Correlations in concentrations, xylem and phloem flows, and partitioning of elements and ions in intact plants. A summary and statistical re-evaluation of modelling experiments in *Ricinus communis*

Andreas D. Peuke*
ADP International Plant Science Consulting, Talstrasse 8, D-79194 Gundelfingen-Wildtal, Germany
* E-mail: andreas@peuke.de

Received 11 August 2009; Revised 5 November 2009; Accepted 6 November 2009

**Abstract**

Within the last two decades, a series of papers have dealt with the effects of nutrition and nutrient deficiency, as well as salt stress, on the long-distance transport and partitioning of nutrients in castor bean. Flows in xylem and phloem were modelled according to an empirically-based modelling technique that permits additional quantification of the uptake and incorporation into plant organs. In the present paper these data were statistically re-evaluated, and new correlations are presented. Numerous relationships between different compartments and transport processes for single elements, but also between elements, were detected. These correlations revealed different selectivities for ions in bulk net transport. Generally, increasing chemical concentration gradients for mineral nutrients from the rhizosphere to the root and from the xylem to leaf tissue were observed, while such gradients decreased from root tissue to the xylem and from leaves to the phloem. These studies showed that, for the partitioning of nutrients within a plant, the correlated interactions of uptake, xylem and phloem flow, as well as loading and unloading of solutes from transport systems, are of central importance. For essential nutrients, tight correlations between uptake, xylem and phloem flow, and the resulting partitioning of elements, were observed, which allows the stating of general models. For non-essential ions like Na$^+$ or Cl$^−$, a statistically significant dependence of xylem transport on uptake was not detected. The central role of the phloem for adjusting, but also signalling, of nutrition status is discussed, since strong correlations between leaf nutrient concentrations and those in phloem saps were observed. In addition, negative correlations between phloem sap sugar concentration and net-photosynthesis, growth, and uptake of nutrients were demonstrated. The question remains whether this is only a consequence of an insufficient use of carbohydrates in plants or a ubiquitous signal for stress in plants. In general, high sugar concentrations in phloem saps indicate (nutritional) stress, and high nutrient concentrations in phloem saps indicate nutritional sufficiency of leaf tissues.

**Key words:** Castor bean, flow model, long distance transport, nutrient deficiency, nutrients, phloem transport, signalling, uptake, xylem transport.

**Introduction**

On land, Higher Plants face the problem of having photosynthesis, i.e. the site for the capturing of light energy and CO$_2$, displaced from the site where water and mineral nutrients are taken up. Therefore, one of the chief requirements for land plants is the presence of long-distance transport systems. In cormophytes, these demands are fulfilled by the actions of phloem and xylem. The xylem transports water, mineral nutrients, metabolic products, and signals from the root to the shoot. By contrast, the phloem transports assimilation products from photosynthetically active or remobilizing ‘source’ tissues, to growing areas within the shoot and the root, the so-called ‘sinks’, via
In particular, the relationship between C and N metabolism has been the target of numerous studies.

For plant nutrition, knowledge of nutrient and assimilate transport in the xylem and phloem is of basic importance. But, since they depend on highly variable parameters, such as volume flow and solute concentrations in the transport stream, these long-distance events are especially difficult to model.

An elegant solution is provided by the method of Pate et al. (1979a), Jeschke et al. (1985), and Jeschke and Pate (1991a). In this method, incremental data and concentration ratios in the transport saps were used to model the flows of nutrients. Within the last two decades, a series of papers using this method has been published, dealing with effects of nutrient deficiency and nutritional disorder on long-distance solute transport and partitioning, including an emphasis on the stress signal abscisic acid in castor bean plants. Variations in nutritional conditions included N source (Peuke and Jeschke, 1993), salt stress (Peuke and Jeschke, 1995; Peuke et al., 1996; Jeschke and Pate, 1991a, b, c), foliar application of N (Peuke et al., 1998a, b), as well as deficiencies in N (Peuke et al., 1994a), P (Jeschke et al., 1996, 1997a, b), and K⁺ (Peuke et al., 2002). These studies permit the quantification of uptake, transport in xylem and phloem between, and incorporation into, the shoots and roots.

These papers gave interesting results and flow profiles, but were only valid for a particular set of nutritional conditions. What are required are flow models that can be extrapolated to other conditions, particularly for photosynthetic partitioning (Minchin and Lacointe, 2005). The question arises if general rules can be discerned, that can describe the behaviour in long-distance transport and flows in intact plants, including the distribution and partitioning of nutrients between organs. For example: Does the nutrient concentration in the rhizosphere have a direct effect on the concentration in root tissue and/or xylem sap that is mathematically describable by a regression model? Is the export by the xylem or the increment in root affected by the uptake of the root? And most general: is there a central control mechanism that organizes the co-operation of these processes?

The present paper aims not only to summarize the observations of previous papers, but also to demonstrate correlations between different compartments and processes in the long-distance transport of single elements and ions. General flow models for nutrients between roots and shoot in Ricinus, based on 12 nutritional conditions, are presented.

Materials and methods

Plant cultivation

The sources of data are previous experiments in which Ricinus communis plants were cultivated under comparable environmental conditions, experimental design, and time schedule. The principal question in these studies was how the elemental flows within an intact plant are affected by nutritional conditions (12 different treatments, see papers summarized below), during vegetative...
growth. Thirteen days after sowing, seedlings were transferred to quartz sand culture (one plant per 5.0 l pot and supplied daily with Long Ashton nutrient solution (Hewitt, 1966). The water capacity of the quartz sand was approximately 10% nutrient solution. Different nutritional conditions required some changes in concentrations; details on the composition of the nutrient solutions is given in the original papers, as listed below. In brief, the nutrient solutions contained: (i) variable nitrate concentrations [0.2 (N-deficiency), 1.0, 4.0 or 12.0 mM] (Peuke and Jeschke, 1993; Peuke et al., 1994; Jeschke et al., 1996); (ii) ammonium (1.0 mM) (Peuke and Jeschke, 1993); (iii) low Pi (Jeschke et al., 1996a, b) or low K+ (Peuke et al., 2002); (iv) foliar N (nitrate or ammonium) supply without N in the nutrient solution (Peuke et al., 1998a, b); and (v) in experiments providing a moderate salt treatment: 1.0 mM

(a) times by applying pneumatic pressure to the root system the time of harvest and, in addition, between the two harvesting periods where exponential growth of the plants was observed. The flows of C and N were modelled according to the method of Jeschke et al. (1998a, b); (ii) foliar N supply without N in the nutrient solution, Peuke et al. (1998a, b); (ii) ions returned to the roots solely by phloem transport; and (iii) transport exchange took place by mass flow in the xylem or phloem.

For C, the contribution of photosynthesis (photosynthesis) and respiration (respiratory losses) must be included:

\[ \Delta_{\text{C, shoot}} = J_{\text{C, x}} + C_{\text{fix}} - C_{\text{res}} - J_{\text{C, P}} \]

The net-uptake of an element can be calculated by the sum of increments in all organs:

\[ \Delta_{\text{uptake}} = \Delta_{\text{shoot}} + \Delta_{\text{root}} \]

Based on these assumptions and fundamental equations, the calculation of the flow of C in the phloem can be made:

\[ J_{\text{N, x}} = \frac{[N]_{\text{p}}}{[C]_{\text{p}}} \]

i.e. the relation of the flow of N to that of C in the phloem is equivalent to that of the respective concentrations:

\[ \left( \frac{[N]_{\text{p}}}{[C]_{\text{p}}} \right) \]

The increment of N in the shoot (\( \Delta_{\text{N, shoot}} \)) resulted from the difference between that supplied by the xylem (\( J_{\text{N, x}} \)) and that removed in the phloem flow (\( J_{\text{N, P}} \)):

\[ \Delta_{\text{N, shoot}} = J_{\text{N, x}} - J_{\text{N, P}} \]

For C, the contribution of photosynthesis (\( C_{\text{fix}} \)) and respiration (\( C_{\text{res}} \)) must be included:

\[ \Delta_{\text{C, shoot}} = J_{\text{C, x}} + C_{\text{fix}} - C_{\text{res}} - J_{\text{C, P}} \]

\[ \Delta_{\text{uptake}} = \Delta_{\text{shoot}} + \Delta_{\text{root}} \]
In the next step, in relation to the concentrations, the flow of N in the phloem is calculated:

\[
J_{C.P} = \left( \frac{([C]_P/[N]_P) \times (([C]_P/[N]_P) - ([C]_X/[N]_X))}{\Delta C_{\text{nut}} + C_{\text{res}}} - ([C]_X/[N]_X) \times (\Delta N_{\text{nut}} - N_{\text{take}}) \right)
\]

In the next step, in relation to the concentrations, the flow of N in the phloem is calculated:

\[
J_{N,P} = J_{C.P} \times (([C]_P/[N]_P)^{-1}
\]

Including the increment of N in the shoot, the flow of N in the xylem can be estimated:

\[
J_{N,X} = \Delta N_{\text{shoot}} - J_{N,P}
\]

In the final step, C flow in the xylem is evaluated:

\[
J_{C.X} = J_{N,X} \times ([C]_X/[N]_X)
\]

On the basis of the flows of total C, those of other ions or elements can be estimated, for example the flow of K⁺ in the phloem:

\[
J_{K,P} = J_{C.P} \times ([K]_P/[C]_P)
\]

On the basis of the flows of total N, those of nitrate can be estimated. The calculation of flows of nitrate and reduction is described in more detail by Peuke et al. (1996).

