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# Effects of Moisture Deficits on $^{14}C$ Translocation in Corn (*Zea mays* L.)[1]

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E. R. BREVEDAN[2] AND H. F. HODGES
*Department of Agronomy, Purdue University Agricultural Experiment Station, West Lafayette, Indiana 47907*

## ABSTRACT

**Corn plants (*Zea mays* L.) were grown in the field on two soils. On a droughty soil, water was withheld from some plants during the grain-filling period while other plants were irrigated. Carbon-14 was fed to the leaves, and translocation to different plant parts was determined. Translocation appeared to be more sensitive to moisture stress than was photosynthesis. More radioactive carbon was retained in both the fed portion and the nonfed portion of the leaf of stressed plants than in nonstressed plants. The stalk segment between the treated leaf and ear-node also contained less radioactivity in stressed plants than in nonstressed plants. On a soil with higher water-holding capacity, moisture stress was imposed on plants by root pruning. Plants under severe stress continued to translocate photosynthetically assimilated $^{14}C$ nearly as well as nonstressed plants for 90 minutes. Between 90 and 120 minutes after labeling, there was a major reduction in amount translocated in stressed plants compared to the nonstressed plants. At longer translocation times the rates of translocation appeared again to be more nearly equal.**

Almost every plant process is affected directly or indirectly by water deficits. Some processes are quite sensitive to water stress, but others are relatively insensitive. When plants are subjected to water stress, there is a decrease in photosynthesis and cell enlargement (10). There is considerable retention of carbohydrates in photosynthetic tissues (8, 10). Although translocation proceeds, its rate is reduced (3, 6, 10). Reduced translocation is rarely mentioned as a factor in reduced plant growth under limited moisture. This is surprising, since the pressure flow hypothesis would require a pressure potential gradient between the leaves and the receiving organs before any translocation of sugars could occur. Such a pressure potential gradient would be reduced as the internal moisture deficit increased. If this hypothesis is correct, translocation could be one of the chief physiological factors limiting growth under unfavorable moisture conditions. Quantitative measurements of water stress imposed on plants during a translocation study are rare. This study was conducted to determine the effects of plant water stress on the translocation and distribution of $^{14}C$ photosynthate in corn plants during the grain-filling period.

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[2] Present address: Department of Agronomy, University of Kentucky, Lexington, Ky.

## MATERIALS AND METHODS

**Experiment I.** Corn seeds (*Zea mays* L., PAG SX-29 single cross) were planted by hand, two seeds per hill, on June 1, 1971. Row spacings of 75 cm, with 60 cm between hills within a row gave a population of 44,440 plants/ha. Each of four plots contained 19 rows with 26 plants/row. Two plots were irrigated and two were not irrigated ("dry treatment"). The soil was Warsaw sandy loam with a low water-holding capacity.

Treatments were imposed after 54 days growth. For the dry treatment, the soil was completely covered with plastic sheets 90 cm wide which did not allow the penetration of rain. The plants in the irrigated treatment were watered regularly using perforated plastic hose lines between rows.

Measurements of soil moisture content were made with a neutron probe (Troxler Model 104) at 30-cm increments of soil depth via an aluminum tube installed in the center of each plot to a depth of 120 cm. Observations were made at 7-day intervals.

Leaf water potential values were determined by the pressure chamber technique developed by Scholander *et al.* (7). Paired plants in each hill allowed the determination of leaf water potential on one plant while the other was being fed $^{14}CO_2$. The second leaf above the ear was used for both leaf water potential measurements and feeding $^{14}CO_2$.

Pollination started on July 28, and silking dates were recorded for each plant. On August 19 and 22, 19 days after pollination, 40 plants with one ear were selected at random. A segment (10 × 7 cm) of the second leaf above the ear (approximately 60 cm from the leaf collar) was enclosed in a Plexiglas chamber (total internal volume approximately 190 $cm^3$) in which approximately 50 $\mu c$ of $^{14}CO_2$ were generated. The leaf was exposed to $^{14}CO_2$ for 5 min, after which the chamber was removed. All labeling was done between 10:30 AM and 2:30 PM.

Translocation times, which did not include feeding time, were: 0, 60, 120, and 360 min, selected on the basis of Eastin's results (2). Six plants were used for each translocation time.

