# Light and Translocation of $C^{14}$ in Detached Blades of Sugarcane [1, 2]

**Constance E. Hartt**
Experiment Station of the Hawaiian Sugar Planters' Association, Honolulu, Hawaii

## Introduction

An effect of light upon the translocation of photosynthate has interested several investigators. Vernon and Aronoff (22) reported that light had no effect upon translocation from soybean leaves other than forming the translocate. However, different distributions of the translocate up and down the stem were obtained in the soybean in light and darkness (15, 20). Increases in translocation were obtained in bright light compared with shade in wheat (4), in rice (18), and in soybean (20). Peel and Weatherley (16) using leafy rooted cuttings of Salix reported that aphid stylet exudation responded immediately to light conditions of the leaves, more than half a meter below the site of assimilation. This response, however, was attributed to differences in diffusion pressure deficit. According to Jones and Eagles (12), the main mechanism resulting in translocation from leaves of tobacco and variegated *Pelargonium* appeared to be located in the veins and did not act in darkness. In the study of the diurnal periodicity of translocation in several plants, Anisimov et al. (1) found: A) in the potato, the rate of translocation was higher at night than by day; B) in the cucumber, the highest rate was between 2 and 4 PM; while C) in maize, the highest rate was between 10 AM and 2 PM. Anisimov concluded that special investigations were needed to determine whether the daily periodicity in translocation was due to growth processes, to a diurnal rhythm in the accumulation of carbohydrates, to the direction of enzyme transformations, or to periodic changes in the state of the protoplasm.

Nelson (14) stated that it is generally agreed that the major portion of translocation takes place by day. He also reported that light intensities of 250 and 2500 ft-c had little or no difference in their effects upon translocation to the roots of pine seedlings.

Thrower (21) reported that darkening a young, expanding leaf of soybean caused its premature abscission, decreased its growth, and depressed its importation of $C^{14}$-photosynthate made in the leaf next below it, although the length of time that import continued was lengthened. Similar results were obtained by supplying the leaf with $CO_2$-free air in the light. Therefore stopping photosynthesis in the young leaf did not increase its activity as a sink, but instead decreased its ability to import sugar. The ability of the darkened leaf to import sugar from below was increased by spraying with kinetin.

In sugarcane, translocation takes place by day and by night (11). The percentage of radioactivity translocated from the fed blade is greater by day than by night, and this difference is more conspicuous when the roots are maintained at 16.7° than at 22.2° (6, 7). Translocation from a blade was decreased by darkening it after administering the $C^{14}O_2$ (10). This effect was attributed to the need for further photosynthesis to wash the radioactive sugar out of the leaf and to enable the fed leaf to compete with other streams of translocating sugar.

In detached blades of sugarcane, translocation is basipetally polar; light or a light-formed factor is required; darkness reverses polarity; and sugar moves into darkened parts (9). It was suggested that the presence or absence of a sink, as well as the changes in the physico-chemical properties of protoplasm might play a role in the reversal of polarity in darkness. The small percentage of radioactive sucrose translocated basipetally in darkness by blades cut in the morning is not a starvation phenomenon, since standing cut blades with their bases in a solution of sucrose increased the concentration of sucrose in the blade but did not increase translocation, either basipetal or acropetal. Instead, there was a decrease in basipetal translocation, both in distance and in percentage. Neither is the small basipetal translocation due to a lack of respiratory energy in the dark, since a comparison of several tests indicated greater respiration in the dark than in the light (9).

Thus, studies with sugarcane have demonstrated a definite effect of light upon translocation. The effect of light was attributed to the need for further photosynthesis (10), to the presence or absence of a sink, and to possible changes in the physico-chemical properties of the protoplasm (9). In an attempt to determine which explanation is correct studies of the effects of duration, intensity, and quality of illumination were undertaken.

---

[1] Manuscript received January 4, 1965.

[2] Published with the approval of the Director as Paper No. 152 of the Journal Series of the Experiment Station, Hawaiian Sugar Planters' Association.

This paper reports work on the effect of the time of day, the time course of translocation, the duration, and the intensity of illumination, upon polarity and upon the percentage of translocation.

