

## SOIL CHEMISTRY AND PLANTS IN FENNOSCANDIAN BOREAL FOREST AS EXEMPLIFIED BY A LOCAL GRADIENT

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**Abstract.** In Fennoscandian boreal forests, in which productivity in general is N limited, there are regular, topographically related variations in forest productivity and plant community composition. Regional surveys have demonstrated strong correlations among soil pH, N content, and base saturation on the one hand and plant productivity and community composition on the other, but the nature of these relationships is poorly understood. We studied in detail the variation in and controls of soil acidity, availability of N and P, and changes in community composition and plant nutrition along a short (only 90 m long) but extreme forest productivity gradient in northern Sweden, which ranged from a groundwater recharge area with low productivity to a very productive discharge area.

The pH in the soil solution of the mor layer ranged from 3.5 in the recharge area to 6.4 in the discharge area, and it was strongly correlated with the base saturation of the exchange complex. Neither the acid strength of organic matter, the ionic strength of the soil solution, nor the quantity of acids could explain more than a minor part of this variation in pH. There were strong correlations between total N in the mor layer and soil solution pH ( $r = 0.97$ ) and base saturation of the exchange complex ( $r = 0.88$ ). At the poor end of the transect the concentration of inorganic N was very low in the mor, and plants with either ectomycorrhizae (ECM) or ericoid mycorrhizae (EM) dominated. With increasing pH, there was an increase in  $\text{NH}_4$  concentrations, while plants that potentially have arbuscular mycorrhizae (AM) became prominent along with ECM and EM species. In the discharge area, which comprised only the last 10 m of the transect,  $\text{NO}_3$  dominated over  $\text{NH}_4$  in the soil solution, the soil had a high capacity for net nitrification, and the vegetation was totally dominated by potentially AM or nonmycorrhizal herbs, some of which had high foliar nitrate reductase activity. Foliar and root N concentrations increased steeply towards the discharge area, but foliar P/N ratios declined below critical levels at the end of the transect. Root  $^{32}\text{P}$  uptake bioassays also indicated a P deficiency in the discharge area, where the soil total P content was high, while the concentration of  $\text{PO}_4$  in the soil solution was very low. The high capacity of the mor in the discharge area to adsorb  $\text{PO}_4$ , due to the presence of organically complexed Fe and Fe-oxihydroxides, may explain the low  $\text{PO}_4$  concentrations.

Our data indicate that the underlying factors influencing both productivity and community composition are pH and supply of base cations. Fundamental differences in exchange characteristics of soil and soil water underlie other related nutrient supply features, in particular the amount and availability of N. Our study of a single short topographic transect supported a previous suggestion based on a regional survey in Norway that variability in soil pH and the supply of base cations affects plant productivity and community composition via effects on N supply. Our data also encompass the interrelations between soil pH, soil N turnover, and the mycorrhizal type of dominant plant species, which, according to Read (1991), occur along long latitudinal or altitudinal climatic gradients. Through millennia discharge areas like the one observed by us have probably provided a relatively stable environment for plants demanding high soil pH and N supply, at the same time as surrounding recharge areas have been acidified naturally through podzolization.

**Key words:** base saturation; boreal forests; Fennoscandia; groundwater discharge; mor layer; mycorrhizae; nitrogen; pH; phosphorus; plant communities; soil chemistry.

### INTRODUCTION

In Fennoscandian boreal forests there are regular and apparently interrelated variations in hydrology, plant

community composition, and forest productivity (e.g., Cajander 1926, Hägglund and Lundmark 1977). More productive forests and field layer communities are commonly found in groundwater discharge areas (flushed areas sensu Gorham 1953) in toe slope areas. As numerous field experiments have shown that N is strongly limiting productivity in these forests (Tamm 1991, Pet-

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tersson 1994), these variations likely reflect variations in soil N supply. Similar relations between hydrology, nitrogen supply, and plants have been reported from tundra ecosystems (e.g., Chapin et al. 1988, Giblin et al. 1991). Why then is the amount and availability of N higher in discharge areas than in recharge areas? Tamm (1991) proposed three possibilities for an accumulation of N in discharge areas: (1) conditions more conducive for  $N_2$  fixation, at present or earlier in the site history, (2) less loss of N during wildfires because of wetter conditions, and (3) an influx of N from surrounding recharge areas, which in turn can be affected by fire and other disturbances. We would like to add (4) a higher in situ flux of solutes, including N species, to plant roots and mycorrhizae (Chapin et al. 1988), and that (5) the supply of water in itself is important to soil microbial activity, in particular N mineralization, and may limit plant growth during dry periods.

Some authors have suggested that N availability could be determined by the availability of P, which has positive effects especially on  $N_2$  fixation (Cole and Heil 1981, Vitousek and Howarth 1991). It is also clear that soil pH should be important as it strongly determines the composition of the soil microbial community. Read (1983, 1986, 1991) proposed a model to describe and explain interrelations between soil pH, humus type, nitrogen mineralization pattern, and the dominance of plants with certain types of mycorrhizae in ecosystems ranging from tundra through boreal and nemoral forests to steppes. In cold, wet climates with slow decomposition and acid soils, he suggested that organic N and  $NH_4$  should be the predominant sources of N and that species with ectomycorrhizae (ECM) and/or ericoid mycorrhizae (EM) should dominate. By contrast, arbuscular mycorrhizal (AM) species should dominate in warmer drier environments with a higher pH, more rapid N mineralization, and substantial nitrification, and hence a significant use of  $NO_3$  by plants. Similar transitions from systems dominated by ECM and EM species to systems dominated by AM species occur also along local hydrochemical gradients in boreal forests (Högberg et al. 1990).

Regional surveys in Fennoscandia have demonstrated strong correlations among soil pH, N content, base saturation, and plant community composition (Dahl et al. 1967, Lahti and Väisänen 1987). To obtain more knowledge about interactions among soil chemistry, soil microorganisms, and plants, we undertook a number of detailed studies along a single short, but extreme, forest productivity gradient in northern Sweden. In a pilot study at the site (Högberg et al. 1990) it was shown that soil total N increased along the gradient together with an increase in soil pH. At the lower, least acid end of the transect, plant nitrate reductase activity (NRA), an indicator of  $NO_3$  availability, was clearly elevated. In this paper we focus on interactions between soil chemistry and availability of N and P to plants. The objectives of this study were (1) to identify factors

responsible for the change in acidity along the transect, and (2) to identify linkages between soil chemistry and plant-available nutrients, especially N and P. Subsequent contributions will examine links between soil chemistry and soil microorganism community composition and activity.

## MATERIALS AND METHODS

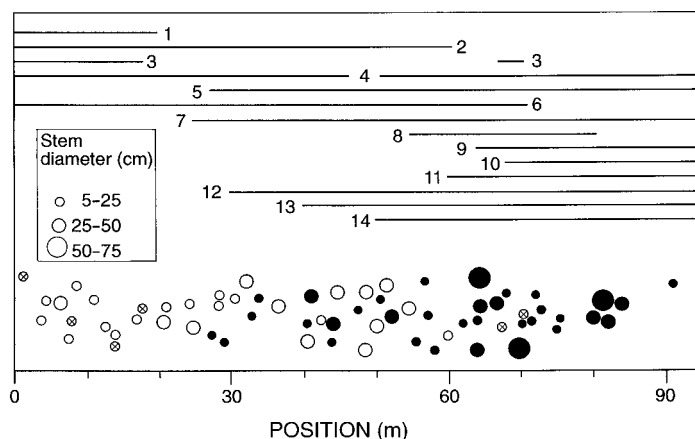
### Site description

The 90-m transect is located at the bottom of the Umeå River valley northwest of Betsele, in northern Sweden ( $64^{\circ}39' N$ ,  $18^{\circ}30' E$ , 235 m above sea level). The site was deglaciated 9200 yr ago, and is situated at the probable position of the highest shoreline. The transect has a rather constant slope of 2%. Larger steep slopes are not found closer than 800 m away, where the bottom of slopes reaching up to 175 m above the river are found. In the springtime (i.e., during snow melt) the discharge area becomes flooded by groundwater during a few weeks; this may occur also after exceptionally rainy weather during summer and autumn. Mean annual temperature and precipitation are  $1.0^{\circ}C$  and 570 mm, respectively. On average, the site is covered by snow from late October to early May.

At the poor upper end of the transect (0 m) there is an open *Pinus sylvestris* (nomenclature of species follows Tutin et al. (1964–1980)) forest with an average age  $\sim 125$  yr and a site height index  $H_{100}$  of 17 m, while close to the rich end there is a closed *Picea abies* forest of similar age (probably established after the same wildfire), but with a  $H_{100}$  of 28 m (Fig. 1). The basal area in the pine forest was 22  $m^2/ha$  and the tallest tree 22 m, while in the spruce forest the basal area was 32  $m^2/ha$  and the tallest tree 36 m. Photosynthetically active radiation (400–700 nm, LI-190SB, LI-COR, Lincoln, Nebraska, USA) between 0.3 and 1 m above the ground varied between  $\sim 600 \mu mol \cdot m^{-2} \cdot s^{-1}$  in the pine forest (0–30 m along the transect) and  $\sim 100 \mu mol \cdot m^{-2} \cdot s^{-1}$  in the spruce forest (40–80 m along the transect), and increased to 400  $\mu mol \cdot m^{-2} \cdot s^{-1}$  at 90 m, when the radiation was 2100  $\mu mol$  photons  $\cdot m^{-2} \cdot s^{-1}$  in an open area. At 90 m, there is a glade created by tree falls and there is poor regeneration of spruce in the dense and tall field layer. The poor upper end of the transect has a field layer dominated by ericaceous dwarf shrubs under the pine canopy. About 40 m along the transect, they become gradually intermingled with short herbs and finally replaced by tall herbs at the rich end (Table 1, Fig. 1). Three forest types have been defined along the transect (Table 1), a dwarf-shrub forest type (DS) between 0 and 40 m, a short-herb forest type (SH) between 50 and 80 m, and a tall-herb forest type (TH) at 90 m. The dwarf-shrub and short-herb forest types are in the recharge area, whereas the tall herb is in the discharge area.

The present river channel is 250 m to the north, and the river level is  $\sim 5$  m below the end of the transect

FIG. 1. Distribution of plant species numbers 1–14 (Table 1), and positions of tree stems in a 10 m wide belt along the transect at Betsele. ○ = *P. sylvestris*; ● = *P. abies*; ⊗ = *B. pubescens*. Sizes of symbols give stem diameter at breast height according to key in insert.



at 90 m. Along the transect, soils are uniform sandy till soils with many boulders. Possibly, finer fractions have been eroded away by turbulent river flow in the past. The soils show morphological characteristics of podzols and are classified as Haplic Podzols (FAO 1988). The mor layer (O horizon) is ~0.07 m thick along the transect. At the upper part of the transect the mor is dominated by the fermentation layer (F), while the humus layer (H) is thin. Along the gradient the thickness of the H layer increases gradually. At 90 m the mor is completely dominated by a H layer and no distinction can be made between the F and H layers. The E horizon is throughout ~0.05 m thick, irregular, and with an abrupt boundary to the Bs horizon. The Bs horizon (upper 0.05 m) is yellowish red to dark reddish brown (5 YR, 3/3–4/6, moist; Munsell Color Company, Baltimore, Maryland, USA) from 0 to 80 m.