The models of flows not included are potential losses by root exudation (i.e., organic acids etc.) or gaseous compounds from the shoots (e.g., nitrogenous gases NH₃ or NOₓ).

Since the growth of the plants was strongly affected by the nutrient conditions, the flows were related to the logarithmical mean fresh weight (Jeschke et al., 1985) of the plants [μmol g⁻¹ FW (10 d⁻¹)] in order to facilitate comparison.

To demonstrate the principal mechanism, and for presentation of 'general' flow models depending on different nutritional conditions, the flow data of the previous studies are summarized here and re-evaluated using regression analysis (see below). The effect of uptake on xylem and phloem flows, as well as increments in the root and shoot were tested (in addition to the xylem flow on the increment in shoots and phloem flow). The generalized flows per plant are given as 100% of uptake ± standard error of the estimated slope of the regression in the models.

Statistics

Determinations of fresh and dry weight, and element and ion concentration of the plant parts were obtained from 7–9 plants for both harvests in each study. Concentrations of solutes in xylem and phloem saps and elements and ions in tissues are given as means ± SD or SE as indicated.

Analysis of correlation was performed on the whole data set using the CORR procedure of SAS (Kₚ₀ and P-value for H₀: Kₚ₀=0).

In the regression analysis by the REG procedure of SAS, two linear models were tested, one with and the other without an intercept. By selection of only significant estimates (slope as well as intercept), non-significant estimates/models were eliminated (H₀: estimates=0). Minimum ρ² was set at 0.5. For the regression analysis, the mean values of the different treatments/studies were used.

Results

Correlation between compounds in xylem and phloem saps, and tissues

In xylem saps, nitrate was the major anion and K⁺ the major cation (Table 1a). A number of consistently positive correlations were detected. Nitrate correlated very well with the cations K⁺, Mg²⁺, and Ca²⁺, but also with amino acid (N) concentrations. Anions (especially Pi) as well as cations (e.g., Mg²⁺, Ca²⁺, and K⁺) correlated fairly well with each other. Na⁺ only correlated with Cl⁻ and slightly with SO₃²⁻.

In the phloem saps, sucrose was the dominant solute, as was to be expected, followed by amino acids and K⁺ (Table 1b). In contrast to the xylem, only a few correlations were detected in phloem saps. K⁺, the major cation, correlated very well with malate. As in xylem sap, Pi correlated with other anions, except the dominant anion Cl⁻. However, Cl⁻ correlated with Na⁺.

In the roots, K⁺ correlated negatively with C, N, and Na⁺, but positively with Pi (Table 2a). Pi was strongly negatively correlated with N. In addition, slight positive relationships between nitrate and malate, and between sulphate and Cl⁻ were calculated. In the axes the strongest correlation was detected between Na⁺ and Cl⁻ (Table 2b). Ca²⁺ correlated fairly well with nitrate and malate, and slightly with K⁺ and negatively with C. In addition, small positive correlations between N and Mg²⁺ or nitrate, K⁺ and malate, and Cl⁻ and sulphate were observed. Compared with the other organs, fewer correlations were observed in the leaves (Table 2c). Most prominent was, again, the relationship between Na⁺ and Cl⁻ and between malate and Ca²⁺. In contrast to the other organs, C in the leaves was slightly negatively correlated with Mg²⁺, and Pi positively with Mg²⁺ or malate. Throughout all plant parts, a significant correlation for concentration in tissues was only observed for Na⁺ and Cl⁻.

Correlation among compartments on the transport pathway of compounds from the rhizosphere to the leaves, and recycling back to the root

A strong effect of the concentration in the rhizosphere (nutrient solution) on the root concentration was detected for Na⁺ and Cl⁻, including a significant intercept, and a slight effect for NO₃⁻ (Fig. 1A). All slopes were greater than 1 [2.0±0.1 (Na⁺) to 4.0±0.5 (NO₃⁻)], and, generally, the concentrations in roots were higher than in the nutrient solution. This reflects the capacity of roots for the accumulation of minerals against their chemical gradient. A similar effect of the rhizosphere on the xylem concentration was observed, but, here, an effect for N and Ca²⁺ was also detected. The slopes for Na⁺ and Cl⁻ from the rhizosphere to the xylem were clearly below 1. The concentrations in the root tissue correlated with those in the xylem only for N, Na⁺, and Cl⁻ (Fig. 1C), although the slopes were rather low. Also some concentrations in the leaves were correlated with those in xylem sap (Fig. 1D). The data of the divalent Mg²⁺ and Ca²⁺ and SO₄²⁻ and Pi may point to homeostasis of these ions in leaf tissue. The high slopes and the comparison of concentrations demonstrate a strong enrichment in the leaves from the xylem sap, except for Na⁺.

In Fig. 2, the regression analysis for xylem-borne minerals from the xylem sap and leaves on the phloem sap
and the phloem sap on the root tissue are presented. For N, Na⁺, Cl⁻, and NO₃⁻ the concentrations in the xylem saps were well correlated with those in the phloem sap. Only for Cl⁻ was this correlation weak. For N and Na⁺, the slopes point to enrichment in the phloem sap compared to the xylem sap. A very tight, significant correlation for concentrations was detected between leaf tissue and phloem saps, with \( r^2 \approx 0.9 \) (Fig. 2B). The slopes ranged from 0.01 (Ca²⁺), to values of 0.47 (K⁺) and 0.87 (Na⁺). Only for Pi was no correlation between leaf and phloem sap concentration found. Finally, the concentration in root tissue seems to be apparently correlated with the phloem concentration in all cases (Fig. 2C), except for Mg²⁺ and SO₄²⁻ and the less phloem-mobile Ca²⁺. The slopes were between 0.85 (Pi) and 23 (NO₃⁻), which reflects a gradient in phloem mobility.

**Correlation between uptake, flows in xylem and phloem, and increment**

For the essential nutrients C, N, K⁺, Mg²⁺, and Ca²⁺, strong correlations (\( r^2 \geq 0.9 \)) were found between uptake, flow in xylem and phloem, and incremental accumulation in shoot and root for the same element. These observations,

### Table 1. Correlations between solutes in xylem saps (a: \( n=323; \) collected by root pressure as well as by applying pneumatic pressure) and phloem sieve tube saps (b: \( n=144–147 \)) in *Ricinus communis* grown under different nutritional conditions 41–51 d after sowing. Given are the means and standard deviation of the whole data set. Significant (\( P < 0.05 \) for \( H_0: K_p = 0 \)) Pearson Correlation Coefficients (\( K_p > 0.50 \)) are indicated by numbers, \( K_p > 0.75 \) additionally by bold numbers. (\( H_0: \) estimate = 0; –, not significant; *, \( P < 0.05; **: P < 0.01; ***: P < 0.001 \)). AA-N: amino acid nitrogen.

#### (a) Xylem saps (mM)

<table>
<thead>
<tr>
<th></th>
<th>Cl⁻</th>
<th>NO₃⁻</th>
<th>Pi</th>
<th>SO₄²⁻</th>
<th>Malate</th>
<th>Mg²⁺</th>
<th>Ca²⁺</th>
<th>Na⁺</th>
<th>K⁺</th>
<th>AA-N</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean</td>
<td>1.25</td>
<td>7.16</td>
<td>0.70</td>
<td>0.64</td>
<td>0.34</td>
<td>1.14</td>
<td>1.75</td>
<td>0.65</td>
<td>5.21</td>
<td>4.90</td>
</tr>
<tr>
<td>SD</td>
<td>±1.83</td>
<td>±0.18</td>
<td>±0.72</td>
<td>±0.93</td>
<td>±0.69</td>
<td>±1.07</td>
<td>±1.71</td>
<td>±1.93</td>
<td>±4.97</td>
<td>±6.34</td>
</tr>
<tr>
<td>n</td>
<td>323</td>
<td>323</td>
<td>323</td>
<td>323</td>
<td>323</td>
<td>323</td>
<td>323</td>
<td>323</td>
<td>323</td>
<td>324</td>
</tr>
</tbody>
</table>

**Table continued...**

#### (b) Phloem sieve tube saps (mM)

<table>
<thead>
<tr>
<th></th>
<th>AA-N</th>
<th>Cl⁻</th>
<th>NO₃⁻</th>
<th>Pi</th>
<th>SO₄²⁻</th>
<th>Malate</th>
<th>K⁺</th>
<th>Na⁺</th>
<th>Mg²⁺</th>
<th>Ca²⁺</th>
<th>Sucrose</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean</td>
<td>67.5</td>
<td>12.0</td>
<td>0.59</td>
<td>6.56</td>
<td>1.29</td>
<td>8.02</td>
<td>67.1</td>
<td>6.96</td>
<td>3.71</td>
<td>1.21</td>
<td>433</td>
</tr>
<tr>
<td>SD</td>
<td>±44.6</td>
<td>±12.8</td>
<td>±0.97</td>
<td>±3.48</td>
<td>±1.03</td>
<td>±5.23</td>
<td>±15.3</td>
<td>±13.59</td>
<td>±2.48</td>
<td>±0.50</td>
<td>±70</td>
</tr>
<tr>
<td>n</td>
<td>145</td>
<td>147</td>
<td>147</td>
<td>147</td>
<td>147</td>
<td>147</td>
<td>147</td>
<td>146</td>
<td>146</td>
<td>146</td>
<td>146</td>
</tr>
</tbody>
</table>

**Table continued...**
Table 2. Correlations between elements in roots (a), axes (b), and leaves (c) of *Ricinus communis* grown under different nutritional conditions 51 d after sowing (*n*=12)

Given are the means ± SD of element concentration in the dry matter of tissues, *n*=57–69 replicates from 12 different treatments. Significant (*P* <0.05 for *H₀: Kₚ=0*) Pearson Correlation Coefficients (*Kₚ*) >0.50 are indicated by numbers, *Kₚ* >0.70 additionally by bold numbers. AA-N: amino acid nitrogen.