## Materials and Methods

The varieties of sugarcane used in these experiments were H 37-1933 and H 50-7209 described previously (9). The plants were grown in full light with adequate nutrition in the field at the Experiment Station. The detached blade method (9) was used. With the exception of experiment 1 (fig 1), all of the experiments reported in this paper were conducted with blades detached in the morning, before 8:30 A M. The methods of the application of $C^{14}O_2$, sampling, preparation, and counting were as previously described (11).

Light during preillumination and application of $C^{14}O_2$ to the detached blades was from water-cooled incandescent lamps. A General Electric light meter placed at the surface of the blade showed the light measurement to be 2000 ft-c.

To vary the intensity of the light during the periods of translocation, the blades were placed at different distances from General Electric cool-white fluorescent tubes and the number of the tubes was varied. Most of the experiments on light intensity were conducted in air-conditioned chambers with the temperature approximately 21°. In some tests, the cabinets were ventilated at room temperature but not thermostatically controlled. Low intensities of light were measured with a Norwood light meter. Higher intensities of radiation were measured with a General Electric radiation meter.

Carbon$^{14}$ results are expressed as: relative specific activity, which is the net cpm at infinite thickness; as relative total counts, which is the relative specific activity times the total dry weight in milligrams; and as percentage of relative total counts in the blade. Relative total counts in the blade is obtained by adding the relative total counts of each part.

## Results

*Time of Day.* Hartt and Kortschak (9) reported that blades detached from the plant in the early morning could not translocate in total darkness as well as blades detached in the afternoon, and the ability to translocate in the dark gradually increased during the day if the blades remained attached to the plant. The effect of light upon translocation in blades detached in the afternoon compared with blades detached in the morning was measured after 24 hours in the dark compared with 24 hours at 0.1 g-cal/cm$^2$ per minute (fig 1). In the light, the blades detached in the morning translocated better than the blades detached in the afternoon; but in the dark, the afternoon blades translocated better, confirming previous tests (9). Basipetal translocation in blades detached in the morning was increased 15.7 times by light. However, in blades detached in the afternoon, basipetal translocation was increased only 1.9 times by light. Acropetal translocation in the light was not affected by the time of day; but in the dark, acropetal translocation was considerably more in the blades detached in the morning than in those detached in the afternoon.

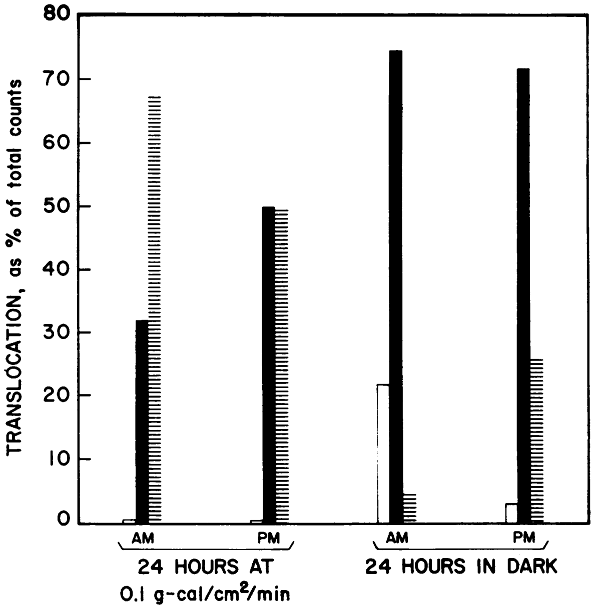

FIG. 1. Effect of time of day upon translocation in the light or the dark. The dosage, time and illumination during feeding were the same as in the legend to table I. The blades to translocate in the light were placed in the air-conditioned cabinets with light (supplied by alternating red and blue fluorescent tubes) which measured 0.1 g-cal/cm$^2$ per minute beside the blades. To translocate in the dark the blades were wrapped in aluminum foil and kept at room temperature. A M: The blades were cut at 8:30–8:40 A M on September 9. P M: The blades were cut at 2:10–2:20 P M on September 11. Each plot is the average of 4 blades. Designation: □, percent translocating to apex; ■, percent remaining in fed part; parallel lines, percent translocated to base.

These experiments indicate that basipetal translocation in sugarcane blades was better in the light than in the dark.

