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Effect of mineral nutritional status on shoot–root partitioning of photoassimilates and cycling of mineral nutrients

H. Marschner[1,4], E. A. Kirkby[2] and I. Cakmak[3]

[1] *Universität Hohenheim, Institut für Pflanzenernährung, D-70593 Stuttgart, Germany*

[2] *Department of Applied Biology, University of Leeds, Leeds LS2 9JT, UK*

[3] *Department of Soil Science and Plant Nutrition, University of Cukurova, 01330 Adana, Turkey*

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Abstract

Mineral nutrients taken up by the roots are, as a rule, transported in the xylem to the shoot, and photoassimilates transported in the phloem to the roots. According to the Thornley model of photosynthate partitioning, nutrient deficiencies should favour photosynthate partitioning to the roots. Examples are cited to show that this preferential partitioning is dependent on phloem mobility and hence on nutrient cycling from shoot to roots. Thus, root growth is enhanced under nitrogen and phosphorus deficiencies, but not under deficiencies of nutrients of low mobility in the phloem, such as calcium and boron. Enhanced root growth under nutrient deficiency relies on the import of both photosynthates and mineral nutrients.

Cycling of mineral nutrients serves a number of other functions. These include the root supply of nutrients assimilated in the shoot (nitrate and sulphate reduction), maintenance of cation–anion balance in the shoot, providing an additional driving force for solute volume flow in the phloem and xylem, and acting as a shoot signal to convey nutrient demand to the root.

Cycling of certain mineral nutrients through source leaves has a considerable impact on photosynthate export as demonstrated in impaired export under magnesium, potassium, or zinc deficiencies. Mineral nutrient deficiency can, therefore, affect photosynthate partitioning either directly via phloem loading and transport or indirectly by depressing sink demand.

Key words: Biomass partitioning, phloem mobility, nutrient cycling, cation–anion balance.

Introduction

The limited understanding of the mechanisms that govern the partitioning of captured resources (carbohydrates, mineral nutrients) between different plant parts and organs is considered to be the main factor restricting the development of process-based modelling of whole plant growth (Dewar, 1993; Cannell and Dewar, 1994). For biomass partitioning between shoot and roots, which is the main topic of this contribution, Thornley (1972) has proposed a simple model which is widely used (Wilson, 1988; Cannell and Dewar, 1994). In the model, growth is dependent on the supply of carbon from the shoot and nitrogen from the root, i.e. the flux of carbon from shoot to roots (phloem transport) and that of nitrogen from roots to shoot (xylem transport). The fluxes are dependent on the concentration gradients of carbon and nitrogen between these two compartments, shoot and roots. According to Thornley's model, conditions which lead to an increase in carbon concentration should, therefore, lead to an increase in biomass partitioning towards the roots, whereas an increase in nitrogen concentration should favour biomass partitioning towards the shoot. In principle, the model is also considered suitable to take into account the effects of various environmental factors including mineral nutrients on the shoot:root ratio (Wilson, 1988).

The well-documented increases in both carbon allocation to roots and in the root–shoot dry weight ratio under conditions of nitrogen limitation (Levin *et al.*, 1989; Peuke *et al.*, 1994) are consistent with the Thornley concept, despite nitrogen cycling from the shoot to roots (Cooper and Clarkson, 1989) and the key role played by

[4] To whom correspondence should be addressed. Fax: +49 711 459 3295.

root-borne phytohormones, particularly cytokinins, in the effect of nitrogen supply on the root–shoot ratio (Kuiper, 1988; Kuiper *et al.*, 1989; Fetene and Beck, 1993). Preferential partitioning of photosynthetic carbon to the roots and increase in root–shoot dry weight ratio are also well documented for plants under phosphorus deficiency (Fredeen *et al.*, 1989; Cakmak, 1994). However, the opposite is true, for example, with magnesium or potassium deficiency (Cakmak *et al.*, 1994*a*; Ericsson and Kähr, 1995), indicating that the effect of mineral nutritional status on shoot–root partitioning of photoassimilates and shoot–root dry weight ratio is markedly element-specific. In this paper examples are presented of the effects of various nutrients on photosynthate partitioning giving special emphasis to cycling of mineral nutrients between shoot and roots. These examples take into account the physiological mechanisms which underlie the Thornley model and help to explain its limitations. The term 'cycling' is used here to describe the translocation of nutrients from shoot to roots, i.e. the completion of a full cycle

$$\text{root} \xrightarrow{\text{xylem}} \text{shoot} \xrightarrow{\text{phloem}} \text{root}.$$

When these nutrients are loaded again into the xylem and transported to the shoot, the term 'recycling' is used.

