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Xylem and Phloem Transport and the Functional Economy of Carbon and Nitrogen of a Legume Leaf[1]

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ABSTRACT

Exchanges of CO_2 and changes in content of C and N were studied over the life of a leaf of *Lupinus albus* L. These data were combined with measurements of C:N weight ratios of xylem (upper stem tracheal) and phloem (petiole) sap to determine net fluxes of C and N between leaf and plant. Phase 1 of leaf development (first 11 days, leaf to one-third area) showed increasing net import of C and N, with phloem contributing 61% of the imported C and 18% of the N. ^{14}C feeding studies suggested the potential for simultaneous import and export through phloem over the period 9 to 12 days. Phase 2 (11–20 days, leaf attaining maximum area and net photosynthesis rate) exhibited net import through xylem and increasing export through phloem. Eighty-two% of xylem-delivered N was consumed in leaf growth, the remainder exported in phloem. Phase 3 (20–38 days) showed high but declining rates of photosynthesis, translocation, and net export of N. Phase 4 (38–66 days) exhibited substantial losses of N and declining photosynthesis and translocation of C. C:N ratio of xylem sap remained constant (2.3–2.6) during leaf life; petiole phloem sap C:N ratio varied from 25 to 135 over leaf development. The relationships between net photosynthesis and N import in xylem were: phase 1, 4.8 milligrams C per milligram N; phase 2, 24.7 milligrams C per milligram N; phase 3, 91.9 milligrams C per milligram N; and phase 4, 47.7 milligrams C per milligram N.

During its relatively short life span, the leaf of a higher plant makes a series of significant demands upon and contributions to the nutrition of the plant on which it is borne. By investigating these interactions in relation to ontogenetic changes in leaf structure (3, 9, 15), gas exchange, and water loss (5–7, 10, 23) and transport to and from the leaf (4, 6, 10, 11), much has already been learned of how the development and functioning of specific foliar surfaces impinge upon the economy of the rest of the plant. This paper extends this approach by examining the nutritional interrelationships for C and N during the life of a leaf of the annual grain legume white lupin (*Lupinus albus* L.). Techniques for collecting xylem and phloem fluids are combined with studies on the growth and CO_2 exchange of the leaf to model its day by day exchanges of C and N with the parent plant, and thus establish its overall contribution in processing of N and providing photosynthate during plant development. The modeling procedure adopted is essentially similar to that developed in earlier studies on *L. albus* in relation to whole plant functioning (18), or to nutritional studies of fruits (19), root nodules (14), and root and shoot apices (13).

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MATERIALS AND METHODS

Plant Material. Two thousand effectively nodulated (*Rhizobium* WU425) plants of white lupin (*Lupinus albus* L. cv Ultra) were grown with N-free mineral nutrients (8) in 8-L pots (six plants/pot) of quartz sand in a naturally lit glasshouse during July to October in Perth, Western Australia (daylengths, 10–12 h during study period). The study involved the uppermost main stem leaf (developed at node 15 or 16) which was initiated at or close to 35 d after sowing and had a subsequent life span of 68 to 72 d. All plants selected for study had an uppermost main stem leaf 1 to 2 mm in length (1 d after initiation) on the 36th d after germination.

Measurements of Ontogenetic Changes in Dry Weight, C and N Content, Area, and Chl Content. These measurements involved harvest of the study leaf from 80 plants at each of 18 harvests made during a 66-d period following initiation of the leaf. Subsamples from the initial sample of 80 leaves were used for determining area (measurements of 20 individual leaves), dry weight, and C and N content (eight replicate samples in subsamples of 40 leaves including the leaves used for area measurements), and Chl content (five replicate measurements in a sample of 20 leaves). The remaining subsample (20 leaves) was used for determination of total N in ethanol-soluble and ethanol-insoluble fractions of leaf tissue.

Total N and ethanol-soluble N were then determined by Kjeldahl analysis and total C of leaf dry matter measured using a Perkin Elmer model 240 CHN analyzer (13). Leaf area was measured from photocopied images, with partly unfolded leaves at young stages opened manually before photocopying. Chl was measured in acetone extracts of freshly harvested leaves, using techniques described elsewhere (1).

Measurement of CO_2 Exchange. Net CO_2 exchanges of attached leaves were measured continuously using an open gas exchange system incorporating a six-way sampling device and an infra red gas analyzer (IRGA) (Series 225 Gas Analyzer; Analytical Development Co. Ltd., Hoddeson, England) operated in the differential mode to monitor CO_2 levels sequentially (6 min sampling times) in the gas streams passing over five enclosed leaves and a reference (empty) cuvette. Each Plexiglas cuvette was ventilated continuously with air (340 μl CO_2/l) at a flow rate such that the CO_2 level dropped by less than 10% in concentration in passing through the cuvette. A water screen (2 × 1 × 0.1 m) mounted above the plants restricted temperature rise in the cuvette to less than +3°C of ambient.

