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The Relationship Between Photosynthesis and Translocation in a C-3 Plant

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ABSTRACT. The basal bifoliate leaf of broad bean on separate plants was supplied with $^{14}CO_2$ at four stages during the development of the species and the distribution of radiocarbon products determined quantitatively 24 h later. The fed leaves retained substantial amounts of the radiocarbon they fixed initially. Determination of the dry weight of the basal bifoliate leaf at four stages of development, from a plant with two expanded leaves to one with developing pods showed no statistically significant change of leaf dry weight during this time. Whole plants of broad bean were also allowed to assimilate $^{14}CO_2$ for one hour. Samples of leaf 3 were then harvested after 1h, 3h, 6h, 24h and 7 days, dried and prepared for autoradiography. The results show that the intensity of ^{14}C in leaf 3 declined with time but with a trace of radiocarbon retained by the 7th day. A survey of published information about the loss of photosynthetically fixed $^{14}CO_2$ from leaves is included. The present results do not support some previously published conclusions that the rate of export of photosynthetic products from the leaves regulates the rate of photosynthesis.

The acquiring of knowledge of the influence of photosynthesis on translocation or for control of photosynthesis by translocation is a central problem in agricultural plant production since it allows plant breeders to judge in selecting and crossing for varieties of crops with high photosynthetic productivity and efficient translocatory ability (source-sink relationship).

One of the most common and most commonly ignored features of translocation studies where $^{14}CO_2$ has been used is the substantial amount of radiocarbon retained by fed leaves. Table 1 summarizes previous data on the proportions of radiocarbon retained by leaves fed with $^{14}CO_2$. It is clear that there are species which show rapid rates of export from leaves *e.g.* sugar-cane, corn and dura, and species with slower export rates *e.g.* tomato, *Vicia faba* L., cotton and wheat. The

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former group comprises C-4 plants while the latter species are C-3 plants (Hatch and Slack 1966, Hatch *et al.* 1967). Despite this easy primary separation of species into C-4 and C-3 types, there is great variation within C-3 plants.

Although there are several suggestions in the literature that a relationship exists between photosynthesis and translocation a consensus of opinion does not exist (Neales and Incoll 1968). Nelson *et al.* (1961) showed for soybean (*Glycine max* L.) that translocation and assimilation were not related and that the amount of ^{14}C fixed was not affected by the age of the fed leaf. Hofstra and Nelson (1969a and b) after studying a range of species demonstrated a correlation between the fixation of $^{14}CO_2$ and the export of radiolabelled assimilates from the fed leaves. Geiger (1976) reviewed a number of reports which revealed that (a) increased demand for export of assimilates resulted in an increased rate of net photosynthesis, (b) reduced demand produced a reduction in net photosynthesis rate, (c) there was a close correlation between sink demand and net photosynthesis and (d) there was no correlation between photosynthesis and sink demand (see Geiger 1976, Table 1).

In a previous paper (Ismail 1984) it was shown that fed broad bean leaves failed to export within 24 hr more than 50% of the ^{14}C which they initially fixed. Overall, the present investigation is meant to provide information on (a) the relationship between photosynthesis and translocation (b) the rate of the fixed and retained ^{14}C in the fed leaf (Table 1).

Table 1. The proportion (%) of fixed radiocarbon retained by fed leaves of different species

Species	Time after feeding (hr)	Percentage retained	Reference
	C - 4 Plants		
Panicum miliacium L.	24	15	Hofstra and Nelson (1969a)
Saccharum officinarum L.	1.5	43	Hartt *et al.* (1963)
	4	20	Hartt and Kortschak (1967)
	24	9	Hartt *et al.* (1963)
	96	2	Hartt *et al.* (1963)
Sorghum vulgare Pers.	24	15	Hofstra and Nelson (1969a)
Zea mays L.	0.5	50	Hofstra and Nelson (1969b)
	24	10-15	Hofstra and Nelson (1969b)
	C - 3 Plants		
Beta vulgaris L.	0.5	82	Mortimer (1965)

Table 1.–(Continued)