TABLE 1. Plant species sampled (x), and found but not sampled (o), in late July 1990 in the dwarf-shrub (DS), short-herb (SH), and tall-herb (TH) forest types at 0, 65, and 90 m, respectively, along the transect at Betsele. Numbers refer to Fig. 1. Nomenclature follows Tutin et al. (1964–1980).

Number	Species	Forest type		
		DS	SH	TH
1	<i>Empetrum hermaphroditum</i> L.	x		
2	<i>Vaccinium myrtillus</i> L.	x	o	
3	<i>Betula pubescens</i> L.	x	x	
4	<i>Linnaea borealis</i> L.	x	x	o
5	<i>Picea abies</i> (L.) Karsten	x	x	o
6	<i>Vaccinium vitis-idaea</i> L.	x	x	
7	<i>Maianthemum bifolium</i> (L.) Schmidt		x	o
8	<i>Solidago virgaurea</i> L.		x	
9	<i>Aconitum septentrionale</i> L.		x	x
10	<i>Actaea spicata</i> L.		x	x
11	<i>Galium triflorum</i> L.		x	x
12	<i>Gymnocarpium dryopteris</i> (L.) Newman		x	x
13	<i>Oxalis acetosella</i> L.		x	x
14	<i>Rubus idaeus</i> L.		x	x

At 90 m the soil color of the Bs is dark brown (10YR 3/1) and the structure becomes aggregated. Selected chemical and physical soil properties are presented in Table 2.

#### Soil solution and exchangeable cations

On 28 June 1994, soil sampling was performed every 10th m along the transect (from 0 to 90 m). Four to five mor samples were taken at random within 3 m from each sampling center with an auger (0.10 m diameter), and the thickness of the mor layer was measured in the hole. The sampled cores were kept separately in polyethylene bags. Mineral soil samples (10–15 samples at each spot) were taken with a narrower auger (0.01 m diameter) and bulked into one composite sample per 10 m. The mineral soil samples were separated into the E horizon and the upper 0.05 m of the Bs horizon.

In the laboratory, mor samples were divided into two equally thick layers, the upper O1 and lower O2. The mor samples were then centrifuged to extract the soil solution with a centrifuge drainage technique (Giesler and Lundström 1993: 14 000 rpm, 60 min, 5°C) within 16 h from the sampling. The average relative centrifugal field was  $16\,500 \times g$  ( $r = 75$  mm). Centrifuged mor samples were sealed in polyethylene bags after centrifugation and stored at 4°C for further analyses. Soil solution collected from the mor layer by centrifugation will give higher concentrations of most solutes compared to percolating soil solution collected by zero-tension lysimeters immediately below the mor layer (Giesler et al. 1996). Giesler et al. (1996) concluded that the centrifugation method might better reflect plant-available concentrations in the mor layer than zero-tension lysimetry, and the method is thus appropriate for this study.

Extracted soil solutions were filtered through a 0.45- $\mu$ m mesh filter (Syrfil-M, Costar Corporation, Cambridge, Massachusetts, USA). Soil solution pH was determined immediately after centrifugation on a sub-

TABLE 2. Selected chemical and physical properties of the O, E, and Bs horizons. The values represent average and standard deviations for the different forest types. The dwarf-shrub (DS) type represents 0–40 m, the short-herb (SH) type represents 50–80 m, and the tall-herb (TH) type represents 90 m along the transect at Betsele.

For- est type	Layer	<i>n</i>	CEC <sub>e</sub> † (mmol <sub>e</sub> /kg OM [d.m.])	CEC <sub>7.0</sub> ‡ (mmol <sub>e</sub> /kg OM [d.m.])	BC <sub>e</sub> § (mmol <sub>e</sub> /kg OM [d.m.])	EA <sub>e</sub> (mmol <sub>e</sub> /kg OM [d.m.])	TA <sub>7.0</sub>	Loss-on- ignition (% of dry mass)	Bulk density (kg/dm <sup>3</sup> )
DS	O1	21	322 ± 49	1182 ± 176	278 ± 55	23 ± 9	904 ± 194	94 ± 2	0.05 ± 0.01
	O2	21	316 ± 44	1312 ± 182	252 ± 52	53 ± 15	1061 ± 176	81 ± 10	0.06 ± 0.02
	E	5	968 ± 318	ND	275 ± 113	689 ± 340	ND	3 ± 1	ND
	Bs	5	620 ± 326	ND	162 ± 123	456 ± 222	ND	7 ± 1	ND
SH	O1	16	647 ± 78	1150 ± 97	638 ± 86	3 ± 2	511 ± 140	83 ± 6	0.05 ± 0.01
	O2	16	657 ± 144	1317 ± 154	634 ± 151	7 ± 4	683 ± 93	56 ± 15	0.10 ± 0.02
	E	4	1052 ± 45	ND	891 ± 93	149 ± 74	ND	4 ± 1	ND
	Bs	4	863 ± 250	ND	406 ± 125	455 ± 163	ND	9 ± 2	ND
TH	O1	5	791 ± 47	1372 ± 29	783 ± 47	5 ± 2	581 ± 22	84 ± 2	0.08 ± 0.02
	O2	5	813 ± 41	1580 ± 42	803 ± 40	8 ± 2	777 ± 25	58 ± 11	0.13 ± 0.04
	E	1	1314	ND	1244	70	ND	4	ND
	Bs	1	1619	ND	1490	127	ND	5	ND

Notes: In the "Layer" column, O1 and O2 denote upper and lower halves of the mor layer, respectively. Mineral soil samples are bulked within each sampling site. ND = not determined.

† Effective cation exchange capacity, 1.0 mol/L NH<sub>4</sub>NO<sub>3</sub>, soil : solution ratio 1:50.

‡ BC<sub>e</sub> + EA<sub>7.0</sub> (BC<sub>e</sub> = effective exchangeable base cations, EA = exchangeable anions at pH 7.0).

§ Effective exchangeable base cations,  $\Sigma 2\text{Ca} + 2\text{Mg} + \text{K} + \text{Na}$ , 1.0 mol/L NH<sub>4</sub>NO<sub>3</sub>, soil : solution ratio 1:50.

|| Total acidity, 1.0 mol/L NH<sub>4</sub>acetate pH 7.0, soil : solution ratio 1:50.

sample of the soil solution. Another subsample was acidified with concentrated HNO<sub>3</sub> before further analyses of cations. The soil solution was kept at 4°C until ready for analysis.

The mor samples (after centrifugation) and the mineral soil samples were passed through a 2-mm mesh sieve to remove coarse fragments. After gentle homogenization, the water content and percent loss-on-ignition (LOI) was measured on a subsample—105°C for 24 h, followed by ignition at 550°C for 6 h. (Note that these soils have negligible carbonate mineral content.) The soil organic matter (OM) content is defined as LOI times dry mass (d.m.). Soil pH (H<sub>2</sub>O, 1:5, soil : soil solution mass ratio, denoted pH<sub>H<sub>2</sub>O</sub>) was determined on mineral soil samples. The soils were stored at 4°C until further analyses ~2 mo later. In all following extractions we used a solution/OM ratio of 50:1 unless otherwise stated.

Exchangeable cations were extracted with an unbuffered salt solution of 1.0 mol/L NH<sub>4</sub>NO<sub>3</sub>. Soil samples of 2.5, 0.4, and 0.3 g OM were used for the O, E, and Bs horizons, respectively. On the mor samples, total acidity (TA<sub>7.0</sub>) was determined using a buffered 1.0 mol/L NH<sub>4</sub>C<sub>2</sub>H<sub>3</sub>O<sub>2</sub> solution (pH 7.0). The suspensions were shaken for 2 h, filtered first through number 00H Munktell analytical paper filter (STORA AB, Grycksbo, Sweden) and then through a 0.45-μm mesh filter. Thereafter solutions were kept at 4°C until further analyses. Solution pH was determined on a portion of the filtrate immediately after extraction and filtration. Total acidity, TA<sub>7.0</sub>, was estimated as the difference in the amount of NaOH added to the filtrate and a blank to reach pH 7.0.

Effective cation exchange capacity (CEC<sub>e</sub>), expressed as millimoles of charge per kilogram organic

matter, was calculated as the sum of 1.0 mol/L NH<sub>4</sub>NO<sub>3</sub> exchangeable cation charges (CEC<sub>e</sub> = 3Al<sup>3+</sup> + 2Ca<sup>2+</sup> + 2Mg<sup>2+</sup> + 2Mn<sup>2+</sup> + K<sup>+</sup> + Na<sup>+</sup> + H<sup>+</sup>). The concentration of H<sup>+</sup> was calculated from the pH of the filtrate. The cation exchange capacity at pH 7.0 (CEC<sub>7.0</sub>) was calculated as TA<sub>7.0</sub> + 1.0 mol/L NH<sub>4</sub>NO<sub>3</sub> exchangeable base cation charges. Base saturation (BS) is defined as the ratio between the sum of base cation charges (2Ca<sup>2+</sup> + 2Mg<sup>2+</sup> + K<sup>+</sup> + Na<sup>+</sup>) and CEC. BS<sub>e</sub> and BS<sub>7.0</sub> refer to CEC<sub>e</sub> and CEC<sub>7.0</sub>, respectively.

The relative charge fraction of cation *i* (*E<sub>i</sub>*) on the cation exchange complex is defined as

$$E_i = Zq_i/Q \quad (1)$$

in which *Z* is the valence of the cation *i*, *q<sub>i</sub>* is the adsorbed quantity of the cation *i* (expressed as millimoles per kilogram organic matter) and *Q* = CEC<sub>e</sub>. The relative charge fraction in the soil solution (*E<sub>i</sub>*) is defined in a similar way, however, *Q* in the soil solution is the equivalent sum of all ions of the same valence sign (i.e., cations or anions) and *q<sub>i</sub>* is exchanged with the concentration *C<sub>i</sub>* (cf. Sposito 1989).

The relationship between soil solution pH and dissociation of titrable organic functional groups was described by the extended Henderson-Hasselbalch equation (cf. Katchalsky and Spitnik 1947):

$$\text{pH} = \text{pK}_a^{\text{app}} + n \log([A^-]/[HA]) \quad (2)$$

in which dissociated organic acids (A<sup>−</sup>) are assumed to be represented by cation-exchange sites binding base cations and protonated organic acids (HA) by sites binding H, Al, and Fe. The term *n* is an empirically estimated constant (cf. Stevenson 1982) and pK<sub>a</sub><sup>app</sup> is the apparent acidity constant. Thus, the quotient [A<sup>−</sup>]/[HA] could be represented by BS/(1 − BS).



On 14 June 1995, a complementary soil sampling was undertaken along the transect to determine dissolved organic carbon (DOC) in the soil solution. Two mor samples were taken at the same 10-m interval as previously sampled, centrifuged the same day, and soil solutions were analyzed for cations, anions, DOC, pH, and conductivity as before.

On 27 July 1995 an additional sampling of the mor layer was made at 0, 50, 80, and 90 m. The samples were composited and passed through a 2-mm mesh sieve and homogenized. Soil solution pH and conductivity were determined from a centrifuged subsample of the homogenized soils. Effects of ionic strength on pH, buffer capacity upon dilution, and titration curves for the four soil samples were determined on the homogenized soils. The batch experiments started the same day as the sampling using the homogenized soil.

