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Partitioning of Carbon and Nitrogen and the Nutrition of Root and Shoot Apex in a Nodulated Legume[1]

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ABSTRACT

Empirically based models depicting exchanges of C, N, and H_2O in phloem and xylem among organs of nodulated white lupin (*Lupinus albus* cv Ultra) were constructed for the interval 51 to 58 days after sowing. Information was incorporated on the economy of C, N, and H_2O in plant parts, the solute composition of transport fluids collected at selected sites on the plant, and the photosynthetic inputs, transpirational losses, and translocatory activities of different age groups of leaflets and stem + petiole segments of the shoot. Partitioning of C and N showed preferential transfer of N to the shoot apex, which imported 13 milligrams C per milligram N, compared with 54 milligrams C per milligram N for the nodulated root. Leaves translocated assimilates at a C:N weight ratio of 43 to 59, and older leaves serving the roots produced the translocate most rich in N relative to C. The shoot apex was enriched with N, additional to its intake from leaves, by direct uptake of xylem fluid (C:N ratio, 2.4) and receipt of nitrogenous solutes transferred from xylem to upward-moving phloem streams in upper regions of the stem. The models for flow of N and H_2O indicated that xylem streams passing to leaves were substantially less rich in N than the adjacent stream moving through the body of the stem and that a progressive increase in concentration of N occurred within stem xylem elements from base to top of the shoot. This apparently resulted from an abstraction of N from xylem of departing leaf traces, possibly by xylem transfer cells, and a subsequent feedback of this N to xylem streams passing on up the shoot. Upper leaves and shoot apex, therefore, acquired more N from xylem per unit of H_2O transpired than lower parts of the shoot.

Roots and unexpanded apical regions of the shoot are heavily dependent on photosynthesizing leaves for assimilates yet are likely to differ markedly in the relative extents of their requirements for translocated C and N. Roots generally produce dry matter of lower N content than shoots (2, 3, 22), incur high respiratory losses which cannot be offset by photosynthesis (6, 19), and have the potential for deriving their own N through activities, such as NO_3^- reduction, NH_4^+ assimilation, and N_2 fixation (23). These features indicate a basically greater demand for C relative to N by roots than shoot apices and suggest that physiological mechanisms are present in plant shoots for dispensing C-rich assimilate streams to roots and translocate more rich in N to shoot apices.

The problem of understanding how the movement of a range of solutes is controlled in relation to the specific demands of a receiving organ has led some workers (*e.g.* ref. 25) to suggest that solutes of the phloem stream are able to move independently of one another. However, considerable evidence has accumulated (*e.g.* refs. 1, 4, and 5) supporting a mass flow hypothesis for phloem transport in which all solutes are pictured as flowing together as a common stream from source to sink. The study presented here, which models the C, N, and H_2O flow and utilization in white lupin (*Lupinus albus* cv Ultra), assumes that a mass flow system of this nature operates in long-distance transport in xylem and phloem, and any conclusions drawn from the study here rest on the truth of such an assumption. By combining information on solute composition in transport channels with data for C and N utilization in plant parts, an attempt is made to define the relative importance of stem tissue and different age groups of leaves in nourishing the growing parts of the plant with C and N. The investigation extends earlier modeling studies on the species (7, 12, 17–21).

MATERIALS AND METHODS

Plant Material. Effectively nodulated (*Rhizobium* WU425) plants of white lupin (*L. albus* L. cv Ultra) were grown with N-free nutrients in lidded 11-liter containers (four plants/container) of organic matter-free quartz sand in a naturally lit glasshouse during July to August in Perth, Western Australia. Day temperatures averaged 22 C; night temperatures averaged 12 C.

Plant Harvest and Analysis. Samples of 40 plants were harvested at 51 and 58 days after sowing and were separated into nodulated roots, stems + petioles, leaflets, and terminal shoot apices (primary inflorescence and adjacent axillary apices). The stem + petiole and leaflet samples were further subdivided into those from nodes 1 to 4 (stratum A), nodes 5 to 8 (stratum B), nodes 9 to 12 (stratum C), and nodes 13 to 16 or 17 (stratum D) (Fig. 1).

Fresh weight and dry weight of all samples of organs were measured and internode lengths and leaflet areas were determined in the four age groups of shoot parts. Total N of plant parts was measured by Kjeldahl analysis; total C was measured using an elemental analyzer (Perkin Elmer, model 240). The increase in total plant N was assumed to have resulted from N_2 fixation.

Measurements of CO_2 Exchange. The CO_2 released from enclosed root systems was collected using Pettenkoffer assemblies as described previously (7, 13). Measurements were made on 10 containers (40 root systems) for consecutive 2- or 3-day intervals throughout the week of study. Night respiration of shoots of intact plants and CO_2 exchange of attached leaves day and night were studied using open gas-exchange systems incorporating a six-way gas sampling device and an IRGA[3] operated in the differential

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[3] Abbreviation: IRGA, infrared gas analyzer.