Species	Time after feeding (hr)	Percentage retained	Reference
	1	42	Mortimer (1965)
	3	30-40	Mortimer (1965)
	24	20	Mortimer (1965)
	168	9-67	Joy (1964)
	96-192	20	Krieddemann (1969)
Brassica napus L.	24	75	Chapman *et al.* (1984)
Cucumis sativus L.	24	65-70	Kanahma and Hori (1980)
Cucurbita melopepo torticollis Bailey	3	50	Webb and Gorham (1964)
Dianthus caryophyllus L.	16	50	Harris and Jeffcoat (1972)
Fragaria x ananassa Duch.	8 96	60 20-30	Antoszewski and Dzieciol (1973)
Glycine max. L.	2	55	Thrower (1962)
	6	75	Clauss *et al.* (1964)
	24	56	Hofstra and Nelson (1969a)
Gossypium hirsutum L.	2	93	Ashley (1972)
	8	68	Ashley (1972)
	24	43	Ashley (1972)
Helianthus annuus L.	24	30	Hofstra and Nelson (1969a)
Hordeum vulgare L.	3	40	Felippe and Dale (1972)
Lolium multiflorum Lam.	24	40-50	Marshall and Sagar (1968a)
Lycopersicum	2	84	Tanka *et al.* (1974)
esculentum Mill.	6	83	Khan and Sagar (1969b)
	24	70-80	Khan and Sagar (1966, 1967)
	24	97	Rangnekar (1974)
	24	40	Hofstra and Nelson (1969a)
	48	70	Tanaka *et al.* (1974)
	144	83	Rangnekar (1974)
	240	40	Tanaka *et al.* (1974)
	360	44	Khan and Sagar (1969b)
Malus sylvestris Mill.	120	10-20	Hansen (1967)
Medicago sativa L.	24	40	Wolf (1967)
Nicotiana tabacum L.	3	70	Yamamoto (1967)
	5	70	Jones *et al.* (1959)
	5.5	78	Shiroya *et al.* (1961)
	8	56	Jones *et al.* (1959)
	21	30	Yamamoto *et al.* (1967)
Nicotiana affinis Moore	24	50	Hofstra and Nelson (1969a)
Nicotiana tabacum L.	96	32	Jones *et al.* (1959)

Table 1.–(Continued)

Species	Time after feeding (hr)	Percentage retained	Reference
Phaselous vulgaris L.	24	55-60	Hale and Whitbread (1973)
		43-72	Olufajo *et al.* (1982)
Phalaris arundinacea L.	24	25	Wolf (1967)
Pisum sativum L.	3	64-78	Lovell *et al.* (1972)
	24	22-37	Lovell *et al.* (1972)
Raphanus sativus L.	24	40	Hofstra and Nelson (1969a)
Ricinus communis L.	24	50	Hofstra and Nelson (1969a)
Triticum aestivum L.	3	52	Dodson *et al.* (1964)
	24	40-50	Carr and Wardlaw (1965)
	48	15-33	Wardlaw (1965)
Vicia faba L.	24	65-83	Ismail (1984)

Materials and Methods

Experiment 1

Seeds of the broad bean (*Vicia faba* L. cv. Express Longpod) were sown two seeds per 15-cm pot in John Innes No. 1 Compost. Plants were thinned to one per pot at the one leaf-stage. The plants were maintained in a temperate glass-house; natural light was supplemented by 400 W mercury lamps to give a daylength of 16 hr; minimum temperature during the day was 20°C and during the night 17°C.

The application of $^{14}CO_2$ was always made between 09.00-11.00 hr. On four different occasions during the life of the species: (a) when the plant had two expanded leaves, (b) when the plant had five expanded leaves, (c) when the plant had 7-8 expanded leaves and flower buds were visible and (d) when the plant had more than 12 expanded leaves and some pods had begun to appear, leaf 1 (basal) was allowed to assimilate $^{14}CO_2$. The method of labelling assimilates was that described by Lovell *et al.* (1972). The treated leaf was enclosed in a transparent perspex chamber (dimensions 6 × 13.5 × 8 cm). The petiole of the leaf was placed in a notch cut into the lower half of the chamber and after replacing the top, the notch was sealed using plasticine. Radioactive carbon dioxide ($^{14}CO_2$) was liberated in the chamber from $Na_2{}^{14}CO_3$ solution (specific activity 59 m Ci per mM) by the addition of excess N HCl). The reaction took place in an aluminium planchette (diameter 2.5 cm). Five microcuries of ^{14} CO_2 were supplied to each treated leaf and the dose remained constant for all the experiment. The leaf fed with $^{14}CO_2$ was confined to the feeding chamber for 1 hr after which time the chamber was removed. There were four replicates of each treatment. The plants were harvested 23 hr later and four plants from each treatment were divided into parts above the fed leaf, parts below the fed leaf and the fed leaf (Ismail 1984). These parts were dried separately in an oven at 60-70°C and weighed. Radioactivity was estimated using the procedures described by Lovell (1969). Sub-samples of known weight were taken, suspended in a constant volume of 98% alcohol, and two 0.5 cm^3 aliquots of each suspension plated onto planchettes, dried and then counted by a Tracerlab multipurpose counting system. Automatic background subtraction facilities were used. The results were examined and expressed in two ways:

