THE REDISTRIBUTION OF STEM SUGARS IN WHEAT DURING GRAIN DEVELOPMENT

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Summary

In wheat, a study of the distribution of ^{14}C assimilated by single leaves near the time of anthesis showed that, during ear development, sugars previously accumulated in the stem internodes were in part redistributed to other plant organs and in part probably converted to polysaccharides within the stem. Only a small proportion of the stem sugar (including fructosans) was lost in respiration. Upward movement of sugars occurred almost entirely from the top two internodes only. The contribution to the final ear dry weight, however, was at the most only 5–10%. There was downward movement of sugars from the third and lower internodes and under the conditions of these experiments much of these went to newly formed tillers. There was little or no redistribution to the roots.

I. Introduction

Sugars, including fructosans, increase in concentration and amount in cereal stem internodes until a few days after anthesis (Archbold 1945). There follows a decline from this maximum until, by the time the grains ripen, little or none remains. Even if it is assumed that the sugar moves to the ear following anthesis, this contribution can only account for at the most 10% of the final grain weight (cf. Archbold 1945; Asana 1959). It was suggested (Archbold and Mukerjee 1942) that loss of stem sugar is in fact a feature of senescence and due at least in part to respiratory losses, and is independent of the requirements of the grains. However, the rate of stem respiration was found to be inadequate to account for all the stem sugar lost in either barley (Archbold 1945) or wheat (Stoy 1965). Moreover there is now some direct evidence of movement of material from the stem to the ear in the work of Murayama, Oshima, and Tsukahara (1961) with rice and Stoy (1963) with wheat using ^{14}C-labelled assimilates. The present experiments were designed to examine more closely the redistribution of sugar carbon from the stems of wheat during grain development. Carr and Wardlaw (1965) have shown that following the pulse application of $^{14}CO_2$ to single wheat leaves distribution of ^{14}C proceeds rapidly at first, but after about 24 hr a relatively stable pattern of slow continuing movement out of the leaf is established. Accordingly $^{14}CO_2$ was supplied to either the top (flag) leaf or the second (from the top) leaf at or soon after anthesis and the initial distribution of ^{14}C was determined 2 days after exposure and the subsequent redistribution 35 days after anthesis when the ears were ripe. Conditions of relatively low temperature and high light intensity were imposed at first with the object of promoting sugar accumulation in the stem, followed by a higher temperature and reduced light intensity which might favour utilization of the stored sugar.

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II. Methods

(*a*) *Cultural Conditions*

Wheat plants (*Triticum aestivum* cv. Gabo) were grown singly in perlite in 5-in. pots. Air temperatures were controlled at 21 °C for 8 hr of the daylight period and at 16 °C for the remainder of the 24-hr cycle and day length was extended to 16 hr by low-intensity incandescent lamps. All plants were supplied with standard nutrient solution [Hoagland's No. 2, with half phosphorus and iron-EDTA instead of tartrate — Bonner and Galston (1952)] in the morning and with water each afternoon. Periodic removal of young shoots limited each plant to a single main stem. One day prior to assimilation of $^{14}CO_2$ by the selected leaves the plants were transferred to an artificially lit (L.B.) cabinet (Morse and Evans 1962).

(*b*) ^{14}C *Assimilation*

The leaves to be labelled were enclosed in a Perspex assimilation chamber with a cross-section of 2 by 15·5 cm and 1650 ml in volume. $^{14}CO_2$ was generated by the addition of 50% lactic acid to weighed amounts of $Ba^{14}CO_3$ and circulated through the chamber for 5 min in darkness to obtain uniform distribution and then for 20 min in light at 3500 f.c. at a rate of 2 litres/min. Excess $^{14}CO_2$ was then removed by passing the air stream through 10% sodium hydroxide.

The terminal 15·5 cm of up to 16 leaves could be exposed simultaneously to $^{14}CO_2$ in this way with an enclosed area for each leaf of approximately 20 cm^2. The initial concentration of CO_2 was 0·69 or 1·14% by volume depending on the number of leaves and allowed 9·3 – 12·3 mg CO_2 per dm^2 of exposed leaf area, which it was felt would not limit photosynthesis during the 20-min assimilation period.