### Roots (µmol g⁻¹)

<table>
<thead>
<tr>
<th>Element</th>
<th>C</th>
<th>N</th>
<th>Na⁺</th>
<th>K⁺</th>
<th>Mg²⁺</th>
<th>Ca²⁺</th>
<th>Cl⁻</th>
<th>NO₃</th>
<th>Malate</th>
<th>SO₄²⁻</th>
<th>Pi</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean</td>
<td>32445</td>
<td>1224</td>
<td>364</td>
<td>871</td>
<td>227</td>
<td>188</td>
<td>587</td>
<td>65</td>
<td>221</td>
<td>118</td>
<td>137</td>
</tr>
<tr>
<td>SD</td>
<td>±1494</td>
<td>±404</td>
<td>±498</td>
<td>±472</td>
<td>±84</td>
<td>±35</td>
<td>±506</td>
<td>±81</td>
<td>±144</td>
<td>±52</td>
<td>±103</td>
</tr>
<tr>
<td>n</td>
<td>69</td>
<td>69</td>
<td>69</td>
<td>69</td>
<td>69</td>
<td>69</td>
<td>69</td>
<td>69</td>
<td>69</td>
<td>69</td>
<td>60</td>
</tr>
<tr>
<td>Correlation</td>
<td>1:1</td>
<td>27:1</td>
<td>89:1</td>
<td>37:1</td>
<td>143:1</td>
<td>172:1</td>
<td>55:1</td>
<td>497:1</td>
<td>147:1</td>
<td>276:1</td>
<td>236:1</td>
</tr>
<tr>
<td>C</td>
<td>–</td>
<td>–</td>
<td>Na⁺</td>
<td>K⁺</td>
<td>Mg²⁺</td>
<td>Ca²⁺</td>
<td>Cl⁻</td>
<td>NO₃</td>
<td>Malate</td>
<td>SO₄²⁻</td>
<td>Pi</td>
</tr>
<tr>
<td>N</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Na⁺</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>K⁺</td>
<td>–0.62</td>
<td>–0.65</td>
<td>–0.54</td>
<td>–0.54</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Mg²⁺</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Ca²⁺</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Cl⁻</td>
<td>–0.66</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>NO₃</td>
<td>0.64</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Malate</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>SO₄²⁻</td>
<td>–0.78</td>
<td>–0.68</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
</tbody>
</table>

### Axes (µmol g⁻¹)

<table>
<thead>
<tr>
<th>Element</th>
<th>C</th>
<th>N</th>
<th>Na⁺</th>
<th>K⁺</th>
<th>Mg²⁺</th>
<th>Ca²⁺</th>
<th>Cl⁻</th>
<th>NO₃</th>
<th>Malate</th>
<th>SO₄²⁻</th>
<th>Pi</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean</td>
<td>33413</td>
<td>870</td>
<td>158</td>
<td>556</td>
<td>175</td>
<td>326</td>
<td>438</td>
<td>68</td>
<td>188</td>
<td>44</td>
<td>97</td>
</tr>
<tr>
<td>SD</td>
<td>±1386</td>
<td>±302</td>
<td>±311</td>
<td>±257</td>
<td>±54</td>
<td>±131</td>
<td>±452</td>
<td>±111</td>
<td>±199</td>
<td>±19</td>
<td>±55</td>
</tr>
<tr>
<td>n</td>
<td>69</td>
<td>69</td>
<td>69</td>
<td>69</td>
<td>69</td>
<td>69</td>
<td>69</td>
<td>69</td>
<td>69</td>
<td>69</td>
<td>61</td>
</tr>
<tr>
<td>Correlation</td>
<td>1:1</td>
<td>38:1</td>
<td>212:1</td>
<td>60:1</td>
<td>190:1</td>
<td>102:1</td>
<td>76:1</td>
<td>488:1</td>
<td>178:1</td>
<td>758:1</td>
<td>344:1</td>
</tr>
<tr>
<td>C</td>
<td>–</td>
<td>–</td>
<td>Na⁺</td>
<td>K⁺</td>
<td>Mg²⁺</td>
<td>Ca²⁺</td>
<td>Cl⁻</td>
<td>NO₃</td>
<td>Malate</td>
<td>SO₄²⁻</td>
<td>Pi</td>
</tr>
<tr>
<td>N</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Na⁺</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>K⁺</td>
<td>–0.65</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Mg²⁺</td>
<td>–0.65</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Ca²⁺</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Cl⁻</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>NO₃</td>
<td>0.64</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Malate</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>SO₄²⁻</td>
<td>–0.78</td>
<td>–0.68</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
</tbody>
</table>

### Leaves (µmol g⁻¹)

<table>
<thead>
<tr>
<th>Element</th>
<th>C</th>
<th>N</th>
<th>Na⁺</th>
<th>K⁺</th>
<th>Mg²⁺</th>
<th>Ca²⁺</th>
<th>Cl⁻</th>
<th>NO₃</th>
<th>Malate</th>
<th>SO₄²⁻</th>
<th>Pi</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean</td>
<td>35675</td>
<td>2456</td>
<td>49</td>
<td>473</td>
<td>176</td>
<td>374</td>
<td>203</td>
<td>4</td>
<td>164</td>
<td>134</td>
<td>49</td>
</tr>
<tr>
<td>SD</td>
<td>±906</td>
<td>±725</td>
<td>±207</td>
<td>±129</td>
<td>±55</td>
<td>±127</td>
<td>±336</td>
<td>±8</td>
<td>±141</td>
<td>±74</td>
<td>±23</td>
</tr>
<tr>
<td>n</td>
<td>69</td>
<td>69</td>
<td>69</td>
<td>69</td>
<td>69</td>
<td>69</td>
<td>69</td>
<td>69</td>
<td>69</td>
<td>69</td>
<td>60</td>
</tr>
<tr>
<td>Correlation</td>
<td>1:1</td>
<td>15:1</td>
<td>727:1</td>
<td>75:1</td>
<td>203:1</td>
<td>95:1</td>
<td>175:1</td>
<td>849:1</td>
<td>218:1</td>
<td>266:1</td>
<td>723:1</td>
</tr>
<tr>
<td>C</td>
<td>–</td>
<td>–</td>
<td>Na⁺</td>
<td>K⁺</td>
<td>Mg²⁺</td>
<td>Ca²⁺</td>
<td>Cl⁻</td>
<td>NO₃</td>
<td>Malate</td>
<td>SO₄²⁻</td>
<td>Pi</td>
</tr>
<tr>
<td>N</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Na⁺</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>K⁺</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Mg²⁺</td>
<td>–0.58</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Ca²⁺</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Cl⁻</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>NO₃</td>
<td>0.63</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Malate</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>SO₄²⁻</td>
<td>–0.78</td>
<td>–0.68</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Pi</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
</tbody>
</table>
based on a wide range of nutritional conditions, were performed by regression analysis of the average flow data of the summarized studies. Therefore, general valid models of nutrient flow between roots and shoots, and vice versa, can be presented on the basis of (net) uptake rates per unit fresh weight, during vegetative growth (monitored over a 10-d period). The models incorporate data of xylem and phloem flow and increments in root and shoot (Figs 3–6), and will be termed ‘general models’, in contrast to the more specific models presented in the previous studies, valid only for a special nutrition condition.

Approximately 44% of newly assimilated carbon is incorporated into carbon skeletons (both structural and non-structural) in the shoot, and 14% is lost through dark respiration in the shoot (Fig. 3, left). The models incorporate data of xylem and phloem flow and increments in root and shoot (Figs 3–6), and will be termed ‘general models’, in contrast to the more specific models presented in the previous studies, valid only for a special nutrition condition.

Nearly the entire proportion of N taken up by roots is transported in the xylem to the shoot, where ~75% is incorporated (Fig. 3, right). One quarter of the xylem-borne N is recycled via the phloem back to the root. A similar proportion of N is incorporated in the root. What remains unclear is the origin of root-incorporated N, whether it originates directly from uptake or from phloem-recycled N, but both pathways are possible.

K⁺ is strongly transported in Ricinus demonstrated by the amount of 114% of K⁺ uptake transported in the xylem to the shoot (Fig. 4, left). Around half of the K⁺ transported in the xylem is recycled back in the phloem, most of which was incorporated into the root. This interaction of transport systems resulted in a slightly favoured incorporation of K⁺ in the shoot compared to the root.

