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Effects of P deficiency on the uptake, flows and utilization of C, N and H_2O within intact plants of *Ricinus communis* L.

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Abstract

The influence of P deficiency on the uptake, flow and utilization of C, N and H_2O by intact NO_3-fed castor bean plants (*Ricinus communis* L.) was studied over a 9 d period in the middle of their vegetative growth. The modelling techniques incorporated data on net increments or losses of C, N and H_2O in plant parts, photosynthetic gains in and respiratory losses of C, molar C : N ratios of solutes in phloem and xylem sap and transpirational losses of H_2O. Plant growth was inhibited within 3 d of withholding P supply and dry matter production was less than one-third of the controls. Leaf growth was particularly depressed, while root growth was much less affected than that of the shoot. Shoot : root ratio of low-P plants was 1.5 compared with 2.6 under P supply. Over the 9 d study period total plant C and N increased by 560 and 47 mmol, respectively, in the controls, but by only 113 and 6.9 mmol in the low-P treatment. The particularly low increment of N in P-deficient plants was due principally to decreased NO_3^- uptake. Flows of C and N during the study period were markedly different between control and P-deficient plants. The partitioning profile for C in P-deficient plants showed a dramatic inhibition of net photosynthesis and attendant photoassimilate flow. Proportional downward to upward allocation of carbon increased with increase in sink size of the root relative to shoot. This was reflected in greater relative allocation of C to root dry matter and root respiration than in P-sufficient plants, and suppressed cycling of C from root to shoot via xylem. Nitrogen intake and xylem transport to the shoot of P-deficient plants were only 15% of the control and, as in the case of C, downward allocation of N predominated over upward phloem translocation. Apart from these severe changes, however, the basic patterns of N flows including xylem-to-phloem and xylem-to-xylem transfer of N were not changed, a feature highlighting the vital nature of these transfer processes even under deficiency conditions. The alterations in flows and partitioning of C, N and H_2O in response to low-P conditions are discussed in relation to the corresponding effects of moderate salt stress in *Ricinus* and the conclusion is reached that changes in nutrient flows under P deficiency were more highly co-ordinated than when plants experience salt stress. Flow profiles under P deficiency which favour root growth and activity are viewed as a means for increasing the potential capability of the plant to acquire P from the nutrient medium.

Key words: *Ricinus communis* L., P deficiency, carbon, nitrogen, water, partitioning, xylem transport, phloem transport.

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Abbreviations: DAS: days after sowing, DM: dry matter, C_{min}: minimal concentration down to which the plants can reduce external ion concentration in the aqueous phase of the rooting medium.

Introduction

Phosphorus is an essential element for higher plants and required in substantial concentrations in plant tissues, particularly during vegetative growth. When P concentrations in dry matter fall below about 0.1–0.2% typical deficiency symptoms usually occur, including a marked reduction in leaf expansion and leaf surface area (Fredeen *et al.*, 1989), and a decrease in the number of emerging leaves (Lynch *et al.*, 1991). Cell and leaf expansion are retarded to a greater extent than chloroplast and chlorophyll formation (Hecht-Buchholz, 1967) resulting in darker green leaf colour under P deficiency but little change in protein content (Rao and Terry, 1989) and chlorophyll per unit leaf area (Fredeen *et al.*, 1989). Nevertheless, photosynthetic efficiency per unit chlorophyll tends to be much lower in P-deficient leaves (Lauer *et al.*, 1989). Additionally, P deficiency affects the plant water relations with the leaves showing higher ABA accumulation and with stomatal closure beginning at less negative leaf water potential (Radin, 1984).

In terms of dry matter yield, the root is much less affected than the shoot so that P-deficient plants are typically low in shoot-to-root dry weight ratio (Fredeen *et al.*, 1989; Heuwinkel *et al.*, 1992). This lower ratio appears to relate to preferential partitioning of carbohydrate towards the roots (Cakmak *et al.*, 1994*a*; Khamis *et al.*, 1990). Another feature of plants inadequately supplied with P is a marked depression that occurs in the uptake of NO_3-N (Heuwinkel *et al.*, 1992; Pilbeam *et al.*, 1993), leading to a disturbance in plant N metabolism and a potential for acidification of the rhizosphere (Heuwinkel *et al.*, 1992).

In an earlier study (Jeschke and Pate, 1991) the application of an empirically-based modelling technique to *Ricinus communis* was reported, which allowed the flows and utilization of C, N or H_2O within the plant to be depicted quantitatively. The modelling procedures are based on the solute composition of xylem and phloem fluid and the ratios of C:N therein, on net increments of these elements in organ dry matter, respiratory losses and photosynthetic gains in C by organs during a study interval. *Ricinus communis* is a species from which phloem sap can easily be collected from the shoot of the intact plant, and which lends itself to such studies. Since lack of P greatly affects physiological processes involving C, N and H_2O utilization, this same modelling approach has been used in the present paper in which a quantitative investigation on the effects of P deficiency on the uptake, allocation and transport of C, N and H_2O by *Ricinus* over a defined growth period was undertaken. As a point of reference to these changes those induced by another stress, namely salinity, were used. For this reason, similar experimental conditions to those applied in a previous study of *Ricinus* exposed to salinity (Jeschke and Pate, 1991) were used and a direct comparison of the effects of the two classes of stress on the species was made.

Material and methods

Culture of plants

Plants of castor bean (*Ricinus communis* L.) were grown in quartz sand culture during May and June 1994 in a greenhouse. At 11 d after sowing (DAS) in vermiculite, seedlings were transplanted into 5 dm^3 pots, 1 plant per pot, and watered daily with an excess of a nutrient solution containing in mM: 4 KNO_3, 4 $Ca(NO_3)_2$, 1.5 $MgSO_4$, 0.5 NaH_2PO_4, with micronutrients present in the following concentrations in μM: 100 Fe (as Fe-sequestrene (Ciba-Geigy)), 46 B, 1.8 Mn, 0.8 Zn, 0.3 Cu, 0.7 Mo, and 0.2 Co. During the initial phases of growth until 44 d after sowing, natural light was supplemented by Osram HQL lamps (16 h light at 350–500 $\mu E\ m^{-2}\ s^{-1}$), but later on the natural light was sufficient and provided up to 700 $\mu E\ m^{-2}\ s^{-1}$. Temperatures were between 22 and 32 °C during the day and between 15 and 18 °C at night. Relative humidity was between 50% and 70%.

At 29 DAS half of the pots were rinsed 10 times with 1 dm^3 of deionized water and 4 times with 1 dm^3 of a P-free nutrient solution (NaH_2PO_4 replaced by NaCl). Phosphate levels were monitored in the eluates from the rooting media and concentrations fell eventually to within 1.5–2.9 μM. The 'low-P' plants were then watered with P-free solution and then from 41 DAS and throughout the study period from 44–53 DAS with a solution containing 5 μM PO_4. This low but deficient supply of P was required to promote a low but measurable uptake of P during the time of the experiment. Had no external P been supplied, some PO_4 loss might have occurred leading to difficulties in constructing and interpreting flow models for P and other elements.

For purposes of comparison, equivalent models of uptake, flow and distribution of C, N and H_2O for *Ricinus communis*, treated with 128 mM NaCl, for the same study period 44–53 DAS were utilized, using already published data provided by Jeschke and Pate (1991).

Monitoring of plant development

The development of leaf area was monitored in a subset of 4 of each of the control and low-P plants by measuring leaf area on the basis of the length of the midrib (mr). Leaf area (A) was then calculated as $A = \alpha mr^2$. The proportionality factor α which was determined empirically increased from 0.88 for leaf 1 to 1.3 in leaf 5 and then declined to 1 in leaf 8. As can be seen in Fig. 1, the 9 d study period 44–53 DAS for control plants coincided with the final phase of expansion in leaf 4, rapid expansion of leaves 5 and 6, and the early, exponential phases of leaf development of leaf 7 and 8. In the low-P plants the corresponding developmental stages were noticeably delayed, as seen for example, for leaves 6 and 7 in Fig. 1.

Monitoring the nutrient concentration in the substrate

When applying fresh nutrient solution every 2–3 d, the first 20 ml of solution draining from four representative pots were collected and analysed for PO_4 and pH.