Using the above system continuously throughout the study period, the net daytime or nighttime CO_2 exchanges on a total of 7 to 20 separate leaves were made during each interval (1.5–4 d duration) of the first 24 d of leaf growth, and on 20 to 30 separate leaves during each 4- or 7-d interval of the remainder of the study period. From these data, mean values were obtained for net photosynthesis and night respiration by the study leaf for each day of the experiment (13).

Collection and Analysis of Transport Fluids Serving the Leaf.

Xylem sap was collected either as root bleeding sap or as tracheal fluid obtained by vacuum extraction of 5 cm segments of upper main stem tissue adjacent to (immediately below) the study leaf. Root bleeding sap showed solute concentrations 5 to 8 times higher than in corresponding samples of tracheal xylem sap, as might be expected from the higher rates of water flux from roots of transpiring as opposed to decapitated plants. The two classes of xylem sap did not, however, show appreciable differences in balance of organic solutes and hence in C:N weight ratio. Data from the tracheal sap samples was used in construction of the models of C and N exchanges of the leaf.

Over 80% by weight of xylem sap solutes consisted of amides and amino acids, and, with 60 to 70% of the sap N consistently as asparagine and glutamine (2), C:N ratios of sap varied only slightly over the study period.

Phloem sap was collected from shallow incisions in the petiole of the study leaf, as described earlier (16, 20). At a series of times throughout the study, collections of phloem sap and xylem sap were made from sets of five plants sampled on each of two occasions during the photoperiod and on a set of five plants sampled once during the night.

With the small volumes (0.1 μl) of phloem sap available from the petiole of each leaf, it proved necessary to bulk each day's sap collections prior to analysis, thereby preventing determination of the extent of variation in C:N ratios between plants and with time of day.

The decision to combine two daytime samples of sap with one nighttime sample was based on the results of earlier studies on diurnal variations in leaves of *Lupinus* (16, 21), in which it was indicated that, under climatic conditions similar to those used here, rates of translocation from leaves during the photoperiod were 2 to 3 times higher than in the subsequent night period.

The likely extent of diurnal variations in C:N ratio of phloem sap was obtained by analyzing a series of petiole sap samples collected at 3-h intervals over a 24 h period, using eight leaves (20 d age) at each time of sampling. C:N weight ratios for the nine sap samples ranged from 73 to 89 (daily mean, 82), indicating a diurnal fluctuation of approximately ±10%, somewhat less than the ±15% fluctuation recorded for leaves of *L. albus* in an earlier study.

The bulked samples for each day of sampling were assayed for the major solutes of C and N (sucrose, malate, amino acids, and amides) as detailed elsewhere (16, 21). These analyses were used to determine the C:N weight ratios of transport fluids (see also 21).

[^{14}C]Urea Feeding Experiments. The age at which leaves commenced to export photosynthate was determined by feeding urea (1 μCi/leaf applied at noon) to leaflets of leaves aged from 6 to 16 d. Two h after feeding, the petiole of the fed leaf and shoot parts above and below the fed leaf were harvested and assayed for ^{14}C to test for export from the fed leaf. Using a similar age range of leaves, import through phloem by the study leaf was tested by feeding [^{14}C]urea to the four leaves below the study leaf (0.5 μCi/leaf applied at noon) and harvesting the study leaf 1 h later and assaying for ^{14}C. By conducting such experiments over a period of several weeks, a picture was built up of the time span in leaf growth when the study leaf appeared capable of both exporting and importing phloem-mobile materials. The use of [^{14}C]urea (as alternative to $^{14}CO_2$) in studying assimilate translocation in *Lupinus* has already been reported (17).

RESULTS

Leaf Growth and Changes in Dry Weight and Content of C, N, and Chl with Leaf Age. The study leaf required 20 d to attain maximum content of dry matter and 24 d to reach full area and maximum Chl content (Fig. 1A). Leaf Chl content fell steadily from day 30 to the end of the study period (66 d). Dry weight per leaf was maintained until day 50; after which it decreased significantly. Total C and N per leaf rose parallel with increasing area and dry weight until 20 d (Fig. 1B); contents of C and N then fell slightly (20–30 d) and were maintained at a relatively constant level for a period (31–52 d) before falling substantially as the leaf continued to senesce (50–66 d). The ranges of SE obtained for measurements of dry matter C and N in the samples of leaves were ±3% to ±11% of the mean; for determinations of leaf area, ±4% to ±14%; and for determinations of Chl content, ±5% to ±16%. SE values were higher in samples of old than young leaves, suggesting that precision of model building would be significantly less for older stages of leaf development.

