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Carbon Transfer and Partitioning between Vegetative and Reproductive Organs in *Pisum sativum* L.

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ABSTRACT

Assimilate partitioning was studied in the common pea (*Pisum sativum* L.) by feeding $^{14}CO_2$ to whole plants and measuring radioactivity in different organs 48 hours after labeling. Two experimental protocols were used. For the first, one reproductive node was darkened with an aluminum foil, to prevent photosynthesis during labeling. The aim was to study assimilate translocation among nodes. The second was carried out to assess any priority among sinks. Whole plants were shaded, during labeling, to reduce carbon assimilation. Various developmental stages between the onset of flowering and the final stage in seed abortion of the last pod were chosen for labeling. When all photosynthetic structures at the first reproductive node were darkened at any stage of development after the formation of the first flower, the first pod was supplied with assimilates from other nodes. In contrast, later developed pods, when photosynthetic structures at their node were darkened, received assimilates from other nodes only when they were beyond their final stage in seed abortion. Reducing illumination to 30% did not change distribution of assimilated carbon between vegetative and reproductive structures, nor among pods. It appears that the relative proportion of ^{14}C allocated to any one pod, compared to other pods, depends on the dry weight of that pod as a proportion of the total reproductive dry weight. When the plant was growing actively, following the start of the reproductive phase until a few days before the end of flowering, the top of the plant (*i.e.*, all the organs above the last opened flower) had a higher sink strength and a higher relative specific activity than pods, suggesting that it was a more competitive sink for assimilates. The pattern of assimilate distribution described here provides an explanation for pod and seed abortion.

In peas the seed number per unit area of soil is highly variable, with a concomitant effect on yield. Final seed set of most flowering plants is the result of a large number of flowers being produced, followed by a certain percentage of abortion. Pea is an indeterminate plant whose pods and seeds are set on successive reproductive "nodes" (a "node" includes the attached leaf and pods) of the plant. Flower abortion percentages, in pea as in soybean, vary according to their position on the plant. In soybean (cv Clark isoline E_1t) for example, only 17% of the flowers of the basal end of the raceme abscise, while 75% of those located at the distal end abort (4). Overall, under field conditions, an average of 50% of pea flowers give pods (13, 21).

Many studies suggest that pod set is regulated by the availability of assimilates to developing reproductive organs. First, a strong correlation between seed number and maximum vegetative dry weight per plant (or stem dry weight at maturity) has been found in soybean (19). Second, Schou *et al.* (22) were able to increase soybean pod number per plant and seed weight per plant by placing reflective boards in the canopy, thereby supplying short-term supplemental light. Furthermore, depodding treatments decreased flower abortion (13), while defoliation (13) and shade (12, 22) increased it.

The development of a pod can be divided into two phases. The first begins at anthesis of the parent flower (stage 0.5 on the decimal scale established by Maurer *et al.* [17]) and ends at the FSSA[1] (20) of the pod. All seeds which pass FSSA go on to achieve maturity. From this point therefore, the final number of seeds in a pod can be counted. This first phase is the period of seed formation and corresponds to a period of active cell division in the seeds (10). The second phase lasts from FSSA until maturity. It corresponds to the filling period of the formed seeds in the pod, characterized by a dramatic increase in seed dry weight. On a pea plant, pods of the different RN are not all at the same stage at the same time: anthesis, FSSA and maturity occur successively on each RN, starting low on the plant and subsequently progressing upward. Moreover, the number of flowering nodes on a given cultural variety can vary, depending on environmental conditions (24). Thus, to understand seed formation, it is necessary to study patterns of assimilate distribution among organs, especially during the period of seed development, as well as the possible competition among the different organs.

Carbon transfer from the subtending leaf and the pod walls of the first RN (RN1) to the seeds of that pod has been measured (9). Two thirds of the carbon required by the ripening seeds came from stipules, leaflets, tendrils and the pod walls of the same node. Some transfer of assimilates from other nodes to the pod does occur. The timing of the transfer is however unknown. Moreover, it is unlikely that all flowering nodes have the same carbon budget as they are in different stages of development at any one time. Assimilate translocation may depend on the relative developmental stages of the pods, the number of RN and the number of pods on the

[1] Abbreviations: FSSA, final stage in seed abortion; RN, reproductive node; RN1, first reproductive node; RSA, relative specific activity (% dpm/% mg C); FSSA1, final stage in seed abortion of the first reproductive node; RDW, reproductive dry weight.

plant. In the field, Turc (24) found a strong relationship, at each RN, between seed number and intercepted radiation (calculated from anthesis to FSSA of the node). This result suggests that little translocation of assimilates occurs among nodes. In contrast, Szynkier (23), using the carbon-isotope technique and pea plants (cv Alaska) bearing only two flowering nodes, showed that competition for assimilates among the pods of the two nodes was accentuated by removal of the subtending leaf of the first pod. The existence of competition among pods on a single plant has been confirmed by Hole and Scott (14), by comparing the growth of pods located on plants bearing different numbers of other pods at variable locations. They showed that individual pod growth was lower with more competing pods on the plant.

