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Xylem sap composition : A tool for investigating mineral uptake and cycling in adult spruce

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Key words: nutrient translocation, remobilization, spruce (*Picea abies* Karst.), uptake, xylem sap

Abstract

Xylem sap composition of spruce is influenced by several factors, such as the sampled organ, the sampling period, the availability of soil nutrients, and the soil water potential. Based on literature data and ongoing investigations carried out with adult trees, we present an overview on the main factors influencing xylem sap concentrations of Norway spruce. Direct measurements of nutrient fluxes in the xylem sap are then used to suggest a general scheme of mineral element cycling within adult trees. In Norway spruce (*Picea abies* Karst.), nutrient concentration in the xylem sap was higher in twigs and fine roots compared to the bottom of the trunk, the highest concentrations being observed in spring during the shoot elongation. Xylem sap concentrations were higher in spruce growing at nutrient rich sites than at poor sites. The combination of twig and trunk xylem sap analysis, together with xylem flow measurements in the trunk during the course of a vegetation period allowed the quantification of mineral fluxes via xylem sap flow in the trunk and twigs. These results were compared to gross mineral uptake measurements at the same site. Ca flux in the trunk xylem sap was lower than the gross uptake of Ca. Mg flux in trunk sap was approximately equivalent to Mg gross uptake whereas P and K fluxes in trunk sap were much higher than the gross uptake. Fluxes of Ca, Mg, K and P in the twig sap were much higher than that in trunk sap. Data suggest that internal cycling is responsible for a large part of the nutrient fluxes in the xylem sap of the crown. Xylem sap composition thus appears to be a tool which can complement other sources of information on mineral uptake and cycling in adult spruce.

Introduction

Perennial plants rely on two major sources of nutrients: root uptake of soil mineral elements and tissue nutrient remobilisation (Marschner, 1986). In forest ecosystems, nutrient uptake by tree stands is mainly evaluated by summation of (i) the annual increment of mineral content in the tree, (ii) the content of elements in the litterfall, and (iii) the net leaching from the crown. Remobilisation is evaluated by studying the variation in mineral content of the current year organs compared to older ones (Fife and Nambiar, 1984). Such calculations performed both on seasonal and annual basis have shown that remobilisation provides a large part of the annual demand for elements such as P, N and Mg (Dierberg et al., 1986; Oren et Schulze, 1989). In addition to measurements of the changes in biomass

and mineral content of nutrient sinks, quantification of nutrient fluxes provides another approach for assessing nutrient uptake. The xylem is the main pathway for nutrient transport from the soil to the shoots. Thus, quantification of mineral fluxes in the xylem sap is the key to this flux-based alternative. However, xylem sap flow rates of solutes are the sum of net uptake from the soil plus recirculation of solutes via the phloem sap. The relative importance of these mechanisms is still a matter of discussion. The xylem sap composition was used as a diagnostic tool of soil nutrient availability in relation to nutrient requirements in adult trees (Stark et al., 1989). In contrast, Kazda and Weilgony (1988) stressed that the xylem sap composition reflects mainly the internal element translocation rather than the soil nutrient availability. Direct measurements of nutrient

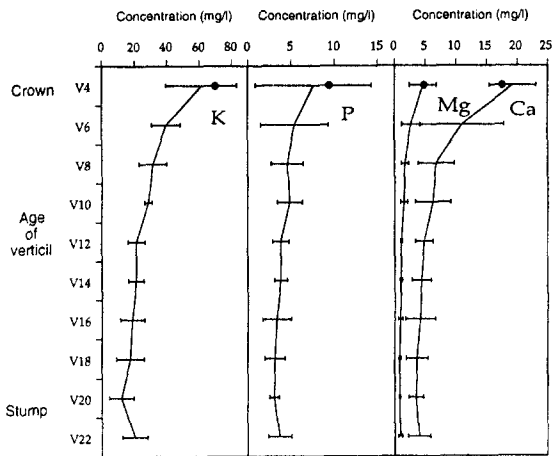


Fig. 1. (—) Variation in the Ca, Mg, P and K concentrations (mg L^{-1}) in the xylem sap of Norway spruce along the bole in relation with the age of the whorl. Xylem sap was extracted by displacement from four 30-year-old trees in July 18. (●) The black dot at the top of each graph represents the mean concentration in the xylem sap extracted from 12 twigs of the fourth whorl from the same trees. Twig sap was extracted with a Scholander chamber using a pressure of 1MPa over the water potential. Data from Dambrine et al. (1992).

