SELECTIVITY AND DISCRIMINATION IN ION UPTAKE UNDER FIELD CONDITIONS

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THEORY

Calculation of nutrient uptake

The study of ion uptake under field conditions requires a soil-plant system in a steady state. For a coniferous forest of trees the same age, it is known that the litter production, B, from trees between 30 and 100 yr remains constant; for a site of normal productivity a mean litter production, B, of 3000 kg/ha per yr is usually assumed:

$$\frac{\overline{B}}{t} = \text{const.} \simeq 3000 \text{ kg/ha per yr} \qquad (1)$$

From Eq.(1) it follows that

$$\frac{d\overline{B}}{dt} = 0 \qquad (2)$$

which means a steady state for litter fall.

The litter fall can be expressed as a flux where all fluxes are calculated for 1 ha and 1 yr:

$$\Phi_{\overline{B}} = \text{const.} \simeq 3000 \text{ kg} \qquad (3)$$

Since the mean litter fall (i.e. the mean mass of needles), consisting of the sum of different old needles ($B_1+B_2+B_3+\ldots$), is usually assumed to be constant, the mean yearly formation of needles must be equal to the mean yearly litter fall:

$$\Phi_{\overline{B}_1} = \Phi_{\overline{B}} \qquad (4)$$

This equation enables the calculation of the net mean yearly nutrient uptake in the needles from the amount of litter and the nutrient content of the litter. If the yearly wood production, H, and the nutrient content, c, of the wood, c_H, is known, the net mean yearly nutrient uptake in the total shoots, $\overline{A}_n$, can be calculated. Calculations of this type have been published by Ehwald [1] and Madgwick [2]. Since the mean nutrient content, $\overline{c}$, of litter and wood is independent of the age of the trees, $\Phi_{\overline{A}_n}$ is constant.

In these calculations the "wash-out", K, of nutrients from the crown of the trees is not included. Since the removal of nutrients from tree crowns by rain can reach appreciable amounts (e.g. potassium in Refs. [3, 4]) the crown wash-out must be considered in calculating the total nutrient uptake in the shoots, A_b:

$$\Phi_{\bar{A}_b} = \Phi_{\bar{B}} \times \bar{c}_B + \Phi_{\bar{H}} \times \bar{c}_H + \Phi_{\bar{K}} \times \bar{c}_K \tag{5}$$

For simplification, the sign for flux (Φ) will be left out of the following equations.

Cycling factors

It is evident from Eq. (4) that in the wash-out of nutrients from tree crowns, the real nutrient uptake is higher than assumed on the usual basis of dry matter production and nutrient content of the dry matter. The fraction of total uptake, f_{cycl}, which is given off from the tree again either by litter fall or by crown wash-out, is calculated as follows:

$$f_{cycl} = \frac{\bar{B} \times \bar{c}_B + \bar{K} \times \bar{c}_K}{\bar{A}_b} \tag{6}$$

The relationship between both ways of cycling may be expressed as the fraction washed out, f_{wash},

$$f_{wash} = \frac{\bar{K} \times \bar{c}_K}{\bar{B} \times \bar{c}_B + \bar{K} \times \bar{c}_K} \tag{7}$$

Ion uptake selectivity coefficients

In a heterogeneous system, whose behaviour cannot be described by a mathematical expression, the simplest way of representing selectivity properties is to compare equivalent fractions in both phases – the liquid and the solid. In ecological studies on ion uptake, the liquid phase is the equilibrium soil solution (ESS), the solid phase is represented by the annual ion uptake $\bar{A}$, as calculated above. If the cation composition of both these phases is expressed in cation equivalent fractions, X, an ion uptake selectivity coefficient, k_{upt}, can be calculated:

$$k_{upt} = \frac{X_{\bar{A}}}{X_{ESS}} \tag{8}$$

Values of $k_{upt} > 1$ indicate selective uptake and values < 1 indicate discrimination.

EXPERIMENTAL RESULTS

The experimental results are only a rough approximation of the theoretical concept because part of the data needed had to be estimated from data in the literature, and for the data obtained experimentally the actual period measured did not allow the calculation of mean values in respect to time.

