The Distribution and Utilization of 14C Labelled Assimilate Fixed at Anthesis in Oilseed Rape *(Brassica napus)*

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Summary

Field grown plants of winter oil-seed rape cv. Jet Neuf were exposed to $^{14}CO_2$ at anthesis.

Labelled assimilates moved progressively from the leaves into the stem and reproductive parts. At maturity 9 % of ^{14}C fixed at anthesis had been mobilized into reproductive organs.

Introduction

Studies on the distribution of ^{14}C-labelled assimilate between plant parts have mainly been carried out under controlled environmental conditions on isolated oil-seed rape plants, often following 24 or 48 h after labelling (Brar & Thies, 1977) or using varieties not currently recommended in the UK (Major, Bole & Charnetski, 1978). At present no information is available for oil-seed rape on the distribution at maturity of ^{14}C fixed at anthesis. In cereals pre-anthesis assimilation has been shown to make a substantial contribution to grain yield especially under conditions of stress (Daniels, Alcock & Scarisbrick, 1982). It is possible that pre-anthesis reserves are also important in oil-seed rape.

During 1982/83, a field experiment was carried out to investigate the contribution of such reserves to reproductive growth in the winter cultivar Jet Neuf. The amount of photosynthate fixed just before the start of flowering was measured using a $^{14}CO_2$ labelling technique and changes in distribution with time were followed.

Procedures

Experimental details are summarized in Table 1. On 26 April 1983 (H1, Table 2) stakes (2.5 cm x 2.5 cm x 180 cm) were driven into the ground to form a 50 cm x 50 cm square enclosing three rows of plants. Two shorter stakes were positioned in the centre of each square, one supporting a small vial and the other a battery powered fan. 3.7 MBq (100 μCi) of $Na_2\ ^{14}CO_3$ was accurately measured into the vial and a polythene bag 50 cm x 50 cm x 250 cm was then positioned over the taller stakes. In order to prevent gas leakage, the chamber was laid flat at the bottom and carefully sealed with soil. With the aid of a syringe, an excess of 5 N-H_2SO_4 was introduced into the vial containing the radioactive base to generate $^{14}CO_2$. The syringe was quickly withdrawn, the insertion hole sealed with tape and the fan started. 0.5 h of exposure was allowed after which the chamber was removed. Two plants were immediately harvested and taken to the laboratory for dissection as described in Fig. 1. Plant parts were dried at 80 °C for 48 h and stored. A further sample was taken 24 h later and thereafter at approximately 4 week intervals, H_2-H_5 (Table 2).

Dried plant parts were subsequently weighed and ground to a fine powder in a Dangoumau analytical grinder. Approximately 100 mg of each milled sample was weighed in a porcelain boat and oxidised for 4 min in a Harvey OX400 biological oxidiser. After combustion CO_2 plus $^{14}CO_2$ were absorbed by 14 ml of scintillation cocktail (27 % phenylethylamine, 27 % industrial methylated spirit and 46 % NE 233 liquid scintillator) in a glass trap. The ^{14}C activity of each sample was counted for 10 min. in an SL Kontron Inter-technique liquid scintillation counter. Standards of 5000 counts min^{-1} and blanks were also counted.

Data were expressed as disintegrations per min/g. The ^{14}C present in each plant part was expressed as a percentage of the total recovered in each plant.

Results

Total plant dry weight increased between H1 to H5 from 7.7 to 43.7 g per plant. Changes in dry weights of leaves, stem material, reproductive parts and roots, H1-H5 are presented in Fig. 2.

The percentage distribution of ^{14}C activity within each plant part and changes which occurred with time are presented in Fig. 3-6. At H1 leaf material fixed the highest percentage of ^{14}C, whilst stems and reproductive parts assimilated 38 % and 4 % of the total respectively. Leaf and stem materials in the lower parts of the canopy were the major sites of ^{14}C fixation (89 %, Fig. 3). Assessment of the percentage ^{14}C assimilated by each of the upper four internodes and leaves at the bases of primary branches 1-4 indicated that the amount of photosynthate fixed by these parts increased progressively towards the lower sections of the canopy. Leaves at the bases of B1, B2, B3 and B4 fixed 0.20 %, 0.42 %, 0.62 % and 0.97 % ^{14}C respectively. The terminal raceme assimilated a greater percentage of ^{14}C (1.8 %) when compared with the individual primary branches.