As pea is an indeterminate plant, vegetative development continues during formation of reproductive structures. The beginning of the reproductive phase is thus characterized by the simultaneous presence of vegetative and reproductive sinks, probably resulting in strong competition for assimilates. Kelly and Davies (15) showed that the relative strength of the reproductive and vegetative sinks of pea plants are regulated by photoperiod and genotype. In short days, more of the ^{14}C allocated to the apical bud of G2 peas was delivered to young leaves than to flower buds, as compared to long days.

In this paper, we report the results of an analysis of ^{14}C-distribution in pea plants carried out to determine: (a) the importance of internodal translocation during the period of seed formation (*i.e.*, from anthesis of the first flower to FSSA of the last formed pod on the plant); and (b) the existence or otherwise of a priority in the carbon distribution among pods, or in the carbon distribution between reproductive structures and developing vegetative organs.

MATERIALS AND METHODS

Plant Culture

Pea seeds (*Pisum sativum* cv Solara, on which leaflets of each node are replaced by tendrils) were sown four to a pot on November 25, 1988, in 1 L pots containing 51% sand, 27% vermiculite, and 22% loam material. Seeds were inoculated with a N_2 fixing strain of *Rhizobium leguminosarum* at sowing and again three weeks later. Plants were grown in a glasshouse, where the average minimum and maximum temperatures were, respectively, 11 and 17°C. The plants were thinned to one plant per pot at the two- to three-leaf stage. Three daily irrigations, with a nutritive solution devoid of nitrogen, maintained the soil near field capacity. Supplementary light was supplied (about 500 $\mu mol \cdot m^{-2} \cdot s^{-1}$ at maximum plant height) to achieve a photoperiod of 16 h day and 8 h night. Under this photoperiod the first flower appeared at a node similar to that observed in the field (2). At each RN, there were either one or two pods. Lateral branches were cut off as soon as they began to develop.

^{14}C-Labeling and Detection

$^{14}CO_2$-Labeling was carried out at midday, using a technique already described (26) and summarized as follows: whole plants were placed in a plastic gas-tight chamber for 90 min, and exposed to $^{14}CO_2$ (specific activity: 5.9×10^3 Bq · mg C^{-1}), generated from $Na_2{}^{14}CO_3$ added to sulfuric acid. The CO_2 concentration was maintained around 350 ppm by automatic addition of $^{14}CO_2$, using an IR gas analyzer which operates a solenoid valve located on the $Na_2{}^{14}CO_3$ flask. The temperature was maintained at 20°C by circulating refrigerated air, and light was supplied by two lamps (400 W) delivering 600 $\mu mol \cdot m^{-2} \cdot s^{-1}$ at maximum plant height. Plants were then replaced in the glasshouse. The chase period lasted 48 h, which was long enough to allow transfer of ^{14}C-assimilates from the sources to the sinks, particularly roots and nodules (1, 25). Samples were then taken from different organs: roots and nodules, the top of the plant (*i.e.*, all the organs above the last opened flower), stem of the entire plant except the top of the plant, leaves from strictly vegetative nodes together, individual developed leaves from each RN and the pods and seeds of each RN. The organ samples were oven-dried for 2 d at 80°C, weighed, ground, and two subsamples per organ were analyzed to determine their total carbon and radioactivity content using the method developed by Bottner and Warembourg (3): purified oxygen carries the gases coming from dry combustion (900°C), a small quantity is delivered to a carbon titration cell, while another portion goes to a methyl-cellosolve + mono-ethanolamine mixture where the CO_2 is absorbed. This mixture provides aliquots for two ^{14}C measurements by scintillation counting. The mean of the four measurements per organ was calculated and used in the statistical analysis.

To analyze the distribution of assimilates, including source/sink relations as defined by Warren-Wilson (27), three criteria were used: (a) proportion of plant radioactivity in each organ (% dpm), indicating the sink strength (27), (b) dry weight of the organs, corresponding to their sink size (27), and (c) the ratio of the percentage of plant radioactivity in an organ to the percentage distribution of its total carbon content (% dpm/% mg C), called RSA (18).

One Darkened Node

To study carbon translocation among nodes, carbon assimilation (photosynthesis) was suppressed on one RN. For this, an aluminum foil sheet was put on the photosynthetic organs of this node (*i.e.*, leaf and pods (16)) to completely exclude light, starting three hours before labeling. The Al foil was in place for 28.5 h. The corresponding pods were then analyzed for assimilate supply, coming from other nodes. The $^{14}CO_2$-labeling was repeated before and after FSSA1 (RN1 darkened), and FSSA3 (RN3 darkened). Three replicates were used for each treatment. It has been considered that FSSA had been completed at a node when at least one seed at that node had exceeded the length of 6 mm (6). Seed length was measured nondestructively: pods were held to the light and the seeds viewed through the transparent pod walls.

