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Optimum nutrition and nitrogen saturation in Scots pine stands

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Abstract

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Long-term field experiments are described, in which nitrogen and other plant nutrients were added regularly to young Scots pine stands at two sites in Sweden, Lisselbo (1969–1988) and Norrliden (1971–1989; some treatments still in progress). A main aim was to establish a range of needle nitrogen concentration levels, as stable as possible, and to study the effects of these and of other factors (other added nutrients, soil acidity changes, irrigation) on tree growth and tree nutrient status. The results confirmed previous experience that nitrogen supply normally is a growth-limiting factor in boreal forest, but showed that regular nitrogen additions can induce boron and magnesium deficiency, and low internal concentrations in the trees, *e.g.* of potassium and phosphorus. Other aspects of ecosystem functioning at varied nitrogen supply–biomass production, nutrient balances for several elements, vegetation changes, soil acidity changes, nitrification, studied by ourselves or by cooperating research groups–are reviewed. The importance of long-term field experiments in the study of urgent environmental problems, such as nitrogen saturation and soil acidification, is discussed.

Key words: Pinus sylvestris, Picea abies, mineral nutrition, nutrient store, nutrient recovery, nutrient depletion, base saturation, exchange capacity, foliar sampling, litterfall

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Preface

This report contains results from the Swedish Optimum Nutrition Experiments in Pine (*Pinus sylvestris* L.) Stands. The experiments were carried out at two sites, Lisselbo (E40–E42) and Norrliden (E55–E58). Although many results have already been published, a full description of the experiments and their background is lacking. The individual experiments started in 1969 and 1971; since most plots have been actively treated for two decades or more, then kept under observation for several years, a very large dataset exists, and this gives rise to problems concerning the degree of detail in the publication. In most cases, we have presented treatment means, where possible with confidence intervals or other statistics. Data at individual plot level have been illustrated in scatter diagrams. However, many of the basic data for tree stands may be found in the 'Ekologen Database System' (Gay, Tamm, Aronsson, Flower-Ellis & Linder, 1994). Some results considered less central to the main problems are reported in a separate publication (Aronsson, Flower-Ellis, Popovic & Tamm, 1999). That paper includes some checks on methodology when results from different experiments are compared, and estimates of some components considered to be of minor importance for our ecosystem budgets. It also contains some soil and biomass data for individual plots.

Ecosystem-oriented projects, such as the present one, have many aspects and are therefore not easy to present. It may help the reader to indicate how we have arranged the material, including some deviations from a strictly consistent description experiment by experiment.

The report falls into eleven sections: The introduction (*Section 1*) presents the scientific background to the project, which in addition to the pine experiments described here, also contains experiments in stands of Norway spruce (*Picea abies* (L.) Karst.). The Introduction also lists questions considered important when the experiments were planned. Not all of the questions posed around 1970 have been satisfactorily answered, for reasons explained in Section 9. Even if the questions originally asked are still relevant, there has been an increasing emphasis on the behaviour of the whole ecosystem at optimal and supra-optimal nitrogen supply.

Section 2 describes the experimental sites, treatments, and methods for measurement and sampling, although some methodological checks are reported in connexion with the presentation of data or in Aronsson *et al.* (1999).

Sections 3–7 discuss the 'main experiments' E55U, E55AN and E40, which deal with the effects of various levels of N, with or without addition of PK fertiliser. Some results from the other experiments at both sites are mentioned where they can supply information missing from the main experiments.

Section 3 deals with soil conditions in E55U and AN, first with chemical concentrations in four soil strata, then with estimates of quantities of chemical constituents per unit area.

Section 4 deals with the elemental composition of aboveground biomass components in E55U and AN (for N, also E40). The long series of annual collections of 'diagnostic' needle samples are presented first, followed by the chemical composition of other parts of the tree biomass (with complementary data from Expt E57).

Section 5 presents conventional tree growth data: stem height, basal area, and volume.

Section 6 deals with biomass fractions of trees aboveground, and their stores of nutrients.

Section 7. The main purpose of the section is to place the information presented earlier in an ecosystem perspective. The section begins with data on litterfall (from Expt E42). The next subsection reviews results obtained by collaborating scientists, which are interesting in an ecosystem context. A further subsection deals with the relationships between tree growth and nutrients, particularly N. Finally, we present data on the relative distribution of plant nutrients between stand and soil, as affected by the nutrient treatments, and on how much of the added N can be recovered in different N regimes.

Section 8 concentrates on results from supplementary experiments at the Norrliden and Lisselbo sites. The discussion deals with effects of other plant nutrients (E41 and E56), of interaction between irrigation and fertilisation (E58), of discontinued annual addition of nitrogen (E58) and of soil acidity manipulations (E42 and E57). The distribution of N and C in various

treatments of E42, E57 and E58, and the frequency of snow-damage in 1988 in relation to nutrient regimes at the Lisselbo site, are also described.

Section 9 compares the original aims (*cf.* Section 1) with what has been achieved within the project. It is concluded that the proposals formulated at the beginning of the project focussed on problems well worth scientific study, even if they might in some cases have been expressed more strictly. Some of the problems would also have required greater resources—or a longer duration than was available to us—to provide fully satisfactory answers.

Section 10 deals with some key problems related to our objectives, which are now much more at the centre of debate than was the case in 1970. Three subsections discuss *(i)* the shape of nutrient response curves, *(ii)* the relations between nutrient optimum and tree age, and *(iii)* the fate of applied N. We have not attempted to review all the rapidly growing literature in these fields, but have tried to compare our results with the most relevant extraneous studies.

In *Section 11* there is a discussion of some key problems, which might be elucidated by further sampling or experimental work on our plots or on other sites where nutrient regimes have been varied in a controlled manner: *(i)* behaviour of forest ecosystems at or above N saturation, especially with respect to N losses and sequestration, *(ii)* recovery of N-saturated systems after interrupted additions, and *(iii)* between-year variations in both tree growth and plant nutrient concentrations and their mutual interdependence, as well as their relationship with climatic variables.

Appreciation

In the more than two decades during which the Optimum Nutrition Project was the principal activity of the (then) Section for Forest Ecology, our working environment underwent many changes. In 1977, the College of Forestry became the Forestry Faculty of the Swedish University of Agricultural Sciences, and migrated from Stockholm to Umeå and Uppsala. Many of those who originally took part in the work have now retired, or have moved elsewhere. We wish to acknowledge here the part played by colleagues within the Section: this study could not have been carried out without the patient and skilled cooperation of all members of the Section, where almost everyone contributed in some way, in fieldwork, in the laboratory, and in the process of transforming raw data into conclusions.

We have greatly appreciated the cooperation of colleagues from other departments, and from other universities and organisations after scientific exchange intensified when the SWECON project started fieldwork in 1973. In the following we wish to acknowledge those whose contributions are not clear from references cited in the text, but still important to us: Folke Andersson, who coordinated activities with SWECON; Bertil Andersson and the staff of the Jädraås Experimental Forest, for much biomass processing and chemical analysis; Björn and Elisabet Axelsson, for access to unpublished data; Björn Berg, for comments on the manuscript; Johan Bergholm, for unpublished data; Leif Hallbäcken, for help with data files and for unpublished data; Bertil Matern, for statistical advice in planning and data processing; Göran Möller, for discussions; Hans Persson, for root data; Tryggve Persson and Mikael Sjöberg, for unpublished soil data; Tryggve Troedsson, for joint planning of irrigation experiments; and the staff of the Svartberget Experimental Forest, for maintenance of the Norrliden experiment. Hilmar Holmen, Sune Linder and Peter Högberg were jointly responsible with us for funding applications and participated actively in the project.

Unfortunately, it is too late to thank Torsten Ingestad for many discussions on stable nutrient levels in trees; Arne Hansson, then secretary of the Foundation for Plant Nutrition Research, who actively supported our work from the planning stage in the mid-1960s and thereafter; and Svante Odén, who first discussed the ecological consequences of long-range air transport of acidifying and fertilising substances.

Uppsala, December 1999

COT AA BP JGKF-E

Contents

1. Introduction

Agricultural scientists began extensive experimentation with fertilisers in the 1840s, when Liebig published his discoveries on the role of mineral nutrients and introduced the concept of 'limiting factors'. Although some forest scientists early realised that forest trees needed the same essential elements as crop plants (Obbarius, 1857; Ebermayer, 1876), the high price of commercial fertilisers made it impossible even to contemplate practical forest fertilisation, and systematic experimentation did not start until the present century. Most experiments laid out before World War II tested cheap products such as slag from ironworks, lime, gypsum, finely ground basalt, or wood-ash. The main purpose was often to find alternative uses for waste products, in the hope that they might also stimulate forest growth. Much of this experimentation was reviewed by Wiedemann (1932).

However, a few field experiments of new types were laid out in the 1920s and 1930s, both in Europe (Hesselman, 1937; Romell & Malmström, 1945; Nemec, 1939) and in the United States (Mitchell & Chandler, 1939). The new experiments were either intended to extend work in forest nurseries—where normal agricultural rules for fertilisation had been shown to be valid—or were based upon theoretical considerations. Süchting (1949) criticised most of the early experiments for their poor design, and provided detailed recommendations for well replicated experiments with large plots. After World War II, the number of systematic experiments began to increase rapidly, since some of the early experiments, both of the trial-and-error type and more scientific ones, had shown dramatic responses. A limited addition of plant nutrients could change a site from wasteland to a well-growing forest (Malmström, 1935; Stoate, 1951; Zehetmayr, 1954; Heiberg & White, 1951; Young, 1948).

Understandably, experimentation with fertilisers advanced more rapidly in agriculture and horticulture. The principle of diminishing returns on increasing addition of a nutrient was mathematically expressed by Mitscherlich (1909). The balance between the nutrient elements was emphasised, *e.g.* in viticulture by Lagatu & Maume (1924) in France, who invented a graphical method for defining the balance between the N, P and K (later extended to other elements, see Prevot & Ollagnier, 1961). Lundegårdh (1945) invented and tested rapid methods for analysing the common nutrients, and suggested leaf sampling for cereals early in the season, for correcting nutrient imbalances before they affected yield. Much of the early work on orchard and crop plants was reviewed by Goodall & Gregory (1947).

During the first half of the 20th century, crop physiologists often discussed the concepts 'limiting factors' and 'physiological optimum' in relation to various environmental factors, including nutrient supply. The Mitscherlich equation, which had more or less replaced Liebig's 'law of the minimum', was developed further, by including several factors in multiplicative models, and by attempts to describe mathematically the growth decrease at high ('supraoptimal') values of a certain factor. Since the factors responsible for the decrease were far more variable than the dose-response relationships below optimum, these models never received the same acceptance as the 'law of diminishing returns'. Researchers who found difficulty in adapting their results to Mitscherlich's and other equations, sometimes found a way out by distinguishing an 'ecological optimum', differing from the physiological optimum by competition from other species.

Some of the new activities in forest nutrition research during the 1930s and after World War II had a wider scope than the nutrient conditions on specific sites. Mitchell & Chandler (1939) attempted to generalise their results with N fertilisation to an entire region. Hesselman (1937) studied stands of different ages, partly by experiment. Research of this kind required a combination of experiments with comparative methods, already used in horticulture and agriculture, such as foliar (or more generally, plant) analysis or soil analysis (for review, see Leyton, 1958; Tamm, 1964*a*).

When the Swedish Forest Research Institute was reorganised in the mid-1940s, it was decided to devote a major effort to forest nutritional research. The decision was based on earlier work by Hesselman, Malmström and Romell, but also inspired by Mitchell & Chandler (1939). The programme was led by C. Malmström and L.-G. Romell; the senior author (COT) of this paper

was employed in 1949 to work on the project, which initially had limited resources but for which funding increased during the 1950s and 1960s, when it became clear to silviculturists that some of their problems had a nutritional background.

According to Malmström and Romell, the research should be 'ecosystem-oriented' and the field experiments 'analytical', thus stressing that the aim was not to promote practical forest fertilisation. However, it was thought that a better insight into the role of nutrients in forest ecosystems might lead to silvicultural applications, such as a better adaptation of methods to sites of differing quality and with different history. It was recognised that competition for nutrients, N in particular, was an essential component of many regeneration problems.

The senior author's field experiments with nutrient additions in the early 1950s were directly inspired by the work of Mitchell & Chandler (1939). Since there is a direct line from experience obtained during this early phase to the experiments described here, it is appropriate to review briefly the approach used by Mitchell and Chandler, as well as some of our own experimentation in the 1950s and 1960s.

In the 1930s, H.L. Mitchell worked with with tree seedlings in pot culture, to test soil fertility, a method widely used at that time. However, he also analysed the foliage of the seedlings and realised that foliar analysis might be a more promising way of diagnosing tree nutrient status. With R.F. Chandler, he started a series of six N-dosage experiments in mixed hardwood forests in New York State. After nutrient application early in the growing season, mature leaves were collected before yellowing, from the top of the crown of dominant and co-dominant trees of all species occurring in sufficient number within quarter-acre plots. Radial growth was measured on increment cores collected from the sample trees, usually at the end of the next growing season.

Mitchell and Chandler plotted foliage N concentrations for each site and species against the amount of N added, and found that the Mitscherlich equation (1) could be fitted to all sets of data, usually with high correlation coefficients. By assuming that, for each species, the same foliar concentration meant the same N supply, they could combine the site-specific curves to one curve:

$$N\% = A(1-10^{-c(N+b)}) \quad (1)$$

where N is the amount of fertiliser N added, A, b and c are constants and the dependent variable is foliar N concentration. The constant b represents the natural N supply on the control plot of the poorest site, measured in the same units as the added N. It should be borne in mind that a certain b (or $b+N$) value should be used for comparative purposes only, not as an exact measure of N availability in the soil. For ten of the eleven species studied, the correlation coefficient of the Mitscherlich equation (combined for the different experiments as described) varied between 0.97 and 0.99, while for the remaining species it was 0.84.

When radial growth data were plotted against soil N supply ($b+N$) measured from the combined equation (1), new equations of the Mitscherlich type could be fitted to the data, although at different levels for different sites. All species reacted positively to N fertilisation; for some species, the reaction also continued at high soil N supply, while for others, the growth curve levelled off at moderate supply. Mitchell and Chandler classified the last group as 'nitrogen-deficiency tolerant', and the first group as 'nitrogen demanding'. A third group was called 'intermediate'.

A further use of equation (1) was as a standard for comparing foliar N data for 36 stands sampled throughout the Northeastern United States. A majority of the stands had leaf N concentrations within the range of the controls of the six experiments, but the distribution curve was highly skewed, implying that a few stands had values comparable with experimental stands with relatively high N additions.

Mitchell and Chandler found no growth decrease at their highest additions, in contrast to the situation in Mitchell's earlier experiments with seedlings (Mitchell, 1934, 1939). They therefore used the term 'estimated optimum supply' for the range of N additions at which the curve for the growth response flattened out. Higher values were said to fall within the 'region of tension'. The lowest part of the curve, including most control plots but also some plots fertilised with up to 56–84 kg ha^{-1} of N, was called the 'region of minima', within which the response to N additions was virtually linear.

Between the region of mimima and the optimum range they distinguished the 'working region'.

Our first N dosage experiment at Mölna, south of Jönköping, which began in 1951, had a design similar to that used by Mitchell and Chandler, with single applications of ammonium nitrate (50, 100, and 200 kg N ha^{-1}). The stand had been planted in 1922, with Scots pine (*Pinus sylvestris* L.) as the main species, but with an admixture of birch (*Betula pendula* Roth) and Norway spruce (*Picea abies* (L.) Karst.), the latter only as suppressed individuals. Foliar samples were collected from all three species, but only the pines could be cored for growth measurements.

The results were described by Tamm (1956), using foliar analyses from each of the years 1950–1954 for all three species, and increment core measurements for pine, from which diameter growth for each of the years 1951–1953 could be determined. He found a dynamic development of both foliar N concentrations and diameter growth. Foliar N culminated in the autumn of the year of fertilisation, then decreased, more rapidly in pine than in spruce and birch. Diameter growth in pine increased in the first summer, peaked in the next year, then declined, though more slowly than needle N. Mitscherlich equations could be fitted to different combinations of data, growth 1951 versus N% in 1951, growth 1952 versus N% in either 1951 or 1952, or growth 1953 versus N% in 1952. However, growth 1953 plotted against N% in the same year gave a very poor correlation. Tamm's results supported the choice of sampling dates made by Mitchell and Chandler, but at the same time, made it clear that there was room for arbitrariness in the selection of dates for measurement.