Shoot-root partitioning and phloem mobility

In the simple Thornley source–sink model it is envisaged that roots provide the sole direct source of mineral nutrients. This is true in principle, only for mineral nutrients of very low phloem mobility like calcium, boron, and manganese. According to the model, for plants deficient in these nutrients, photosynthetic carbon might first increase in the shoot and subsequently be preferentially partitioned to the roots and the root–shoot dry weight ratio should increase. Accumulation of carbohydrate in the leaves of plants deficient in calcium (Gossett *et al.*, 1977) or boron (van de Venter and Currier, 1977) is well known, but the predicted shifts in root : shoot ratio are not observed in plants suffering from these deficiencies (Johann, 1957; Cakmak *et al.*, 1995). These findings possibly suggest that retranslocation of mineral nutrients from shoot to roots is at least involved in the preferential partitioning of carbon to the roots under conditions of limited nutrient supply to roots from the external medium. Under manganese deficiency shoot–root dry weight ratio can even increase because of impaired photosynthesis, i.e. a drop in source capacity and thus in carbon supply to the roots (Vielemeyer *et al.*, 1969; Ericsson, 1995).

In contrast to calcium, boron, and manganese, retranslocation of phloem-mobile mineral nutrients such as potassium and nitrogen from shoot to roots together with photosynthetic carbon is a normal feature during ontogenesis (Cooper and Clarkson, 1989; Jeschke and Pate, 1991*a*, *b*). Whilst this retranslocation may serve specific regulatory functions for any particular mineral nutrient, it might also be the consequence (or a side-effect) of the mechanism of phloem loading of photoassimilates (sucrose in particular) in the source leaves (Komor, 1994) and the pressure-flow driven transport of solutes in the sieve tubes to sink organs such as shoot apices and roots (Fig. 1). The specific demand of the various shoot sink organs (e.g. apex, seeds) for solutes delivered through the phloem is adjusted by leakage and retrieval along the pathway and accumulation in, or release by, the adjacent parenchyma cells (Martin, 1989; Grimm *et al.*, 1990; Hayachi and Chino, 1990). Because of the gradients in water potential of the various shoot organs, retranslocation (backflow) of solutes in the xylem from these shoot organs in a basal direction rarely occurs, except in fleshy fruits (Marschner, 1995), for example, of calcium (Mix and Marschner, 1976) and water (Pate *et al.*, 1985).

In contrast to the above-ground sink organs, solutes delivered to the roots by mass flow in the phloem in excess of the demand required for growth and maintenance, can recycle back in the xylem from the roots to the shoot (Fig. 1). In the following discussion, examples are