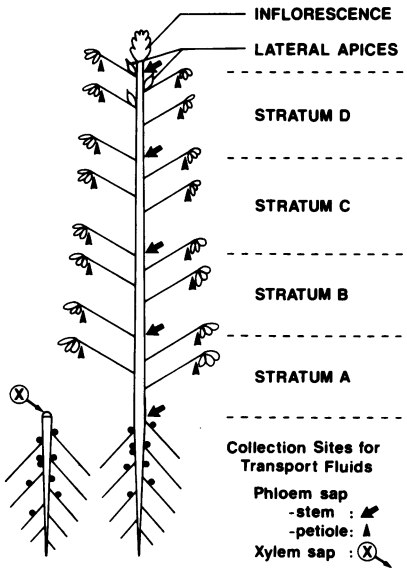

FIG. 1. Diagrammatic representation of plant of *L. albus* for the period 51 to 58 days after sowing to show strata of shoot parts and sites for collection of phloem and xylem sap used in the modeling studies.

mode to monitor CO_2 levels sequentially (6-min sampling times) in the gas streams. Shoot night respiration used four containers (16 plants) on each of four nights of sampling, each container of four plants being enclosed in a 108-liter cuvette through which air (340 μl CO_2/l) was passed at 1 to 3 l/min. Release of respired CO_2 from roots to the cuvette was prevented by sealing the lid of the container around the base of the shoots using Terostat VII (Teroson, GmBH, Heidelberg). CO_2 exchanges of attached, randomly chosen leaves from the four strata (A to D) (Fig. 1) were measured using 120-ml clear Plexiglas cuvettes ventilated with air (340 μl CO_2/l at 1.5 l/min. Plants with cuvettes attached to their leaves were maintained under a water screen which restricted temperature fluctuations in the cuvettes to less than ±4 C of ambient. Every second day, leaves from a fresh set of plants were enclosed for measurement so that, with five cuvettes operating continuously, average daytime exchange of CO_2 by each leaf stratum was estimated from a series of four or five successive measurements during the study period.

Short-term CO_2 efflux studies on freshly excised plant parts were made over 15- to 30-min periods during the night (17). The data, comprising measurements during three different days of the study period, were used to estimate the relative contributions of specific shoot parts (leaflets and stem + petioles of Strata A to D, and lateral shoot apices + inflorescence) to the total CO_2 efflux of the shoot at night. Identical series of measurements of stem + petiole CO_2 exchange were made in natural light during daytime.

[^{14}C]Urea-feeding Studies and Translocatory Commitments of Leaflets. At three times during the week of study, 0.1-ml drops of [^{14}C]urea (0.1 μCi) were applied to leaflets of leaves selected at random from the shoot strata A to D. One h later, phloem sap was collected from incisions in the stem 2 cm above and 2 cm below the node of insertion of the fed leaf. Phloem sap samples were assayed for ^{14}C by liquid scintillation (Packard Tri-Carb, model 2003) with appropriate correction for quenching. The ratio of ^{14}C activity in phloem sap from the two sampling sites was used as an index of the activity of the leaf in donating assimilates to the upward- and downward-moving phloem streams of the stem.

Measurement of Relative Rates of Photosynthesis of Shoot Organs Using a Short-term $^{14}CO_2$-fixation Technique. At eight randomly chosen times during the photoperiods of the week of study, a container of two intact plants was enclosed in a 108-liter clear Plexiglas cuvette. While darkening the cuvette momentarily, $^{14}CO_2$ (1×10^7 dpm ^{14}C/l) in air was introduced to the cuvette and mixed thoroughly with a fan. The cuvette then was exposed to full sunlight for 5 min, after which the shoots were removed and immediately separated into component organs (Fig. 1). Each part was frozen in liquid N_2 and later extracted with 80% (v/v) ethanol. After acidification of the extracts (pH 3.0) to release any unfixed $^{14}CO_2$, aliquots of the extracts were assayed for ^{14}C by liquid scintillation. Percentage distribution of ^{14}C was taken as an indication of relative photosynthetic performances of shoot parts at the time of feeding.

Collection and Analysis of Transport Fluids. Root bleeding sap (xylem exudate) and phloem exudate were collected as described previously (14) from the sites depicted in Figure 1. Collections were made each day, at 11 times throughout the study period, including three night samples and eight samples spanning the photoperiod. The resulting 11 samples from each collection site were combined and analyzed as representative of average sap composition at the respective sites during the study period. Each sample was analyzed for the major solutes of C and N (sucrose, malate, amino acids, and amides) as described elsewhere (9, 14) and the analyses were used to determine the C:N weight ratios of the transport fluids. C:N ratios of the sap samples determined on the CHN analyzer were in close agreement with ratios computed as above from solute composition of the samples.

Measurement of Transpiration Loss. Water loss from shoots of intact potted plants were measured gravimetrically (19) for each 24-h period of the study and compared with water loss over the same time from similarly aged defoliated plants. The difference between the two sets of values was taken as representing transpiration of leaflets, whereas the water loss of the defoliated plants was used to indicate the contribution of petioles, stem, and apical parts to shoot transpiration.