fluxes in the xylem sap may contribute to clarify this dispute.

Based on literature data and current studies carried out in the Vosges (France) and in Northern Sweden, we present here an overview on the main factors influencing xylem sap concentrations of Norway spruce (*Picea abies* Karst.). Direct measurements of nutrient fluxes in the xylem sap are then used to draw a general scheme of mineral element cycling within adult trees.

Various factors influencing the xylem sap concentration

According to published data, mean concentrations of major nutrients in spruce xylem sap are highly variable (Table 1). The extraction procedure, the type of organ from which sap was extracted, the sampling time and season, the soil nutrient availability and the soil water potential are proposed factors responsible for this variability.

Extraction procedures

Xylem sap can be extracted by different methods: (i) using the natural spring rise of sap (Huguet, 1973), (ii) displacement by miscible (Denayer de Smet, 1967) or non miscible liquids (Moreno and Garcia Martinez,

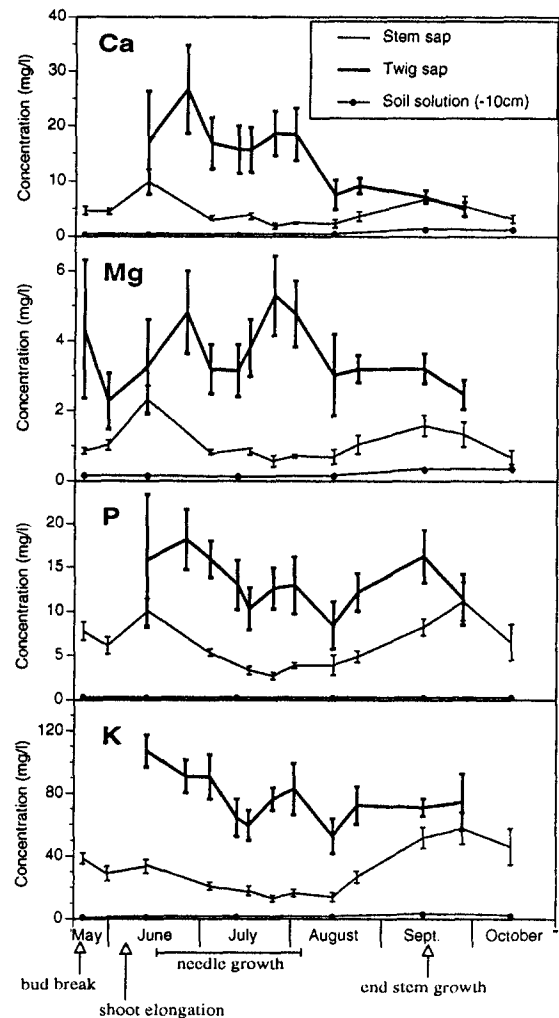


Fig. 2. Time course of Ca, Mg, P and K concentrations in the xylem sap from the twigs and the bottom of the trunk of Norway spruce, and in zero tension lysimeter water at the same site. At each sampling date, stem sap was extracted from three 60-cm-10 long portions cut at the bottom of the stem (between 1 and 3 metres height above the soil) of four trees. Twig sap was extracted by pressure from eight twigs of the whorl 4 and in the same trees. Data from Dambrine et al. (1992).

1980), (iii) applying a pressure by the mean of a Scholander et al. (1965) chamber, or (iv) a vacuum (Bollard, 1953).

