DISTRIBUTION OF ASSIMILATE DURING STEM ELONGATION IN WHEAT

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Abstract

During the phase of stem extension in plants of *Triticum aestivum* L. cv. Stewart, the distribution of assimilated ^{14}C appeared to be related to sink size, proximity to the source, and a canalizing effect imposed by the vascular system on the movement between leaves. Evidence was found of a greater resistance to export from a leaf in the upward than in the downward direction and this is consistent with the observed arrangement of the sieve elements linking the bundles at the nodes. The cross-sectional area of the phloem did not appear to impose a limitation on the amount of material transported to the apex. The bulk of carbon imported by a growing leaf was consistently transported from the second lamina below. Import from other leaves continued after the emergence of a lamina and accounted for some 80% of its final dry weight and 50% of that in the attached sheath. The elongating internodes either side of the leaf formed large sinks for its photosynthate. Ear growth, prior to its emergence, was supported by the upper three leaves. After emergence the flag leaf was the main supplier.

I. INTRODUCTION

The movement of the products of carbon fixation to and from each leaf continually changes as it and the plant develop. A very young leaf imports all of its requirements; as it expands it enters a phase where it may be exporting photosynthate although still a net importer and then it becomes a net-exporting organ with virtually no import. In cereals and grasses, import into a leaf continues until it is fully emerged (Quinlan and Sagar 1962). Initially, most of the export goes to the apex but, with development of the leaves above it, an increasing amount moves downward (Rawson and Hofstra 1969).

Generally, it may be concluded that, during the vegetative phase, the pattern of distribution reflects primarily the physiological activity of the leaf sources and the growing sinks, with some restrictions imposed by the transport channels. For example, in tobacco, there appears to be preferential transport between leaves on the same orthostichy (Jones, Martin, and Porter 1959). In cereals and grasses, ^{14}C-distribution patterns suggest that morphological restrictions on movement are unlikely (Doodson, Manners, and Myers 1964; Quinlan and Sagar 1962). However, few attempts have been made to explore the relationship between the pattern of distribution of photosynthate and the vascular network in the Gramineae. Inosaka (1958) concluded from ^{32}P translocation studies and anatomical observation in rice that the connections between one leaf and the second above it were more direct than those between it and the next.

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During stem extension of wheat, the pattern of distribution may well be different from that of the vegetative phase outlined above, because of the presence of additional sinks and the possible transient destruction of the transport channels as the internodes elongate (Forde 1965; Patrick 1972*b*). As so little is known about the events during this phase, it was studied in detail and the results are reported herein. The partitioning of assimilates from the five upper leaves on the main tiller was followed, together with estimates of growth of the component organs and sieve-tube numbers in the nodes and internodes. These findings were then related to stem structure as recently described (Patrick 1972*a*, 1972*b*).

II. Materials and Methods

(*a*) *Plant Culture*

Plants of *Triticum aestivum* L. cv. Stewart were grown in a controlled-environment cabinet at temperatures of 24°C during a 15-hr light period and of 17°C during the 9-hr dark period. The pots were rotated once every 48 hr along the radiation gradient, the mean visible radiation received at plant level being 0·18 cal cm^{-2} min^{-1}. The plants were grown from similar-sized seed in leached river sand provided with an adequate supply of mineral elements and water.

When the third leaf on the main tiller was half emerged (about 14–16 days from sowing), the plants were thinned to two uniform seedlings per pot. Measurements of assimilate movement were commenced 5 days later, when the sixth leaf was about to emerge. Each of the laminae (numbered from the base of the tiller upward) from 4 to 8 (flag leaf) were exposed to a pulse of $^{14}CO_2$ at intervals of 2 days, only one leaf being fed on any one plant. There were four replicates. Feeding was continued until anthesis (49 days from sowing), i.e. over the whole period of stem elongation.

(*b*) $^{14}CO_2$ *Assimilation*

Each leaf was fed $^{14}CO_2$ as follows. Four hours after the beginning of the light period, the leaf was sealed into a Perspex assimilation chamber (30 by 2 by 2 cm) covered with aluminium foil to exclude light. The $^{14}CO_2$ was generated by an excess of A.R. lactic acid from $1{\cdot}3 \times 10^{-7}$ moles Na_2CO_3 (buffered at pH 9 with 0·001M Tris) containing 5 μCi ^{14}C placed in an unstirred reservoir at one end of the chamber. After 10 min, to allow for partial release and diffusion of $^{14}CO_2$ throughout the chamber, the foil was removed. After 2 hr, the chambers were removed. The plants were harvested 48 hr later.