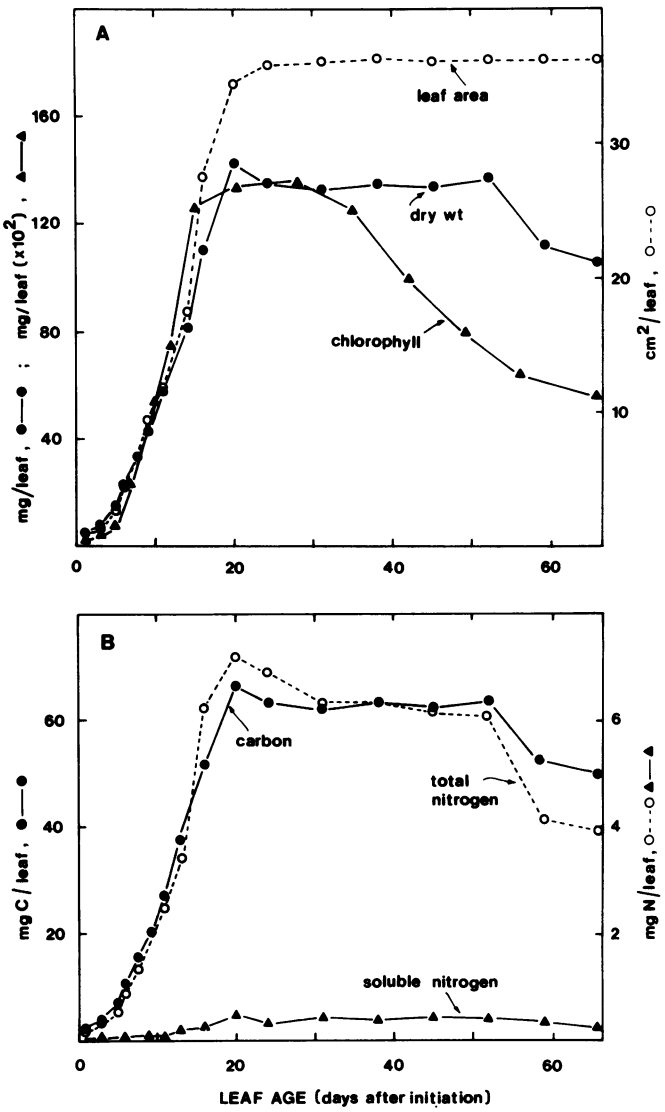

FIG. 1. Changes with age in (A) area, dry weight, Chl content; and (B) total C, total N, and ethanol-soluble N of the uppermost main stem leaf of effectively nodulated plants of *L. albus*. SE for measurements of dry weight, C, and N lay within the range 3% to 11% of the mean; for leaf area, 4% to 14%; and for Chl, 5% to 16%.

CO_2 Exchanges and the Balance of Carbon in Leaves of Different Age. The developing leaf exhibited net losses of CO_2 during the day as well as the night for the first 5 d of its life. Net gains of C from the atmosphere during the day were made from day 5 onwards; the leaf first showed a net positive balance for CO_2 over the 24-h period beginning on day 5, after which photosynthetic activity increased sharply. Maximum rate of net daily uptake of CO_2 (net photosynthesis) was achieved at full expansion, at which

time the daytime gain of C from the atmosphere was more than 20 times the nightly loss of C through respiration. The ranges of SE for gas exchange measurements for the five leaves studied on a daily basis were ±6% to ±21% of the mean for night respiration and ±6% to ±25% for daytime CO_2 uptake.

The gross balance of carbon in the leaf was estimated by comparing these atmospheric exchanges of CO_2 with the net daily increments or losses of C in leaf dry matter (Fig. 2A). For the first 11 d of growth, much more C was required for leaf growth and respiration than was available from net photosynthesis. Over the period 11 to 16 d, when the leaf was incorporating C into dry matter most rapidly, sufficient C was fixed from the atmosphere to satisfy growth and give rise to an exportable surplus of C. Over the period 20 to 24 d, near maximum rates of photosynthesis and a declining rate of C incorporation into dry matter resulted in maximum rates of translocation of C from the leaf. During the remainder of the study period, when the dry matter content and night respiration losses of the leaf remained fairly constant, the amounts of C available for export were essentially determined by photosynthetic rate. The latter fell sharply from day 24 to day 40 and was then maintained at near constant rate until the end of the study period.