The values estimated were the mean litter production, $\bar{B} = 3000$ kg (all values expressed per ha per year), the mean wood production, $\bar{H}$, and the nutrient content of the wood, $\bar{c}_H$. The litter production varied considerably from year to year according to weather conditions. The nutrient content of the litter was either directly determined or set equal to the nutrient content of a 5-yr-old spruce needle. The crown wash-out was determined as the difference between the amount of nutrients in the canopy drip and in rain water, allowing for the interception of rain water by crowns. The equilibrium soil solution corresponds to the saturation extract of a fresh field sample of soil.

Table I gives calculated data for nutrient uptake in a Norway spruce stand on acid water-logged soil, as well as the fraction cycling and the fraction washed out. The yearly turnover includes 76-92% of the nutrients taken up, and seems to be more or less the same for all nutrients. Big differences exist in the way of cycling: P and N cycle predominantly with the litter fall; Na, K, Al and Fe predominantly with crown wash-out. The crown wash-out measured may be higher than the mean value, because the measuring period (6.11.1964-10.9.1965) followed a dry summer and autumn. The wash-out of H and S is probably much lower than the values given in Table I; it is reasonable to assume that SO_2 and SO_3 in the air equilibrate with the water in pore spaces of dead twigs, giving rise to high concentrations of H^+ and SO_4^{2-} in the canopy drip.

Figures 1(a) and (b) show data for soil analyses, exchangeable cations and cations in the ESS. From these data the sorption selectivity coefficients can be calculated, which are listed in Table II. Gapon constants can also be calculated. The selectivity coefficients and the Gapon constants of K and Al depend on the content of organic matter in the soil, both ions being more specifically bound by clay than by organic matter. The selectivity coefficients of Na and Ca depend on the degree of Al saturation of the soil, both ions being more specifically bound the lower the saturation.

The uptake selectivity coefficients and the data from which they are calculated are listed in Table III. K, Ca and Mg are taken up selectively; Fe, Al and especially Na are discriminated against. For Al and Fe, the discrimination occurs mainly by crown wash-out as the uptake of these ions corresponds closely to their presence in the soil solution. On the other hand, the discrimination of Na is due mainly to the root.

CONCLUSIONS

The data given in this paper are not accurate enough to draw definite conclusions. Nevertheless, assuming the values given are close to mean values, some hypothetical conclusions may be drawn mainly to get as much

TABLE I. NUTRIENT FLUXES IN A NORWAY SPRUCE STAND ON ACID WATER-LOGGED SOIL

	H	Na	K	Ca	Mg	Al	Fe	Mn	N	S	P
						(moles/ha per yr)					
Canopy drip (K+N) (589 mm)	4201	599	924	1002	136	188	83	69	1647	4738	26
Rain water (N) (777 mm)	394	143	83	146	34	27	10	2	663	909	14
Crown wash-out (K)	(3807)	456	841	856	102	161	73	67	984	(3829)	12
3000 kg litter (B)		45	303	684	93	24	18	84	2616	300	81
Twigs, wood and bark (H)		?	100	400	60	?	?	?	900	?	30
Net shoot nutrient uptake (A_n)		45	403	1084	153	24	18	84	3516	300	111
Total shoot nutrient uptake (A_b)		501	1244	1940	255	185	91	151	4500	(4129)	123
f_{cycl}		-	0.92	0.79	0.76	-	-	-	0.80	-	0.76
f_{wash}		0.91	0.74	0.56	0.52	0.87	0.80	0.44	0.27	(0.93)	0.13

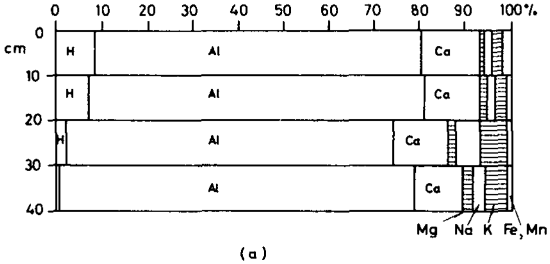

FIG. 1 (a). Results of soil analyses. Exchangeable cations in percentage of the cation equivalent sum