The relative contributions of different shoot parts to water loss of the whole shoot were assessed by determining weight loss of freshly excised leaflets, stem + petiole segments, inflorescences, and lateral apices over a 1-min period using a torsion balance (White Electrical Instruments, United Kingdom). A second series of measurements of the transpirational activities of the different strata of leaflets was made using a porometer (Mark II, Delta-T Devices, United Kingdom).

RESULTS

Relative Growth Rates and C, N, and H_2O Increments of Plant Parts (Table I). Highest relative growth rates were recorded for the inflorescence + lateral apices, followed by the expanding leaflets and stem + petioles of stratum D of the shoot. These parts and the nodulated root were the major sinks for C and N. Leaflets of stratum A showed net losses of C and N, leaflets of B showed a net loss of N and a very small gain of C. Stem + petiole segments from all levels of the shoot incorporated C into dry matter, due principally to secondary thickening of the stem at levels A to C and to extension growth in the stem of stratum D. The ratio of the increments of C and N in dry matter of the whole plant was 17:1; in stem + petioles, 22 to 210:1; in leaflets C and D, 15 and 9:1, respectively; in shoot apices, 10:1; and in the nodulated root, 16:1.

Respiration Losses. Rates of CO_2 efflux of root and shoot remained fairly constant over the study period (Fig. 2A). The night losses of CO_2 from the nodulated root from 51 to 58 days amounted to 288 mg C/plant; the total night respiration of shoot parts was 185 mg C/plant. Estimates of the separate contribution of shoot parts to total night respiration showed greater losses from leaflets than from stem + petioles (Table II).

Transpiration. Comparisons of the rate of water loss of whole shoot and defoliated shoots (Fig. 2B) indicated that leaflets consistently accounted for more than 95% of shoot transpiration. A similar conclusion was reached from the torsion balance studies (Fig. 3A; Table II), which included estimates of the contributions

Table I. *Relative Growth Rates and Increments of C, N, and Tissue H_2O in Organs of Nodulated L. albus over the Period 51 to 58 Days after Sowing*

Plant Part[a]	Relative Growth Rate	Increments in		
		Carbon	Nitrogen	Tissue Water
	mg dry matter/g·day	*mg/plant*	*mg/plant*	*g/plant*
Nodulated Root	55	165 ± 9.2[b]	10.1 ± 0.54	2.3 ± 0.10
Stratum A: stem + petioles	48	42 ± 1.8	0.6 ± 0.04	0.6 ± 0.02
leaflets	−3	−2 ± 0.1	−1.3 ± 0.06	0.0 ± 0.02
Stratum B: stem + petioles	55	42 ± 2.2	0.2 ± 0.01	0.4 ± 0.02
leaflets	3	3 ± 0.1	−1.3 ± 0.07	0.2 ± 0.02
Stratum C: stem + petioles	93	55 ± 2.6	1.1 ± 0.08	0.9 ± 0.03
leaflets	37	49 ± 1.9	3.3 ± 0.15	0.7 ± 0.03
Stratum D: stem + petioles	195	49 ± 3.7	2.2 ± 0.24	0.9 ± 0.04
leaflets	123	122 ± 7.3	13.1 ± 0.91	1.3 ± 0.08
Terminal inflorescence + lateral shoot apices	232	64 ± 6.7	6.7 ± 0.73	0.8 ± 0.08
Total Plant	59	588 ± 21.1	34.8 ± 1.75	8.1 ± 0.28

[a] Plant parts and strata of shoot as designated in Figure 1.
[b] Values are expressed ± SE of mean.

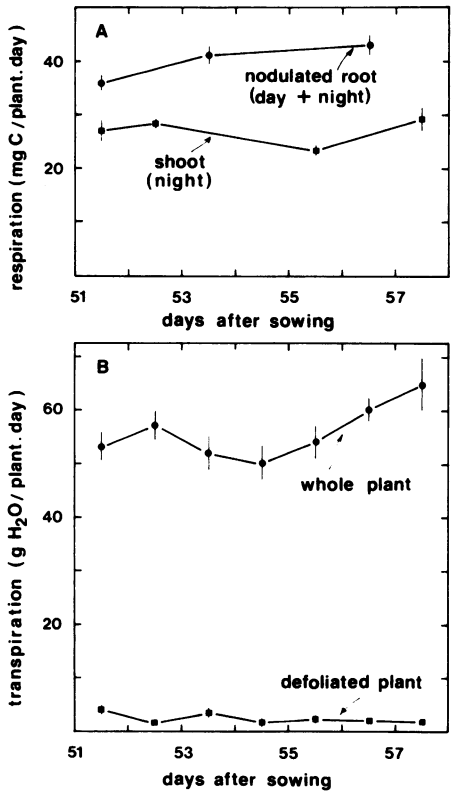

FIG. 2. Respiration losses (A) and gravimetric measurements of water loss (transpiration) (B) of nodulated plants of white lupin for the period 51 to 58 days after sowing. Vertical bars represent values for SE of mean.