The temperature during the experiment varied between 26 and 32 C. Solar radiation during the feeding period averaged 65.4 and 54.7 langleys/hr on August 19 and August 22, respectively.

The plants were harvested and individually separated into $^{14}CO_2$-treated part of the fed leaf, the remainder of that leaf, the stalk between the node of the treated leaf and the node of the ear, the husk and shank, and the kernels which were divided into three equal parts: the portion on the bottom of the ear, the portion on the middle, and the portion on the tip of the ear. Plants harvested 360 min after feeding were individually separated into the same parts as the others, plus all the leaves below the ear, all the leaves above the fed leaf, the

first leaf above the ear, the ear leaf, the stalk above the treated leaf, the stalk below the ear, and the tassel.

The plants were excised, dissected, and immediately frozen at −15 C. The samples were dried, weighed, and ground. Two 10-mg subsamples were taken from each sample (except in the case of the treated leaf part, from which three subsamples were taken). These were digested in 0.5 ml of a mixture of $HClO_4$ and $H_2O_2$ (1:1), heated for 3 hr at 65 C, and then 10 ml of a mixture consisting of 500 ml of 2-ethoxyethanol, 500 ml of toluene, and 4 g of Omnifluor were added.

All radioactive measurements were made in a liquid scintillation spectrometer (Packard Tricarb Model 3003). Samples were counted for 10 min or to a total of 100,000 counts, whichever came first. Values for all samples were corrected for background radiation and quenching.

The amount of $^{14}C$ in each plant part was expressed as per cent distribution of the "relative total activity" (counts/min · mg × weight of the part plan/the sum of the radioactivity in all plant parts).

Of the remaining plants with only one ear, 45 were chosen at random from each treatment, and the ear was harvested after ripening. These samples were dried, and the kernel weight for each sample was determined.

**Experiment II.** Corn was planted May 28 on a Chalmers silty clay loam (a soil with relatively high water-holding capacity). Row spacing was 75 cm, distance of plants within the row was 20 cm, and density of plants 66,700 plants/ha. Pollination of the treated plants was on July 27.

Three treatments were imposed: (1) normal plants, (2) plants with part of the roots cut, and (3) plants without roots. The morning of the day before feeding the plants with $^{14}CO_2$, a trench was dug along the row on both sides at a distance of approximately 15 cm from the plants. This treatment removed many of the roots but left some supporting the plant. Plants in that row were selected at random to be used for treatments 2 and 3. The plants for treatment 3 were removed from the soil with approximately 1 $dm^3$ of soil and roots after feeding them with $^{14}CO_2$. The stem was immediately recut underwater to ensure water continuity to the stem and leaves, and left standing with the base of the stalk in the container of water. Plants for treatment 1 were selected at random from adjacent undamaged rows.

Plants with only one ear were used in all cases. The selected plants were fed $^{14}CO_2$ as described in experiment 1. Translocation periods were 0, 0.5, 1, 1.5, 2, 4, 8, 20 hr, 2 and 4 days.

Solar radiation was recorded at a weather station about 200 m from this experimental site. Solar radiation averaged 61.9, 70.3 and 68.4 langleys/hr on August 10, 12, and 17, respectively, the days when plant labeling occurred.

Table I. *Average Leaf Water Potential Observed Hourly During the Translocation Period of Experiment I*

| Time from Exposure to $^{14}CO_2$ | Irrigated | Dry |
|---|---|---|
| *hrs* | *−bars* | |
| 0 | 13.4 | 17.9 |
| 1 | 15.3 | 20.2 |
| 2 | 17.6 | 21.8 |
| 3 | 16.7 | 20.8 |
| 4 | 15.6 | 19.6 |
| 5 | 13.6 | 17.9 |
| 6 | 11.9 | 16.6 |

Table II. *Soil Water Content (Percentage Volume Basis) and Soil Moisture Tension Before and After Labeling*

| Depth | Aug. 17 | | Aug. 24 | |
|---|---|---|---|---|
| *cm* | % | *−bars* | % | *−bars* |
| Not irrigated | | | | |
| 0–30 | 11.0 | <15.0 | 9.0 | <15.0 |
| 31–60 | 15.1 | 5.0 | 13.0 | 10.5 |
| 61–90 | 15.8 | 4.1 | 14.2 | 7.5 |
| 91–120 | 15.2 | 4.7 | 15.3 | 4.8 |
| Irrigated | | | | |
| 0–30 | 28.6 | 0.4 | 32.1 | 0.2 |
| 31–60 | 31.0 | 0.2 | 34.8 | 0.1 |
| 61–90 | 27.0 | 0.6 | 29.4 | 0.3 |
| 91–120 | 13.8 | 8.0 | 14.6 | 5.6 |