Displacement of sap and pressure were the major approaches used to extract sap from Norway spruce (see Table 1). The first method was used to extract sap from large organs, such as trunks and branches. It is reliable and pollution by the impaired cells is minimal because of the large volume collected (Glavac et al., 1989). The latter method allowed the collection

Table 1. Literature data of nutrient concentrations (mgL^{-1}) in the xylem sap of spruce

Authors	Sampling level	Month	Method	Soil and stand conditions	Mean concentrations in sap			
					Ca	Mg	K	P
Osonubi et al. (1988)	Current year twig or n-1	8-10	Pressure 1 MPa/potential	Podzolic, Mg deficient	26.5	4.1	60.1	
				Cambisol, healthy	32.8	6.1	60.6	
Kazda and Weilgony (1988)	6-year-old branches	5-11	Pressure (3 MPa)	Podzolic, declining	8	4.4	69	
				Strongly declining	6.7	3.5	70	
Dambrine et al. (1992)	Branches, whorl 2-10	7	Pressure 1 MPa/pot.	Brown soil/limestone healthy	26.2	4.7	100.7	7.5
	Upper part of the stem	7	Displacement		18.1	3.1	95	3.8
	Lower part of the stem	7	Displacement		12.8	2.6	51.3	2.7
	Large roots ($d > 1$ cm)	7	Displacement		15	3	45	3.3
	Fine roots ($d < 1$ cm)	7	Displacement		39.7	6.3	106	7.3
Dambrine et al. (1992)	branches	5-10	Pressure 1 MPa/pot.	Acid brown soil Mg deficient	16.2	3.8	87	13.1
	Bottom of the stem	5-10	Displacement		4	1	23	5.3
This study	Bottom of the stem	8	Displacement	Podzol control, N deficient	12.7	2.2	36.6	3.8
		8	Displacement	Podzol fertilized, healthy	20.2	3.6	58.6	8.2
		8	Displacement	Podzol, drought stress	11	2.3	28.8	4.6

of sap from small organs (e.g. twigs), but the minute amounts of sap extracted increase the potential contamination. The applied pressure does not affect the sap concentration up to 1 MPa over the twig water potential (Osonubi et al., 1988). Sap concentration of Ca, K, Mg, and P obtained by displacement from trunk portions of the upper crown, and by pressure from attached twigs, were identical (Fig. 1) (Dambrine et al., 1992). This suggested that experiential artefacts were limited and thus, the observed discrepancies (Table 1) are mainly related to biological processes.

Variation in xylem sap concentration in relation to analysed organs

An analysis of mineral concentrations in the xylem sap from twigs, trunks and roots of 17-year-old spruces (Dambrine et al., 1992) indicated that these concentrations were higher in twigs and fine roots. Conversely, lower concentrations were obtained at the bottom of the trunk. This variation in sap concentration was correlated to the nutrient concentrations of the organs from which sap was extracted. No difference in 4-year-old twigs sap concentrations of Ca, Mg, P and K were detected between the top and the bottom of the crown. Data confirmed the results obtained with Douglas fir (*Pseudotsuga menziesii*) (Stark et al., 1984). Xylem sap collected along the bole of 30 year-old spruce showed a gradient of increasing concentrations from

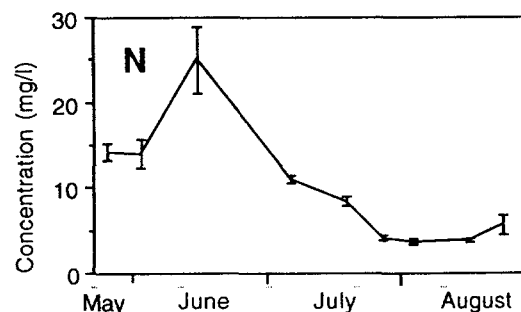


Fig. 3. Time course of total N concentration in the xylem sap at the bottom of the trunk from Norway spruce.

the bottom of the living crown to the top (Fig. 1). Over the vegetation period, twig xylem sap was more concentrated than the sap from the bottom of the bole (Fig. 2). This is in agreement with patterns obtained by Ferguson et al. (1981) in kiwi fruit (*Actinidia chinensis*).