to water loss made by the inflorescence + lateral shoot apices and the strata of stem + petioles. Estimates of transpiration of leaflets A to D by porometer measurement (Fig. 3B) agreed closely with those based on torsion balance measurements (Fig. 3A). There was increasing proportional loss during the study period from the growing leaflets of stratum D and a progressive decline in the contribution of the oldest (stratum A) leaflets. Estimates of transpirational losses of leaflets based on the gravimetric studies of whole shoots and torsion balance values were as shown in

Table II. *Net Photosynthesis, Respiration, and Transpiration of Plant Parts of Nodulated L. albus over the Period 51 to 58 Days after Sowing*

Plant Part	Respiration[a]	Photosynthesis	Transpiration
	mg C/plant	*mg C/plant*	*g H_2O/plant*
Whole plant	473 ± 19[b]	1061 ± 40	391 ± 22
Nodulated roots	288.5		
Shoot parts			
Stratum A: stem + petioles	13.8	nil	5.1
leaflets	13.2	172.0	63.2
Stratum B: stem + petioles	13.3	nil	5.0
leaflets	24.1	291.8	113.3
Stratum C: stem + petioles	11.8	nil	5.6
leaflets	41.8	370.0	123.1
Stratum D: stem + petioles	7.7	nil	1.5
leaflets	37.0	227.6	68.4
Apical inflorescence	22.5	nil	6.0

[a] Respiration of nodulated roots was measured day and night, that of shoot parts, night only.
[b] Values expressed ± SE of mean.

Table II.

Net Photosynthesis of Shoot and Photosynthetic Contributions of Strata of Shoot Parts. As in earlier studies (17–20), net photosynthesis of the plant was defined as daytime gain of C as CO_2 by the shoot from the atmosphere and estimated (Table II) as 1061 mg C/plant for the week of study. This comprised 588 mg C incorporated into plant dry matter (Table I), 288 mg C respired from nodulated roots (Table II), and 185 mg C lost in shoot night respiration (Table II). Distribution of photosynthesis among shoot parts estimated by the short-term $^{14}CO_2$-feeding studies (Fig. 3C) indicated that leaflets of strata A to D accounted for 98% of the shoot's photosynthetic capacity, with the inflorescence, lateral shoot apices, and stem + petioles (marked "other," Fig. 3C) accounting for the remaining 2%. Freshly excised stem + petiole segments were shown to be at or near CO_2 compensation point during daytime under conditions of illumination similar to those within the leaf canopy. This agreed with the $^{14}CO_2$-feeding experiments showing insignificant photosynthetic contributions by these shoot parts.

Estimates of relative photosynthetic activities of the four strata of leaves by $^{14}CO_2$-feeding (Fig. 3C) agreed closely with the

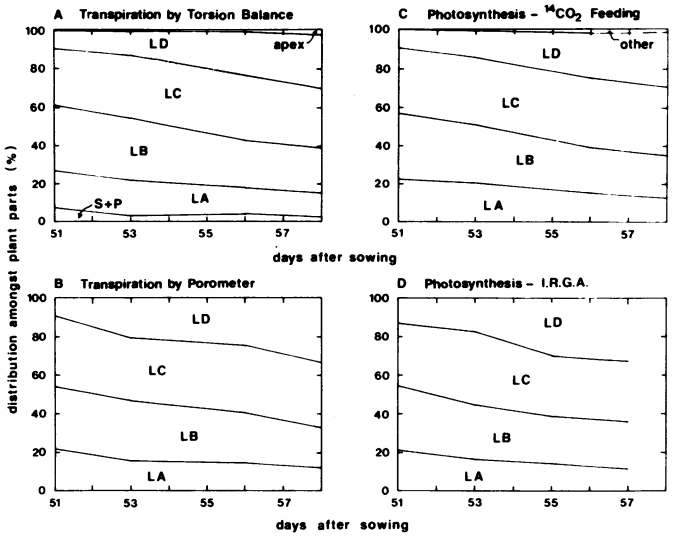

FIG. 3. Estimates of relative activities of leaflets of the four shoot strata (LA, LB, LC, and LD) in transpiration as measured by torsion balance (A) or porometer (B) and in photosynthesis as measured by short-term $^{14}CO_2$ feeding (C) or by IRGA (D). The torsion balance studies (A) included measurements of water loss of stem + petioles (S + P) and the inflorescence + lateral apices (apex) and the $^{14}CO_2$-feeding studies (C) included assessment of the contribution of shoot parts other than leaflets in the photosynthesis of the total shoot.

measurement of net CO_2 uptake by these groups of leaves using the IRGA (Fig. 3D). There was an increase during the study period in the relative contributions from the upper story (stratum D) leaflets and a corresponding decline in the contributions from the older leaflets of strata A and B. The proportioning of whole plant net photosynthesis among the strata of leaflets was estimated (Table II) by averaging data for the $^{14}CO_2$-feeding and IRGA measurements of relative photosynthetic activities of each stratum of leaflets (see Fig. 3). Other shoot parts were assumed to be at CO_2 compensation point (net daytime CO_2 exchange was 0).