(*c*) *Sampling and Measurement*

At each harvest, the main tiller was dissected into those individual laminae, sheaths, internodes, and ear located at and above the fifth node from the base. Below the fifth node, the internodes did not elongate to more than 10 mm and this portion of the tiller was not included in the analysis. Each node was included with the internode above it. The leaves and internodes were numbered successively from the base upward, such that internode 1 was bounded by leaves 1 and 2 and so on. Individual lengths of all organs were measured and the fractions dried for 48 hr at 80°C. The loss of radioactivity on drying was found to be less than 0·5%.

The ^{14}C present in each organ was determined separately, using the oxygen combustion technique of Kalberer and Rutschmann (1961). All of the material was combusted but if the dry weight of any organ exceeded 200 mg it was divided into components not exceeding 200 mg. The released carbon dioxide was trapped as ethanolamine carbonate in a 1 : 9 (v/v) ethanolamine–methylcellosolve mixture (Jeffray and Alvarez 1961). An aliquot of the carbonate solution was added to a scintillant of toluene–*p*-terphenyl–dimethyl-POPOP (867 : 8 : 0·2 by weight) and counted in a Tri-carb spectrometer (efficiency of 80%). The recovery efficiency from the oxygen combustion was found to be 90%.

The data are expressed as absolute counts (disintegrations/min) and specific activity. The specific activity is the absolute counts incorporated by a growing organ divided by its increment increase in dry weight over the same time interval (48 hr).

It should be noted that, throughout the paper, the term "leaf" is used in the strict morphological sense, in that it refers collectively to a lamina and its attached sheath.

III. Results

(a) *Fixation and Export of* ^{14}C

(i) *Fixation of* $^{14}CO_2$.—Measurements of $^{14}CO_2$ activity in the chamber containing a leaf after 10 min exposure to light (Table 1) indicated that the CO_2 concentration had been seriously depleted below the initial concentration of 500 p.p.m. $^{12}CO_2$ (300 p.p.m. in air plus 200 p.p.m. from the $Na_2{}^{14}CO_3$) and 100 p.p.m. $^{14}CO_2$ (i.e. assuming $^{12}CO_2$ was assimilated at a rate proportional to that for $^{14}CO_2$). Although $^{14}CO_2$ continued to be released (at a decreasing rate), the total CO_2 concentration would have been expected to fall to the compensation point of 60–80 p.p.m. CO_2 (Moss 1962) within 20–30 min of exposure to light. However, the final activity of the ^{14}C fixed by each lamina was the same (i.e. about 9×10^6 disintegrations/min) after the 2-hr assimilation period irrespective of leaf age and the initial rate of CO_2 depletion in the chamber (Table 1).

Table 1

Measured activity of $^{14}CO_2$ in the chamber atmosphere 10 and 120 min after exposure of laminae at different ages to light

Data based on four replicates. Activity released after 10 min exposure to light was $4 \cdot 7 \times 10^6$ disintegrations/min and total activity released was $9 \cdot 5 \times 10^6$ disintegrations/min

Leaf age (days from full emergence)	$10^{-5} \times$ Activity (disintegrations/min) in chamber after		Calculated CO_2 concn. after 10 min (p.p.m.)
	10 min	120 min	
2	19·2	4·4	274
6	17·0	3·1	239
10	12·3	3·6	173
14	20·5	—	281

(ii) *Effect of* CO_2 *Concentration during Feeding.*—As there was a period of about 1·5 hr during the ^{14}C assimilation when the leaf was near its CO_2-compensation point, an experiment was conducted to investigate if this resulted in a distribution pattern different from that expected with CO_2 at 300 p.p.m. throughout. The seventh leaf, at the time of peak photosynthetic activity, on each of four plants was fed $^{14}CO_2$ by the standard procedure and on four separate plants by the same procedure but containing a reservoir of $Na_2{}^{12}CO_3$ from which sufficient CO_2 was generated at

10-min intervals to maintain the concentration at about 300 p.p.m. The distribution of activity after 48 hr (Table 2) indicates little difference between the two procedures,

TABLE 2

EFFECT OF CO_2 CONCENTRATION DURING THE INCORPORATION OF $^{14}CO_2$ BY THE SEVENTH LEAF ON THE DISTRIBUTION OF ^{14}C WITHIN THE PLANT

Each result is the mean of four replicates ± S.E.