The effect of ionic strength on solution pH was determined in suspensions of NaCl with measured conductivities of 50, 150, 250, and 500  $\mu\text{S}/\text{cm}$ . These conductivities spanned the range measured in centrifuged soil solution from mor layer samples along the transect. Thirty milliliters of solution were added to 10 g fresh mass (f.m.) of mor layer soil and the suspensions were shaken for 2 h. The pH was measured in the supernatant after 1 h of sedimentation. Corrections for the conductivity of the soil water remaining after centrifugation were made, assuming a similar conductivity as in the centrifugate. The relationship between the ionic strength ( $I$ ) and conductivity was determined from a calibration curve using known concentrations of a KCl solution. The linear relationship was  $I = 68 \times 10^{-7} \times \text{conductivity } (\mu\text{S}/\text{cm}) - 2.9 \times 10^{-4}$ .

The effect of the buffer capacity on pH was determined by measuring pH in soil suspensions with different solution/soil ratios [henceforth abbreviated s/s ratio, in milliliters of solution per gram organic matter (dry matter, d.m.)], ranging from 2 to 270. Corrections were made for the water content in the soil. NaCl solutions with the same conductivities as those measured in centrifuged soil solutions were added to keep ionic strengths constant. The soil suspensions were shaken for 2 h, and pH was measured in the supernatant after 1 h of sedimentation. The ability of the mor soil to buffer the soil solution on dilution will depend on the concentration of protonated acid functional groups with  $\text{pK}_a$  values around the prevalent pH in the soil solution and is thus assumed to give an estimate of influence of the acid quantity (cf. Skjellberg 1995). The slope of the linear relationship between solution pH and s/s ratio (Skjellberg 1995) was used as an estimate of the soil to buffer against dilution. A lower value of the slope will thus indicate a larger buffer capacity.

Titration curves were developed by adding HCl or  $\text{Ca}(\text{OH})_2$  (s) to soil suspensions with  $\sim 1.0$  g OM (d.m.) suspended in 50 ml 0.04 mol/L NaCl. At least seven titration points were obtained within the pH interval from 2 to 8. Duplicate samples were used for each

titration point. The samples were shaken for 48 h and pH was measured in the supernatant after 1 h of sedimentation. The valence of the cation in the added hydroxide will affect the shape of the titration curve (Aitken and Moody 1994). Therefore  $\text{Ca}(\text{OH})_2$  was used as the base since  $\text{Ca}^{2+}$  was the major counterpart to  $\text{H}^+$  on the exchange complex. The acid neutralizing capacity (ANC) was determined as the quantity of  $\text{H}^+$  (as HCl) required to titrate the soil to pH 3.0, and the base neutralizing capacity (BNC) was determined as the quantity of  $\text{OH}^-$  needed to titrate the soil to pH 7.0. The base saturation (BS) was calculated for each titration point as  $\text{BS}_{3-7} = \text{ANC}/(\text{ANC} + \text{BNC})$  (cf. Binkley et al. 1989). The quantity of  $\text{H}^+/\text{OH}^-$  needed to reach pH 3 and 7, respectively, was estimated by interpolation using the closest data points above and below pH 3 and pH 7, respectively. Differences in the solution pH at the same BS are interpreted as mainly reflecting differences in acid quality (Skjellberg 1996).

An incubation at  $4^\circ\text{C}$  was also performed on the soil samples from 27 July 1995 to evaluate the effect of sample storage in darkness in sealed plastic bags on soil pH and net nitrification. Subsamples from the 0, 50, 80, and 90 m soils were centrifuged after 2 mo of storage. The pH value, conductivity and  $\text{NO}_3$  concentrations in soil solutions were compared with centrifugates from the day of the soil sampling.

#### *Extractable pools of inorganic N*

On 8 June 1994, the F, and/or H layers from an area of  $0.4 \times 0.4$  m were sampled for analyses of extractable inorganic N (i.e.,  $\text{NH}_4$  and  $\text{NO}_3$ ) at every 10th m along the transect. All samples were separated by horizons and sieved (5-mm mesh) and stored at  $4^\circ\text{C}$ . Twenty grams (f.m.) soil was extracted with 50 mL of 2 mol/L KCl for 2 h on a shaker and thereafter filtered on the day of sampling.

#### *Phosphate adsorption experiment*

A batch equilibrium experiment was conducted on mor samples from 80 and 90 m to evaluate the  $\text{PO}_4$  adsorption capacity of the soils. For comparison, a Bs horizon sample from 70 m was included. The experiment followed Nodvin et al. (1986). The ability to remove or release  $\text{PO}_4$  can be described by the relationship between the amount removed or released from the solution (RE: in millimoles per kilogram) and the initial amount of  $\text{PO}_4$  added ( $X_i$ : in millimoles per kilogram), and is defined by the linear isotherm:

$$\text{RE} = mX_i - b. \quad (3)$$

The slope ( $m$ ) is defined as the partition coefficient of the initial mass isotherm (Nodvin et al. 1986), i.e., the fraction of total reactive substance in a soil/water system that is retained by the soil. A value of 1.0 thus indicates total adsorption, whereas a value of 0 indicates no adsorption.

We equilibrated 20 mL of either 0, 50, 200, 400, 600,

1000, or 2000  $\mu\text{mol/L}$   $\text{Na}_2\text{HPO}_4$  with 1 g (d.m.) of soil on a shaker (16 h, 20°C). After the equilibration period, particulate matter was removed by centrifugation (15 000 g, 15 min) and the centrifugate was filtered (0.45  $\mu\text{m}$ ) and analyzed for  $\text{PO}_4$ .

Since the presence of Al and Fe oxihydroxides in soils affects  $\text{PO}_4$  adsorption and availability (Bohn et al. 1985, Guzman et al. 1994) extractable pools of Al and Fe were also determined in five more samples from 80 and 90 m. Three extraction methods were used: 0.5 mol/L  $\text{CuCl}_2$  (2 h), 0.1 mol/L  $\text{Na}_4\text{P}_2\text{O}_7$  (sodium-pyrophosphate, PYRO, 16 h) and citrate-bicarbonate-dithionite (CBD). For the CBD extraction a solution/soil OM (d.m.) ratio of 100:1 was used (15 min). The  $\text{CuCl}_2$  extraction is assumed to extract organically complexed Al (Hargrove and Thomas 1984), whereas the PYRO extraction is assumed to extract all organically bound Fe and Al (McKeague 1967), while CBD extracts amorphous and crystalline Al and Fe-oxihydroxides as well as organically bound Al and Fe forms (McKeague et al. 1971).

Determinations of nitric and perchloric acid digestable contents of P (total P) were conducted on the soil samples taken on 8 June 1994.

#### Foliar analyses

On 31 July 1990, three 10  $\times$  10 m plots were laid out along the transect: one (I) at 0 m in the dwarf shrub forest type, one (II) at 65 m in an intermediate forest type with both dwarf shrubs, short herbs, and tall herbs (short herb forest type), and one (III) at 90 m in the tall herb forest type. Foliar samples of >5 g (f.m.) each of fresh leaves were taken from individual shoots ( $N = 6-8$ ) of a range of species on each plot (Fig. 1, Table 1), dried (70°C, 48 h), and ground in a ball mill before analyses of N, P, K, Mg, and Ca. Only fresh leaves were sampled. Samples from *P. abies* contained several year classes of needles.

#### Plant nitrate reductase activity

On 16 June 1994, foliar samples of a few grams (f.m.) of four species (cf. Table 1) were collected at 10-m intervals along the transect: *L. borealis* (0–80 m), *O. acetosella* (30–90 m), *R. idaeus*, and *A. septentrionale* (70–90 m). Assays of NRA were conducted as described by Högberg et al. (1986) to indicate availability of nitrate in the soil–plant system.

#### Root bioassays

We conducted root bioassays to assess whether plants were deficient in N or P. In these assays roots were immersed in solutions labelled with  $^{15}\text{N}$  or  $^{32}\text{P}$ . Plants will show high specific uptake rates for the element in which they are deficient. Samples ( $n = 6-11$ ) of >3 g f.m. of fine roots each were taken from *P. abies* at 0, 40, 70, and 90 m, and from *R. idaeus* ( $n = 10-11$ ) at 70 and 90 m on 19 June 1995. Samples represented roots traced from individual shoots; around 0 m an area

of  $\sim 0.1$  ha was used to obtain samples from *P. abies*, while at 40, 70, and 90 m the corresponding areas were from 0.01 to 0.04 ha. In addition, at 0, 40, and 70 m, half the samples were from tall trees and the other half from specimens <2 m tall. At 90 m there were only tall trees in the vicinity and roots from these were traced into the center of the 90 m area for sampling. The analytical protocols followed Jones et al. (1994), except that the activity of  $^{32}\text{P}$  was doubled and we present  $^{32}\text{P}$  data in counts per minute (CPM) instead of picograms of P. After immersion in the labeled solutions,  $^{15}\text{NH}_4$  and  $^{32}\text{PO}_4$  adsorbed on root surfaces were desorbed in solutions of  $\text{CaSO}_4$  and unlabeled  $\text{KH}_2\text{PO}_4$ , respectively.

#### Analysis

Soil solutions were analyzed for Si, Fe, Al, Mn, Mg, Na, Ca, K, and P using inductively coupled plasma-mass spectrometry (ICP-MS, Perkin Elmer SCIEX, Norwalk, Connecticut, USA). An ion chromatograph (Dionex model 4000i, Dionex Corporation, Sunnyvale, California, USA) was used to determine Cl, F,  $\text{PO}_4$ ,  $\text{NO}_3$ , and  $\text{SO}_4$  concentrations. Soil solution P analyzed with ICP-MS was considered to represent the total P content ( $P_T$ ) in the soil solution. In the phosphate adsorption batch experiment, a flow injection analyzer (5020 Analyser, Tecator, Höganäs, Sweden) was used to determine  $\text{PO}_4$  concentrations. Soil solution  $\text{NH}_4$  concentrations were analyzed spectrophotometrically with a flow injection analyzer as above. Soil solution pH was measured with an Orion Research Model 601/digital ionalyzer and an Orion 8103 SC Ross combination electrode (Orion Research, Cambridge, Massachusetts, USA). DOC was analyzed on a total organic carbon analyzer (TOC-5000, Shimadzu Company, Tokyo, Japan). Ionic strength ( $I$ ) was calculated as

$$I = 0.5 \sum C_i Z_i^2 \quad (4)$$

where  $C_i$  = concentration and  $Z_i$  = charge of ion  $i$ . The anion deficit was calculated as the sum of cation charges minus the sum of anion charges. Aluminum was treated as completely organically complexed and not contributing to net charge.

Extractable cations were analyzed using inductively coupled plasma-atomic emission spectrometry (Perkin-Elmer Plasma II emission spectrometer, Norwalk, Connecticut, USA). Titratable acidity ( $\text{TA}_{7.0}$ ) was determined on Mettler DL 70 titrator using a Mettler DG 111-SC combination electrode (Mettler Institut AG, Greifensee, Switzerland).

Dried soil and plant material were digested in a mixture of nitric and perchloric acid (ratio 10:1) and analyzed for total P, Ca, Mg, and K using ICP-AES (as above). Foliar N was analyzed colorimetrically on a Kjeldahl digest, while soil total N was analyzed on an elemental analyzer coupled to an isotope ratio mass spectrometer (ANCA-NT solid/liquids preparation

module coupled to a Model 20-20 IRMS, Europa Scientific Limited, Crewe, England).