Translocatory Destinations of Assimilates from Leaflets. The study combining [^{14}C]urea feeding of leaflets with collections of stem phloem sap concluded, as in a previous study (24), that the translocate from leaflets of the upper stratum (D) were almost entirely committed to supplying the shoot apex and that the leaflets of the lower strata (A and B) were equally highly involved in providing assimilates to roots. The leaflets of stratum C were translocating in both directions, the upper leaf of the stratum principally towards the shoot apex and the lower three leaves principally towards the root.

Composition and C:N Weight Ratios of Transport Fluids (Table III). Xylem sap had a high level of amides, had low levels of other amino acids and malate, and recorded a C:N ratio of 2.4 (14). Phloem sap C:N ratios varied from 20:1 to 59:1, the variations being due more to differences in amide than in sucrose level. As in earlier studies (14, 20), the lowest C:N ratios were obtained for phloem sap collected from stem tissue close to the shoot apex. C:N ratios in phloem tended to be higher in collections from petioles of leaflets than from stem tissue, and there was an upward gradient of increasing C:N ratio in petiole phloem sap for the successive groups of leaves of the shoot. A notable result was the very high level of amide in phloem sap collected at the top of the stem.

Modeling Flow and Utilization of C, N, and H_2O. As before (12, 18–20), models for flow of C and N between plant parts through xylem and phloem were derived from data on C and N increments in dry matter (Table I), respiratory losses from plant parts (Table II), and C:N weight ratios of transport fluids (Table III). The equations used to calculate the fluxes of C and N between

Table III. *Solute Concentrations and C:N Weight Ratios of Transport Fluids Collected from Nodulated L. albus over the Period 51 to 58 Days after Sowing*

Collection Site[a]	Solute Concentrations[b]				C:N[c] Ratio
	Sucrose	Malate	Amino Acids	Amides	
	μmol/ml				*g/g*
Xylem bleeding sap					
Root/shoot junction	—[d]	1.2	1.7	6.1	2.4
Phloem bleeding sap					
Petioles, leaves stratum A	588	2.2	48.7	49.6	42.8
Petioles, leaves stratum B	535	2.4	31.9	37.7	53.9
Petioles, leaves stratum C	497	2.8	25.6	34.2	56.5
Petioles, leaves stratum D	473	2.0	28.7	28.7	59.2
Stem below stratum A	526	3.3	38.8	44.0	44.5
Stem below stratum B	459	1.5	24.5	40.9	46.2
Stem below stratum C	438	1.9	32.4	42.6	39.9
Stem below stratum D	412	3.0	26.1	48.9	36.0
Stem at apical inflorescence	345	2.3	36.2	77.8	20.2

[a] See Figure 1.
[b] Bulked sap samples from 11 collections during the period of study.
[c] Computed from concentrations of solutes given in this table.
[d] —, not detected.

specific plant parts were as published earlier (20), and the basic assumptions and levels of precision in model construction indicated in that publication applied here. The present models carried additional information on transpirational losses and photosynthetic inputs of shoot parts and C:N ratios of phloem sap of petioles and stem tissue from the four strata of the shoot. It was assumed that: (*a*) net photosynthate was generated by the strata of leaflets in proportions indicated by averaging the data of $^{14}CO_2$-feeding and IRGA studies (see Table II); (*b*) as shown by the [^{14}C]urea-feeding study, lower leaves (strata A and B) supplied the nodulated root, the upper leaves (stratum D) fed the shoot apices and mid leaves (stratum C) fed shoot apex and root; (*c*) shoot organs other than leaflets were, on average, at compensation point for CO_2 during the photoperiod and were, therefore, dependent on leaflets for their net gains of C in dry matter and for maintenance of their respiration at night; (*d*) exchanges between plant parts took place by mass flow in xylem and phloem and in the relative amounts of C and N, indicated from the C:N weight ratio of the nearest relevant sampling point for xylem and phloem sap (see Fig. 1 and Table III); (*e*) water and N were carried from root to shoot exclusively through the xylem (any N which was translocated from shoots surplus to the requirements of the root in dry matter production was returned to the shoot via xylem); (*f*) leaflets of stratum D, although not all fully expanded and still increasing in C and N content, imported only through xylem.

Information derived from the flow models for C and N (Fig. 4, A and B) was combined with data on transpirational loss, the balance of water in plant parts, and concentration values for phloem solutes to construct a model for water flow and utilization. It was assumed that: (*a*) water accompanied C and N in phloem in amounts indicated from levels of solutes in phloem sap (Table III); (*b*) the xylem stream entering the shoot was the only source of water for transpiration, tissue water increments, and water in phloem; (*c*) transpirational losses of the various parts of the shoot were in the relative proportions indicated from torsion balance studies (Fig. 3A; Table II). (*d*) amounts of "metabolic" H_2O utilized in photosynthesis or released in respiration were calculated as 1.5 mg H_2O/mg C of carbohydrate fixed or respired. These values were added to or subtracted from the increment in free H_2O for an organ (Table I) to estimate its net consumption of H_2O.