At H2 (Fig. 4) the percentage of ^{14}C in the main stem leaves below 14 was 15.9 % less than at H1. These leaves were therefore the major source of ^{14}C. By comparison leaves higher in the canopy (L1 to L4) imported ^{14}C presumably because they were immature and still expanding. The lower stem internodes imported large amounts of ^{14}C (+ 9.84 %) compared with the upper parts. Reproductive parts, mainly buds and flowers at this stage accumulated + 3.14 % of the labelled carbon. A higher percentage of ^{14}C was recovered in the terminal raceme than primary branches 1 to 4 (Fig. 4).

During reproductive development when lower pods were filling (H3) more ^{14}C was exported from the lower leaves for the maintenance of the reproductive parts although leaves at the bases of branches 1 to 4 also exported some assimilates to the primary branches. Lower stem internodes imported large amounts of ^{14}C (Fig. 5). The percentage ^{14}C in the reproductive parts of the terminal raceme and branches 1 and 2 declined between H2 and H3, probably due to the high rate of respiration characteristic of oil synthesizing tissues rather than export of assimilates.

During the main period of pod and seed development (H4 to H5) reproductive parts imported a higher percentage of labelled assimilates from leaves situated in the lower parts of the canopy. Fig. 6 shows the percentage distribution of ^{14}C on July 5th, nine days before the crop was harvested.

Discussion

Assessment of the photosynthetic capacity of various plant organs at first flowering (H1) indicated that leaves were the major site of ^{14}C fixation. Assimilate was subsequently exported to developing stems, reproductive parts and roots after 24 h (Fig. 4). Similarly when Chapman, Daniels & Scarisbrick (1984) exposed whole rape plants to $^{14}CO_2$ at initial flowering, leaves fixed 66.8 % of the total ^{14}C and exported 24.9 % to other plant parts after 24 h. Lower leaves exported some carbon for the maintenance of newly formed leaves higher in the canopy as indicated by Brar & Thies (1977) although at later harvests upper leaves also exported some photosynthate to the upper primary branches.

The percentage of ^{14}C translocated to the reproductive parts mainly increased over time with the exception of a slight decline within the reproductive parts of the terminal raceme and the top two primary branches between H2 and H3. Bilsborrow & Norton (1984) using growth analysis concluded that mobilized materials were not important in seed growth. Yet results obtained in the present experiment suggest that photosynthate fixed by leaves and stem material at first flowering were mobilized into reproductive organs later in the season. At maturity 9 % of the labelled assimilates were translocated to the reproductive organs. This figure excludes labelled assimilate respired by these organs. Unfortunately neither respiration no refixation were quantified in the experiment.

The percentage of ^{14}C fixed by individual internodes and leaves at the bases of primary branches increased progressively towards the lower sections of the canopy. This is because dry weights of these plant parts and leaf area increase with increasing canopy depth. Thus although leaves in lower regions are less favourably positioned for light interception they are favoured by their larger size and area. Leaves below internode 4 fixed a majority of ^{14}C at anthesis and were the major source of labelled assimilates exported to other plant parts.

Chapman *et al.* (1984) also found that leaves situated in the upper parts of the canopy fixed little ^{14}C when compared to the middle and lower sections. Major *et al.* (1978) have indicated that proximity of source to sink is important in the export of assimilates. Yet results obtained in the present experiment showed that although lower branches were near the source of carbon supply, they imported less carbon when compared to the terminal raceme and primary branches 1 to 4 situated higher in the canopy. Because the terminal raceme and the uppermost branches are the first to be initiated and are developmentally superior they have a higher sink capacity and hence a competitive advantage over lowermost branches. This partly explains why fewer pods with smaller seeds are formed on the lowermost branches.

It must be remembered that in addition to mobilized materials, reproductive growth and deve-

lopment during and after flowering largely depends on current assimilation by the stem and developing pods themselves. Brar & Thies (1977) working under glasshouse conditions estimated that during the most intensive period of seed dry matter accumulation 31 % of assimilated ^{14}C delivered to the growing seeds came from the stem, and Chapman *et al.* (1984) found that during seed filling the stem exported 15 % of labelled carbon to the developing pods in field rape. A number of ^{14}C studies have shown that rape pods assimilate $^{14}CO_2$ and after flowering play an important role in the production of their own structural and seed assimilates (Brar & Thies, 1977 ; Major *et al.* (1978).

The results of this experiment have demonstrated that assimilates fixed at first flowering are mobilized into reproductive organs during pod and seed development. It is suggested that in future experiments a series of labellings should be carried out at various growth stages and changes with time in ^{14}C distribution patterns assessed. Further work is also required to examine the contribution of pre-anthesis reserves to seed growth under a range of environmental conditions.