The sampling time and season

N, K and Mg concentrations in twig xylem sap of Norway spruce do not present diurnal variations (Osonubi et al., 1988) in spite of large changes in transpiration velocities. So far, diurnal variations in nutrient concentrations were not investigated in trunk xylem sap. Seasonal variations in xylem sap concentrations of spruce have been studied by Kazda and Weilgony

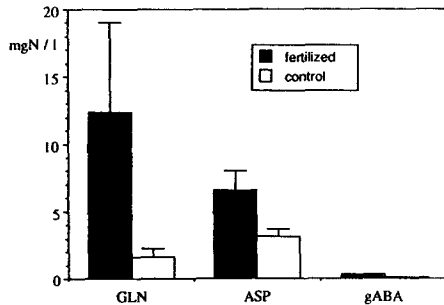


Fig. 4. Glutamine, aspartate, and γ -aminobutyrate concentrations in the xylem sap extracted by displacement from the bottom of the trunk of four N-deficient and four N-fertilized trees at Flakaliden (Northern Sweden).

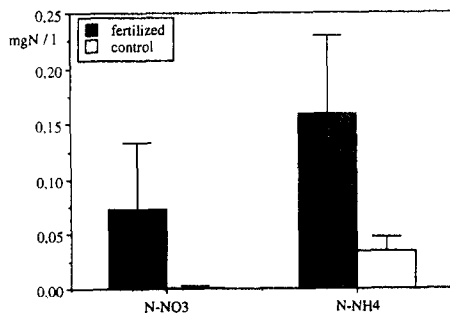


Fig. 5. N-NO₃⁻ and N-NH₄⁺ concentrations in the xylem sap extracted by displacement from the bottom of the trunk of four N-deficient and four N-fertilized trees at Flakaliden (Northern Sweden).

(1988) and results were confirmed by Dambrine et al. (1992). In our study, twig sap concentrations (e.g. P, N, Ca, N and Mg) were higher after bud break at the beginning of needle growth (Fig. 2, 3). A second peak (except for Mg) occurred when needle growth was completed. Then concentrations decreased (e.g. Ca, Mg) or remained stable (e.g. P, K). In trunk, the first concentration peak occurred during the elongation of the buds, slightly earlier than in the branches (Fig. 2). Then, concentrations decreased and remained at a low level during needle growth. A second peak of concentration was observed at the end of trunk growth. The N concentration in trunk sap exhibited the same temporal pattern (Fig. 3) (Carisey, 1990). Glutamine and aspartate were the main components of this N fraction whatever the phenological stage. Nitrate was not detected in trunk xylem sap.

Similar temporal variations patterns of nutrients in trunk xylem sap were described in beech (*Fagus sylvatica* L.) (Glavac et al., 1989, 1990) and kiwi fruit (Ferguson et al., 1983).

Nutrient availability

Sap was extracted from twigs of Mg-deficient and non-deficient spruce growing on acid soils (Osonubi et al., 1988). Sap concentrations of Ca and Mg at the poorer site was approx. 70% of that obtained at the richer site (Table 1). In contrast, concentrations in N and K were similar. Kazda and Weilgony (1988) have compared the concentration of mineral elements in the sap of 6-year-old branches and in soil solutions at three sites with low (8%) to very low (2%) soil base saturation during the course of a vegetation season. Ca and Mg concentrations were lowest at the poorest site, but the ratio of xylem sap concentration to soil solution concentration was highest at this site suggesting a compensatory translocation. According to these authors, xylem sap cannot be directly used as a diagnosis tool to appreciate the site fertility. Our data (Dambrine et al., 1992) support this contention. Sap concentrations were several order of magnitude higher than those observed for soil solutions, except for Ca and Mg in trunk sap at the end of needle growth (Fig. 2). In addition seasonal fluctuations of nutrient concentrations in sap and soil solutions were apparently independent. It should be noticed that mean Mg and K concentrations in branch xylem sap of spruces growing on poor and acid soils are close (See the data from Dambrine et al., 1992 in Table 1; Kazda and Weilgony, 1988; Osonubi et al., 1988). On the other hand, Ca concentrations differ widely between these studies.