A further complication was the existence of considerable between-year variation in foliar nutrient concentrations, both at the experimental site and elsewhere. Although dose/response curves made separately for dominant and dominated trees (co-dominant, intermediate and suppressed) were both significant and of the same general shape, the curves for dominated trees had a steeper slope, suggesting that these trees had been less successful in the competition for N, than had the dominants. The relationships found must, in any case, be considered empirical and difficult to generalise.

By the method of Mitchell and Chandler, Scots pine needles were calculated to contain *ca.* 20 mg N g^{-1} DM (dry mass) when the growth response levelled off, *i.e.* at N optimum *sensu* Mitchell and Chandler. However, as noted above, the estimate was based on comparisons between two highly dynamic developments, that in foliar concentrations and that in radial growth. New experiments with annual application of N were therefore planned, in which growth and concentrations could be compared under less variable conditions. Since both growth and foliar concentrations vary markedly with season in both boreal and temperate species, we could at best hope for constant conditions over a period of some years. The first experiment was a factorial N (levels N0, N1, N2 and N4)*PK. The treatments were initially planned for five successive years. Height growth was measured annually, and current needles sampled each autumn. Basal area was measured at intervals, and the plan was to make annual ring measurements at the end of the experiment.

This experiment (E1 Hökaberg) was laid out in the spring of 1957 in a plantation of Norway spruce on an abandoned field at Remningstorp in SW Sweden. When the experiment was planned, the spruce exhibited slight chlorosis, suggesting N deficiency (confirmed by low needle N concentrations). In 1958, a smaller ancillary experiment (E2 Petersburg) was laid out in a spruce plantation of the same age, but on cleared forest land. Here the spruce had been held back by frost damage and competing field-layer vegetation, but the needles had a dark green colour and higher N concentrations.

The different N regimes showed well-separated foliar concentrations of N, but there was considerable between-year variation, and it was difficult to establish the high foliar N concentrations reported as optimal for seedlings in nurseries or solution culture. Two biomass samplings were made, one after four years and one nine years later, when the experiment was discontinued because of drought and barkbeetle damage to some plots.

The results of the Remningstorp experiments have been reported in several publications (Tamm, 1964*b*, 1968, 1971, 1975, 1980; Tamm & Popovic, 1974).

Several lessons were learned from the Remningstorp experiments, which may be con-

sidered the first and not fully successful member of a new generation of forest nutrition experiments:

(i) Experiments should be planned for lengthy periods (at least a decade), and comprise large plots and several replicates.

(ii) Continuous measurements of growth parameters are needed, and biomass samplings are essential.

(iii) Interactions between N and other factors should be considered, although some compromises are necessary, to limit the size of each experiment.

(iv) Stand age, from seedlings to old-growth, is a possible source of variation in nutrient demand and tolerance.

On the positive side, the Remningstorp experiments showed that foliar N concentration could be kept at separate levels by annual additions, that other element concentrations in general were decreased by N additions (partly compensated by PK additions), and that PK additions scarcely affected the N concentrations (Tamm, 1968, 1980).

Nutritional conditions may well differ between tree stands of different age, as discussed by Hesselman (1937), and strongly emphasised by Miller (1981). Some experiments were therefore laid out *ca.* 1960 in old stands of pine and spruce on poor sites in a cold climate, also with the aim of maintaining elevated nutrient levels for a prolonged period. These experiments were cooperative between the Section for Forest Ecology and the Department of Forest Yield Research, then led by Ch. Carbonnier. Some results from the pine experiments have been reported by Burgtorf (1981), Popovic & Andersson (1984) and Hallbäcken & Popovic (1985). Data from these less intensive experiments will be used in the discussion in Section 10, together with data from other relevant long-term experiments.

We consider long-term optimum nutrition experiments to be particularly useful in providing answers within the following problem areas (the wording is quoted from funding applications from the mid-1970s):

Area 1. Primary production of forest ecosystems at nutrient levels for optimum growth.

Area 2. Importance of different nutrients, of canopy density (or leaf area index), and of water supply for actual and potential production at selected sites.

Area 3. Disturbances in ecosystem functions at optimum and supra-optimal nutrient regimes.

Area 4. Between-year variation in growth and foliage nutrient concentrations of trees under different nutrient regimes.

Area 5. Interactions between added nutrients, lime, and other factors.

Area 6. Effects of interrupted fertilisation on forest plots maintained at elevated nutrient levels (N regimes in particular) for extended periods.

Area 7. Long-term effects of often repeated N additions, comparable with the loads of N compounds in atmospheric deposition in polluted areas.

In the discussion in Section 9, the extent to which the experiments described have provided answers to the questions asked is considered. Comparison with results from other projects will help to answer the question whether the results obtained are valid beyond the local conditions in which they were obtained. In Sections 10 and 11, the discussion is extended to the role of long-term experiments in illuminating currently urgent problems, and to the need for cross-fertilisation between different methodologies.

This paper describes two experimental areas in pine forest, and results obtained since the start of the experiments in 1969 and 1971, respectively. Work reported was primarily carried out at the former Section for Forest Ecology, first at the College of Forestry in Stockholm, later at the Forestry Faculty of the Swedish University of Agricultural Sciences, Uppsala. Several other scientists and technical staff were involved, either from the Section or from other institutes or universities. Results already published are, as a rule, reviewed briefly, but in some cases it is necessary to report background material for data presented earlier in condensed form only, in symposium proceedings or similar publications. Results from collaborating

research groups are reviewed in conjunction with our own results, when appropriate, otherwise in a separate subsection of Section 7.

The nutrient optimisation experiments in Norway spruce stands, mentioned in the Preface, are not discussed here except as reference material in some comparisons, but an annotated bibliography of the spruce experiments is planned.

Sites and methods

Sites and climate

The location of the experimental sites is shown in Fig. 2.1 and some geographical and climatic data are presented in Table 2.1. The Norrliden site can be considered typical of large areas of boreal forest in N. Sweden, while Lisselbo represents a site on coarse-textured glacifluvial sediments at the southern margin of the boreal zone.

In forest, measurement of the total deposition of S and N compounds is methodologically difficult (Westling, Hallgren-Larsson, Sjöblad & Lövblad, 1992). Forest stands collect particles and gases from the air to a larger extent than does an open field. However, in areas remote from local sources of pollutants, wet deposition normally represents the largest component of atmospheric deposition. The deposition data in Table 2.1 were provided by Dr. L. Granat and adapted for our sites from as yet unpublished data (Granat, in press). There are no deposition data for the sites themselves (*cf.*, however, Degermark 1984–1996; recent data from Svartberget, 17 km S of Norrliden). The data in Table 2.1 are therefore based upon precipitation concentrations in Gävle (for Lisselbo) and Umeå (for Norrliden), recalculated for the mean precipitation at our sites. There is, however, a gradient in deposition, contaminants decreasing with distance from the coast in N. Sweden, whereas this is not a problem in the Gävle area. However, the data in the table fall within the range given on the maps published by Westling *et al.* (1992), in which particle deposition in the canopy is considered. Although the period covered in Table 2.1 is short, the data demonstrate the decrease in S deposition from the 1960s onwards, which has been observed elsewhere and which agrees with the trend in S emissions in western Europe. In contrast, N deposition appears to be increasing, which also agrees with a European trend.

Norrliden

The experimental site Norrliden is situated 70 km NW of Umeå (Table 2.1), north of the river Vindelälven on a gentle slope (5% to NE and N) at an altitude of 260–275 m, *i.e.* above the highest coastline after the latest glaciation (Fig. 2.1).

The former forest was an old spruce-dominated stand, harvested in 1951. Prescribed burning in 1952 was followed by planting with two-year-old Scots pine plants in 1953 (Fig. 2.2, 2.3, 2.4).

The soil material is glacial till, fine sand being the dominant fraction. The soil is a haplic podzol (Anon., 1988). In Expt E57, Si_{30cm} varies between 20.2–28.0, corresponding to stone percentages between 34.2–8.7 (Tamm & Popovic, 1989); see Plate III. In Expt E55U and AN, Si_{30cm} varies between 13.4–27.8 (Fig. 2.6).

Soil profiles and their mineralogy were thoroughly studied by Melkerud (1989) on two plots of experiment E57, one control and one acidified plot.

Detailed descriptions of sites and the experimental designs, together with some early results, were published by Tamm, Nilsson & Wiklander (1974*b*; Lisselbo) and Holmen, Nilsson, Popovic & Wiklander (1976; Norrliden).

Lisselbo

The Lisselbo site is situated on a low (*ca.* 5 m) glacifluvial eskar, 80–85 metres above sea level, 100 km north of Uppsala (Table 2.1; Fig. 2.1, 2.5). The area is below the postglacial coastline, and wave action during land uplift has redeposited much of the eskar material. The experimental area includes the eskar ridge, although most plots are situated on the gentle slope towards the west, or on flat ground. The soil is well drained, the groundwater level varying from a few metres in the lowest part to almost 10 m. The stoniness index (Si_{30cm}; Viro, 1952) varies between 10–30 cm (Fig. 2.7) According to Viro, this corresponds to stone percentages from 67 to near zero. The texture varies from gravelly to fine sand; along the ridge of the eskar in particular, there is a high frequency of stones (Tamm & Popovic, 1989). The soil is a haplic

Table 2.1. *Geographical data and some climatic data, from Degermark (1984–1993); Helmisaari & Helmisaari (1992); wet deposition from L. Granat (pers. comm.)*

Site	Lisselbo	Norrliden
Experiment	E40 E41 E42	E55 E56 E57 E58
Lat. °N	60°28'	64°21'
Long. °E.	16°57'	19°45'
Altitude, m (lowest-highest)	80–85	260–275
Mean annual temperature, °C	4.8	1.2
Mean annual precipitation, mm	593	595
Wet deposition element kg ha^{-1} yr^{-1}	(Gävle)	(Umeå)
S		
1965–1970	6.7	7.2
1971–1980	6.4	6.8
1981–1990	5.2	5.5
NH_4-N		
1965–1970	1.2	1.3
1971–1980	1.7	1.7
1981–1990	1.9	1.9
NH_3-N		
1965–1970	1.4	1.6
1971–1980	1.8	2.1
1981–1990	1.9	2.2

podzol (Anon., 1988) with an irregular and mostly shallow A_2 horizon, such as is often found in pure pine stands (Plates I and II).

The former Scots pine stand at Lisselbo was destroyed by a storm early in 1954, which threw down about one-third of the standing forest volume in the parish of Hedesunda, in which Lisselbo is situated. The new stand was established in 1954 by a combination of natural regeneration and sowing with seed of a local provenance. The spacing of the young stand was adjusted in 1965 by cutting a number of saplings.

Experimental design and treatments

All experiments have a randomised block design. They are designated 'E' (for Forest Ecology) followed by a number, to distinguish them from experiments laid out by other departments at the (former) College of Forestry; some experiments designated 'P' (for Forest Production) and a number are discussed in Section 10. When plot data for tree stands are presented in tables, plot numbers are arranged by blocks, even where block numbers are not given explicitly. For E41 and E56 they may be found in Table 2.6 in this paper, for all Lisselbo experiments in Tamm *et al.* (1974*b*) and for all Norrliden experiments in Holmen *et al.* (1976). They are also listed by Aronsson *et al.* (1999).

At Lisselbo, where treatments began in 1969, three different experiments were laid out, E40–E42 (Fig. 2.5), while at Norrliden, started two years later, there are four, E55–E58 (Fig. 2.4). All plots are 30 × 30 m (treated area). Fertiliser was broadcast by hand early in the growing season. The net plots are 20 × 20 m, and all measurements of tree growth, needle sampling and other non-destructive measurements were carried out within these areas. Biomass sampling and other disturbances, such as excavation of soil pits have, as a rule, taken place on the 5-m buffer strip outside the net plot, except in experiments E55U and AN and E57, where thinning made possible biomass sampling from trees felled on the net plots.

Nitrogen was added in all experiments. The source of N was ammonium nitrate (AN) in all cases except Expt E55U, which received urea (U).

The N dosage experiments (E40 and E55U and AN) have four levels of N, including the control. Each N-level was tested with or without PK. There are four replicates in E40 (in total 32 plots). In each of the E55 experiments there

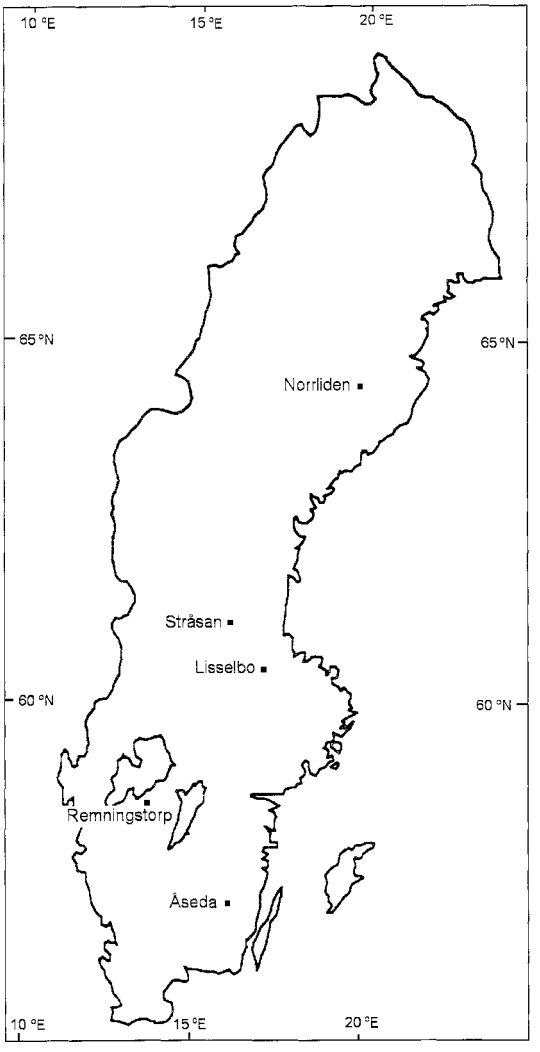

Fig. 2.1. Site locations: Norrliden and Lisselbo, Stråsan, Åseda and Remningstorp.

Fig. 2.2. The Norrliden site before the start of the experiments. Note charred stump. October 1969. (Photo COT).

Fig. 2.3. E55AN: On the left, plot 37 (control), on the right plot 44 (N3). June 1993. (Photo P. Högberg).

are two complete blocks (with and without PK) and one incomplete block (no PK additions). There were thus 20 plots in each of the two E55 experiments. For fertiliser additions, see Table 2.2.

E41 and E56 are experiments with N-fertilisation of all plots at level N2, in combination with one or more of the nutrients P, K, Mg, S in an incomplete balanced block design. The plot arrangement (Table 2.6) makes it possible to compare eight plots to which each of the four nutrients has been added, with eight plots without the nutrient in question, but with the same amounts of the other three nutrients, though in different combinations. A mixture of micronutrients was given to one additional plot in each block, to which the most complete combination of the four elements P, K, Mg and S occurring in that block was supplied. This provides four comparisons between plots with and without 'micro', but otherwise similarly treated (Tables 2.3, 2.6).