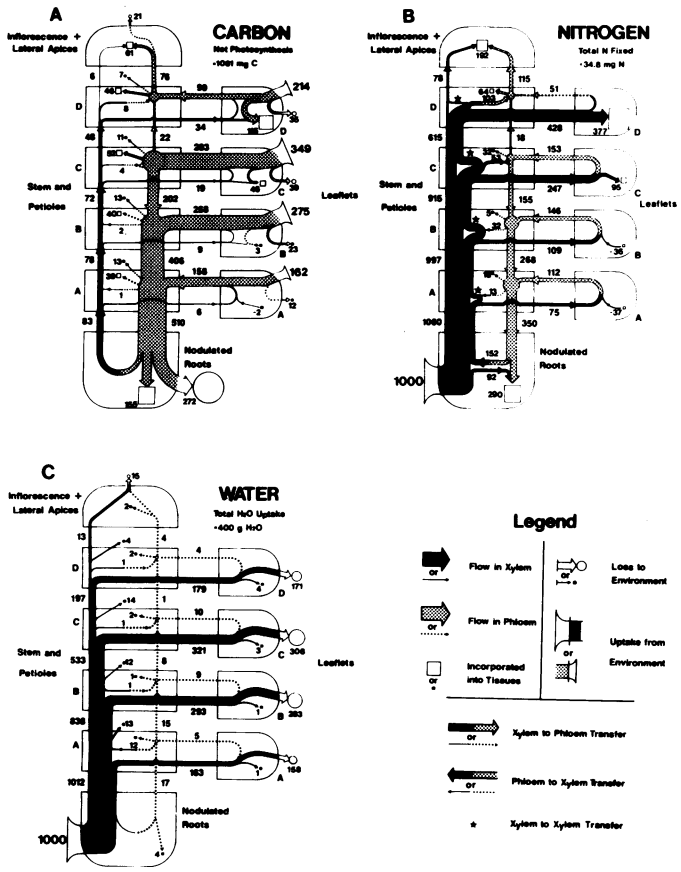

FIG. 4. Flow profiles for uptake, transport and utilization of C (A), N (B), and H_2O (C) by nodulated plants of *L. albus* over the period 51 to 58 days after sowing. Amounts of C, N, and H_2O transported and utilized are expressed in terms of a net intake by the plant of 1000 units by weight of a specific quantity. Direct incorporation of fixed N into nodules is assumed to have provided 50% of the N increment of nodules (see ref. 12). Total amounts of C and N fixed and H_2O consumed by the plants are also given.

C Flow and Utilization (Fig. 4A). The model for C agreed closely with earlier studies (18–20) in showing a large commitment (51%) of net photosynthate to roots, especially to respiration of root and nodules (27%), and a conversion of over half (55%) of the C of net photosynthate to dry matter. The demand for C by the inflorescence + lateral apices was less than one-sixth of that of the root and was met largely by translocate from leaflets D with only a small contribution from leaflets C. A relatively small proportion (8.3%) of C was cycled through roots and returned to the shoot in xylem (black lines, Fig. 4A), principally in the form of amides and amino acids (Table III).

Combining data from leaflet photosynthesis with information on leaf area, D leaflets were shown to have the lowest average net photosynthetic rate (37 mg $C/dm^2 \cdot day$) and exhibited the lowest percentage export (46%) of their net photosynthate. Leaflets A to C showed similar average net photosynthetic rates (46 to 55 mg $C/dm^2 \cdot day$) so that the apical gradient in increasing net photosynthesis (Table II) was caused by increasing average leaflet areas from the base to the top of the primary shoot. Stratum C leaflets exported a lesser proportion (81%) of their net photosynthate than did A and B leaflets (94 to 97% export), but still donated significantly more net photosynthate to the plant than any other stratum.

N Flow and Utilization (Fig. 4B). Roots received in phloem translocate an amount of N equivalent to 35% of the total fixed N or 90% of the N cycled through leaves. The model indicated that delivery of N in phloem exceeded the nodulated roots' demand for N in dry matter production. This extra N (15% of the total fixed N) was depicted as returning to the shoot in xylem.

Leaflets D constituted the major sink for N in the shoot but exported in phloem only 12% of the N they imported through xylem. Leaflets C, although cycling more N than any other group of leaflets, were still accumulating dry matter and retained 38% of their net intake of N through xylem. Leaflets A and B showed net losses of N and, therefore, recorded greater N export in phloem than import in xylem.

Inflorescence + lateral apices acquired 19% of the fixed N but only 8% of net photosynthate. These regions were depicted as relying for their N supply on (*a*) direct intake of xylem fluid, (*b*) phloem translocation from leaves, and (*c*) xylem to phloem transfer in the stem.