(*c*) *Experiments*

Four experiments were carried out. In the first two the second leaf was exposed to $^{14}CO_2$, in the third the flag leaf, and in the fourth both the second and flag leaves. In experiments I, II, and III the plants were transferred, 1 day prior to supplying $^{14}CO_2$, to a chamber maintained at 15 °C during a high-intensity light period (3500 f.c.) of 16 hr and at 10 °C during an 8-hr dark period (15/10 °C). Eight days after anthesis the cabinet temperature was raised to 21/16 °C and the light intensity reduced to 700 f.c. In experiment IV the temperature was maintained at 21/16 °C throughout, but the light intensity was varied as for the other experiments. $^{14}CO_2$ was supplied during the light period and an initial harvest was made 2 days (expts. I, II, and III) or 4 days (expt. IV) after assimilation. In all experiments a final harvest was made 35 days after anthesis, but in experiment III an additional harvest was made at 20 days after anthesis. The details for each experiment are set out in Table 1.

(*d*) *Harvesting and Sampling*

On harvesting each plant was immediately cut into the parts required and the part either oven-dried at 80 °C or placed into boiling 80% ethanol. The plant was divided into the flag leaf or second leaf (including both sheath and blade) or both parts; ear; top internode of the stem (bearing the ear); second internode (recording from

the top); remaining lower internodes, tillers, and the crown together with the roots. For measurements of dry weight and of material soluble in ethanol and water the fresh stem sections were weighed and then split lengthways and each part weighed. One part was used for extraction and the other for determination of dry weight and ^{14}C activity in the stem.

(e) *^{14}C Analyses*

The distribution of ^{14}C in the plant was determined by the direct counting of dried powdered material (O'Brien and Wardlaw 1961). The results are expressed as "total activities" in counts per minute derived from the product of "relative specific activity" (counts/min/30 mg) and dry weight in grams of the part concerned.

TABLE 1

DETAILS OF $^{14}CO_2$ LABELLING EXPERIMENTS

Expt. No.	Expt. Uptake Leaf	$^{14}CO_2$ Supplied* (mg)	$^{14}CO_2$ Supplied* (μc)	Time from Anthesis for $^{14}CO_2$ Uptake (days)	Time from Anthesis to First Harvest (days)	No. of Plants in Each Harvest
I	Second	22·3	240	0	2	6
II	Second	22·3	240	4	6	6
III	Flag	36·9	320	3	5	5
IV	Flag	22·3	240	0	4	8
	Second	22·3	240	1	4	8

* In experiments I, II, and IV, 12 leaves were fed simultaneously, additional plants for separate analysis were included to make up the number when necessary. In experiment III, 15 leaves were fed simultaneously.

(i) *Extraction.*—One split half of each stem internode was cut into short lengths, dropped into boiling 80% ethanol, and allowed to cool for 5 min. The ethanol extract was decanted and evaporated to 1 ml or less at room temperature *in vacuo*. The stem pieces were further extracted in water at room temperature for 16 hr and then for 10 min more in fresh water. The combined ethanol and water extracts were then evaporated under vacuum and made to a final volume of 5 ml in water for chromatographic analysis. The stem material remaining after extraction was then dried and weighed (residual dry weight), ground, and counted in the usual way.

(ii) *Chromatography.*—20-μl aliquots of extract were spotted onto Whatman No. 1 chromatographic strip paper. Descending chromatograms were run for 48 hr, using the upper fraction of a n-butanol–acetic acid–water (4 : 1 : 5 v/v) mixture as solvent. Sucrose and glucose were run as reference sugars on a separate strip at the same time as the extracts. The location of sugars on the chromatograms was determined by spraying with benzidine–trichloroacetic acid and heating to 120°C in a drying oven which gives a reaction with both free and combined glucose and to a lesser extent fructose (Bacon and Edelman 1951). Finally, a ^{14}C marker was

placed 2 cm before the start line and each strip was run through a chromatogram scanner to locate the position of radioactive materials.