*Time Course of Translocation in Blades Detached in the Morning.* Translocation at 2000 ft-c (fig 2) was compared with translocation in similar blades with fed part plus apex darkened with foil (fig 3) for 0.5 to 6 hours. The blades in the light translocated primarily basipetally each time tested. The blades with fed part plus apex darkened with foil translocated much less than the blades in the light. Translocation with the fed part plus apex darkened was chiefly basipetal for 2 hours, and chiefly acropetal at 4 and 6 hours. With the fed part plus apex dark, sugar started toward the base but did not have

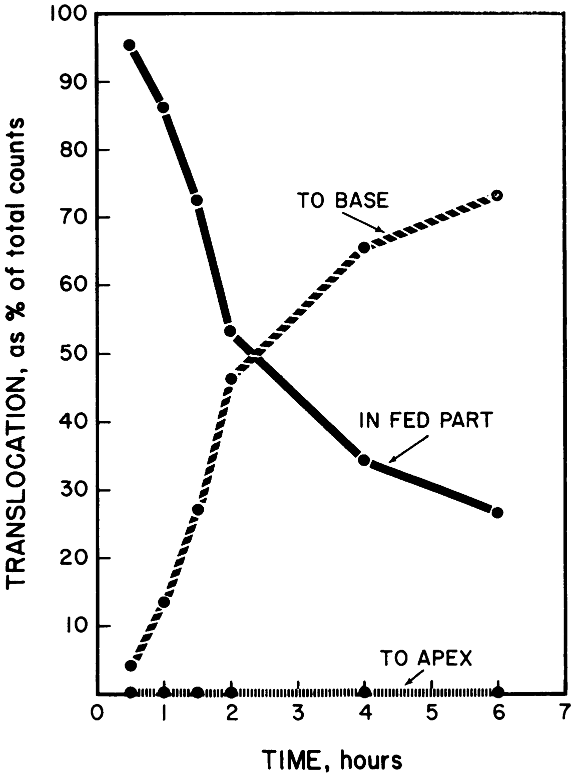

FIG. 2. Time-course of translocation for 0.5 to 6 hours in the light. The dosage, time and illumination during feeding were the same as in the legend to table I. Light during translocation was 2000 ft-c (incandescent illumination).

the necessary push to continue basipetal translocation throughout the experiment. That which could not go to the base during the first 2 hours remained in the fed part. Between 2 and 4 hours, the "door to the apex opened." The removal of radioactivity from the fed part to the apex increased, and some radioactive sugar that had already gone to the base returned back up to the apex. In other words, between 2 and 4 hours, something happened which resulted in a reversal of polarity.

To sharpen the time of reversal of polarity, the experiment was repeated with sampling every half hour from 1 to 4 hours. Translocation with the fed part plus apex darkened with foil was not as much as in the previous test but showed the same trend. A reversal in polarity took place between 2.5 and 3 hours.

Thus, acropetal translocation rather than basipetal, in morning blades with fed part plus apex dark, started at about 3 hours.

*Duration of Light.* The effect of intermittent light upon blades detached in the morning was studied by brief exposure of darkened blades to 2000 ft-c illumination for a few seconds every 30 minutes. Translocation was no better than in continuous darkness.