## RESULTS AND DISCUSSION

**Experiment I.** Plants did not show signs of wilting, even though there were differences in plant water potential as shown by the pressure chamber data in Table I. The plant water potential changed during the translocation period reflecting the evaporative demand associated with insulation and temperature. Water volume percentages in the soil (Table II) decreased, particularly in the surface layer (0–30 cm) under the dry treatment. Soil water was at tensions normally considered available to plants only at depths greater than 30 cm. The control plots had only slight fluctuations of soil water content and were maintained near field capacity during the experiment.

The distribution of $^{14}C$-photosynthates at various times after labeling are shown in Table III. In this experiment each plant

Table III. *Distribution Percentages and Standard Deviations of $^{14}C$ in Various Plant Parts Relative to Total Activity Recovered, Experiment I*

Data are means of three replications.

| Translocation Period | Treatment | Treated Part of Fed Leaf | Remainder of Fed Leaf | Stalk between Treated Leaf Node and Ear Node | Husk and Shank | Kernels | Stalk below Ear Node | Activity Recovered |
|---|---|---|---|---|---|---|---|---|
| *hr* | | % ± *SD* | | | | | | *cpm* × $10^{-3}$ |
| 0 | Irrigated | 98.3 ± 2.0 | 1.7 ± 2.1 | ... | ... | ... | . | 3215 |
| | Dry | 97.3 ± 2.1 | 2.7 ± 2.1 | ... | ... | ... | ... | 2733 |
| 1 | Irrigated | 55.9 ± 3.6 | 22.2 ± 1.2 | 18.0 ± 0.8 | 1.7 ± 1.2 | 2.2 ± 1.5 | ... | 5248 |
| | Dry | 64.6 ± 1.5 | 25.1 ± 1.6 | 7.0 ± 1.1 | 1.8 ± 0.6 | 1.6 ± 1.0 | ... | 4206 |
| 2 | Irrigated | 41.9 ± 3.7 | 7.6 ± 2.1 | 20.6 ± 3.3 | 11.2 ± 1.0 | 18.6 ± 2.0 | ... | 4065 |
| | Dry | 58.1 ± 1.9 | 20.5 ± 3.8 | 6.9 ± 1.1 | 3.4 ± 0.5 | 11.0 ± 0.9 | ... | 3617 |
| 6 | Irrigated | 24.3 ± 2.9 | 5.8 ± 1.0 | 13.4 ± 0.8 | 8.6 ± 0.4 | 40.0 ± 3.0 | 7.8 ± 0.4 | 5048 |
| | Dry | 39.5 ± 3.2 | 18.2 ± 2.9 | 7.5 ± 1.3 | 3.9 ± 0.9 | 23.4 ± 3.9 | 7.5 ± 1.3 | 3512 |

Table IV. *Average Hourly Leaf Water Potential During the First 8 Hr of the Translocation Period of Experiment II*

| Time from Exposure to $^{14}CO_2$ | Treatment | | |
|---|---|---|---|
| | 1 | 2 | 3 |
| *hr* | *—bars* | | |
| 0 | 14.8 | 18.7 | 19.3 |
| 2 | 20.0 | 25.1 | 25.3 |
| 4 | 17.6 | 22.6 | 26.2 |
| 6 | 15.0 | 19.0 | 21.5 |
| 8 | 12.1 | 16.4 | 18.5 |

was exposed to $^{14}CO_2$ for exactly 5 min. The plants in the irrigated plots absorbed an average of 20% more $^{14}C$ than did those in the stressed plots. Sixty per cent more labeled assimilate was retained in the treated segment of the stressed plants than in those of the nonstressed plants after 6 hr. A greater portion of the label was also retained in the remainder of the fed leaf in the stressed plants than in that of the irrigated plants. This appeared to be the case at all time intervals. The lower percentage values in the untreated portion of the leaf of the irrigated plants may have been caused by a higher flux of labeled assimilates through the intervening tissue. Perhaps there was a greater accumulation of label in the leaves of stressed plants due to more mixing of the translocated stream with pools of soluble sugar in the mesophyll cells near the translocate stream than in the nonstressed plants. A lower flux through the conducting cells would provide more time to allow such exchange to take place and explain this result.