III. Results and Discussion

The overall amounts of ^{14}C in the plants at each harvest are recorded in Table 2. The values are mean values of the sums of ^{14}C in the several organs. The distribution of ^{14}C between the plant organs, together with dry weight and in some cases residual dry weight, is shown in Tables 3 and 4 and Figure 1. The detailed results of experiment I closely resembled those of experiment II and are not presented.

Table 2

CHANGE IN TOTAL ^{14}C PER PLANT THROUGHOUT EACH OF FOUR EXPERIMENTS

Mean values per plant ± standard error are given (see Table 1 for details)

Expt. No.	Expt. Uptake Leaf	Total ^{14}C per Plant (counts/min)			Change in ^{14}C from Initial to Final Harvest	
		Initial Harvest	Intermediate Harvest*	Final Harvest†	Whole Plant	Stem
I	Second	16,493±656	—	13,560±1344	−2933±1496	−3900±731
II	Second	16,361±1191	—	15,467±516	− 894±1298	−3773±998
III	Flag	16,608±1211	15,508±342	17,738±238	+1130±1234	−3924±1320
IV	Flag and second	37,204±2800	—	31,848±2698	−5356±3888	−8942±2373
Mean		21,667±1464		19,653±1199	−2013±1979	−5135±1355

* 20 days after anthesis. † 35 days after anthesis.

(a) *Respiratory Losses and Conversion of Sugars*

For the four experiments taken together the mean values of total ^{14}C at the two harvests show a difference of 10%, the value after 35 days being the lower. However, neither this difference nor any of those for single experiments exceed twice the calculated standard errors of these differences. Loss of ^{14}C by respiration was therefore too small to be measured in terms of the sum of differences between plant parts as determined here. It can only be assumed that about 10% of the ^{14}C present at the first harvest was evolved as CO_2 in the subsequent 30–35 days. Losses from the stems (Table 2, derived from the data of Tables 3, 4, and Figure 1), however, amounted to an average of 23% of the ^{14}C originally present (or 40% of that in the stems alone). Here the differences are three or more times as great as the appropriate standard error. It is therefore reasonable to conclude that stem losses were at least twice as great as total respiration losses and so direct evidence is provided that there is some redistribution of ^{14}C from the stem internodes while ears are developing.

In the two experiments (II and III) in which sugars (including fructosans) were extracted from the stem internodes, it appeared from chromatograms of the extracts