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Table 1 – Experimental details 1982-83

Previous crop	Winter wheat
Soil type	Calcareous loam, pH 7.8
Row width (cm)	18.3
Seed rate (kg/ha)	9.5 (168 seeds/m²)
Variety	Jet Neuf
Drilling date	25 August 1982
Plot size (m)	10.53 x 3.66
Fertilizer (kg/ha)	Basal dressing of 22.5 kg/N 60 kg P_2O_5, 60 kg K_2O 42 kg/N, 9 September 1982 75 kg/N, 2 March 1983 128 kg/N, 12 April 1983
Weed control	Pre-emergence TCA (8.9 kg/ha)
Pest control	Triazophos (840 g ai/ha)
Disease control	Benomyl (0.5 kg ai/ha) Iprodione (1.0 kg ai/ha)
Harvest date	14 July 1983

Table 2 – Sampling dates

Sampling dates	Growth stage*
H1 26th April 1983	4.1 First flower open. Terminal raceme and branches mainly green-yellow buds. Most leaves green.
H2 27th April 1983	4.1 As for H1 except that a few more flowers had opened on the terminal raceme.
H3 17th May 1983	4.2-4.3 Terminal raceme and branches in full flower ; seeds enlarging in lower pods of terminal raceme and branches 1-4. Other branches bearing only flowers. Secondary branches buds present.
H4 8th June 1983	4.4 Flowering on all branches completed. Seeds enlarging in all pods. Leaves still green.
H5 5th July 1983	5.2-5.3 Seeds in lower pods green to green-brown mottled. Leaves on main stem mainly senescent. Stem still green.

* Growth stage key as described by Harper & Berkenkamp (1975).

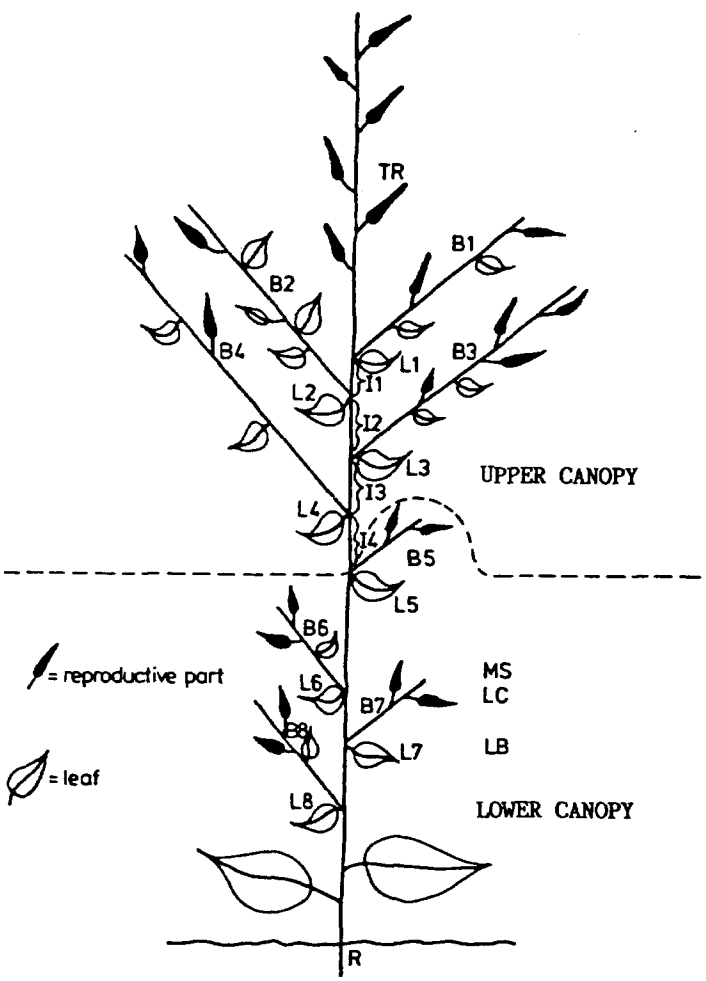


Fig. 1 – Dissection of plants

KEY

R, Root ; MS, main stem below I_4 ; LC, leaves subtending B_5-B_8 ; I_4, internode 4 ; L_4, leaf subtending B_4 ; I_3, internode 3 ; leaf subtending B_3 ; I_2, internode 2 ; L_2, leaf subtending B_2 ; I_1, internode 1; L_1, leaf subtending B_1 ; *TR, terminal raceme ; B_1, branch 1 ; B_2, branch 2 ; B_3, branch 3 ; B_4, branch 4 ; LB, branches 5-8.

* Terminal raceme and branches were subdivided into reproductive parts, leaves and stem.