E42 and E57 are primarily acidification/liming experiments, the results of which have been reported elsewhere (Tamm & Popovic, 1989; 1995). Some of the treatments (control and N2PK) were identical with those in E40 and E55, so useful comparisons can be made (Table 2.4). E42 also contained irrigation treatments, which at Norrliden were in a separate

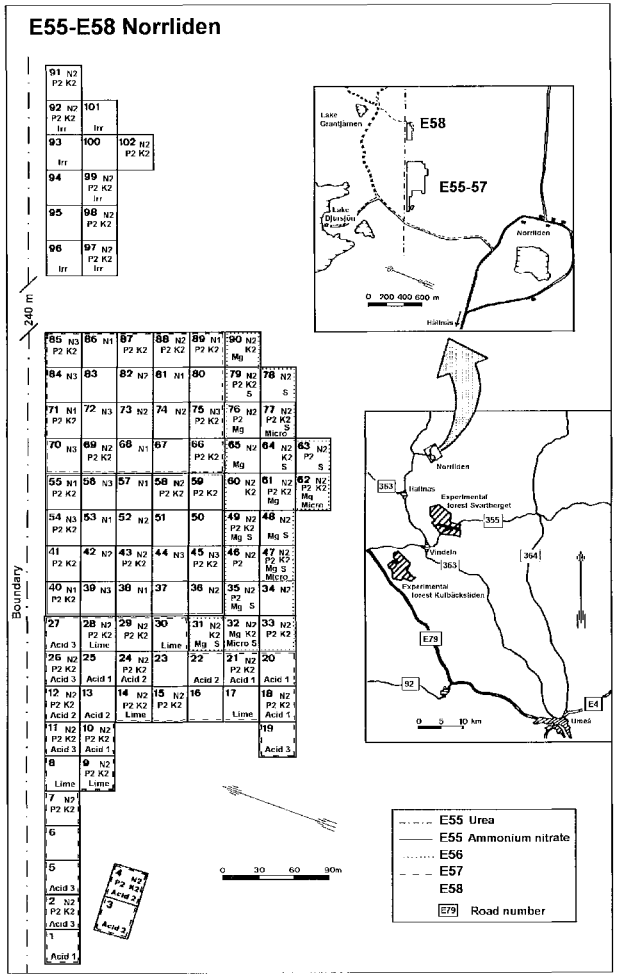

Fig. 2.4. Situation and plan of the experimental area Norrliden, showing Expt E55, E56, E57 and E58. Expt E57 is at the bottom and E58 at the top of the plan, while E56, E55U and E55AN are distinguished by different frames.

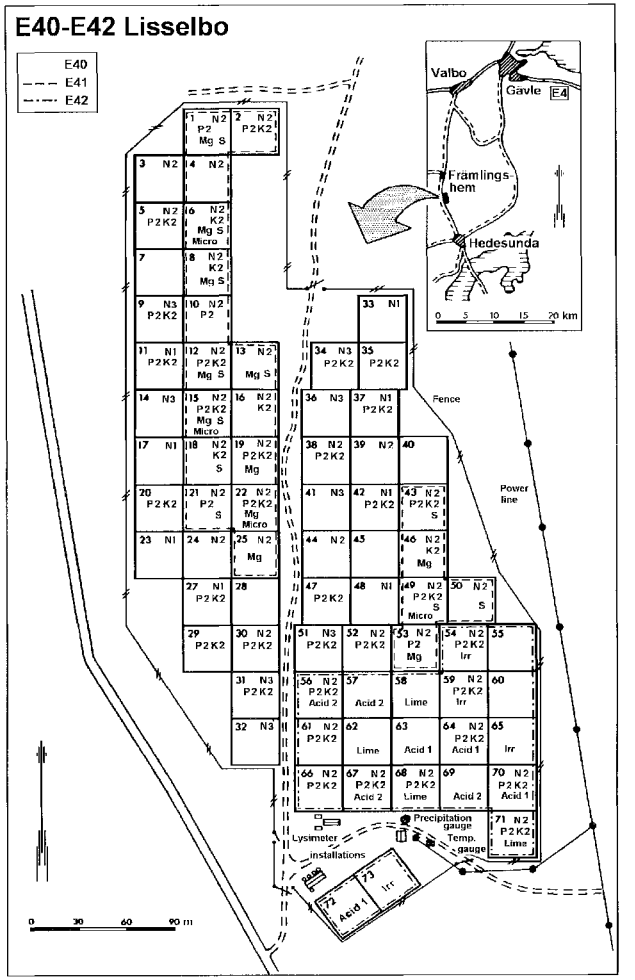

Fig. 2.5. Situation and plan of the experimental area Lisselbo, showing Expt E40 (32 plots), E41 (20 plots) and E42 (20 plots).

Table 2.2. *Fertilisation treatments of Expts E40, Lisselbo, and E55U and AN Norrliden. They are N dosage experiments, each level with and without a PK-treatment. E40 was fertilised with ammonium nitrate (four replicates). E55U was fertilised with urea and E55AN with ammonium nitrate. For each source of N, there were three replicates for controls and plots with N only, and two for plots receiving PK (with or without N). All figures are kg ha^{-1} element. Together with the P and K fertiliser were also added the amount of other elements indicated as follows. Added total amounts of other elements in E40: Ca=610, S=340, Cl=500. In E55: Ca=660, S=370, Cl=540*

	E40	Lisselbo					E55	Norrliden				
Year	N1	N2	N3	P	K	B	N1	N2	N3	P	K	B
1969	60	120	180	40	76							
1970	60	120	180									
1971	40	80	120				60	120	180	40	75	
1972	40	80	120	20	38		60	120	180			
1973	40	80	120				60	120	180			
1974	40	80	120				40	80	120	40	75	
1975	30	60	90	40	78		40	80	120			
1976	30	60	90				40	80	120			
1977	20	40	60	40	78	2.5	30	60	90	40	78	
1978	20	40	60				30	60	90			
1979	20	40	60				30	60	90			
1980	20	40	60	40	78		30	60	90	40	78	2.5
1981	20	40	60				30	60	90			
1982	20	40	60				30	60	90			
1983	20	40	60	40	78		30	60	90	40	78	
1984	20	40	60				30	60	90			
1985	20	40	60				30	60	90			
1986	20	40	60	40	78		30	60	90	40	78	
1987	20	40	60				30	60	90			
1988	20	40	60				30	60	90			
1989	–	–	–				30	60	90	40	78	
1990	–	–	–				30	60	90			
Sum	580	1160	1740	260	504		720	1440	2160	280	540	

experiment, E58. The irrigation treatment aimed at reducing summer drought effects rather than optimising water supply, and was tested with or without NPK-fertilisation (Table 2.5).

Foliar sampling

From the year before treatments started and throughout the experimental period, needles were sampled in autumn each year, as far as possible from the same ten trees on each net plot. At sampling, one or two well-exposed branches were cut from the second whorl from the top of the saplings during the early years of the experimental period. When the trees had become too tall to be sampled by pole secateur, a shotgun was used to obtain samples from the uppermost part of the crown. Current needles were removed and dried at 70°C.

Soil sampling

Determination of soil stores of chemical constituents is commonly less accurate than determination of concentrations, or requires more sampling points for the same accuracy (Troedsson & Tamm, 1969). A detailed study of soil stores by digging pits within measurement plots might give accurate values, but would be a destructive operation on fairly small permanent plots. We therefore used an indirect method to determine soil mass per hectare, which may introduce errors. However, the likelihood that random sampling errors will create significant experimental effects is small, and is included in the criteria for statistical significance. Two comments may, however, be made on this statement: *(i)* Simultaneous testing of a large number of possible relationships increases the risk of 'type I error', *i.e.* that a correct null hypothesis of 'no relationship' is rejected, and *(ii)* error in a conversion factor (such as from stoniness index to soil mass, see below) introduces bias in the same direction in several parameters.

The soil was sampled in Expt E55U and AN Norrliden in September 1975 (humus layer only) and in June 1988, and in Expt E58 Norrliden in September 1986. The samples were collected at

Table 2.3. *Expt E41 Lisselbo and E56 Norrliden are experiments with 'incomplete balanced blocks', intended to test, at a sufficient N supply (N2), the effects of addition of P, K, Mg, S and the micronutrients Cu, Zn, Mn, B, and Mo. P-fertiliser: triple superphosphate, K: potassium chloride, M: magnesium carbonate, and S: sodium sulphate. Additions in kg ha^{-1} element. For a detailed plan of the plot arrangements, see Table 2.6. Added total amounts of other elements in E41: Ca=314, Cl=415, Na=288. In E56: Ca=285, Cl=378, Na=288*

	E41	Lisselbo					E56	Norrliden				
Year	N2	P	K	Mg	S	Micro	N2	P	K	Mg	S	Micro
1969	120	40	80	50	40							
1970	120					(a)						
1971	80						120	40	80	50	40	(a)
1972	80	20	40				120					
1973	80			50	40	(a)	120					
1974	80						80	40	80			
1975	60	40	80				80			50	40	(a)
1976	60						80					
1977	40	40	80	50	40	(b)	60	40	80	50	40	(b)
1978	40						60					
1979	40						60					
1980	40	40	80	50	40		60	40	80	50	40	
1981	40						60					
1982	40						60					
1983	40	40	80	50	40		60	40	80	50	40	
1984	40						60					
1985	40						60					
Sum	1040	220	440	250	200		1140	200	400	250	200	

Note (a). 12 kg of each Cu, Zn, and Mn per ha, 5 kg B per ha, and 1 kg Mo per ha on each occasion. The proportions of elements and their chemical form was that of an additive used by the fertiliser company 'Supra' in their 'complete' fertilisers. Note (b). As (a) but without B.

regular intervals along the diagonals of the plots, using an auger. The diameter of the auger was 70 mm in the humus layer samplings. The 18–20 individual samples were bulked into one composite sample per plot. The mineral soil samples at Norrliden (Expt 58 1986, Expt 55U and AN 1988) were collected using a special auger (diameter 34 mm, with a lateral orifice). All mineral soil samples extended to 20 cm depth (for stones, see below) and were separated into three strata (0–5, 5–10 and 10–20 cm).

Sampling points falling wholly or partly on stones were included, humus layer and mineral soil (if present) being collected. However, a few points (at most two per plot) falling entirely or partly beneath tree stems or stumps, were discarded (see below).

Most soil sampling at Lisselbo was done within the acidification experiment E42, most extensively in June 1985, and is described by Tamm & Popovic (1989), together with the samplings from experiment E57 Norrliden, made in late June, 1985.

Mass data from auger samplings were used for calculating the mass of the humus layer, while mineral soil mass was calculated from the stoniness index (Si_{30cm}).

Si_{30cm} was determined for individual plots of the Norrliden and Lisselbo experiments (except E56 and E58) by the rod-testing method (Viro, 1952). Rod tests were made at 25 points distributed over the plot, which should give an estimated plot standard error of ± 1.6 cm (Viro, 1958). Calculations for transforming Si_{30cm} values into the mass of soil particles >2 mm are described by Tamm & Popovic (1989). The stoniness index was also used as a covariate in statistical analyses, testing its assumed relationships with tree growth (see Sections 5 and 7).

There was patchy variation in Si_{30cm} at both Lisselbo and Norrliden (Fig. 2.6, 2.7). Unfortunately, this was not known when the experiments were laid out. The attempts to minimise variation within blocks were instead based on the appearance of the stand. Stoniness differs systematically between E55U and AN (Table 2.7).

Expts E55U and AN were not designed to show differences in fertiliser effects between urea and ammonium nitrate, and the difference in

Table 2.4. *Treatments in Expts E42 Lisselbo and E57 Norrliden. Both experiments contained manipulation of soil acidity by adding dilute sulphuric acid one or more times during summer, or calcium carbonate at start. In addition, E42 contained irrigation plots; see Table 2.5. The treatments mentioned were given either alone or together with fertilisers (NPK). E42 had duplicate plots and E57 triplicate plots for each treatment. The figures are given for elements in kg ha^{-1}, for sulphuric acid as H_2SO_4 (note, however, that the sums at the bottom of the table concern the element S). Total amounts of other elements added with the PK fertiliser in Expt E42: Ca=520, Cl=420, S=290. In Expt E57: Ca=285, Cl=230, S=160*

	Espt	E42					Expt	E57					
Year	N2	P	K	H_2SO_4 Acid1	Acid2	Ca as $CaCO_3$	N2	P	K	H_2SO_4 Acid1	Acid2	Acid3	Ca as $CaCO_3$
1969	120	40	76		2 × 50	2000							
1970	120			50	2 × 50								
1971	80			50	2 × 50		120	40	76	50	2 × 50	3 × 50	2000
1972	80	20	38	50	2 × 50		120			50	2 × 50	3 × 50	
1973	80			50	2 × 50		120			50	2 × 50	3 × 50	
1974	80			50	100		80	40	76	50	100	150	
1975	60	40	78	50	100		80			50	100	150	
1976	60			50	100		80			50	100	150	
1977	40	40	78				60	40	78				
1978	40						60						
1979	40						60						
1980	40	40	78				60	40	78				
1981	40						60						
1982	40						60						
1983	40	40	78				60	40	78				
1984	40						60						
1985	40						60						
Sum	1040	220	426	110 (as S)	251 (as S)	2000	1140	200	386	98 (as S)	188 (as S)	282 (as S)	2000

Table 2.5. *Expt E58 Norrliden and part of E42 Lisselbo are fertilisation and irrigation experiments. E58 and the irrigation section of E42 consists of four treatments (control, irrigation, NPK and NPK+irrigation). E58 had three replicates and E42 two replicates. Elements in kg ha^{-1}; irrigation in mm per summer. Added total amounts of other elements in E42: Ca=520, Cl=420, S=290. In E58: Ca=285, Cl=230, S=160*

	E42 Lisselbo				E58 Norrliden			
Year	N2	P	K	Irr	N2	P	K	Irr
1969	120	40	76					
1970	120			92				
1971	80			70	120	40	75	92
1972	80	20	38	47	120			120
1973	80			36	120			53
1974	80			113	80	40	75	30
1975	60	40	78	50	80			106
1976	60			12	80			135
1977	40	40	78		60	40	78	88
1978	40				60			
1979	40							
1980	40	40	78					
1981	40							
1982	40							
1983	40	40	78					
1984	40							
1985	40							
Sum	1040	220	426		720	120	228	

Table 2.6. *Arrangement of element additions to individual plots in Expts E56 Norrliden and E41 Lisselbo. The basic design, 'incomplete balanced blocks', comprises four blocks, each with four plots; but in each block, one additional plot with micronutrients was added, for comparison with another plot in that block, viz. that which had received identical additions of elements other than 'Micro'. The five plots were randomised together, but for effects of single elements (P, K, Mg, S) only four plots should be used. Amounts of elements added are shown in Table 2.3*

Expt	Block	Element(s) added Plot	N	P	K	Mg	S	Micro
E56	7	31	+	−	+	+	+	−
		32	+	−	+	+	+	+
		33	+	+	+	−	−	−
		34	+	−	−	−	−	−
		35	+	+	−	+	+	−
	8	46	+	+	−	−	−	−
		47	+	+	+	+	+	+
		48	+	−	−	+	+	−
		49	+	+	+	+	+	−
		60	+	−	+	−	−	−
	9	61	+	+	+	+	−	−
		62	+	+	+	+	−	+
		63	+	+	−	−	+	−
		64	+	−	+	−	+	−
		65	+	−	−	+	−	−
	10	76	+	+	−	+	−	−
		77	+	+	+	−	+	+
		78	+	−	−	−	+	−
		79	+	+	+	−	+	−
		90	+	−	+	+	−	−
E41	5	1	+	+	−	+	+	−
		2	+	+	+	−	−	−
		4	+	−	−	−	−	−
		6	+	−	+	+	+	+
		8	+	−	+	+	+	−
	6	10	+	+	−	−	−	−
		12	+	+	+	+	+	−
		13	+	−	−	+	+	−
		15	+	+	+	+	+	+
		16	+	−	+	−	−	−
	7	18	+	−	+	−	+	−
		19	+	+	+	+	−	−
		21	+	+	−	−	+	−
		22	+	+	+	+	−	+
		25	+	−	−	+	−	−
	8	43	+	+	+	−	+	−
		46	+	−	+	+	−	−
		49	+	+	+	−	+	+
		50	+	−	−	−	+	−
		53	+	+	−	+	−	−