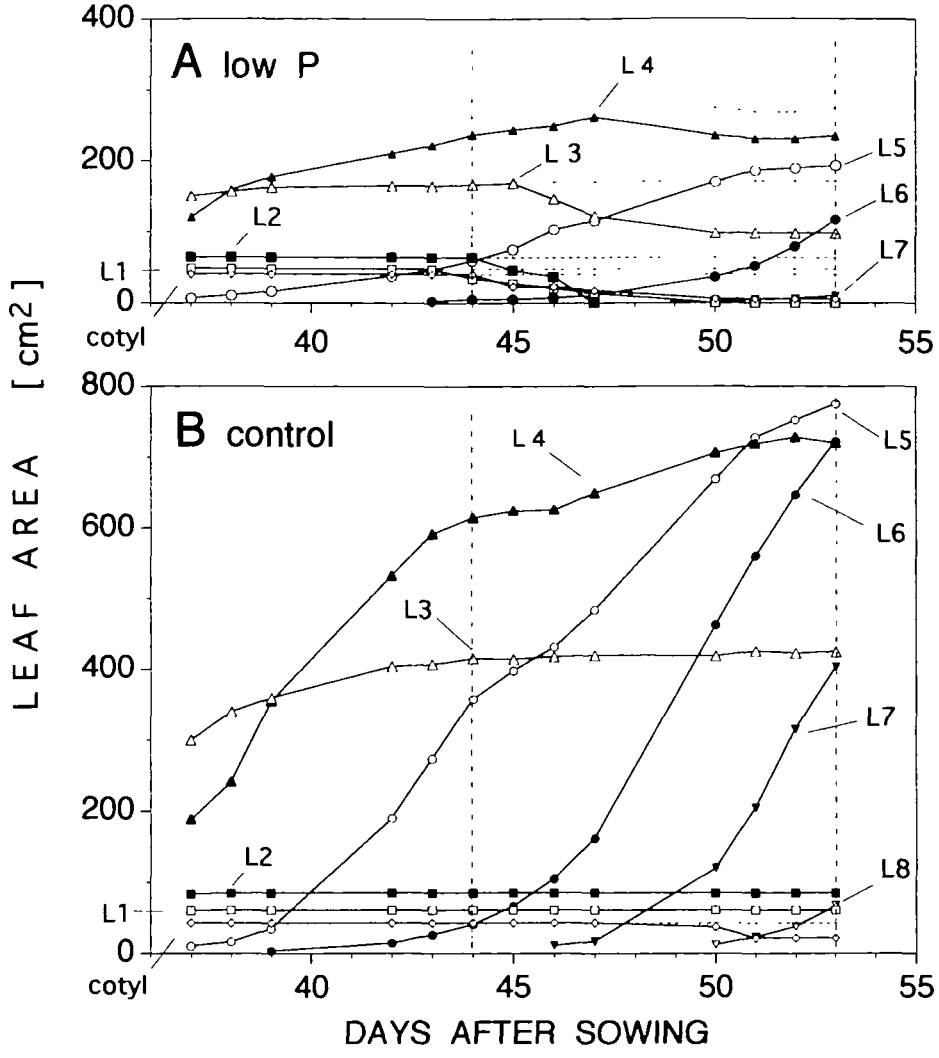

Fig. 1. Leaf area development over the period 37–55 DAS in the plants of castor bean (*Ricinus communis*) grown in sand culture and used for modelling the uptake, flow and utilization of C, N and H_2O. Dashed lines indicate the study period 44–53 DAS. (A) Control plants supplied with 0.5 mM $H_2PO_4^-$ and (B) low-P plants deprived of phosphate supply at 29 DAS and then supplied with 5 μM $H_2PO_4^-$ from 42 DAS onward, in this upper graph the dotted lines depict the hypothetical leaf area development without leaf abscision, the full lines show the leaf area with leaf loss. Each data point is the average of 4 leaves.

Harvests and assessment of incremental gains in tissue carbon, nitrogen, phosphorus, and water

A subset of 7 of each of the control and low-P plants was harvested at the beginning and end of the study period and separated into root and shoot material. The latter was further subdivided into its variously aged leaf laminae and petioles and the stem segments subtending each age class of leaf. Fresh and dry weights of plant parts were measured individually for each plant before and after freeze-drying. Organs were then either bulked according to age and class or processed individually depending on the available sample size. Samples were ground and thereby mixed before being analysed for C and N using a CHN analyser (CHN-O-Rapid, Heraeus, Hanau). Increments or losses of C, N and H_2O in each plant part during the study period were calculated from the resulting data. Phosphorus was analysed using an ICP spectrometer (JY 70 plus, ISA, Instrument S.A. Division, Jobin-Yvon, France).

Measurement of transpiration and net photosynthesis

Whole shoot transpiration was assessed on a daily basis by weighing a subsample of four of each of the control and low-P plants and applying corrections for the water loss of pots without plants. The partitioning of transpiration between various plant parts was determined gravimetrically by first measuring the water loss of a whole potted plant and then that of its separate organs by 11 consecutive weighings over a 3 min period immediately following detachment of laminae, petioles or stem parts. The measurements resulted in highly reproducible rates (SEM on average 3.8–5.7%) of organ transpiration. Also the sum of transpiration of all detached organs of a plant was in close agreement with that obtained initially for the whole plant. Transpiration was additionally measured by porometry using a LICOR-1600 steady-state porometer.

Total net photosynthesis of the plants was obtained from the sum of all gains in carbon and of respiration losses. The

partitioning of photosynthetic activity between the individual leaves was assessed on three occasions by enclosing a plant in a 30 dm^3 perspex cuvette, darkening the plant for a period of 2 min and introducing 50 μCi $^{14}CO_2$. After thorough mixing of the atmosphere the plants were exposed for 10 min in the light and then harvested quickly and dissected in the manner described above. The leaf blade tissues were extracted with 80% methanol in the cold. Soluble ^{14}C was measured by scintillation counting and total ^{14}C content of each plant part then assumed to be proportional to its contribution to photosynthesis of the whole plant (Jeschke and Pate, 1991).

Respiration

Root respiration was assessed by two methods. In the first using intact plants it was measured continuously on duplicate subsets of three control and three low-P plants each growing with the roots enclosed in aerated but air-tight vessels. Using the Pettenkofer gas flow system described by Pate *et al.* (1979) and Layzell *et al.* (1981) CO_2 evolved was absorbed in KOH solution and subsequently measured gravimetrically as $BaCO_3$. Alternatively excised roots were enclosed in sealed, gauged Erlenmeyer flasks and the build-up of CO_2 measured over four consecutive 30 min intervals by infrared analysis (225 Mark 3, ADC Instruments, Hoddesdon, UK) (Pate *et al.*, 1979). Data obtained by the two methods agreed well.

Shoot night respiration was measured on four occasions for control and low-P plants by enclosing the whole plants used for Pettenkofer measurement (roots enclosed) in a 300 dm^3 cuvette and measuring the build-up of CO_2 concentration between dusk and dawn. Partitioning of respiration between shoot parts was assessed using detached parts as described for excised roots.

Collection and analysis of phloem and xylem sap

Phloem sap was obtained from shallow incisions into the petioles of all leaves and into the stem at various locations from the hypocotyl upwards to young internodes. Bleeding proceeded readily in the control plants, but occurred more slowly in low-P plants, to the extent that it was not possible always to collect sufficient amounts of sap at all sites from these plants. Sap was collected on two occasions from 7 plants of each of the control and low-P treatments.

Xylem sap was collected both by pressurizing the moist quartz sand substrate and the root system contained in a pressure vessel (Passioura, 1980) as described in Jeschke and Pate (1991) and by sampling root pressure exudate from detopped hypocotyl stumps. The cut surface was carefully washed and the first exudate discarded to avoid contamination from cut cells. Xylem and phloem sap were kept on ice during collection and stored at −22 °C prior to analyses. Sap samples were analysed for amino acids (Amino acid analyser LC 5001, Eppendorf/Biotronik Co., Maintal, Germany), for anions including NO_3^-, malate and oxalate (Anionenchromatograph IC 1000, same manufacturer) and for sucrose by refractometry (Billingham and Stanley Ltd., Tunbridge Wells, UK). The virtual absence of sucrose in the xylem sap was confirmed by HPLC (Jeschke and Pate, 1991).

Modelling of the flows of C, N and of H_2O

By the use of primary data, namely, increments of C and N, net photosynthesis, respiration of all organs, and the molar C:N ratios in the transport fluids, it proved possible to calculate net flows of C and N through phloem and xylem for the study period using the methods described initially by Pate *et al.* (1979) and Layzell *et al.* (1981) and as further refined by Jeschke and Pate (1991). In addition, the flows of H_2O over the same period were estimated from data on transpiration, water use by all individual organs, and water transport in the phloem, as calculated from the flows and from the concentration of C in the phloem. Procedures and formulae used for constructing models were precisely used as described earlier (Layzell *et al.*, 1981; Jeschke and Pate, 1991).

Statistical treatment

Dry weight increments were obtained from seven replicates of each of both treatments at the first and the second harvests. All further analyses were made usually with two to three bulked and sometimes with seven individual samples for each organ. Only for small plant parts was a single bulked sample used. All analyses were done in duplicate with two weighings. Where appropriate, data are presented as ±standard error (SE) of the mean. As has been discussed by Pate *et al.* (1979) because of a strong positive, growth-related correlation between increments in DM, in C and in N, the variation limits of increments tended to be less than would be expected were these attributes to vary independently of one another.

Results

Effect of P deficiency on biomass production and leaf development

Withholding the P supply severely inhibited plant growth within 3 d as seen from the development of total leaf area (Fig. 2). At the time of withdrawal of P from the root medium, leaf 2 had attained 66% and leaf 3 2.5% of their respective final areas; in low-P plants final areas attained by these leaves were only 74% and 40% of the respective controls (Fig. 1). Growth of leaves still yet to emerge after withdrawal of P was even more depressed as, for example, that of leaf 5 of P-starved plants down to 25% of controls (Fig. 1). In addition to expansion of existing leaf primordia, P-deficiency reduced the number of newly emerged leaves as seen for leaves 6–8 in Fig. 1 and it led to a dark green discoloration of the leaves and to severe grey-brown intercostal necroses. Shortly before and during the study period abscission occurred for cotyledons, leaves 1 and 2 and some of leaves 3 and 4 (Fig. 1). Total leaf area of low-P plants therefore remained about static, whereas that of controls doubled (Fig. 2).

Twenty-four days after imposing the low-P stress the dry matter (DM) of P-deficient plants was 31% (Table 1) and the gain in DM over 9 d was 22% of the P-sufficient plants. Root growth was clearly less inhibited than that of the shoot, its final DM being 52% (Table 1) and its DM gain 32% of the controls. Expressed in another way, 49% of the DM increase of low-P plants occurred in the root, compared with only 28% in the controls. As a consequence, the final shoot-to-root ratio was 1.5 in low-P and 2.6 in sufficiently supplied plants.