Water Flow and Utilization (Fig. 4C). Transpiration accounted for 92% of the 400 ml H_2O taken up by the plant during the study period. Proportional water losses of leaflets A, B, C, and D were 17, 31, 33 and 19%, respectively, correlating closely with values of 16, 28, 35, and 21% for the respective contributions of net photosynthate by the same groups of leaflets (Fig. 4A). This indicated a strong positive correlation between transpiration and CO_2 fixation. Distribution of water to the strata of leaflets (Fig. 4C) was, however, very different from their respective imports of N (Fig. 4B), proportional intake of A, B, C and D being 17, 31, 33, and 19% for water *versus* 9, 12, 29 and 50% for N, respectively. The models thus suggested that the xylem fluid supplying upper leaflets had a significantly higher N concentration than that entering lower leaflets, and it was possible to estimate the magnitude of the difference by using the data of Figure 4, B and C, to calculate mean concentrations of N in xylem fluid entering the petioles or moving through the main body of stem tissue of each stratum of the shoot. From this information and data on internode lengths, it was possible to estimate gradients for average xylem N concentration with height and nodal position on the shoot. These calculations (Fig. 5) indicated that the mainstream of xylem fluid in

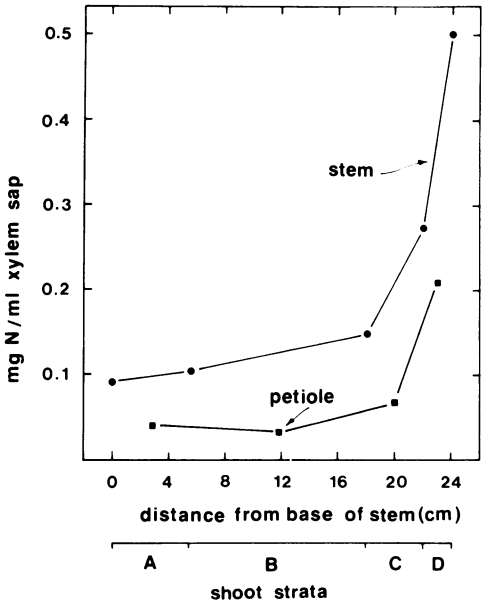

FIG. 5. Estimates of average concentration of N in xylem of different parts of the shoot of *L. albus* over the period 51 to 58 days after sowing. The figure shows gradients up the stem and between the different shoot strata for N concentration in xylem streams moving to leaves (values marked petioles) or ascending the main stem towards the shoot apex (values marked stem). Data were obtained from the flux values for N and H_2O given in Figure 4 and measurements of internode lengths of the shoot.

the stem was at all levels significantly more concentrated in N than that entering adjacent leaflets through petioles and that particularly steep upward gradients in N concentration in xylem occurred in the top region of the stem.

It was therefore concluded that N was removed from the xylem streams of vascular tissue committed to supplying leaves and that this N was subsequently fed back into the xylem of other traces supplying higher regions of the shoot. This process was depicted in the model as looped flow-paths for N in the xylem stream (see black stars, Fig. 4B), the relative thicknesses of which portrayed the amounts of N removed from departing leaf traces and released back to xylem streams continuing further up the stem.

DISCUSSION

The shoots of white lupin plants of the age studied here achieved a partitioning of assimilated C and N in which growing apices of the shoot received 13 units by weight of C/unit by weight of N, compared with an intake by the nodulated root from the shoot of 54 C:N. Four distinct but interacting processes were depicted (Fig. 6) to be involved in this differential transport of N relative to C. First, translocation to shoot apex and nodulated root occurred from photosynthesizing leaves. The phloem translocate from the different strata of leaves carried solutes with an average C:N ratio close to that of the roots' requirements for these elements, but markedly deficient in N relative to C as far as nutrition of the shoot apex was concerned. Since the C:N ratio of translocate from upper leaves serving the shoot apex was higher than that of lower leaves serving roots, the transfer of fixed C and cycled N from leaves worked against preferential flow of N to apical growing parts of the shoot. As viewed in Figure 6, leaves were envisaged to supply the root with virtually all of its C requirement and 65% of its N increment over the study period, while supplying the shoot apex with 82% of its C but with only 2% of its N.