Whole Plant Shading

To reduce the total quantity of assimilates produced per plant, some plants were shaded with commercial nets which stop 70% of the incident radiation, while control plants were kept in full light. Five labeling dates were chosen between flowering of RN1 and the final stage in seed abortion of the

Table I. *Total Assimilated Radioactivity and Specific Activity per Plant, at Four Stages of Development*

Stages of Labeling	Total Radioactivity per Plant[a]		Whole Plant Specific Activity	
	C[b]	T	C	T
	×10³ dpm		dpm/mg C	
Before FSSA1 (1)[c]	2590 ± 28[d]	2841 ± 454	1705 ± 31	1952 ± 282
Before FSSA3 (3)	1961 ± 217	2217 ± 382	1118 ± 39	1234 ± 236
After FSSA1 (1)	1661 ± 207	1264 ± 42	795 ± 99	717 ± 59
After FSSA3 (3)	2505 ± 310	3335 ± 145	949 ± 167	1036 ± 25

[a] Mean of three plants. [b] C = control plants; T = plants with a darkened node. [c] Number of the darkened node. [d] Standard error of the mean.

pods at node 3 (FSSA3). These were: (i) flowering of RN2, (ii) flowering of RN4, (iii) FSSA1, (iv) FSSA2, and (v) FSSA3. Shades were placed on the treated plants at the beginning of the last night period before labeling, and removed at the end of the labeling period (8 h after the onset of the light period).

RESULTS

Effect of Darkness on the Distribution of ^{14}C-Photoassimilates among Organs

Total darkness of one RN (number 1 or 3), whatever its stage of development, did not significantly decrease total activity per plant (dpm/plant) nor the specific activity (dpm/mg C) (Table I). Thus net photosynthesis per plant did not appear to be modified by this treatment. However, due to plant heterogeneity, variations in leaf area (which was not measured) may have masked differences between control and treated plants.

The darkened leaf contained consistently fewer ^{14}C-assimilates than the same leaf on control plants (Fig. 1). The Al foil prevented the leaf from carrying out photosynthesis and there was little or no ^{14}C translocation from other source organs to this leaf: at no date was the leaf a sink for assimilates. For each of the illuminated leaves, the differences of activity between the control and the treated plants were not significant at any labeling date (Fig. 1). Therefore, the treatment did not modify photosynthesis or translocation from the lighted leaves.

Darkened pods nevertheless contained a certain quantity of ^{14}C-assimilates (Fig. 2). However, the relative quantity of assimilates depended on the location and the developmental stage of the pod. When RN1 was darkened, the quantity of assimilates recovered in its pods was not significantly different from that of the first pods of control plants (Fig. 2, A and B), whatever the stage of labeling. For the illuminated nodes, distribution of assimilates was not different between control and treated plants. Similar results were obtained for the pods of RN3 after the FSSA3 (Fig. 2D): no difference of ^{14}C was found in these pods between control and treated plants. In contrast, prior to FSSA3, the pods of RN3 of treated plants had much less labeled carbon than the pods of RN3 on control plants (Fig. 2C). The ability of these pods to attract assimilates produced on other nodes clearly depends on their stage of development. Furthermore, for the two last labeling dates, it appears that the pods of RN2 and RN4 had a significantly different response on the control and treated plants. The comparison of their RSA reveals that there was no significant difference between the pods of RN2 of the control and those of the treated plants (Table II). This indicates that the difference of sink strength (% dpm) was only due to a difference in organ dry weight (in our sample, and for both dates, respectively, the pods weights of RN2 were 286 and 757 mg on the controls, and 455 and 1178 mg on the treated plants). At the last two labelings, the pods on RN4 were very young and had not reached the same stage of development on the control (respectively 4 and 15 d after flowering) and on the treated plants (respectively 6.5 and 13.5 d after flowering). At that age, differences of developmental stage can induce big differ-

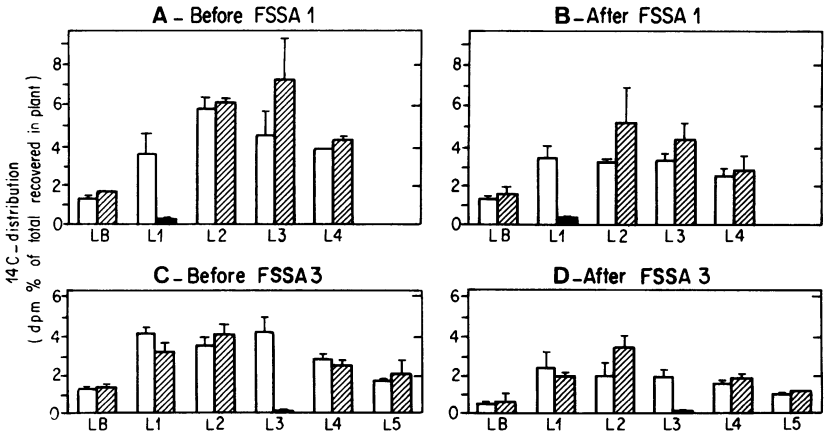


Figure 1. Relative distribution of current assimilated carbon among leaves, at four stages of development. Comparison between control plants and plants with one darkened node. Vertical bars indicate half standard errors. LB = mean per leaf below RN1. L1, L2, L3, L4, L5 = leaf of RN1, RN2, RN3, RN4, RN5, respectively. Open bars (□) indicate control plants; of plants with a darkened node, a solid bar (■) indicates the darkened node, and a shaded bar (▨) indicates other leaves.