Nearly 70% of Mg²⁺ taken up is exported to the shoot, where most of it (61% of uptake) is incorporated (Fig. 5, right). Only ~12% of xylem import (9% of uptake) is recycled back to the root. As a final result of these processes, 39% of Mg²⁺ taken up is accumulated in the root. Similarly, some 80% of Ca²⁺ taken up is transported

![Fig. 1. Regression analysis between compartments on the way of single elements or ions from the nutrient solutions to the root (A), nutrient solution to the root pressure xylem sap (B), root to the root pressure xylem sap (C), and root pressure xylem sap to the leaf tissue (D) in Ricinus communis in a vegetative growth period 41–51 d after sowing. For the calculations, the means of the summarized studies/treatments were used. Significant relationships (H₀: estimate=0; P<0.05) are indicated by dotted (0.5 < r² < 0.7), dashed (0.7 < r² < 0.9), or solid bold (r² > 0.9) lines, the numbers indicate the estimates of the slopes ± SE and confidence limits of the mean are indicated by dashed/dotted lines. The degrees of freedom were: for the model=1, for the error=11, and uncorrected total=12. All axes start at 0 and significant intercepts are indicated if the regression lines are not going through the origin.)
Fig. 2. Regression analysis for compartments on the way of single elements or ions from the xylem saps to the phloem saps (A), from leaf tissue to the phloem saps (B), and from the phloem saps to root tissue (C). For further details see the legend to Fig. 1.

Fig. 3. General flow model for the transport and utilization of carbon (left) or nitrogen (right) in shoot and root of *Ricinus communis* in the vegetative growth period 41–51 d after sowing. Photosynthesis (100%) is indicated by a yellow arrow and uptake by the root by a black arrow. The arrows on the left site indicate flow in the xylem; on the right site flow in the phloem. The squares indicate the increment in the plant parts. The arrows leaving the plant indicate the respiration. PS, photosynthesis; \( J_x \), phloem flow; \( J_x \), xylem flow; \( \text{resp}_R \), respiration in the root; \( \text{resp}_S \), respiration in the shoot; \( \text{inc}_R \), incorporation in the root; \( \text{inc}_S \), incorporation in the shoot. The flow models were propounded by a regression analysis of flow values from models on 12 different nutritional conditions. Numbers indicate 100% of uptake ±SE.
Almost all of this is incorporated in the shoot, since the recycling via phloem back to the root is negligible, with only 2% of xylem flow or 1% of uptake, respectively.

For Na⁺ and Cl⁻, no complete general flow patterns were detected, since, most importantly, there was no correlation between uptake and xylem flow and shoot increment (Figs 4, right, 6, left). However, for both elements a significant correlation between xylem flow and shoot increment and recycling in the phloem was observed. Na⁺ was incorporated at around 80% in the root, and about 70% of xylem-borne Na⁺ was incorporated in the shoot, while the rest (31%) was recycled in the phloem back to the root. Around 80% of xylem transported Cl⁻ is incorporated in the shoot. 15% of the xylem-imported Cl⁻ is recycled back to the root.

For nitrate, a model for uptake and xylem transport including reduction can be presented (Fig. 6, right). 38% of nitrate taken up is reduced in the root, and the rest is exported via xylem to the shoot, where 94% of the xylem import or 53% of original uptake is reduced. Incorporation or remobilization of nitrate in the root and shoots were observed, but played no significant role.

---

**Fig. 4.** General flow model for the uptake, transport, and utilization of K⁺ (left) or Na⁺ (right) in the shoot and root of *Ricinus communis* in the vegetative growth period 41–51 d after sowing. For further details see the legend to Fig. 3. Grey or dashed lines indicate statistically not correlated flows or increments.

**Fig. 5.** General flow model for the uptake, transport, and utilization of Ca²⁺ (left) or Mg²⁺ (right) in the shoot and root of *Ricinus communis* in the vegetative growth period 41–51 d after sowing. For further details see the legend to Fig. 3.
With the exception of Cl\(^{-}\), the uptake of C correlated very well with those of the other modelled elements, which was also true for N (Table 3a). The strong varying mean uptake rates demonstrate a clear ranking, in the sequence C>N>K\(^{+}\), while the rest of ions studied, Na\(^{+}\), Mg\(^{2+}\), Ca\(^{2+}\), and Cl\(^{-}\), had comparable uptake rates. These data also include, in part, a release of elements. Mg\(^{2+}\) and Ca\(^{2+}\) correlated very well with each other, and with nitrate. A similar picture can be found for the increments in roots (Table 3b), but no correlation of K\(^{+}\) with C and N was found, and nitrate showed no correlation with any nutrient except Ca\(^{2+}\), probably due to conversion of nitrate by reduction in the root. In xylem flow (Table 3c), a number of correlations for C, N, and K\(^{+}\) were observed, in this case in addition to those of Cl\(^{-}\) flow. Nitrate flow was correlated with all cation flows, except Na\(^{+}\). The increments in the shoots showed strong correlations for the essential nutrients C and N (positively), as well as K\(^{+}\) (negatively) (Table 3d). For phloem flow, good correlations were observed between C and N, Mg\(^{2+}\), Ca\(^{2+}\), and NO\(_3\)\(^{-}\), as well as between N and K\(^{+}\), Mg\(^{2+}\) and Cl\(^{-}\) (Table 3e). The good correlation between Ca\(^{2+}\) and NO\(_3\)\(^{-}\) demonstrates, as with C and N, that less phloem-mobile ions are also transported in the phloem, if C export via the phloem is high.

To demonstrate the possible effects of phloem-borne nutrient signals on uptake, growth, and photosynthesis, a regression analysis for phloem concentrations of sugar, N, and K\(^{+}\) was performed (Fig. 7). The concentration of sugar in the phloem saps correlated negatively with photosynthesis, growth, N\(^{-}\), and K\(^{+}\)-uptake. Other significant and relevant \(\rho^2 > 0.5\) correlations were not detected. Phloem sugar was negatively correlated with Mg\(^{2+}\) and Ca\(^{2+}\)-uptake (data not shown).

**Discussion**

**Concentration and correlations of compounds in transport saps and tissues**

Nitrate was the major anion and K\(^{+}\) the dominating cation in the xylem sap of *Ricinus*. Nitrate is usually the dominant anion and N-compound in the xylem sap of many species (Atkins et al., 1980; Arnozis and Findenegg, 1986; Murphy and Lewis, 1987; van Beusichem et al., 1988; Gouia et al., 1994; Gerendaš and Schurr, 1999). In addition, amino acids and amides are found as N-compounds in varying concentrations and proportions in the xylem (Lalonde et al., 2004). Similarly, in the xylem sap of many species, K\(^{+}\) is detected in high concentrations (wheat: Barneix and Breteler, 1985; bean: Cakmak et al., 1994; rye: White, 1997; lupinus: Jeschke et al., 1985). However, the xylem concentrations of solutes of *Ricinus* (Table 1a) were analysed in root pressure saps as well as in saps collected under pressure in the rhizosphere (0.1–0.2 MPa above the compensation point). It is a well-known fact that solute concentrations decrease hyperbolically when flux rates increase, with the highest values seen under root exudation conditions, and the lowest values seen under transpiration conditions (Schurr and Schulze, 1995; Gerendaš and Schurr, 1999).

Phloem saps are typically much more concentrated than xylem saps. Sugars, amino acids, and K\(^{+}\) are the dominant solutes and account for the majority of the osmotic potential (Komor, 2000; Lalonde et al., 2003). Nitrate was found to be loaded into the phloem in low amounts only, and ammonium not at all (Schobert and Komor, 1992). In addition, Schobert and Komor (1989) and Caputo and Barneix (1997) found that amino acids and amides were loaded into and exported by the phloem to different degrees, which also pointed to discrimination against particular amino acids.
Table 3. Correlations between uptake, increment in roots, xylem flow, increment in shoots, or phloem flow for single elements and ions in *Ricinus communis* grown under different nutritional conditions 41–51 d after sowing (n=12).

Also given are the means ±SD of flows or increments from 12 different treatments.

(a) Uptake (μmol g⁻¹ FW 10 d⁻¹):

<table>
<thead>
<tr>
<th></th>
<th>C</th>
<th>N</th>
<th>K⁺</th>
<th>Na⁺</th>
<th>Mg²⁺</th>
<th>Ca²⁺</th>
<th>Cl⁻</th>
<th>NO₃⁻</th>
<th>Mean</th>
<th>SD</th>
</tr>
</thead>
<tbody>
<tr>
<td>C</td>
<td>####</td>
<td>**</td>
<td>*</td>
<td>*</td>
<td>***</td>
<td>***</td>
<td>–</td>
<td>–</td>
<td>2915</td>
<td>±1339</td>
</tr>
<tr>
<td>N</td>
<td>0.86</td>
<td>0.68</td>
<td>0.65</td>
<td>0.67</td>
<td>0.68</td>
<td>0.76</td>
<td>0.65</td>
<td>0.76</td>
<td>102</td>
<td>±77</td>
</tr>
<tr>
<td>K⁺</td>
<td>0.67</td>
<td>0.68</td>
<td>0.65</td>
<td>0.67</td>
<td>0.68</td>
<td>0.76</td>
<td>0.65</td>
<td>0.76</td>
<td>30.0</td>
<td>±19.9</td>
</tr>
<tr>
<td>Na⁺</td>
<td>0.65</td>
<td>0.67</td>
<td>0.67</td>
<td>0.68</td>
<td>0.68</td>
<td>0.76</td>
<td>0.67</td>
<td>0.76</td>
<td>9.3</td>
<td>±4.4</td>
</tr>
<tr>
<td>Mg²⁺</td>
<td>0.90</td>
<td>0.87</td>
<td>0.90</td>
<td>0.87</td>
<td>0.88</td>
<td>0.91</td>
<td>0.89</td>
<td>0.91</td>
<td>10.7</td>
<td>±8.7</td>
</tr>
<tr>
<td>Ca²⁺</td>
<td>0.91</td>
<td>0.88</td>
<td>0.91</td>
<td>0.88</td>
<td>0.91</td>
<td>0.88</td>
<td>0.91</td>
<td>0.88</td>
<td>17.6</td>
<td>±13.7</td>
</tr>
<tr>
<td>Cl⁻</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>13.7</td>
<td>±24.3</td>
</tr>
<tr>
<td>NO₃⁻</td>
<td>0.89</td>
<td>1.00</td>
<td>0.89</td>
<td>1.00</td>
<td>0.89</td>
<td>1.00</td>
<td>0.89</td>
<td>1.00</td>
<td>116</td>
<td>±80</td>
</tr>
</tbody>
</table>

