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9. ABSTRACT
Maize (Zea mays L.) growing in the field was labeled with $^{14}CO_2$ at four leaf positions 15 to 18 days after flowering. On four occasions after labeling, entire plants were harvested and ^{14}C in several plant fractions was analyzed by liquid scintillation spectroscopy to reveal patterns of translocation within the plants losses of ^{14}C by respiration, and patterns of mobilization and redistribution of ^{14}C among and within organs. The first and third leaf blades above the ear (+1 and +3, respectively), and the first blade below the ear (-1), exported ^{14}C mainly to kernels of the developing ear. Among these three leaf blades, the extent of export of ^{14}C was more rapid from upper positions than from lower ones. Movement of ^{14}C from the fifth leaf blade (-5) below the ear was much slower than that from the upper three blades, but kernels of the developing ear ultimately became the principle sink for C exported by this blade. Compared with the upper three leaf blade positions, however, appreciable label from -5 accumulated in the lower stem and roots. Labeling plants bearing partly-fertilized ears caused a large accumulation of C in the stem, roots and to a lesser extent, husks, compared with completely-fertilized controls. About 20% of the ^{14}C assimilated by the +1, +3, and -1 blades was lost by respiration in the 5 weeks following labeling. During the same interval, nearly 70% of the ^{14}C assimilated by the -5 blade was lost by respiration. Approximately half of the carbon assimilated by +3, +1, and -1 blades was translocated directly to kernels within 24 hr after assimilation. A similar quantity of label assimilated by =3,+1, and -1 blades was deposited in cobs and husks within 24 hr after assimilation. Estimates of redistribution of label within the plants suggest that 60 to 80% of the ^{14}C accumulated in kernels between days 1 and 35 following labeling was derived from ^{14}C originating in upper leaves and deposited in the cob and husk within 24 hr.

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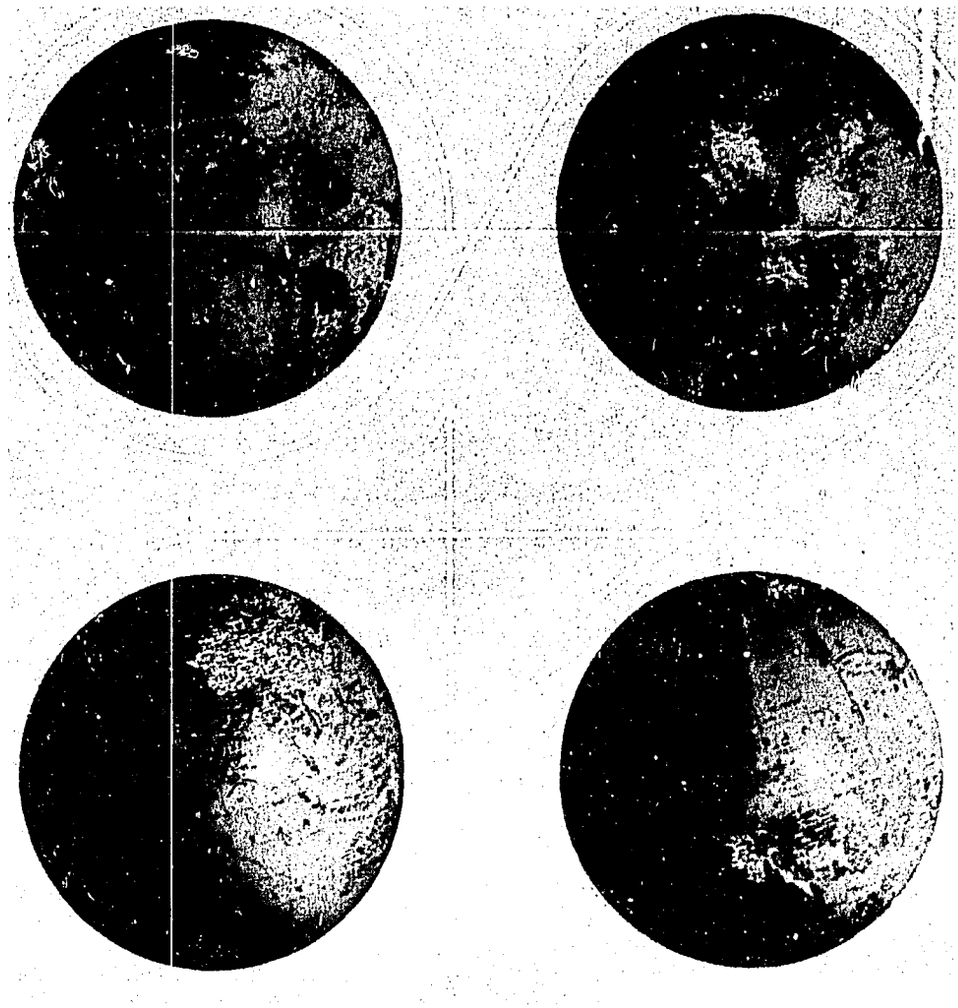

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A. F. E. Palmer, G. H. Heichel, and R. B. Musgrave

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Patterns of Translocation, Respiratory Loss, and Redistribution of ^{14}C in Maize Labeled after Flowering[1]