A second partitioning process was direct absorption by the shoot apex from the xylem. With a C:N ratio of only 2.4:1, xylem fluid had considerable impact in enriching the apex with N, and its uptake was shown (Fig. 6), somewhat hypothetically, to consist

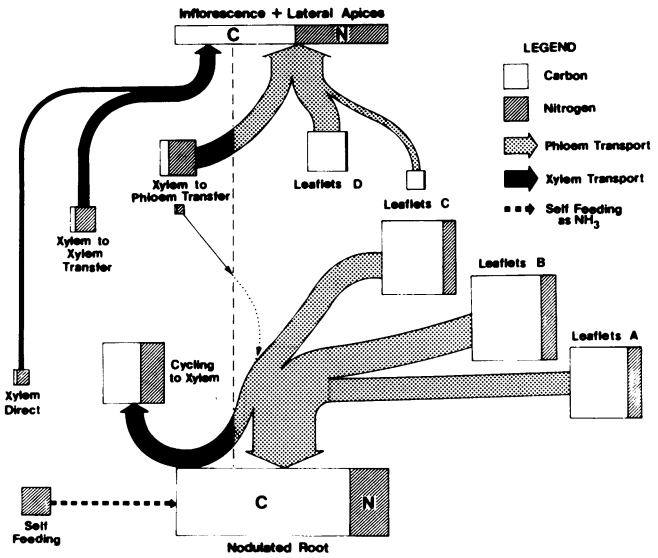

FIG. 6. Diagrammatic representation of the principal components of C and N partitioning from mature shoot to root and shoot apex in 51 to 58 day *L. albus*. Plants were relying on root nodules for their N supply. The areas of the rectangles for C and N are drawn to proportions (10 g C equivalent in area to 1 g N), indicating the relative sizes of the contribution of C and N made by each partitioning process to shoot apex or root. Information drawn entirely from Fig. 4.

of two components, one a direct mass flow through xylem of nitrogenous solutes at the same concentration as that leaving the root, the other an "extra" fraction of N provided by lateral abstraction of xylem solutes destined for leaves and the feeding back of these solutes into xylem streams serving the shoot apex. The well-developed transfer cells which line the xylem elements of departing leaf traces of white lupin [and many other species (16)] were likely sites of retrieval of N from xylem and the traces above the nodes closing the "gaps" caused by departure of leaf traces were the most likely location for subsequent transfer of the nitrogenous solutes to xylem streams progressing further up the stem. Termed "xylem to xylem transfer" (Figs. 4 and 6), this mechanism was estimated to provide 29% of the intake of N by the shoot apex.

The third component of differential partitioning to root and shoot apex was the loading of N solutes by upper stem tissue onto the upward-moving phloem streams from leaves. It was concluded that this process, indicated also in earlier studies (18, 19), depended directly on xylem as a principal source of additional N and was, therefore, termed xylem to phloem transfer in Figures 4 and 6. The process was responsible for changing the average C:N ratio of phloem translocate from upper leaflet strata from 58:1 to 20:1 as it passed through the top four or five internodes of the shoot. As in the case of the xylem to xylem transfer mentioned above, abstraction from departing leaf traces was judged to be the most likely source of solutes for phloem loading with N, although direct xylem to phloem transfer within the cauline bundles of internodes might also have contributed significantly. Xylem parenchyma transfer cells have been found in internode tissue of white lupin (11), and, although these cells exhibit less well-developed sets of wall ingrowths than do the transfer cells of departing leaf traces, their presence throughout the length and in the majority of bundles of an internode would provide an extensive pathway for solute retreival from xylem and a more direct route to phloem than in the case of nodal sets of transfer cells. The process of xylem to phloem transfer emerged from the models as a dominant activity in N partitioning, meeting 58% of the intake of N by the shoot apex.

The final, somewhat speculative component of the partitioning process was the possible cycling of N through the root system. The models constructed here (Fig. 4), and in other studies of *L. albus* (17–20), indicated that, in certain stages of growth, the shoot provided the root with an amount of N considerably in excess of the current requirements of nodules and root in dry matter production. The presence of low, but significant, levels of amino compounds in xylem exudate collected from below the nodulated region of lupin roots (15) supported the assumption that this excess N supplied to roots was being returned to the shoot in the xylem. If this were so, the cycled N would elevate N concentrations in the xylem and thereby stimulate N supply to the upper parts of the shoot. This possibility was indicated in Figures 4 and 6 as a cycled component for N solutes involving transfer from phloem to xylem in the root.

As in any modeling exercise, the accuracy of the various predictions derived from the study was limited by the validity of the assumptions used in the construction of the models. Although previous studies on other species (8, 10, 26) have shown that developing leaves are capable of simultaneous import and export of assimilates in the phloem, the study on white lupin presented here assumed that all exchanges of C and N in phloem between leaflets and the rest of the plant involved export by the leaflets. This was likely to have applied to the three lower strata of leaflets, but the uppermost leaf of stratum D, less than half expanded at the commencement of the study, was probably importing C and N through phloem for at least the early part of the experimental period. If the model was inaccurate in this respect, the importance of xylem in the N nutrition of upper leaflets would have been

overestimated, and an underestimate of similar magnitude then would have been involved in xylem to phloem transfer of N in the upper portion of the stem to which this young leaf was attached.

It would be of interest to determine how the partitioning processes for C and N in white lupin change ontogenetically or in response to nutritional and environmental conditions. Already measurable differences have been indicated for patterns of C and N utilization of NO_3-fed, non-nodulated, and N_2-fixing nodulated plants of the species (18) and the mechanistic bases of these differences await evaluation.

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