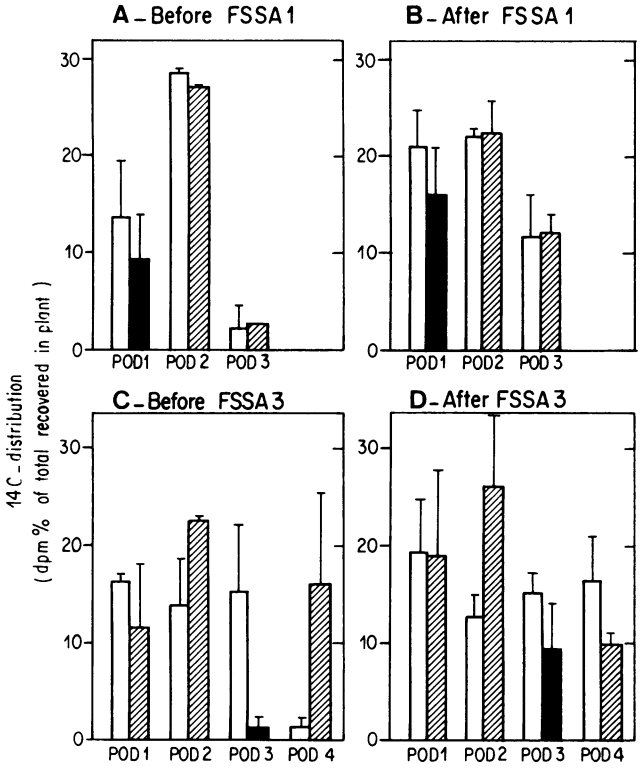


Figure 2. Relative distribution of current assimilated carbon among pods, at four stages of development. Comparison between plants with one darkened node and control plants. Vertical bars indicate half standard errors. POD1, POD2, POD3, and POD4 = pods of RN1, RN2, RN3, and RN4, respectively. Open bars (□) indicate control plants; of plants with a darkened node, a solid bar (■) indicates the pod of the darkened node and a shaded bar (▨) indicates other pods.

ences of sink strength as indicated by the RSA (4). Furthermore, it was not clear whether or not these pods had recently aborted. Should the pods abort, the RSA is very low (4).

Effect of Whole Plant Shading on ^{12}C-Assimilate Partitioning

The total amount of ^{14}C-assimilates recovered from shaded plants was one-fourth that recovered from controls at each stage of labeling (Fig. 3). The response of photosynthesis (about 25% of the control) was consistent with the reduction in incident radiation (to 30% of the control). These results

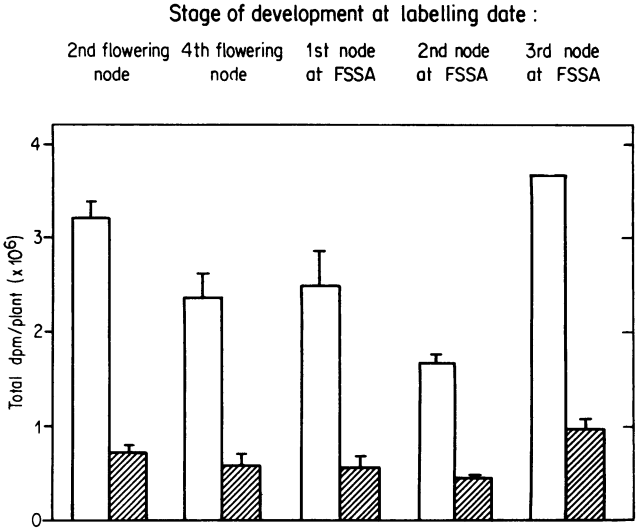


Figure 3. Total radioactivity per plant, at five stages of development. Comparison between control (□) and shaded (▨) plants. Vertical bars indicate half standard errors.

suggest that the conditions used were on the linear part of the response curve of photosynthesis to radiation (5).

At each date, the proportion of carbon exported from the leaves was not significantly different between control and shaded plants (Fig. 4). The total amount of ^{14}C exported from the leaves of the shaded plants was therefore 25% that exported from the leaves of the control plants if one refers to Figure 3.

Partitioning of ^{14}C-assimilates among the different leaves was not affected by shade (Fig. 5): there was no significant difference of sink strength (% dpm) between control and shaded leaves, regardless of labeling date. Assuming that respiration is not modified by the treatment, the proportion of assimilates exported by a leaf, in reference to the total amount incorporated, is therefore independent of the radiation level.

Differences in newly assimilated carbon partitioning among vegetative and reproductive structures were not significant between shaded and control plants, for any of the five labeling dates (Fig. 6). Samples of stems, roots and nodules, all the leaves below the first flowering node, individual leaves of the flowering nodes, and tops of the plants were analyzed for ^{14}C content. The partitioning of the label in treated plants was not distinguishable from that of control plants (Fig. 5).

Table II. *Relative Specific Activity (% dpm/% mg C) of Pods 2 and 4, Labeled at Two Different Stages*

Stage when Labeling	Treatment	Pods on the Second Node	Pods on the Fourth Node
Before	Control	2.06 ± 0.30[a] a[b]	1.96 ± 0.91 a
FSSA3	Third node darkened	2.30 ± 0.20 a	4.13 ± 0.53 a
After	Control	1.29 ± 0.35 a	2.81 ± 0.28 b
FSSA3	Third node darkened	1.74 ± 0.06 ab	1.50 ± 0.06 a

[a] Standard error of the mean. [b] For a same stage of labeling, means followed by a same letter are not significantly different at the 5% level (*t* test).