### Statistics

For statistical comparison of solute concentrations and exchangeable cations at different sampling spots along the transect one-way ANOVA was used ( $df = 9$ ). The two layers, O1 and O2, were analyzed separately. To test for differences between the two mor layers, we used paired  $t$  test for each forest type separately. Multiple comparisons in variance analyses were performed with Scheffé's test for multiple contrast following the procedure of Zar (1984). The Scheffé test allows us to test hypothesis where mean values from several sampling plots are compared, i.e., sampling plots grouped as DS, SH, and TH. The null hypothesis for a comparison of, for example, DS and SH will thus be

$$H_0: [(\mu_0 + \mu_{10} + \mu_{20} + \mu_{30} + \mu_{40})/5] \\ - [(\mu_{50} + \mu_{60} + \mu_{70} + \mu_{80})/4] = 0$$

where  $\mu$  denotes the average value for the sampling plot and the index denotes the plot. Statistical analysis was performed using SYSTAT statistical software (SYSTAT, Evanston, Illinois, USA). Significant differences refer to the  $P < 0.05$  level unless otherwise stated.

### RESULTS

#### Soil solution pH

Soil solution pH in the mor layer spanned  $>3$  pH units along the transect. The lowest pH values were found at 0 m (Fig. 2a). Between 40 and 50 m there was an increase in pH of  $\sim 1$  pH unit and between 80 and 90 m there was another increase of 1 pH unit. The  $\text{pH}_{\text{H}_2\text{O}}$  in the E horizon followed the pattern observed in the mor layers (Pearson correlation:  $r = 0.86$ ,  $P < 0.001$ ). In the Bs horizon there was no increase in  $\text{pH}_{\text{H}_2\text{O}}$  between 0 and 80 m but an increase between 80 and 90 m (data not shown).

Soil solution pH correlated strongly to base saturation, except for the 90-m samples, which formed an outlying group and were excluded in the correlation ( $r = 0.87$  and  $r = 0.94$  using  $\text{BS}_e$  or  $\text{BS}_{7.0}$ , respectively). When the extended Henderson-Hasselbalch equation (Eq. 2) was applied (Fig. 3a), a similar positive correlation was found (90-m soil samples excluded). The correlation was, however, not improved ( $r = 0.95$  and  $r = 0.93$  using  $\text{BS}_e$  or  $\text{BS}_{7.0}$  in the equation, respectively).

In contrast to the above results, the 90-m soil did not form an outlying group when we correlated the pH determined in the 1.0 mol/L  $\text{NH}_4\text{NO}_3$  solution to the base saturation (Fig. 3b). A similar positive correlation (including the 90-m soil samples) was also found when soil solution pH in the soil samples from

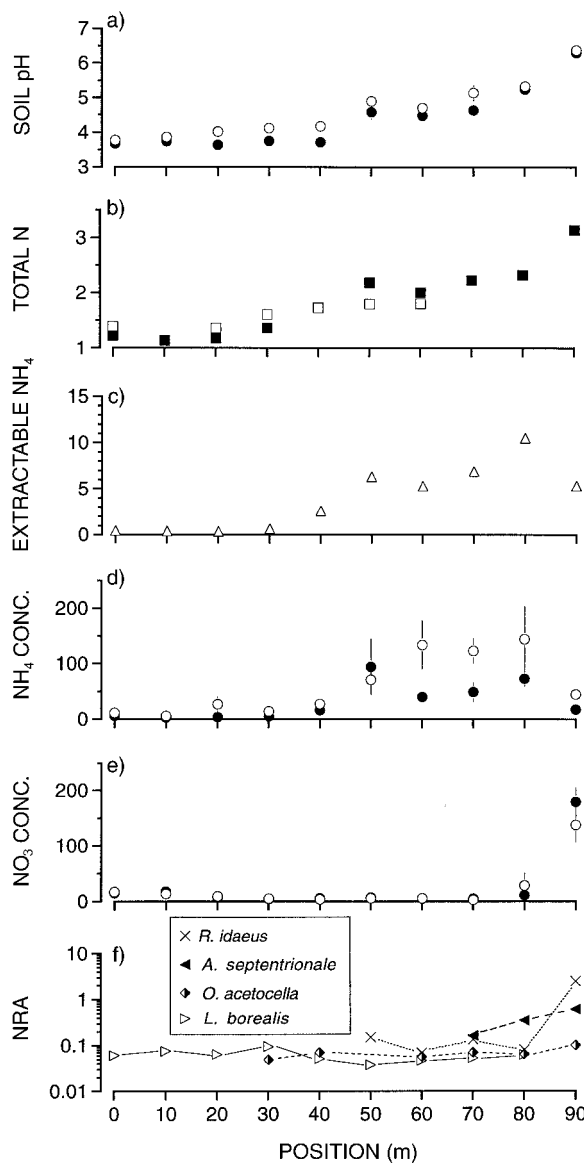


FIG. 2. Soil solution pH and N parameters along the transect at Betsele. (a) pH in soil solution: ○ denotes upper half of the mor layer (O1), and ● denotes lower half of the mor layer (O2). (b) Total N content (% of OM): □ = F layer, ■ = H layer. (c) 2.0 mol/L KCl extractable  $\text{NH}_4$  (mmol/kg OM), average value of F and H layers. (d)  $\text{NH}_4$  concentrations ( $\mu\text{mol/L}$ ) in the soil solution (symbols as in part a). (e)  $\text{NO}_3$  concentrations ( $\mu\text{mol/L}$ ) in the soil solution (symbols as in part a). (f) Plant nitrate reductase activity [NRA,  $\mu\text{mol NO}_2^- \cdot (\text{g fresh mass})^{-1} \cdot \text{h}^{-1}$ ] in four plant species (cf. insert). Bars represent  $\pm 1$  SE ( $n = 4-5$ ).

July 1995 were correlated to the base saturation determined from the titration data (not shown).

Comparing pH values from the titration at the same base saturation showed that the 80- and 90-m soils generally had lower pH values than the 0- and 50-m soils at the same base saturation (Fig. 3c). The max-

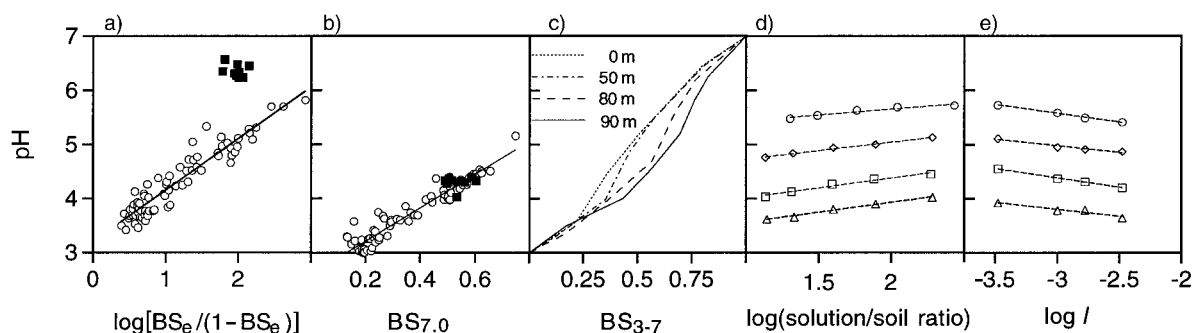


FIG. 3. Variations in soil chemistry along the transect at Betsele: (a) soil solution pH vs.  $\log[BS_e/(1 - BS_e)]$  (Eq. 2) ( $\circ$  = 0–80 m,  $\blacksquare$  = 90 m;  $BS_e$  refers to base saturation at  $CEC_e$  [effective cation exchange capacity]), (b) pH in 1.0 mol/L  $NH_4NO_3$  vs.  $BS_{7.0}$  ( $\circ$  = 0–80 m,  $\blacksquare$  = 90 m;  $BS$  = base saturation), (c) pH vs base saturation determined from titration curves, (d) the relationship between pH and  $\log(s/s \text{ ratio})$ , the  $s/s$  ratio expressed as L/kg OM (d.m.), and (e) the relationship between pH and  $\log I$ , where  $I$  = ionic strength. Symbols in (e) and (f) are:  $\circ$  = 90 m,  $\diamond$  = 80 m,  $\square$  = 50 m, and  $\triangle$  = 0 m.

imum difference found at the same base saturation was 0.9 pH units.

The ability of the soil samples from 0, 50, 80, and 90 m to buffer pH upon dilution increased (a lower value indicates a higher buffering capacity) from 0.37 at 0 m to 0.22  $\Delta pH/\Delta \log(s/s \text{ ratio})$  at 90 m (Fig. 3d). A tenfold increase in the  $s/s$  ratio will thus increase pH by <0.4 pH units. The  $s/s$  ratios (expressed as liters per kilogram OM), in the field ranged from 2.11 to 4.33, which is equivalent to log ratios of 0.32–0.64. The difference in  $s/s$  ratios will thus contribute at most 0.13 pH units of the pH variation along the transect, according to calculations based on the smallest buffering capacity (0.37), and the maximum difference in  $s/s$  ratio observed.

Changes in the ionic strengths ( $I$ ) in suspensions with soil samples from 0, 50, 80, and 90 m gave at the most a difference of 0.35 pH units, based on maximum and minimum values of  $I$  in the centrifuged soil solutions (Fig. 3e). The average  $\Delta pH$  per unit  $\log I$  was 0.46 for the four soil samples. Assuming that the ionic strength is constant and equal to the average  $I$  for all samples enables a correction for observed differences in ionic strengths using the estimated  $\Delta pH$  per unit  $\log I$  value of 0.46. A correction for observed differences in ionic strength gave a maximum pH correction of 0.27. The average correction was, however, less:  $0.09 \pm 0.01$  (mean  $\pm 1$  standard error).

Incubation of soil samples at 4°C for 2 mo decreased soil solution pH by 0.71 pH units in the 90-m soil samples. In soil samples from 0, 50, and 80 m pH increased by 0.16, 0.16, and 0.21 units, respectively. Nitrate concentrations in the 90-m soil samples increased from about 180 to 13 000  $\mu\text{mol/L}$  during the same time period and the conductivity rose from 184 to 1575  $\mu\text{S/cm}$ . In the other soil samples concentrations of  $NO_3^-$  were <22  $\mu\text{mol/L}$ , and changes were minor during storage.

#### Exchangeable pools of base cations

The increase in base saturation in the mor layer along the transect was mainly caused by increased Ca

saturation, and decreased H saturation of the exchange complex (Fig. 4c). In the mineral E horizon a similar trend was found (Fig. 4d). However, Al was the major cation replacing Ca at the more acid part of the transect (Fig. 4d). In the upper Bs horizon there was also an increase in base saturation, which, however, was not as pronounced as in the E horizon (Fig. 4e). Between 80 and 90 m, however, the base saturation increased from 49 to 92%.

#### Soil solution

The three major cations in the soil solution were Ca, K, and Mg, which comprised >75% of the total cation concentration (expressed as micromoles of charge per liter). Concentrations of cations were generally higher in the O1 than in the O2 layer (Table 3). Inorganic anions in the soil solution were dominated by  $PO_4$ ,  $SO_4$ , and Cl (Table 3).

Cation concentrations increased along the transect from 0 to 80 m. The increase in cation concentration was mainly due to Ca. At 90 m, concentrations of both cations and anions, except  $NO_3^-$ , decreased (Table 3). The increase in cations along the first 80 m of the transect was balanced by an increase in the anion deficit because inorganic anions remained relatively constant (Fig. 4a, Table 3). The increase in the anion deficit also corresponded to an increased ionic strength in the soil solution (the anion deficit was not accounted for in the calculation of ionic strength). There was no relationship between the water content and the ionic strength.