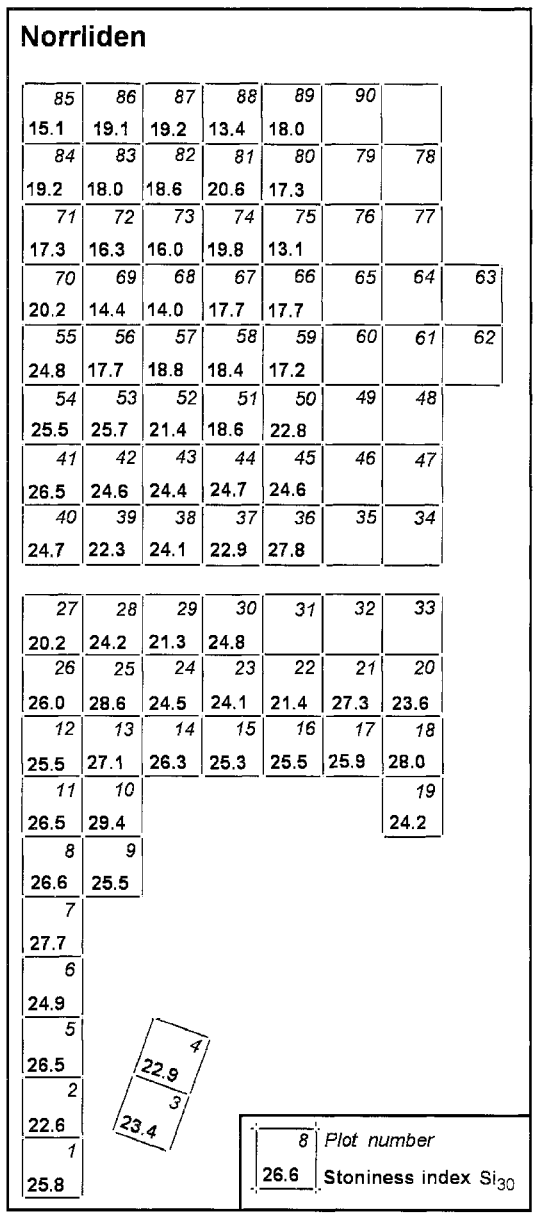

Fig. 2.6. Map of stoniness (Si_{30}) at Norrliden (E55U and AN, E57).

soil emphasises the need to consider them as independent experiments. However, since the experimental treatments run parallel in E55U and AN, the results are presented together in diagrams and tables, with separate subdiagrams for U, AN, UPK and ANPK, or with different symbols in histograms and scatter diagrams. Occasionally, it has been necessary to substitute information missing from one experiment by

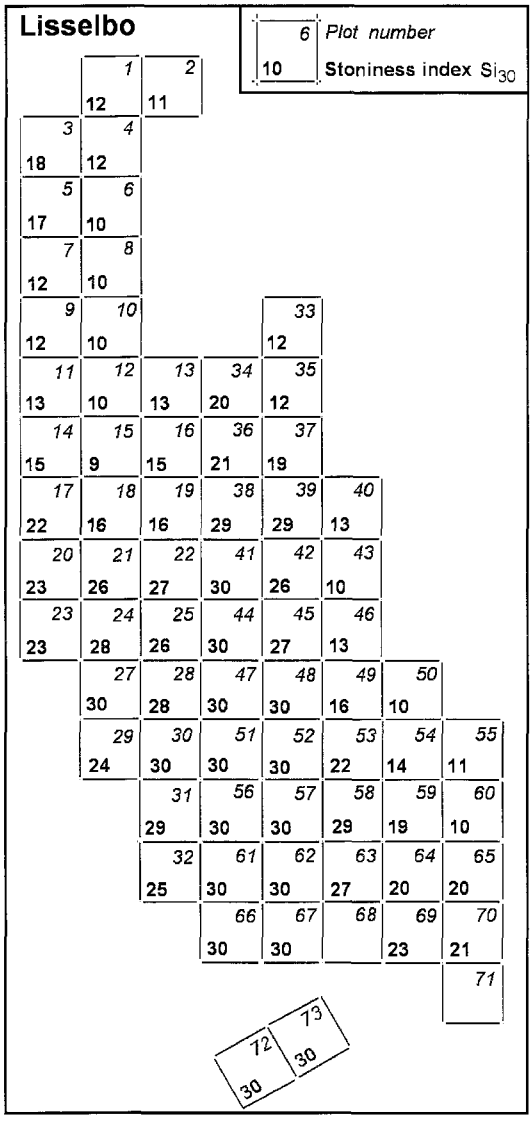

Fig. 2.7. Map of stoniness (Si_{30}) at Lisselbo. One missing value (plot 53) was interpolated.

Table 2.7. *ANOVA test on stoniness data for Expt E55 Norrliden (data in Fig. 2.6) concerning differences between blocks fertilised with urea and with ammonium nitrate. Note that differences reflect pretreatment conditions*

Source of variation	D.f.	Sum of squares	Mean square
Total variation	39	603.85	
Between U and AN	1	316.41	316.41
Within N forms	38	287.45	7.56
Between blocks	4	92.01	23.00
Within blocks	34	195.43	5.75

F ratio N form/Error: 41.85*** (D.f. 1/38)
F ratio Block effect: 4.00** (D.f. 4/34)

material from another; this is discussed where relevant (see Section 6).

Sources of error

Auger-sampling of the humus layer is fairly straightforward, and sampling error may be estimated approximately from the number of subsamples (Troedsson & Tamm, 1969; Falck, 1973). Twenty auger samples should yield standard errors around $\pm 7\%$ for plot means of humus N (N_{tot} mg dm^{-2}), in a spruce ecosystem on glacial till, according to Troedsson & Tamm (1969). For the same parameter, individual analyses of 20 samples cut out with a knife from areas of 4 dm^2, yielded a higher standard error from the 0 and A horizons (0 $\pm 10\%$, A_1 $\pm 9\%$), but for the B horizon the standard error was relatively small ($\pm 6\%$). No comparison was made with auger samples. The profile studied had an irregular and often weakly developed A_2 horizon which, where it occurred, was included in the A_1. The variability of the soil in amount of N was surprisingly similar on an apparently more uniform outwash sand studied by the same authors. A small bias, ascribable to the regular spacing of sampling points and to the occasional reduction of the number of points from 20 to 19 or 18, may have slightly increased the error in the Norrliden sampling, but we do not consider this a serious source of error. Forest soils formed on stony glacial till are among the most heterogeneous substrates for sampling, so conclusions should be based on means for as many plots as possible.

Lisky (1995) studied in great detail the variation in amounts of carbon (kg m^{-2}) in a Scots pine stand on glacifluvial sand in south Finland, and arrived at even higher coefficients of variation than did Troedsson & Tamm (1969). However, part of the variation was caused by a few high values close to stems and stumps, which led to skewed distributions. Since we avoided sampling beneath tree stems and stumps, our data may be considered more reproducible, but also biased, in the sense that some very high values close to tree stems were missed. Nevertheless, we consider that errors arising in this way would be larger for C than for N and most other bioelements, since they are ascribable to the uneven distribution of woody litter and bark, and of dissolved organic matter in stemflow, both of which involve material with

a high C/N ratio. Another Finnish study (Hokkanen, Järvinen & Kuuluvainen, 1995) confirms the influence of trees on qualitative soil properties, but does not discuss quantitative properties other than humus-layer thickness.

A possible source of error would arise, if the treatments had affected the morphology of the soil horizons, in particular the boundary between the humus layer and the mineral soil. This often happens in liming experiments on moderately fertile sites. Morphological changes, of a kind that might complicate the distinguishing of the horizons, were not observed at Norrliden and Lisselbo. This does not exclude minor colour changes (due to liming or to changed transport of humic substances into the mineral soil). We cannot explain the observations by Lohm (1988), concerning differences in depth of the A_2 horizons between controls and strongly acidified plots in experiment E57. Lohm's observations were not confirmed in the extensive soil survey of that experiment in 1985 (Tamm & Popovic, 1989).

Chemical analysis of soil and plant material

Soil

Humus and mineral soil samples were mixed well and sieved fresh; using a 3-mm screen for humus and 2 mm for mineral soil.

The pH_{H_2O} was estimated after 24 hours in water suspension (*w/v* relation 1:3 for humus and 1:2 for mineral soil, roughly corresponding to sample: water fresh mass relations of 1:5 and 1:3, respectively).

Loss on ignition was determined at 550°C and dry mass at 105°C. In the 1975 sampling, carbon was calculated for humus samples by multiplying the loss on ignition by 0.58. The total N content was determined by Kjeldahl digestion, with measurements on an autoanalyser. Total C and total N in samples from 1988 were estimated on the Carlo Erba Elemental Analyzer NA 1500 (see Kirsten & Hesselius, 1983).

Exchangeable base cations were extracted with 1 M NH_4Ac solution (adjusted to *p*H 7.0; Balsberg, 1975). Base cations were determined using an atomic absorption spectrophotometer (IL-AAS-551). Titratable acidity was obtained from measurements of *p*H on the buffer solution, using a glass electrode. Cation exchange capacity (CEC) and degree of base saturation (V%) were calculated from base cations and titratable acidity.

Exchangeable aluminium was extracted with 1 M KCl solution and measured on the AAS (after 1984, on IL Plasma-200).

Ammonium and nitrate N were extracted by shaking fresh soil with 1 M $KAl(SO_4)_2$ solution in the 1975 samples. Ammonium N was measured colorimetrically on the autoanalyser after reaction with indophenol (Selmer-Olsen, 1971). Nitrate was reduced with cadmium amalgam to nitrite and measured on the autoanalyser (Popovic, 1977). The 1988 samples were extracted with 0.5 M KCl solution for estimation of ammonium and nitrate N by flow injection analysis, FIA (Tecator FIA 5010).

Needle and biomass samples

For chemical analysis, needle samples were weighed after drying at 105°C and wet-combusted in a mixture of nitric acid/perchloric acid (ratio 2.5:1.0). K, Ca and Mg were determined using a flame-photometer (until 1970), an atomic absorption spectrometer (1971–1984), or on the ICP emission spectrometer (type Plasma 200 after 1984). P and Mn were determined colorimetrically until 1984, thereafter on the Plasma 200. After 1984 S, Al and micronutrients were also determined by Plasma 200. Parallel analyses were made at every change in methods.

The chemical analyses of the annual 'diagnostic' needle samples were normally made on one sample per plot, but lists of plot values for each element were scrutinised for deviations from previous values; when unexpected irregularities occurred, duplicate analyses were made. Samples which could not be checked by comparison were run in duplicate (some biomass samples, soils, incubation experiments).

Incubation experiments

In 1975, incubation experiments were made at a temperature of 20°C in 300 ml Erlenmayer flasks, with 40 g of fresh soil material, after sieving and adjustment of the moisture content to 60% WHC (water-holding capacity) for periods of six and nine weeks, with duplicate flasks for each period (Popovic, 1971; 1977; 1984). The flasks were sealed with very thin polyethylene film, permeable to O_2 and CO_2 (Bremner & Douglas, 1971).

Tree growth measurements

All trees within the net plots were measured at intervals in the same way as permanent yield plots of the Yield Research Department, *i.e.* all trees above breast height (1.3 m) were numbered and breast height diameter (DBH) was measured by cross-calipering at permanent marks on the stem. The initial height of all trees in the young stands was measured. After canopy closure, every second tree was measured, plus a few dominant trees. Some trees which had not reached breast height at the first measurement, but which were thought likely to become part of the future canopy, were also numbered and their height was measured. The interval between stand measurements was 3–5 years. At Lisselbo, where the first stand measurements were made in 1971, leading shoots were measured back to 1968, the year before treatment began.

The volume of individual stems, or of mean trees by diameter classes, was estimated using formulae from Näslund (1940–41 and 1947, Norrliden and Lisselbo, respectively) and Andersson (1954, for small trees).

Increment cores cannot be taken from small-diameter trees without risking damage. Therefore, at Norrliden in the spring of 1985, basal area measurements were made on cores from 20 trees per plot, which had been removed as thinnings. At Lisselbo, at least five trees per plot were cored, for preference trees overthrown or broken by heavy snow in late 1988. These were supplemented where necessary by cores from trees outside the net plots (on plots with few damaged trees). At Norrliden, trees to be removed were, with few exceptions, not selected individually but were taken out as a proportion of the numbers on a list. Therefore, the selection of trees should not be seriously biased. The Lisselbo samples are less satisfactory in this respect. The results should therefore only be relied upon when they show reactions essentially similar to those demonstrated by measurements on standing trees.

The two methods of measuring basal area increment of trees, by calipering in the field and from ring width under the microscope, both have merits. For both types of measurement, the precision of comparisons can be increased by analysis of covariance (ANOCOVA), in which some measure of tree vitality is used as covariate. For basal area growth, either basal area (BA) or basal area growth (BAG) before treatment was used as covariate. The advantage of this is that the covariate is measured on the same core as the growth variable, *i.e.* at exactly the same position in the stem and with the same precision. The influence of the covariate is initially very strong, but decreases as the stand grows older. The adjustment calculated from the ANOCOVA also decreases relatively. In most cases it was statistically significant; in the few cases where this was not so, we continued to adjust the values to maintain comparability over time.

Growth estimates based on periodic field measurements have the advantage of being more directly related to stand characteristics, such as yield and site quality. The precision of the measurements is, however, lower and the time resolution is much lower than for core measurements, in which annual values are still accurate. Intervals of 3–5 years were used in our measurements, but for statistical analyses, longer periods are preferable. Adjustments were made by ANOCOVA for both basal area and stem volume, but since the results were very similar for both of these measurements (for reasons explained in Section 5), most of the growth data presented here are stem volumes or volume increment, adjusted either by means of stem volume at the start of treatment or by 'Bjørgung's index', ($\sqrt{n \cdot h^2}$; Bjørgung, 1968). The index combines initial stand density (n stems ha^{-1}) with arithmetic mean height (h), which is related to tree vigour. At least until the canopy is fully closed, the index and volume growth are linearly related, as reported by Bjørgung (1968) and confirmed in our experiments. In the same way as for core measurements, diagrams for the progression of stem volume are shown (Section 5). In these the adjustments have been continued, even though the adjustment variable is not fully significant during the latest period. Examples of the size of the adjustments are given by Aronsson *et al.* (1999).

When tree measures (stem volume or basal area) are used to estimate biomass or storage of bioelements in the stand, measured values have been used as far as possible. The reason for this is that the individual plot, with its actual stand and soil, is regarded as a sample of an ecosystem, for which the data for components should be coherent, not 'smoothed' by adjustment oper-

ations, which are justified only when studying treatment effects on single components.

Selection of sample trees for biomass

Sample trees from five treatments, N0, N1, N2, N3 and N2PK, were used at Lisselbo. Trees within each net plot were divided into three groups with similar basal area, small, average, and large trees. The mean tree for each group was calculated, and for most plots, a tree outside the net plot but within the treated area, was selected from the diameter class in question. This tree should not deviate by more than 5% from the arithmetic mean height for the group. The first tree to fulfil these criteria was felled as a sample tree, unless it showed stem or crown damage. There were 60 sample trees (5 treatments*4 replicate plots*3 trees). On plot 3 (N2) and plot 5 (N2PK), the sample trees were taken within the net plots, and root samples were also taken; these plots were thereafter regarded as disturbed, and were excluded from most tree growth calculations (Section 5). The principles for estimating biomass fractions by allometric equations are described by Albrektson (1980).

The sampling at E55 Norrliden in 1985 was similar, but the larger number of treatments (two N sources) and the much larger trees necessitated modifications. Since approximately 20% of the basal area was removed by thinning at the same time, the sample trees could be taken from the net plots. The biomass sample trees were taken from two U blocks and two AN blocks, but were selected differently. Within U blocks, two trees per plot were sampled, *viz.* one tree close to the tree of mean basal area, and one close to the tree of mean basal area +1.5 standard deviations (sd). On average, the larger tree had a basal area 70% greater than the mean tree.

On AN blocks, four trees were sampled from each of two controls, two PK plots, two N2 plots and two N2PK plots. Of the four trees from each plot, one was close to the tree of mean basal area, one tree represented mean basal area −0.75sd, one tree mean basal area +0.75sd, and one tree +1.5sd. In all, 16 trees were selected from U plots and 48 from AN plots, but two AN trees were discarded at an early stage, because of damage. Some trees were also felled on plots within E56, but only a few stem data from them have been used. Here, as at Lisselbo, some trees with top or stem damage were avoided as not being fully representative, and the next tree on the list to meet the size criteria was taken.

The biomass sampling in E57 also comprised trees close to mean basal area, as well both as smaller and larger trees (Popovic, 1990/1991) from some treatments. Here, the control and N2PK treatment are especially valuable, since they had been treated in the same way as the controls and N2PK AN in E55.

Methods of calculation and statistical analysis

The measurements and formulae used for estimating biomass fractions are described in Section 6. They are based on allometric relationships between biomass fractions and stem measurements, but simple proportionality factors have sometimes been used, when this could be done without serious loss of accuracy.

The statistical calculations of all large data sets (chemical analyses, relationships between tree growth with foliar composition, *etc.*) were made with the help of SAS (SAS Institute Inc., 1982), while some simpler tests (ANOVA or ANOCOVA on limited numbers of data) were made on a programmable calculator (HP41CV). Most regressions shown in the figures were calculated by the KaleidaGraph data analysis/graphics application for Macintosh computers (Anon., 1993).