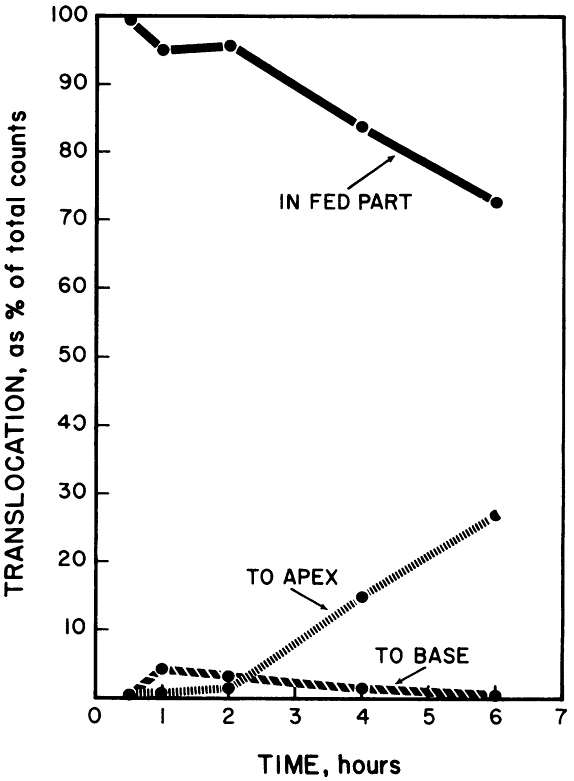

FIG. 3. Time-course of translocation for 0.5 to 6 hours with the fed part plus the apex darkened with foil. The dosage, time and illumination during feeding were the same as in the legend to table I.

Table I. *Effect of Intermittent Light upon Translocation*

$C^{14}O_2$ (10 μc) was fed to a 20-cm portion of blade 5 for 5 minutes at 2000 ft-c. After removing the feeding chamber, the blades to translocate in the dark were wrapped in aluminum foil. The blades to receive intermittent light were placed in the dark room and exposed to 2000 ft-c for 5 minutes every 30 minutes for 6 hours.

| Part | Entirely in dark | | Intermittent light | |
|---|---|---|---|---|
| A. Distribution as % of relative total counts | | | | |
| Apex | 1.5 | 1.0 | 0.2 | 0.5 |
| Fed | 79.4 | 86.6 | 76.8 | 85.6 |
| Base | 19.1 | 12.4 | 23.0 | 14.0 |
| RTC × $10^6$ | 5.4 | 5.4 | 5.3 | 6.2 |
| B. Relative specific activity as cpm | | | | |
| A2* | 10 | 10 | 0 | 10 |
| A1 | 160 | 120 | 30 | 30 |
| Fed | 4210 | 5190 | 4770 | 4860 |
| B1* | 1060 | 930 | 1870 | 1090 |
| B2 | 550 | 270 | 760 | 390 |
| B3 | 330 | 110 | 190 | 120 |
| B4 | 140 | 20 | 40 | 30 |
| B5 | 20 | 0 | 0 | 0 |

* A = Apical sections, above the fed part; B = Basal sections, below the fed part.

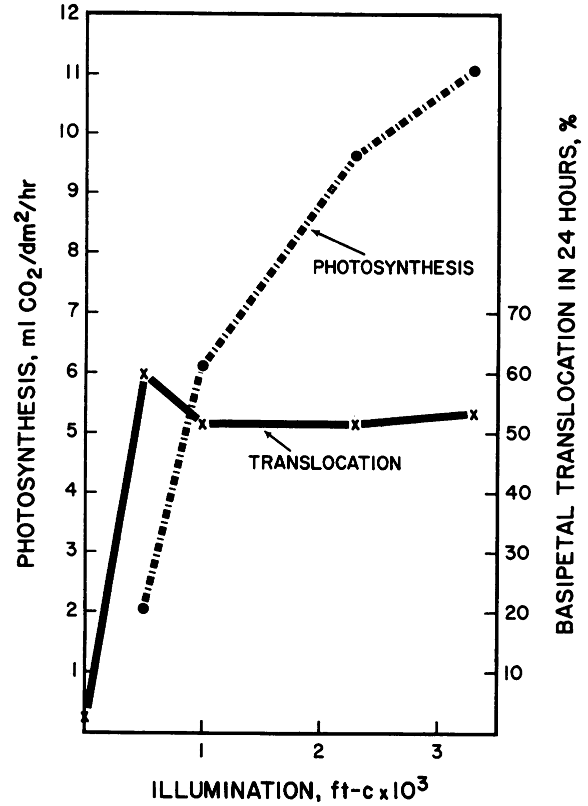

FIG. 4. Effect of light intensity upon photosynthesis and translocation in blades from the same plot: blade 5 of the variety H 50–7209. Photosynthesis was measured with the infrared analyzer, at 500, 1000, 2300, and 3300 ft-c. Translocation was measured at the same intensities of light and in the dark.