Organ	Distribution of ^{14}C (% of total)	
	Normal procedure	CO_2 maintained at 300 p.p.m.
Lamina 7 (fed)	23·1±3·2	15·4±1·6
Sheath 7	8·8±2·0	10·8±2·9
Lamina 8	3·9±0·9	3·5±0·3
Sheath 8	2·0±0·1	1·9±0·4
Internode 6	14·0±2·6	13·3±2·5
Internode 7	0·6±0·1	0·7±0·1
Ear	1·1±0·2	1·0±0·3
Remainder	46·5±3·2	53·4±6·8

the slightly greater export (8%) from the lamina held at 300 p.p.m. CO_2 being partitioned in closely the same proportions as that from the one fed using the standard method. Similar results have been obtained in tall fescue grass (Jewiss 1967).

TABLE 3

SPECIFIC ACTIVITIES OF THE VARIOUS PLANT FRACTIONS DETERMINED OVER A NUMBER OF HARVESTS PRIOR TO THE EMERGENCE OF THE EAR

Specific activities expressed as thousands of disintegrations per minute per milligram dry weight increase

Organ	Specific activity	Organ	Specific activity
Lamina exposed to $^{14}CO_2$	222·8±29·5	Internode 5	57·8±5·6
Sheaths of exposed laminae	86·2±15·8	Internode 6	41·8±2·5
Laminae of unexpanded leaves	42·3± 3·4	Internode 7	31·4±1·3
Sheaths of unexpanded leaves	35·5± 3·2	Internode 8	27·2±2·8
		Ear	34·3±3·0

(iii) *Mean Specific Activity of ^{14}C in the Plant Organs after 48 Hr.*—The mean specific activity was determined as the total counts incorporated from all the fed laminae by each organ per unit increase in its weight, both measured over a time interval of 48 hr. If the absolute distribution of assimilated ^{14}C was proportional to that of the exported photosynthate, then the mean specific activities of each organ should be similar and remain constant with time. The mean specific activity of the laminae exposed to $^{14}CO_2$, averaged over all time intervals, was higher than that of all other organs (Table 3). This retention of ^{14}C was also apparent in the sheaths of the leaves exposed to $^{14}CO_2$. There was not much variation in the specific activities

of the other organs with time, although there was some suggestion that with progress up the stem the total activity per unit dry weight increase was progressively diluted, this pattern being most evident in the internodes. It probably resulted from a greater contribution from the photosynthesis of the sheaths, of which the exposed surface area increased markedly from sheath 5 up the main tiller.

Thus, the data given in Tables 2 and 3 demonstrate that the distribution of ^{14}C reflects the proportionate amounts of photosynthate exported from the source laminae to the various sinks. However, the amounts of radioactivity retained by the source laminae and their attached sheaths must be interpreted with caution.

(*b*) *Distribution of* ^{14}C *Exported*

In respect of the uppermost three leaves, the proportioning of ^{14}C exported above and below the source lamina (considering only that portion of the main tiller above and including leaf 5) followed a pattern similar to that shown in Figure 1.

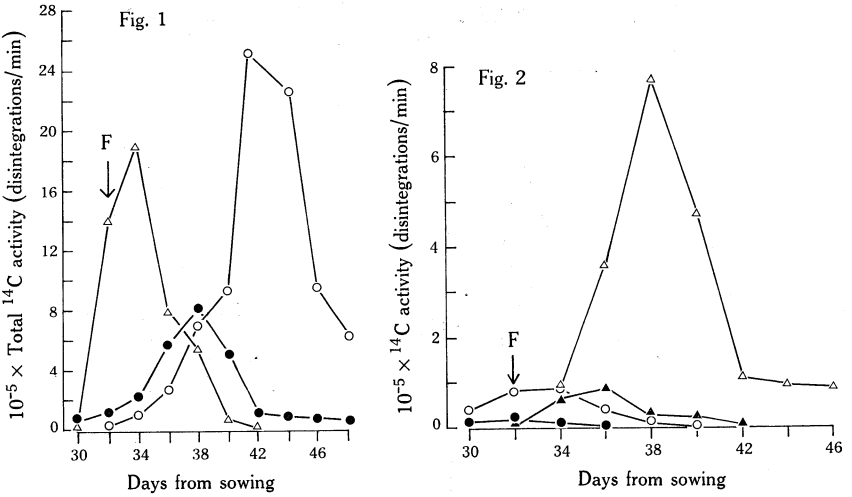

Fig. 1.—Total activity of ^{14}C exported above (○) and below (●) lamina 7 (only that portion above and including leaf 5) and the amount retained by its attached sheath (△) when it was fed at different stages. F = full emergence.