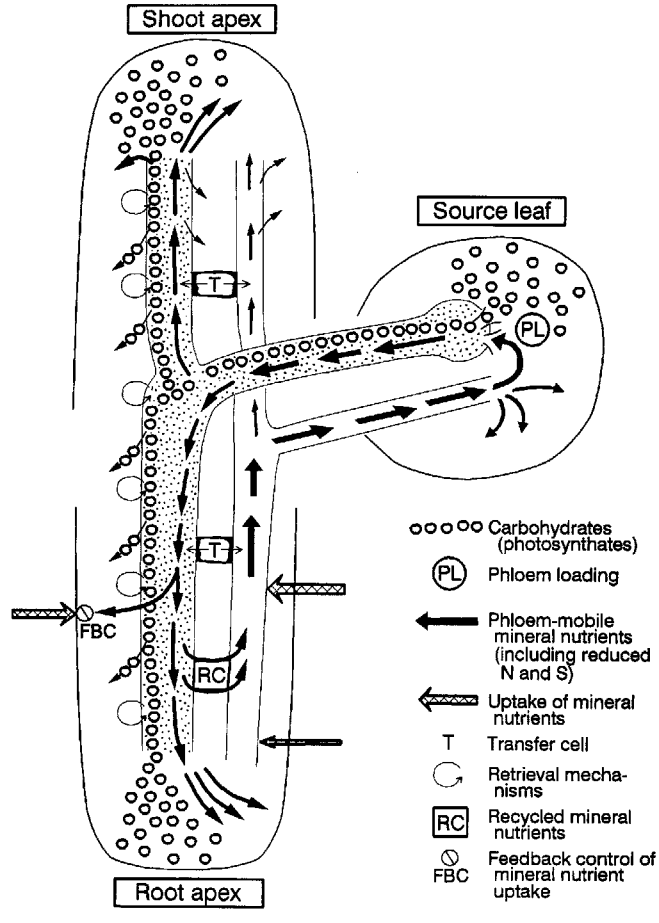

Fig. 1. Model for the partitioning of photoassimilates and mineral nutrients and the cycling and recycling of mineral nutrients in plants.

given for such cycling of mineral nutrients between shoot and roots and their possible regulatory functions, not only for mineral nutrition *per se*, but also allocation of photosynthates between shoot and roots.

Nutrient cycling and nutrient assimilation in the shoot

In plant species which predominantly or exclusively reduce nitrate in the shoots, retranslocation of reduced nitrogen as amino acids in the phloem together with sugars to the roots is required for root growth (Fig. 1). In such instances, the term 'photoassimilates' also includes nitrogen. In nitrate-fed barley plants up to 79% of the nitrogen translocated in the xylem to the shoot was retranslocated in the phloem as reduced nitrogen back to the roots; of this fraction about 21% was incorporated into the root tissue and the remainder recycled back in the xylem to the shoot (Simpson *et al.*, 1982). In young wheat and rye plants, over 60% of the reduced nitrogen in the xylem sap represented a recycling fraction (Cooper and Clarkson, 1989). Even when nitrate reduction takes place in roots, a considerable proportion of the reduced nitrogen transported in the xylem to the shoot is retranslocated in the phloem to the roots and recycles back in the xylem to the shoot (Jeschke and Pate, 1991*a*).

In general, reduction of sulphate takes place predominantly in leaves (Fankhauser and Brunold, 1978) and reduced sulphur is retranslocated in the phloem to the sink sites including roots (Herschbach and Rennenberg, 1994). In wheat, throughout ontogenesis, 12–33% of the sulphur recycles back in the xylem (Larsson *et al.*, 1991). Thus, just as a substantial portion of the reduced nitrogen in the xylem sap will have already recycled at least once through the plant, the same may also hold true for reduced sulphur (Schupp *et al.*, 1991).

In ammonium-fed plants most ammonium is assimilated in the roots (Pilbeam and Kirkby, 1992) and translocated as amino acids to the shoot. Part of this amino-N is directly loaded from the xylem into the phloem along the pathway to the shoot (Fig. 1, transfer cells) and transferred to the sink sites in the shoot (Da Silva *et al.*, 1990). Another part may follow a similar fate as described for nitrate after reduction, namely retranslocation together with photoassimilates back to the roots (Table 1). Although the amount of reduced nitrogen retranslocated to the roots is lower in ammonium-fed than in nitrate-fed plants (0.26/0.81 mmol), this amount, nevertheless, exceeds the amount of total nitrogen accumulated in the roots of ammonium-fed plants (0.20 mmol). Thus, in ammonium-fed plants, part of the reduced nitrogen in the xylem sap can represent a cycling fraction (Peuke and Jeschke, 1993).

Ammonium assimilation in roots has a large requirement for carbon skeletons of which only a small fraction

Table 1. *Cycling of nitrogen between roots and shoot of nitrate and ammonium-fed maize plants (C. Engels, unpublished)*

	N supply to the roots	
	NO_3^-	NH_4^+
	(mmol N plant^{-1} d^{-1})	
Root uptake	0.98	1.06
Root accumulation/incorporation	0.21	0.20
Xylem transport to shoot	1.58	1.12
Shoot accumulation/incorporation	0.77	0.86
Phloem export to roots	0.81	0.26

is provided by increased PEP carboxylase activity and 'CO_2 dark fixation' (Cramer *et al.*, 1993). For ammonium assimilation in roots the photosynthetically fixed carbon provided by phloem import can become a limiting factor, and lead to impaired root growth. This is particularly the case at high root zone temperatures which lead to correspondingly high root respiration rates (Kafkafi, 1990), and which are always higher in ammonium as compared with nitrate-fed plants (Peuke and Jeschke, 1993).