Table II. *Effect of Darkness after Illumination for 6 Hours*

| Part | 6 hr at 2000 ft-c | | 6 hr at 2000 ft-c + 18 hr in foil | | 24 hr in foil | |
|---|---|---|---|---|---|---|
| | Distribution as % of relative total counts | | | | | |
| Apex | 0.3 | 0.2 | 8.4 | 4.2 | 15.8 | 18.4 |
| Fed | 45.5 | 40.3 | 46.9 | 48.9 | 68.5 | 74.2 |
| Base | 54.2 | 59.6 | 44.6 | 46.9 | 15.7 | 7.4 |
| RTC × $10^6$ | 15.3 | 14.5 | 16.0 | 14.5 | 9.4 | 9.5 |

Lengthening the time of the 2000 ft-c exposure to 5 minutes had no effect upon basipetal translocation (table I). However, the 5-minute periods of light were apparently sufficient to keep acropetal translocation in the normal range, as shown by the relative specific activity of the Al part (table IB). Thus, the 5-minute exposures to light were sufficient to control polarity but not enough to drive basipetal translocation. Apparently, less light is needed to control polarity than to drive basipetal translocation.

The reversal of polarity by darkness, in blades detached in the morning, could take place even after exposure to 2000 ft-c for 6 hours (table II). Additional translocation in the dark, after 6 hours at 2000 ft-c, was all acropetal. The percentage data indicate that some of the radioactive sugar which had gone to the base while in the light, went back up toward the apex in the subsequent darkness. The blades in the light for 6 hours followed by darkness did not differ appreciably in relative total counts from the blades in the light. The blades in the dark, however, definitely had less total radioactivity. Apparently the loss in total activity, which was associated with darkening the fed part and attributed to respiration (9), was prevented by the 6-hour exposure to light.

*Intensity of Light.* Photosynthesis in sugarcane, measured with the infrared analyzer, saturated at 5000 to 7000 ft-c in the varieties used in this investigation (8). Since basipetal translocation in detached blades was better in the light than in darkness (9) (fig 1), tests were conducted to determine the light saturation value for translocation and compare it with the light saturation value for photosynthesis in similar blades of the same variety.

Translocation and photosynthesis were measured in blade 5 of variety H 50-7209 at 500 to 3300 ft-c (fig 4). Basipetal translocation was saturated at 500 ft-c, the lowest intensity used, whereas the assimilation of $CO_2$ increased rapidly from 500 ft-c.

When the low level of light intensity was extended down to 250 ft-c (fig 5), basipetal translocation was saturated at that level whereas photosynthesis was very weak. The compensation point was located at

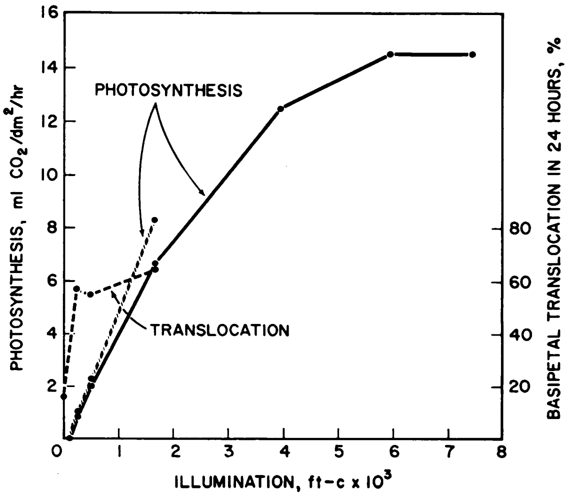

FIG. 5. Light saturation and compensation point for photosynthesis in blade 5 of the variety H 50-7209, measured with the infrared analyzer, compared with basipetal translocation in similar blades.

120 to 125 ft-c (fig 5). The saturation of translocation at 250 ft-c in this experiment agrees with the results reported by Nelson (14) who stated that intensities of 250 and 2500 ft-c had little or no difference in effect upon translocation to roots in young pine seedlings.

No significant differences in basipetal translocation were obtained until the intensity of illumination was reduced to 50 ft-c (fig 6). When all the results for the variety H 50-7209, blade 5, illuminated or in the dark for 24 hours (a total of 17 tests and 67 blades) were studied statistically, the differences for basipetal translocation were significant at the 0.01 level comparing 0 with 50 and 50 with 100 ft-c. But the differences from 100 to 3300 ft-c were not significant. Basipetal translocation for 24 hours was, therefore, saturated at 100 ft-c.