A. F. E. Palmer, G. H. Heichel, and R. B. Musgrave[2]

ABSTRACT

Maize (*Zea mays* L.) growing in the field was labeled with $^{14}CO_2$ at four leaf positions 15 to 18 days after flowering. On four occasions after labeling, entire plants were harvested and ^{14}C in several plant fractions was analyzed by liquid scintillation spectroscopy to reveal patterns of translocation within the plants, losses of ^{14}C by respiration, and patterns of mobilization and redistribution of ^{14}C among and within organs. The first and third leaf blades above the ear (+1 and +3, respectively), and the first blade below the ear (−1), exported ^{14}C mainly to kernels of the developing ear. Among these three leaf blades, the extent of export of ^{14}C was more rapid from upper positions than from lower ones. Movement of ^{14}C from the fifth leaf blade (−5) below the ear was much slower than that from the upper three blades, but kernels of the developing ear ultimately became the principle sink for ^{14}C exported by this blade. Compared with the upper three leaf blade positions, however, appreciable label from −5 accumulated in the lower stem and roots. Labeling plants bearing partly-fertilized ears caused a large accumulation of ^{14}C in the stem, roots and to a lesser extent, husks, compared with completely-fertilized controls. About 20% of the ^{14}C assimilated by the +1, +3, and −1 blades was lost by respiration in the 5 weeks following labeling. During the same interval, nearly 70% of the ^{14}C assimilated by the −5 blade was lost by respiration. Approximately half of the carbon assimilated by +3, +1, and −1 blades was translocated directly to kernels within 24 hr after assimilation. A similar quantity of label assimilated by +3, +1, and −1 blades was deposited in cobs and husks within 24 hr after assimilation. Estimates of redistribution of label within the plants suggest that 60 to 80% of the ^{14}C accumulated in kernels between days 1 and 35 following labeling was derived from ^{14}C originating in upper leaves and deposited in the cob and husk within 24 hr.

Additional index words: **Growth, Dry matter distribution, Carbon balance, Source-sink relations.**

STUDIES of the growth of maize (*Zea mays* L.) reveal that dry matter in grain is produced by leaf photosynthesis occurring after fertilization of the ear (1, 8, 28). Development of varieties having the number and arrangement of leaves that support large grain yields requires knowledge of the movement of assimilated carbon from leaves at various positions on the plant to developing ears and other organs. Recent studies showed that after flowering the upper leaves of maize exported carbon principally to the ear (6, 7). The position of a leaf blade relative to the developing ear strongly influenced rate and direction of translocation (27). In young plants, however, all leaves exported carbon to all other organs of the plant (16).

To elucidate the translocation of carbon in maize, we measured, under field conditions, the patterns of distribution of ^{14}C, from leaf blades labeled at four positions on the plant, after complete fertilization of the ear. The distribution of ^{14}C in plants having partly-fertilized ears was also measured to determine if altering a developing organ modified the fate of assimilated carbon. Entire plants, including the roots, were sampled to facilitate measuring the loss of carbon by respiration and estimating the redistribution of carbon within the plant.

MATERIALS AND METHODS

These experiments were conducted on the Central Experiment Station, College of Agriculture, University of the Philippines, near Los Baños, Laguna between August and October, the rainy season of the tropical monsoon climate. *Zea mays* L. var. 'Philippine Hybrid No. 1d' was planted on beds shaped to hasten drainage and oriented east-west with rows oriented north-south. The photosynthetic characteristics of this variety were previously reported (13, 14). Seeds were planted by hand at 19-cm intervals in rows 75 cm apart (69,000 plants ha^{-1}). Each seed was planted so that leaves of each plant would be oriented at right angles to the row. All plants were grown on Lipa silty clay. A typical profile description is given by Raymundo, Carandang, and Bruce (24). Plots were well fertilized.

In the field, attached leaves were sealed into an acrylic plastic leaf chamber that was only slightly larger than a corn leaf blade (13, 14). Leaf temperatures (30 ± 2 C) and wind speeds (4 m sec^{-1}) in the chamber were assured by attaching the chamber to a portable refrigeration unit containing a centrifugal fan. The closed labeling circuit included a $^{14}CO_2$ generator, leaf chamber, hose pump, drier column, and Beckman infrared CO_2 analyzer. The chamber was displayed normal to incident sunlight. As photosynthesis occurred, CO_2 concentration in the chamber quickly decreased. When CO_2 concentration was about 250 ppm, excess lactic acid was injected by a syringe into the sealed generator that contained 2 ml of $Na_2{}^{14}CO_3$ in NaOH. Two hundred μCi of $^{14}CO_2$ were released into the flowing gas stream and swept into the chamber. The $^{14}CO_2$ and $^{12}CO_2$ released from Na_2CO_3 caused a transient increase of 10 ppm CO_2 or less in the chamber. Thereafter, the CO_2 concentration in the closed system was monitored for 20 to 30 min until the leaves attained their CO_2 compensation concentration. The leaves were maintained at the CO_2 compensation concentration for 5 min to assure maximum fixation of $^{14}CO_2$. Subsequently, the chamber was removed and the plants remained under field conditions until sampling.

Plants with 14 to 16 leaves, one developing ear, no tillers, and without disease or mechanical damage were labeled 15 to 18 days after fertilization of the ear. Four leaf blade positions were selected to receive label and the leaf blades were identified by their proximity to the ear using the following protocol. Leaf 0 was attached to the same node as the ear. Leaves one and three above the ear, designated +1 and +3, and leaves one and five below the ear, designated −1 and −5, were chosen.