(1) Total ^{14}C recoveries = the total radioactivity in each plant.

(2) The radiocarbon recovered in the whole plant excepting the fed leaf expressed, as a percentage of the total ^{14}C recovery from these parts.

Over similar stages of development leaf 1 (the basal) from other uniform plants was harvested, dried in an oven at 70°C and weighed. There were four replicates of each treatment.

Experiment 2

Broad bean plants were raised as described previously in Experiment 1. Whole plants of broad bean at the vegetative phase (with 5-6 expanded leaves) were allowed to assimilate $^{14}CO_2$ (10 µ Ci) following the method of Oo (1968). Samples of leaf 3 (a basal leaf) were harvested after 1 hr, 3hr, 6hr, 24hr and 7 days, dried, and prepared for autoradiography and exposed to Kodirex X-ray film for three days (Yamaguchi and Crafts 1958 and Little 1962).

Results

Twenty four hours after the basal leaf was supplied with $^{14}CO_2$ the proportion retained in the fed leaf was 86, 65, 73 and 80% during Experiments 1a, 1b, 1c and 1d respectively.

Figure 1 illustrates that there is no correlation between photosynthesis (measured as total ^{14}C assimilation) and translocation (measured as the export of ^{14}C-labelled compounds). The amount of $^{14}CO_2$ fixed by the basal leaf in Experiment 1a was higher than the amounts fixed by the corresponding leaf in subsequent experiments while the amount of ^{14}C exported did not fall with time (Table 1).

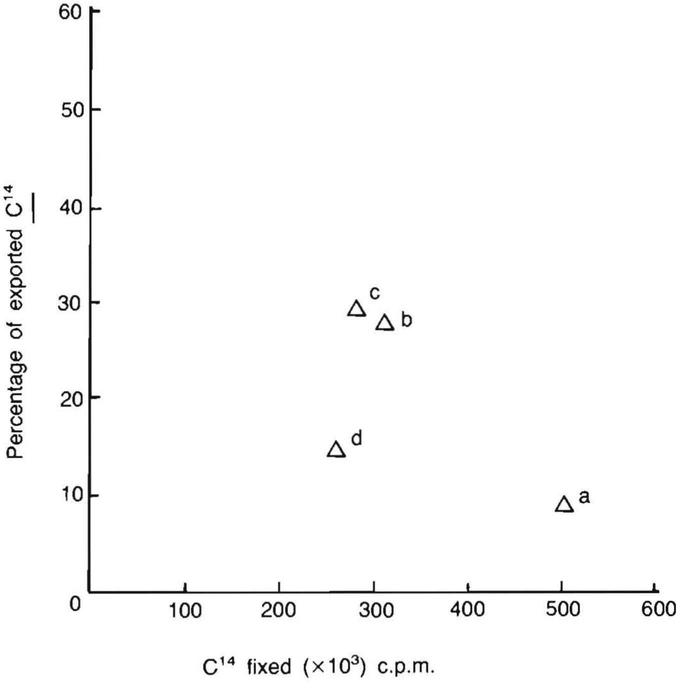

Fig. 1. The relationship in *Vicia faba* L. between total radiocarbon recovered from the whole plant (C^{14} fixed) and the percentage of the recovered carbon exported from the source leaf; a, b, c and d refer to experiments 1(a - d) respectively, c.p.m. = count per min.

It can be seen that the dry weight of leaf 1 of broad bean did not increase with time (Table 2).

Plate 1 shows that over the first three harvests the veins and the petioles were labelled but the intensity of labelling declined with time and by the 7th day there was still a trace of radiocarbon retained in the source leaf (Plate 1).