The complementary analyses of soils sampled on 14 June 1995 gave no difference between the average DOC concentrations in soil solutions in the dwarf-shrub forest type and the short-herb forest type, whereas the average anion deficit was significantly higher for the short-herb forest type (Table 4). A calculation of the charge density (i.e., the equivalent amount of negative charges per DOC expressed as micromoles of charge per milligram DOC) showed that the average value was significantly higher in the



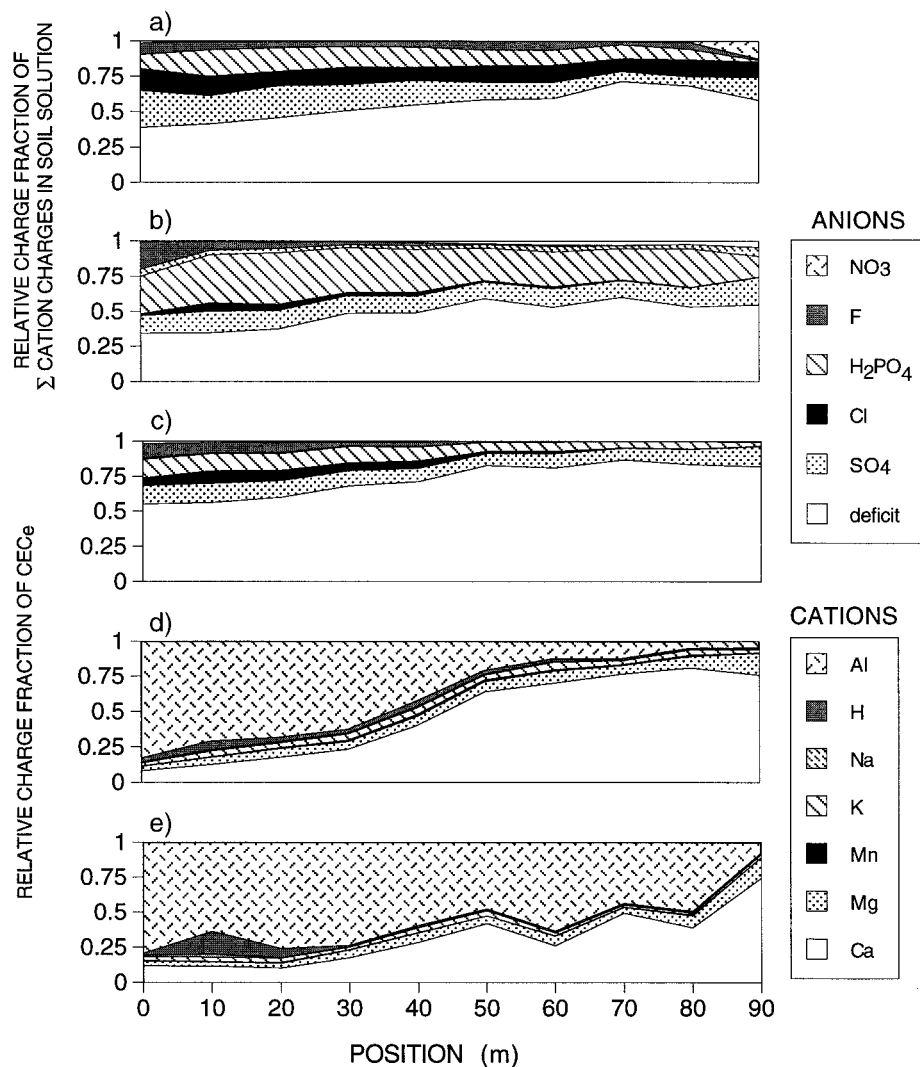


FIG. 4. The relative charge fraction of ions in soils and soil solutions along the transect at Betsele: (a) anions in soil solution (average values, O1), (b) cations in soil solution (average values, O1), (c–e) the relative charge fraction of exchangeable cations in (c) the mor layer (average values, O1), (d) the E horizon, and (e) the upper Bs horizon.  $CEC_e$  = effective cation exchange capacity.

short-herb forest type than in the dwarf shrub forest type. The concentrations of DOC in soil solutions from 90 m (tall-herb forest type) were significantly lower as compared to average soil solutions from the two other forest types (7 vs. 33 mmol/L, respectively). The decrease in DOC also corresponded to a decreased anion deficit at 90 m. The charge density at 90 m was similar to the value observed in the short-herb forest type (Table 4).

The relative charge fraction of the major cations in the soil solution was positively correlated with the relative charge fraction of exchangeable cations (Fig. 4, Table 5) with the exception of Na. The amount of cations in the soil solution comprised a small portion relative to the exchangeable pool (<1% for the divalent ions and ~6% for K).

#### *Nitrogen: total capital and availability*

There was an increase in total N concentrations (Fig. 2b) in the mor layer, which was strongly correlated with soil solution pH and  $BS_{7.0}$  ( $r = 0.97$ ,  $P < 0.001$  and  $R = 0.88$ ,  $P < 0.01$ , respectively). On a kilogram per hectare basis, the total N pool in the mor increased from ~400 kg/ha at 0 m to 1300 kg/ha at 90 m. The average values for nitrogen in the three forest types, dwarf shrub (0–40 m), short herb (50–80 m), and tall herb (90 m), were 370, 700 and 1330 kg/ha, respectively.

Extractable  $NH_4$  increased along the transect from 0 to 80 m (Fig. 2c), whereas extractable  $NO_3$  did not exhibit any trend (data not shown). The average amount of extractable  $NO_3$  was 0.2 mmol/kg OM (d.m.). The

TABLE 3. Solute concentrations (means  $\pm$  1 SD) and ionic strength ( $I$ , mmol/L) of soil solutions ( $\mu\text{mol/L}$ ) in the mor in the three forest types (cf. Table 2) at Betsele. Asterisks (\*) denote significant differences between the upper (O1) and lower (O2) half of the mor, whereas different letters denote significant difference between sites, the first letter denoting O1 and

Layer	pH	F	Cl	NO <sub>3</sub>	SO <sub>4</sub>	PO <sub>4</sub>	P	Al	
Forest type									
DS	O1	4.00 ± 0.24 * a a	146 ± 83 a a	331 ± 113 * a a	10 ± 8 a a	285 ± 217 a a	388 ± 147 * a a	453 ± 173 * a a	36 ± 16 a a
	O2	3.71 ± 0.16	125 ± 93	240 ± 126	10 ± 10	245 ± 144	221 ± 118	284 ± 139	34 ± 14
SH	O1	5.03 ± 0.39 * b b	236 ± 22 * a a	508 ± 328 a a	11 ± 23 a a	206 ± 107 a a	421 ± 156 * a b	498 ± 213 * a b	12 ± 4 * b b
	O2	4.75 ± 0.41	82 ± 53	345 ± 201	7 ± 7	223 ± 118	121 ± 56	149 ± 57	20 ± 6
TH	O1	6.39 ± 0.15 * c c	8 ± 5 a a	115 ± 31 * a b	138 ± 70 b b	88 ± 21 * a a	12 ± 9 b a	23 ± 7 * b a	23 ± 5 ab ab
	O2	6.32 ± 0.03	8 ± 4	57 ± 21	180 ± 58	72 ± 21	4 ± 0	13 ± 3	23 ± 5
<i>P</i> values									
	O1	<0.001	0.123	0.028	<0.001	0.667	<0.001	<0.001	0.002
	O2	<0.001	0.001	<0.001	<0.001	0.012	<0.001	<0.001	<0.001

increase in extractable NH<sub>4</sub> was also reflected in soil solution NH<sub>4</sub> concentrations (Fig. 2d). At 90 m both extractable NH<sub>4</sub> and soil solution NH<sub>4</sub> were lower than at 80 m. Instead, NO<sub>3</sub> concentrations in the soil solution increased from almost nondetectable amounts between 0 and 70 m to concentrations of up to 160  $\mu\text{mol/L}$  at 90 m (Fig. 2e).

#### Phosphorus: total capital and availability

The total P content (in kilograms per hectare) in the mor layer increased along the transect with especially high values in the tall-herb forest type at 90 m (Fig. 5a), where the amount of P was  $\sim$ 2.5 times higher than in the short-herb forest type.

Soil solution phosphate concentrations in the mor were always higher in the O1 layer than in the O2 layer (Table 3). The largest difference was found at the short-herb site (50–80 m); concentrations in the O1 layer were almost 3 times higher than in the O2 layer. The PO<sub>4</sub> concentration was  $\sim$ 83% of total P (P<sub>T</sub>) content in the soil solution and was correlated to total P ( $r = 0.99$ ,  $P < 0.001$ ).

Phosphate added to the 90-m soil was almost completely removed in the adsorption experiment, i.e., the slope of the regression line was close to 1 ( $m = 0.95$ ). A similar degree of phosphate retention was found for the Bs horizon from 70 m (Fig. 6a). In contrast, the 80-m mor layer showed almost no ability to retain phosphate ( $m = 0.08$ ) (Fig. 6a). The 80-m mor also released 1.37 mmol/kg (d.m.) initially, while the amounts released initially by the 90 m and Bs soils were much lower, 0.08 and 0.03 mmol/kg (d.m.), respectively.

The CBD-extractable pool of Fe in the mor was 15 times larger at 90 m compared to at 80 m (Fig. 6c). Similarly, the PYRO-extractable pool was 24 times higher in the 90-m mor soil (Fig. 6c). For Al similar differences were found (Fig. 6b). The CBD-extractable

Fe pool was 2.3 times larger than the PYRO-extractable Fe pool at 90 m. For Al there was no significant difference between the CBD- and PYRO-extractable pools.

#### Foliar analyses

There was a continuous and clear increase in %N in foliage of the species sampled along the transect (Table 6, Fig. 7); at 0 m %N was below 1.0% in three species out of six, while at 90 m %N exceeded 2.5% in all six species sampled. Generally, there was a large variation in the foliar concentrations of nutrients both between plant species and in the degree of change in concentrations along the transect (Table 6, Fig. 7). Percentage P increased slightly between 0 and 65 m. In *L. borealis* the increase was significant ( $P = 0.009$ ). Thereafter, from 65 to 90 m, there was a significant decrease in %P between the short-herb and tall-herb forest type. The rate of change differed, however, between the species. Percentage P showed a decreasing trend in four species, but a slight increasing trend in two. However, the P:N ratio decreased significantly between 65 and 90 m to average ratios below 0.1 for all species (Fig. 7). As regards K, species found at both 0 and 65 m on an average had lower concentrations than species found at both 65 and 90 m (Fig. 7). There was a significant increase in %K in two out of four species between 0 and 65 m, but no further increase between 65 and 90 m. Above all, there was a large variation in %Ca between plant species. At 65 and 90 m there was a variation in %Ca from  $>2.5\%$  in *A. septentrionale* and *A. spicata* down to  $\sim 0.5\%$  in *G. dryopteris*. As regards Mg, no significant difference was found between 0 and 65 m. Between 65 and 90 m five species showed increasing trends in %Mg, while a slight negative trend was found in a sixth.

the second O2. *P* values for one-way ANOVA ( $df = 9$ ,  $n = 42$ ) are presented at the bottom of the table. The anion deficit is equal to cations – anions (mmol/L).