Fig. 2 – Dry weights of various plant organs at each harvest date (Control).
Each point is the mean of 8 plants. I, SE of the means

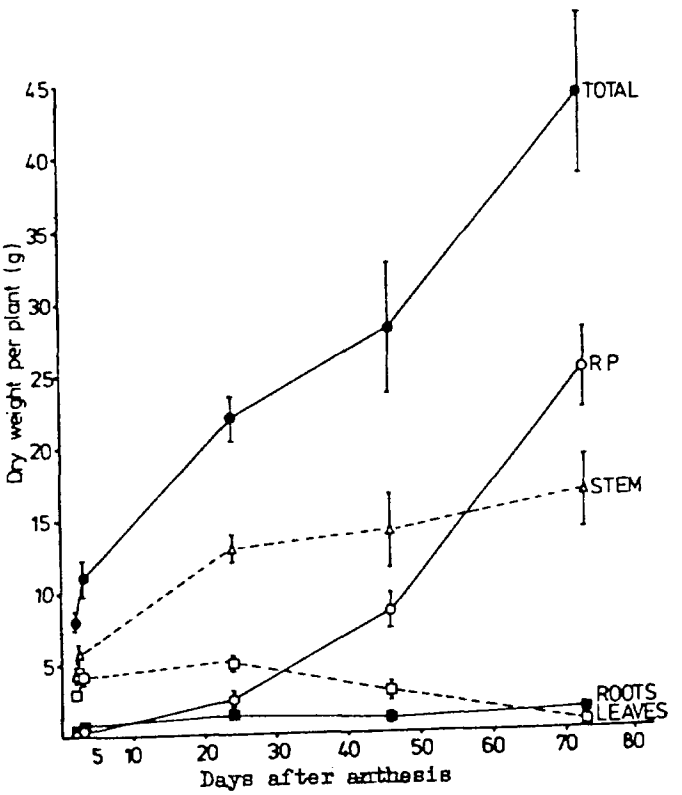
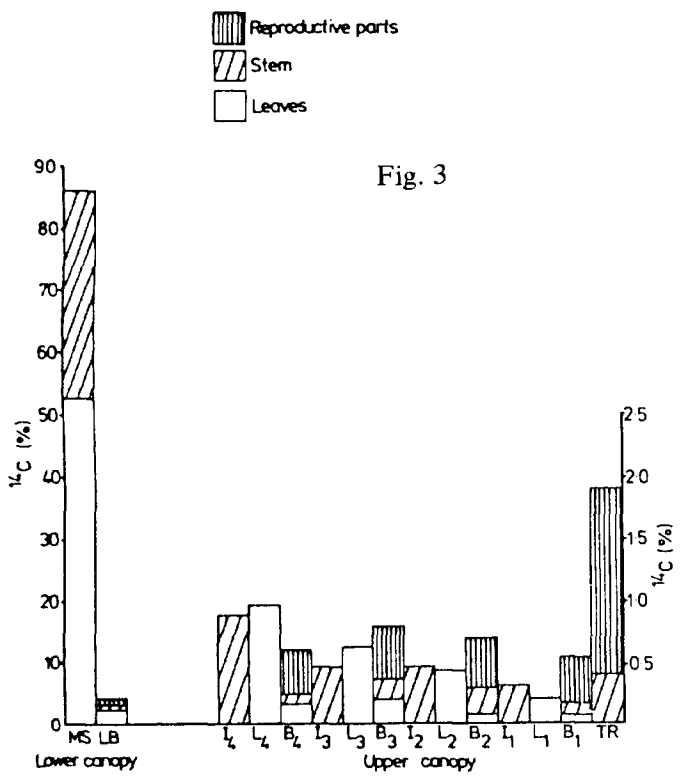


Fig. 3-6 – Percentage ^{14} carbon within various plant parts defined in Figure 1