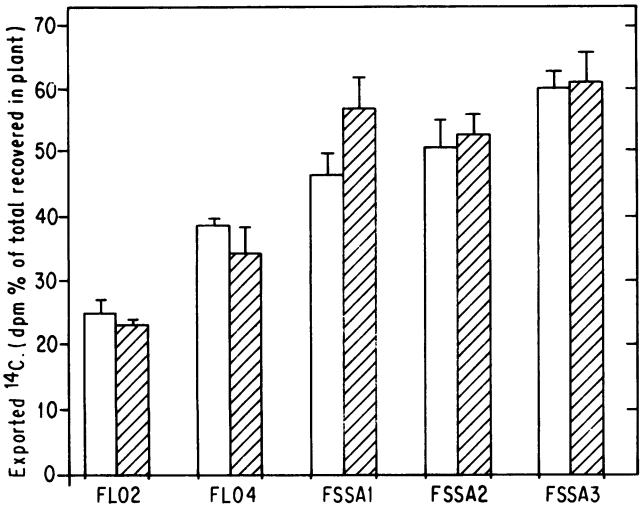


Figure 4. Proportion of carbon exported from the leaves, at 5 stages of development. Comparison between control (□) and shaded (▨) plants. Vertical bars indicate half standard errors. Symbols as in Figure 3.

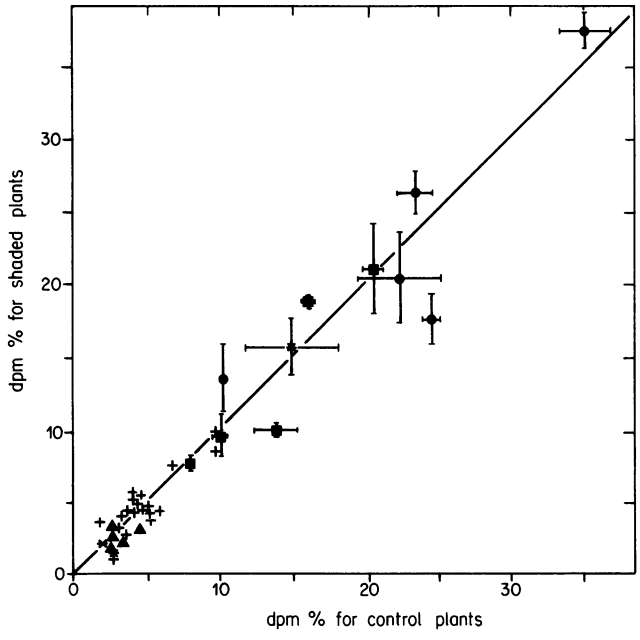


Figure 5. Relative distribution of ^{14}C-assimilates among vegetative organs (dpm % of total recovered in plant). Comparison between control and shaded plants. Bars indicate standard errors (only for the high % dpm). (●) Leaves below the first flowering node, together; (+) leaf of a flowering node; (■) stem of the plant; (*) top of the plant; (▲) roots and nodules.

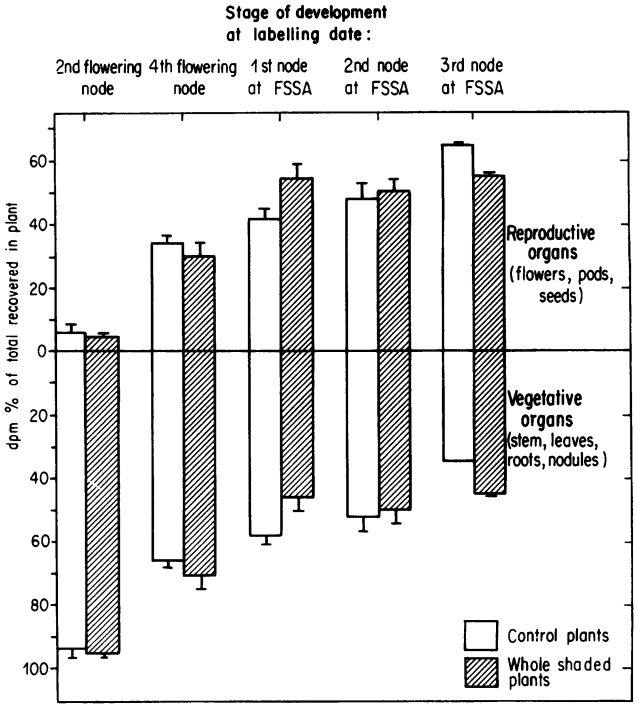
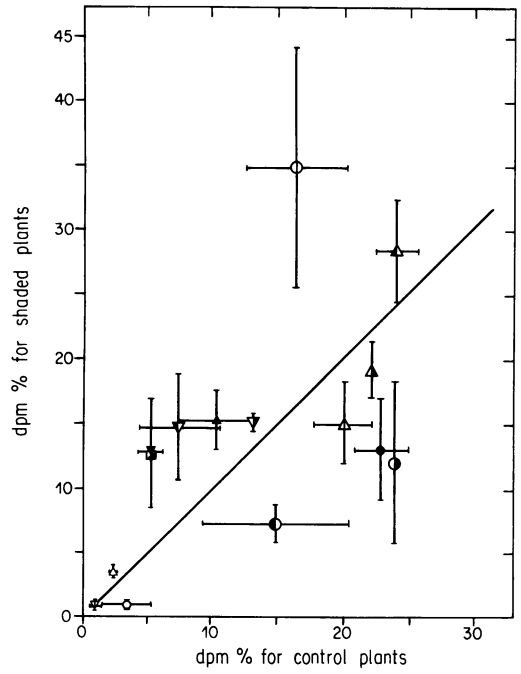