Statistical significance is shown by the conventional symbols, one, two or three asterisks, for probability values $p \leq 0.05$, 0.01 and 0.001, respectively. In most tables, the actual p values from the SAS program are shown, down to $p < 0.0001$. LSD in some tables represents least significant difference, at the level $p \leq 0.05$.

3. Soil chemical changes related to N and PK regimes

The effects of treatment manipulation on soil chemical conditions, mainly in Expts E55U and AN, are dealt with here. The material is arranged in four parts: First, concentration data for biologically important parameters. Secondly, estimates of the amounts of chemical constitu-

ents per unit area. Thirdly, soil biological activity, especially N turnover. Fourthly, the recovery of added N from the soil under different N regimes.

Changes in soil concentrations of biologically important constituents

The soil was comprehensively sampled in Expts E55U and AN at Norrliden in June, 1988. The effects on soil variables of N and PK treatments are summarised in Table 3.1. Treatment differences are given with their signs and conventional significance symbols, more to give an overview of the variables studied than to present final results. Since simple ANOVAS do not utilise the full information in the experimental design—the N regimes form arithmetic series—linear and quadratic regressions between soil variables and N regimes were tested. Those resulting in significant and relevant relationships are presented here in diagrams, Fig. 3.1–3.4 for concentration variables, in Fig. 3.5–3.11 for variables expressed as amount per hectare. The type of diagram varies, depending on the need for further testing of the significance values in Table 3.1 (Table 3.2 for amounts) or the need to illustrate changes relative to the conditions on control plots. For further details, see Aronsson *et al.* (1999), where soil data for individual plots are presented.

Changes in soil acidity and base saturation

Fig. 3.1*a-d* presents relationships between pH_{H_2O} and N regimes as linear regressions. Three only of the 16 linear regressions were not statistically significant (ANPK and UPK in the humus layer, UPK in the uppermost mineral soil—all with only six degrees of freedom compared with ten for those without PK).

Fig. 3.1*c-d* show the influence of N addition on soil *p*H in the two lowest horizons, where it falls by about one unit at the highest rate of addition. In contrast, humus layer *p*H tends to increase with increasing N addition (Fig. 3.1*a*). It follows that the treatment effect is least marked in the horizon 0–5 cm (Fig. 3.1*b*). PK treatment does not affect *p*H as much as N addition, but the less steep slope of the regressions with PK than without PK in Fig. 3.1*c-d* is consistent with two occurrences of negative interaction N*PK in the same horizons in Table 3.1, where interactions are otherwise rare.

The acidity changes are further illustrated in Fig. 3.2*a-d* and compared with changes in base saturation (V%) in Fig. 3.3*a-d*. Base saturation (V%) is often considered a better expression of the acid/base status of a soil than *p*H, but the two variables provide somewhat different information and are therefore both of interest. In undisturbed podzol profiles in North Sweden, *p*H increases and V% decreases with depth (O. Tamm, 1950; Tamm & Hallbäcken, 1988). This is also the case on control plots at Norrliden. With increasing N addition, *p*H increases in the humus layer and decreases in the mineral soil, as discussed above. V% decreases with increasing N addition, but increases with PK addition, as is shown when Fig. 3.3*a* is compared with *c* or *b* with *d*. Not all PK differences are statistically significant, partly because the analytical accuracy is low at the very low values in mineral soil. On the other hand, all the curves in Fig. 3.3 are very similar.

In summary, the two higher N regimes, irrespective of the form of N, completely change the *p*H trends with depth, and all N additions decrease V%. PK addition increases V%, apparently more in the humus layer than in deeper mineral horizons, but has little effect on *p*H.

The decrease in V% with increasing N regime is of course connected to losses of 'base' cations. These losses are more appropriately discussed in the next subsection, in connexion with changes in constituents, expressed as amounts per unit area. Some of the metal cations lost have been replaced by ammonium ions, which conventionally are not included in V%. The question whether adsorbed ammonium ions might play a part in the change in V%, has been studied by Aronsson *et al.* (1999), who concluded that the difference in V%, calculated with or without ammonium ions, was fairly small and scarcely affected the conclusion that annual N additions deplete the mineral soil of base cations.

Changes in concentrations of soil N fractions and in C/N ratio

Since E55 U and AN are primarily N dosage experiments, it is especially interesting to study changes in N fractions during the experimental period. However, large quantities of organic matter, containing N, are stored in the soil. Hence treatment effects on concentrations of

Table 3.1. *ANOVA test on soil properties in Expt E55, Norrliden. Chemical concentration variables: H, K, Mg, Ca, CEC, Al and NH_4N, NO_3N are expressed as μeq g^{-1}, C and N as mg g^{-1}. For full explanation, see Table 3.2*

Treatment effect	D.f.	*p*H	H	K	Mg	Ca	CEC	V%	Al	C	N	C/N	NH_4N	NO_3N
Humus														
								Urea						
N	3	+0.22*	+35.5	−1.87***	+0.12	+10.2	+44.1	− 0.2	− 2.1	+ 9.5	+3.8***	−10.0***	+118.8	+19.3
PK	1	+0.07	− 7.1	+0.66	−2.58*	+94.3***	+85.3	+12.6***	−13.7***	+32.0*	−0.1	+ 2.9*	− 82.7**	− 0.6
NxPK	3	−	−	+	−	+	+	+	−	+	−	+	−	−
								Ammonium nitrate						
N	3	+0.23*	+32.3	−1.99*	−0.66	−29.2**	+ 2.4**	− 5.7**	+ 9.6	− 5.8	+1.7	− 5.9***	+141.8*	+12.9*
PK	1	+0.01	− 5.8	+0.71	−5.78**	+83.5***	+74.4***	+11.2***	−14.2*	+11.2	−0.6	+ 2.8**	−134.6**	− 2.9
NxPK	3	−	−	+	−	+	+	+	−	+	−	+	−	−
Mineral soil 0–5 cm														
								Urea						
N	3	−0.15**	+ 9.0	−0.13	−1.30	− 0.13	+ 7.4	− 2.9*	+ 3.6	+ 2.1	+0.24**	− 6.7***	+ 15.1***	+ 1.8***
PK	1	−0.05	− 4.6	+0.73***	+0.11	+ 6.7***	+ 2.9	+ 9.7***	− 8.9***	− 0.6	−0.07	+ 1.3*	− 5.6*	+ 0.1
NxPK	3	−	−	+	+	+	−	+	−	−	−	+	−	+
								Ammonium nitrate						
N	3	−0.29**	+ 8.6	+0.07	−0.14	− 4.5***	+ 3.9	− 8.4***	+ 5.8	+ 2.6	+0.16**	− 2.5*	+ 21.8*	+ 4.2**
PK	1	−0.04	+ 3.2	+1.24***	+0.01	+ 5.2***	+ 9.6*	+ 8.2***	− 4.9*	− 0.2	−0.02	+ 0.4	+ 2.8	+ 0.4
NxPK	3	−	+	+	+	+	+	+	−	−	−	+	+	+
Mineral soil 5–10 cm														
								Urea						
N	3	−0.48***	+16.3**	−0.25**	−0.19*	− 2.1**	+13.7*	− 5.1***	+ 5.2	+ 3.4**	+0.19**	− 0.8	+ 1.8*	+ 6.7***
PK	1	−0.08	+ 1.5	+0.89***	+0.02	+ 2.1***	+ 4.6	+ 3.8***	+ 4.0	− 2.5**	−0.11*	− 0.2	+ 0.4	− 1.8
NxPK	3	−*	+	+	+	+	+	+	+	−	−	+	−	
								Ammonium nitrate						
N	3	−0.70***	+ 8.7**	−0.55*	−0.25***	− 4.6***	+ 3.4*	− 9.3***	+ 6.4	+ 2.2*	+0.10**	+ 2.2	+ 7.64***	− 0.1
PK	1	+0.41	+ 7.4*	+1.14***	+0.04	+ 1.6***	+10.2**	+ 3.0***	+ 1.3	− 1.8	−0.02	+ 0.3	+ 0.99	+ 2.6
NxPK	3	−	+	+	+	+	+	+	+	−	−*	+	+	+
Mineral soil 10–20 cm														
								Urea						
N	3	−0.62***	+ 0.5	−0.46*	−0.28	− 2.0**	− 2.3	− 5.2***	+ 0.7	+ 0.6	+0.03	− 0.1	+ 0.20	+ 4.7***
PK	1	−0.19*	+ 6.9*	+0.90***	−0.03	+ 0.7	+ 8.4**	+ 2.0*	+ 3.7*	+ 0.9	+0.04	+ 0.1	− 0.26	− 1.3
NxPK	3	−**	+	+	+	+	+	+	+	+	+	+	−	−
								Ammonium nitrate						
N	3	−0.74***	+ 4.3	−0.58***	−0.12**	− 2.1***	+ 1.5	− 6.6***	+ 3.4**	+ 0.4	+0.06	− 1.8**	+ 0.93*	+ 5.2*
PK	1	−0.15	+10.9*	+1.15***	+0.01	+ 0.2	+12.2**	+ 1.2	+ 2.2*	+ 1.1	+0.02	+ 1.2**	+ 0.26	− 0.5
NxPK	3	−	+	+	+	+	+	+	+	+	−	+	+	−

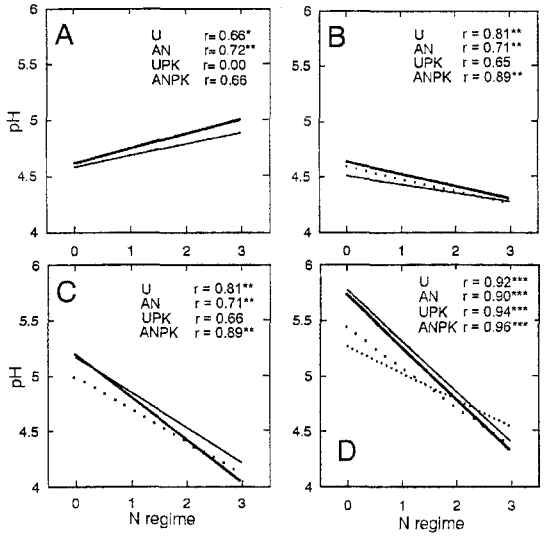

Fig. 3.1. Soil pH_{H20} in different soil horizons at the sampling in June 1988, as a function of N regime in E55 Norrliden, calculated for each treatment group separately (U, AN, UPK, ANPK). Only statistically significant regression lines are shown. Correlation coefficients (r) are shown for all four groups; when statistically significant, they are marked with asterisks. (A) Humus layer (O or A_o). (B) Mineral soil 0–5 cm, (C) 5–10 cm, (D) 10–20 cm. Thin lines denote urea treatments, heavy lines ammonium nitrate; solid lines are treatments without PK and broken lines, those with PK.

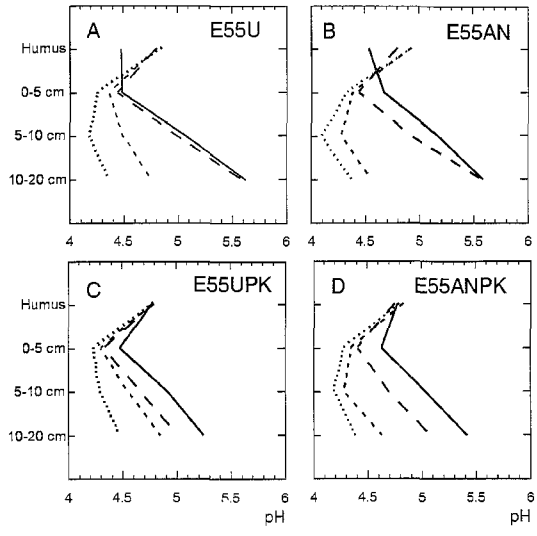

Fig. 3.2. Variation in pH_{H20} with soil depth and treatment in Expt E55 Norrliden. Sampling in June 1988, when N1 plots had received 630 kg N (17 applications 1971-1987); and PK plots 240 kg P and 462 kg K (in six applications 1971–1986). Source of N: urea in subdiagrams (A) and (C), ammonium nitrate in (B) and (D). Arithmethic means for three plots (A and B, treatments without NPK) or two plots (C and D, treatments with NPK). For individual plot data, see Aronsson *et al.*, 1999). Legend: solid lines: no N; broken lines: N added; long dashes: N1; intermediate dashes: N2; short dashes: N3.

total N and total C tend to be masked, even if several cases are confirmed statistically in Table 3.1. The carbon/nitrogen (C/N) ratio is a more sensitive measure of the same changes (Fig. 3.4), and shows clear changes in the humus layer between no-N and N treatments, and similar, though less clear, tendencies in the mineral soil. NPK treatments have higher C/N ratios than the corresponding treatment with N only, especially in the humus layer.

The differences in mineral N concentrations (ammonium N and nitrate N) show much clearer treatment effects in Table 3.1, but will be discussed in greater detail in connexion with the storage data and N turnover (p. 31–33).

Changes in soil stores of biologically important constituents

General comments

The tests made to relate soil mass (fine earth, <2 mm grain size) to stoniness index, Si_{30cm} (Tamm & Popovic, 1989), gave no indication of differences in bulk density between the three horizons studied here. Consequently, there is no

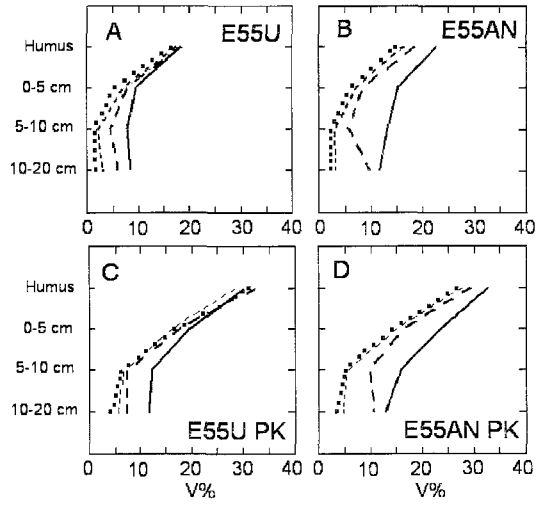

Fig. 3.3. Variation of base saturation (V%) with sampling depth in E55 Norrliden. For explanation, see Fig. 3.2.

reason to report storage values for separate mineral horizons in this case. Differences in soil storage for the N and PK regimes are summar-

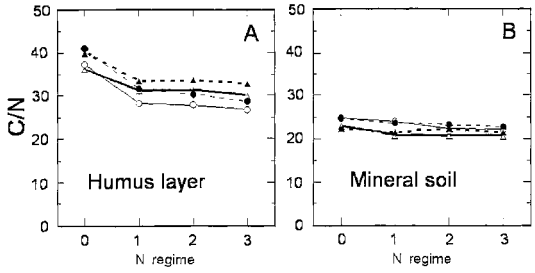

Fig. 3.4. Carbon/nitrogen ratio in the soil in E55 in different nutrient regimes, measured in June 1988. (A) in humus layer, (B) in mineral soil 0–20 cm. Calculated from plot data presented by Aronsson *et al.* (1999). Legend: Thin lines urea; heavy lines ammonium nitrate. PK treatments with broken lines.

ised in Table 3.2, for the humus layer and mineral soil (0–20 cm).

As noted above (Section 2), spatial variation in the mass of soil strata is large, which affects estimates of all constituents expressed as amounts per unit area. Even though most of the variation in stratum mass may be regarded as random, for single plots it affects all constituents similarly. The only way to minimise this source of error is to compare the means of as many plots as possible. This is done in Fig. 3.5, where means are compared for N and C stores and dry masses for combinations of treatments in each N regime: all five U plots, all five AN plots, all six plots without PK, and all four plots with PK. This presentation can show only main effects, not interactions, but it may still help to distinguish between possible treatment effects and pure 'noise' in the statistical sense.

Examples of the agreement between humus layer mass, C content and N content are given in Fig. 3.5. All three parameters differed consistently between no-N plots and fertilised plots; to this we shall briefly return. The mineral soil on U and AN plots differed in mass at all N levels, which agrees with the difference in stoniness (Table 2.7), but there were no systematic differences between treatments with or without PK. Parallels between N and C stores in the mineral soil will also be discussed further. Since most differences between treatments in Table 3.2 are larger (in relative terms) than those for total N and total C, plot differences in dry mass may be considered to be of minor importance when differences in element stores (Table 3.2, Fig. 3.6–3.11) are large and consistent.