Fig. 2.—^{14}C exported from lamina 7 during its ontogeny to the various organs below it: sheath 6 (○); sheath 5 (●); internode 6 (△); internode 5 (▲). F = full emergence.

Until 2–4 days after the full emergence of the source lamina, the attached sheath formed the major sink for its assimilate. The amounts of ^{14}C exported above and below the source lamina were similar but increased with time for some 4–6 days after full leaf emergence. Then, the contribution to the basipetal region decreased, whilst that transported above continued to increase before declining 10–12 days after full leaf emergence (except with lamina 8 where the acropetal contribution increased continually over the period investigated—see Fig. 3).

The distribution of assimilates *below* the fed lamina was similar for each source leaf. For example, most of the activity exported downwards from lamina 7 (Fig. 2)

early in its ontogeny was moved to the nearest sheath (sheath 6) but, as the intervening internode (internode 6) began to elongate, increasing amounts were found in this organ. Although the second internode below the source leaf (internode 5) was accumulating dry matter, little activity was exported to it. The reason(s) for this were not clarified. Negligible amounts of activity were found in the fully expanded laminae (laminae 5 and 6) and the second sheath below (sheath 5).

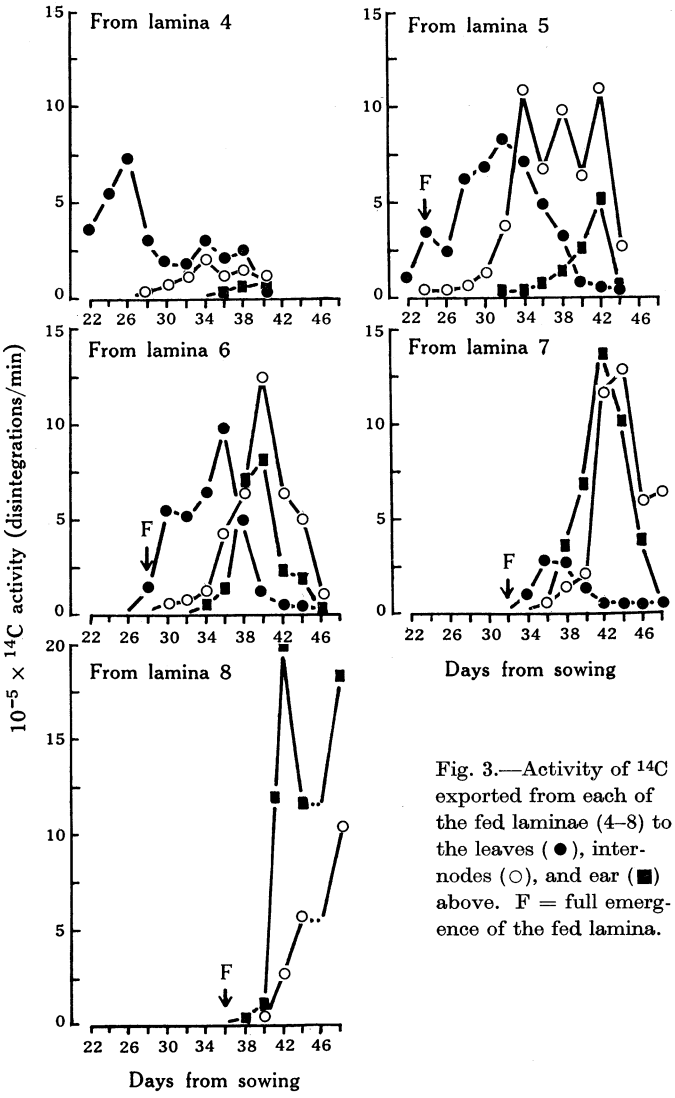

Fig. 3.—Activity of ^{14}C exported from each of the fed laminae (4–8) to the leaves (●), internodes (○), and ear (■) above. F = full emergence of the fed lamina.

The distribution of that portion of ^{14}C exported to the leaves. internodes, and ear *above* the source leaf appeared to vary with leaf position and age (Fig. 3). At all times, most of the export from lamina 4 was incorporated in the leaves above but, whereas movement from lamina 5, 6, and 7 was initially to the upper leaves, as the internodes and ear began to grow, increasing amounts were diverted to these organs.