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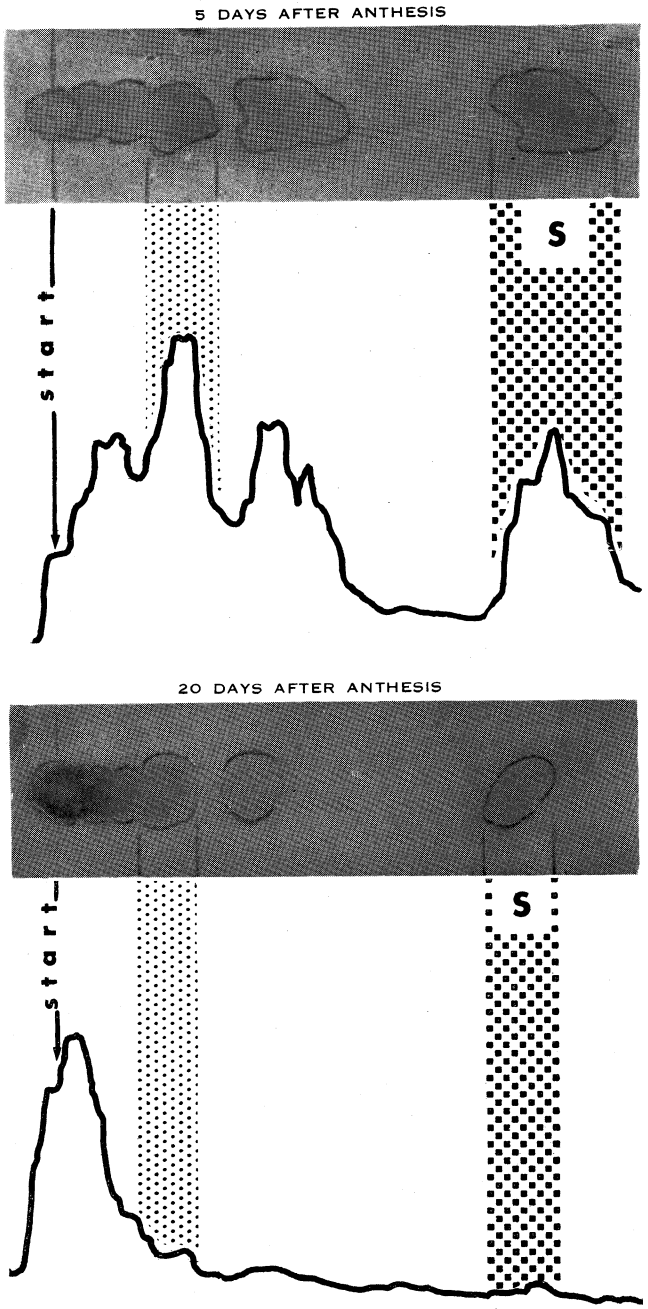

Chromatograms and radioactivity traces of an ethanol and water extract taken from the second internode of the stem of Gabo wheat of plants in which the flag leaf blades were allowed to assimilate $^{14}CO_2$ 3 days after anthesis and subsequently samples were taken for analysis at 5 days and 20 days after anthesis. The lightly stippled area indicates the highest peak of activity observed at the initial harvest, while the more heavily stippled area S compares with the sucrose reference.

that all the radioactivity was associated with these carbohydrates, apparently in the form of 3- and 4-unit oligosaccharides as well as sucrose. This is illustrated in Plate 1 by the chromatogram of an extract taken from the second internode during the initial harvest of experiment III. Loss of ^{14}C from the constituents of the extracts can therefore be attributed to sugars. Such losses were in fact somewhat greater than the total losses from the stem, suggesting that there was a small but continuing conversion of sugars to polysaccharide in the stem (cf. Lopatecki, Longair, and Kasting 1962). In experiment II (Table 3), for example, where $^{14}CO_2$ was supplied

TABLE 3

ANALYSIS OF EXPERIMENT II: SECOND LEAF FED $^{14}CO_2$ 4 DAYS AFTER ANTHESIS

Results given for each plant part are the means of six replicates ± standard error

Plant Part	Dry Weight (mg)		Total ^{14}C (counts/min)		^{14}C Distribution (%)
	Total	Residual*	Total	Residual*	
Harvest 6 days after anthesis					
Ear	551±52		241±97		1·3±0·4
Top internode	422±33		277±28		1·7±0·1
Second internode	467±25	254±12	1448±343	492±181	8·8±2·1
Lower internodes	487±41	313±35	6013±474	1471±344	36·9±2·2
Roots and crown	1292±128		2655±589		16·4±3·9
Tillers	—		—		—
Flag leaf	400±33		229±24		1·4±0·1
Second leaf	289±18		5498±562		33·5±1·8
Harvest 35 days after anthesis					
Ear	1975±75		1568±285		10·0±1·6
Top internode	395±24		234±47		1·5±0·3
Second internode	340±20	281±15	602±245	460±174	3·7±1·5
Lower internodes	495±43	429±37	3129±354	3038±341	20·2±2·0
Roots and crown	1644±61		3499±314		22·9±2·6
Tillers	6395±278		5761±506		37·3±3·0
Flag leaf	255±14		75±4		0·5±0·02
Second leaf	205±8		599±19		3·9±0·2

* Residual weight, or residual activity, after extraction with ethanol and water.