Low-P conditions led to severe decreases in tissue P

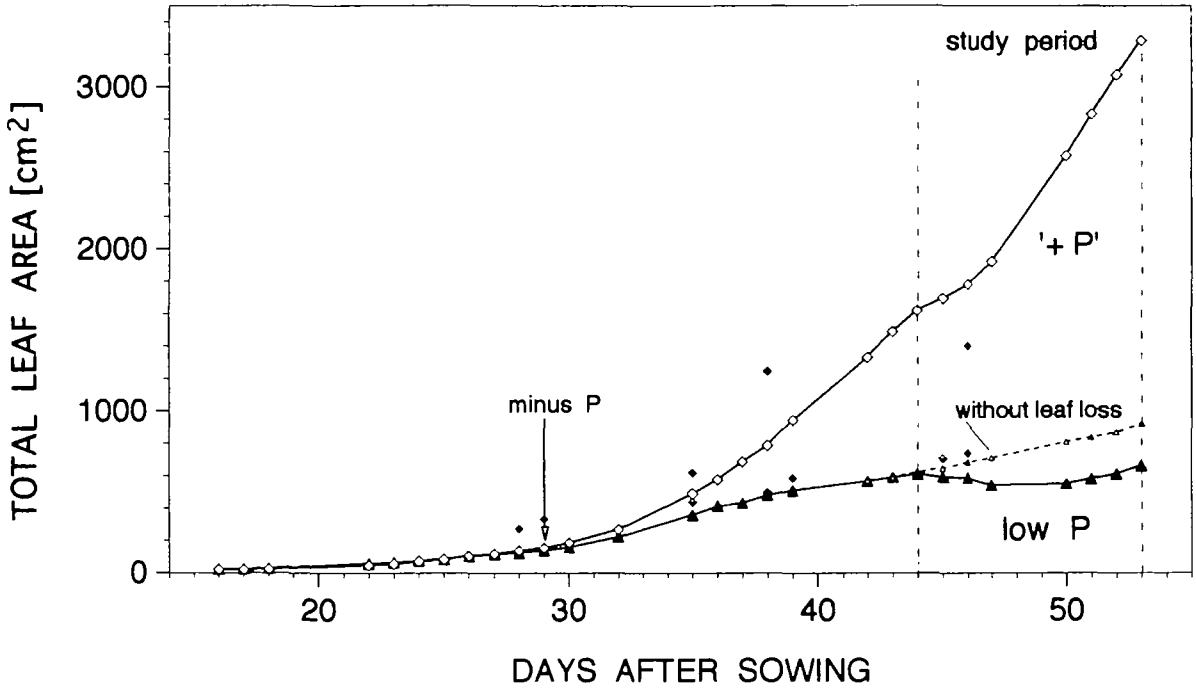

Fig. 2. Development of total leaf area in the plants of castor bean (*Ricinus communis*). Treatment of control and low-P plants as described in the legend to Fig.1. (◆) Leaf area in plants treated with 128 μm NaCl, (◇) leaf area in the corresponding controls.

concentrations (Table 1), the lowest ones being found in root tissues.

Effect of P deficiency on the partitioning of carbon and nitrogen among plant parts

Total plant C increased by 560 mmol in control and by 113 mmol in low-P plants over the 9 d study period. Increases in N were 47 mmol in control and only 6.9 mmol in low-P plants. These increments corresponded in the controls to a doubling of the initial values in parallel with leaf area development (Fig. 2), but to only 44% or 37% increases in C or N in low-P plants. The low N (NO_3^-) uptake was also reflected in an acidification of the low-P rooting medium as opposed to an alkalinization in the controls.

Figures 3 and 4, A and C, compare the distribution of C and N between plant parts at the first harvest with that of the increments in C and N (Figs 3B, D, 4B, D), thereby indicating absolute sink sizes for C and N and, by comparison, proportional changes relative to respective initial contents. Absolute increments were particularly high in the massively expanding leaf 6 (Fig. 1), while the exponentially growing leaf 7 showed the highest relative gains in C and N. Increments decreased strongly with higher leaf age and older leaves, particularly leaf 3, showed some net mobilization of N and C (Figs 3, 4).

Low P supply led to substantial decreases in the initial contents of C and N and to severely lowered increments, particularly in N (note the increased scale in Figs 3D, 4D). Moreover, the largest increments were shifted from leaf 6 (control) to leaf 5 (low-P), since leaf development was retarded. Net mobilization of N from older leaves was smaller than in the controls in absolute terms. However, there were substantial losses in C and N owing to leaf abscission, losses which almost matched the gains recorded for younger leaves (Figs 3D, 4D).

The low increments in N occurring in low-P plants (Fig. 4D) resulted from decreased dry matter production compounded with low N concentrations in plant tissues (Fig. 5). As in controls, N concentrations in low-P plants decreased with organ age, but in general at a lower level. For example, laminae of low-P plants contained, on average, 72% and 54% of the control plant N levels at the first and second harvests, respectively.

Effect of P deficiency on the carbon and water balance of Ricinus

The balances of C exchanges during the experimental period are given in Table 2, which also includes for comparison previously published data for identically aged salt-affected *Ricinus* (see Jeschke and Pate, 1991). Total photosynthesis amounted to 790 (control), 190 (low-P) and 270 mmol C (salt-treated), highlighting the unusually severe effect of low-P as opposed to salt stress on C accumulation. In control plants 71% of the photosynthates served for plant DM gain, about 14% for root respiration and the remaining 15% for shoot night respiration. In low-P plants the data were 60% for DM gain,

Table 1. *Effect of P deficiency of plant growth and P concentrations in tissues at the end of the study period (53 DAS and 24 d after P withdrawal)*[a]

	Control					Low-P plants				
	Lamina	Petioles	Stem	Root	Whole plant	Lamina	Petioles	Stem	Root	Whole plant
Dry weight [g plant^{-1}]	14.1 ± 0.9	3.6 ± 0.3	6.2 ± 0.5	9.2 ± 0.7	33.0 ± 2.3	3.3 ± 0.25	0.64 ± 0.06	1.56 ± 0.15	4.7 ± 0.3	10.3 ± 0.6
Shoot : root DW ratio					2.63					1.54
Leaf area [dm^2]					3.5					6.8
Specific leaf area [cm^2 g^{-1}]					2.4					2.1
Total P [mmol plant^{-1}]	1.8 ± 0.1	0.28 ± 0.03	0.73 ± 0.08	0.65 ± 0.05	3.4	0.15 ± 0.01	0.021 ± 0.002	0.051 ± 0.003	0.12 ± 0.003	0.34
% of whole plant P	51%	8%	21%	19%		44%	6.1%	14.8%	35%	
P concentration[b] [mg P g^{-1} DW]	3.7	2.6	3.6	2.7		1.6	1.4	1.1	0.9	

[a] DW, dry weight.
[b] Standard errors are not given because concentrations change along the stem axis. Standard errors for individual organs were on average 8%.

28% for root and 12% for shoot respiration. Particularly large differences between the three sets of plants were seen in the root DM gain, to which 20% of total C was allocated in controls, 27% in low-P plants, but only 10% in salt-treated ones.

The corresponding balance sheets for water (Table 3) showed a predominance of transpirational losses, amounting to 96–97% of the water intake for all three conditions, which decreased in absolute terms strongly from 324 mol H_2O per plant and 9 d in controls to 59 in low-P or 60 in salt-treated plants. When related to the mean leaf area, the water loss corresponded to 2.4 g $H_2O\,cm^{-2}\,d^{-1}$ in controls versus 1.7 and 1.6 (same units) in low-P and salt-treated plants, respectively. Partial stomatal closure and hence reduced overall water loss per unit leaf area in these latter two treatments was confirmed by porometer measurements (data not shown).

Quantities of water deposited in tissues or involved in net photosynthesis played only a minor role in the water balance of all three treatments (Table 3).

Molar C : N ratios of phloem and xylem sap

C : N ratios in phloem sap collected from petioles or the stem are given in Table 4. Both in control and in low-P plants the ratios varied longitudinally along the stem axis in a similar way as shown earlier (Jeschke and Pate, 1991) and the mean ratios of controls were very similar to values of salt-treated *Ricinus* (Table 4). Low-P conditions, however, led to markedly higher C : N ratios, a feature related to noticeably lower concentrations of amino acids (70% of the control), particularly of Gln (55%), the principal amino acid in the phloem sap, compounded with 36% higher concentration of sucrose.

C : N ratios in xylem sap and in root pressure xylem exudates were decreased rather than increased by low-P conditions (Table 4). As noted for phloem sap, levels of amino acids and particularly Gln were much lower than in the controls. However, in xylem sap C : N ratios are principally determined by the balance of NO_3^- to Gln and in low-P plants this balance was shifted towards NO_3^-, even though the absolute NO_3^- concentration was lower than in the control. C : N ratios of xylem sap collected from the midribs of different leaves varied only slightly up the shoot, as has been shown similarly for salt-treated *Ricinus* (Jeschke and Pate, 1991). Interestingly, these data for salt-treated plants showed higher C : N ratios compared with controls (Table 4).

Models of uptake, flow and utilization of carbon and nitrogen

Using the increments of C and N, net photosynthesis and night respiration in shoot organs, day and night respiration of the root, and the molar ratios of C : N in xylem and phloem the flows of these basic nutrients in xylem