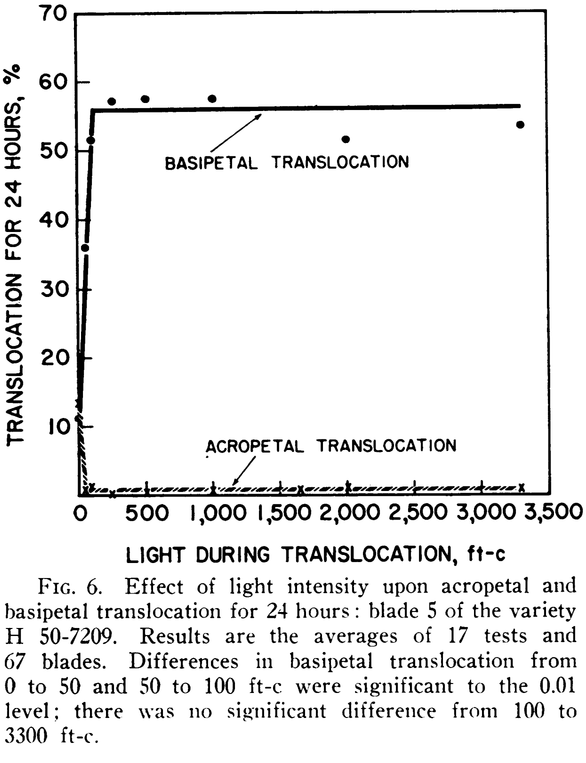

FIG. 6. Effect of light intensity upon acropetal and basipetal translocation for 24 hours: blade 5 of the variety H 50-7209. Results are the averages of 17 tests and 67 blades. Differences in basipetal translocation from 0 to 50 and 50 to 100 ft-c were significant to the 0.01 level; there was no significant difference from 100 to 3300 ft-c.

The factor preventing acropetal translocation (and therefore controlling polarity) was saturated at only 50 ft-c (fig 6). These results indicate that less light is required to control polarity than to drive basipetal translocation. This finding is in agreement with the results on duration of light.

The experiments on intensity of light show that translocation is a low light intensity process.

## Discussion

The object of this investigation was to determine, if possible, whether light has any effect upon translocation other than to make the sugar which is translocated. The results appear to indicate that light may affect 2 aspects of translocation, the polarity or direction of movement, and the percentage of basipetal transport.

The effect of light upon polarity appears not to be connected with further photosynthesis in $C^{12}O_2$ after the photosynthetic production of radioactive sucrose, for the following reasons. There was much less effect of light upon polarity in the blades detached in the afternoon than in the blades detached in the morning, although both sets of blades in the light were presumably making $C^{12}$ sucrose. Moreover, the factor controlling polarity was saturated at a light intensity of only 50 ft-c, which is well below the compensation point for photosynthesis.

Basipetal translocation was significantly increased by an illumination of 50 ft-c and was saturated at 100 ft-c. If further photosynthetic assimilation of $CO_2$ were the explanation for the stimulating effect of light upon translocation, there should be a net uptake of $CO_2$. It is true that the photosynthetic pool may be small and not much uptake required for the photosynthetic pool to overflow into translocation. But without a net uptake, could there be an overflow? Because basipetal translocation was saturated at a light intensity below the compensation point, it appears to the writer that basipetal translocation was independent of the assimilation of $CO_2$. The independence of translocation and the assimilation of $CO_2$ was previously demonstrated by Shiroya et al. (19), who found better translocation in a pine seedling illuminated at the $CO_2$ compensation point (66 ppm) than in one at 400 ppm $CO_2$.

Because basipetal translocation was increased by light intensities which give no net uptake of $CO_2$, and thus was apparently independent of the assimilation of $CO_2$, some other explanation is needed for the effect of light upon translocation. Because of these results the writer has referred to the possibility that translocation is under photocontrol (7). There may be alternative interpretations. A tentative suggestion is that light controls translocation by an electrokinetic mechanism similar to that proposed by Fensom (3), or by the formation of ATP known to be important in translocation (13). The process of photosynthetic phosphorylation is also independent of the assimilation of $CO_2$ (2) and could be the source of energy which drives the translocation of sugar.