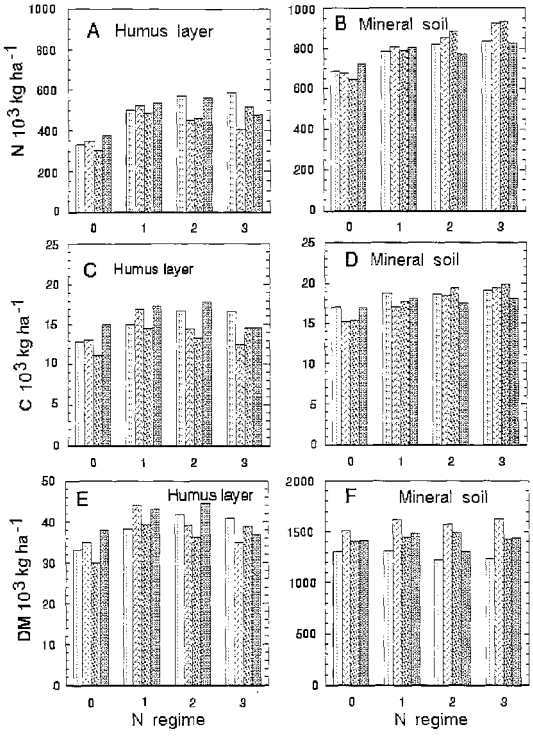

Fig. 3.5. N, carbon and dry mass of horizon in humus layer (left) and mineral soil 0–20 cm (right) in June, 1988, by treatment combinations in E55. The bars for each N regime correspond to (in order) U ± PK, AN ± PK, U ± AN, UPK ± ANPK. Further explanation in text.

Changes in amounts of exchange capacity, acidity and cations

The data in Table 3.2 follow from those in Table 3.1. Both types of experimental treatment, N and PK fertilisation, appear to increase the cation exchange capacity (CEC), but in the ANOVA tests in Table 3.2, statistical significance is attained once only for N (ammonium nitrate in mineral soil) and twice for PK (urea in humus layer and ammonium nitrate in mineral soil). These increases may be explained by an increase in amounts of organic matter upon fertilisation, possibly also by a quality change in this material.

Significant interactions N*PK are few (occurring only in E55AN, mineral soil). Exchangeable H^+ and Al increase significantly with N in E55AN, mineral soil. In E55U, the differences in Table 3.2 are in the same direction, but do not attain significance.

In Table 3.2 the negative effect of increasing N regime on Ca and Mg stores in the mineral

Table 3.2. *Expt E55, Norrliden. Results of ANOVA tests of treatment effects on chemical variables in amounts per hectare. There were 12 degrees of freedom (D.f.) for the error in the test of N and PK effects. Asterisks denote P levels (* ≤ 0.05, ** ≤ 0.01 and *** ≤ 0.001) in the ANOVA test. For main effects, the sign and numerical difference are shown for situations with and without treatment (for N-fertiliser, an average of N 1–3 is compared with N 0). For interactions, only the sign and asterisks for significance (if any) are shown. Sampling in June 1988*

Treatment effect	D.f.	H keq	K keq	Mg keq	Ca keq	CEC keq	Al keq	C kg 10^3	N kg	NH_4N kg	NO_3N kg
						Variables					
Humus											
						Urea					
N	3	+ 4.42	+0.007*	+0.089	+1.19	+ 5.71	+0.07	+3.21	+223.88**	+ 4.67**	+0.78**
PK	1	+ 2.44	+0.084*	−0.034	+4.43***	+ 6.93*	−0.44**	+3.73*	+ 73.01	− 2.85**	+0.06
NxPK	3	+	+	−	+	+	−	+	−	−	+
						Ammonium nitrate					
N	3	+ 3.70	−0.015	+0.058	−0.51*	+ 3.32	+0.41	+1.80	+118.42	+ 6.25**	+0.50
PK	1	+ 4.75	+0.055	−0.112	+3.54***	+ 9.54	−0.51*	+1.77	+ 13.76	− 5.12**	−0.18
NxPK	3	−	+	−	+	+	−	+	−	−	−
Mineral soil 0–20 cm											
						Urea					
N	3	+ 6.69	−0.471*	−0.302	−2.64**	+ 3.29	+2.70	+1.84	+137.46	+ 5.45***	+5.70***
PK	1	− 2.92	+0.992***	+0.009	+2.94***	+ 0.95	−0.99	−2.12	−104.00*	− 2.40**	−1.94
NxPK	3	−	+	+	+	−	−	−	−	−	−
						Ammonium nitrate					
N	3	+14.80***	−0.527	−0.220**	−4.75***	+ 9.30*	+8.68**	+3.26**	+199.97***	+10.76*	+8.99**
PK	1	+15.56***	+1.914***	+0.057	+2.96***	+20.42***	+1.34	+1.23	+ 25.84	+ 1.99	+0.92
NxPK	3	+*	+	+	+	+*	+	+	−*	+	+

soil is numerically larger and more significant in E55AN than in E55U. The same is true of the positive effect on H^+ and Al. Because of the experimental design, these differences cannot be statistically confirmed as treatment effects. However, such differences are to be expected from a generally accepted theory, the 'mobile anion concept' (Seip, 1980). In acid soils, anions of strong acids (NO_3, SO_4, Cl) are not much retained by soil colloids—in contrast to cations such as H^+, Ca, K and Mg—and percolate down the profile, accompanied, for the sake of electroneutrality, by cations from the soil solution and the exchange complex. When ammonium nitrate is added, a large part of the ammonium ions is rapidly absorbed, but is also assimilated into organic N by plants and microorganisms. As is discussed below (p. 33), ammonium N is preferred to nitrate N by most organisms in acid forest soils. When urea is added, it is rapidly transformed into ammonium ions, and is then either adsorbed or transferred to organic N. Transformation to nitrate may occur slowly, and proceeds more rapidly only at high levels of available ammonium N in the soil.

Seip (1980) used the concept 'mobile ions' to explain how 'acid deposition', with a *p*H between 4 and 4.5, due mainly to sulphur compounds, could pass a humus layer of similar acidity and then acidify surface waters. However, the process begins already in the soil horizons below the humus layer, and the theory applies equally well to the effect of nitrate, either added as ammonium nitrate or, in nitrifying soils, formed in upper soil horizons.

When PK fertilisers are added, the mobile sulphate ions are compensated by the addition of Ca and K, which increases base saturation in the humus layer. Part of the sulphate ions still percolates.

In the humus layer, the amount of Al decreases with PK addition—presumably because much Ca and K has been added—while the effects of N addition are less clear. In the mineral soil, N increases the amount of exchangeable Al (statistically significant at the 1% level with ammonium nitrate). In the regression analysis (Fig. 3.6*d*), three of the four groups show clear relationships between Al stores and N regimes.

The humus layer has not been acidified by N addition, and the stores of base cations show

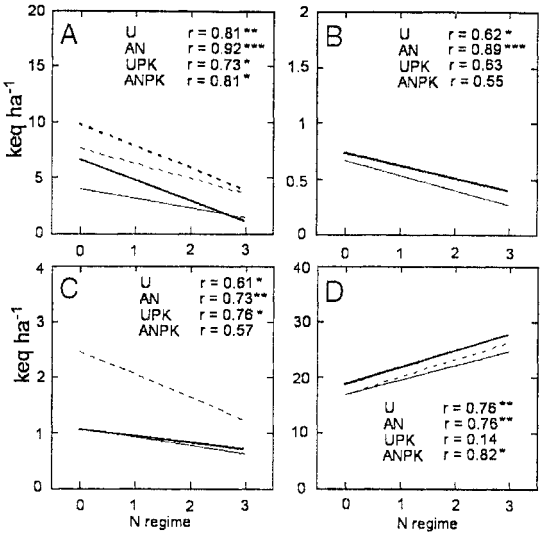

Fig. 3.6. Amounts of exchangeable Ca (A), Mg (B), K (C) and Al (D) in the mineral soil (0–20 cm), as a function of N regime in E55. Values in keq ha^{-1}. Symbols, regression lines and *r* values as in Fig. 3.1.

one instance only of significant changes with this treatment (negative at the 5% level with ammonium nitrate). PK addition positively affects the stores of K, and especially that of Ca (both of which are added with the fertiliser). The PK effect on the Mg store is not statistically significant, but has a negative sign in the humus layer.

In the mineral soil, where strong acidification has occurred following N addition, clear negative effects have been observed in the stores of all three elements, most consistently for Ca (Table 3.2). Fig. 3.6*a*, *b* and *c* give a more detailed picture of the decline of the cation stores with increasing N regime. The decrease in equivalents of exchangeable Ca accounts for a considerable part of the increase in exchangeable Al (Fig. 3.6*d*), while the decreases in K and Mg (in keq ha^{-1}) are much smaller. Full equivalence cannot be expected between increases in Al and decreases in Ca + Mg + K, as there are also changes in hydrogen ions and ammonium ions. Furthermore, the basis for calculation of V% is somewhat artificial, *viz.* CEC at *p*H 7.

Changes in stores of soil N fractions

With the help of Table 3.2 and Fig. 3.5, 3.7 and 3.8, the differences in total N, ammonium and nitrate between treatments are briefly presented below. Some of the data are discussed in a more

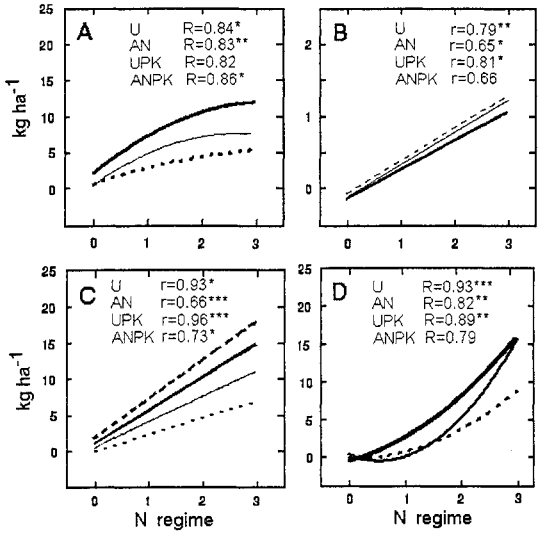

Fig. 3.7. Amounts of ammonium and nitrate N (kg ha^{-1}) in humus layer and mineral soil (0–20 cm) in E55 Norrliden, as a function of N regime, June 1988. (A) Ammonium N in humus layer. (B) Nitrate N in humus layer. (C) Ammonium N in mineral soil. (D) Nitrate N in mineral soil. See further Fig. 3.1.

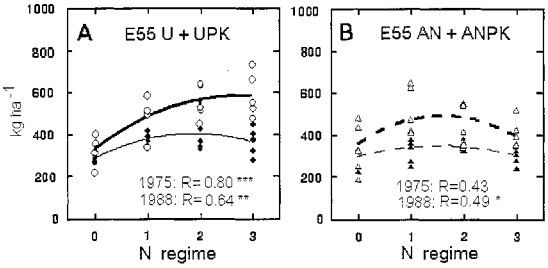

Fig. 3.8. Total N, kg ha^{-1}, in E55 U and AN in humus layer. (A) E55U: in humus layer in 1975 and 1988. (B) E55AN: in humus layer in 1975 and 1988. Symbols: circles for U, triangles for AN; filled symbols for treatments with PK. The 1975 data were calculated from dry mass and N percentages presented by Popovic (1977).

dynamic perspective, with the aid of the detailed presentation of plot data (Fig. 3.9–3.11). Finally, other studies carried out in our experimental areas are discussed.

Total N

As the effects of treatments on total soil N in both the humus layer and the upper mineral soil tend to be masked by variation in the amount present before the experiments began, we have already discussed Fig. 3.5, in which the means of all plots with the same N regime are compared, independently of PK addition or N source. The comparison showed *(i)* that in the humus layer there are consistent differences in stratum mass, and amount of C and N between no-N treatments and all treatments with N; *(ii)* that in the mineral soil, differences in mass between E55U and AN are consistent (U < AN), while there is no consistent difference in mass between +PK and −PK; *(iii)* in the mineral soil there are several similarities of pattern in the N and C stores, both of which show a slight increase with increasing N regime. Conclusion *(i)* merits further discussion (Fig. 3.8*a* and *b*), as it may indicate a treatment effect. Conclusion *(ii)* is in agreement with the difference in stoniness between U and AN (Table 2.7), which suggests that E55AN may have a higher site quality than E55U. Conclusion *(iii)* calls for statistical tests where individual plot values are used, see Fig. 3.8*c* for N stores (*cf.* also Table 3.5).

Fig. 3.8*a* and *b* explore individual plot data for N stores in the humus layer in E55U and AN, and compare conditions in 1988 with a sampling made in 1975 (Popovic, 1977). For E55U, both samplings resulted in significant curvilinear relationships, which explain much of the variation. For E55AN, the last sampling alone resulted in a significant relationship (at the 5% level). However, it seems safe to conclude that addition of N has increased the N store in the humus layer in both E55U and AN. The difference between the two sampling dates seems plausible, considering that the ecosystem is in the aggrading phase of development (Bormann & Likens, 1979). However, small differences in the sampling procedure may well have affected the size of the difference.

For the mineral soil a single sampling exists, that in 1988 (Table 3.5), which is discussed in more detail at the end of Section 3. Here, we can only conclude that the increase in the N store, from N0 to N1, seems well established for both E55U and AN, but that most of the differences between N levels are non-significant.

Several authors have demonstrated a higher retention of urea-N in the soil, compared with ammonium N, in short-term experiments (Overrein, 1969, 1971; Nõmmik & Popovic, 1971; Nõmmik & Möller, 1981; Melin, 1986). Melin & Nõmmik (1988) indicated that high retention of urea in the soil was followed by a lower uptake of N by the trees during the duration of their experiment (two growing seasons).

Our study demonstrates only moderate differences between the N forms; however, neither the C/N ratios (Fig. 3.4) nor the data in Fig. 3.8 exclude the possibility of such differences in retention. A simple test for correlation between the amounts of N in the humus layer and mineral soil under different regimes, was therefore made (Table 3.3).

The result is not entirely convincing, perhaps because of the small number of plots. As might be expected from general considerations, there is a positive r value for no-N plots, but no statistical significance. The only significant value ($r = -0.63$; $p < 0.05$) in the table is that within N regimes in E55U; which might suggest that the more urea-N is retained in the humus layer, the less is retained in the mineral soil. There is no corresponding trend in E55AN.

The data were inspected for a possible influence of PK on N-sequestration or on the partitioning of added N between the two soil strata. There was no indication of an effect in either direction. To split the material further would result in very few degrees of freedom for each factor and, consequently, a small chance of obtaining conclusive results.

Thus we conclude from the soil N studies that the most obvious treatment effect on the amount of total N in the soil profile is that between N addition and no N. Smaller differences in effect between N levels, and between E55U and AN, are neither excluded nor demonstrated by our data. In the preliminary compilation of the data (Tamm, 1992; see also Högberg & Nohrstedt, 1992), a negative effect of PK addition on N retention appeared. However, when the differences in horizon masses (Fig. 3.5*e* and *f*) are taken into account, most of the effect can be explained by variations in mass. The hypothesis that the addition of PK should decrease N retention is supported only by the trends in C/N ratios, mentioned earlier (Fig. 3.4). Circumstantial evidence can also be found in the earlier discussion of treatment effects on acidity characteristics, where we noted an interaction N*PK in the effect on H^+ as well as on the N store (Table 3.2, AN, mineral soil).

Table 3.3. *Correlation coefficients (r) for the relationships between the amount of N in the humus layer (A_0) and mineral soil (0–20 cm) in experiment E55 Norrliden, 1988. The r values were calculated directly for the N levels (degrees of freedom n−2), while the values for the combined treatments concern 'within-treatment' correlation (degrees of freedom n−4)*

Treatments	No. of plots n	r
N0 ± PK	10	0.45
N1 ± PK	10	−0.20
N2 ± PK	10	−0.41
N3 ± PK	10	−0.50
N1−N3 U ± PK	15	−0.63*
N1−N3 AN ± PK	15	0.12

Ammonium N

Nitrogen addition increased the amounts of adsorbed ammonium ions in both humus layer and mineral soil (Table 3.2). Fig. 3.7*a* suggests that the curves for enrichment of the humus layer are of the diminishing-return type, while straight lines give an equally good fit for the mineral soil (Fig. 3.7*c*). However, as there is considerable between-plot variation (Fig. 3.10), too much weight should not be given to curve shape.