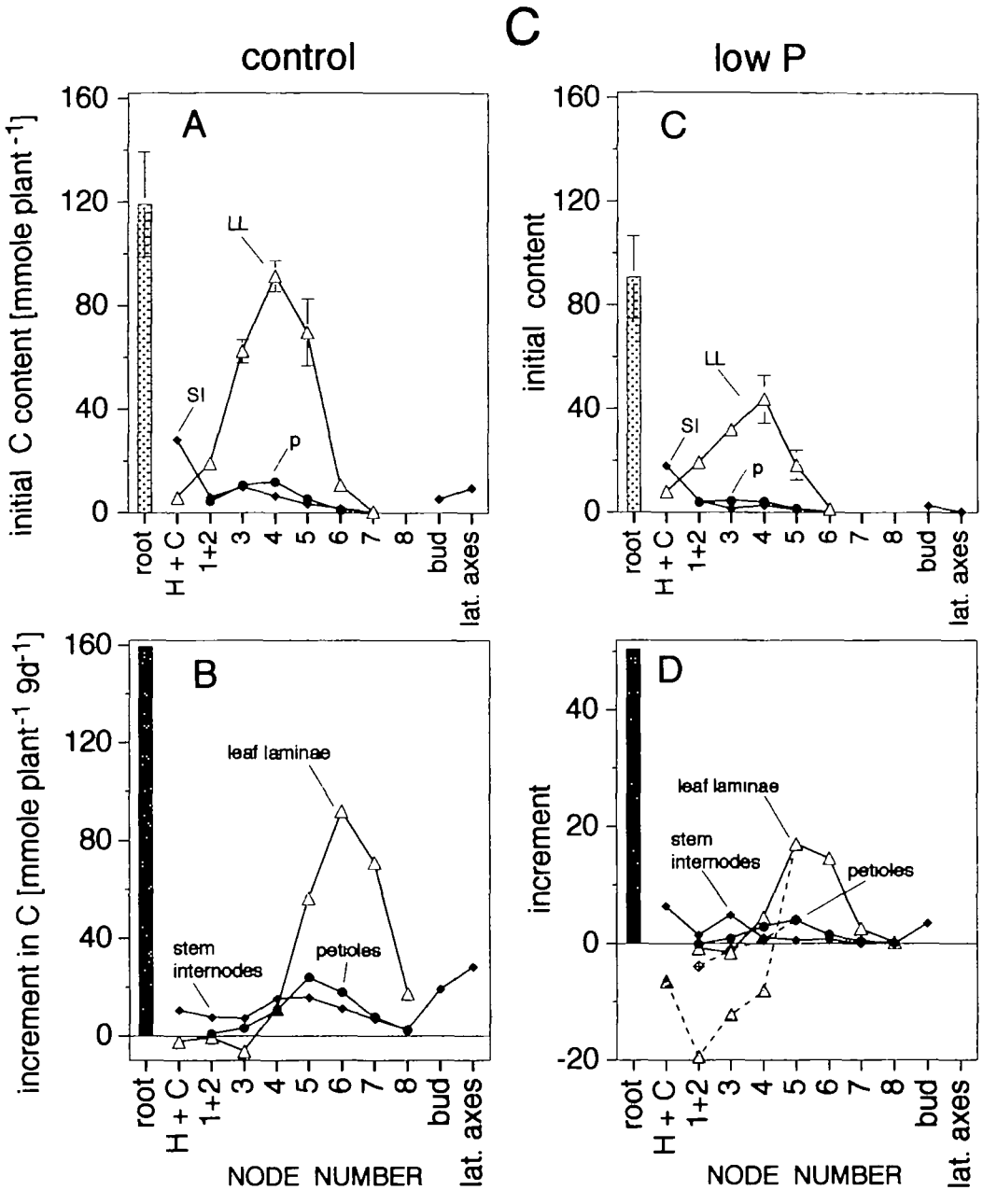

Fig. 3. Initial carbon contents at 44 DAS (top) and carbon increments or losses (bottom) during the period 44–53 DAS in root (▦, □), leaf laminae (△), petioles (●) and stem segments (◆) of sand-cultured *Ricinus communis*, grown in the presence of 0.5 mM $H_2PO_4^-$ (A, B) or under conditions of P deficiency (C, D), (see legend to Fig.1). Losses due to abscision of laminae (—▲—) or petioles (—◆—) were also depicted in graph D. H+C=hypocotyl and cotyledons.

and phloem have been calculated. The resulting models, involving flows between each individual stem internode, the petioles and laminae, and detailed as depicted in Jeschke and Pate (1991) were used to bulk and combine the data of all developmentally-related organs. These were the laminae of (a) the young and exponentially growing leaves 7 and 8 in the controls or 6 and 7 in low-P plants (cf. Fig. 1), (b) the maturing or already mature but still expanding leaves 4 to 6 (controls) or 4 and 5 (low-P), and (c) the older leaves. Additionally, stem internodes and petioles have been combined, the resulting models being as depicted in Figs 6–9. The numbers on arrows depicting flows, on squares depicting deposition of C and N and on circles designating respiration are expressed in terms of ‰ relative to total net photosynthesis or total N uptake. In this way the allocation of C and N to various organs is directly comparable. The width of arrows depicting the absolute rates of net flows through xylem and phloem (Figs 6–9) are drawn to the same scale for the two treatments and are, therefore,

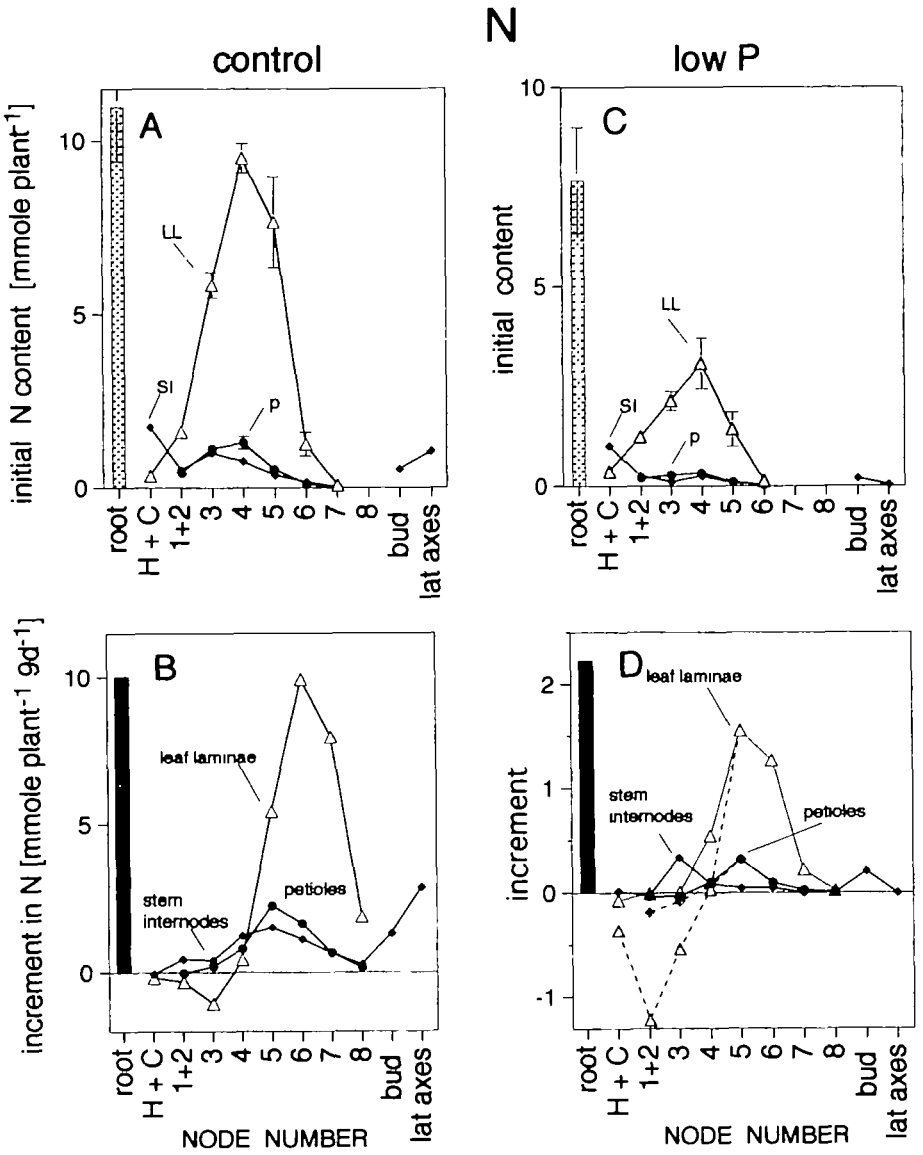

Fig. 4. Initial nitrogen contents at 44 DAS (top) and nitrogen increments or losses (bottom) during the period 44–53 DAS in root (▣, □), leaf laminae (△), petioles (●) and stem segments (◆) of sand-cultured *Ricinus communis*, grown in the presence of 0.5 mM $H_2PO_4^-$ (A, B) or under conditions of P deficiency (C, D), (see legend to Fig.1). Losses due to abscision of laminae (—▲—) or petioles (—◆—) were also depicted in D. H + C = hypocotyl and cotyledons.

directly comparable. In the case of low-P plants the abscised leaves have not been included in the calculations, but the quantities of N lost in these leaves are indicated in Fig. 9.

The flow schemes of carbon in Figs 6 and 7 highlight the dramatic inhibition of net photosynthesis and assimilate flows by P deficiency. Although outwardly similar to that of control plants assimilate flows under low-P conditions were typified by the following proportional shifts in allocation profiles for C:

(a) accentuated downward as opposed to upward phloem translocation from leaves, compare the C flows originating from mature internodes 4–6 in control or 4 and 5 in P starved plants,

(b) a clear increase in the relative sink size of the root under P starvation, reflecting the formation of a correspondingly larger root system,

(c) a substantial proportional increase of C utilization for root respiration compared to control plants,

(d) a particularly strong proportional decrease in xylem cycling of C to the shoot.

The situation regarding nitrogen partitioning (Figs 8,

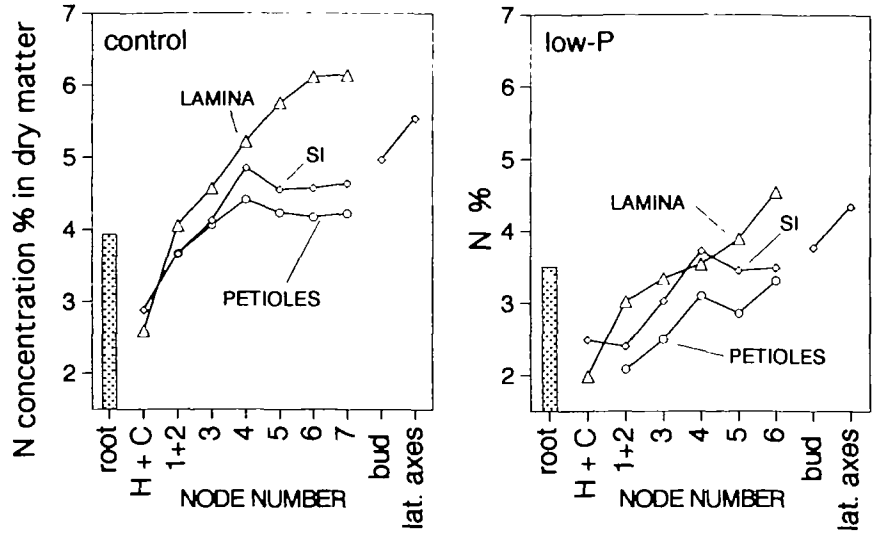

Fig. 5. Concentrations of nitrogen (% by weight in dry matter) of root and shoot organs of sand cultured castor bean (*Ricinus communis*) at the initial harvest, i.e. at 44 DAS Plants were cultivated in the presence of 0.5 mM phosphate (left) or under conditions of P deficiency (right). SI = stem segments.