(b) Increment in roots (μmol g⁻¹ FW 10 d⁻¹):

<table>
<thead>
<tr>
<th></th>
<th>C</th>
<th>N</th>
<th>K⁺</th>
<th>Na⁺</th>
<th>Mg²⁺</th>
<th>Ca²⁺</th>
<th>Cl⁻</th>
<th>NO₃⁻</th>
<th>Mean</th>
<th>SD</th>
</tr>
</thead>
<tbody>
<tr>
<td>C</td>
<td>####</td>
<td>**</td>
<td>–</td>
<td>–</td>
<td>**</td>
<td>**</td>
<td>–</td>
<td>–</td>
<td>650</td>
<td>±391</td>
</tr>
<tr>
<td>N</td>
<td>0.81</td>
<td>0.81</td>
<td>0.81</td>
<td>0.81</td>
<td>0.81</td>
<td>0.81</td>
<td>0.81</td>
<td>0.81</td>
<td>26.3</td>
<td>±21.6</td>
</tr>
<tr>
<td>K⁺</td>
<td>0.54</td>
<td>0.54</td>
<td>0.54</td>
<td>0.54</td>
<td>0.54</td>
<td>0.54</td>
<td>0.54</td>
<td>0.54</td>
<td>14.4</td>
<td>±9.4</td>
</tr>
<tr>
<td>Na⁺</td>
<td>0.54</td>
<td>0.54</td>
<td>0.54</td>
<td>0.54</td>
<td>0.54</td>
<td>0.54</td>
<td>0.54</td>
<td>0.54</td>
<td>6.21</td>
<td>±3.05</td>
</tr>
<tr>
<td>Mg²⁺</td>
<td>0.86</td>
<td>0.86</td>
<td>0.86</td>
<td>0.86</td>
<td>0.86</td>
<td>0.86</td>
<td>0.86</td>
<td>0.86</td>
<td>4.11</td>
<td>±4.09</td>
</tr>
<tr>
<td>Ca²⁺</td>
<td>0.81</td>
<td>0.81</td>
<td>0.81</td>
<td>0.81</td>
<td>0.81</td>
<td>0.81</td>
<td>0.81</td>
<td>0.81</td>
<td>4.13</td>
<td>±2.73</td>
</tr>
<tr>
<td>Cl⁻</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>1.99</td>
<td>±1.92</td>
</tr>
<tr>
<td>NO₃⁻</td>
<td>0.76</td>
<td>0.76</td>
<td>0.76</td>
<td>0.76</td>
<td>0.76</td>
<td>0.76</td>
<td>0.76</td>
<td>0.76</td>
<td>0.32</td>
<td>±1.55</td>
</tr>
</tbody>
</table>

(c) Xylem flow (μmol g⁻¹ FW 10 d⁻¹):

<table>
<thead>
<tr>
<th></th>
<th>C</th>
<th>N</th>
<th>K⁺</th>
<th>Na⁺</th>
<th>Mg²⁺</th>
<th>Ca²⁺</th>
<th>Cl⁻</th>
<th>NO₃⁻</th>
<th>Mean</th>
<th>SD</th>
</tr>
</thead>
<tbody>
<tr>
<td>C</td>
<td>####</td>
<td>**</td>
<td>–</td>
<td>–</td>
<td>**</td>
<td>**</td>
<td>–</td>
<td>–</td>
<td>113</td>
<td>±121</td>
</tr>
<tr>
<td>N</td>
<td>0.64</td>
<td>0.64</td>
<td>0.64</td>
<td>0.64</td>
<td>0.64</td>
<td>0.64</td>
<td>0.64</td>
<td>0.64</td>
<td>99.8</td>
<td>±78.6</td>
</tr>
<tr>
<td>K⁺</td>
<td>0.65</td>
<td>0.65</td>
<td>0.65</td>
<td>0.65</td>
<td>0.65</td>
<td>0.65</td>
<td>0.65</td>
<td>0.65</td>
<td>33.2</td>
<td>±27.8</td>
</tr>
<tr>
<td>Na⁺</td>
<td>0.65</td>
<td>0.65</td>
<td>0.65</td>
<td>0.65</td>
<td>0.65</td>
<td>0.65</td>
<td>0.65</td>
<td>0.65</td>
<td>5.32</td>
<td>±7.10</td>
</tr>
<tr>
<td>Mg²⁺</td>
<td>0.67</td>
<td>0.67</td>
<td>0.67</td>
<td>0.67</td>
<td>0.67</td>
<td>0.67</td>
<td>0.67</td>
<td>0.67</td>
<td>7.62</td>
<td>±6.21</td>
</tr>
<tr>
<td>Ca²⁺</td>
<td>0.82</td>
<td>0.82</td>
<td>0.82</td>
<td>0.82</td>
<td>0.82</td>
<td>0.82</td>
<td>0.82</td>
<td>0.82</td>
<td>13.8</td>
<td>±11.6</td>
</tr>
<tr>
<td>Cl⁻</td>
<td>0.93</td>
<td>0.93</td>
<td>0.93</td>
<td>0.93</td>
<td>0.93</td>
<td>0.93</td>
<td>0.93</td>
<td>0.93</td>
<td>15.4</td>
<td>±18.6</td>
</tr>
<tr>
<td>NO₃⁻</td>
<td>0.97</td>
<td>0.97</td>
<td>0.97</td>
<td>0.97</td>
<td>0.97</td>
<td>0.97</td>
<td>0.97</td>
<td>0.97</td>
<td>62.0</td>
<td>±47.9</td>
</tr>
</tbody>
</table>

(d) Increments in shoots (μmol g⁻¹ FW 10 d⁻¹):

<table>
<thead>
<tr>
<th></th>
<th>C</th>
<th>N</th>
<th>K⁺</th>
<th>Na⁺</th>
<th>Mg²⁺</th>
<th>Ca²⁺</th>
<th>Cl⁻</th>
<th>NO₃⁻</th>
<th>Mean</th>
<th>SD</th>
</tr>
</thead>
<tbody>
<tr>
<td>C</td>
<td>####</td>
<td>**</td>
<td>–</td>
<td>–</td>
<td>**</td>
<td>**</td>
<td>–</td>
<td>–</td>
<td>1237</td>
<td>±760</td>
</tr>
<tr>
<td>N</td>
<td>0.86</td>
<td>0.86</td>
<td>0.86</td>
<td>0.86</td>
<td>0.86</td>
<td>0.86</td>
<td>0.86</td>
<td>0.86</td>
<td>75.8</td>
<td>±59.5</td>
</tr>
<tr>
<td>K⁺</td>
<td>0.83</td>
<td>0.83</td>
<td>0.83</td>
<td>0.83</td>
<td>0.83</td>
<td>0.83</td>
<td>0.83</td>
<td>0.83</td>
<td>15.6</td>
<td>±15.0</td>
</tr>
<tr>
<td>Na⁺</td>
<td>0.83</td>
<td>0.83</td>
<td>0.83</td>
<td>0.83</td>
<td>0.83</td>
<td>0.83</td>
<td>0.83</td>
<td>0.83</td>
<td>3.14</td>
<td>±4.97</td>
</tr>
<tr>
<td>Mg²⁺</td>
<td>0.93</td>
<td>0.93</td>
<td>0.93</td>
<td>0.93</td>
<td>0.93</td>
<td>0.93</td>
<td>0.93</td>
<td>0.93</td>
<td>6.54</td>
<td>±5.63</td>
</tr>
<tr>
<td>Ca²⁺</td>
<td>0.91</td>
<td>0.91</td>
<td>0.91</td>
<td>0.91</td>
<td>0.91</td>
<td>0.91</td>
<td>0.91</td>
<td>0.91</td>
<td>13.5</td>
<td>±11.5</td>
</tr>
<tr>
<td>Cl⁻</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>11.7</td>
<td>±15.7</td>
</tr>
<tr>
<td>NO₃⁻</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>3.38</td>
<td>±12.80</td>
</tr>
</tbody>
</table>
In the composition of xylem sap, numerous correlations were observed, particularly for N and its compounds. These analyses demonstrate that the hypothesis on K⁺ being the preferred counterion for nitrate in the xylem may not be true, since nitrate was correlated in a similar way with Mg²⁺ and Ca²⁺. Nevertheless, K⁺ contributes, due to its abundance, the largest complement of positively charged ions in the xylem. By contrast to the xylem sap, in phloem saps only a few significant correlations were detected. One reason may be that, in the xylem sap, charged ions are dominating, which must be compensated for by counterions. By contrast, in the phloem sap, sugars (around 75%) and amino acids (around 15%) are the major solutes, with K⁺ ranking third, accounting for approximately 5% of total solutes. All transport saps must be electrically neutral, which can only be accomplished in part by H⁺ or OH⁻ (Gerendás and Schurr, 1999; Roberts, 2006).