C:N Weight Ratios and Concentrations of Organic Solutes in Xylem and Phloem Streams Serving the Leaf. Xylem sap, obtained by vacuum extraction of a 5 cm segment of main stem tissue immediately below the point of attachment of the study leaf, showed a C:N ratio which did not vary outside the range 2.3 to 2.6 during the life of the leaf. Amides and amino acids (contributing 95% of the xylem sap N and 80% of its C) and organic acids (10% of sap C) were the principal organic solutes of xylem and the balance between these constituents did not change appreciably during the study period (2). By contrast, the C:N ratio of petiole phloem sap changed markedly during the development of the leaf (Fig. 2B). In the first 7 d when the leaf was heavily dependent on phloem translocate, the entering sap had a mean C:N ratio within the range 20 to 40. The ratio then rose rapidly as the leaf began exporting solutes through phloem, achieving a maximum ratio of 135 (C:N) at 13 d. At this time, the leaf had reached 60% of its final area and was making fastest gains of dry matter, C, and N (Fig. 1). After this, the C:N ratio of the phloem sap fell sharply to a value of 26 at the end of the study. This marked pattern of changes in C:N ratio of phloem sap was caused principally by ontogenetic variations in the concentrations of amides and amino acids. Sucrose, the major contributor of C to phloem sap, varied relatively less in concentration (175–289 mg/ml) during leaf life than did nitrogenous solutes (4.4–20.1 mg/ml). Organic acids (3.3–6.1 mg/ml) made relatively small contributions to sap total C and hence to the variations in C:N ratio of the sap.

Net Transport Exchanges of C and N in Xylem and Phloem between the Leaf and Parent Plant. Values for these quantities were derived for each interval between successive harvests of the study period, using data for C and N increments or losses in leaf