Export to the leaves ceased when the sheath stopped increasing in weight. Except for lamina 8 (flag lamina), export to the ear declined to negligible amounts during the period from ear emergence (day 43) to anthesis (day 49). Movement from lamina

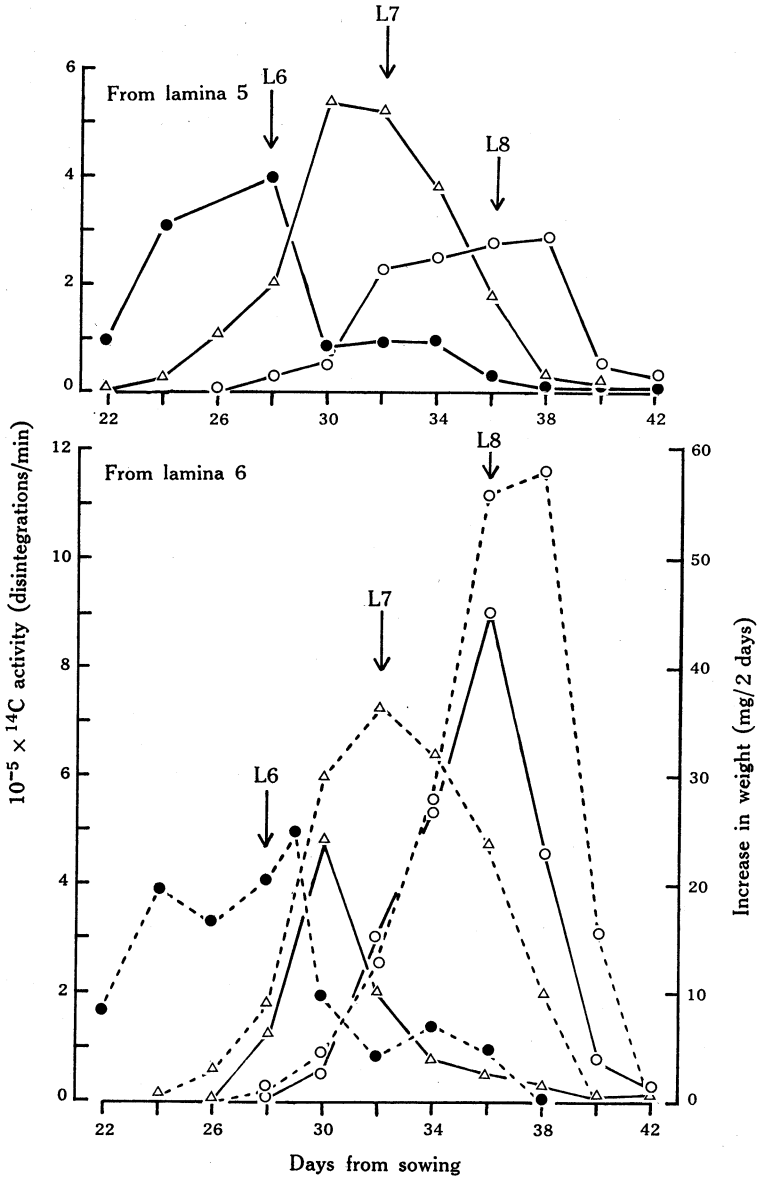

Fig. 4.—Activity of ^{14}C imported by leaves 6 (●), 7 (△), and 8 (○) from laminae 5 and 6. The dotted lines represent the increment increases in weight (mg per 2 days) of leaves 6 (●), 7 (△), and 8 (○). The arrows indicate the time of full leaf emergence of laminae 6, 7, and 8.

8 to the ear decreased temporarily, but that to the stem (mainly the flag internode) continued to increase during this time.

Internal competition for assimilate is always possible when two or more organs import appreciable quantities at the one time. These data (Fig. 3) suggest that leaves never compete significantly with the stem and ear tissue: There was little demand by the stem plus ear prior to day 32 and by this time the flag lamina (lamina 8) had just emerged. It was fully expanded 4 days later and may be reasonably assumed to have had the photosynthetic capacity to meet the demand for assimilates by its sheath during its growth over the succeeding 4 days. On the other hand, the stem and the ear developed more or less concurrently and similar quantities of assimilate were imported from each of the three uppermost leaves. There exists, then, the possibility of competition between these two organs but whether or under what circumstances this may be significant has not been examined.