The distribution of ^{14}C assimilated during photosynthesis was determined by sampling plants labeled at each of the four leaf positions 1, 7, 14, and 35 days after incorporation of $^{14}CO_2$. The mean dry matter contents of ears at the 1, 7, 14, and 35 day harvests were 30 ± 2%, 43 ± 1%, 52 ± 1%, and 68 ± 1%, respectively. Therefore, labeling occurred when ears contained about 30% dry matter. The four leaf positions and four dates of sampling gave 16 treatments. Hereafter a single treatment will be designated by the leaf position, and the days from labeling to sampling will be a subscript. For example, $+3_{14}$ shows that the third leaf blade above the ear was labeled, and that the plant was sampled 14 days after labeling. To obtain the maxi-

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mum amount of new information, a compromise between number of treatments and number of replications was necessary. We chose to use a relatively large number of treatments and accept a smaller precision of measurement than if a smaller number of treatments had been equally replicated. Two treatments, $+3_{14}$ and $+1_{14}$, were replicated six times to allow calculations of standard errors. Eleven treatments were replicated twice, and three were conducted once.

At sampling time, the plants were cut immediately below the first node above the attachment of the brace roots and dissected into leaf blades, leaf sheaths, stem internodes, husk including shank, and ear. A pit was dug adjacent to the plant and the root system was sampled using a pin-board method (26). This technique permitted efficient recovery of the roots because the plants were shallow-rooted. A block of soil about 75 cm wide, 60 cm deep, and 30 cm thick that contained the roots was removed, and the roots were washed free of soil using a gentle water spray. The upper two or three internodes of the root system were separated and the lower internodes and roots were bulked. All plant parts were dried to constant weight at 75 C and the ear was partitioned into cob and kernels. The samples were ground in a Wiley mill to pass a 40-mesh sieve.

A 30 mg subsample of each plant part was mixed with a small quantity of CuO, wrapped in aluminum foil, and combusted in flowing O_2 in a Coleman model 33 carbon-hydrogen analyzer. The effluent gases were passed through $MgClO_4$ to remove H_2O and through MnO_2 to remove oxides of S and N. The $^{14}CO_2$ and $^{13}CO_2$ evolved were quantitatively trapped in a bubbler containing 5 ml of 1 M Hyamine hydroxide 10-X [p-(diisobutylcresoxyethoxyethyl) - dimethyl benzylammonium hydroxide] in CH_3OH (21). A 3 ml aliquot of each sample and 10 ml of a scintillator solution containing 5 g l^{-1} PPO (2,5-diphenyloxazole) and 0.3 g l^{-1} dimethyl POPOP [1,4-bis-2-(4-methyl-5-phenoloxozolyl)-benzene] in toulene were counted for 10 min in triplicate in a Packard Series 314 Tri-Carb liquid scintillation spectrometer. The counting efficiency was 65.5% accorling to the internal standard and channels ratio methods. Results are expressed as a percent of the total radioactivity recovered in the plant on each sampling date unless otherwise specified.

RESULTS

The distribution of label assimilated at four leaf positions among the organs of the plant and among the fractions of the ear shows consistent patterns that merit emphasis. On each date of sampling, the amount of ^{14}C recovered from the labeled leaf blade and its sheath was less for upper than for lower leaves on the plant (Fig. 1-4). The patterns clearly show that leaf blades rank $+3 > +1 > -1 > -5$ in rapidity and thoroughness of export of label. Similar patterns of distribution of label occurred at each sampling, but the proportion of recovered radioactivity in the labeled leaf blade and its sheath decreased with time as translocation and respiration continued.

The patterns of distribution reveal that developing ears and specifically kernels were major sinks for ^{14}C assimilated by $+3$, $+1$, and -1 leaf blades (Fig. 1-4, A to C). Twenty-four hours after labeling, 60 to 70% of the recovered label was in the ear and only 8 to 11% remained in the labeled blade. Seven to 35 days after labeling, kernels continued to be the major sink for ^{14}C arising from $+3$, $+1$, and -1 leaves (Fig. 1-4, A to C).

Movement of ^{14}C from the -5 blade was very slow compared with that from the upper three blades, and 58% of the recovered label remained in the blade and sheath after 24 hr. The bulk of ^{14}C transported from the -5 blade accumulated in lower stem internodes and roots instead of the ear during the first 24 hr after labeling (Fig. 1, D). The kernels became the major sink for ^{14}C from the -5 blade after 7 days had elapsed, and on subsequent dates, kernels continued to be the major repository for ^{14}C exported from the -5 blade (Fig. 2-4, D). Nevertheless, export

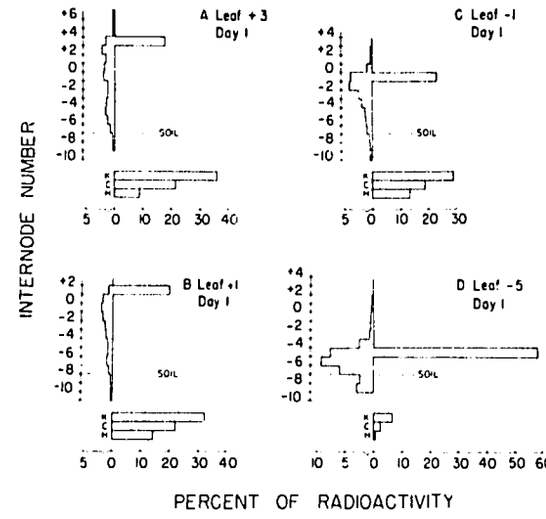

Fig. 1. Patterns of distribution of ^{14}C in maize plants sampled 1 day after labeling at four leaf positions. Results are expressed as a percent of total radioactivity recovered in the plant on day 1. In the upper histogram of each quadrant, bars to the left of the vertical axis indicate retention or accumulation of label in stem internodes above the soil surface and in internodes of the root system below the soil surface. Similarly, bars to the right of the vertical axis denote the retention or accumulation of ^{14}C by leaf blades plus sheaths. See text for numbering of leaves and internodes. The lower histogram of each quadrant shows the accumulation of label in three fractions of the ear, kernels (K), cob (C), and husk plus shank (H). Note that the scale for histograms to the left of the vertical axis is double that to the right of the vertical axis.