Table 2. Dry weight of leaf 1 (basal leaf) over the period of the four experiments

	Experiment No.			
	1a	**1b**	**1c**	**1d**
Dry weight* (mg)	134 ± 10	142 ± 16	132 ± 12	132 ± 16

* (Values are means of 4 replicates) ± S.E. given.

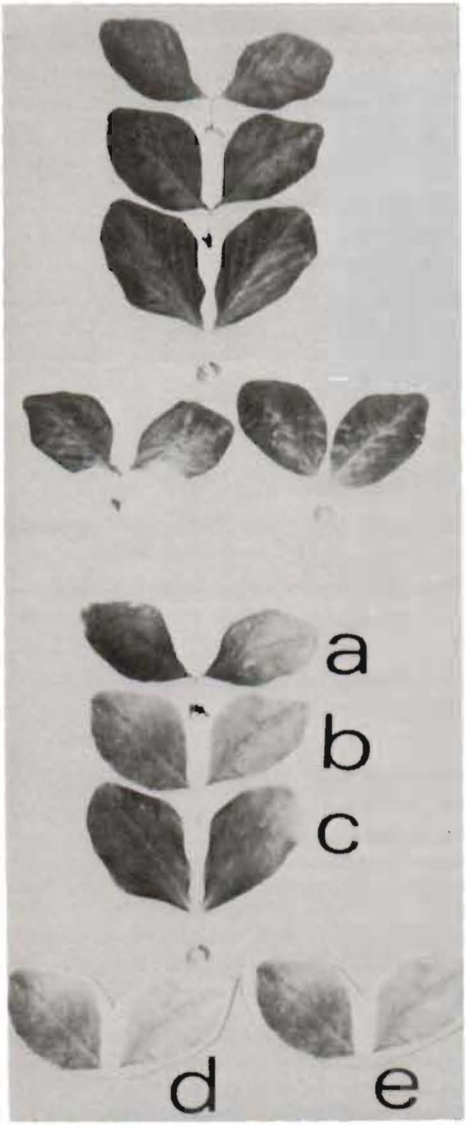

Plate 1.

Translocation of ^{14}C-labelled compounds from L3 of vegetative plants of *Vicia faba* with time.

Whole plants of broad bean were allowed to assimilate $^{14}CO_2$ liberated from 10 μCi of $Na_2\,^{14}CO_3$ for 1 h. Samples of L3 were harvested after 1, 3, 6 and 24 h and after 7 days. Exposure to Kodirex X-ray film was for 14 h. The upper block of 5 leaves is a photograph of the plant material, the lower block is a photograph of the autoradiographs of the corresponding leaves.

a. after 1 h	d. after 24 h
b. after 3 h	e. after 7 days
c. after 6 h	

Discussion

Assimilate accumulation or retention in leaves has been known to plant physiologists since the 19th century (Boussingault 1886) but the relationship between rate of translocation and rate of photosynthesis is still neither agreed nor fully understood although several hypotheses exist (Humphries 1967, Neales and Incoll 1968 and Geiger 1976). Accumulation of assimilates in leaves has been reported when (a) sinks are removed (Moss 1962, Burt 1964, Nosberger and Humphries 1965, and Olufajo *et al.* 1982) (b) leaves are infected with a fungal pathogen - *Uromyces fabae* Pers. (Thrower and Thrower 1966) (c) leaves are under drought stress (Kemper *et al.* 1961, Wardlaw 1967, and Munns and Pearson 1974) and (d) rates of photosynthesis are low (Hofstra and Nelson 1969b). It has been suggested that rapid rates of translocation are associated with (a) more efficient sinks (Khan and Sagar 1969a) (b) less sources per plant (Khan and Sagar 1969a, Lovell and Sagar 1972, Thorne and Koller 1974, and Geiger 1976) (c) more efficient and quicker vein loading (Liu *et al.* 1973) (d) higher photosynthetic rate (Servaites and Geiger 1974) (e) more vascular bundles per unit leaf width (Crookston and Moss 1974) and (f) more phloem (Evans *et al.* 1970).

Unlike tomato leaves (Khan and Sagar 1969b) broad bean leaves do not continue to increase their weight after expansion is completed. However, in *Vicia faba* L. all the leaves had exorted within 24hr between 14 and 40% of their fixed carbon. These values are within the range of C-3 plants although at the lower end (Table 1). Hofstra and Nelson (1969a and b) after studying a range of species demonstrated a correlation between the fixation of $^{14}CO_2$ and the export of radiolabelled assimilates from the fed leaves.