A substantial amount of the assimilated $^{14}C$ had been translocated to the kernels within 2 hr after labeling. The kernels of stressed plants had only 59% as many counts as the kernels of irrigated plants at both 2 and 6 hr. These differences are greater than the 20% differences in amounts of $^{14}C$ fixed at 0 hr, suggesting that translocation may be more sensitive to stress than is photosynthesis. Hartt (3) also observed that translocation in sugarcane was more sensitive to moisture stress than photosynthesis. The stalk segment between the treated leaf and the ear as well as the husk and shank segments appeared to function as tissue through which the labeled assimilate was transported, with no evidence that more accumulated in these areas of the stressed than of the nonstressed plants. In fact, more radioactivity was contained in the intervening stalk segments of the irrigated plants than of the stressed plants. The stalk below the ear node accumulated small amounts of radioactivity, but differences between treatments were insignificant. The remaining plant segments were found to contain insignificant levels of radioactivity 6 hr after labeling and data are, therefore, not reported.

Since no differences in specific activity were found at any time among the three divisions of kernels (from the butt, midsection, or tip of the ear), the data are not presented. Highly significant differences in yield were observed between the plants grown without irrigation after July 24 and the irrigated plants. The average kernel weight/ear was 195.4 g for the control plants and 165.4 g for the stressed plants.

**Experiment II.** Wilting occurred in treatments 2 and 3. Wilting was more severe, especially in treatment 3, during the longer translocation times, *i.e.* times > 4 hr. Table IV shows the leaf water potentials observed at different times after labeling the plant. Average leaf water potentials of −15.9, −20.3, and −22.2 were observed for treatments 1, 2, and 3, respectively.

Translocation patterns of photosynthetically assimilated $^{14}C$ from the leaves are presented in Figures 1 and 2. The average number of cpm/plant recovered for treatments 1, 2, and 3, respectively, were $4013 \times 10^3$, $3564 \times 10^3$, and $3576 \times 10^3$. The percentage of $^{14}C$ remaining in the fed area after 1.5 hr of translocation was significantly different among treatments. The loss of $^{14}C$ from the fed area of control plants was rapid, about 60% moving out in 2 hr, and a total of more than 75% in 8 hr (Fig. 1). However, significant amounts of the assimilated $^{14}C$ were retained in the fed area of plants in treatments 2 and 3.

The control plants translocated more than 60% of the assimilated $^{14}C$ from the leaf by 4 hr. This value is similar to that found by Eastin (2) in corn during grain filling and by Hartt (3) in sugarcane, but is lower than that observed by Hofstra and Nelson (4) in corn seedlings. Approximately 8 hr were required for the leaf to export 50% of $^{14}C$ photoassimilated in plants from which all roots were excised. Less than 5% of the $^{14}C$ was found after 4 hr in the portion of the fed leaf not labeled in treatment 1, but in the case of plants under water stress, the percentage of $^{14}C$ was greater, approximately three times greater in treatment 3 plants than in treatment 1 plants. The assimilated $^{14}C$ was retained at a fairly steady high level in the nonfed portion of the leaves of plants in treatment 3 for several hours; after 20 hr the concentration of $^{14}C$ decreased.