The correlation between K⁺ and malate in phloem sap points to the old theory of Ben Zioni *et al.* (1971) that secondary products of nitrate reduction in the shoot control the uptake of nitrate by the roots. Nitrate, transported together with K⁺ in the xylem, is reduced in the shoot and, at the same time, malate is produced stoichiometrically. From the rates of nitrate reduction (OH⁻ production) and rates of malate synthesis (2H⁺ production), it was calculated that malate accumulation contributed 76, 45, or 39% to the pH-stat system during nitrate reduction in plants fed with 0.2, 1.0, or 4.0 mM nitrate (Peuke *et al.*, 1996). Part of the K⁺-malate pool moves down to the root system. The observed correlation between sugar and Pi in phloem saps seems to be in contrast to the inhibition of sucrose loading into the phloem by Pi (and sulphate) described in *Ricinus* (Schobert *et al.*, 1998).

The correlations between Na⁺ and Cl⁻ in transport saps and, indeed, all tissues (Tables 1, 2) can be attributed to the supply of NaCl in the experiments with salinity. In both transport systems, no competition among either cations or anions appears to exist. Even some anions and cations (e.g. Mg²⁺ and Ca²⁺ in both xylem and phloem: Table 1a, b, as well as for xylem flow: Table 3c) correlated very well in xylem or phloem saps. This is surprising, since some transporters and channels are transporting different ions like nitrate and Cl⁻ with differing selectivity (Gilliham and Tester, 2005). Different anions (see review by Roberts, 2006) or cations (Mäser *et al.*, 2001; Demidchik and Maathuis, 2007) can be transported via the same transport system. A selectivity ranking for the transport of anions has been observed (Roberts, 2006), but this does not result in competition at the level of net transport or tissue content of ions. For example, the inhibition of nitrate uptake was caused mainly by the osmotic effects of applied salts, and, specifically, the high-affinity transport system (HATS) was inhibited non-competitively by NaCl (Peuke and Jeschke, 1999). Only for the loading of sugars and amino acids into the phloem pathway has competition been reported (Schobert and Komor, 1989).

**Correlations between rhizosphere, root, xylem sap, and leaves**

The regression analysis for the effects of sequential compartments in the transport pathway of single solutes from the rhizosphere to the root and following transport steps in the plant revealed several relationships. This is not surprising, since, within a plant, these transport compartments are not independent, but also of interest are the strength ($r^2$) and performance (slope) and also the gaps – the cases where no significant satisfying correlation were found. First, the high capacity of the root for the accumulation of minerals from the rhizosphere and for the accumulation in the leaves after xylem transport was evident. These data demonstrate uptake from apoplastic compartments into the tissue against a chemical gradient.

For both roots and shoots, numerous uptake systems for the most important nutrients have been found and, in part, physiologically characterized (Chrispeels *et al.*, 1999; Raghothama, 1999; Grossman and Takahashi, 2001; Rausch and Bucher, 2002; Munns, 2005; Roberts, 2006). Ions are taken up mostly by active means by high affinity transport systems against concentration and electrical gradients (Clarkson and Hanson, 1980; Chrispeels *et al.*, 1999; Raghothama, 1999; Véry and Sentenac, 2003; Roberts, 2006; Miller *et al.*, 2007). However, it is important that cations and anions be discussed separately with respect to electrochemical driving forces for transport. Electrical gradients have opposite effects on cations and anions. High negative voltages across the plasma membrane and buffered cytosolic concentrations allow the uptake of cations...
through ion channels or uniporters (e.g. K⁺: Véry and Sentenac, 2003; Na⁺: Tester and Davenport, 2003; Ca²⁺: White and Broadley, 2003), whereas only very high external concentrations of anions can allow their uptake through ion channels or uniporters (e.g. Cl⁻ in saline environments: White and Broadley, 2001).

Transport systems for ion influx across the plasma membrane of root cells have been characterized by a ‘dual uptake system’ (Epstein et al., 1963; Chrispeels et al., 1999; Raghothama, 1999; Grossman and Takahashi, 2001; Forde, 2002b): high-affinity transport systems (HATS) that mediate uptake from relatively low concentrated solutions (<1 mM) at relatively low rates, and low-affinity transport systems (LATS) that operate at higher rates and higher external concentrations (>1 mM), depending on the nutrient plant system. The HATS is described as a saturable system, whereas the nature of the LATS shows linear responses to substrate concentrations. In the present paper, studies were analysed in which the concentration of nutrients in the rhizosphere were in the mM range, far away from HATS.

Fig. 7. Regression analysis for the effects of phloem sieve tube sap concentration of sugars, N, and K⁺ on photosynthesis, growth, N-, and K⁺-uptake in *Ricinus communis* in a vegetative growth period 41–51 d after sowing. Significant relationships (H₀: estimate=0; \( P < 0.05 \)) are indicated by lines and confidence limits of the mean are indicated by dotted lines.
saturable Michaelis–Menten kinetics never resulted in models where all the estimates were significant (whereas \( V_{\text{max}} \) could be estimated satisfactorily, \( K_d \) was never significant, data not shown). However, the amount of data was too low to allow the calculation of dual systems.

Ions taken up by the roots can be used either for growth and accumulation in the root, or subjected to export via the xylem to the shoot. Nitrate, sulphate, and \( \text{Pi} \) can also be assimilated in the root and converted to other chemical forms (Clarkson and Hanson, 1980; Crawford and Glass, 1998; Grossman and Takahashi, 2001;Amtmann and Blatt, 2009). Therefore, competition can be assumed in the roots between use and/or metabolism and export via the xylem. Nonetheless, for \( \text{P} \) and \( \text{S} \), the inorganic forms represent the major compounds for storage, and sulphate is the major form of transported sulphur as well (Buchner et al., 2004). Another problem comes from the nutrient distribution within a plant organ, between symplastic and apoplastic compartments, as well as within individual cells, most importantly cytosolic concentrations versus vacuolar. In the present study, only the overall concentration in the bulk material was used.

The electrochemical gradients for the transport of ions from the root symplast to the xylem are generally opposite those for the uptake of ions from the nutrient solution to the root symplast. Thus, different transport mechanisms are required for the uptake of ions from the nutrient solution to the symplast and their efflux from the symplast to the xylem. In stelar cells, a number of anion and cation channels have been detected and characterized (Mäser et al., 2001; White and Broadley, 2001; Tester and Davenport, 2003;Véry and Sentenac, 2003; Roberts, 2006;Amtmann and Blatt, 2009). However, some loading processes like those for sulphate and \( \text{Pi} \) still require clarification (Raghothama, 1999; Buchner et al., 2004; Rausch and Bucher, 2002;Smith et al., 2003). There are a number of reports that xylem loading is a passive process (Köhler and Raschke, 2000; Roberts, 2006). Wegner and Raschke (1994) suggested that cations and anions are released simultaneously from the xylem parenchyma into the xylem apoplast and vessels through channels, following electrochemical gradients set up by the ion uptake processes in the cortex. Zhu et al. (2007) characterized an electrogenic pump in the plasma membrane of xylem parenchyma that was not directly involved in the loading of ions, but contributed to the establishment of membrane potentials, such that electroneutral salt transport and acid release can proceed. These assumptions can be supported by the present analysis, since the slopes for \( \text{loading of the xylem} \) from the root tissue are mostly below 1. They are also supported by the comparison of concentrations in roots and xylem root pressure saps (Fig. 1C).

\( \text{Ca}^{2+} \) seems to be a special case, since no statistical relations were found between the rhizosphere and root, root and xylem or between phloem and root, but a correlation between nutrient solution and xylem sap was seen, with a slope approximating 1. Reasons may be that uptake is restricted to the root tip, and an apoplastic pathway for radial transport of \( \text{Ca}^{2+} \) in the root for xylem loading cannot be excluded (Clarkson and Hanson, 1980; White, 2001). Generally, the identification of genes encoding \( \text{Ca}^{2+} \) influx channels in plants is still a problem (Mäser et al., 2001). White and Broadley (2003) list several gene families encoding putative \( \text{Ca} \) channels. Especially for the long-distance transport of \( \text{Ca}^{2+} \), however, many unsolved questions remain (White, 2001). Once taken up by a plant cell, the mobility of intra- and intercellular \( \text{Ca}^{2+} \) is relatively low (Clarkson and Hanson, 1980; Hirschi, 2004). Similarly, the molecular details of \( \text{Mg}^{2+} \) transport seem to be poorly understood (Shaull, 2002). It seems highly likely that many gene families are involved in \( \text{Mg}^{2+} \) transport in plants (Gardner, 2003).

**Correlation between xylem saps, phloem saps and leaves**

As shown before for the xylem, the loading of the phloem from the source tissue, in the present case the bulk root or leaf material, seems to follow chemical gradients, since the calculated slopes (from 0.01 ± 0.001 for \( \text{Ca}^{2+} \) up to 0.87 ± 0.11 for \( \text{Na}^+ \)) were always below 1. Including data from the axes (Table 2b), the flowing solution in the sieve tubes is less concentrated than source, sink, and transit tissue. The only, but most important, difference is sucrose in the sieve tube sap, which is highly concentrated. The bulk material of root or leaf may be a rough estimate as a 'source tissue' for xylem and phloem loading, since only a few cells are directly connected to the xylem elements or companion cell/sieve tube complexes. On the other hand, there are only few tissues in plants which are symplastically and apoplastically isolated.