The results obtained in the present work (Fig. 1) do not support the generalization of a relationship between photosynthesis (measured by total ^{14}C assimilation) and translocation (measured by the export of ^{14}C-labelled compounds). This result is consistent with the report by Pearson (1974) that in *Vicia faba* L. the daily course of translocation was not related either to rate of photosynthesis or to changes in carbohydrate concentration. Munns and Pearson (1974) reported that translocation and photosynthesis in potato were under independent metabolic control. Inspection of Plate I shows a continual decline in the amount of ^{14}C-compounds retained by the source leaf and by the 7th day there was a minor retention of ^{14}C fixed by the leaf evincing that export from the fed leaf continued for several days. Gordon (1986) indicated that 20-50% of the photosynthetically fixed carbon is retained in the leaf for subsequent export in many species.

The nature of the compounds retained by a fed leaf has been described by several authors. Clauss *et al.* (1964) for soybean, Ashley (1972) for cotton and Webb and Gorham (1964) for straight-necked squash, showed that the initial rapid rate of export of radiocarbon by a leaf coincided with the disappearance of ^{14}C-ethanol-soluble compounds from the fed leaf. Mullen and Koller (1988) experimenting the soybean showed that daytime rates of export were closely related to net CO_2 assimilation while the total amount of starch depleted during the night increased as starch concentration at the beginning of the night increased. It is not clear whether conversion of assimilates to ethanol-insoluble forms is a cause or an effect of retention of ^{14}C-labelled assimilates in leaves fed with $^{14}CO_2$. A possible explanation at this stage is that leaving the leaf in the feeding chamber for an hour means that CO_2 level starts somewhat above 340 ppm and goes to near 50 ppm perhaps by 20 min. There is an uncontrolled factor of changing CO_2 concentration which will change the biochemistry of photosynthesis and further allocation of C to compounds. However, when the proportion of current photosynthesis being exported is not a maximum, an increase in photosynthates will not cause an increase in translocation. The amount of carbon translocated will depend on the requirements of the sink and excess carbohydrate will accumulate in the source (Ho 1979, and Marowitch *et al.* 1986). Sawada *et al.* (1986) by manipulating growth conditions of a single rooted primary leaf of soybean indicated that surplus assimilate not translocated to the sink organ was accumulated in the source organ and that the photosynthetic metabolism was influenced by the amount of sucrose accumulated in the cytoplasm rather than by the starch content in chloroplast. Grange (1987) experimenting with mature pepper leaves indicated that the retention of assimilates observed was due either to export limited by processes occurring after the synthesis of sucrose, or export probably impeded at the loading step.

In summary, it is suggested that further significant progress in understanding the mechanisms which control the rate of photosynthesis and translocation in plants may be achieved by more detailed studies of sources and sinks. The process involved in loading or unloading of metabolites merits much more attention than they have received.

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العلاقة بين التمثيل الضوئي والانتقال في نبات ك٣

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في هذا البحث تم تزويد الورقة السفلى لنبات الفول بثاني أكسيد الكربون الموسوم بالكربون المشع $^{14}CO_2$ وذلك في أربع مراحل مختلفة من حياة النبات. وبعد ٢٤ ساعة من بداية المعاملة تم حساب الكربون المشع في كل حالة وجد أن الورقة المعاملة احتفظت بكمية هائلة من الكربون المشع، بينما لم يزد وزن الورقة (المصدر) نفسها.

وفي تجربة أخرى تم تزويد نباتات الفول الكاملة ب $^{14}CO_2$ وتم أخذ عينات من الورقة السفلى بعد فترات: ساعة ـ ٣ ساعات ـ ٦ ساعات ـ ٢٤ ساعة، وسبعة أيام وبعد تجفيف هذه العينات أخضعت للتصوير الإشعاعي الذاتي ولقد أوضحت نتائج هذه التجربة أن كثافة الكربون المشع قلت مع مرور الزمن حتى اليوم السابع.

يتبين من التجارب السابقة أن تكوين وبقاء السكر والنشويات في الورقة (المصدر) وعدم انتقالها حالا إلى مصبات أخرى في النبات قد يؤدي إلى إعاقة عملية التمثيل اضوئي ومن ثم نستنتج أنه لا يوجد ارتباط طردي وثيق بين عمليتي البناء الضوئي والانتقال في النبات.

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