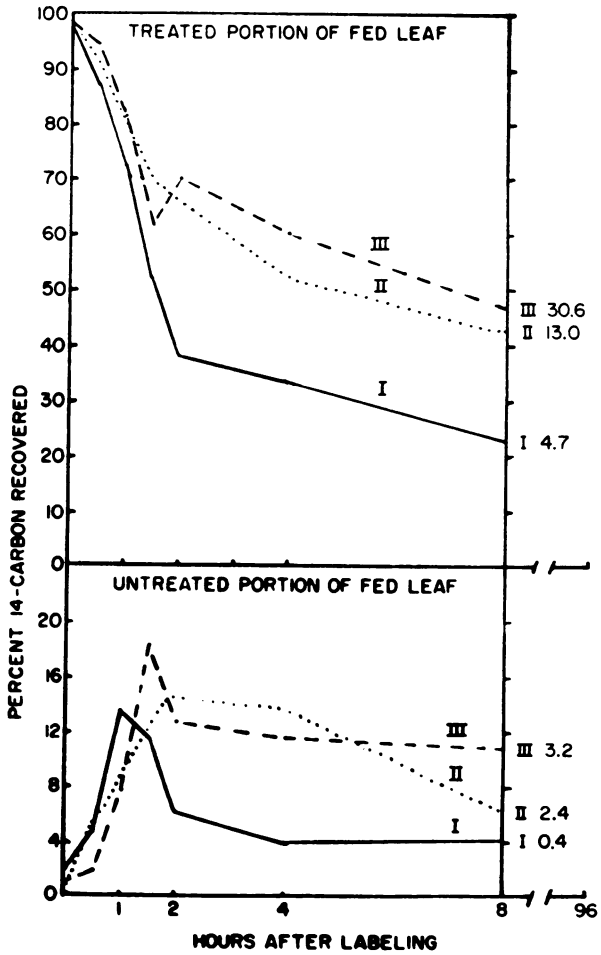


FIG. 1. Percentages of recovered radioactivity in fed portion and in the remainder of labeled leaf. I: no root removal; II: partial root removal; III: complete removal during translocation period. Values in margin are percentages of total radioactivity remaining in tissue 96 hr after labeling the plants.

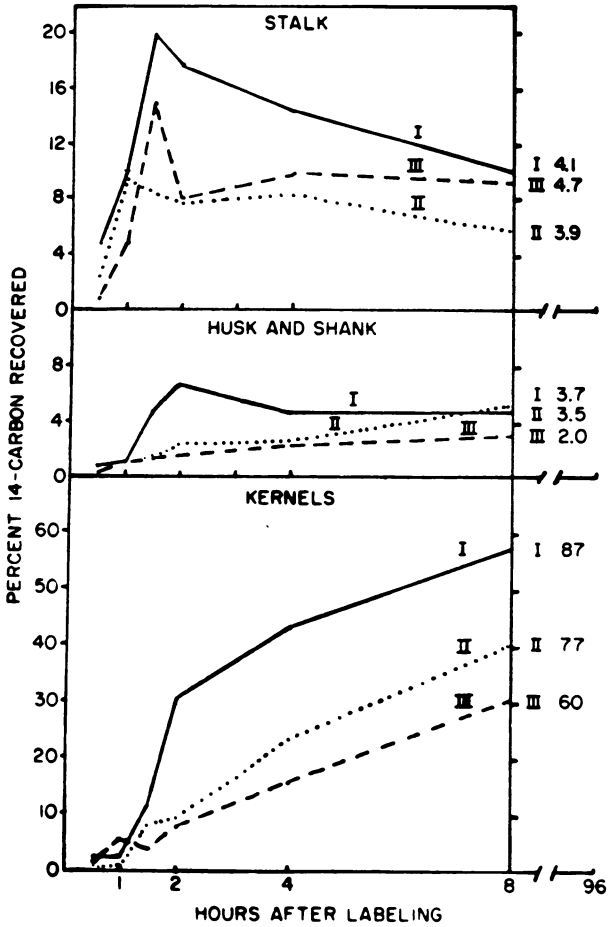


FIG. 2. Percentages of recovered radioactivity in stalk segment between labeled leaf node and ear node, husks and shank, and kernels. I: no root removal; II: partial root removal; III: complete root removal during translocation period. Values in margin are percentages of total radioactivity remaining in tissue 96 hr after labeling the plants.

Higher (less negative) plant water potentials during the night may have allowed translocation of that carbohydrate.

Accumulation of $^{14}C$-photosynthates in kernels continued throughout the translocation period but was slower in treatment 2 and especially in treatment 3. Forty per cent of the $^{14}C$ recovered was found in the kernels at approximately 3, 8, and 20 hr in treatments 1, 2, and 3, respectively.