Figure 6. Cumulative distribution of ^{14}C-assimilates among vegetative and reproductive organs, at different stages during the period of seed formation. Comparison between control and shaded plants. Vertical bars indicate half standard errors.

Comparison of the relative distribution of assimilated carbon among pods located at the different reproductive nodes in shaded plants and in control plants is not easy because of the great variability in the pod responses through time (Fig. 7). For any stage of development, one pod from each of the two plants, at the same age and at the same position on the plant, contained a significantly different proportion of assimilates. However, there was no clear-cut priority since this distribution did not depend at all time on the total amount of assimilates produced (*e.g.*, shaded and control plants) and the data points for the same pod are either on one or on the other side of the 1/1 diagonal (Fig. 7). The increase of pod ^{14}C content with time suggests that assimilate distribution depends on pod's age but the relative proportion also depends on pod's location on the plant. This shows for the pods of RN2 on labeling date iv which received a higher amount and a higher proportion of assimilates than the pods of RN3 at the same age (labeling date v). It seems also probable that assimilated carbon distribution to a pod depends on that pod's "environment," *i.e.*, the number and size of the other pods located at other RN of the plant.

The relative ^{14}C distribution scored for pods of each RN was divided by that of all the pods (% dpm of pods of one RN/total dpm for all pods). Similarly, the proportion of total pod dry weight in each pod was calculated (% dry weight of pods of one RN/total RDW). The relationship between the two values is shown in Figure 8. For pods representing more than 10% of the RDW, assimilate partitioning was correlated with the proportion of each pod in this RDW. This constitutes



Pods of the 1st node Pods of the 2nd node Pods of the 3rd node Pods of the 4th node	○ △	● ▲ ▼	◑ ◬ ▽	◐ ◬ ▽	◑ ◬ ▽ ◪
pod position	2nd flowering node	4th flowering node	1st node at FSSA	2nd node at FSSA	3rd node at FSSA
	Stage of labelling				

Figure 7. Relative distribution of ^{14}C-assimilates among pods (dpm % of total recovered in plant). Comparison between control and shaded plants. Bars indicate standard errors.

the model for partitioning. The shading treatment appeared to have no significant effect on this relationship. Thus, assimilate partitioning among pods did not depend on total amount of assimilates produced by the plant (Fig. 7). At any given stage, no pod seemed to have priority over the others. When the plant produced a smaller quantity of assimilates at a given date (*e.g.*, the shaded plants), every pod received a proportionally lower quantity. The proportion of ^{14}C allocated to the pods of each RN depended on the proportion of total dry weight in these pods: within a plant, the larger the pod, the more ^{14}C it received. However, the pods located on RN1 seemed to receive significantly less assimilates than was predicted by the model.

Each pod representing less than 10% of the RDW had a much lower allocation of ^{14}C than was suggested from this model (Fig. 8). This model for partitioning does not therefore apply to smaller pods.

Competition between Developing Vegetative and Reproductive Organs

A further consequence of the indeterminate flowering pattern of *P. sativum* is that the formation of reproductive structures is concomitant with vegetative development. The vegetative and reproductive periods overlap by a variable period. In our experiment, the overlap included the three first labeling dates, at which there were both vegetative and reproductive sinks. Plant shading did not significantly modify sink strength of the top of the plant, nor that of the pods (Fig. 9, top). Thus it cannot be considered that any one of these organs had priority over the others. Yet, at the first date of labeling, the RSA of the top of the plant was higher than those of the pods of RN1 and RN2 (3, 1.1, and 1.6, respectively, in control plants, Fig. 9, bottom). At the second labeling date, the RSA of the top decreased to about 2 and RSA of the pods of RN1 and RN2 increased to 3 and 4, respectively. It also appears that the top of the plant attracted more assimilates early in plant flowering, and that this capacity decreased thereafter (Fig. 9, top).