Export to the growing leaves followed the pattern described by Doodson, Manners, and Myers (1964) in so far as it was switched from one leaf to the next and the greatest amount was moved to the second leaf above (Fig. 4). Movement to the second leaf above appeared to be closely related to its sink size (i.e. increment increase in weight per unit time) but that to the first and third leaves were not. Amounts moved per unit sink activity showed that export to the second leaf above occurred more readily than that to the other leaves (Table 4). This may be due to the more

TABLE 4

SPECIFIC ACTIVITY OF THE ^{14}C MOVED TO LEAVES 7 AND 8 FROM LAMINAE 5 AND 6

Specific activities expressed as thousands of disintegrations per minute per milligram dry weight increase

Days from sowing	Specific activity of ^{14}C moved from:			
	Lamina 5 to leaf 7	Lamina 5 to leaf 8	Lamina 6 to leaf 7	Lamina 6 to leaf 8
32	24·8	16·5	9·6	21·7
34	24·1	9·2	5·5	20·0
36	20·3	6·5	6·5	21·2

comprehensive interconnection between the vascular bundles associated with each second leaf (Patrick 1972*a*). Indeed, 60% of the ^{14}C imported by a leaf during its growth came from the second leaf below.

Import into the expanding lamina and its attached sheath continued after the lamina emerged (Fig. 4). The amount of dry matter contributed during this period may be estimated assuming the specific activity of the imported ^{14}C remains constant following the emergence of the lamina. (This contention is supported by the data in Table 3.) On this assumption, photosynthate moved from the lower leaves accounted for about 80% of the dry weight increase of the lamina during the first 2–3 days after emergence, falling to 25% at full expansion (4 days from the appearance of the lamina tip). Some 50% of the final weight of the sheath was imported from sources other than the attached lamina.

The amount exported to the individual internodes and ear appeared to depend on a relationship between sink size of the importing organ and the number of intervening sinks and sources (Fig. 5). The form of this relationship could not be clarified

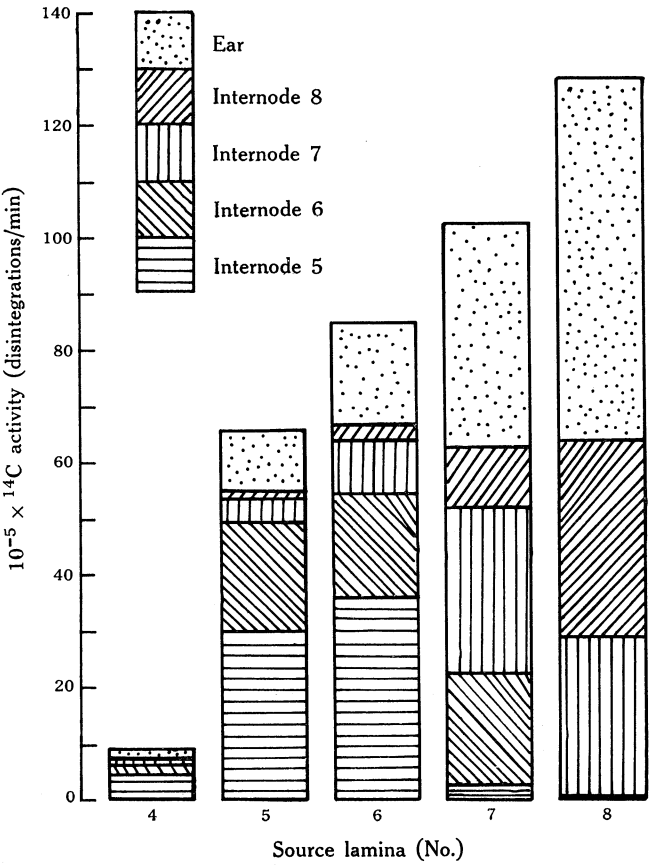

Fig. 5.—Sum of the ^{14}C imported from the various sources by internodes 5, 6, 7, 8, and the ear between days 22 and 48 presented additively in order from the base of the main tiller.

from the data, except that the amounts incorporated from the various sources did not necessarily depend upon the quantities passing through the intervening internodes. Some kind of selective unloading process appeared to be superimposed upon the normal supply and demand relationship. However, several general features of ^{14}C distribution emerged. For example, export from all sources to the ear was as great or greater than that to the uppermost two internodes. The internodes immediately above and below a lamina formed the largest stem sinks for its export whilst internodes further down the stem retained negligible amounts. The specific activity of the export to the internodes on either side of the source lamina indicated 2–5 times as much activity per unit change in weight moved to the lower than to the upper

internode (Table 5). This occurred irrespective of the actual rates of growth of the respective internodes. These results may mean that, at the node of attachment of the source leaf, there was a greater resistance to the flow of assimilates exported in the acropetal than in the basipetal direction.