to the second leaf, the apparent increase in ^{14}C in the ethanol- and water-insoluble material of the lower internodes was 1567±484 counts/min. In experiment III, where the flag leaf assimilated $^{14}CO_2$, the increase in the second internode was 945±354 counts/min and in the top internode 1327±871 counts/min. This conversion of simple sugars to higher-unit oligosaccharides and polysaccharides is also illustrated for experiment III in Plate 1, where the chromatogram of an extract taken from the second internode at the initial harvest is compared with a chromatogram of an extract taken 20 days after anthesis. By this time most of the ^{14}C was incorporated in the oligosaccharides retained on the start line, which now constituted most of the soluble sugars in the internode. It should be noted that starch which is present as a storage form of carbohydrate in the leaves and stems of other cereals such as rice (Murayama,

Oshima, and Tsukahara 1961) has not been detected in these organs in wheat (Barnell 1938; Lopatecki, Longair, and Kasting 1962). Confirmation of the earlier conclusion reached in respect of barley (Archbold 1945) is therefore also forthcoming in wheat, in that respiratory losses proved insufficient to account for all the sugar loss from the stems during ear development.

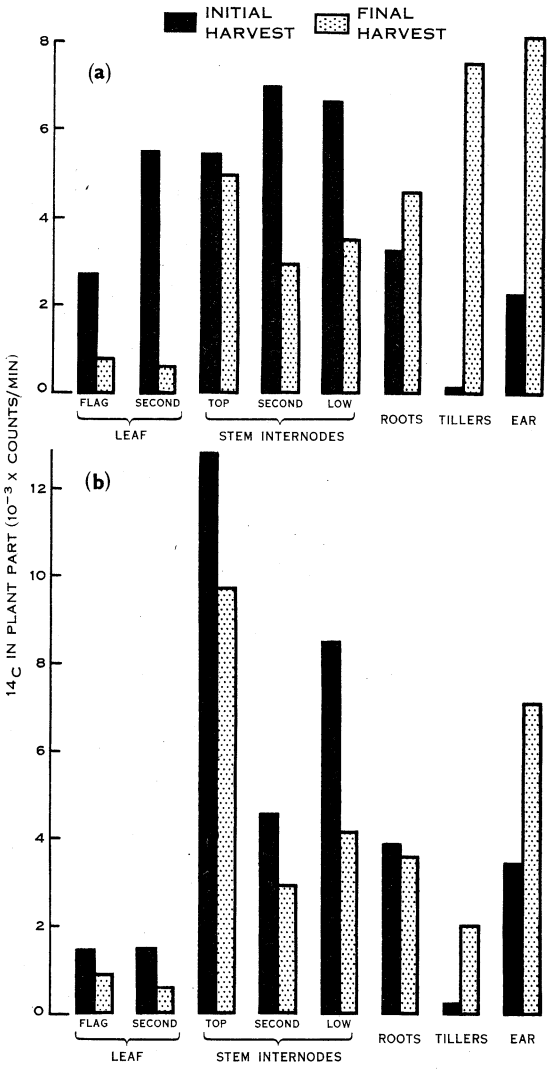

Fig. 1.—Distribution of ^{14}C between plant parts at the initial and final harvests. (*a*) Experiments II and III combined. (*b*) Experiment IV.

(*b*) *Distribution of Second Leaf Assimilates* (*Table 3*)

Two days after uptake of $^{14}CO_2$, 33·5% of the ^{14}C was still in the second leaf and its sheath. 53% had moved downwards from the point of insertion of the sheath

and 13% upwards of which only 1·3% had reached the ear. Immediate export from the second leaf was thus mainly downwards to the lower internodes (37%) and the roots (16%). During the subsequent 30 days while the grain was developing there was only a small increase in the amount of ^{14}C in the part of the plant above the second node and consequently little sugar had moved up from the lower internodes. There was nevertheless a small but significant increase of radioactivity in the ear accompanied by a barely significant loss (difference equals twice the standard error) from the second internode, which must be regarded as the source for the increase in the ear. Although nearly all the ^{14}C disappeared from the leaf and sheath by the 35th day it is unlikely that this provided ^{14}C for the ear because of the absence of net increase above the node. Material redistributed from the leaf and sheath therefore moved downwards and together with sugar from the lower internodes was translocated to newly growing tillers. There was no significant change in the activity of the roots in this or any of the other experiments, so roots do not participate in sugar redistribution.

