture supply (table I). One beneficial effect of a low moisture supply may therefore be a lessening of hydrolysis in transit resulting in the arrival of more sucrose at the storage sink. The importance of the action of invertases for the transfer of sucrose from the sieve tubes to the storage parenchyma has been shown by Hawker and Hatch (22). However, even after 2 days of treatment, the stalks of the plants at the higher osmotic concentrations of the nutrient solution had higher sucrose-reducing sugar ratios than the controls on the dry weight basis (fig 8). Thus, both radioactive and inactive sugars were affected by moisture supply. Other plants were allowed to ripen for 1 month. The results for moisture and sugars in internodes 8 to 10 (fig 9) showed improvement in sucrose-reducing sugar ratios and higher percentages of sucrose associated with lower percentages of moisture.

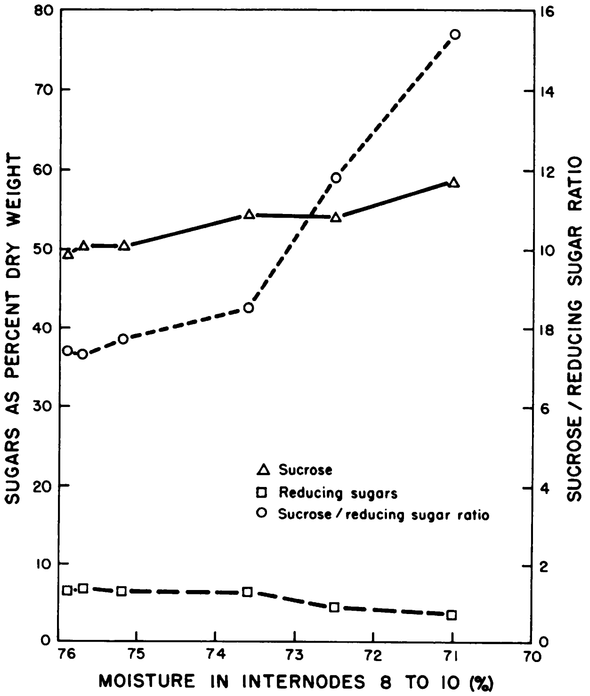

FIG. 9. Effect of moisture percentage upon ripening for 1 month, in internodes 8 to 10. Differences in moisture percentage of the stalk resulted from adding or withholding NaCl from complete nutrient solutions.

Total Fixation Compared with Translocation. Photosynthesis, as measured by total activity in the plant after translocation for 90 minutes (thus before much differential could be caused by respiration), decreased 18 % in each of the plants with low moisture supply (fig 1). This decrease is in agreement with previously reported results on photosynthesis in sugarcane (1, 7, 8, 9, 15) and in other plants (6, 24, 28, 31, 32, 38). Whereas total fixation decreased 18 %, translocation from the same leaves decreased 93 % at 4.4 atm and 94 % at 6.4 atm (fig 1). Apparently, translocation was affected more severely than photosynthesis in the same leaf.

Discussion

In the discussion of the paper by Roberts (28), Nelson said that the effect of moisture upon translocation itself is not known, because the effect upon translocation might be a secondary result of the well-known inhibition of photosynthesis by moisture stress. The writer is of the opinion that the deleterious effect of low moisture upon translocation reported herein was a primary effect, because translocation was affected so much more severely than photosynthesis in the same leaf. Since decreasing the assimilation of CO_2 to compensation by low light intensity had no effect upon translocation (13), similarly decreasing the assimilation of CO_2 by low moisture supply should not affect translocation, unless the low moisture supply itself affects translocation directly. Moisture stress affected translocation more severely than photosynthesis, for which reason it is possible that the primary effect was upon translocation rather than photosynthesis: and the piling up of sugar in the leaf caused by slow translocation decreased further photosynthesis in that leaf (10).

The decrease in velocity of transport and the poorly developed profile of the cut and wilted stalk compared with the attached, turgid stalk was thought to result from moisture stress rather than from the loss of a pulling force exerted by the roots, for these reasons: A) No such decrease occurred in a cut, nonwilted stalk. B) The wilted stalk had considerably lower moisture percentages than the attached stalk, and apparently had lost its moisture gradient. C) Deradication leaving the stubble intact did not decrease translocation in a sugarcane stalk (20).

The effect of moisture supply upon the profile of radioactivity in the stem reported herein (figs 5 and 6) and by Plaut and Reinhold (27) is of interest because the mass-flow hypothesis of translocation predicts a flattening when translocation is accelerated (26). Müller and Leopold (25) reported that basipetal transport of ^{32}P in the phloem of detached corn leaves is enhanced by localized application of kinetin to the leaf. Because the ^{32}P profiles were flattened by kinetin treatment, and because kinetin enhanced the movement of other solutes, e.g. ^{22}Na, Müller and Leopold (26) concluded that the mechanism of kinetin-induced transport is a mass-flow rather than diffusion. They considered the most likely cause of the mass-flow to be a gradient in osmotic potential, resulting in either a pressure-flow or, preferably, a suction-flow. On the other hand, Webb and Gorham (35), from their studies of the effect of node temperature upon translocation of ^{14}C in squash plants, concluded that translocation of sugar through the node and basal region of the petiole is under direct physiological control: it cannot be a physical flow of solution moving within an inert conduit along a turgor pressure gradient. Either the flow of solution is metabolically regulated, or the structural integrity of the conduit is metabolically maintained, according to Webb and Gorham.