Mn	Mg	Ca	Na	K	NH <sub>4</sub>	Anion deficit	<i>I</i>
54 ± 37 * a a	185 ± 68 * a a	581 ± 298 * a a	70 ± 31 a a	904 ± 287 * a a	17 ± 14 * a a	1367 ± 741 * a a	3.19 ± 1.21 * a a
20 ± 16	104 ± 51	297 ± 147	73 ± 53	547 ± 302	7 ± 9	626 ± 267	2.05 ± 0.88
18 ± 10 * a a	289 ± 143 * a a	1233 ± 459 * b b	130 ± 67 * a a	1135 ± 699 * a a	119 ± 76 * b b	2889 ± 1318 * b b	4.78 ± 1.96 * a a
11 ± 6	109 ± 39	619 ± 165	96 ± 43	567 ± 295	65 ± 54	1231 ± 379	2.58 ± 0.68
4 ± 2 a a	105 ± 11 * a a	292 ± 35 * a a	69 ± 8 a a	154 ± 32 * a a	46 ± 16 * ab ab	619 ± 71 * b b	1.25 ± 0.15 * b b
4 ± 1	77 ± 10	207 ± 31	81 ± 9	78 ± 19	18 ± 7	320 ± 35	0.94 ± 0.16
0.014	0.028	<0.001	0.001	0.030	<0.001	<0.001	0.008
0.042	0.003	<0.001	0.162	0.001	0.003	<0.001	<0.001

#### Plant NRA activity

In *L. borealis* sampled from 0 to 80 m, and in *O. acetosella* sampled from 30 to 90 m, NRA was at constitutive levels  $<0.2 \mu\text{mol NO}_2^- \cdot (\text{g f.m.})^{-1} \cdot \text{h}^{-1}$  (Fig. 2f). In *R. idaeus* the same was found from 50 to 80 m, but the activity at 90 m ( $2.5 \mu\text{mol NO}_2^- \cdot (\text{g f.m.})^{-1} \cdot \text{h}^{-1}$ ) was  $>10$  times constitutive levels. In *A. septentrionale* NRA increased more gradually from constitutive levels at 70 m to  $0.61 \mu\text{mol NO}_2^- \cdot (\text{g f.m.})^{-1} \cdot \text{h}^{-1}$  at 90 m.

#### Root bioassays

There were no differences in P uptake rates in excised roots between tall and short *P. abies* from 0, 40, and 70 m. There were, furthermore, no differences in P uptake between fine roots of *P. abies* from 0, 40, and 70 m, but the activity at 90 m was significantly higher (Fig. 5c, one-way ANOVA,  $df = 3$ ,  $P < 0.001$ ). In *R. idaeus* a similar difference was observed between samples from 70 and 90 m (*t* test:  $P < 0.01$ ). There was no directional variation in N uptake rates in excised roots of *P. abies* along the gradient. However, the %N in roots increased significantly from  $1.20 \pm 0.03$  at 0 m to  $1.97 \pm 0.10$  at 90 m (one-way ANOVA,  $df = 3$ ,  $P < 0.001$ ).

TABLE 4. DOC (dissolved organic carbon) in soil solution, 14 June 1995, in the three forest types at Betsele (cf. Table 2). Previous year's data are in parentheses. Different superscript letters denote significant differences among forest types.

Forest type	<i>n</i>	DOC (mmol/L)	Deficit (μmol/L)	pH	Charge density (μmol <sub>c</sub> /mg)
DS	8	33.7 <sup>a</sup>	1004 <sup>a</sup> (996)	3.57 <sup>a</sup> (3.85)	2.65 <sup>a</sup>
SH	8	32.7 <sup>a</sup>	1727 <sup>b</sup> (2060)	4.42 <sup>b</sup> (4.89)	4.59 <sup>b</sup>
TH	2	7.3 <sup>b</sup>	471 <sup>a</sup> (470)	6.61 <sup>c</sup> (6.36)	5.34 <sup>b</sup>

#### DISCUSSION

The Betsele transect is an extreme example of the catenary sequences found in hilly terrain in the Fennoscandian boreal forest. In this context the correlation between slope length and plant productivity is so strong that site productivity can be estimated reasonably well from slope length alone (Hägglund and Lundmark 1977, Holmgren, 1994). Ample experimental evidence has shown that N is the limiting nutrient in the majority of these forests on mineral soils (Tamm 1964, 1991). Additions of other elements (e.g., P, K, Ca, and Mg) have not resulted in immediate growth responses unless the N limitation was removed (Tamm 1985), although larger survey data usually show a strong correlation between base saturation and site productivity. This, and the fact that N is not supplied from the bedrock, lead to the hypothesis that the availability of base cations or soil pH affects tree growth via effects on soil N supply (Dahl et al. 1967). In the following section we will first concentrate on the chemistry of base cations and determinants of soil pH. We will thereafter examine relations between soil chemistry and plants, notably the variations in N and P availability and plants.

#### The exchange complex and the composition of the soil solution

The increase in base saturation of the mor layer from 0 to 90 m was mainly caused by an increase in

TABLE 5. Correlation coefficients between the relative charge fraction (*E*) for cation *x* in the soil solution and the relative charge fraction for cation *x* on the exchange complex (1.0 mol/L NH<sub>4</sub>NO<sub>3</sub>). Values represent all mor samples collected along the Betsele transect ( $n = 84$ ).

Ca	Mg	Mn	K	Na
0.89	0.73	0.88	0.78	0.41

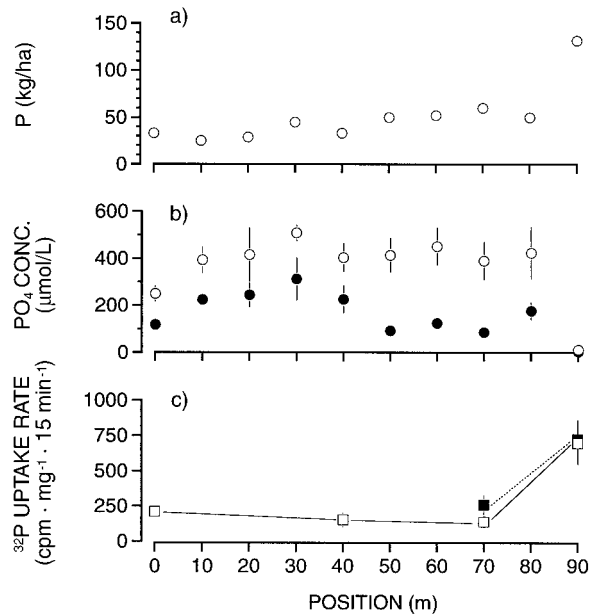


FIG. 5. (a) Total P in the mor layer. (b) PO<sub>4</sub> concentrations in the soil solution (symbols as in Fig. 2). (c) Uptake rates of <sup>32</sup>P for excised roots of *R. idaeus* (■) and *P. abies* (□) along the transect at Betsele (mean ± 1 SE) (cpm = counts per minute).

TABLE 6. Tests of differences in concentration of macro-nutrients and P:N ratios in foliage between forest types and species (cf. Fig. 7). Results are based on two-way ANOVA with balanced design ( $n = 8$  for N and  $n = 4$  for the other elements).

Nutrient	Forest type comparison	Number of species	P		
			Species	Forest type	Species × forest type
N	DS vs. SH	4	<0.001	<0.001	<0.001
	SH vs. TH	6	0.001	<0.001	0.220
P	DS vs. SH	4	<0.001	<0.001	0.027
	SH vs. TH	6	0.137	0.014	0.003
Ca	DS vs. SH	4	<0.001	0.002	0.009
	SH vs. TH	6	<0.001	0.011	0.008
K	DS vs. SH	4	<0.001	<0.001	<0.001
	SH vs. TH	6	0.003	0.407	0.759
Mg	DS vs. SH	4	<0.001	0.658	0.239
	SH vs. TH	6	<0.001	<0.001	0.006
P:N	DS vs. SH	4	<0.001	0.005	0.027
	SH vs. TH	6	0.627	<0.001	<0.001

Ca on the exchange complex. In the E and Bs horizons in the dwarf-shrub forest type, however, Al was the dominant cation on the exchange complex (CEC<sub>e</sub>). This is expected in podzols (cf. Ugolini and Sletten 1991), and is in accordance with a survey of Swedish forest soils (Nilsson 1988). There was a marked increase in the Ca saturation in the E horizon between the dwarf-shrub and short-herb forest types, whereas a similar pronounced increase in the Bs was only

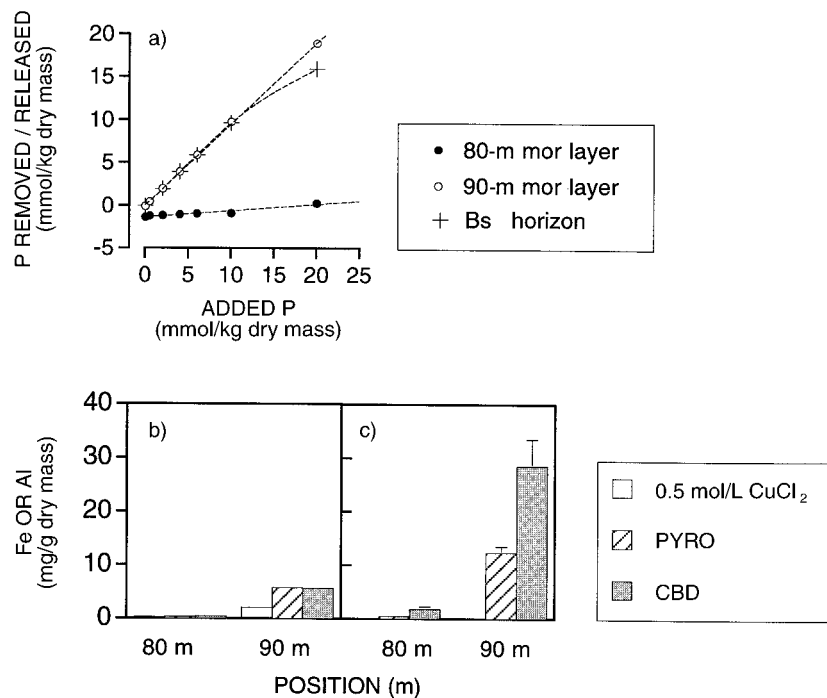


FIG. 6. (a) Adsorption isotherms for phosphate in mor soils from 80 and 90 m and Bs horizon soil from 70 m; a steeper slope indicates a higher phosphate adsorption capacity. (b) The extractable amounts of Al. (c) Fe in 0.5 mol/L CuCl<sub>2</sub>, 0.1 mol/L sodium-pyrophosphate (PYRO), and citrate-bicarbonate-dithionite (CBD) (mean ± 1 SE).