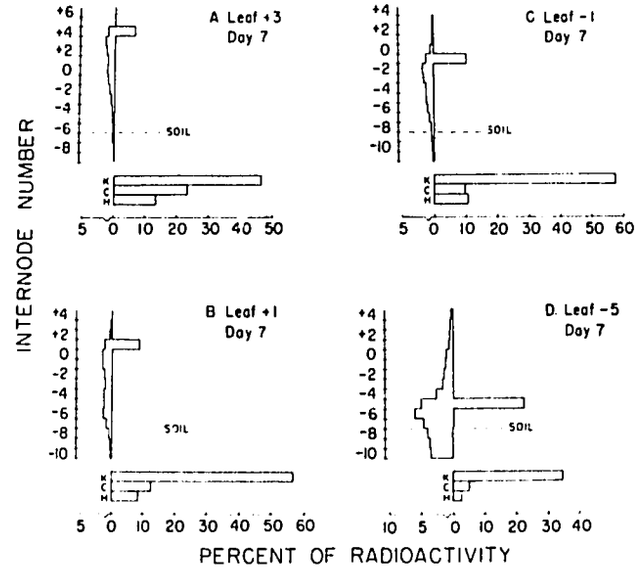

Fig. 2. Patterns of distribution of ^{14}C in maize plants sampled 7 days after labeling at four leaf positions. Results are expressed as a percent of total radioactivity recovered in the plant on day 7. See legend of Fig. 1 for further explanation.

from the -5 blade to the ear was less complete than that from the upper three blades. Clearly the upper and lower blades have greatly different abilities to serve as sources of carbon for the developing ear.

Recovery of ^{14}C in fractions of the ear ranked kernels > cob > husk. Although plants were continually losing ^{14}C by respiration and reapportioning ^{14}C

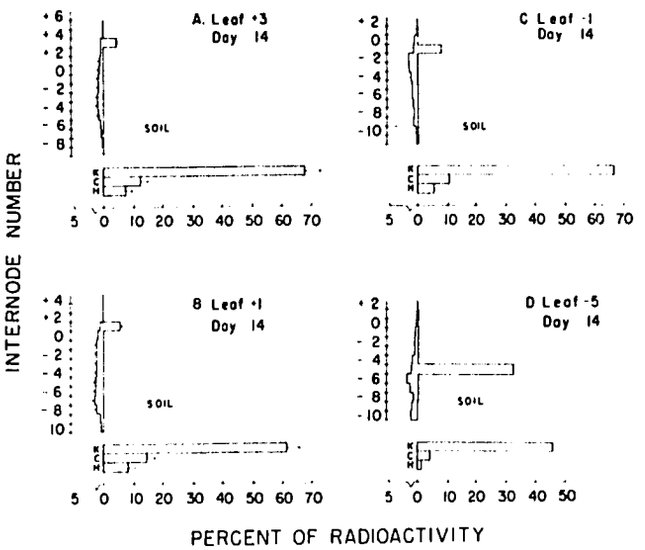

Fig. 3. Patterns of distribution of ^{14}C in maize plants sampled 14 days after labeling at four leaf positions. Results are expressed as a percent of total radioactivity recovered in the plant on day 14. The length of the line to the left or right of the bars of the histogram for A and B indicate the standard error of six replications. See legend of Fig. 1 for further explanation.

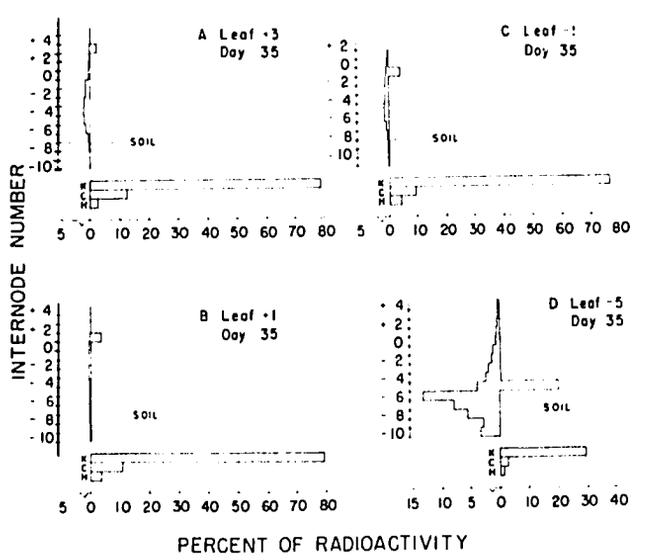

Fig. 4. Patterns of distribution of ^{14}C in maize plants sampled 35 days after labeling at four leaf positions. Results are expressed as a percent of the total radioactivity recovered in the plant on day 35. See legend of Fig. 1 for further explanation.

among organs, the proportion of label in kernels increased with time except for the -5_{35} treatment.