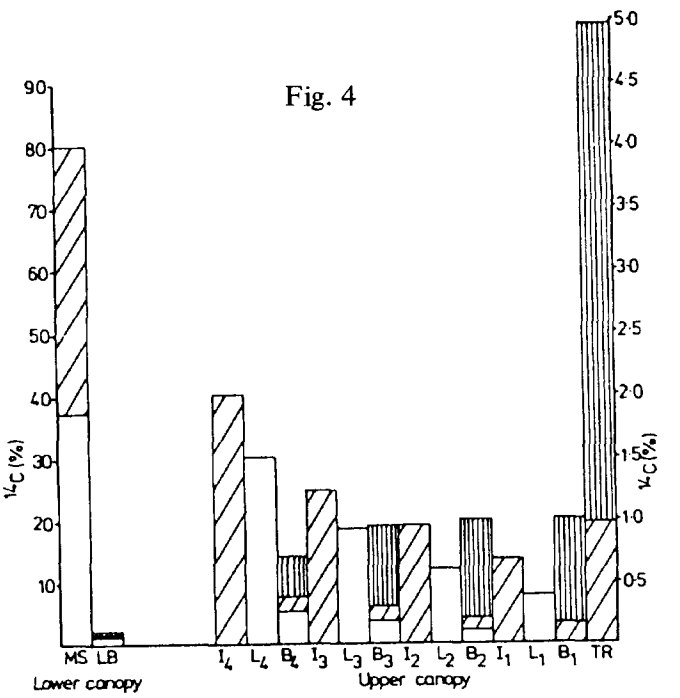


Fig. 5

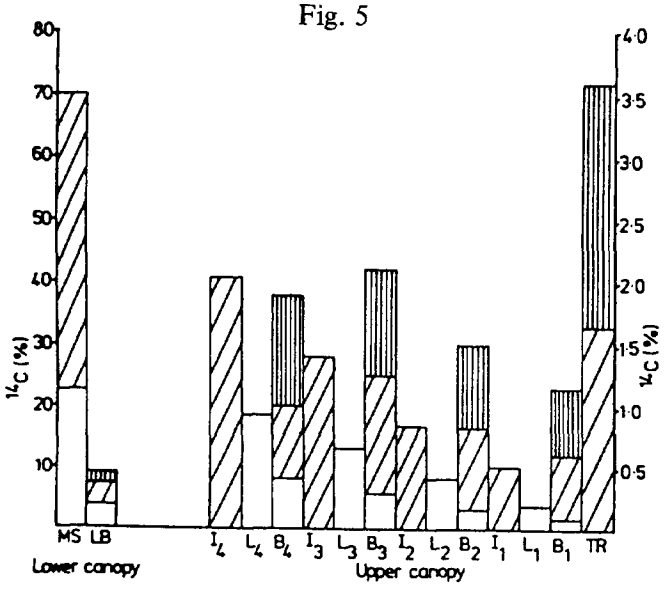
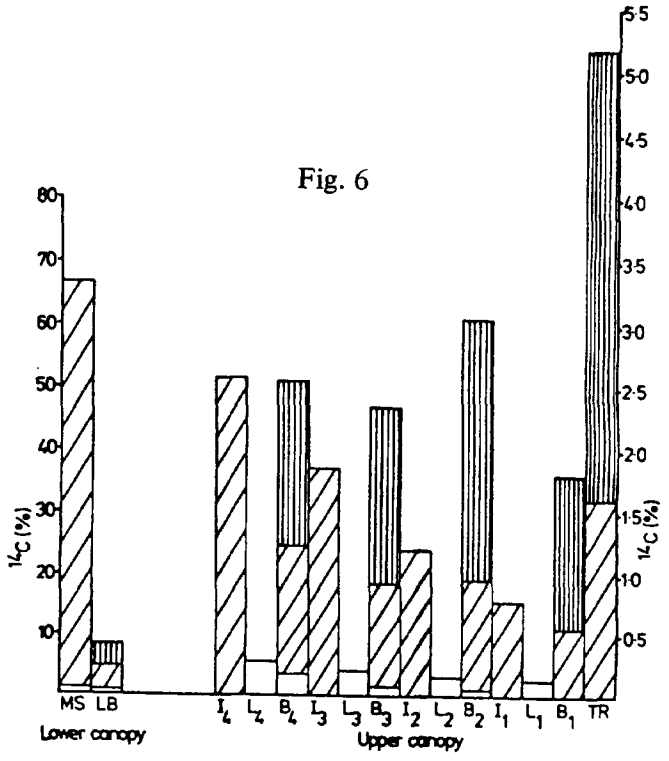

^{14}C (%)
80
70
60
50
40
30
20
10
4·0
3·5
3·0
2·5
2·0
1·5
1·0
0·5
MS LB
Lower canopy
I_4 L_4 B_4 I_3 L_3 B_3 I_2 L_2 B_2 I_1 L_1 B_1 TR
Upper canopy

Fig. 6


^{14}C (%)
80
70
60
50
40
30
20
10
5·5
5·0
4·5
4·0
3·5
3·0
2·5
2·0
1·5
1·0
0·5
MS LB
Lower canopy
I_4 L_4 B_4 I_3 L_3 B_3 I_2 L_2 B_2 I_1 L_1 B_1 TR
Upper canopy