While \( \text{Ca}^{2+} \) and \( \text{NO}_3^- \) are found in low concentrations in phloem sap, other elements such as \( \text{N} \), \( \text{K}^+ \), and \( \text{S} \) are found in high concentrations in phloem saps and their phloem mobility is considered high (Marschner, 1995). For the potentially toxic ion \( \text{Na}^+ \), the highest slope (0.87 ± 0.11) was found for the effect of leaf tissue on sieve tube sap concentration, indicating an effective retrieval from leaves and export to the root. While excess \( \text{Cl}^- \) may be problematic in woody plants (citrus and grapevine), \( \text{Na}^+ \) is considered to be the more significant player in effecting toxic damage, especially so in leaves (White and Broadley, 2001; Tester and Davenport, 2003; Munns, 2005). In glycophytes, tolerance to salinity depends on mechanisms to avoid high \( \text{Na}^+ \) concentration in leaves, which includes restricting uptake in roots and transport to shoot (loading and reloading from the xylem, Shi et al., 2002), while...
maintaining recycling from the shoot in the phloem. The capacity to exclude Na\(^+\) and Cl\(^-\) from the xylem is correlated with salt tolerance (Teakle et al., 2007). Davenport et al. (2007) demonstrated that a Na\(^+\) transporter (ATHKT1) appears to control both retrieval of Na\(^+\) from the xylem and root vacuolar loading. Na\(^+\) recycling via the phloem seems to be of importance for salt tolerance (Berthomieu et al., 2003), and HKT genes have been implicated in this as well. The present study revealed evidence for all three assumptions. The slopes for Na\(^+\) from the nutrient solution to the root tissue and xylem sap, as well as from xylem sap to leaf tissue (Fig. 1) were found to be relatively low, but a relatively high slope was seen from the leaf tissue to phloem sap (Fig. 2).

The forces (hydrostatic pressure differences) that drive phloem transport and dictate the direction of flow originate in the source–sink relations between the phloem and its surrounding tissue (van Bel, 1993, 2003; Komor, 2000; Patrick et al., 2001; Lalonde et al., 2003; Thompson and Holbrook, 2003). Due to molecular studies, numerous carriers, pumps, and channels in the plasma membrane of the sieve tubes are known to be responsible for phloem loading, particularly for sugars, but also for amino acids (for reviews see Van Bel, 1993, 2003; Patrick et al., 2001; Lalonde et al., 2003, 2004). In addition, K\(^+\) channels (Véry and Sentenac, 2003; Chérel, 2004; Ashley et al., 2006), Na\(^+\) transporters (Berthomieu et al., 2003; Munns, 2005), sulphate transporters (Takahashi et al., 2000; Yoshimoto et al., 2003), and Pi transporters (Raghothama, 1999) have been found and characterized in phloem tissue. Volk and Franceschi (2000) found evidence that Ca\(^{2+}\) activity is higher in sieve tubes than in adjacent cells, and related this observation to the activity of Ca\(^{2+}\) channels. However, only sucrose, and probably some amino acids, are loaded apoplastically into the sieve tube/companion cell complexes, by proton symporters (Lalonde et al., 2003). It was demonstrated that phloem-mediated carbon export is correlated with the sucrose concentration in green leaves (Komor, 2000).

**Uptake, transport, and partitioning of elements and effects of nutrient deficiency**

For C, N, K\(^+\), Ca\(^{2+}\), and Mg\(^{2+}\) complete correlating flow models between roots and shoots were found which included a statistically significant connection between uptake, incorporation in root tissue, xylem flow, increment in shoot tissue, and phloem flow. In the case of Na\(^+\) and Cl\(^-\) no statistically significant correlation between uptake and xylem transport was detected. In addition, the phloem flow was not statistically connected to the increments (processes) in roots.

The major portion of most of the investigated elements was incorporated in the shoots of *Ricinus* during the experimental period following uptake: Ca (79% of uptake) >N (75%) >Mg (61%) >K (56%) >C (44% of uptake, 67% of totally incorporated C). This pattern is well documented for N. The shoot consumes the largest part of N in several species: 60% in ryegrass (Bowman and Paul, 1988), 71% in lupin (Pate et al., 1979a; Jeschke et al., 1985), 70–92% in wheat (Lambers et al., 1982; Simpson et al., 1982; Larsson et al., 1991). Most of the N taken up was initially transported to the shoot as observed previously in wheat and barley (Lambers et al., 1982; Larsson et al., 1991; Agrell et al., 1994). Due to a different recycling in the phloem, in well-fed wheat 11% (Lambers et al., 1982) or 10–17% (Larsson et al., 1991), but also 60% (Cooper and Clarkson, 1989) of the xylem-borne N was found to be recycled in the phloem back to roots.

The pattern in well-fed plants, that most acquired minerals are accumulated in the shoot during vegetative growth, changes in favour of the root when nutrients are limited. Increased root growth has been detected repeatedly under nutrient deficiency (Clarkson and Hanson, 1980; Marschner, 1995; Raghothama, 1999; Lacointe, 2000; Forde, 2002b; Wissuwa et al., 2005; Hermans et al., 2006). Under N deficiency, this has frequently been observed and discussed in terms of efforts to increase the interception of roots with soil N (Rufy et al., 1990; Duarte and Larsson, 1993; Fetene et al., 1993; Lacointe, 2000). Consequently, relatively more N is needed to be incorporated in the roots of many species (Pate et al., 1984; Rufy et al., 1990; Duarte and Larsson, 1993; Agrell et al., 1994; Peuke et al., 1994). One reason for this is that in N-limited plants higher retranslocation from the shoot is observed (Pate et al., 1979b; Lambers et al., 1982; Rufy et al., 1990), and even a net export of N from the shoot has been found (Pate et al., 1984; Peuke et al., 1994). Similar effects to those seen under N deprivation (Peuke et al., 1994) have also been observed under P- (Jeschke et al., 1996) and K\(^+\) limitation (Peuke et al., 2002) in *Ricinus*. By contrast, under conditions of salinity, relatively more N was incorporated in the shoot in lupin (Jeschke et al., 1992), while no such effects were seen in bean and cotton (Gouia et al., 1994).

Hermans et al. (2006) postulated an increase in carbohydrate transport to the roots in the cases of N and P limitation, but not under K\(^+\) or Mg\(^{2+}\) deficiency. Our former results confirm this for N (Peuke et al., 1994) and P deficiency (Jeschke et al., 1996), although it was also documented for K\(^+\) limitation (Peuke et al., 2002), where increased C export via the phloem was observed. These studies also demonstrated that other nutrients were preferentially accumulated in root tissues.

The uptake of C by photosynthesis was very well correlated with those of other nutrients, demonstrating that plants can perform photosynthesis when they are well supplied with nutrients. The limitation of an essential nutrient, in general, results in decreased photosynthesis (Paul and Driscoll, 1997; Wissuwa et al., 2005) and in lowered uptake of other ions. This was true for N-deficiency in *Ricinus* for all other essential nutrients: K\(^+\), Ca\(^{2+}\), Mg\(^{2+}\) (Peuke et al., 1994). Under P deficiency (Jeschke et al., 1996), and similarly K\(^+\) limitation (Peuke et al., 2002), photosynthesis and N uptake were inhibited. However, Wissuwa et al. (2005) pointed out that, even under severe P deficiency, photosynthesis produced enough assimilate for
growth. Therefore, reduced growth was more due to limited minerals than to photosynthesis.

On the contrary, for the purpose of charge balance, the uptake of a given ion may also be coupled to the enhanced uptake of others. This was Cl⁻ in the case of imposing low or no nitrate pedospherically (N deficiency: Peuke et al., 1994, ammonium nutrition: Peuke and Jeschke, 1993; shoot application: Peuke et al., 1998b). Under K⁺ limitation, the uptake of Ca²⁺ and Mg²⁺ was about 120% and that of Na⁺ even 244% of the control (full-strength K⁺ 1.3 mM). The sum of charges from these uptake events will compensate for the uptake of the limited ion (Peuke et al., 2002).

For many years the idea has existed that nutrient transport systems in the roots are regulated by ‘demand of the shoot’ (Marschner, 1995). It might be hypothesized that the shoot is the site where partitioning of N is determined. Since the amount of the recycled N is normally more than enough to supply the roots, Lambers et al. (1982) suggested that the distribution of N is determined in the shoot. Gojon et al. (1986) showed that N status of the roots was highly dependent on translocation from the leaves. However, contrary to these assumptions, N deficiency can sometimes lead to an increase rather than a decline in amino acid cycling. A number of studies postulated an effect of nutrients recirculated via the phloem on uptake in roots. This has been proposed for N, particularly for nitrate uptake (Imsande and Touraine, 1994; Forde, 2002a, b; Miller et al., 2007). NO₃⁻ is not only a major N source for the nutrition of plants, it also acts as a signal to modulate plant metabolism and development (Crawford and Glass, 1998). However, it has been questioned whether nitrate concentration in the root itself can regulate nitrate uptake, and it was proposed that sugars delivered from the shoot to the root may be the chief signals (Rideout and Raper, 1993). Specifically, a role for sucrose in regulating expression of nitrate transporter genes has been proposed (Forde, 2002b). Further, several amino acids recycled in the phloem may play a key role in N uptake in roots (Cooper and Clarkson, 1989).