Nutrient cycling, regulatory functions

Nutrient cycling from shoot to roots (Fig. 1) may also serve other important functions such as in the maintenance of cation-anion balance in the shoot, providing an additional driving force for solute volume flow in the phloem and in the xylem, and acting as a shoot signal to convey shoot demand for a particular mineral nutrient to regulate uptake from the external medium and xylem loading (Engels and Marschner, 1992).

Nitrate reduction in the shoot produces equivalent amounts of organic acid anions for charge balance. These organic acids are either stored together with cations in the vacuoles of leaves, or are retranslocated in the phloem together with potassium to the roots (Fig. 2). Retranslocation of potassium malate is the most well-known mechanism. After decarboxylation of the organic acids, potassium can again act as the counter-ion for nitrate transport in the xylem to the shoot. In soybean, in which about 90% of the nitrate is reduced in the shoot, experimental data are in full agreement with this model (Touraine *et al.*, 1990). In addition, both light and stem feeding of potassium malate enhance net release of HCO_3^- and net uptake of nitrate.

Potassium concentrations in the phloem sap are usually in the range of 50–150 mol m^{-3}. Apoplasmic phloem loading of sucrose in source leaves mediated by a proton-sucrose co-transport requires a steep transmembrane pH gradient and maintenance of high potassium concentrations in the sieve tubes. High potassium concentrations therefore enhance phloem loading of sucrose and also amino acids (Baker *et al.*, 1980). High potassium concentrations in the sieve tubes also substantially contribute to

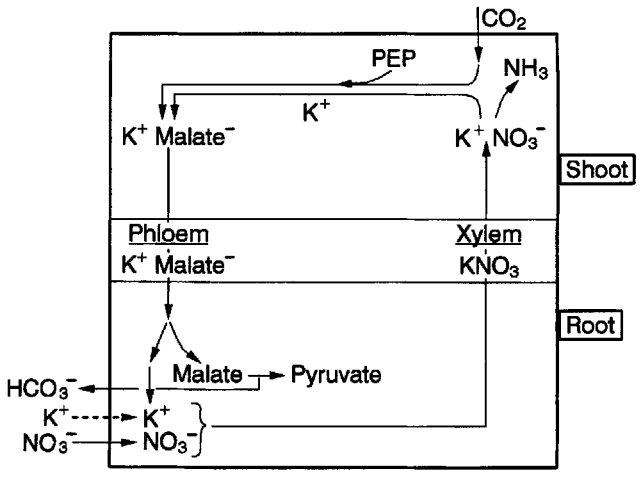

Fig. 2. Model for the circulation of potassium between roots and shoot in relation to nitrate and malate transport (PEP, phosphoenol pyruvate) (based on Ben-Zioni *et al.*, 1971, and Kirkby and Knight, 1977).

the volume flow rates (Table 2) and, thus, enhance photosynthate transport from source to sink (Hartt, 1969; Collins and Duke, 1981). These high concentrations of potassium are balanced by both organic and inorganic anions, presumably including bicarbonate.

Typically, in shoot organs the concentration and composition of the phloem sap changes along the pathway from source to sink by release and retrieval (Fig. 1). Inverse changes in concentrations of sucrose and potassium (Hayashi and Chino, 1990) may provide an important means of fine regulation of the pressure-driven solute volume flow in the phloem from source leaves to sinks such as developing cereal grains with high sucrose but low potassium demand (Martin, 1989).

These various functions of potassium in photosynthate transport from source to sink are presumably a main reason for the high cycling of potassium between shoot and roots (Table 3). In the roots, most of the phloem-derived potassium is released again to the xylem, i.e. recycles through the roots, and can act again as the counter-ion for anions (e.g. nitrate) and as an osmotic driving force for root pressure-driven xylem transport (Fig. 1). Compared with potassium, not only is the concentration of magnesium in the phloem sap much lower (usually ~5 mol m^{-3}), but so too is the proportion recycling through the roots (Table 3), suggesting substantial utilization of magnesium for root growth. Retranslocation of sodium from shoot to roots most likely functions mainly to maintain a low shoot concentration of sodium. Retranslocation of sodium from shoot to the roots and substantial net release into the external solution of this phloem-derived sodium is a typical feature in many natrophobic plant species (Lessani and Marschner, 1978).