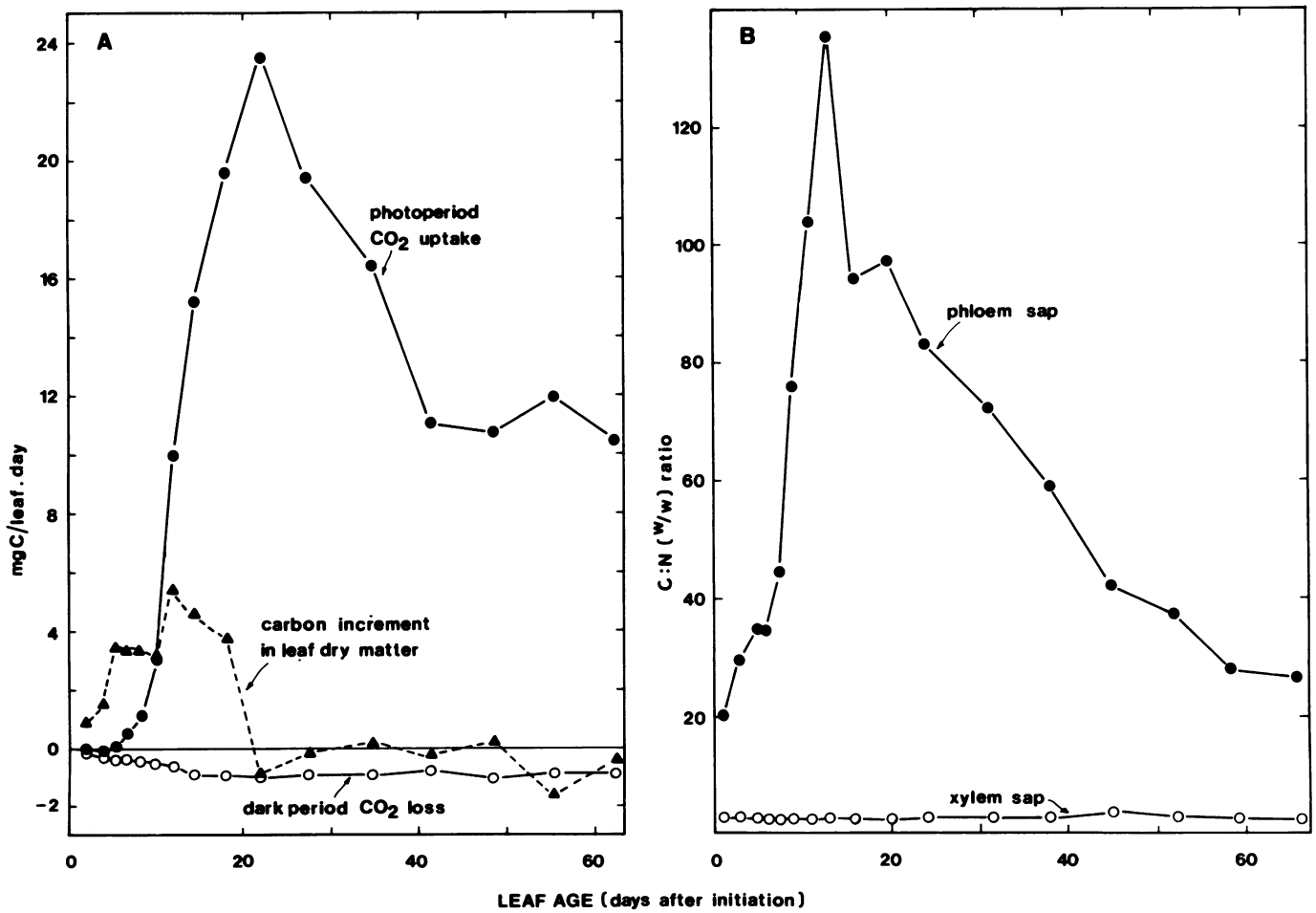

FIG. 2. Ontogenetic changes in C economy and transport exchanges of the uppermost main stem leaf of *L. albus* L. A, Day and night net CO_2 exchange and net daily losses or gains of C in leaf dry matter; B, C:N weight ratio of solutes of upper stem tracheal xylem sap and phloem sap from the upper region of the petiole of the study leaf. SE for measurements of CO_2 exchange were from 6% to 21% of the mean for night respiration and from 6% to 25% of the mean for daytime respiration. Precision of data for C:N ratios as discussed in text.

dry matter, gaseous exchanges of C by the leaf in night respiration, and net daytime photosynthesis and C:N weight ratios of xylem sap and petiole phloem sap. Using essentially similar formulae to those of earlier publications (18, 19), exchanges of C and N in xylem and phloem between the study leaf and plant were computed. As in earlier studies (13, 18, 19), the modeling procedure assumed that transport exchanges of C and N took place exclusively by unidirectional mass flow in xylem and phloem, and that such exchanges occurred at the C:N ratios recorded at that time for xylem sap or petiole phloem sap.

Data for daily rates of C import or export through xylem and phloem and for incorporation of C into leaf dry matter were as indicated in Figure 3A. Corresponding values for N were as shown in Figure 3B.

A phase of continuous net import through xylem and phloem was recorded for the first 11 d of development, during which increasingly rapid gains were made in C and N content of the leaf. Phloem import accounted for the bulk of C transported into the leaf, but xylem assumed the major role in import of N from day 5 onwards.

There then followed a period of more intensive growth (11–16 d) with increasing rates of gain of C and N in leaf dry matter (Fig. 1). Import of C through xylem was equivalent to one-sixth to one-half of the C increment of the leaf, while net fixation of CO_2 provided the remaining C for growth and a progressively increasing surplus of C for export in the phloem. The corresponding picture for N (Fig. 3B) showed the bulk of the imported N to be leaving the leaf in phloem.

The next 5 d of leaf development (16–20 d) spanned the completion of leaf growth, and showed declining rates of import of N through xylem and increases towards maxima in rates of translocation of C and N from the leaf in the phloem (*cf.* Figs. 1–3). The interval from 20 to 38 d showed little changes in C and N of leaf dry matter or in rates of import of C and N in xylem and N export through phloem, but a sharp decline in export of C, which matched closely the declining rate of net photosynthesis of the leaf (Fig. 2A). The final period of development (39–66 d) showed net losses of N from the leaf, and a corresponding increase in rates of export of N. Import of C and N in xylem remained at about the same rate as in the previous period, while the rate of translocation of C from the leaf was maintained at around half of the maximum value attained over the period 20 to 24 d.

Evidence of Simultaneous Import and Export of Photoassimilates in Phloem. The [^{14}C]urea studies testing for phloem export and phloem import were conducted on 12 replicate leaves (six for export, six for import) at each day of the life of the study leaf from 6 to 18 d after its initiation. At ages up to 8 d, no evidence was obtained of export; two of six leaves aged 9 d showed export; four of six of age 10 d recorded export of ^{14}C and, at all ages thereafter, high levels of export of ^{14}C.