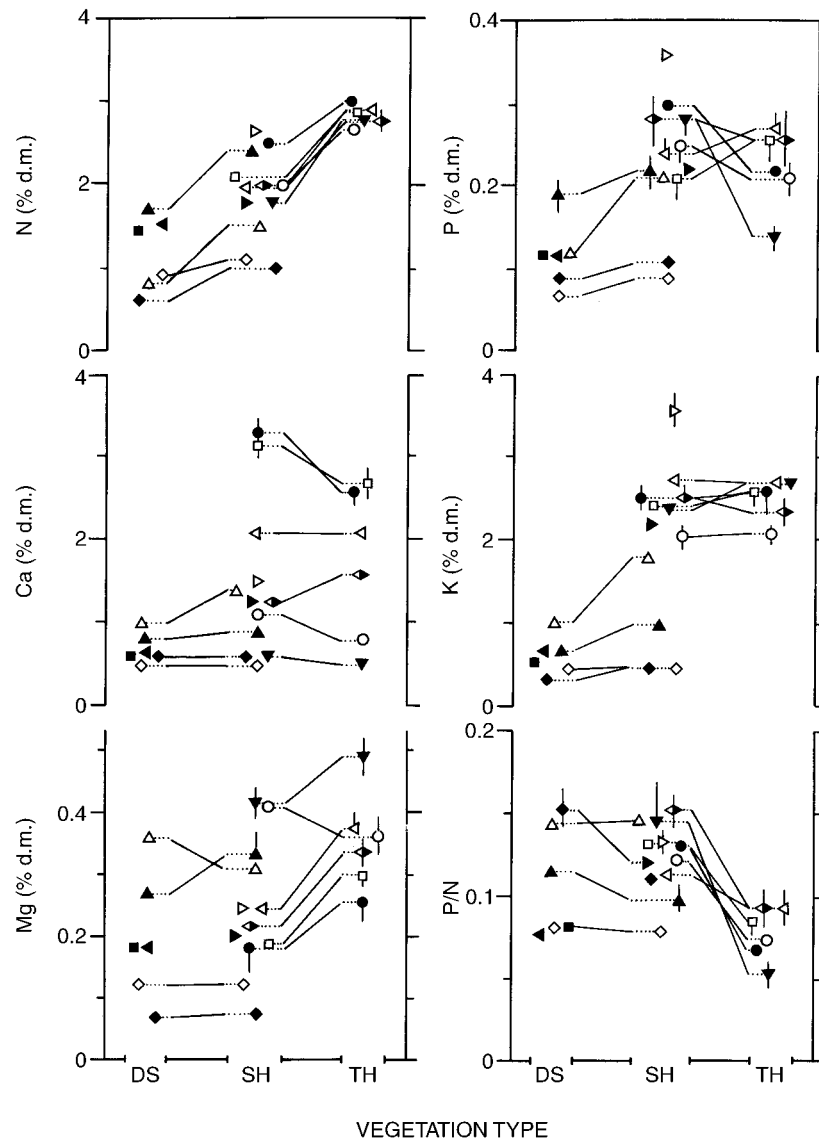


FIG. 7. Foliar concentrations of N ( $n = 6-8$ ), P ( $n = 4$  for P, Ca, K, and Mg), Ca, K, Mg, and the ratio N/P in: *E. hermafroditum* ■, *V. myrtillus* ▲, *B. pubescens* ▲, *L. borealis* △, *P. abies* ◆, *V. vitis-idaea* ◇, *M. bifolium* ►, *S. virgaurea* ►, *A. septentrionale* ●, *A. spicata* □, *G. triflorum* ◀, *G. dryopteris* ▼, *O. acetocella* ◀, and *R. idaeus* ○, sampled in late July 1990 in the DS forest type at 0 m, the SH forest type at 65 m, and the TH forest type at 90 m along the transect at Betsele. Values are means  $\pm$  1 SE.

found between the 80 and 90 m sites. The steep increase in base saturation in the Bs from 49 to 91% within 10 m (from 80 to 90 m) supports the assumption that groundwater discharge is very local at 90 m, and that discharge of groundwater rich in base cations and bicarbonate explains the high base saturation in the mor layer and mineral soil there. A similar increase in Ca saturation and soil solution pH was also shown by Ross et al. (1991, 1994) in a small area with a local groundwater seep. The relatively high Ca content in the mor layer and E horizon from 50 to 80 m has to be linked to other factors. One possibility is that deep-rooted plants take up nutrients from the subsurface

groundwater flow and redistribute Ca onto the surface soil through litterfall. Uptake of nutrients in the discharge area by the tall spruce trees surrounding it could also contribute to a stepwise redistribution upslope by litterfall. This would expand the effects of the local groundwater discharge and explain why the Ca content was higher in the mor and E horizon in the short-herb forest type than in the dwarf-shrub forest type (Fig. 4).

The distribution of cations in solution followed changes on the exchange complex. This was especially pronounced when the solute fractions were compared with the equivalent fractions on the exchange

complex for Ca, Mg, and K, the three major cations in the soil solution (Table 5).

The results from the soil solution sampling on 17 June 1995 showed a strong correlation between DOC and anion deficit, which suggests that the anion deficit is accounted for by dissociated organic acids. The large increase in Ca concentrations between the dwarf-shrub and short-herb forest types was balanced by an increase in the anion deficit, since no increase in inorganic anions was observed. However, this was not due to an increase in DOC, since DOC concentrations were similar between the dwarf-shrub and short-herb forest types. Assuming the same total charge density of DOC would suggest that the increased charge density per milligram DOC at the short-herb forest type is due to the fact that acid functional groups on the DOC are more dissociated in the short-herb than in the dwarf-shrub forest type. This is also in accordance with the higher pH and the increased dissociation of the OM in the short-herb type.

The most pronounced difference in solute concentrations was found between the short-herb forest type and the adjacent tall-herb forest type, where concentrations for most solutes dropped. The exception was  $\text{NO}_3^-$ , which was higher in the tall-herb forest type. Water contents in the tall herb mor soil were about twice as high as in the mor from the short-herb forest type and can thus only explain a small part of the decrease in concentrations. The anions F and  $\text{PO}_4$  showed the most drastic decreases (over 10 times, compared to the short-herb forest type), whereas DOC and the anion deficit decreased  $\sim 4$  times, compared to concentrations in the short-herb forest type. Since charge balance has to be maintained, there was also a decrease in cations in the soil solution (Table 3).

Several processes might contribute to the decrease in the solute concentrations at the 90-m site. Differences in the water content could not explain the large difference between the 90-m site and the adjacent sites. The large adsorption capacity of  $\text{PO}_4$  (and most likely F) might, however, also explain the low concentrations of cations. Wiklander (1978) showed that the adsorption of  $\text{PO}_4$  ions also decreased the concentrations of added balancing cations. He proposed that the adsorption of  $\text{PO}_4$  ions will generate negative charges on the surface of Fe hydroxides and thus create new cation exchange groups. Further studies on the 90-m soil will be undertaken to study the adsorption mechanisms of  $\text{PO}_4$  and the effect on cation retention.

The adsorption isotherm of the 90-m mor showed that the capacity to adsorb  $\text{PO}_4$  equaled the capacity of a Bs horizon sample, while the adsorption capacity was very limited for the 80-m mor. Adsorption of  $\text{PO}_4$  in acid soils is generally considered as a process linked to adsorption on Al and Fe oxihydroxides (Bohn et al. 1985), which are found in the Bs horizons of podzols. In the 90-m soil the amounts of extractable Al and Fe forms were considerably higher than in the 80-m soil.

The difference between the CBD- and PYRO-extractable Fe also indicate that Fe oxihydroxides are present in the mor. The presence of both Fe oxihydroxides and organically complexed Fe will largely increase the  $\text{PO}_4$  adsorption capacity in the mor layer (Gerke 1993). This is also in accordance with earlier findings, where the phosphorus retention capacity has been correlated with the presence of Fe oxihydroxides in peat lands (Cuttle 1983, Richardson 1985). The higher total P content in the tall-herb forest type compared to the dwarf-shrub and short-herb forest types is also in agreement with the higher adsorption capacity. Further studies will be undertaken to determine the different P pools in the 90-m mor. The high adsorption capacity can probably also explain why lower concentrations of F and possibly also DOC were found in the mor layer at 90 m (cf. Nodvin et al. 1986).

The accumulation of both organically bound and amorphous Al and Fe in the mor at the 90-m site can be a result of several processes. The local discharge in the 90-m site will create conditions of an upward transport of Al and Fe. This could be as  $\text{Fe}^{2+}$  under reducing conditions, which probably occurs during part of the year or as organically complexed ions. Another alternative would be a mixing of mineral soil particles from the Bs into the mor by soil faunal activity. This was suggested by Pare and Bernier (1989) in a study on P deficiency in mull and mor soils in declining sugar maple stands in Canada. There was, however, no major change in our study in LOI between the short-herb and tall-herb forest types, and hence no evidence of increased mixing in the tall-herb forest type.

#### *Determinants of soil pH*

One of the more striking features along the transect was the increase in pH by  $>3$  pH units in the soil solution of the mor layer. This variation can theoretically be attributed to four major factors; (1) the degree of neutralization of the acid functional groups on the OM; (2) the acid strength of the OM; (3) the ionic strength of the soil solution; and (4) the acid quantity.

The strong relationship between soil pH and the degree of neutralization (measured as base saturation) suggests that the acid neutralization is a major factor explaining differences in soil pH along the transect. This is also in accordance with earlier studies. For instance, Valentine and Binkley (1992) suggested that the degree of neutralization was the major factor responsible for the variation in pH in different plant communities in a tundra landscape. Similarly, Skjellberg (1996) showed that much of the small-scale variation in pH in some Swedish mor soils could be explained by differences in degree of neutralization.

The maximum difference of 0.9 pH units when comparing pH values at the same base saturation from the titration curves (Fig. 3c) indicates that there were differences in acid strengths and/or inorganic buffering constituents. The latter is especially valid for the 90-m

samples with large amounts of extractable Al and Fe. This seems, however, to be of minor importance since the largest differences in pH were found between the soils from the 0 and 50 m compared to the 80- and 90-m soils. The results from the titration curves also show that differences in "acid strength" cannot explain the entire variation in pH of over 3 pH units along the transect.

The total acidity, measured as  $TA_{7.0}$ , largely exceeded the acidity in the soil solution in all forest types. The maximum value of 0.37 in  $\Delta pH/\Delta \log (s/s \text{ ratio})$  showed that the capacity to buffer pH was large for all soils at the ambient pH values. This shows that the differences in water contents we found are of minor importance. It also indicates that the concentrations of protonated acid functional groups with  $pK_a$  values around the ambient pH values did not differ substantially among the soil samples.

Corrections for the effect of ionic strength had generally only a minor effect on the soil solution pH (cf. Richter et al. 1988). The correction decreased the difference in soil solution pH between 80 and 90 m from  $\sim 1.0$  to 0.8 pH units. This correction was not sufficient to explain why the 90-m soil did not conform to the general linear relationship found between soil solution pH and base saturation (Fig. 3a). The incubation of soil samples, however, showed that the 90-m soil had a large capacity for net nitrification even at low temperature ( $4^\circ\text{C}$ ). The pH decrease in the stored 90-m soil samples did not account for the large proton production that should have been induced by nitrification (assuming a net production of one proton for each  $\text{NO}_3^-$ , i.e., ammonification plus nitrification). The pH of 4.89 in the soil solution after the incubation is equal to  $\sim 5 \times 10^{-5}$  mmol  $\text{H}^+/\text{g OM}$  (assuming the same pH in the extracted and remaining soil solution, and a solution: soil ratio of 3.86). The net production of  $\text{H}^+$  from nitrification is equal to  $5 \times 10^{-2}$  mmol  $\text{H}^+/\text{g OM}$  (a  $\text{NO}_3^-$  increase in the soil solution of 12 820  $\mu\text{mol/L}$ , soil solution ratio as above), which is 1000 times larger than the actual amount of  $\text{H}^+$  in the soil solution. Thus, the proton production must have been buffered by the acid functional groups on the OM and thus lowered the base saturation of the 90-m soil samples. Using the titration data for the 90-m soil also shows that a decrease from 5.62 to 5.29 is equal to an increase of  $5 \times 10^{-2}$  mmol  $\text{H}^+/\text{g OM}$  on the exchange complex (the pH value of 4.89 after the incubation was corrected for the larger ionic strength in the stored soil solution using the  $\Delta pH$  per unit  $\log I$  value for the 90-m soil of 0.43). This would lead to a discrepancy between the measured pH values in the centrifugate and the estimated base saturation determined 2 mo later. This is also supported by the fact that the 90-m soil did not diverge from the rest when base saturation was related to pH values, when storage effects could be neglected, i.e., when using pH values from the 1.0 mol/L  $\text{NH}_4\text{NO}_3$  extraction (Fig. 3b) and the titration data.