Retranslocation of readily phloem-mobile mineral nutrients like potassium, phosphorus or reduced nitrogen from the shoot to the roots is also required to cover the high demand of apical root zones for growth. In fast-growing roots the uptake capacity of apical root zones for these mineral nutrients from the external solution is insufficient and most of these required mineral nutrients have to be supplied either from basal root zones (Marschner and Richter, 1973), or, together with photosynthates from the shoot. Presumably the latter source of supply is quantitatively more important (Fig. 1). Jeschke and Wolf (1988) demonstrated that potassium retranslocation via the phloem can supply all of the potasssium required for root growth. Retranslocation of mineral nutrients from shoot to roots might also be important in smoothing out fluctuations in the external supply (Cooper and Clarkson, 1989; Komor, 1994), thereby maintaining rapid root growth in soil-grown plants despite spatial and time-dependent heterogenity in external supply.

Mineral nutrients like potassium and nitrogen also provide the major osmotic driving forces for xylem volume flow from roots to the shoot ('root pressure'). Recycling of these mineral nutrients (Fig. 1) might therefore play a substantial role in maintaining xylem volume flow, particularly in field-grown plants late in the season when nutrient availability in the rooting zone decreases because of depletion (Engels *et al.*, 1994). In field-grown maize, at flowering the concentration of sucrose in the xylem exudate can be substantial (Canny and McCully, 1989), reaching concentrations between 20 and 44 mol m^{-3} (Table 4), thus, becoming a major component as

Table 2. *Effect of potassium supply to castor bean plants on the composition of phloem sap and rate of phloem sap exudation (based on Mengel and Haeder, 1977)*

	Potassium supply in the growth medium	
	0.4 mol m^{-3}	1.0 mol m^{-3}
Phloem sap concentration (mol m^{-3})		
Potassium	47	66
Sucrose	228	238
Osmotic potentials (MPa)	1.25	1.45
Exudation rate (ml (3 h)$^{-1}$)	1.35	2.49

Table 3. *Partitioning, translocation and cycling of mineral elements in* Ricinus communis *L. (based on Jeschke and Pate, 1991*b)

Parameter	Proportion of total uptake (%)			
	K	Na	Mg	Ca
Import (leaf lamina) through xylem	138	11	51	39
Export (leaf lamina) through phloem	93	9	13	2
Phloem transport to roots	85	9	15	1
Recycling through roots	78	–[a]	7	–[a]

[a] Could not be quantified.

an osmotic driving force for xylem volume flow. Remobilization of sugars in the roots might probably account for the sugars in the xylem (Canny and McCully, 1988). However, the marked increase in the concentrations of both sugars and reduced nitrogen in the xylem exudate of plants where the cob as a major sink had been removed (Table 4) suggests that in annual species recycling of photosynthates such as sucrose from roots to shoot may also become important, particularly in plants with a large source-sink ratio (Komor, 1994).

Cycling of mineral nutrients from shoot to the roots may also act as an important signal of feedback control for nutrient uptake (Fig. 1), depending on plant demand for growth (Drew and Saker, 1984). Evidence for such a role has been found for potassium (Drew *et al.*, 1990), phosphorus (Drew *et al.*, 1984), iron (Maas *et al.*, 1988; Grusak, 1995), sulphur (Herschbach and Rennenberg, 1994; Herschbach *et al.*, 1995) and amino acids on nitrate uptake (Müller and Touraine, 1992). Zinc deficiency-induced phosphorus toxicity is another example which demonstrates the role of cycling of mineral nutrients in providing a feedback control. In zinc-deficient plants, cycling of phosphorus from shoot to roots is impaired and, thus, also the negative feedback control which restricts phosphate uptake from the external solution. Thus under zinc deficiency phosphate continues to be supplied via the xylem to the shoot, which is already high in phosphorus, and phosphorus toxicity results (Marschner and Cakmak, 1986).