From plants labeled at any of the upper three leaf positions, less than 0.7% of the ^{14}C recovered on each date was found in blades and sheaths that were originally unlabeled. Twenty-four hours after the —5 leaf was labeled, 0.6% of the ^{14}C was recovered from blades and sheaths that were originally unlabeled. On subsequent dates, 2 to 3% of the recovered label from plants fed $^{14}CO_2$ at the —5 leaf was found in blades and sheaths that were originally unlabeled (Fig. 1-4, D). Clearly, a very low proportion of ^{14}C is recovered from unlabeled leaves and sheaths, and recovery in the upper leaves is greater when a lower, not an upper, blade is offered $^{14}CO_2$. There was no evidence that lower, older leaves were parasitic on the plants.

On each of the dates there was little difference in the proportion of ^{14}C recovered from stem internodes when plants were labeled at +3, +1, and —1 positions. Nevertheless, the proportion of label recovered from the stem decreased with time, and about 14, 9, 8, and 4% of the recovered ^{14}C was found in the stem 1, 7, 14, and 35 days following labeling (Fig. 1-4, A to C). When the —5 position was labeled, the lower stem internodes accumulated more ^{14}C than those of plants labeled at the upper three leaf positions (Fig. 1-4, D). The proportion of label in the stem decreased with time, and about 27, 26, 11, and 31% of the recovered label was found in the stem 1, 7, 14, and 35 days after labeling of the —5 leaf.

When a blade above the ear was labeled, little ^{14}C moved above the internode subtending the labeled blade, but appreciable ^{14}C was recovered in internodes between the labeled blade and the ear and in internodes below the ear. When blades below the ear were labeled, ^{14}C moved further downwards in the stem and upwards to the internode above the attachment of the ear, but little ^{14}C moved into higher portions of the plant. The recovery of ^{14}C was greatest in the internode immediately below the one subtending the labeled blade, and recovery of label declined linearly or exponentially with distance from the peak. These patterns were similar on all dates of sampling (Fig. 1-4).

Less than 0.7% of the recovered ^{14}C was found in roots when +3, +1, and —1 blades were labeled, and recovery in roots was an extension of the trend established in lower stem internodes on all dates of sampling. Compared with upper leaf positions, a larger proportion of ^{14}C moved to the root system when the —5 leaf was labeled. The proportion of ^{14}C in roots generally decreased with time when the upper three blades were labeled, but the proportion of ^{14}C in roots increased with time when the —5 position was labeled except for the -5_{14} treatment (Fig. 1-4). Like plants labeled in the upper blades, the recovery of ^{14}C in roots of plants labeled at the —5 position was an extension of the trend established in lower stem internodes on all dates.

Observing plants bearing partly-fertilized ears provided convincing evidence that the development of kernels was the major process determining the fate of carbon assimilated after flowering in maize (Table 1). An ear that was only 20% fertilized on a plant labeled at the +1 position accumulated 40% as much ^{14}C in kernels and 35% as much ^{14}C in the cob during the first 14 days following labeling as did a completely-fertilized ear on a comparably-labeled plant. The plant bearing a partly-fertilized ear retained 77%

Table 1. Comparison of the distribution of ^{14}C in plants bearing partly and completely fertilized ears 14 days after labeling.

Leaf position	Organ	% recovered radioactivity: Extent of fertilization 100%	20%	Leaf position	Organ	% recovered radioactivity: Extent of fertilization 100%	50%
+1	Ear	84.1	44.2	-5	Ear	50.5	14.0
	Kernels	61.5	24.8		Kernels	45.4	11.0
	Cob	14.6	5.2		Cob	4.0	1.2
	Husk	8.0	14.2		Husk	1.1	1.8
	Leaves	6.1	10.8		Leaves	34.5	21.3
	Stem	8.8	34.2		Stem	11.2	41.3
	Roots	0.4	10.8		Roots	3.8	23.4

Table 2. Recovery of assimilated radioactivity, offered at four leaf positions, in entire plants on four dates following labeling.

Leaf position	Percent of assimilated radioactivity			
	Days after labeling			
	1	7	14	35
+3	100.0	79.3	82.0 ± 1.5*	81.2
+1	100.0	81.0	85.0 ± 1.2*	82.6
-1	100.0	80.1	83.8	74.1
-5	100.0	85.2	67.7	31.4

* Standard errors are given for treatments having six replications.

more ^{14}C in the labeled blade and accumulated 77, 290, and 2600% more label in the husk, stem, and roots than the control.

An ear that was 50% fertilized on a plant labeled at the —5 position accumulated 24% as much ^{14}C in kernels and 30% as much ^{14}C in the cob during the first 14 days following labeling as did a completely-fertilized ear on a comparably-labeled plant. The plant bearing a partly-fertilized ear accumulated 63, 270, and 530% more label in the husk, stem, and roots, but did not retain ^{14}C in the labeled blade compared with the control. The decline in accumulation of label in kernels was not directly proportional to the decrease in fertilization; the decrease in kernel mass did not mirror the decrease in fertilization of the ear. Partial fertilization clearly alters the distribution of assimilated carbon in the plant. The stem, roots, and, to some extent, husks accumulate carbon that would be translocated to kernels of a completely-fertilized ear.

A measure of losses of carbon through respiration was obtained by sampling the entire plant and comparing the amount of label recovered with that assimilated (Table 2). Our techniques were not sufficiently sensitive to detect the loss of ^{14}C by respiration during the 24 hr following labeling, so the amount of label recovered after 24 hr was equal to the label originally assimilated. The losses of ^{14}C from all plants will be underestimated in proportion to the small quantities of roots lost in sampling, but this error is slight. The lower leaves were all recovered; their senescence did not contribute to error in calculating respiratory losses.