In the ANOVA test, the effect of PK addition on adsorbed ammonium (Table 3.2) is mostly negative, which is confirmed in Fig. 3.7*a* (humus layer), and for E55U in Fig. 3.7*c*. In E55AN (mineral soil), there was no significant PK effect in Table 3.2, and in the curves in Fig. 3.7*c*, the difference between ANPK and AN is positive.

The amounts of exchangeable ammonium in the humus layer had not increased much from 1975 (Fig 3.9) to 1988 (Fig. 3.10), There were also ammonium stores in the mineral soil (not studied in 1975). As some ammonium normally also occurs in forest soil profiles on unfertilised plots (Fig. 3.10), we cannot conclude that all ammonium ions on fertilised plots come from the addition. Since, however, control and fertilised differ by an order of magnitude, we may assume that the high values on plots with added N are either fertiliser ammonium or ammonium mineralised in an environment in which N turnover has been stimulated by N additions.

Nitrate N

The amounts of nitrate in the humus layer are virtually zero on no-N plots, but rise linearly with N additions (Fig. 3.7*b*). In the mineral soil, nitrate is also near-zero at N0 and low at N1, but rises steeply with higher regimes. Both quadratic and exponential functions were tested with

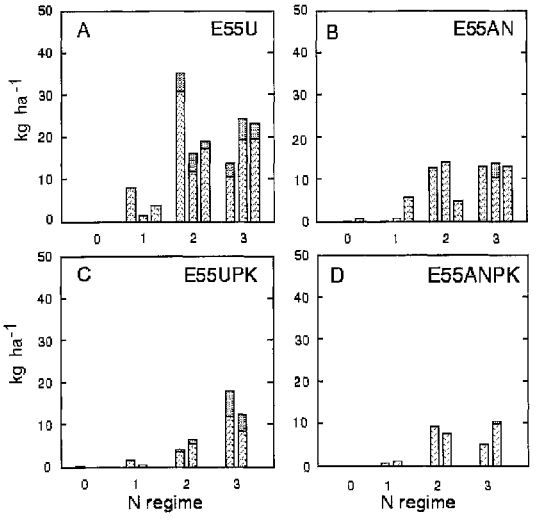

Fig. 3.9. Total amount of inorganic N in the laboratory (recalculated as kg ha^{-1}) in humus samples collected in September 1975 from differently treated plots of E55 Norrliden. Upper part of the bars: nitrate N. Accumulated N addition before sampling, 260 kg N ha^{-1} for N1, 520 for N2 and 780 for N3. (Data from Popovic, 1977.).

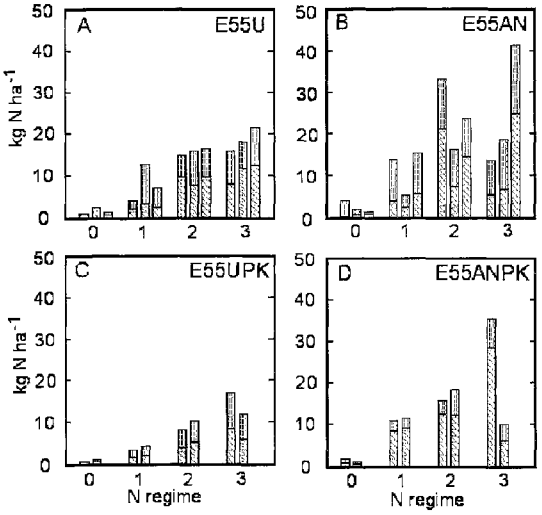

Fig. 3.10. Expt E55. Ammonium nitrate in humus layer (upper part of bars) and mineral soil 0–20 cm (lower part) at the sampling in June 1988. (A). U plots, (B) AN, (C) UPK, (D) ANPK. (Data from Tamm, 1991.).

equally good fits; the quadratic function has been used (Fig. 3.7*d*). For nitrate, too, there is considerable between-plot variation (Fig. 3.11).

The amounts of nitrate in the humus layer on N2 and N3 U plots were smaller in 1988 than in 1975, but traces of nitrate also occurred on N1 U plots, in contrast to 1975 (Fig. 3.11). N2

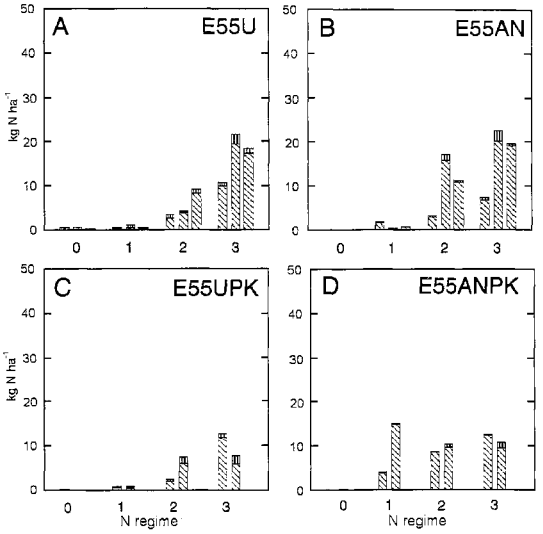

Fig. 3.11. Expt E55. Nitrate nitrogen at the sampling in June 1988. See legend to Fig. 3.10.

and N3 AN plots all contained nitrate, although in small amounts. In addition, all N2 and N3 plots—both U and AN—contained more nitrate in the mineral soil than in the humus layer. The two N1ANPK plots also contained nitrate in the mineral soil, but not in the humus layer.

Changes in soil biological activity, N turnover in particular

Incubation experiments

The traditional method of estimating changes in soil N turnover has been incubation experiments. However, incubation experiments, whether in the laboratory or in the field, are a type of model experiment in samples disturbed at least by cutting off roots, and often in other ways. The results should therefore not be accepted as showing what happens under undisturbed conditions, but may still provide useful information on potential biological activity in the soil (Romell, 1935). Some studies made using traditional incubation of samples from Expt E55 Norrliden (Popovic, 1977) are reviewed here. Incubation tests were also made on samples from experiments E57 Norrliden and E42 Lisselbo. These results are briefly reviewed, together with the direct information concerning the content of N fractions at Norrliden, which were discussed earlier but which are presented in greater detail in Fig. 3.9–3.11.

The incubation experiments with E55 samples

were carried out in the autumn of 1975 (Popovic, 1977), when the accumulated N additions amounted to 260 (N1), 520 (N2) and 780 (N3) kg N ha^{-1}. At the start of incubation, all samples from plots with no added N contained very small amounts of ammonium-N and virtually no nitrate-N (Fig. 3.9). At level N1, mineral N was somewhat higher, but was still present as ammonium ions only. At levels N2 and N3 in E55AN, mineral N was higher, and showed considerable between-plot variation. With a single exception, nitrate occurred in very small amounts. There was little difference between E55U and AN at level N1, but at levels N2 and N3, mineral N was higher in E55U, and the nitrate-N amounted to 15 and 24% of the total mineral N for treatments N2 U and N3 U, respectively.

According to Popovic (1977), the amount of mineral N had increased after six and nine weeks in samples from all plots with added N. The increase was higher in U samples than in AN samples. For levels N2 and N3, the proportion of nitrate-N was also higher than at the start, while the nitrate concentrations were close to or below the detection limit at level N1 for both types of fertiliser. In samples from the AN plots, only the sample from the N3 plot which had a higher initial value, contained a noteworthy amount of nitrate after nine weeks, and even then the amount was lower than that in any of the N2 U and N3 U urea plots.

We conclude from this study that the Norrliden humus offers a considerable resistance to nitrification, which agrees with conditions in other samples from boreal forests with low *p*H and a high C/N ratio. However, it is known that this resistance can be overcome by disturbances such as clearfelling or forest fire (Hesselman, 1926; Popovic, 1975) and by fertilisation, especially with urea (Overrein, 1971). It is thus interesting that 260 kg ha^{-1} urea-N (in four applications) was unable to induce nitrification in the Norrliden humus, while level N2 (520 kg ha^{-1}) appeared to be above the threshold value. In 1988, no incubation tests were made, but the small amount of nitrate on the N1 U plots suggests that the rate of nitrification there was still low, although the total amount of N added by then was 630 kg ha^{-1} (in 17 applications). Evidently, nitrification does not begin automatically when a certain threshold value of urea addition is exceeded. Presumably, both the timing of the application and the dose on each occasion play some part.

From Popovic's results, it is not possible to determine a threshold value for the induction of nitrification caused by applying ammonium nitrate. Of the five AN plots with regimes N2 and N2PK, incubation led to little or no nitrification in samples from four plots. The exception was one N2PK plot with measurable, but still low, nitrification in the 1975 incubations. In regimes N3(AN) with or without PK, samples from four plots either already contained traces of nitrate at the outset or formed small amounts of nitrate during incubation. The fifth plot contained some nitrate at the start (Fig. 3.9*b*), and the amount increased more than tenfold during nine weeks, although it did not attain the level found in N2 and N3 U plots (Popovic, 1977). The accumulated N addition in 1975 was 520 and 780 kg ha^{-1}, respectively. We conclude that the absence of nitrate from the humus layer of N1 AN plots in 1988 (Fig. 3.11) indicates that 630 kg N ha^{-1} had not yet induced appreciable nitrification in the humus layer.

Incubation tests from the Stråsan site (Expt E26A, Nilsson, Berdén & Popovic, 1988) confirm that nitrification can be induced by ammonium nitrate fertilisation, although the amounts of nitrate measured after six weeks' incubation were also relatively small in the N2 regime.

Further short-term incubation experiments were carried out on samples from the acidification-liming experiments E57 Norrliden and E42 Lisselbo (Popovic, 1984; Tamm & Popovic, 1989). The primary goal of these studies was to reveal possible effects of experimental changes in soil acidity, but comparisons can also be made between controls and plots treated with N2PK. On the whole, these studies confirm that the mor layer from both sites offers a considerable resistance to nitrification, which can, however, be induced by fertilisation, especially in combination with liming. As in E55 U and AN, large differences in nitrification rates were found between samples from duplicate plots, which further emphasises that we do not yet possess full insight into the processes which induce nitrification. It should also be mentioned that the N2PK treatment decreased soil respiration in experiment E57 (Popovic, 1984).

Persson, Wirén, Andersson & Gahne (1989) carried out long-term incubation experiments with humus samples from E57 Norrliden, to study effects of experimental acidity changes on carbon and N mineralisation. However, their study also allows comparisons to be made between treatment N2PK and Control and N2PKLime with Lime only. It is clear that N2PK depressed CO_2 release during the whole experimental period (290 days). Lime increased CO_2 release, but only initially, while acidification decreased it, though less than fertilisation. The effect of N2PK on N mineralisation was strongly positive at the beginning of the incubation, where no lag period appeared, as is otherwise normal in incubated mor humus. However, the effect changed to negative at the end of incubation. Lime (without N2PK) had a clear, negative effect on the amount of mineralised N, strongest initially. The effect of acid on N mineralisation was small and was not tested statistically, but had a positive sign and was most pronounced in the middle of the incubation, after the end of the lag period mentioned above.

Amount and distribution of ammonium and nitrate in the soil in Expt E55 U and AN

We have already discussed the occurrence of exchangeable ammonium and nitrate in humus layer and mineral soil as influenced by treatments (Table 3.2, Fig. 3.7). These data can also provide some information on N dynamics, especially if they are studied in detail and combined with information from other sources. Detailed data, for individual plots, are supplied in Fig. 3.9–3.11.

In E55U we can assume that virtually all nitrate present was formed by nitrification. In E55AN we cannot exclude the possibility that part of the nitrate in the mineral soil is a residue from the previous fertilisation (one year earlier). Nõmmik & Möller (1981) applied ammonium nitrate (150, 300 and 600 kg N ha^{-1}) on 10 July 1974. At a sampling in autumn 1974, nitrate was found in the soil at the two higher rates, mainly in the mineral soil and in amounts corresponding to about 10% of the total amounts of N applied. In the spring of 1975, most of this nitrate had disappeared, but at the highest rate (600 kg ha^{-1}) 5 kg was still present, half of it in the horizon 5–15 cm. Since leaching is driven by highly variable hydrological processes, large between-year variation can be expected. However, with the addition rates used at Norrliden, we would expect the amounts of remaining fertiliser nitrate to be small a year after addition.

The question remains whether it is possible to fit the data reviewed above, into a coherent pattern. To be able to do this, we must use other known facts about N uptake and leaching in boreal forest soil.

The rapidly increasing amounts of nitrate in the mineral soil when the level N1 is exceeded (Fig. 3.11), can be interpreted as symptoms of N excess. Nitrate is only weakly adsorbed to soil colloids (in acid soils), and most of the absorbing plant roots and their mycorrhizal hyphae occur in the humus layer or just below it (Persson, 1980). In addition, many plants, among them many of the species characteristic of the boreal forest, appear to prefer ammonium-N to nitrate-N when both are available (Ingestad, 1973; Lee & Stewart, 1978). We therefore suspect that a large part of the 5–20 kg ha^{-1} of nitrate N in the mineral soil in regimes N2 and N3 will leave the ecosystem with the percolating water, as will much of the nitrate from the 1988 application (added shortly after the sampling). The nitrate present in the mineral soil (but not the humus layer) of the two N1PK AN plots does not really contradict this hypothesis, as we have earlier discussed evidence for a more rapid leaching of added ions, both cations and anions, from the humus layer when PK has also been added.

Berdén, Nilsson & Nyman (1997), in lysimeter studies in the optimum nutrition experiment E26A Stråsan, found no nitrate leaching during 1987–1990 from treatment N1, but treatment N2 regularly lost some nitrate. After the spruce stand was felled in 1989–1990, leaching from N2 increased dramatically, but N1 lysimeters also showed nitrate leaching.

Very small amounts of nitrate were found in soil water during 1990–1991 by Andersson *et al.* (1995) in an experiment in a spruce forest in south Sweden, which had been supplied with 3*200 kg N ha^{-1} in three additions, in 1976, 1980 and 1985.

Apparently, a forest soil may immobilise large amounts of N, even of urea, despite the fact that urea stimulates nitrification under certain cir-

cumstances (*cf.* Popovic, 1977, 1984, 1985). Detailed data on the retention of fertiliser N have been reported by Melin (1986) from an experiment with ^{15}N-labelled urea, calcium nitrate and ammonium nitrate. Melin found that a large fraction of the added urea was immediately retained in the organic layer and top mineral soil (0–5 cm) as exchangeable ammonium ions, but was later transferred to non-exchangeable form and (to a small extent) to nitrate. In Melin's study, no evidence was found for leaching of fertiliser N from applied urea, and 87% of the added urea N could be accounted for in the ecosystem after two growing seasons. Eight per cent was estimated to have disappeared as gaseous ammonia. When N was applied as ammonium nitrate or calcium nitrate, labelled fertiliser N rapidly appeared in lower horizons.

Studies of nitrate reductase in leaves

Nitrate reductase (NRA) is an enzyme present in plant tissues in concentrations related to the concentrations of nitrate to which the cells have been exposed. In plants which have efficient nitrate reduction in the roots, aboveground tissues will contain very low concentrations (unless they are exposed to atmospheric nitrate or NO_x), but in many plants, a large part of the nitrate reduction takes place in connexion with photosynthesis. A common forest species with aboveground nitrate reduction is the grass *Deschampsia flexuosa* (L.) Trin. Leaves of this grass at Expt E55 Norrliden were used by Högberg *et al.* (1986) for a bioassay on the occurrence of nitrate in the soil. The results are given in Table 3.4.

Control plots show low values of NRA as measured by NO_2 reduced under standardised conditions (Table 3.4). Samples from all plots with regimes N2 and N3 show more than twice the activity of those from control plots. This is the case for N1AN, too—not surprisingly, since the AN plots hade received nitrate earlier in the summer. However, the most interesting point is that regime N1U did not show elevated enzyme activity. This may be taken as evidence that nitrification on these plots was so low in July 1985 that no appreciable amounts of nitrate entered the roots of *D. flexuosa*, a well-known 'nitrate plant', assumed to be favoured by the presence of nitrate. These results agree with our conclusions from the incubation tests ten years earlier, reported above. The lack of mineral soil acidification at level N1 U (Fig. 3.2) may also be taken as indicating a lack of nitrate, which is of interest in connexion with 'mobile anions' as the mechanism for the downward transport of acidity (p. 28).