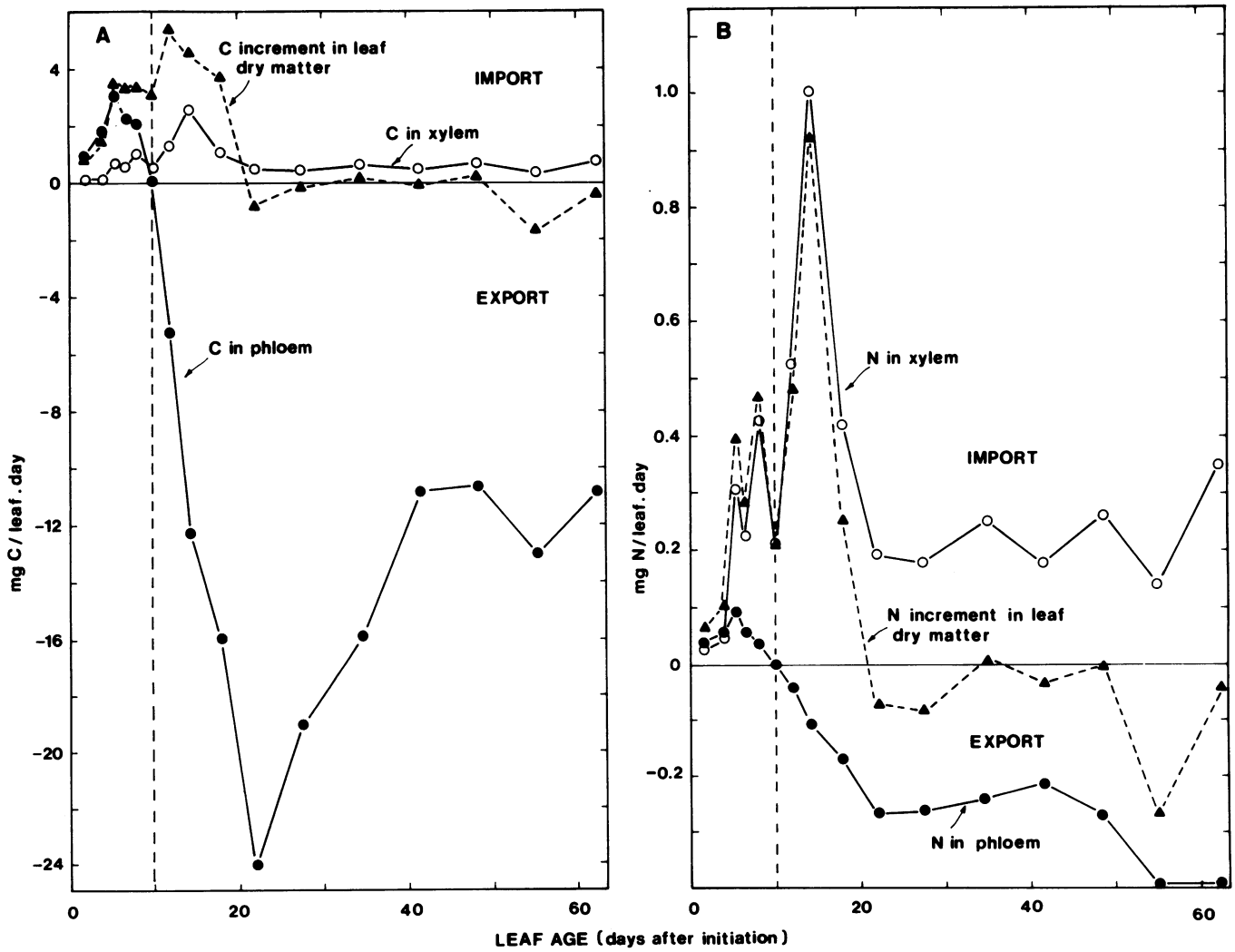

FIG. 3. C and N economy of uppermost main stem leaf of effectively nodulated *L. albus*. A, Net daily intake of C in xylem, import or export of C in phloem, and increment or loss of C in dry matter; B, net daily intake of N in xylem, import or export of N in phloem, and increment or loss of N in dry matter. The vertical dashed lines in A and B mark the point of change from net import to net export through phloem.