(*c*) *Distribution of Flag Leaf Assimilates* (*Table 4*)

Two days after the uptake of $^{14}CO_2$, 14·5% of the ^{14}C remained in the flag leaf and its sheath. 13% had reached the ear and only 8% moved down to the lower internodes and roots. Over 60% was distributed about equally between the top and second internodes of the stem. That in the top internode was mainly in an insoluble form and reflects the fact that this internode was still growing at the time of the CO_2 assimilation. In the second internode three-quarters of the ^{14}C was incorporated into the soluble sugars. This type of distribution is similar to that already reported by Carr and Wardlaw (1965). Export from the flag leaf is therefore distributed above and below the node of insertion in approximately equal amounts, but of that moving downwards very little proceeds below the second internode. During the subsequent period of grain development the flag leaf and second internodes were depleted of ^{14}C, while there was accumulation in the ear, until at the 35th day the ear contained 37% of the total. Simultaneously with the movement of sugar to the ear from the second internode there was a much smaller downward movement to the newly growing tillers. The flag leaf thus supplies the ear with assimilates first directly and then, over a longer time, indirectly by means of the sugar stored in the second internode. There was no movement from the top internode which acts only as the channel of translocation to the ear.

Results of an intermediate analysis, 20 days after anthesis, are also included in Table 4. They serve to confirm the general pattern of distribution already discussed and show as well that it was virtually complete after 20 days. There was little further change in the location of ^{14}C after 20 days except for a barely significant accumulation in the ear.

(*d*) *Distribution from the Flag and Second Leaves*

It is evident from Table 2 that the amounts of ^{14}C assimilated in the several experiments agree very closely and the distribution from the flag and second leaf in experiment IV can therefore be compared directly with the sums of the estimates of ^{14}C in the various organs obtained from experiments II and III. This comparison is

set out in Figure 1. The distribution is broadly similar in the two cases. The longer time between assimilation and the first harvest combined with higher temperatures in experiment IV, resulted in less retention of ^{14}C in the fed leaves at this harvest. The main point calling for remark is the greater amount of activity in the top internode in experiment IV. This may be attributed to the fact that here the CO_2 was supplied at anthesis when this internode was actively elongating and also the growth rate

TABLE 4

ANALYSIS OF EXPERIMENT III: FLAG LEAF FED $^{14}CO_2$ 3 DAYS AFTER ANTHESIS

Results given for each plant part are the means of five replicates ± standard error

Plant Part	Dry Weight (mg)		Total ^{14}C (counts/min)		^{14}C Distribution (%)
	Total	Residual*	Total	Residual*	
Harvest 5 days after anthesis					
Ear	631±36		2089±346		13·0±2·6
Top internode	526±19	394±13	5152±732	3449±672	30·5±2·3
Second internode	388±36	256±13	5621±438	1234±226	34·1±2·5
Lower internodes	578±32	416±23	696±194	268±96	4·0±0·8
Roots and crown	1187±26		679±243		3·9±1·1
Tillers	—		—		—
Flag leaf	313±23		2371±115		14·5±0·9
Harvest 20 days after anthesis					
Ear	1418±50		4687±357		30·4±2·9
Top internode	543±16	468±15	4898±309	3651±461	31·6±2·0
Second internode	415±6	334±7	2699±203	2171±272	17·4±1·2
Lower internodes	529±12	427±20	526±168	600±101	3·4±1·0
Roots and crown	1279±97		969±330		6·1±2·0
Tillers	1091±92		896±231		5·7±1·4
Flag leaf	315±15		833±51		5·4±0·5
Harvest 35 days after anthesis					
Ear	1966±55		6584±985		37·3±5·9
Top internode	525±16	422±66	4734±321	4776±554	26·7±1·8
Second internode	349±21	288±17	2424±253	2179±198	13·7±1·4
Lower internodes	418±17	343±15	387±120	390±95	2·1±0·7
Roots and crown	1231±89		1093±398		6·1±2·2
Tillers	2157±173		1823±448		10·2±2·4
Flag leaf	273±16		693±35		3·9±0·2