To test the effects of soil nutrient availability, xylem sap from the trunk of heavily fertilised trees and control trees grown at the experimental site of Flakaliden (Northern Sweden) were analysed. N-deficient spruce stands were fertilised for several years with a complete nutrient solution to reach the optimal growth. Height increment of spruces was multiplied by a factor of approx. 3 (Linder and Flower-Ellis, 1992). Mineral and free amino acid (e.g. glutamine) concentrations in trunk sap of the fertilised trees were much higher (Table 1, Fig. 4, 5). Traces of nitrate (<1% total N) were detected in the xylem sap of fertilised spruces.

Thus, the availability of mineral elements in the soil influenced the sap concentration on the long term as shown by Stark et al. (1989) and Glavac et al. (1989). However, relationships between short-term changes in soil nutrient availability and xylem sap concentrations have not been investigated yet.

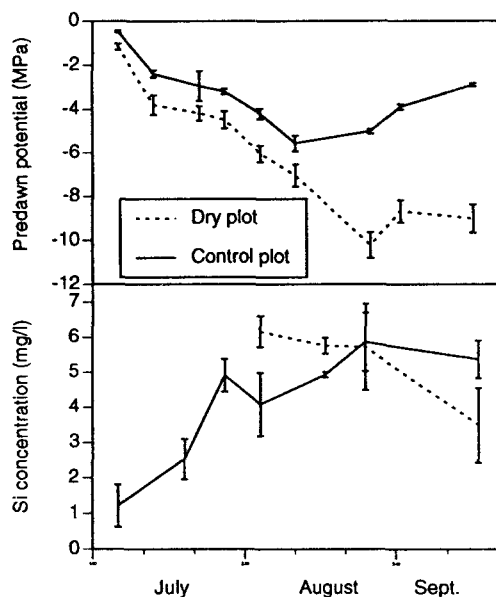


Fig. 6. Variation of predawn potential and trunk xylem sap Si concentration in Norway spruce during a drought experiment (Dambrine et al., 1992).

The soil water potential

Kazda and Weilgony (1988) did not observe any relationships between branch sap concentrations and the water potential of the soil, in spite of a prolonged dry period. However a control plot was not included in their study. Sap was extracted from twigs and trunks of trees in two stands experimentally stressed by drought as compared to control plots. In the first experiment, the soil of a 30-year-old spruce plot of the Vosges mountains was protected from rainfalls during a two-month summer period. Soil water potential and tree transpiration (Lu, 1992) drastically decreased in the dry plot compared to the control. No difference between the trunk sap concentrations of Ca, Mg and K in the two plots was detected until the end of August, where Ca, K and Mg concentrations decreased in the trunk sap of the drought plot as compared to the control (Dambrine et al., 1993). This decrease was possibly related to (i) the low availability of Ca and Mg at the depth (B horizon) to which drought stressed trees were forced to absorb water, (ii) the cumulated effect of a low uptake in Ca and Mg during the previous month, or (iii) the impairment of fine roots by drought. In the same experiment, Si concentration in trunk sap increased progressively with soil drought until the soil water potential reached 1 MPa, at the end of August

(Dambrine et al., 1992)(Fig. 6). This increase was related to a possible increase in soil solution Si concentration when soil moisture progressively decreased (Atteia et al., 1993). The fact that Si concentration in the sap of the stressed trees fell below the control value in September suggests a limitation of root activity by drought. In the second study mentioned above, the soil of a 25-year-old, N-deficient spruce plot from Northern Sweden was partly (2/3 of the surface) protected from rainfalls during three successive summers. Trunk sap extractions, which were carried out in August during the third year of experimental drought, did not revealed significant difference in mineral concentration related to drought (Table 1). The discrepancies between the results of these studies might be explained by the large demand for base cations imposed by the strong growth of the Vosgian stand as compared to the low demand of the poorly growing Swedish stand. Nevertheless, the relationships between sap concentrations and soil water potential clearly require additional investigations.