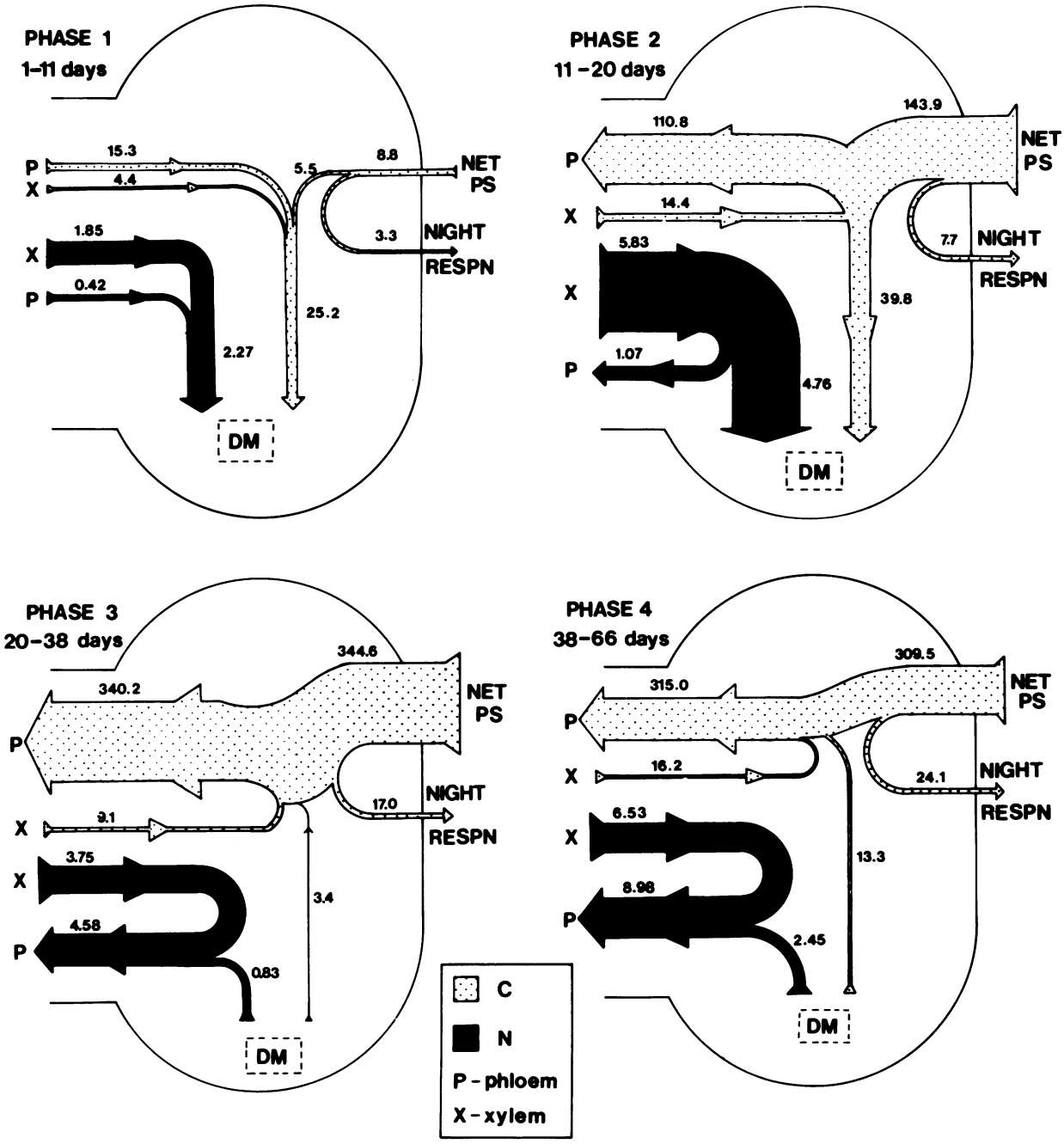

FIG. 4. Four main ontogenetic phases in economy of C and N in uppermost main stem leaf of effectively nodulated *L. albus* L. Gaseous exchanges of C as CO_2, increments or losses of C and N in leaf dry matter, and exchanges of C and N through xylem and phloem are given as mg C or mg N for each phase. Thicknesses of lines are drawn proportionally to mean daily fluxes of C and N, so that the relative intensities of different activities can be compared between phases of development.

In the complementary experiments on import, leaves aged up to 10 d were heavily labeled after application of ^{14}C to adjacent older nurse leaves; in the sample of leaves aged 11 d, all six showed very slight import of ^{14}C; in leaves aged 12 d, only one of six showed detectable import of ^{14}C; whereas all older leaves studied (13–18 d) showed no import of translocate.

It was concluded from these experiments that the 3-d period from 9 to 12 d after leaf initiation was a time when leaves might possibly begin importing and exporting simultaneously through the phloem. However, since the experiments involved separate studies of either export or import, the data were not regarded as conclusive proof of ability of a single leaf to simultaneous export and import through its phloem (*cf.* other studies [e.g. 12, 15, 22] giving evidence of a graded sink-source transition, with evidence of bidirectional flow of photosynthate in the petiole of an individual leaf).