Among the different factors determining soil solution pH along the transect, the effect of base saturation clearly is the most important. The increase in base saturation was primarily due to a decrease in protonated sites and an increase in Ca on the exchange sites. This emphasizes the importance of the Ca input to the mor and also shows that the increased base saturation is not due to a change in the acid quantity. Biological processes, such as nutrient uptake, mineralization, and nitrification, will cause seasonal fluctuations in soil solution pH. For instance, the sensitivity to disturbance of the 90-m mor indicates the potential influence of nitrification on soil solution pH in that forest type. However, the potential buffering capacity is so large that the general trends along the transect will be quite stable. This is supported by the fact that all pH measurements along the transect, independent of method and time of the year, have shown the same general trend (cf. Fig. 2; Högberg et al. 1990).

#### *Plant-soil relationships*

The steep increase in %N in foliage and spruce roots along the transect supported the observations of increased N availability in the soil. We did not, however, observe a lower demand for N in spruce roots in the tall-herb forest type as compared to samples from tall spruce trees elsewhere along the transect. The P/N ratios in foliage and the root uptake bioassay both indicated a P limitation in the tall-herb forest type, where the P/N ratios were under 0.1, which is considered an indication of P limitation (Linder 1995). This is in agreement with the low supply of  $\text{PO}_4^{3-}$  in the soil solution and the high P adsorption capacity of the mor in the discharge area (cf. Guzman et al. 1994). The type of root uptake bioassay we used is based on the fact that plants deficient in N or P demonstrate a high uptake for the element in highest demand (Jones et al. 1994). It is interesting to note that the tall *P. abies* trees surrounding the discharge area displayed this deficiency symptom for P in roots in the discharge area (i.e., in the tall-herb forest type), although a large portion of their roots must have had access to available P in the adjacent recharge area. Foliar analyses of the %Ca, %Mg, and %K concentrations did not reveal any general pattern and showed a large variation among species. High Ca saturation at the discharge area could theoretically affect the uptake of K and Mg. However, even though the K/N ratio was low at the discharge area, K and other base cations were in excessive quantities in relation to N in foliage (Linder 1995) throughout the transect.

The availability of N was closely linked to the changes in pH along the gradient. This was indicated both in the development of the total capital of N in the mor layer, as well as in the concentration of inorganic N in the soil solution. In the dwarf-shrub forest type concentrations of inorganic N species were very low in the mor layer: the sum of  $\text{NH}_4^+$  and  $\text{NO}_3^-$  was  $<50$

$\mu\text{mol/L}$  (Fig. 2). The low concentration of inorganic N in the soil solution suggests a tight cycling of the available inorganic N as well as a general shortage in the N supply. In this forest type, plants are either ECM or EM, with *L. borealis* (AM) as the only exception (Harley and Harley 1987), although *L. borealis* never becomes an important component of the vegetation. Both ECM and EM species have the capacity to use some organic N sources, although this capacity varies widely depending on the fungal symbiont (Leake and Read 1990, Read 1991).

In the short-herb forest type with less acid soils than the dwarf-shrub type (Table 3), concentrations of  $\text{NH}_4$  frequently were in the interval of 50–150  $\mu\text{mol/L}$ , and there was also a substantial pool of extractable  $\text{NH}_4$ . In this forest type the plant species are a mixture of ECM trees, EM ericaceous dwarf shrubs, and potentially AM herbs. The occurrence of potentially AM herbs in the short-herb forest type may be related to increases in soil pH and levels of  $\text{NH}_4$  in the soil solution and on the exchange complex (Figs. 1 and 2). However, uptake of organic N has recently been demonstrated by nonmycorrhizal Arctic sedge (Chapin et al. 1993), and studies on the uptake capacity for organic N sources by species found at Betsele along with determinations of free amino acids in the soil solution are required before definite conclusions can be drawn (cf. Kielland 1995).

In the tall-herb forest type, with the least acid soil and a high supply of  $\text{NO}_3$ , potentially AM herbs dominated, some of which exhibited high current NRA (Fig. 2) or high maximal inducible NRA (Högberg et al. 1990). In this forest type EM species are not present at all. Roots of the ECM spruce trees did, however, enter into the center of the tall-herb glade. Visual inspection of these roots indicated that they were ECM.

Our short transect thus encompassed the interrelated variations among soil pH, plant N sources, mycorrhizal types, and plant community composition described for long latitudinal and altitudinal gradients by Read (1986, 1991). According to Read the acid conditions and slow mineralization of N at either high latitudes or altitudes lead to a situation in which EM and ECM species short-circuit the N cycle by using organic N and leave little N for decomposers, and in particular little inorganic N to plants dependent on  $\text{NH}_4$  and/or  $\text{NO}_3$ . As regards the tall-herb forest type, two important prerequisites for autotrophic nitrification are met: a high supply of  $\text{NH}_4$  and high soil pH. A P limitation to plant production in the discharge area at the center of the tall-herb forest type should lead to a supply of  $\text{NH}_4$  in excess of plant demand, which would further contribute to a competitive advantage of nitrifiers. It may well be that significant gross nitrification occurs also in the other forest types where the buildup of the end product may be prevented by rapid immobilization (Davidson et al. 1992, Hart et al. 1994). In any case, the potential for net nitrification is substantially larger

in soil from the tall-herb vegetation type, as shown by data from stored samples. Preliminary data on soil respiration and C/N ratios of mor layers suggest that N mineralization can vary severalfold with rates increasing with soil pH. Hence, there are considerable variations in the rate of N supply as well as in the mixture of available N sources, and these variations seem to affect the plant species composition in the directions described by Read (1986). Plant communities themselves provide new substrate for decomposition, which in turn affects microbial activity and soil chemistry (e.g., Wedin and Tilman 1990, Hobbie 1992). Interestingly, the change in soil pH was not continuous, but rather discontinuous, with rather abrupt steps from one forest type to another (Figs. 1 and 2), which may be indicative of feedback effects of plants on soil processes.

Based on the data at hand it is difficult to judge whether *in situ* N cycle processes contribute more to the high supply of N in the discharge area than a potential influx from surrounding recharge areas. As said above, preliminary data from microbial studies nevertheless support an influence from *in situ* processes. Further studies at the site also aim at determining the influx of N in discharge water.

#### *The Betsele transect in a wider perspective*

The pH gradient found at Betsele encompasses a large part of the pH variation in Swedish forest soils in an area where the influence of acid precipitation is minor. The development of the pH gradient can be ascribed to two major factors: the formation of podzols and the groundwater discharge at one end of the transect. Podzolization will cause a natural acidity in the soil as can be seen in chronosequences of podzol development (Singleton and Lavkulich 1987, Bowman 1989). This includes both a buildup of the exchange capacity (i.e., organic acids) associated with OM accumulation as well as accumulation of Al and Fe in the Bs horizon as could be seen along the whole transect. The position of the discharge area in the terrain implies that it has received a high supply of base cations and maintained a high soil pH and a relatively stable soil chemical environment for plants demanding high pH through millennia, at the same time as pH (and probably also N availability) has declined in surrounding recharge areas.

Under these conditions a high supply of N was not linked to a high supply of P, in contrast to the situation in many other systems (Cole and Heil 1981, Vitousek and Howarth 1991). Rather, the high supply of N in the discharge area, in particular, could be a result of a P limitation there.

The strong linkage among soil total N, base saturation, and the development of different plant communities at Betsele is strikingly similar with earlier findings in surveys of the Fennoscandian boreal forest (Dahl et al. 1967, Lahti and Väisänen 1987). In Fig. 8



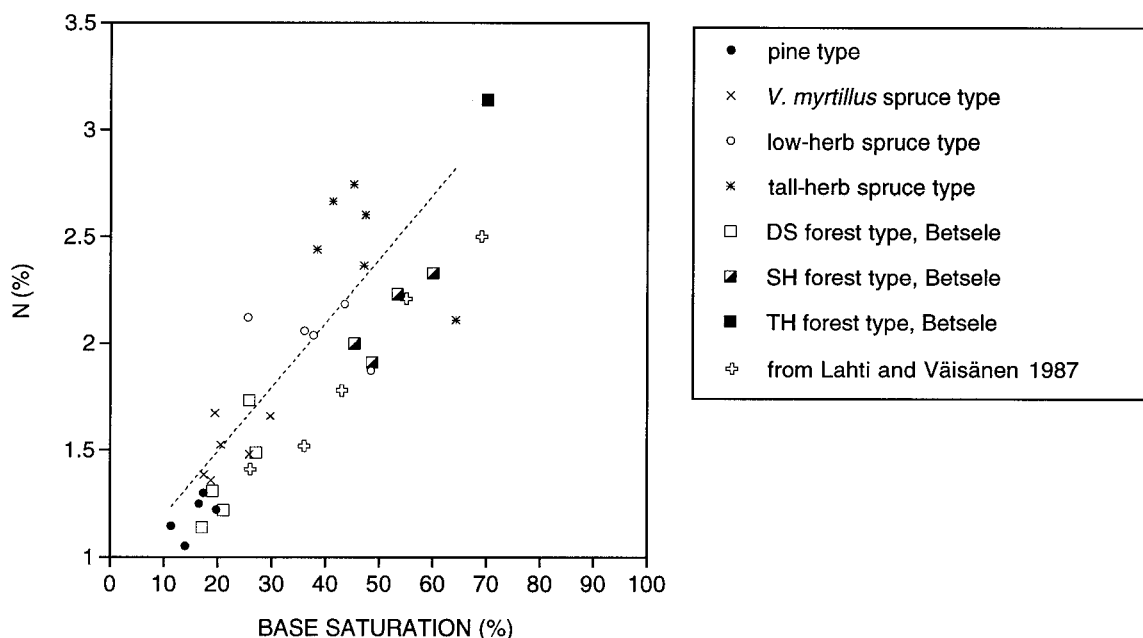


FIG. 8. The relationship between %N and % base saturation (BS) in the mor layer in different forest types. Symbols (●, ×, ○, and \*) are data from Dahl et al. (1967) and represent forest types in Hedmark county, Norway. The dotted line is the regression from Dahl et al. (1967). Squares represent data from the Betsele transect, each square representing a 10-m section of the 90 m long transect. □ = dwarf-shrub forest type (DS), half-filled square = short-herb forest type (SH), and ■ = tall-herb forest type (TH). Plus signs are data from Lahti and Väisänen (1987) and represent 921 forest stands in southern Finland; each plus sign represents a different forest type. The N content is determined as percentage of OM in data from Dahl et al. (1967) and Betsele, while the Finnish data are expressed as percentage of dry humus. Base saturation in data from Dahl et al. (1967) and Betsele is determined in unbuffered 1.0 mol/L  $\text{NH}_4\text{NO}_3$ , whereas the Finnish material represents Ca saturation (extraction method unknown).

the relationship between total N and base saturation along the Betsele transect is compared with the observations of Dahl et al. (1967) from Hedmark county in Norway (~580 km southwest of Betsele) and of Lahti and Väisänen (1987), which represent 921 stands (~500 km southeast of Betsele) from the inventory of forest soil fertility (1980–1983) in southern Finland. This comparison clearly supports the suggestion that Betsele is an extreme gradient encompassing a wide variation observed also in a larger regional perspective.

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