Relation between the flux of nutrients annually transported in the xylem sap and the annual gross uptake and total mineral content of the stand

In a 30-year-old spruce stand, Lu (1992) continuously measured the flux of xylem sap in the lower part of the trunk of 4 trees during the course of a vegetation period, using the constant energy heat probe method described by Granier (1985). Daily transpiration was calculated by multiplying daily fluxes by the sap wood total cross section of the stand. Simultaneously, Dambrine et al. (1992) sampled and analysed the sap from the twigs and the lower part of the trunks (as shown in Fig. 2). Xylem sap flux measured at the bottom of the trunk is equal to that in the crown and the upper crown contributes to approx. 75% of the transpiration flux (Granier and Claustres, 1989). Nutrient concentrations in the trunk and twig sap were multiplied by the transpiration of the corresponding periods in order to estimate nutrient fluxes on the stand area basis for the whole vegetation season (Table 2). Nutrient fluxes were compared with the gross mineral uptake and mineral content measurements obtained at the same site using a traditional biomass and mineral content inventory (Dambrine et al., 1991). Data provided by the different approaches are presented in Table 2 and Figure 7. Annual Ca flux in the sap at the bottom of the trunk was low: $12 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$. This

Table 2. Comparison between the annual nutrient fluxes ($\text{kg ha}^{-1} \text{yr}^{-1}$) in the sap of the crown and the trunk, the gross uptake ($\text{kg ha}^{-1} \text{yr}^{-1}$) and the mineral content of the stand (kg ha^{-1})

	Ca	Mg	P	K
Flux in trunk sap (1)	12.0	2.8	17.2	82.1
Flux in twig sap (2)	42.7	10.9	39.4	226.5
Mineral cycling in the upper trunk and crown (2 - 1)	30.7	8.1	22.2	144.4
Increment of mineral content of the trunk (3)	10.7	1.3	0.6	7.5
Flux in litterfall and crown leaching (4)	10.0	1.5	3.3	25.0
Total gross uptake (3 + 4)	20.7	2.8	3.9	32.5
Mineral content of the trunk (5)	112.4	14.9	12.6	91.2
Mineral content of the crown (6)	180.3	20.7	55.4	206.4
Total mineral content of the stand (5 + 6)	292.7	35.6	68.0	297.6

value is lower than the annual gross uptake of Ca ($20.7 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$). In contrast, the flux of Ca in the sap of twigs ($42.7 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$) was much higher than the annual gross uptake. Fluxes in trunks and twigs represented a low percentage of the total amount of Ca in the stand, thus suggesting a low turn-over-rate. Mg gross uptake and Mg flux in trunk sap were equivalent. On the other hand, Mg flux in branch xylem sap ($10.9 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$) was much higher than the gross uptake ($2.8 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$) and represented approximately 50% of total Mg content in the crown ($20.7 \text{ kg} \cdot \text{ha}^{-1}$). Fluxes of K and P in trunk xylem sap were much higher than the gross uptake rate. By dividing the annual gross uptake by the flux of P and K in trunk sap, it appears that root uptake would supply only 33% of the P and 40% of the K flux in trunk sap. The same calculation applied to the crown showed that root uptake supplied only 48% of the Ca, 25% of the Mg, 10% of the P and 14% of the K fluxes in crown sap. Fluxes of P and K in branch xylem sap were of the same order of magnitude as the total content in P and K of the crown, suggesting a turn-over-time of a few years.