Cycling of mineral nutrients from shoot to roots as a signal of feedback control seems to be of particular importance in nodulated legumes. Nitrogenase activity in the nodules is regulated not only by phloem import of carbohydrates and water, and xylem export of reduced nitrogen (Streeter, 1993) in general, but most likely also by phloem import of reduced nitrogen (Parsons *et al.*, 1993). Negative feedback control of nitrogenase activity in nodules might therefore be achieved by increasing mineral nitrogen supply to the roots (Parsons *et al.*, 1993) or by lowering shoot demand for reduced nitrogen as, for example, under drought stress (Schubert *et al.*, 1995).

Table 4. *Effect of additional late N fertilization (+N) or cob removal after anthesis (−Cob) on xylem exudation rate and exudate composition of field-grown maize 93 and 105 d (compiled) after sowing (based on Engels* et al., *1994)*

Parameter	Control	+N	−Cob
Exudation (ml (3 h)$^{-1}$ plant^{-1})	3.2	2.9	3.8
Potassium (mol m^{-3})	11.5	16.4	13.4
Nitrate (mol m^{-3})	12.9	17.3	9.1
Reduced N (mol m^{-3})	37.4	42.2	63.6
Reduced N (% of total)	69	66	86
Reducing sugars (mol m^{-3})	4.2	5.3	9.6
Sucrose (mol m^{-3})	19.9	26.8	44.5

Nutrient deficiency-induced alteration in photosynthate partitioning

Nutrient deficiency may not only affect the provision of photosynthates by decreasing source capacity (leaf area index, leaf area duration), but also by altering photosynthate partitioning between the source leaves and various sinks (Fig. 1). Some examples are given here showing nutrient deficiency-induced alterations in partitioning of photosynthates during the vegetative growth of plants.

Under nitrogen deficiency, the increase in root–shoot dry weight ratio (Engels and Marschner, 1995; Marschner, 1995) is not only caused by preferential phloem export of sucrose to the roots, but also by export of nitrogen, which can exceed the xylem import of nitrogen from roots to the shoot (Peuke *et al.*, 1994). Similarly, under phosphorus deficiency root–shoot dry weight ratio increases, in soybean for example, from 0.24 in sufficient to 1.0 in deficient plants (Fredeen *et al.*, 1989). This increase in root–shoot dry weight ratio might also be achieved in part by enhanced net retranslocation of phosphorus from shoot to roots in deficient plants (Smith *et al.*, 1990). These results suggest that under nitrogen or phosphorus deficiency not only is a higher proportion of the nutrients taken up from the substrate retained in the roots, as predicted by the Thornley model, but also that cycling from shoot to roots provides additional nitrogen and phosphorus to the roots. This cycled fraction of these nutrients may not only contribute to, but may even cause, the shift in sink strength for photosynthates of the roots at the expense of the shoot apex. Under phosphorus deficiency, despite strongly impaired shoot growth, the chlorophyll concentrations and photosynthetic activity of the source leaves are usually at least maintained (Fredeen *et al.*, 1989; Cakmak, 1994), ensuring continuous photosynthate export to the roots as a dominant sink in the deficient plants.

A typical response to phosphorus deficiency is shown in Table 5. In comparison with the control, shoot dry weight is much lower in the phosphorus-deficient plants, particularly because of the strongly inhibited growth of the shoot apex (Cakmak, 1994). However, in the primary leaves (source leaves) sucrose concentration and sucrose export in phloem exudate are maintained and, therefore, root growth is similar in the deficient and phosphorus-sufficient control plants.

Plants deficient in either potassium or magnesium behave differently in respect to photosynthate partitioning between shoot and roots as compared with plants deficient in nitrogen (Anderson, 1988) or phosphorus (Table 5). Although phloem mobility as well as cycling of potassium and magnesium are similarly high as for phosphorus and nitrogen (Table 3), root–shoot dry weight ratio decreases rather than increases under potassium or magnesium deficiency (Table 5). For plants deficient is magnesium, a

Table 5. *Effect of sufficient (control) and deficient nutrient supply on plant dry weight, chlorophyll and sucrose concentration in, and phloem export from, primary leaves of* Phaseolus vulgaris *L. (compiled data from Cakmak, 1994, and Cakmak* et al., *1994*a, b)