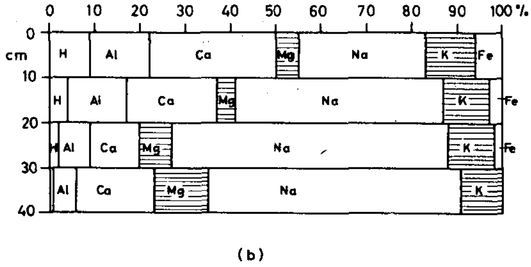

FIG. 1 (b). Results of soil analyses. Cations in the equilibrium soil solution in percentage of the cation equivalent sum

TABLE II. SORPTION SELECTIVITY COEFFICIENTS

Cm	Na	K	Ca	Mg	Al
0-10	0.095	0.25	0.64	0.23	6.4
10-20	0.093	0.28	0.43	0.17	7.4
20-30	0.076	0.48	0.75	0.22	10.8
30-40	0.058	0.52	0.75	0.39	12.6

information as possible from the experiments to improve the experimental set-up for future work.

In studies on ion uptake it must be remembered that crown wash-out may vary considerably; high values are found for areas with high precipitation and zero for plants grown in greenhouses. Figure 2 is a diagrammatic representation of the concentration gradient and fluxes in relation to crown wash-out.

When crown wash-out is high, a low efflux from the root can be assumed since most of the efflux occurs via crown wash-out. A concentration gradient from roots to shoots would be necessary to allow the high rate of

TABLE III. UPTAKE SELECTIVITY COEFFICIENTS FOR 45-YR-OLD SPRUCE ON STAGNOGLEY

	Na	K	Ca	Mg	Al	Fe
Equivalent fraction in 5-yr-old needle X_{B_5}	0.012	0.15	0.68	0.11	0.019	0.0069
Equivalent fraction in ESS 0-40 cm X_{ESS}	0.50	0.10	0.20	0.072	0.10	0.027
$k_{upt} = X_{B_5} : X_{ESS}$	0.024	1.4	3.4	1.5	0.19	0.26
$k_{upt} = X_{B_5+K} : X_{ESS}$	0.048	2.2	2.8	1.1	0.85	0.74

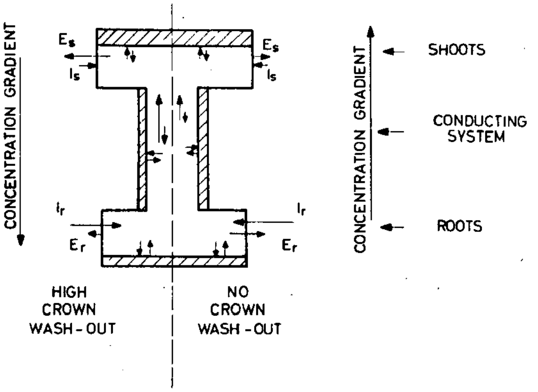

FIG. 2. Diagrammatic representation of concentration gradient and fluxes in relation to crown wash-out. ▨ = persisting parts of the plant; I = influx; E = efflux; s = shoots; r = roots. The length of the arrows indicates flux intensities

ion transport from the roots to the shoots. When there is no crown wash-out and the same influx into the roots, the efflux occurs mainly through the roots; a concentration gradient from shoots to roots would be necessary to lower the rate of transport from roots to shoots.

On this basis, it seems possible that the plant takes up ions in the same ratio as the ions are present in the soil solution. For Na (the dominating cation in the ESS, the largest fraction washed out and the most strongly discriminated against by the root) a concentration gradient would have to be postulated from the shoots to the roots, causing a high efflux from the root. The selective uptake of other cations (K, Ca, Mg) would then be the result of differences in root efflux, in the same way that the discrimination of Al and Fe is the result of shoot efflux.

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