TABLE 5

SPECIFIC ACTIVITY OF THE ^{14}C MOVED TO THE INTERNODE IMMEDIATELY ABOVE AND BELOW THE SOURCE LAMINA AND RATES OF GROWTH OF THE INTERNODES

Specific activities expressed as thousands of disintegrations per minute per milligram dry weight increase

Source lamina	Sink internode	Days from sowing			
		33–35	35–37	37–39	39–41
		Specific activity			
Lamina 6	Internode 5 (below)	27·3	32·5	32·8	—
	Internode 6 (above)	3·9	6·1	8·3	—
Lamina 7	Internode 6 (below)	6·2	15·0	12·7	47·1
	Internode 7 (above)	4·4	3·5	9·5	4·2
Lamina 8	Internode 7 (below)	—	12·8	10·5	8·9
	Internode 8 (above)	—	6·0	2·2	3·6
		Rate of dry weight increase of internodes (mg/48 hr)			
	Internode 5	22·5	20·6	18·7	0·0
	Internode 6	15·0	22·5	24·4	46·8
	Internode 7	0·2	5·6	11·3	30·0
	Internode 8	—	0·1	0·2	7·5

(c) *Vascular Development*

As described previously (Patrick 1972*b*), there is continual destruction and differentiation of sieve-tube elements during the elongation of an internode. The significance of this in translocation was explored by counting the numbers of sieve tubes in each bundle along the entire lengths of internode 6 and sheath 7 at two-day intervals during their elongation, determining the mean lumen area per sieve tube (found to be $32 \pm 1 \cdot 8$ and $61 \pm 2 \cdot 6\ \mu m^2$ for outer- and inner-ring bundles respectively) and calculating the "specific mass transfer" (Canny 1960) as an index of transport capacity. The latter was calculated on the smallest number of sieve elements present along the length of the organ at each harvest and therefore should provide a minimum estimate of the transport capacity. (It may be noted that the rate of sieve-tube differentiation exceeded the rate of destruction so there was a continual increase in the minimum number throughout elongation.) The amounts of material moved were estimated from the relevant dry weight changes before the emergence of lamina 7 and from ^{14}C data thereafter. In keeping with Canny's procedure, respiration losses were ignored.

The values for the specific mass transfer over a number of harvests were determined for the movement of dry matter through (1) sheath 7; (2) internode 6 to leaf

7 assuming all material moved in the leaf 7 traces; (3) internode 6 to the shoot above; and (4) internode 6 to the shoot above assuming all material moved in the leaf 8 traces (Table 6). These assumptions concerning the transport of material within specific channels were anatomically valid until day 36 when node 7 reached maturity (cf. Patrick 1972*b*). Another assumption implicit in these data was that acropetal and basipetal movement were not spatially separated and occurred within the same sieve elements (cf. Trip and Gorham 1967). Comparison of the values of specific mass transfer in Table 6 with that of an average value of 20 g per cm^2 sieve-tube lumen

TABLE 6

SPECIFIC MASS TRANSFER OF DRY MATTER THROUGH (1) SHEATH 7, (2) INTERNODE 6 TO LEAF 7, (3) INTERNODE 6 TO THE SHOOT ABOVE, AND (4) INTERNODE 6 TO THE SHOOT ABOVE LEAF 7

Time of the emergence of the laminae is indicated by E

Days from sowing	Specific mass transfer (g cm^{-2} hr^{-1})			
	1	2	3	4
22	1·7	0·5	0·6	0·9
24 E(6)	4·5	2·1	1·7	0·9
26	4·0	3·7	4·0	4·5
28 E(7)	5·8	8·5	8·2	7·4
30	4·1	29·1	22·7	13·0
32 E(8)	3·1	35·2	21·8	14·5
34	—	15·7	17·7	20·6
36	—	8·5	15·0	—