Feedback from the leaf to the root occurs more specifically via the concentrations of special compounds, rather than the bulk flow of an element. In the present study, positive correlations between flows were demonstrated, resulting in high uptake as well as in high phloem flow. Therefore, negative feedback of the import of an element via the phloem into the root on the uptake may be excluded by the present findings. Frequently, amino acids, particularly glutamine, are implicated, although this is likely to depend on the species (Tillard et al., 1998; Gessler et al., 1998). However, a positive correlation between glutamine (slope 3.0; \( r^2 = 0.49 \)) or asparagine (slope 24; \( r^2 = 0.83 \)) concentration in phloem sap and nitrate uptake was detected in Ricinus (data not shown). Similarly to amino acids and amides for N, glutathione, as a reduced S compound, may play a key role in the regulation of S uptake. The inhibiting effect of glutathione on sulphate uptake and xylem loading was described by Herschbach and Rennenberg (1991). The sulphate to glutathione ratio in the phloem sap may be the shoot-borne long-distance signal controlling sulphate uptake and loading into the xylem (Herschbach et al., 2000). Buchner et al. (2004) stated that many sulphate transporters are regulated by nutritional status for optimal transport, as is the case for Pi transporters and P stress (Raghothama, 1999; Rausch and Bucher, 2002; Smith et al., 2003). Low K⁺ status triggers the expression of high-affinity transporters (Ashley et al., 2006), and White (1997) assumed a negative feedback via K⁺ recycling in the phloem. However, in the case of K⁺, in contrast to N or S, a special form or ratio in the phloem sap cannot be the regulating signal, since K⁺ only exists in the plant in the cationic form. Similarly, Pi is not reduced in plants. Accordingly, no correlations between K⁺ and Pi (data not shown) concentrations in phloem sieve tube saps and uptake as well as photosynthesis and growth were detected in the present study (Fig. 7).

Due to nutrient limitation, sugars are accumulating in all or different plant parts (Caputo and Barneix, 1997; Paul and Driscoll, 1997; Lalonde et al., 1999; Roitsch, 1999; Paul and Foyer, 2001; Rolland et al., 2002; Hermans et al., 2006). Sugars have multiple functions in plants as energy substrates, carbon sources, osmotica, and signals (Lalonde et al., 1999; Rolland et al., 2002; Hermans et al., 2006). It is widely accepted that sugars act as signals in response to biotic and abiotic factors, including nutrient deficiency, resulting in the down-regulation of photosynthesis genes and the up-regulation of storage in response to high sugar concentration (Lalonde et al., 1999; Roitsch, 1999; Paul and Foyer, 2001; Rolland et al., 2002; Hermans et al., 2006; Hammond and White, 2008). Similarly, nitrate has been discussed as a metabolic signal with direct action on genes, locally, and involving long-range signalling pathways (Crawford and Glass, 1998; Forde, 2002a, b; Miller et al., 2007). However, on the basis of the present data set, the effect of nitrate concentration in phloem sap (slope 67, \( r^2 = 0.42 \)) or in root tissue (slope 2.4, \( r^2 = 0.34 \)) on nitrate uptake was relatively low, but always positive (data not shown).

A number of reports support the assumption that sink strength or activity is regulating phloem carbon transport and/or, finally, photosynthesis (Paul and Foyer, 2001; Minchin et al., 2002; Wissuwa et al., 2005; McCormick et al., 2006). The increased transport of sucrose from shoot to root has also been implicated in the responses of root architecture and the release of organic acids to plant nutritional status (Hammond and White, 2008). Different plant parts have different demands on mineral nutrient supply for growth. Leaves have a higher element to C ratio (mol to mol) than roots for K and Mg (75 K and 203 Mg per C) than roots (37 K and 143 Mg per C) (Table 2). On the other hand, in case of N and Ca, this ratio favours the roots (27 N and 172 Ca per C) compared to the leaves (15 N and 95 Ca per C). Theoretically, in the case of nutritional limitation, a plant organ with a lower ratio should grow larger or longer. However, as demonstrated for N in the present paper, the situation is not that straightforward.
Within higher plants, carbohydrates are distributed by the phloem in the form of sugars during the growth period. Therefore, it is not surprising that sugar concentration increases in plants, including in the sieve tubes, if growth is reduced or inhibited as observed here due to mineral deficiency. The question remains if the sugar concentration in the phloem is a consequence only or a signal. The sugar concentration in phloem sap was clearly negatively correlated to net photosynthesis, growth, as well as N and K⁺ uptake (Fig. 7).

Nitrate assimilation

The present observations regarding nitrate concentrations and transport must be interpreted with regard to nitrate reduction in tissues. The site of nitrate reduction depends on plant species and environmental conditions (Pate, 1973; Andrews, 1986). In several species like barley, maize, and cocksfoot (Dactylis glomerata), a relatively high proportion of nitrate is reduced in the shoot (Lewis et al., 1982; Gojon et al., 1986; Murphy and Lewis, 1987; Andrews et al., 1992). By contrast, the root is the major site of nitrate reduction, for example, in bean, non-nodulated lupin, oat, barley, rye, wheat, and peach (Allen et al., 1988; Atkins et al., 1979; Andrews et al., 1992; Gojon et al., 1991). In woody plants, nitrate reductase has also been found in the leaves, but root assimilation is generally predominant, in particular, in Gymnosperms and members of the Proteaceae (Smirnoff et al., 1984). Generally, relatively more nitrate is reduced in the shoots as nitrate supply is increased (Atkins et al., 1979, 1980; Sutherland et al., 1985; Andrews, 1986; Rufty et al., 1990; Gojon et al., 1991; Andrews et al., 1992; and the present results in Ricinus). After recovery from N deficiency or in the induction phase (for nitrate uptake and reduction), nitrate is reduced initially in the root but later shifted, in the steady-state phase, toward the shoot (Bowman and Paul, 1988; Gojon et al., 1986).

The site of nitrate reduction, seems to be strongly affected by the conditions determining the transport of nitrate and by the ionic composition in the xylem. Nitrate is not only a source of N, but may also function as an osmoticum and as an important negative charge carrier in the xylem. Generally, the transport of nitrate in the xylem is closely related to the availability of a counterion. The importance of K⁺ for the uptake, translocation, and reduction of nitrate is well established (Blevins et al., 1978; Barneix and Breteler, 1985; Förster and Jeschke, 1993; Casadesús et al., 1995). The major role of K⁺ in this context is to act as a counterion in the xylem transport of nitrate.

Concluding remarks

In the present statistical re-evaluation of earlier studies, a number of correlations were detected. However, this was not true for all the investigated elements. Essential nutrients/elements seem to be taken up, transported, and cycled within a plant in a well-correlated framework. Consequently, for C, N, K⁺, Mg²⁺, and Ca²⁺, general models could be presented in which the most important processes of uptake, xylem and phloem transport, and incorporation in roots and shoots are well correlated for these elements. By contrast, potentially toxic elements like Na⁺ or Cl⁻ are not so well correlated. Only phloem and xylem flows were correlated with each other, demonstrating an efficient recycling of undesirable elements from the shoots.

The hypothesis that the phloem plays an important role in the delivery of signals to distantly located plant organs can be supported by the present study. This information can be in the form of ions or elements, phytohormones, or even electrical signals. The concentration of solutes in the phloem sieve tube saps were very well correlated with the concentrations in leaf tissue for mobile as well as less mobile nutrients. Therefore, the composition of phloem saps is a good indicator for the nutritional conditions in leaves. The assumption that phloem recycling of nutrients to the roots may regulate uptake there cannot be supported. Under conditions of nutrient limitation, growth seems to be more sensitive than photosynthesis (Wissuwa et al., 2005; Keller, 2005). Consequently, sugars can accumulate in plants due to nutrient deficiency and, since the phloem is the path for sugar distribution, it may be centrally involved in signalling in this important context. The sugar concentration in phloem saps correlated strongly and negatively with the uptake of essential nutrients. The question remains if this is only a consequence of the insufficient use of carbohydrates in plants or a more ubiquitous signal for stress in plants. In any case, high sugar concentrations in phloem saps indicate nutritional stress, while high nutrient concentrations in phloem saps indicate well-supplied leaves.

Acknowledgements

I thank Dr Herbert J Kronzucker, University of Toronto for critical reading of the manuscript and his efforts to improve the quality of this paper.

References


Downloaded from https://academic.oup.com/jxb/article-abstract/61/3/635/476997 by guest on 23 February 2019


Arnozis PA, Findenegg GR. 1986. Electrical charge balance in the xylem sap of beet and Sorghum plants grown with either NO₃ or NH₄ nitrogen. Journal of Plant Physiology 125, 441–449.


Herschbach C, van der Zalm E, Schneider A, Jouanin L, De Kok LJ, Rennenberg H. 2000. Regulation of sulphur nutrition in wild-type and transgenic poplar over-expressing γ-glutamylcysteine synthetase in the cytosol as affected by atmospheric H$_2$S. *Plant Physiology* 124, 461–473.


Peuke AD, Jeschke WD, Hartung W. 1998b. Foliar application of nitrate or ammonium as sole nitrogen supply in Ricinus communis. II. The flows of cations, chloride and abscisic acid. New Phytologist 140, 625–636.


Schurr U, Schulze E-D. 1995. The concentration of xylem sap constituents in root exudate, and in sap from intact, transpiring castor