Treatment	Dry wt. (g plant^{-1})		Chlorophyll (mg g^{-1} DM)	Sucrose (glucose equiv.)	
	Roots	Shoot		Leaves (mg g^{-1} DW)	Phloem exudate (mg g^{-1} FW (8 h)$^{-1}$)
Control	0.52	2.5	11.2	16.2	3.5
P deficiency	0.48	0.8	12.0	20.0	2.9
K deficiency	0.16	1.2	3.7	75.8	1.7
Mg deficiency	0.13	1.5	3.6	108.3	0.7

decrease in root–shoot dry weight ratio is often observed (Ericsson and Kähr, 1995; Marschner, 1995). Despite the requirement of both these nutrients in various steps in photosynthesis, this decrease in magnesium- and potassium-deficient plants is not caused by impaired photosynthesis *per se*, but results from impaired photosynthate export in the phloem, leading to the accumulation of carbohydrates such as sucrose in the source leaves (Fischer and Bremer, 1993), despite their much lower chlorophyll concentrations (Table 5). This impaired export is demonstrated in Table 6. Partitioning of non-structural carbohydrates between shoot and roots is strongly altered in the phosphorus-, potassium- and magnesium-deficient plants, and closely correlated with the effect of the respective deficiency on dry matter partitioning between shoot and roots.

Cycling of potassium and magnesium through source leaves is high (Jeschke and Pate, 1991*b*) and essential for photosynthate export in the phloem (Fig. 1). In potassium-deficient source leaves, both phloem loading of photosynthates and subsequent solute volume flow in the sieve tubes were depressed and sucrose accumulated in these leaves (Table 5). In magnesium-deficient source leaves, accumulation of sucrose was particularly high, suggesting specific inhibition of phloem loading of sucrose, probably as the result of low activity of the proton-pumping ATPase at the sieve tube membranes. In magnesium-deficient leaves, not only is the export of sucrose impaired but also that of other solutes such as potassium and particularly amino acids (Table 7). Resupplying magnesium to the roots of deficient plants for only 12 h in the dark period strongly enhanced phloem export of magnesium, sucrose, amino acids, and to some extent potassium. This interdependence of phloem loading and export of sucrose and amino acids is in agreement with results of Winter *et al.* (1992). The data shown in Table 7

Table 6. *Effect of sufficient (control) and deficient nutrient supply on percentage partitioning of non-structural carbohydrates in shoot and roots of* Phaseolus vulgaris *L. (Cakmak* et al. *1994*a)

	Control	P deficiency	K deficiency	Mg deficiency
Shoot	84.3	77.3	96.6	99.2
Roots	15.7	22.7	3.4	0.8

Table 7. *Effect of Mg deficiency and resupply of Mg for 12 h (in the dark) on phloem export of solutes from primary leaves of* Phaseolus vulgaris *L. (Cakmak* et al. *1994*b)

Treatment	Phloem export (g^{-1} leaf FW (8 h)$^{-1}$)			
	Mg (μg)	Sucrose (mg)	Amino acids (mg)	K (mg)
Control (Mg sufficient)	5.19	2.53	0.33	0.19
Mg deficient	0.78	0.46	0.07	0.08
Mg deficient + resupply	2.48	1.80	0.20	0.11

furthermore suggest that this interdependence includes the mineral nutrients potassium and magnesium. Export of photosynthates could thus rapidly deplete potassium and magnesium at the phloem loading sites unless continuously replenished by the bulk leaf tissue. In source leaves, the phloem loading step might, therefore, be particularly sensitive to magnesium and potassium deficiency.

Accumulation of photosynthates in source leaves, as a result of either impaired phloem loading or export under magnesium and potassium deficiency, or impaired sink activity under zinc deficiency (Marschner and Cakmak, 1989), enhances the formation of toxic oxygen species such as superoxide radicals ($O_2^{\cdot-}$) and hydrogen peroxide (Fig. 3). Accordingly, the activity of detoxifying enzymes in source leaves increases under either magnesium or potassium deficiency (Table 8), but not under phosphorus deficiency where less photosynthates are accumulated.