9) showed particularly strong depression of its translocation in low-P plants. However, all basic elements of the flows were still present, including the occurrence of both xylem-to-phloem transfer (+ in Figs 8, 9) and of xylem-to-xylem transfer (✱ in Figs 8, 9). The extent and direction of transfer between xylem and phloem followed directly from the calculations of flows (Jeschke and Pate, 1991). The occurrence and the size of xylem-to-xylem

Table 2. *Net carbon balance of castor bean* (Ricinus communis) *over the period 44–53 DAS when raised in quartz sand culture with sufficient (control) or deficient P supply (low-P) or exposed to a mean effective salinity of 128 mM NaCl in the rooting medium (salt-treated)*

		Control (mmol C $plant^{-1}$ $(9d)^{-1}$)	Low-P	Salt-treated[a]
(1) Net carbon increments	(a) Leaf laminae	240±30	35±8	67
	(b) Petioles	67±11	10±2	9
	(c) Stem+apex	97±16	18±4	31
	(d) Root	160±30	51±9	28
(2) Respiratory losses (night)	(a) Leaf laminae	79±13	15±2	31
	(b) Petioles	14±2	2.4±0.4	3.2
	(c) Stem+apex	23±3	4.9±1.0	11
(3) Root respiration (day and night)		111±11	54±7	88
(4) Net photosynthesis in shoot (sum of items 1–3)		790±50	190±15	270

[a]Data from Jeschke and Pate (1991).

Table 3. *Net water balance of castor bean* (Ricinus communis) *over the period 44–53 DAS when raised in quartz sand culture with sufficient (control) or deficient P supply (low-P) or exposed to a mean effective salinity of 128 mM NaCl in the rooting medium (salt-treated)*

		Control (mol H_2O $plant^{-1}$ $(9d)^{-1}$	Low-P	Salt-treated[a]
(1) Net increments in tissue water	(a) Leaf laminae	1.8±0.2	0.25±0.08	0.27
	(b) Petioles	1.7±0.3	0.14±0.04	0.16
	(c) Stem+apex	2.1±0.3	0.16±0.03	0.35
	(d) Root	4.0±0.7	1.7±0.3	0.65
(2) Water used in photosynthesis	Leaf laminae	0.8±0.1	0.19±0.01	0.27
(3) Transpiration losses	(a) leaf laminae	307±13	54.2±0.9	56
	(b) Petioles	4.7±0.27	0.8±0.1	1.1
	(c) Stem+apex	2.6±0.1	1.6±0.1	1.0
(4) Uptake from rooting medium (items 1, 2, 3)		324±20	59±4	60

[a]Data from Jeschke and Pate (1991).

Table 4. *Molar ratios of carbon : nitrogen in solutes of phloem and xylem sap of castor bean* (Ricinus communis) *raised in quartz sand culture with sufficient (control) or deficient P supply (low-P) or exposed to a mean effective salinity of 128 mM NaCl in the rooting medium (salt-treated)*

Transport fluids were collected during the study period 44–53 d. Phloem sap was collected from shallow incisions into petioles or stem internodes.

	Control C:N ratio [mol mol^{-1}]	Low-P	Salt-treated[a]
Phloem sap collected from petioles	36.0±9	49.6±8.9	36
Phloem sap collected from stem internodes	27.5±1.9	47.8±2.7	31
Xylem sap collected from midrib of leaves[b]	0.8±0.15	0.71±0.03	1.5
Root pressure xylem exudates[c]	0.98± 0.07	0.68±0.19	Not collected

[a]Data from Jeschke and Pate (1991)

[b]Xylem sap was collected by pressure application, applied pressures were 0.25–0.45 MPa (control), 0.25–0.4 MPa (low-P) and 0.78–0.91 MPa (salt-treated).

[c]Root pressure exudates were collected from hypocotyl stumps. Flow rates were in μl min^{-1}: control: 86–55 (1. harvest) and 155–103 (2. harvest), both descending with time; low-P: 3.8–8.5 (1. harvest) and 3.4–8.4 (2. harvest), both ascending.

transfer, on the other hand, were derived from comparisons of the xylem flows of N with those of H_2O (Figs 10, 11; cf. Jeschke and Pate, 1991). These analyses revealed much lower N concentrations in the xylem streams serving leaves than in the flows leading further up the stem. As suggested earlier by Pate and Layzell (1981) this differential behaviour results from a progressive abstraction of N from the xylem of leaf traces and a subsequent discharge of this N into cauline traces serving upper regions of the stem. Using the concentration difference and the volumes of water flowing in the xylem the quantities of N transferred from xylem-to-xylem (✱ in Figs 8, 9) have been calculated. The transfer was somewhat smaller also in relative terms in low-P than control plants (Figs 8, 9).

Apart from the generally lower translocation in P-starved than control plants there were also shifts in the allocation of N, i.e.

(a) a substantial increase was observed in the predominance of downward relative to upward phloem translocation in mature stem parts under low-P conditions, see the numbers on the arrows.

(b) retranslocation from shoot to root in low-P plants involved a higher proportion of N (Fig. 9) amounting to one-third of that of xylem transport, compared with only one-fifth in controls.

(c) the roots in low-P plants acquired a 1.5-fold higher relative allocation of nitrogen than in the controls.

It should be noted that considerable quantities of N, amounting to 40% of the uptake during the study period, were lost in abscised leaves (Fig. 9). This nitrogen was not, however, included in the flow calculations.

Models of the flows and utilization of water

As in earlier experiments (Layzell *et al.*, 1981; Jeschke and Pate, 1991) flows of water via xylem have been estimated from the quantities transpired, from those deposited in tissues during growth or used for photosynthesis in each organ and from the amounts retranslocated via phloem. These were obtained from the phloem flows of carbon and its concentration in the phloem sap at each translocation site. In the resulting models the thickness of arrows depicting rates of flow are directly comparable for control and low-P plants (Figs 10, 11); the water budget items have been expressed in terms of an uptake of 1000 molar units of water in order to enable comparisons of allocation and utilization of H_2O with that of C and N and between the treatments.

The models (Figs 10, 11) highlight the severe reduction in water uptake, in flows and in transpiration which occur in low-P plants. Interestingly, a higher proportional transpiration was seen in the two mature or maturing leaves 4+5 of low-P (76%) than in the three leaves 4–6 of control plants (70%). Root growth consumed a larger share of water in the P-deficient plants.

Discussion

The severe P-deficiency of low-P *Ricinus* plants is well indicated by tissue P levels of leaves (Table 1) which were far below those needed for adequate growth (2–5 mg g^{-1} DM or 0.2–0.5% of DM are average values from Bergmann, 1988). Nevertheless, some PO_4 uptake did occur during the study period, as indicated by a lowering of the external PO_4 concentration within a day from 5 to a mean of 1.1 μM. Since C_{min} for PO_4 is much lower (0.12 μM for tomatoes, Itoh and Barber, 1983), actual PO_4 concentrations within the rhizosphere may have been lowered to an even greater extent.

In agreement with Fredeen *et al.* (1989) and Lynch *et al.* (1991) low-P conditions severely reduced the area of leaves and retarded further leaf production (Fig. 1). As shown for P deficiency in other species, soybean (Fredeen *et al.*, 1989), maize (Khamis *et al.*, 1990) and

Table 5. *Comparisons of present data on proportional investments of absorbed C, N and H_2O in control and low-P castor bean* (Ricinus communis *L.*) *with data obtained under conditions of moderate salt stress*

The data are given as parts per thousand (‰) of total daytime net photosynthetic gain of C, total uptake of N (as nitrate), or absorption of water from the rooting medium.

		Control[a] (‰)	Low-P[b] (‰)	Salt-treated[c] (‰)
(A) Carbon				
(i)	Shoot carbon increment	510	330	400
(ii)	Root carbon increment	200	270	100
(iii)	Night respiration of shoot	150	120	170
(iv)	Day and night respiration of root	140	280	330
(v)	Leaf laminae, import via xylem	30	21	60
(vi)	Leaf laminae, export in phloem	720	810	730
(vii)	Phloem transport to root	400	580	500
(viii)	Cycling through root system[d]	58	29	77
(B) Nitrogen				
(ix)	Shoot nitrogen increment	790	680	780
(x)	Root nitrogen increment	210	320	220
(xi)	Leaf laminae, intake via xylem	750	840	930
(xii)	Leaf laminae, export in phloem	290	360	400
(xiii)	Phloem transport to root	220	330	320
(xvi)	Cycling through root system[d]	115[e]	170[e]	150[e]
(C) Water				
(xv)	Tissue water increment of shoot	17	9.3	13
(xvi)	Tissue water increment of root	12	29	11
(xvii)	Transpiration of leaf laminae	940	920	940
(xviii)	Transpiration of stem + petioles	22.6	26	35
(xix)	Water involved in phloem transport of leaf laminae	20	25	22

[a]Data derived from Figs 6, 8 and 10 for control plants of castor bean, study period 44–53 d.
[b]Data derived from Figs 7, 9 and 11 for low-P plants of castor bean, study period 44–53 d.
[c]Plants fed 12 mol m^{-3} NO_3 as nitrogen source and grown in moderate salinity (mean root medium concentration 128 mol m^{-3} NaCl), study period 44–53 d after sowing, data from Jeschke and Pate (1991).
[d]Defined as C or N initially translocated to the root in phloem and then returning back to the shoot via xylem.
[e]Takes into account NO_3-N absorbed directly by the root from the rooting medium (see Figs 8, 9)

bean (Cakmak *et al.*, 1994*a*), root growth was relatively favoured and the shoot-to-root ratio accordingly decreased (Table 1). This is borne out by the finding that 51% of the C accumulated during the study period was allocated to the root, compared with only 28% in the controls (Table 2). Favoured root growth clearly did not result from an easier access of the root to soil P, as suggested for soybean by Fredeen *et al.* (1989) since in *Ricinus* root P concentrations were lower than in the shoot (Table 1) and not higher as found in soybean. The shoot-to-root ratio was less decresed in response to P deficiency (to 1.5) than to N deficiency (to 1.1: Peuke *et al.*, 1994).