In sugarcane, a circulatory flow takes place in the phloem (3). Not only ^{14}C, but also other isotopes, including ^{32}P, ^{15}N, and even ^{45}Ca (18) move from 1 stalk to another in the same stool. In transporting sucrose to the stalk, each leaf must compete with the other leaves (particularly those above it) — which indicates competing streams entering the stalk from each leaf (20). In detached blades, basipetal translocation of ^{14}C sucrose in the dark is enhanced by additional sugar entering the apex; the additional sugar may be sucrose, sucrose-forming sugars or nonsucrose-forming sugars (17). All these results favor a flow mechanism rather than diffusion.

Is the flow along an osmotic gradient? If so, is it a pressure flow or a suction flow? Are there additional mechanisms?

Apparently, the flow may be along an osmotic gradient: in some parts an increasing gradient, in other parts a decreasing gradient. The moisture percentage in the blade increases from apex to base (17); the moisture percentage in the stalk decreases from joint 5 or 6 to the lower joints (fig 4). Loss of the moisture gradient in the stalk of the wilted plant was accompanied by a decrease in translocation (fig 6). The translocation mechanism is sensitive to moisture supply, since small differences in moisture percentage (fig 4) were accompanied by considerable difference in translocation (figs 1–3). All of these moisture percentages were obtained from complete sections of blade or stem, including nonconducting and conducting cells. However, if 1 tissue is under moisture stress it may be assumed that other adjacent tissues are also under moisture stress.

Evidence that the translocation of sucrose in sugarcane resembles a pressure-flow mechanism rather than a suction-flow mechanism is as follows: A) Detached blades can translocate basipetally in the dark only when they have an initial positive gradient in sucrose (17). B) Additional water supplied to the cut apex did not produce basipetal translocation in the dark; but additional sugars stimulated basipetal transport (17). C) The conversion of a polysaccharide to sucrose during the night enabled an attached leaf to resume translocation (11, 19). The conversion of polysaccharide to sucrose would increase the osmotic potential at the source which would favor a pressure-flow mechanism at night. D) Water does not accumulate at the sink, since all parts of the plant decrease in moisture percentage with time. E) A circulation of solutes, and presumably of water, takes place (3).

The writer concludes from the above points A to E that a pressure-flow mechanism may be involved in translocation of ^{14}C in sugarcane, particularly at night. But this is not the whole story, since translocation upward and downward in the stalk take place simultaneously (21). This simultaneous bidirectional movement of ^{14}C in the phloem of the stalk indicates either: A) different osmotic gradients in different channels, or B) the operation of some factor in addition to osmotic gradient. Additional factors are growth, kinetin-like mobilizers (25, 26, 33) and light. Superimposed upon the general mass transport moving along a pressure gradient, possibly the only mechanism by night but also operative by day, is the special process of phototranslocation, a light-stimulated process which speeds up translocation by day, is independent of sugar gradients, and causes the accumulation of sucrose at the sink (13, 14, 17).

The question may arise as to which mechanism was affected by water stress, pressure flow or phototranslocation. In the 22-hour test (19), the rate of loss in total counts from 11:30 PM to 3:30 AM, corrected for respiration, was 11.3 % per hour. The rate from 3:30 PM to 5:30 PM was 27.8 % per hour. The night rate may be considered to be that of pressure flow, and the day rate to be that of phototranslocation in addition to pressure flow. Assuming the same rate of pressure flow by day as by night, it would appear that both mechanisms were affected by water stress which resulted in 94 % inhibition of translocation in 90 minutes in the daytime (fig 1).

The writer believes that both suggestions of Webb and Gorham (35) apply. The flow of solution is metabolically regulated during the night by the conversion of polysaccharide to sucrose, and during the day by the process of phototranslocation. The structural integrity of the conduit is metabolically maintained, in that some light-dependent process controls the polarity of translocation in the blade (13, 14, 17).

The results of this investigation may be applied to an understanding of the effect of withholding water upon ripening cane. In this work a low moisture supply decreased photosynthesis less severely than translocation; but in more severe water stress in the field photosynthesis might stop completely. In the plants with low moisture supply, the process of translocation was slowed down presumably giving more time for the transfer of sucrose to storage. Growth was curtailed giving an excess of sugar for storage. Hydrolysis was decreased, which allowed more sucrose to be translocated, albeit slowly, to storage. Unless the moisture stress is very severe, no physiological argument appears from this investigation to be against the withholding of irrigation for the ripening of sugarcane.

Acknowledgments

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