The levels of $^{14}C$ constituents in the labeled portions of the fed leaves were significantly different only after 60 to 90 min. Whether the stress treatments affected rate of movement through the phloem, as suggested by the higher values obtained in the untreated portion of the fed leaves of stressed plants, or some other aspect of the plant's metabolism is not clear. Rate of transport could be as great, but at a lower velocity of flow in the phloem, if the concentration of solutes were higher in stressed plants. Techniques used in this study could not distinguish differences in rate and velocity. Intermediate carbohydrate pool sizes might have been different in experiment I, where the stress was imposed gradually by withholding water. In experiment II the stress was imposed more quickly by root pruning the day before labeling. The discontinuity in the slopes suggest that the translocate may have come from different pools. During the first 60 to 120 min following labeling the translocate may have come directly from chloroplast pools of soluble sugars; whereas after longer time intervals the translocate may come from carbohydrate pools less available for translocation. The logarithmic profile of translocation patterns has been explained by Clauss *et al.* (1) and Hofstra and Nelson (4) as the result of translocate being accumulated in or near the phloem. The higher levels of radioactivity found in the stalk and husk and shank segments of the irrigated plants in the early hours after labeling may have resulted from more labeled carbohydrate moving through these tissues. It is somewhat surprising that an exchange with carbohydrate pools in the tissue adjacent to the conducting cells did not occur in these tissues as apparently did in the nonlabeled portion of the leaf.

An alternative possibility that root pruning modified sink activity seems remote in that the rates of $^{14}C$ accumulation in the kernels of pruned and unpruned plants appeared to be quite similar after 2 hr (experiment II). Levels of $^{14}C$ accumulation in the kernels were affected by the difference in accumulation between 90 and 120 min. One might have expected inconsistent results between experiments I and II because of the differences in the manner in which the moisture stress was imposed; however, the data appear consistent between experiments as well as among treatments in experiment II.

The depressive effect of water stress on photosynthate translocation reported here is in agreement with the observation of several other authors (3, 5, 6, 8–10). It has been suggested that some forms of growth are less sensitive to water stress than cell expansion. Wardlaw (9) found a continued movement of assimilates from the leaf to the developing wheat grain under water stress conditions. He also observed a lower velocity of sugar transport from leaves of stressed plants than from well watered plants. Water potential of the leaf appears to be a critical indicator of the capacity of the corn plant to translocate $^{14}C$-photosynthate. In these studies, the imposition of water stress which lowered the leaf xylem potential from approximately −15 to −20 bars caused a 30% reduction in the movement of $^{14}C$ translocation during the first 2 hr following labeling.

## LITERATURE CITED

1. CLAUSS, H., D. C. MORTIMER, AND P. R. GORHAM. 1964. Time-course study of translocation of products of photosynthesis in soybean plants. Plant Physiol. 39: 269–273.
2. EASTIN, J. A. 1970. Carbon-14 labeled photosynthate export from fully expanded corn (*Zea mays* L.) leaf blades. Crop Sci. 10: 415–418.
3. HARTT, C. E. 1967. Effect of moisture supply upon translocation and storage of $^{14}C$ in sugarcane. Plant Physiol. 42: 338–346.
4. HOFSTRA, G. AND C. D. NELSON. 1969. The translocation of photosynthetically assimilated $^{14}C$ in corn. Can. J. Bot. 47: 1435–1442.
5. NELSON, C. D. 1963. Effect of climate on the distribution and translocation of assimilates. *In:* L. T. Evans, ed., Environmental Control of Plant Growth, Academic Press, New York. pp. 149–174.
6. PLAUT, Z. AND L. REINHOLD. 1965. The effect of water stress on $^{14}C$ sucrose transport in bean plants. Aust. J. Biol. Sci. 18: 1143–1155.
7. SCHOLANDER, P. F., H. T. HAMMEL, E. D. BRADSTREET, AND E. A. HEMMINGSEN. 1965. Sap pressure in vascular plants. Science 148: 339–346.
8. WARDLAW, I. F. 1967. The effect of water stress on translocation in relation to photosynthesis and growth. I. Effect during grain development in wheat. Aust. J. Biol. Sci. 20: 25–39.
9. WARDLAW, I. F. 1969. The effect of water stress on translocation in relation to photosynthesis and growth. II. Effect during leaf development in *Lolium temulentum* L. Aust. J. Biol. Sci. 22: 1–16.
10. WIEBE, H. H. AND S. E. WIHREIM. 1962. The influence of internal moisture stress on translocation. *In:* Radio-isotopes in Soil-Plant Nutrition Studies. International Atomic Energy Agency, Vienna. pp. 279–288.