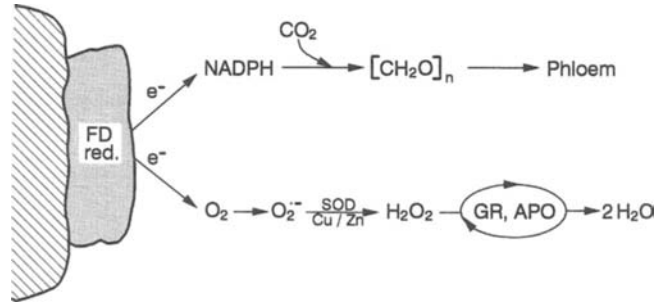

Fig. 3. Alternative utilization of photoreductants for CO_2 assimilation or activation of molecular oxygen, and detoxification (scavenger) systems. SOD, superoxide dismutase; GR, glutathione reductase; APO, ascorbate peroxidase.

Under conditions of high light intensity, however, the production of toxic oxygen species often exceeds the capacity of the detoxifying enzymes leading to photo-oxidation of chloroplast pigments and severe symptoms of chlorosis and necrosis in potassium- and magnesium-deficient leaves. The particularly high light sensitivity of potassium- and magnesium-deficient source leaves can be readily demonstrated by partial shading of the leaf blades, where the shaded plants remain green and the light parts become chlorotic and necrotic (Marschner and Cakmak, 1989). In agreement with this observation, in tobacco and tomato plants with genetically manipulated inhibition of phloem loading of sucrose, accumulation of carbohydrates in the source leaves was associated with severe chlorosis and necrosis of these leaves (Dickinson *et al.*, 1991; Riesmeier *et al.*, 1994).

Zinc deficiency combined with high light intensity, leads to photo-oxidation of chloroplast pigments and, thus, to a particularly evident rapid destruction of functioning of source leaves (Table 9). In zinc-deficient plants, although growth and sink activity of the shoot apex are strongly depressed and carbohydrates accumulate in the source leaves, root growth is not enhanced as would be expected by the Thornley model (Cakmak *et al.*, 1989). Besides the lower export of photosynthates, the activity of Cu/Zn superoxide dismutase (SOD) (Fig. 3) is impaired in zinc-deficient leaves and raises the level of $O_2^{\cdot-}$ in the cells accordingly (Cakmak and Marschner, 1988). The source function of the leaf is thus destroyed.

Table 8. *Activities of antioxidative ($O_2^{\cdot-}$ and H_2O_2 scavenging) enzymes in primary leaves of* Phaseolus vulgaris *L. plants suffering from phosphorus, potassium, and magnesium deficiency (based on Cakmak, 1994)*

Enzyme activity (g^{-1} FW and min.)	Control (sufficient)	Deficient in		
		P	K	Mg
Ascorbate peroxidase (μmol ascorbate)	4.0	2.7	9.2	13.0
Monodehydroascorbate reductase (μmol ascorbate)	1.2	0.4	3.8	4.8
Glutathione reductase (μmol NADPH)	0.28	0.28	0.32	0.80

Conclusions

Partitioning of photosynthates and of mineral nutrients are interconnected in many ways. Solute volume flow in the phloem to sink tissue not only provides photosynthates, but also most of the mineral nutrients required for growth. The demand for photosynthates and mineral nutrients by shoot sinks has to be finely tuned along the pathways because of the absence of recycling. In contrast, in roots no such fine tuning is necessary because of the possibility of recycling. Thus large amounts of nutrients cycle to the roots and recycle back to the shoot in excess of root demand thereby serving various functions. This cycling also has an impact on photosynthate partitioning between shoot and roots in general and under nutrient deficiency in particular. Photosynthate partitioning is markedly dependent on cycling of certain mineral nutrients through source leaves and deficiencies of these mineral nutrients disrupts the export of photosynthates.

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Table 9. *Effect of Zn deficiency and light intensity on shoot dry weight, chlorophyll and carbohydrate concentrations in primary leaves of* Phaseolus vulgaris *L. (Marschner and Cakmak, 1989)*

Light intensity (μE m^{-2} s^{-1})	Shoot dry wt. (g per plant)		Chlorophyll (mg g^{-1} dry wt)		Carbohydrates (mg glucose equiv. g^{-1} dry wt)			
					Sucrose		Total	
	+Zn	−Zn	+Zn	−Zn	+Zn	−Zn	+Zn	−Zn
80	1.24	1.13	19.2	17.3	10	11	40	42
230	2.38	1.13	16.6	7.8	11	54	42	124
490	3.80	1.16	11.2	4.5	17	82	77	138

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