Depending upon the position of the labeled leaf blade on the plant, two patterns of respiratory loss occurred. When ^{14}C was assimilated at +3, +1, and —1 blades, about 20% of the label was lost by respiration in the subsequent 5 weeks. Indeed, no significant loss occurred after the first week following labeling. The ^{14}C assimilated at the —5 leaf was continually lost from plants during the 5 weeks following labeling; 15, 32, and 69% of the original ^{14}C was lost after 1, 2, and 5 weeks. The greater respiratory loss from plants labeled at the —5 leaf might be due to slower movement of ^{14}C to the ear where it could be converted to a form that is respired less readily. A large proportion of ^{14}C administered at the —5 position remained in the labeled blade, the stem internodes, and in root systems compared with plants labeled at higher leaf positions (Fig. 1-4, D). Perhaps ^{14}C in these locations is more labile for respiration than that speedily transported to a developing ear.

DISCUSSION

Sinks for carbon. Many defoliation experiments have suggested that upper and middle leaves on the maize plant are principal contributors of carbon to the ear and that lower leaves contribute relatively little (3, 17). The patterns of translocation of ^{14}C that we observed in intact plants fully support this view and further reveal that lower leaves are major sources of carbon for maintenance of the lower stem and root system during the final third of crop growth. That all of the carbon derived from a lower leaf is not deposited in a site inaccessible for respiration is amply demonstrated by large losses of ^{14}C from plants labeled at the —5 position. The patterns reveal that the ear is the sink for a small fraction of carbon assimilated by lower leaves.

Partial fertilization of the ear drastically altered the distribution of ^{14}C from the +1 and —5 leaves and resulted in accumulation of label in the stem and roots. This observation supports earlier findings that plants bearing unfertilized ears accumulate large concentrations of sugar in the stems (3, 25).

Respiratory losses of carbon. About 20% of the label applied 15 to 18 days after fertilization to +3, +1, and —1 blades was lost through respiration during the ensuing 5 weeks (Table 2). This observation is remarkably consistent with the 22 to 33% losses by respiration in two varieties of 10 to 30 day old maize plants (11), and with theoretical calculations of the respiration by 10 day old maize seedlings (23). The general pattern emerges that maize exhibits a conservative carbon loss by respiration throughout its growth when compared with species like white clover (*Trifolium repens* L.) that respire 38 to 43% of their assimilated carbon (22).

The losses of ^{14}C from the —5 blade are 60 to 70% of that assimilated and suggest that a smaller proportion of the carbon fixed by lower blades is retained by the entire plant. On a whole plant basis, lower blades fix little carbon because of reduced light penetration into the lower canopy (20, 29). Thus, the proportionately larger respiratory loss of carbon by lower blades compared with upper blades is probably of little consequence in the overall carbon balance of the plant.

Redistribution of carbon. Losses by respiration and recoveries of label in various organs or ear fractions can be combined to estimate redistribution of ^{14}C assimilated after flowering among or within organs of plants. However, we must first evaluate whether respiratory losses incurred by the entire plant (Table 2) are reasonable estimates of respiratory losses incurred by individual organs and fractions of the ear.

We found that blades respired about twice as rapidly as ears on a weight basis (unpublished data), and at about 1.0 mg CO_2 g^{-1} hr^{-1} our ear respiration rates were similar to published rates (15). Furthermore, previous work showed that blades respired about twice as rapidly as roots and stems (11). Thus, the assumption that stems, ears, and roots respire at similar, slow rates is reasonable pending more precise measurements.

Blades and sheaths contributed about 12% of the dry wt of the plant after flowering, and ears, stalks, and roots comprised the balance of plant mass. Although leaves respire more rapidly than other organs, they comprise only a small portion of the total plant mass and thus contribute only a small proportion of the total plant respiration. In this experiment, the labeled blade and sheath were the only ones to contain

Table 3. Radioactivity recovered in the fractions of the ear on days 1 and 14 following labeling expressed as a percent of the total radioactivity recovered in the plant on each date (column a) and as a percent of the assimilated label (column b).

Days after labeling	Fraction	Leaf position +3 a	+3 b	+1 a	+1 b	-1 a	-1 b	-5 a	-5 b
1	Kernels	35.8	35.8	32.0	32.0	26.7	28.7	6.4	6.4
	Cob	21.3	21.3	22.1	22.1	18.6	18.6	2.4	2.4
	Husk	8.8	8.8	14.1	14.1	13.2	13.2	0.6	0.6
14	Kernels	67.9	55.7	61.5	52.3	66.9	51.1	45.4	30.7
	Cob	12.2	10.0	14.6	12.4	10.3	8.6	4.0	2.7
	Husk	7.2	5.9	8.0	6.8	5.4	4.5	1.1	0.7
Gain by kernels			19.9		20.3		27.4		24.3
Loss by cob plus husk			14.2		17.0		18.7		-0.4

significant label; we estimate that only about 0.5 to 1% of the total mass of the plant was respiring ^{14}C more rapidly in darkness than the balance of the plant. Furthermore, leaf respiration of maize declines to a steady and slow base rate 2 to 3 hr after darkening (12). Clearly, therefore, over a period of 2 weeks the error will be minor if we assume that all organs and ear fractions respire ^{14}C at the same rate as the entire plant.