Since any differences in growth rates and in developmental patterns are likely to result from the specific partitioning and flow rates of assimilates and nutrients, the flows of C and N and their partitioning patterns in low-P and control plants would be expected to closely prescribe and hence reflect the effects of P-deprivation on growth. This is indeed seen in (a) a general severe restriction of the rates of net flows and (b) in quantitative, but not qualitative, shifts in the directions of flows and in the allocation of C and N (Figs 6–9). The changes in flows resulting from P deficiency can be compared with those induced by salinity, since in a previous study of salt-stressed *Ricinus* plants (Jeschke and Pate, 1991) measurements were carried out on plants of identical age (44–53 DAS) to those used here and the controls of the salt-treated plants showed very similar leaf area development as the present controls (see Fig. 2). This comparison is particularly interesting since salinity × PO_4 interactions have been observed in several species (e.g. cotton, Martinez and Läuchli, 1991, 1994) and since salt-affected soils are often also extremely low in P.

The ratio of molar inputs of N : C : H_2O were 1 : 17 : 6940 for controls, 1 : 27 : 8500 for low-P and 1 : 22 : 4803 for salt-stress conditions. The relatively high N : C utilization of 1 : 17 in control *Ricinus* plants, much higher than in white lupin (1 : 36, Layzell *et al.*, 1981), may reflect the relatively luxuriant N nutrition expected of plants fed 12 mM NO_3^-. The ratio was decreased under salt stress (to 1 : 22) and to an even greater extent after P-deprivation (to 1 : 27), since here NO_3^- uptake was inhibited, as shown for barley (Lee, 1982) and tomato (Heuwinkel *et al.*, 1992; Pilbeam *et al.*, 1993). The molar ratios of C : H_2O, given above, essentially denote overall water use efficiencies of the plants, i.e. 2.4, 3.2 and 4.6 mmol C mol^{-1} H_2O for control, low-P and salt-stress conditions. The apparent increase in water use efficiency of low-P plants was evident at leaf level as reduced transpiration per unit

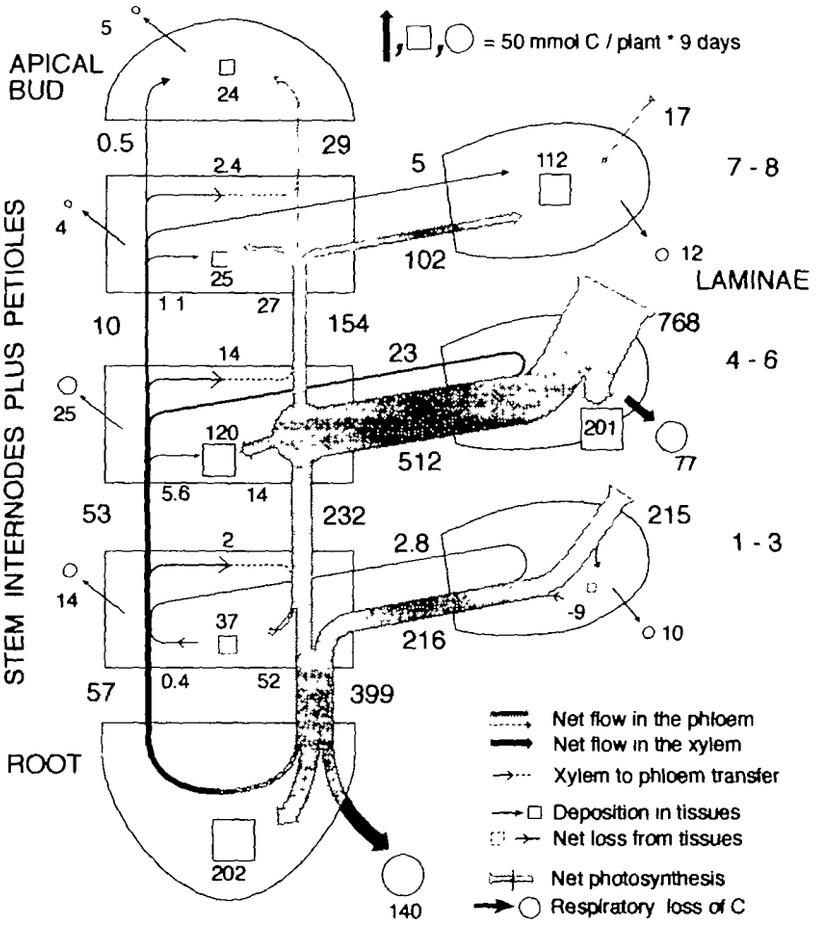

Fig. 6. Flow profiles for uptake, transport and utilization of carbon in control plants of *Ricinus communis* L. over the period 44–53 DAS. The plants were fed with 0.5 mM $H_2PO_4^-$. The width of arrows and the area of squares (incorporation) and circles (respiration) are drawn in proportion to *absolute* rates of net flow of C, of deposition of C into dry matter and loss of C in respiration (see the scale at the top). The *numbers* indicate *relative* flows and the relative partitioning of C and are expressed as ‰ in relation to total net photosynthesis (791 mmol plant^{-1}(9d)$^{-1}$). The numbers under the squares of each stem segment denote uptake from the phloem (right) or the xylem (left). For the sake of clarity flows into the two exponentially growing leaves (7 and 8), into or out of the maturing or mature, but still expanding leaves (4–6), and in the oldest leaves (1–3) and the subtending stem segments plus petioles have been combined.

leaf area (Radin, 1984). Transpiration was also seen to decrease in salt-stressed plants, but was compensated by higher photosynthetic rates. This latter effect was presumably due to the higher light intensities at Perth, Western Australia, where the salt-stressed plants were grown, in comparison with Würzburg, Germany.

Table 5 summarizes the budget items extracted from the flow schemes of Figs 6–11 and for comparison the corresponding data obtained with salt-treated plants. Turning first to the utilization of carbon, the prominent changes under low-P conditions were an increased investment of C for root growth and respiration (items ii and iv), although in terms of fresh weight root respiration was inhibited to 76% of controls as in bean (Rychter and Mikulka, 1990). The evidently increased sink size of the root may, in part, be related to higher starch accumulation (Cakmak *et al.*, 1994*a*). Together with a substantially lowered C utilization in the shoot (item i), the high root sink activity of low-P plants led to increased export from the laminae (item vi) and substantially higher assimilate transport to the root (item vii). This agrees with data of Cakmak *et al.* (1994*b*) suggesting slightly stimulated sucrose export from bean leaves, as indicated on the basis of EDTA-induced phloem exudates. Indeed, phloem sap collected from low-P *Ricinus* contained higher sucrose levels than in controls (Jeschke *et al.*, 1997). Contrasting results have been obtained by Radin and Eidenbock (1986) who estimated assimilate export from the balance of photosynthetic gains and C accumulation in the leaf, and found lowered export in P-deficient cotton. Using the same procedure Rao *et al.* (1990) found higher C export in P-deficient sugar beet, but only during the night. In our experiments net C transport integrates over day and night, but increased C:N ratios and higher sucrose

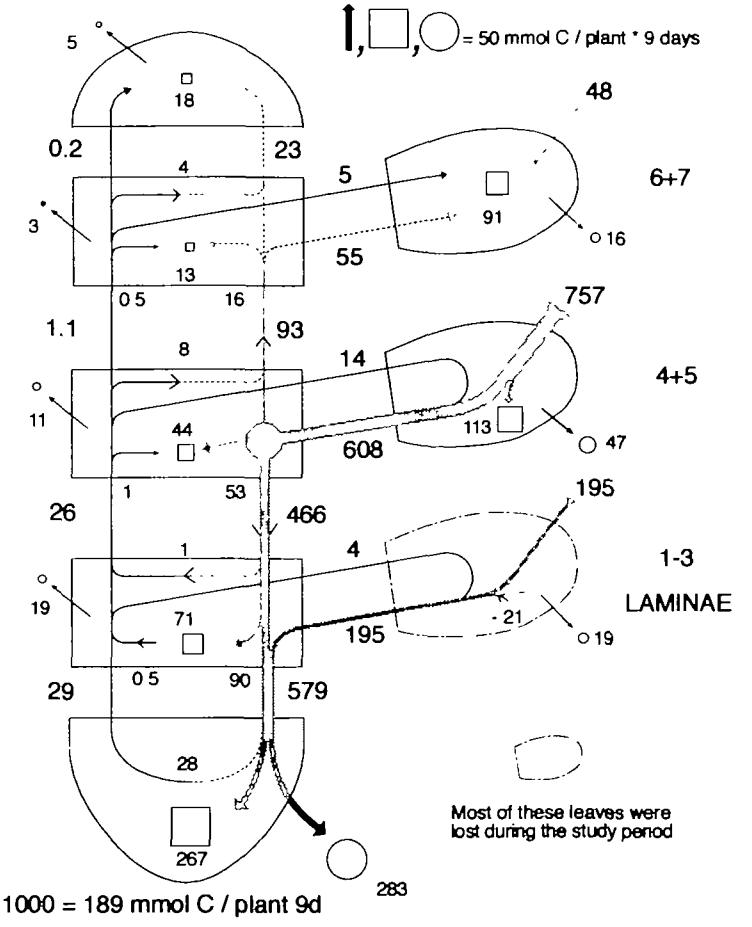

Fig. 7. Flow profiles for uptake, transport and utilisation of carbon in low-P plants of *Ricinus communis* L. over the period 44–53 DAS. Phosphate had been withdrawn at 29 DAS and 5 μM $H_2PO_4^-$ was then given at 41 DAS. As in Fig.6 the width of arrows and the area of squares (incorporation) and circles (respiration) are drawn in proportion to *absolute* rates of flow of C, of deposition of C into dry matter and loss of C in respiration (see the scale at the top). *Numbers* indicate *relative* flows or partitioning of C and are expressed as ‰ in relation to total net photosynthesis (189 mmol plant^{-1}(9d)$^{-1}$). Other details as given in the legend to Fig. 6, except the young leaves (6 and 7) and the maturing or mature leaves (4 and 5) were mathematically bulked. For the labelling of plant organs see Fig 6, the scale of arrows indicating flow rates is identical with that in Fig. 6.

levels were observed during the day and the conspicuously higher C increments of the root hardly appear to be due only to night-time increases.