per hour (Canny 1960) suggests that in each intercalary meristem the sieve tubes are maintained in sufficient number to adequately transport the material moved through them. The only exception occurred during days 30 and 32 when the calculated specific mass transfers in the vascular traces of leaf 7 passing through internode 6 were greater than the average suggested by Canny (1960). This may imply that the cross-sectional area of the phloem—in internode 6 when leaf 7 was approaching full emergence—was restricting transport to and from leaf 7. At this stage, internode 6 was rapidly elongating and the rate of sieve-tube destruction was significantly decreasing the potential cross-sectional area of the phloem in the internode (Patrick 1972*b*). (However, there is no reason to believe that a specific mass transfer of 20 g cm^{-2} hr^{-1} even approaches the limit of sieve tubes for transport.) If transport to the shoot above leaf 7 were principally confined to the traces of leaf 8, then the data would indicate there was no "bottleneck" in the movement to this region through internode 6.

To summarize, internode elongation could possibly produce "bottlenecks" in the transport system. However, these appear to influence transport to and from a leaf only when it is approaching full emergence; movement to the apex was unaffected. The relatively low specific mass transfer indices in a young internode would suggest the vascular system was not limiting the supply of sucrose to those regions with differentiated sieve elements.

IV. Discussion

Since the cross-sectional area of the phloem does not appear to limit the amount of material transported to the apex, vascular restrictions, if any, must be confined to the young nodes in which sieve-tube differentiation of the cross-linkages lags behind that of the leaf traces they interconnect (Patrick 1972*b*). There is some rather circumstantial evidence that supports this contention; that is, the differentiation of vascular links that connect an expanding leaf at the apex with the rest of the plant coincides with the relative growth rate of that leaf reaching a maximum. This may be interpreted to mean that the establishment of a more efficient supply of substrate partially releases the limitations on the growth of the primordium (Williams 1960; Patrick 1972*b*). Similar observations have been made in tobacco, whereby the halt in the decline in the relative growth rate of an expanding leaf is associated with the appearance of sieve tubes in the lamina (Hannam 1968). However, whether or not these are causal correlations requires further investigation.

It is suggested that the source discrimination exhibited by the import into the growing leaves is, at least in part, influenced by the relative conductances of the vascular channels linking the sink to the various sources. Similar conclusions have been drawn from anatomical and ^{32}P tracer studies in rice (Inosaka 1958). Except for some minor details, rice has a comparable vascular system to that of wheat (Patrick 1972*a*). Therefore, it is not surprising to find that, in both species, the second lamina below is the main source of supply for the growth of a leaf. The vascular restraint on assimilate movement between leaves has important physiological implications, especially in terms of lamina growth. Clearly, if the distribution of photosynthate were solely determined by sink demand (and since growth of the lamina is largely dependent on import), the growth activity of the lower sheaths could completely dominate events at the apex. The canalizing effect of the vascular system imposes a constraint on this potential competition.

Import of carbon into a lamina from lower leaves continues through to its full emergence and accounts for some 80% of its final weight. The small contribution by lamina photosynthesis is not surprising when it is considered that the lamina remains erect and furled until full emergence, thus providing a small area for light capture. From emergence onward, movement of assimilates into the leaf may be limited by the cross-sectional area of the transport channel in the internode below.

The distribution of assimilate exported from laminae appeared to be governed by the normally found relationship between source proximity and sink size. However, acting independently of the sink effect there was a bias toward a downward movement. The nature of this was not clear but may, in part, be related to a possible higher resistance to lateral relative to longitudinal transport imposed by the arrangement of the sieve elements linking the bundles (Patrick 1972*a*). That is, acropetal export from the source leaf at the node of attachment, initially, would have involved a lateral flow between neighbouring sieve elements whereas basipetal movement may have continued longitudinally within the same sieve tubes.

The elongating internodes formed large sinks for the carbon exported from the leaves attached at either node. Import from other leaves was confined to those located below the internode. The relative amounts of carbon imported from the

various sources appeared to be dependent on a sink effect coupled with a selective unloading mechanism. The nature of this supposed mechanism could not be clarified. Ear growth prior to emergence was supported mainly by the three leaves below the flag leaf. Assimilate from these leaves was distributed between stem and ear according to sink demand and position of the source leaf. Whether plant photosynthesis was sufficient to meet the demands for stem and ear growth is uncertain but it was clear that, under the experimental conditions, the ear competed successfully with the stem for ^{14}C compounds. Following ear emergence, the contribution from these lower leaves declined rapidly and, as shown by other workers (Quinlan and Sagar 1962; Wardlaw 1965), the flag leaf was the sole supplier to the ear by the time of anthesis.

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