DISCUSSION AND CONCLUSION

Assimilate Translocation among Nodes

Our results confirm that translocation of assimilates between different nodes occurs: when deprived of photosynthezing leaves, pods received assimilates from other leaves, at

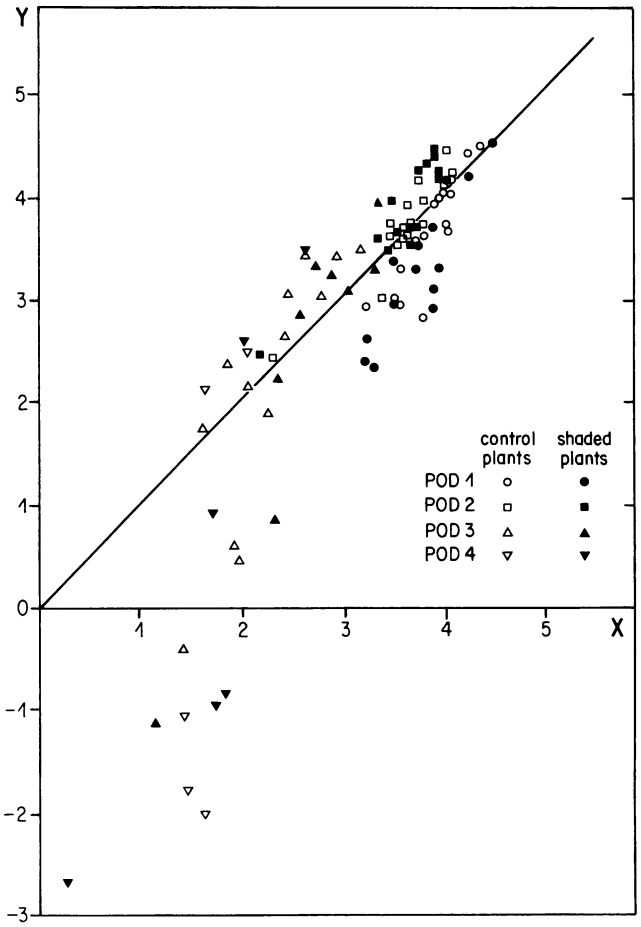


Figure 8. Relationship between the dry weight of each pod, as a proportion of the total, and the relative quantity of ^{14}C-assimilates allocated, for five labeling dates. X = ln[(dry weight of one pod/dry weight of all the pods) × 100]. Y = ln[(dpm of one pod/dpm of all the pods) × 100].

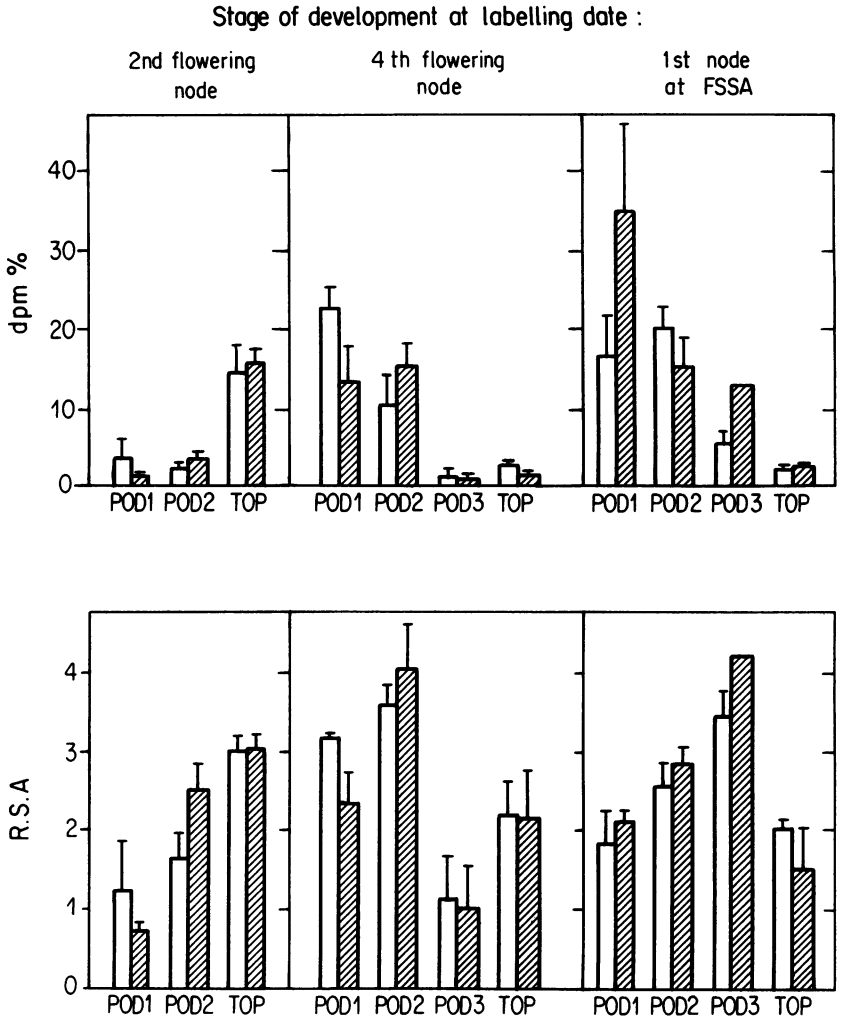


Figure 9. Relative distribution of assimilated ^{14}C among pods and top of the plant, and their relative specific activities, at three stages of development. Comparison between control and shaded plants (see Figs. 3, 4). Vertical bars indicate half standard errors.

any stage of development. However, if the pods of RN1 were supplied with assimilates from other nodes ("external assimilates") at any stage, the pods of RN3 only received a significant quantity of external assimilates after they had passed the point of FSSA3 and all their seeds had started to grow. These results confirm those of Szynkier (23) who showed that the pod of RN2, deprived of its feeding leaf, never received significant quantities of assimilates from the leaf of RN1. In contrast, the pod of RN1, deprived of its feeding leaf, was supplied with assimilates from the leaf of RN2.