The relatively increased sink size of the root, attracting 580‰ of the current photosynthate (item vii), indeed is an underestimate, since it does not allow for the increased exudation of organic acids from roots of P-deficient plants (Dinkelacker *et al.*, 1989; Hoffland *et al.*, 1992). If this were included, then C translocation from shoot to root would be even higher.

In contrast to phloem export, xylem import of C into the lamina (item v) and cycling through the root into the xylem (item viii) were substantially decreased in low-P plants, while being considerably increased under salt-stress. The basis of these changes will be considered together with the translocation of N.

The severely depressed photosynthesis of low-P plants (arrows in Figs 6, 7) resulted primarily from low leaf area (Fig. 2) and to some degree from inhibited photosynthesis. In terms of leaf area net photosynthesis was 90% and $^{14}CO_2$ incorporation on average 80% of the control. Particularly in soybean (Fredeen *et al.*, 1989; Lauer *et al.*, 1989), but also in sugar beet (Rao *et al.*, 1990) and maize (Khamis *et al.*, 1990) photosynthesis was severely inhibited at saturating light, while photosynthesis at ambient light was affected less (Rao *et al.*, 1993).

Changes in salt-stressed *Ricinus* (Table 5) appeared to be far less co-ordinated than in P-deficient plants and included the onset of substantially unrestrained root respiration. Increased respiration rate was in fact accompanied by a correspondingly lower C increment in the root of salt-treated plants (item ii), similar changes have also been observed in *Ricinus* at milder salt stress (Peuke and Jeschke, 1995).

Turning to the flows and allocation of nitrogen, low-P conditions substantially restricted the allocation to and

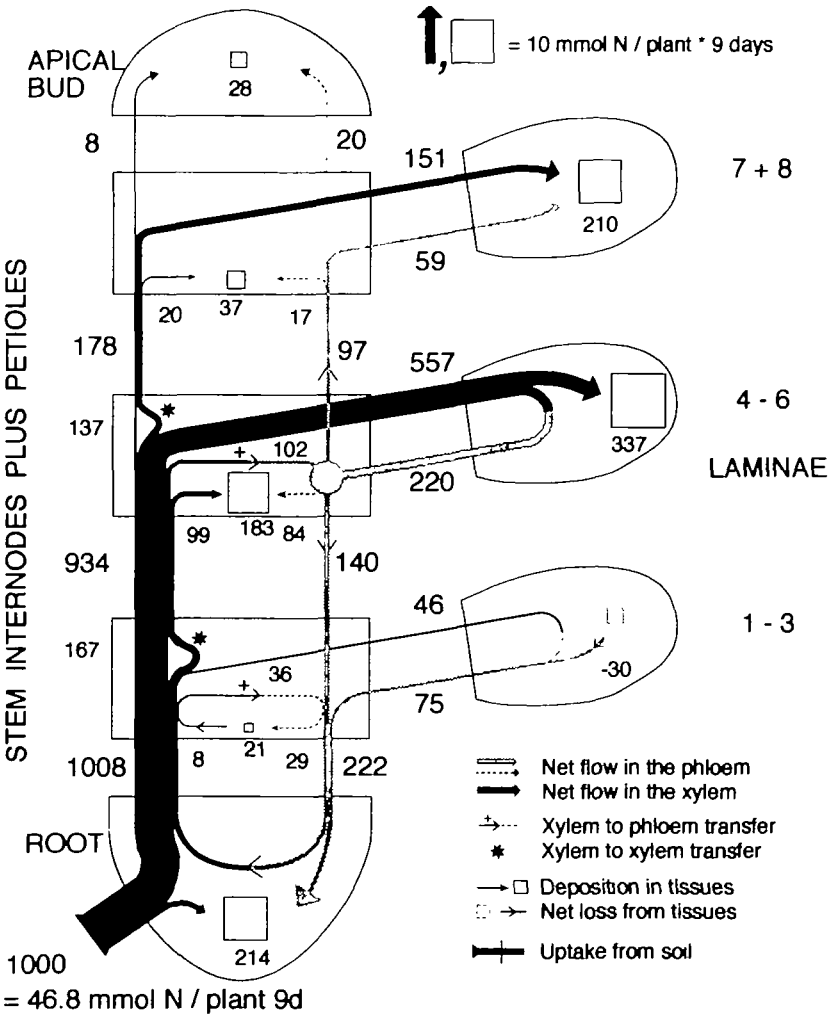

Fig. 8. Flow profiles of uptake, transport and utilization of nitrogen in control plants of *Ricinus communis* L, fed 0.5 mM $H_2PO_4^-$ and 12 mM NO_3^-. Details as in Fig. 6 and as there the width of arrows and the area of squares (N incorporation) are drawn in proportion to *absolute* rates of flow of N and of the deposition of N into dry matter (see the scale at the top). The *numbers* indicate *relative* flows and partitioning of N and are expressed as ‰ in relation to total nitrate uptake (46.8 mmol N plant^{-1}(9d)$^{-1}$) from the rooting medium.

accumulation of N in the shoot (item ix), with an attendant marked enhancement of the sink size of the root for N (item x). In molar terms, however, low-P conditions restricted the allocation of N to the root more than that of C, as depicted by the width of arrows in Figs 6–9. Expressed in mmol N per plant over the 9 d period the flows of N via phloem to the root were 10.4 (control) and 2.4 (low-P = 23%) and those of C were 315 (control) and 109 (low-P = 34%). Depression of N flows may be caused essentially by the well-documented inhibition of NO_3^- uptake typical of P deficiency (Lee, 1982; Heuwinkel *et al.*, 1992; Pilbeam *et al.*, 1993). This interpretation is in accord with the strongly decreased N increments (Fig. 4) and tissue concentrations (Fig. 5). However, Cl^- is also known to depress NO_3^- uptake (Wehrmann and Hähndel, 1984) and its presence in P-deficient, but not control, nutrient solutions partly may have contributed to the observed depression of NO_3^- uptake.

At first sight the findings of increased N import into the lamina (item xi) and concomitantly decreased xylem import of C (item v) might appear contradictory, because almost all of the C translocated via the xylem is in the form of amino acids. The apparent discrepancy may be accounted for, however, when considering the nature of N compounds in the xylem. As will be shown in a subsequent paper (Jeschke *et al.*, 1997), the xylem sap of P-deficient plants carried considerably more NO_3^- than amino acids. The disproportionate changes in N and C translocation in the xylem were, therefore, due to strongly decreased amino acid and relatively increased NO_3^- levels in the xylem sap and are indicative of an inhibited nitrate assimilation in roots of P-deficient *Ricinus*.

Enhanced N mobilization from senescing leaves was somewhat surprisingly not encountered in P-deficient plants (Figs 8, 9), despite the P-deprivation leading to massive premature senescence and shedding of leaves (Fig. 1). Leaf

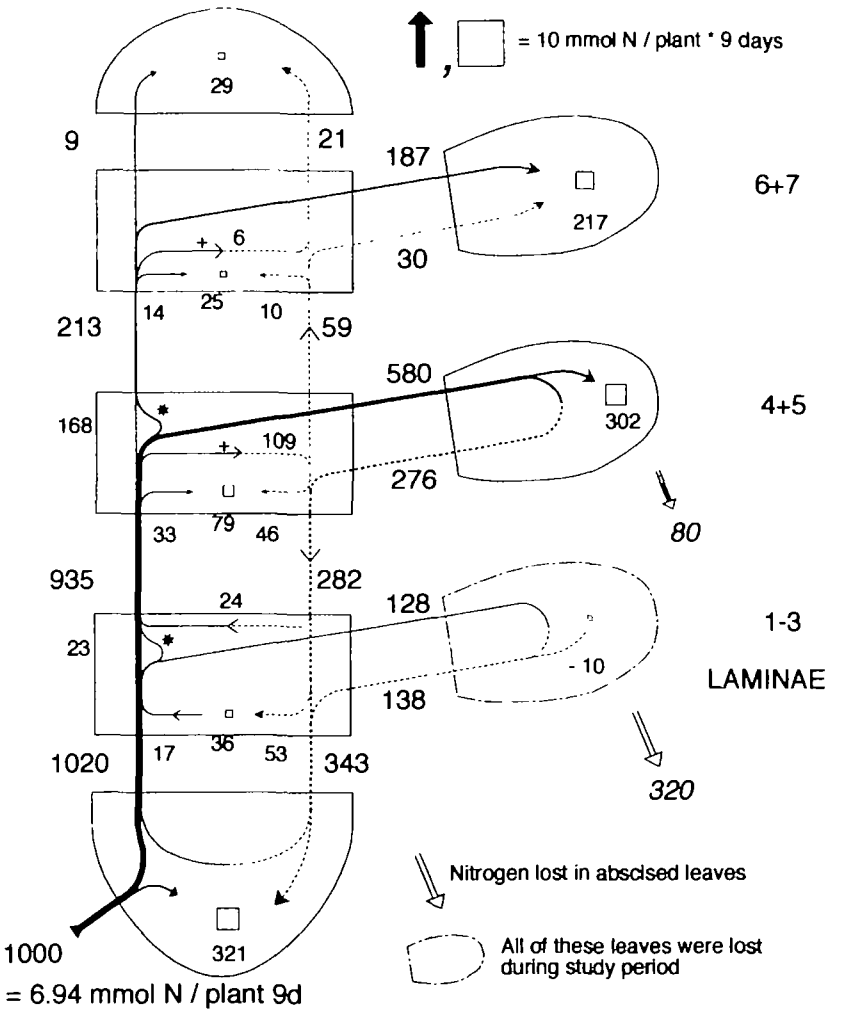

Fig. 9. Flow profiles of uptake, transport and utilization of nitrogen in low-P plants of *Ricinus communis* L., P-deficient since 29 DAS but fed with 12 mM NO_3^-. Details as in Fig. 6, except the young leaves (6 and 7) and the maturing or mature leaves (4 and 5) have been bulked mathematically. Widths of arrows (flow rates) and areas of squares (N incorporation) are drawn in proportion to *absolute* rates of flow of N and of the deposition of N into dry matter (the scale is the same as in Fig. 8). The *numbers* indicate *relative* flows and *relative* rates of deposition of N and are expressed as ‰ in relation to total nitrate uptake (6.94 mmol N $plant^{-1}$ $(9d)^{-1}$) from the rooting medium. For the labelling of plant organs see Fig. 8.

senescence in these plants did not, however, proceed in the normal manner with progressive yellowing and apparent chlorophyll degradation, but was associated with patches of grey to brown intercostal necroses. In soybean low-P treatments have also been found not to enhance N mobilization from leaves (Crafts-Brandner, 1992).