* Residual weight, or residual activity, after extraction with ethanol and water.

would be higher at the higher temperature. With the increased accumulation in the top internode there is a corresponding reduction in accumulation of ^{14}C in the second internode. The total loss of activity from the leaves and stem in experiment IV was greater than accumulation in the ear and tillers, a difference that could perhaps be ascribed to respiratory losses. However, as indicated in Table 2, this was not a statistically significant loss in total activity. Also in experiment IV, in contrast to the previous experiments, the reduction in ^{14}C in the top internode just reached the level of significance.

(e) *Contribution of Redistributed Sugars to the Ear*

If the arguments already put forward are accepted then the second internode is almost the only one participating in the supply of stored sugars to the ear. In terms of dry weight changes the mean loss from the top internode (expts. II, III, IV) was 11 mg, which does not approach the standard error, and similarly the changes in radioactivity in the top internode between harvests do not reach the 5% level of significance in two cases (expts. II, III) and barely in the third (expt. IV). The mean loss from the second internode is 75 ± 25 mg and the gain by the ear is 1416 mg. This gives an estimate for the contribution to the ear by stored sugar of 5% during the interval between harvests or of 3·8% of the final ear dry weight. This should be a maximum contribution because other substances such as proteins or salts may be included. Loss of activity from the second internode gives a less certain estimate when calculated as the amount reaching the ear. The mean loss of activity from the second internode is 1883 counts/min which, on the basis of a loss of 75 mg, is equivalent to 25 counts/min/mg. The mean increase in activity in the ear was 3157 counts/min which, from the above calculation, would account for import of 125 mg, or 9% of the recorded dry weight increase. This will also be an overestimate because it is assumed in the calculation that the ^{14}C is distributed evenly in all the components of the dry weight loss. For the two experiments (II, III) in which sugars were extracted the loss of soluble material and of activity may be used as the basis of the estimate in the same way as for dry weights. Since the values for soluble material involve differences between direct estimates of dry and residual dry weight the errors of the estimates are large and in fact in the case of experiment II where the activity in the second internode is low the loss is somewhat less than twice its standard error. However, where the flag leaf assimilated $^{14}CO_2$ the activity in the second internode is high and the loss significant. Taking the mean values for the two experiments, 113 mg of soluble material and 2478 counts/min in activity were lost, equivalent to 22 counts/min/mg. The mean increase in the ear was 2911 counts/min which would thus account for 132 mg added from the second internode out of a total dry weight increase of 1379 mg, namely 10%. It can therefore be concluded that the contribution from the second internode is not greater than 7% of the final ear dry weight. This conclusion is in accordance with that reached for barley.

This direct type of evidence would appear relevant to studies on the function of "reserve" carbohydrates in the regrowth of pasture plants following defoliation, especially since the significance of the link between strong regrowth and high sugar levels in plants has been called into doubt (May 1960). This partitioning of "reserve" between the ear and new shoots may vary with the amount of accumulated sugar or the growth rate of the grains. The failure to alter the rate of loss of stem sugars by ear removal as noted earlier with barley (Archbold and Datta 1944) may have been caused not so much by the failure of the grains to control the mobilization of stem sugars as by the ability of alternate growing regions, such as young tillers, to utilize these sugars. Relevant to this is the observation that current assimilates from the flag leaf of wheat were redirected to the base of the plant when grains were removed from the ear, without any obvious effects on the movement of assimilates out of the leaf (Wardlaw 1965).

IV. Acknowledgments

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