Many factors are involved in translocation. It is not suggested that light is the only one concerned. With an attached leaf the pull from below is strong (9), especially the pull from the young, growing parts which may be due to kinetin (21). Removal of the pull from the stalk by detachment of the blade facilitates the study of the push from the leaf. More work is needed on the effect of light upon translocation. However, the finding that light or a light formed factor is essential for the translocation of sugar (9), which is saturated below the compensation point, suggests that this transport may actually be a phototranslocation. The possibility of a phototranslocation might be of interest to investigators of photomorphogenesis and other photoregulated processes in plants, since the supply of available carbohydrate affects photomorphogenesis, according to Schwabe (17).

If the transport of sugar from the leaf were indeed initiated by a phototranslocation, this would give a built-in mechanism for the coordination of photosynthesis and translocation now considered essential for maximum yield in sugarcane (5). The slowing down of translocation causes an accumulation of sugar in the blade, which results in an inhibitory effect upon the assimilation of $CO_2$ in that blade (6, 8). A decrease in the assimilation of $CO_2$ means less ATP and TPNH are being used; hence, more energy is available for translocation, and excess sugar is removed from the leaf, which facilitates an increase in the rate of assimilation. So the 2 processes of photosynthesis and phototranslocation continue, both dependent upon light, leading to maximum production by the plant.

## Summary

Investigations are reported on the effect of light upon translocation of $C^{14}$ in detached blades of sugarcane, including the time of day when the blades were detached, the time course of translocation, intermittent illumination, light followed by darkness, and the intensity of illumination.

Aspects of translocation which were affected by light were polarity and the percentage of translocation.

The change in polarity with light and darkness was greater in blades detached in the morning than in blades detached in the afternoon. Therefore, experiments designed to study this phenomenon were conducted with blades detached in the morning.

Darkening the apex plus fed part, after removing the feeding chamber, resulted in a reversal in polarity. This reversal did not take place immediately but after 2 or 3 hours.

To control polarity, light did not have to be continuous. Exposure of the blades to 2000 ft-c for periods of 5 minutes alternating with periods of 25 minutes in absolute darkness, was apparently sufficient to keep acropetal translocation in the normal range.

Sensitivity of the system controlling polarity was not lost even after exposure to 2000 ft-c for 6 hours. Part of the radioactive sugar which was translocated basipetally during the 6 hours at 2000 ft-c was retranslocated acropetally during the subsequent period in darkness.

The factor controlling polarity was saturated at 50 ft-c.

Basipetal translocation, measured as percentage of total counts, was better in the light than in the dark and (in the light) better in blades detached in the morning than in blades detached in the afternoon.

Total translocation (acropetal plus basipetal) was greater in the light than in the dark. The superiority of translocation in the light could be detected even in one-half hour. After 2 hours, and associated with the reversal in polarity, the percentage of counts translocated from the fed part was almost as great in the dark (chiefly acropetal) as in the light (chiefly basipetal).

Exposure of the blades to 2000 ft-c for periods of 5 minutes alternating with total darkness for periods of 25 minutes, was not enough to drive basipetal translocation.

The factor controlling basipetal translocation was saturated at 100 ft-c.

The photosynthetic assimilation of carbon dioxide in blades of the same variety, the same rank, and from the same plot, measured with the infrared analyzer, saturated at 6000 ft-c. The compensation point was located at 120 to 125 ft-c.

Because light affected translocation at intensities which allow no net uptake of carbon dioxide, the effect of light upon translocation is not due merely to the washing out effect of further photosynthesis in ordinary carbon dioxide.

The suggestion is made that the initiation of translocation of sugar from the leaf is under photocontrol.

## Acknowledgments

The author is grateful to Miss Ada Forbes and Mrs. Grace Sadaoka for technical assistance.

It is a pleasure to acknowledge helpful suggestions received from Sterling B. Hendricks, James Lockhart, and George O. Burr during various stages in the preparation of the manuscript.