General interpretation and conclusion

A general scheme for nutrient cycling within Norway spruce can be drawn from the above investigations. Three main factors influence the nutrient concentrations in the xylem sap: (i) the nutrient availability, (ii) the phenological stage and (iii) the type of sampled

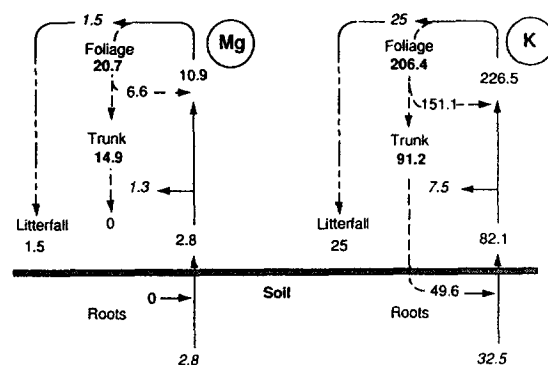


Fig. 7. Budget of Mg and K in adult Norway spruce. Nutrient pools ($\text{kg} \cdot \text{ha}^{-1}$) appear in bold, gross uptake values ($\text{kg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$) appear in italics. (\longrightarrow), xylem fluxes; (\dashrightarrow), phloem fluxes.

organ. The soil fertility influences sap nutrient concentrations over a period of several years. In other terms, nutrient concentrations in sap are high in trees growing at nutrient fertile sites! However the higher nutrient concentrations in xylem sap compared to soil solutions suggest that sap content is mainly affected by the nutrient status of the tree rather than the nutrient availability in the soil. Short term studies during which the nutrient availability will be changed might clarify this contention. Although direct experimental demonstrations are still lacking, variations in spruce sap concentration of nutrients exhibiting low translocation rates (e.g. Ca, Si) following short term changes in nutrient availability have been reported and suggested that xylem sap analysis could be used as an early diag-

nostic tool to detect such changes (Tromp and Ovaa, 1985).

Variations in trunk sap concentrations of the major nutrients throughout the year can be attributed to the temporal ion mobilisation from reserve tissues (Ferguson et al., 1983). Nutrient translocation from bark and parenchyma in spring to meet the growth requirements of shoots accounts for the spring concentration peak in sap (Glavac et al., 1990). The second concentration peak in sap occurs at the end of trunk growth in trunk sap and at the end of needle growth in twig sap. The latter presumably correspond to the slower incorporation of mineral elements in tissues when growth is completed.

In the present comparative study, mineral fluxes in the xylem sap of the trunk are lower (Ca), equivalent (Mg) or much higher (P, K) than the gross uptake. Uncertainties associated with the calculation of a mineral cycling budget are mainly related to (i) the low frequency of xylem sap analysis, (ii) flow measurements ($\pm 10\%$), (iii) stand sap wood area measurements ($\pm 15\%$), and (iv) gross uptake estimates ($\pm 15\%$).

The "lack" of Ca in the xylem sap could be explained by the fact that Ca transport does not occur entirely by mass flow because of Ca adsorption on the xylem vessels (Ferguson and Bollard, 1976). The equivalent amounts of Mg flux in sap and Mg gross uptake suggests that this ion is almost entirely transported by passive mass flow in the trunk, and that internal cycling of Mg in the trunk is low. This unexpected result could be explained by the acute Mg-deficiency of the studied stand. The large excess of K and P in the sap flux at the bottom of the trunk implies that these fluxes should be compensated by downward fluxes in the phloem. Phloem sap is rich in P and K and phloem-to-xylem as well as xylem-to-phloem transfers have been reported for several plants (for a review see Simpson, 1986).