Let us first examine whether carbon from the cob and husk is mobilized and redistributed into developing kernels during the 2 weeks following labeling. Each column (a) in Table 3 summarizes from Fig. 1 and 3 the recovery of radioactivity in kernels, cob, and husk on days 1 and 14. These values must be corrected for loss by respiration before estimates of redistribution can be made. Multiplying each value in column (a) by the proportion of assimilated label remaining in the plant on each date (Table 2) yields column (b): the proportion of the assimilated label remaining in each ear fraction on days 1 and 14. At each leaf position the import of ^{14}C by the kernels between days 1 and 14 is estimated by subtracting the values in each column (b) for kernels on day 1 from the corresponding values for kernels on day 14. Export of label by the cob and husk can be similarly computed.

The import of ^{14}C by the kernels exceeded the export by the cob plus husk for plants labeled at all four positions (Table 3). Mobilization and redistribution was considerable in plants labeled at the three upper leaf positions. Seventy-one, 84, and 68% of the ^{14}C accumulated by the kernels of plants labeled at the +3, +1, and −1 positions between days 1 and 14 could have been mobilized from husks and cobs. These results suggest that at least 15 to 30% of the carbon transported to kernels between days 1 and 14 was mobilized from other plant organs.

We can determine whether mobilization of ^{14}C from leaves, stems, or roots will meet the additional requirements of the kernels for label by computations similar to those of Table 3. Each column (a) in Table 4 summarizes from Fig. 1 and 3 the recovery of radioactivity in the ears, leaves, stems, and roots on days 1 and 14. Multiplying each value in column (a) by the proportion of assimilated label remaining in the plants on each date (Table 2) accounts for losses by respiration and yields, column (b), and gives the proportion of assimilated label remaining in each organ on days 1 and 14. At each leaf position the import of ^{14}C by the ear between days 1 and 14 is estimated by subtracting the values in each column (b) for ears on day 1 from the corresponding values for ears on day 14. Export of label by all other organs can be similarly computed. The export of ^{14}C by leaves, stems,

Table 4. Radioactivity recovered in the organs of the plant on days 1 and 14 following labeling expressed as a percent of the total radioactivity recovered in the plant on each date (column a) and as a percent of the assimilated label (column b).

Days after labeling	Organ	Leaf position +3 a	+3 b	+1 a	+1 b	-1 a	-1 b	-5 a	-5 b
1	Ear	65.9	65.9	68.2	68.2	60.5	60.5	9.3	9.3
	Leaf blade	18.2	18.2	20.1	20.1	23.3	23.3	58.9	58.9
	Stem	15.4	15.4	11.1	11.1	15.5	15.5	26.7	26.7
	Roots	0.5	0.5	0.6	0.6	0.7	0.7	5.1	5.1
14	Ear	87.3	71.6	84.1	71.5	82.6	69.2	50.5	34.2
	Leaf blade	5.1	4.2	6.0	5.1	8.3	7.0	34.6	23.4
	Stem	7.2	5.9	8.8	7.5	8.6	7.2	11.2	7.6
	Roots	0.4	0.3	1.0	0.9	0.5	0.4	3.8	2.6
Gain by ear			5.7		3.3		8.7		24.9
Loss by other organs			23.7		18.3		24.9		57.1

and roots was more than sufficient to meet the additional requirements of the kernels (Tables 3 and 4). Our estimates do not reveal the specific origin of ^{14}C imported by the ear. The stem is probably the principle source since it subtends the ear. Thus, the ear potentially can import carbon mobilized in other organs, but major redistribution appears to occur within the ear.

The patterns of redistribution of ^{14}C revealed in Tables 3 and 4 are consistent with previous observations that decreases in dry wt of the stalk, husk, and cob, and decreases in soluble solids of the stalk, occur during accumulation of dry matter by kernels (1, 2, 4, 10, 18, 19). Labeling experiments that we report support the hypothesis that carbon assimilated after flowering and translocated to stem, cob, and husks can be mobilized and redeposited in kernels at a later date. Calculations based on Hanway's Table 2 and Fig. 4 (9) suggest that grain accumulates about 2 g day^{-1} plant^{-1} by translocation after flowering from organs decreasing in dry wt. Our results clarify this phenomenon by revealing that about half of the carbon accrued by kernels in the period following flowering is translocated directly from the upper leaves within 24 hr. For example, Table 3 shows that 29 to 36% of the label assimilated by +3, +1, and −1 blades is deposited in kernels within 24 hrs of assimilation. An equal quantity, about 30 to 36%, of the label assimilated by +3, +1, and −1 blades is deposited in cobs and husks within 24 hrs of labeling. Furthermore, about 70 to 85% of the label from upper blades that is deposited in cobs and husks is subsequently remobilized and translocated to kernels in the ensuing 2 weeks (Table 3). An even lesser amount of carbon, probably 5 to 10% of the label assimilated after flowering, is first deposited in the stem and later retranslocated to kernels (Tables 3 and 4). Of course this latter estimate is less precise than those for translocation from leaves, and cobs and husks, because static measurements of the accrual of label cannot fully describe the dynamic transport of assimilate.

Nevertheless, our field experiments suggest that cobs and husks may be the principal reservoirs of carbon that allow linear dry matter accumulation in kernels while the dry matter production of the plant fluctuates with daily radiation receipts. Duncan, Hatfield, and Ragland (5) previously ascribed this function to the stem. We conclude that assimilation by leaves during the period of growth after flowering of tropical maize used in these experiments exceeded the capacity of kernels to accept carbon. Emphasis on increasing

sink size or number of kernels may therefore be required to improve yield of other tropical maize varieties that behave similarly. Efforts to increase sink size should parallel attempts to increase photosynthetic capacity of the plant, because plentiful photosynthate during vegetative growth and inception of flowering undoubtedly ensures development of fertile spikelets on the ear.