## Literature Cited

1. Anisimov, A. A., E. K. Fuzina, L. A. Dobryakova, and E. V. Likhovidova. 1963. Diurnal periodicity in translocation of assimilates. Doklady Akad. Nauk SSSR, Biol. Sci. Sec. 146: 1166–69. (Eng. transl.)
2. Arnon, D. I. 1956. Phosphate metabolism and photosynthesis. Ann. Rev. Plant Physiol. 7: 325–54.
3. Fensom, D. S. 1957. The bio-electric potentials of plants and their functional significance. I. An electrokinetic theory of transport. Can. J. Botany 35: 573–82.
4. Grodzinskii, D. M. 1959. The problem of the transport of nutrient substances in the leaves of winter wheat. Nauch. Trudy Ukrain. Nauch-Issledovatel. Inst. Fiziol. Rastenii 20: 53–58. (Transl.) (Biol. Abs. 37: 667, 1962.)
5. Hartt, C. E. 1963. Translocation as a factor in photosynthesis. Naturwissenschaften 21: 666–67.
6. Hartt, C. E. 1964. Translocation of sugar in the cane plant. 1963 reports, 22nd Ann. Conf., Hawaiian Sugar Technologists. 151–67.

7. Hartt, C. E. 1965. The effect of temperature upon translocation of $C^{14}$ in sugarcane. Plant Physiol. 40: 74–81.
8. Hartt, C. E. and G. O. Burr. 1965. Factors affecting photosynthesis in sugarcane. Proc. Intern. Soc. Sugarcane Technologists, 12th Congr. 1965. (In press).
9. Hartt, C. E. and H. P. Kortschak. 1964. Sugar gradients and translocation of sucrose in detached blades of sugarcane. Plant Physiol. 39: 460–74.
10. Hartt, C. E., H. P. Kortschak, and G. O. Burr. 1964. Effects of defoliation, deradication, and darkening the blade upon translocation of $C^{14}$ in sugarcane. Plant Physiol. 39: 15–22.
11. Hartt, C. E., H. P. Kortschak, A. J. Forbes, and G. O. Burr. 1963. Translocation of $C^{14}$ in sugarcane. Plant Physiol. 38: 305–18.
12. Jones, H. and J. E. Eagles. 1962. Translocation of carbon$^{14}$ within and between leaves. Ann. Botany (London) NS 26: 505–10.
13. Kursanov, A. L. 1963. Metabolism and the transport of organic substances in the phloem. Adv. Botan. Res. 1: 209–78.
14. Nelson, C. D. 1963. Effect of climate on the distribution and translocation of assimilates. In: Environmental Control of Plant Growth, L. T. Evans, ed. Academic Press, New York, 449 pp. p 149–73.
15. Nelson, C. D. and P. R. Gorham. 1957. Uptake and translocation of $C^{14}$-labeled sugars applied to primary leaves of soybean seedlings. Can. J. Botany 35: 339–47.
16. Peel, A. J. and P. E. Weatherley. 1962. Studies in sieve-tube exudation through aphid mouth-parts: The effect of light and girdling. Ann. Botany (London) NS 26: 633–46.
17. Schwabe, W. W. 1963. Morphogenetic responses to climate. In: Environmental Control of Plant Growth. L. T. Evans, ed. Academic Press, New York. p 311–34.
18. Shen, G. M. 1960. Translocation and distribution of assimilates from the leaves of rice plant during its various developing periods–experiments with radioactive carbon ($C^{14}$). (In Chinese with Eng. sum.). Acta Agric. Sinica 11: 30–40. (Biol. Abs. 35: 4648–49. 1960.)
19. Shiroya, T., G. R. Lister, V. Slankis, G. Krotkov, and C. D. Nelson. 1962. Translocation of the products of photosynthesis to roots of pine seedlings. Can. J. Botany 40: 1125–35.
20. Thrower, S. L. 1962. Translocation of labeled assimilates in the soybean. II. The pattern of translocation in intact and defoliated plants. Australian J. Biol. Sci. 15: 629–49.
21. Thrower, S. L. 1964. Translocation of labeled assimilates in the soybean. III. Translocation and other factors affecting leaf growth. Australian J. Biol. Sci. 17: 412–26.
22. Vernon, L. P. and S. Aronoff. 1952. Metabolism of soybean leaves. IV. Translocation from soybean leaves. Arch. Biochem. Biophys. 36: 383–98.