Mineral element fluxes in twig sap are much higher than at the bottom of the trunk. Evaporation could increase sap concentration when ions are not incorporated continuously into growing organs. In fact, the needle apoplasm is directly connected to the xylem sap of the twig and its volume is important compared to that of the xylem in the twig. However this is probably not the case for 4-year-old or older branches where xylem is well differentiated and large enough to minimize direct pollution by the needles apoplasmic sap. Moreover, such a process cannot explain the increase in sap concentration of the roots compared to the trunk. Considering the mean sap concentrations found in the

literature (Table 1) and values of transpiration measured at the same site (Werk et al., 1988) or known estimates (300–400 mm), it is evident that the annual flux of nutrients in branches is much higher than the gross uptake of the stands (Schulze et al., 1989). Therefore, these ions must be recycled within the upper trunk and crown. Comparison of the nutrient cycling estimates in the upper trunk and crown (Table 2, line 3) with the total mineral content of the stand (Table 2, line 9) indicated that approx. 10% of the Ca, 23% of Mg, 32% of P and 49% of K total pool in the above part of the tree were cycled annually. The Ca value was low compared to other nutrients but still represents significant amounts of Ca. The remobilisation of Ca is generally considered negligible since this ion accumulates in insoluble forms (pectate and oxalate) in the oldest organs of spruce and Ca concentration in the phloem sap is low (0.5–2.3 mmol.L⁻¹; Hall and Baker, 1972; Hocking et al., 1980). However, by comparing the nutrient content in the tree rings of trees of various ages growing under similar conditions (Colin-Belgrand et al., 1993) or by feeding plants with labelled Ca (Kuhn, 1993), it has been shown that Ca transfers can occur in young trees. The question of Ca translocation pathways obviously needs further investigation. Almost one quarter of Mg, one third of P and one half of K storage in the above ground portion of the tree were cycled annually in the xylem sap. Intense transfer from xylem to phloem and vice versa or from these tissues to the parenchyma are required to explain such fluxes. The fact that the difference in concentration between twig and trunk xylem sap was maintained along the growing season showed that such transfers are not restricted to specific phenologic periods. In this respect, it differs from "classical" remobilisation processes occurring during spring and fall (Marschner, 1986). Since the relative importance of phloem compared to xylem increases considerably toward the extremities of the tree, phloem to xylem translocation could influence the composition of the xylem sap in branches and roots more strongly than in the trunk, where phloem occupies a very restricted area.

Based on these investigations, a simplified scheme of mineral element cycling within Norway spruce stand can be put forward (Fig. 8). three overlapping cycles have been distinguished. The "ecological" cycle corresponds to the flux of nutrients annually taken up by the roots and returned to the soil by litterfall and crown leaching. The "seasonal remobilization" cycle is dominated by the spring nutrient flux mobilized in spring from the root and trunk reserves to growing tissues

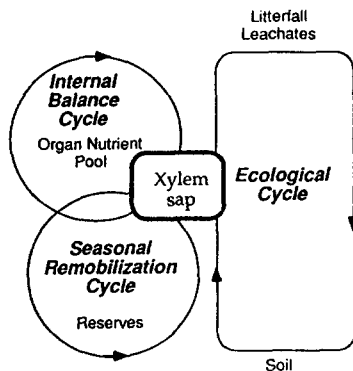


Fig. 8. A simplified model of nutrient cycling in Norway spruce.

and conversely, by fall fluxes to storage tissues. The latter cycle, referred to as "internal balance cycle" corresponds to the permanent cycling of nutrients within each organ. It presumably reflects the source-sink fluxes of nutrients between the developing tissues.

In conclusion, estimation of xylem sap content and fluxes is a complementary approach to quantify internal cycling of mineral elements in adult trees and its variation resulting from environmental stresses. Xylem sap analysis can be used in nutrient uptake studies if the studied nutrients are not cycled intensively within the tree. Recent studies demonstrated that isotope ratio analysis (e.g. $\delta^{18}\text{O}$, $\delta^{15}\text{N}$ - NO_3 , $\delta^{87}\text{Sr}$) of sap and soil solutions offers new possibilities for a better understanding of nutrient cycles (Bishop and Dambrine, 1994; Pate et al., 1993).

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