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REFERENCES

1. Allison, J. C. S. 1969. Effect of plant population on the production and distribution of dry matter in maize. Ann. Appl. Biol. 63:135-144.
2. ———. 1971. Analysis of growth and yield of inbred and crossbred maize. Ann. Appl. Biol. 68:81-92.
3. ———, and D. J. Watson. 1966. The production and distribution of dry matter in maize after flowering. Ann. Bot. N.S. 30:365-381.
4. Daynard, T. B., J. W. Tanner, and D. J. Hume. 1969. Contribution of stalk soluble carbohydrates to grain yield in corn (*Zea mays* L.). Crop Sci. 9:831-834.
5. Duncan, W. G., A. L. Hatfield, and J. L. Ragland. 1965. The growth and yield of corn. II. Daily growth of corn kernels. Agron. J. 57:221-223.
6. Eastin, J. A. 1969. Carbon-14 labeled photosynthate distribution in corn in relation to leaf position and leaf function. Proc. 24th Ann. Corn and Sorghum Res. Conf., Amer. Seed Trade Assn. Publ. No. 24. p. 81-89.
7. ———. 1970. C-14 labeled photosynthate export from fully expanded corn (*Zea mays* L.) leaf blades. Crop Sci. 10:415-418.
8. Hanway, J. J. 1962. Corn growth and composition in relation to soil fertility. I. Growth of different plant parts and relation between leaf weight and grain yield. Agron. J. 54: 145-148.
9. ———. 1969. Defoliation effects on different corn (*Zea mays* L.) hybrids as influenced by plant population and stage of development. Agron. J. 61:534-538.
10. ———, and W. A. Russell. 1969. Dry-matter accumulation in corn (*Zea mays* L.) plants: comparisons among single-cross hybrids. Agron. J. 61:947-951.
11. Heichel, G. H. 1971. Confirming measurements of respiration and photosynthesis with dry matter accumulation. Photosynthetica 5:93-98.
12. ———. 1970. Prior illumination and the respiration of maize leaves in the dark. Plant Physiol. 46:359-362.
13. ———, and R. B. Musgrave. 1969. Varietal differences in net photosyntheses of *Zea mays L.* Crop Sci. 9:483-486.
14. ———, and ———. 1970. Photosynthetic response to drought in maize. The Philippine Agriculturist 54:102-114.
15. Hesketh, J. D., and R. B. Musgrave. 1962. Photosynthesis under field conditions. IV. Light studies with individual corn leaves. Crop Sci. 2:311-315.
16. Hofstra, G., and C. D. Nelson. 1969. The translocation of photosynthetically assimilated ^{14}C in corn. Can. J. Bot. 47: 1435-1442.
17. Hoyt, P., and R. Bradfield. 1962. Effect of varying leaf area by partial defoliation and plant density on dry matter production in corn. Agron. J. 54:523-525.
18. Jain, T. C. 1971. Contribution of stem, laminae, and ear to the dry-matter production of maize (*Zea mays* L.) after ear emergence. Indian J. Agr. Sci. 41:579-583.
19. Johnson, R. R., K. E. McClure, L. J. Johnson, E. W. Klosterman, and G. B. Triplett. 1966. Corn plant maturity. I. Changes in dry matter and protein distribution in corn plants. Agron. J. 58:151-153.
20. Lemon, E. R., and J. L. Wright. 1969. Photosynthesis under field conditions. XA. Assessing sources and sinks of carbon dioxide in corn (*Zea mays* L.) crop using a momentum balance approach. Agron. J. 61:405-411.
21. Lian, S., and A. Tanaka. 1967. Behavior of photosynthetic products associated with growth and grain production in the rice plant. Plant Soil 26:333-347.
22. McCree, K. J., and J. H. Troughton. 1966. Prediction of growth rate at different light levels from measured photosynthesis and respiration rates. Plant Physiol. 41:559-566.
23. Penning de Vries, F. W. T. 1972. Respiration and growth. Proceedings of a Symposium on Crop Processes in Controlled Environments. Academic Press. (In Press).
24. Raymundo. M. E., D. A. Carandang, and R. C. Bruce. 1968. The soils of the U.P. College of Agriculture and the Central Experiment Station. The Philippine Agriculturist 47:298-320.
25. Sayre, J. D., V. H. Morris, and F. D. Richey. 1931. The effect of preventing fruiting and reducing the leaf area on the accumulation of sugars in the corn stem. J. Amer. Soc. Agron. 23:751-753.
26. Schuurman, J. J., and M. A. J. Goedewaagen. 1965. Methods for examination of root systems and roots. Centre for Agricultural Publications and Documentation. Wageningen, Netherlands.
27. Tripathy, P. C., J. A. Eastin, and L. E. Schrader. 1972. A comparison of ^{14}C-labeled photosynthate export from two leaf positions in a corn (*Zea mays* L.) canopy. Crop Sci. 12: 495-497.
28. Van Eijnatten, C. L. M. 1963. A study of the development of two varieties of maize at Ibadan, Nigeria. J. Agr. Sci. 61:65-72.
29. Wright, J. L., and E. R. Lemon. 1966. Photosynthesis under field conditions. IX. Vertical distribution of photosynthesis within a corn crop. Agron. J. 58:265-268.