These results are not in contradiction with the observation that fruits are mainly (or initially) fed with assimilates from their subtending leaf (9, 24). However, in the case of the leaf being deficient for photosynthesis (for example a leaf, low in the canopy, receiving little light), assimilates from other nodes may be allocated to the pods in the axil of that leaf varying with their stage of development, and the presence of other developing pods. In our experiment, the difference of behavior between pods of RN1 and RN3, at a given stage of pod development, can be explained by the presence or absence of older and bigger reproductive sinks. After FSSA1, older pods have priority and the pods located on a higher RN are probably fed mainly by their own leaf, at least until their FSSA; it appears that if the pod has reached its FSSA, it can be fed by the other nodes. Even early in development, pods of the first reproductive nodes can however receive external assimilates as they have no competitive, older pods. Similar movements of assimilates were found on an indeterminate soybean: translocation was also preferentially directed toward the reproductive organs located below the source leaf, early in the period of seed formation, whereas it was both upward (to vegetative structures) and downward at the beginning of flowering (11).

The very low quantity of assimilates allocated to pods of the upper flowering nodes is presumably a result of the competition from the lower, older and heavier pods. Pods on the first reproductive nodes grow very rapidly and reach higher dry weights than the upper pods, and thus receive a larger proportion of assimilates than the upper nodes at the same stage. This could be one of the reasons for the high frequency of abortion on these upper nodes. However, the possible involvement of hormones should not be excluded, as suggested by Heindl and Brun (12) and Brun and Betts (4).

The leaves receiving about the same incident radiation and having similar areas contained similar amounts of radioactivity. However, pods were fed in proportion to their relative

biomass. This is consistent with the existence of assimilate translocation between nodes. It is also true for the control plants, and is presumably true in the field.

Effect of Radiation Level on Assimilate Partitioning

The amount of ^{14}C exported from the leaves was reduced by the shade proportionally to the decrease in ^{14}C assimilation by the plant. However, there was no difference in the ^{14}C partitioning between vegetative and reproductive structures, between pea plants under two different regimes of incident radiation (100% and 30%). This is consistent with studies of three varieties of soybean. Egli (7) and Egli *et al.* (8) did not find any significant effect of year, moisture stress, shade or variable plant densities on dry matter partitioning between fruits and vegetative organs, at any stage of flowering or fruit set. However, their treatments had significantly modified the growth of the plants. Thus our results on pea confirm that the relative long- or short-term distribution of assimilates among vegetative and reproductive sinks is not linked to the total amount produced or available. Partitioning at a given stage appeared to be fixed and independent of the environmental conditions.

It appears that the proportion of assimilates allocated to the reproductive parts of pea increases rapidly during the period of fruit formation. This is consistent with the behavior of soybean (7, 8) and, as apical senescence was occurring in this period, with the results of Kelly and Davies (15) who observed a decline in the sink strength of vegetative organs associated with flowering.

Competition for Assimilates among Pods

Our results show that pods compete for assimilates. When incident radiation was reduced, each pod received a lower quantity of assimilates, but the proportion of the total produced that was received by pods was unchanged. There does not seem to be a clear-cut priority of some pods over others. Reducing photon flux density from 600 to 200 $\mu mol \cdot m^{-2} \cdot s^{-1}$ had no significant effect on relative dry matter partitioning among the fruits retained in the different treatments of Hole and Scott (14). In their experiment as in ours, the partitioning of dry matter among fruits depended on their stage of development: initially the flowers of RN1 received a higher proportion of assimilates; thereafter their share decreased. This would suggest that dry matter partitioning depends on the relative abilities of each sink to attract assimilates. Using $^{14}CO_2$-labeling, we confirmed these results. The relative ability of each sink to attract photoassimilates could be linked to its relative dry weight, as compared to total RDW, particularly when pods have reached a certain dry weight. We believe that seed dry weight is the main characteristic of sink demand, and that this demand regulates partitioning. The same conclusion has been reached by Lovell and Lovell (16). Studying the importance of the carpel as a source of assimilates for its seeds, they established that the percentage of ^{14}C imported by the seeds from the carpel was determined mainly by seed dry weight.

Competition for Assimilates between Young Vegetative Organs and Growing Pods

Just after onset of flowering, when vegetative development was still active, the top of the plant was a significant sink for carbon (high %dpm, and high RSA). At this stage, there was competition between these developing vegetative organs and the young fruit beginning their development on the first reproductive nodes of the plant. On soybean, Grima-Pettenati *et al.* (11) found very high RSA for the buds and growing leaves, particularly in young plants (7 d before flowering, and at flowering). This translocation to the upper vegetative organs lasted longer for an indeterminate than for a determinate variety (11). Competition between developing vegetative nodes and young pods in active growth could explain the high abortion levels, generally observed in the field, on the first reproductive nodes. In the field, abortion is even more frequent than in experimental systems due to the greater number of flowering nodes (24), suggesting a longer-lasting competition between top and pods.

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