Turning to the flows of water, hardly any differences were found between control and salt-affected plants, although water uptake and transpiration were strongly inhibited in the latter (Table 5). In low-P plants, however, a clearly higher proportion of water was incorporated into the root and a slightly lower proportion was lost by transpiration (Table 5). Total transpiration was similarly decreased in low-P and salt-stressed *Ricinus* (Table 3).

Even though P deficiency severely affected rates of flows and greatly perturbed sink sizes for C and N, it did not alter the element-specific properties of flows. In particular, two transfer processes, which are of high importance for the partitioning of N, i.e. xylem to phloem (+ in Figs 8, 9) and xylem-to-xylem transfer (✱ in Figs 8, 9) proceeded unabated in proportional terms in P-deprived *Ricinus*. These transfer processes, first described in *Lupinus albus* (Layzell *et al.*, 1981) and similarly present in *Ricinus* (Jeschke and Pate, 1991) are highly significant for improving the N supply to young organs. As has been discussed recently (Pate and Jeschke, 1995), xylem-to-phloem transfer supplements the N nutrition of phloem-importing organs, as for example the apical bud (Fig. 8, 9), in its high demand for reduced N. Both in control and low-P plants a large proportion of the N translocated upwardly via the phloem from nodes 4–6 or 4+5 and further into the terminal bud originated from a massive xylem to phloem transfer in these stem parts.

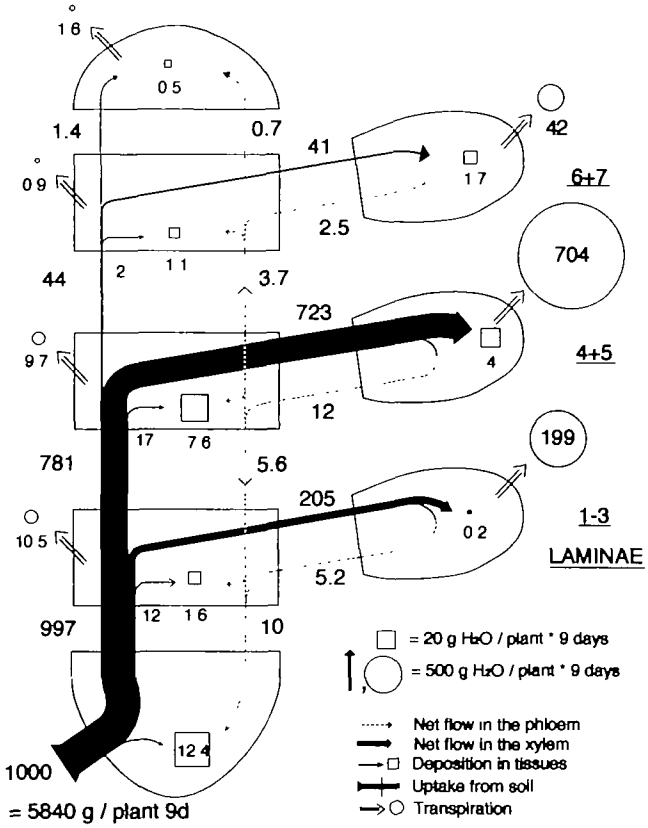

Fig. 10. Flow profiles of uptake, transport, utilization and transpirational loss of H_2O in P-sufficient control plants of *Ricinus communis* L. Details as in the legend to Fig. 6 and as there the width of arrows and the area of squares (H_2O incorporation) and circles (transpiration) are drawn in proportion to *absolute* rates of flow and of water use or transpiration (see the scale at the bottom). The numbers indicate *relative* flows and rates of utilization and are expressed in terms of ‰ in relation to total H_2O uptake (324 mol (5840 g) H_2O $plant^{-1}(9d)^{-1}$) from the rooting medium For the labelling of plant organs see Fig. 8.

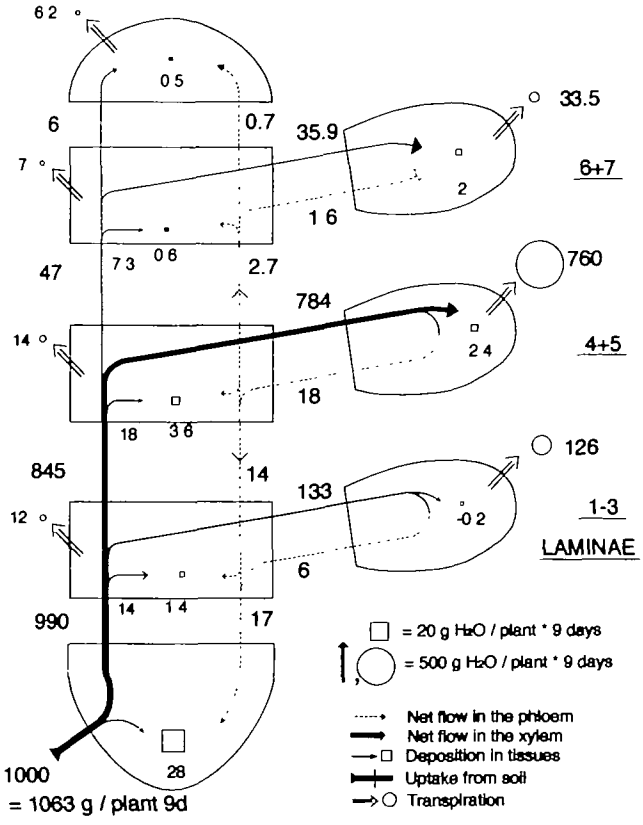

Fig. 11. Flow profiles of uptake, transport, utilization and transpirational loss of H_2O in low-P plants of *Ricinus communis* L., P-deficient since 29 DAS. Details as in the legend to Fig. 6, except the young leaves (6 and 7) and the maturing or mature leaves (4 and 5) have been bulked mathematically. For the width of arrows see legend to Fig. 10, the scale is identical with that in Fig. 10. The numbers indicate *relative* flows and rates of utilization of H_2O and are expressed in terms of ‰ in relation to total H_2O uptake (59 mol (1063 g) H_2O $plant^{-1}(9d)^{-1}$) from the rooting medium. For the labelling of plant organs see Fig. 8.

By contrast to the weakly transpiring, enclosed apical bud, young leaves of *Ricinus* transpire substantially whilst importing from both phloem and xylem before the transition to phloem export occurs when they reach about 2/3 of their final leaf area (Jeschke and Pate, 1992). Leaves 6 and 7 (low-P) and 7 and 8 (control) were in this juvenile condition (cf. Fig. 1). However, owing to their as yet small leaf area (Fig. 1) these leaves contributed together only 3.4–4.2% to the total transpiration (Figs 10, 11). Nevertheless, most of their proportionately high N demand (21–22% of total NO_3^- uptake) originated from xylem import (72% of the import in control and 86% in low-P plants). Considering this high N import alongside low transpiration, it follows that the xylem sap entering these leaves must have been 3.6 or 5-fold more concentrated in N than at the stem base in control or P-deficient plants. Increases in the xylem sap N concentration of this magnitude along the stem axis have been directly measured in *Ricinus* (Jeschke and Pate, 1991). It can be seen that most of the N reaching the upper leaves had been transferred from xylem traces serving the leaf to vessels running further up the stem (✱ in Figs 8, 9). The single loops of xylem-to-xylem transfer depicted in the nodes 4–6 (Fig. 8 ✱) or 4+5 (Fig. 9 ✱) in fact consist of 3 or 2 loops at the site of each node. The augmentation of nitrogenous solutes in the xylem sap by this xylem-to-xylem transfer proceeds in fact in a cascading manner up the stem axis, as can be seen from the progressive increase in nitrogen concentration in detailed models (Jeschke and Pate, 1991) and is present in control and P-deficient plants.

Conclusion

As far as we are aware, the results presented in this paper compares for the first time complete inventories of uptake, transport and utilization of C, N and H_2O between organs and within of an intact plant deprived of P at a given state of growth. Despite much lower intakes under P

deficiency the general patterns of flows and partitioning of C, N and H_2O considered in comparison with the controls (Figs 6–11) appear to be well co-ordinated, well adapted towards allowing the plants to withstand these disadvantageous, deficient conditions. This is evident, for example, in increased water use efficiency and, more specifically, by relatively greater investments of C and N in the root system. The formation of a proportionally larger root system in P-starved plants would clearly offer a means of adaptation to deficiency of this element since acquisition of PO_4 from soil solution is essentially dependent on PO_4 diffusion to the root surface over relatively short distances in which case an enlarging root surface would be especially advantageous (Föhse *et al.*, 1991). As shown in our parallel study (Jeschke and Pate, 1991) plants which are salt-stressed exhibit less evidence of adaptation of this kind, and the responses involved in such plants are less orderly and more detrimental to plant growth.

Acknowledgements

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