DISCUSSION

The data on the C and N economy of the leaf of *Lupinus albus* described in this paper provided an integrated picture of growth, CO_2 exchanges, and transport activities during the various developmental stages of the leaf of a higher plant. Viewed in terms of the net total demands and contributions made during its 66-d developmental period, the study leaf made an initial investment of 66.7 mg C and 7.2 mg N into its structural matter, deriving all

of its N and the equivalent of 51% of its C by import from other parts of the plant through xylem and phloem. A net daytime gain of 807 mg C was made by photosynthesis throughout development, this being equivalent to 12 times the amount of C bound into leaf structural matter and more than 15 times the total C lost by the leaf in night respiration. A total of 18 mg N was imported through xylem and 0.4 mg N through phloem, and of this a total of 14.6 mg (79% of that imported) N returned to the plant with phloem translocate during the 66-d study period. This amount of N cycled was equivalent to almost twice that initially bound into the leaf's structure and to almost 3 times the N content of the leaf at the end of the study period.

Four distinct phases were recognized in leaf development, each exhibiting a highly characteristic pattern of physiological activities in relation to economy of C and N. These phases, as summarized in Figure 4 in which gaseous exchanges of C as CO_2, C, and N incorporation into or losses from leaf dry matter, and exchange of C and N through xylem and phloem were expressed in amounts (mg C or mg N) for a specific interval of growth. The thicknesses of lines in each flow model were drawn proportionally to mean daily fluxes of C or N for each study interval.

Phase 1 (1–11 d), a period of net import through phloem as well as xylem and culminating in the leaf being one-third of its final area, showed phloem to contribute 61% of the C and 18% of the N consumed in leaf growth, xylem 17% of the C and the remainder of the N (Fig. 4). Net photosynthesis provided the remaining 22% of the C fixed into leaf dry matter. Phase 2 (11–20 d) was marked by rapid increases in leaf area, dry weight, and contents of Chl, C, and N (Fig. 1), and by the end of this period near maximum values had been attained for these quantities. For every 100 units of C fixed photosynthetically, an additional 10 entered the leaf through the xylem, and of these 110 units of C, 77 were translocated from the leaf in the phloem, 28 entered leaf dry matter, and five were lost in night respiration (Fig. 4). Despite its high demand for N in growth, the leaf imported more N through xylem than was incorporated into dry matter, such that for every 100 units of N entering the xylem, 18 units of N were available for export in the phloem. Phase 3 (20–38 d; Fig. 4) was a period when photosynthate was translocated from the leaf at a very high rate relative to C intake through xylem or to C losses from leaf dry matter or in respiration. Net loss of N from leaf dry matter provided the equivalent of 22% of the N translocated from the leaf through the phloem. Phase 4 (38–66 d) showed somewhat lower rates of photosynthesis and relatively larger net losses of C and N from leaf dry matter than in the preceding phase but still relatively high rates of translocation of C and cycling of N.

A major problem in modeling C and N flow for the leaf concerned the interval 9 to 12 d (spanning phases 1 and 2; Fig. 4) when evidence was obtained (see [^{14}C]urea feeding studies) of the leaf's potential for simultaneous export and import through phloem. It was not possible to determine the extent, if any, to which export during phase 1 or import during phase 2 affected the models; but, since only 1 or at most 2 d of the 10-d periods over which the models were constructed carried complications due to bidirectional flow in the phloem, it was unlikely that the validity of the general conclusions drawn from the whole phase of development would have been affected. A further problem related to the use of tracheal sap collected from stem tissue below the study leaf to determine the composition of the xylem stream entering the leaf. Recent modeling studies (13) have indicated an ability of upper stem tissue to withdraw N from the xylem streams of departing leaf traces and to transfer this N, or an equal amount of N, to xylem streams moving further up the shoot. Were this the case, stem tracheal sap would provide erroneous information on what was actually passing out to the leaf. In an attempt to test this possibility, xylem (tracheal) sap was collected from petioles of the study leaf (25 d old). Analysis showed it to contain solutes (organic acids and amino compounds) in essentially the same proportions, though at different concentrations than in stem tracheal sap of similarly aged plants. The C:N weight ratios of the sap samples were virtually identical (2.3 for petiole tracheal sap, 2.4 for stem tracheal sap), so that any errors due to site of sampling on the models of Figure 4 would have been of small magnitude.

A prominent feature of Figure 4 was the highly variable relationship between net photosynthesis and intake of N through xylem. During phase 1, 4.8 mg C was fixed as CO_2 per mg N imported through xylem; in phase 2, 24.7 mg C/mg N; in phase 3, 91.9 mg C/mg N; and in phase 4, 47.4 mg C/mg N. The physiological basis for such wide variations in this relationship are not understood, though it is likely to involve interrelationships during leaf aging between CO_2 fixation, transpiration, and levels of N in xylem fluid entering the leaf.

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