Table 3.4. *Average nitrate reductase activity (NRA, μmol NO_2 g^{-1} h^{-1}) and range of activity (n=3), in Deschampsia flexuosa on plots at Norrliden, Expt E55 and, for lime, E57. For treatments, see Tables 2.2 and 2.4. From Högberg* et al. *(1986)*

Treatment	NRA	Range
Urea blocks		
Control	0.18	0.15–0.22
N1	0.20	0.18–0.21
N2	0.55	0.49–0.59
N3	0.61	0.55–0.62
Ammonium nitrate blocks		
Control	0.21	0.15–0.28
N1	0.51	0.44–0.56
N2	0.62	0.47–0.82
N3	0.63	0.58–0.70
Lime (Expt E57)	0.23	0.20–0.26

It is noteworthy that NRA activity was not elevated on limed plots (in Expt E57), in spite of the common belief that liming induces nitrification. The lack of NRA activity may have been connected with the high C/N ratio in the humus layer. (Popovic, 1984; Nõmmik, 1978).

A later study by Högbom & Högberg (1991), comprising samplings from spring, summer and autumn, showed that the mean NRA activity in *D. flexuosa* leaves in 1989 was related to the N regime, with a doubling from the background level (N0) to N1 and a further doubling at N3. Values at level N2 were more scattered than those at the other levels, and there were only small differences between urea and ammonium nitrate. These results agree in principle with those in Fig. 3.11, which show that very small amounts of nitrate occurred in the humus layer on N1 urea plots in the early summer of 1988, but from which we concluded that the near-absence of nitrate in the mineral soil indicated that there was little or no downward movement of nitrate, and in any case, far less than on all other N-fertilised plots, including N1 ammonium nitrate. The difference between the two NRA samplings, with N1 U plots having a

somewhat elevated NRA acitivity in 1989 but not in 1985, may reflect random between-year variation, but we cannot exclude the possibility of an increasing trend, ultimately approaching N saturation.

N isotope studies

In several papers, Högberg and his co-workers have reported studies of the ratio between the two natural N isotopes ^{14}N and ^{15}N on our plots. This method is based on the tendency for several biological processes that cause N losses (nitrification, denitrification, also non-biological volatilisation of ammonia from urea) to discriminate against the heavier isotope ^{15}N, which is thus enriched in the ecosystem. N fertilisers normally have ^{15}N values close to that of atmospheric N, since manufacturing processes discriminate much less between the isotopes than do the biological processes mentioned.

Analyses of stored needle samples from Expt E55 (Högberg, 1990, 1991), indicate an increase in ^{15}N with increasing N regime, particularly in regime N3U, where the values differed significantly from the control by 1975, and remained different until the last sampling (1989). For N3AN, only the two latest samplings (1985 and 1989) deviated significantly from the control. For regime N1, both N forms appeared to decrease ^{15}N temporarily, with a recovery at the last sampling. The interpretation (Högberg, 1990, 1991; Högberg, Johannisson, Högberg, Högbom, Näsholm & Hällgren, 1995) is that considerable amounts of N have been lost from the system under regime N3 (both AN and U), and under regime N2. The rise in ^{15}N under regime N1 might be explained as boundary contamination from 'high-N' plots to 'low-N' plots. There is a good correlation between isotope ratios in pine needles and *D. flexuosa* leaves from the same plots, although the grass shows consistently higher ^{15}N values, possibly because it satisfies a larger proportion of its N demand from nitrate than does pine (Högberg, 1991). In urea-fertilised plots, there are more processes at work which discriminate against the heavier N isotope, *viz.* volatilisation of ammonia on urea hydrolysis and later nitrification, while only half of the ammonium nitrate can be nitrified. Nitrate leaching is not a strongly discriminatory process.

Högberg & Johannisson (1993) also relate their ^{15}N values to calculated N losses from individual plots.

Further isotope abundance studies were reported by Högberg, Johannisson & Hällgren (1993), where ^{13}C abundance was used as an indicator of drought stress, most apparent in dry years on N-fertilised Lisselbo plots (with more needle biomass than the controls). Högberg *et al.* (1995) presented further data on changes in both ^{15}N and ^{13}C abundance at the sites Norrliden, Lisselbo and Stråsan for periods of 20 years or more.

Soil changes in N as part of an ecosystem budget: discussion

Balance sheets can be constructed for the elements listed in Tables 3.1–3.2 from our data, but for most elements they will be very incomplete, since most soil data concern exchangeable ions, and we have inadequate information about the transfers of ions between the exchangeable pool and other pools in the soil.

Here we shall concentrate on soil N budgets. The budgets will be partial only, because leaching and volatilisation have not been studied and uptake by trees cannot be discussed before we have presented data on biomass and its chemical composition. In this section we shall compare added fertiliser N and the excess of N on fertilised plots over that on no-N plots at the soil sampling in June 1988, designated as 'the formal recovery' in Table 3.5.

Before results are presented, a possible source of error must be mentioned. Högberg (1991), in his studies of N isotope ratios within different treatments at Norrliden, found evidence of some contamination between plots. Presumably pine roots from 'low-N plots' have grown into 'high-N plots'. The effects cannot be dramatic, since the foliar levels of N are still well separated (Section 4), and the vegetation boundaries between control plots and fertilised plots are still distinct. However, any between-plot contamination will decrease the differences between controls and fertilised plots, making underestimates of the recovery of fertiliser N more likely than overestimates.

The basic data for the comparison are presented in Table 3.5, separately for Expts E55U and AN for N regimes, for two soil strata (humus layer and mineral soil 0–20 cm). Humus-layer data for 1975 from Popovic (1977)

Table 3.5. *Total amounts of N (kg ha^{-1}) added by fertilisation and found in humus layer and upper mineral soil (0–20 cm) in different N regimes, Expts E55U and AN Norrliden. Samplings in September 1975 and June 1988. Standard errors of the mean of five plots are given below each value. Formal recovery of fertiliser N, % of added, is shown in bold type*

	Nitrogen regime							
	N0U	N1U	N2U	N3U	N0AN	N1AN	N2AN	N3AN
N added 1975	–	260	520	780	–	260	520	780
1988	–	630	1260	1890	–	630	1260	1890
Amount in humus layer 1975	288	382	404	368	309	326	365	302
	±8	±14	±40	±30	±20	±16	±16	±18
Fertiliser N, % recovered 1975	–	**36**	**22**	**10**	–	**7**	**11**	**−1**
Humus layer 1988	322	491	556	590	340	520	442	412
	±30	±40	±36	±47	±55	±51	±44	±30
Fertiliser N, % recovered 1988	–	**27**	**19**	**14**	–	**29**	**8**	**4**
Mineral soil 1988	688	789	832	856	664	801	868	924
	±33	±46	±39	±71	±40	±34	±71	±22
Fertiliser N, % recovered 1988	–	**16**	**11**	**9**	–	**22**	**16**	**14**
Humus layer + mineral soil 1988	1010	1281	1388	1446	1004	1321	1310	1336
	±48	±22	±37	±62	±86	±54	±74	±40
Fertiliser N, % recovered 1988	–	**43**	**30**	**23**	–	**50**	**24**	**18**

are also included). The confidence intervals in Table 3.5 confirm what has been discussed earlier, *viz.* that the differences in N stores between controls and N-fertilised plots are well established (statistically significant except for N1AN–N0AN in 1975), but that most other differences between N levels lack statistical significance, if a *t*-test is applied (*cf.*, however, Fig. 3.8). It seems clear that the amounts of N do not increase much from regime N1 to N3, particularly not in the humus layer.

Consequently, the recovery percentages decrease rapidly with increasing N regime. Losses from the soil system increase in the same direction. The percentage recovery in the humus layer —the only stratum measured in 1975— was on average lower than that in 1988. However, it is always difficult to compare different soil samplings, since small differences in horizon delimitation may bias the results. Since we shall later discuss the fate of the N not recovered in our soil analyses, it may suffice here to recall that the initial annual applications of N were higher during this early period, than later (Table 2.2).

The data in Table 3.5 concern the average effect of N application as U or AN, but without regard to the presence or absence of PK applications. As was mentioned earlier, there is no convincing evidence for an influence of PK on N recovery (Fig. 3.5)

The low soil fertility of boreal forest has traditionally been associated with high C/N ratios in the organic matter (Dahl, Gjems & Kielland-Lund, 1967). In addition, the total amount of both N and organic matter is often low, particularly on dry sites (Tamm & Carbonnier, 1962; Lundmark, 1974). The effect of N addition, implying incorporation of more N in a larger amount of organic matter in both the humus layer and the mineral soil, might thus be interpreted as a very desirable development. However, most of this apparently positive effect has been achieved in regime N1, with a total addition at the time of sampling of 630 kg N ha^{-1}, and much of the N added in the higher N regimes appears to have been lost from the soil. Consequently, the building up of a higher soil fertility by large annual additions of N fertilisers is not a very efficient process. On the Norrliden site, it is not favoured by further amendments with PK fertilisers. We can neither confirm nor disprove the common belief that urea may be more efficient than nitrate-containing fertilisers in increasing the N store in the humus layer. The evidence for a difference is too weak (higher N stores in regime N2U and N3U than in N2AN and N3AN in Table 3.5). Furthermore, the experiment was not designed to evaluate U/AN contrasts.

One of the urgent environmental problems concerning the long-term effects of N deposition is the question of how much added N can be retained in a soil profile, often discussed in terms of 'critical load'. The mode of N application in our experiments is, of course, not fully

analogous with slow deposition from the atmosphere, which seldom creates high concentrations, until some sort of 'N saturation' is attained. We may expect more efficient N retention in the early phases of increased anthropogenic deposition, as witness the normally low nitrate leaching from undisturbed forest land (Grennfelt & Hultberg, 1986). Yet we can find no reason why the processes responsible for retention and leaching in an ecosystem should work in a fundamentally different way, depending on the origin of the N. We regard the increasing losses of N under the higher N regimes in our experiments as alarm signals, in the same way as increasing N losses in areas with high N deposition are alarm signals.

We have earlier noted other effects of N addition on the soil balance of other components (plant nutrients, acidity) with potential negative effects on forest growth, and shall return later to this subject.

4. Changes in plant nutrient levels related to N and PK regimes

Foliar nutrient levels

The data discussed here concern nutrient concentrations in current needles collected in autumn, sampled to follow changes in nutrient status of the trees ('diagnostic samples'). Autumn was chosen to avoid the rapid fluctuations in nutrient concentrations and dry mass during the growing season (Tamm, 1955; Leyton, 1958). The choice of current needles was based on earlier experience that the effect of N fertilisation on N in current and older needles was fairly similar (Tamm, 1956). We also wished to sample the same trees every year, to minimise between-tree variation as a major source of error (Tamm, 1956; Helmisaari, 1992*a*). Sampling of current shoots from the top of a tree instead of needles one year older, reduces the risk of damage to leading shoots and shoots suitable for sampling in a later year. However, sampling of one-year-old (C+1) needles has other advantages: visual symptoms and deficiency concentrations often show up better (Heiberg & White, 1951; Linder, 1995).

Between-plot variation in needle concentration of N was low in Norrliden before fertilisation began (Fig. 4.1*a–d*). The mean value for E55U in 1970 was 12.84 ± 0.01 and for E55AN 13.03 ± 0.04 mg N g^{-1} dry mass (DM).

Plots fertilised with ammonium nitrate increased their foliar N levels more rapidly than urea plots (1971–1974), but these differences were small from 1975 onwards.

Variation between years was considerable, and largely synchronised between experiments (E55 U and AN) and nutrient regimes: peak values for N occurred in 1975 in all treatments —including those without nitrogen—and minima in 1986 (followed by a new but lower peak in 1987).

The intention of establishing separated N levels in the foliage succeeded reasonably well,

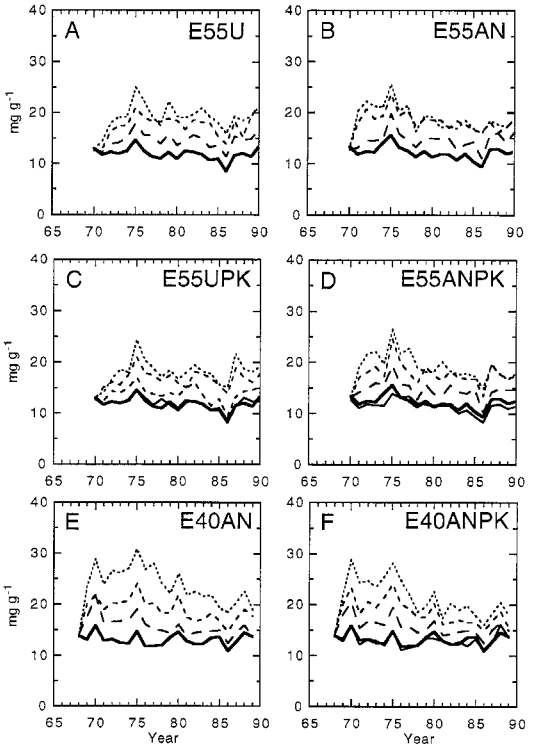

Fig. 4.1. N concentrations, mg g^{-1} DM, in exposed current pine needles sampled annually in autumn from the top of the crown, starting in 1970 in E55 and in 1968 in E40. (A) E55U. (B) E55AN. (C) E55UPK. (D) E55ANPK. (E) E40 without PK, (F) E40 with PK. Treatments without N: solid lines, heavy for control plot means and thin for PK plots. The heavy solid line for controls is repeated in diagrams showing PK treatments. Plots with added N are shown by dashed lines; shorter dashes with increasing N regime (*cf.* Figs. 3.2–3.3). There were three replicates in (A) and (B), two in (C) and (D), and four in (E) and (F).

although the curves for the regimes N2 and N3 touch or even cross each other in single years in some treatment groups.

Addition of PK fertiliser appears to have had little or no effect on the N concentrations—a phenomenon most easily visible in Fig. 4.1*c* and *d*, where the curves for NOPK plots can be compared with the curve for the means of all three control plots from E55U and AN, respectively, in Fig. 4.1.

Addition of N had similar effects in Expt E40 at Lisselbo, where only one form of N (ammonium nitrate) was used (Fig. 4.1*e–f*). The initial foliar N concentration (in 1968) was higher than in E55, 14.18 ± 0.14 mg g^{-1} DM, and more variable between plots, as is seen from the standard error. The total range within 32 plots was 12.3–15.9 in E40, compared with 12.0–14.0 within the 40 plots of E55U and AN.

The slowly decreasing trend in the curves for fertilised plots in E40 can be related to the lower level of N addition (N1 = 20 kg $ha^{-1}yr^{-1}$ from 1977 onwards; see Table 2.2). The between-year variation is considerable, and well synchronised between all treatments. The maximum concentrations of N, attained with regimes N3 and N3PK in 1970 and 1975, are *ca.* 30 mg g^{-1} DM, a value well above suggested optimum values for Scots pine (Ingestad, 1979; Ingestad & Kähr, 1985).

Information about variability in foliar levels of elements other than N between years and between treatments, is given in Figs. 4.2–4.6, containing material analogous to that in Figs. 4.1 for the elements P, K, Ca, Mg and Mn. For treatments without PK (Norrliden subdiagrams *a* and *b*, Lisselbo subdiagram *e*) there is considerable between-year variation in concentrations of these elements; at Lisselbo of P, K, Ca, Mg and Mn, at Norrliden especially in Ca, Mg and Mn. There is a tendency to parallel behaviour between at least lower N regimes and controls. Most of the diagrams also show a clear tendency for N addition to depress the concentrations of the other elements, both with rates of addition and with time. The maxima and minima in the between-year variation do not coincide with the N highs and lows, or between sites, and there are also differences between elements.

The subdiagrams for treatments with PK (Fig. 4.2–4.6*c*, *d* and *f*), show additional variation in P and K levels, which can be related to the PK additions (Table 2.2). For much of the time, concentrations of P and K are highest in either regime N0PK or N1PK. PK fertilisation has partly compensated for the depressive influence of N additions on the foliar levels of P and K. For Ca, Mg and Mn, there are small signs only of fertiliser effects, other than the depressive influence of N. The limited amount of Ca added with the PK fertiliser (Table 2.2) has raised the foliar Ca levels on the N0PK plot in E55U and E40 (Fig. 4.4*c* and *f*).

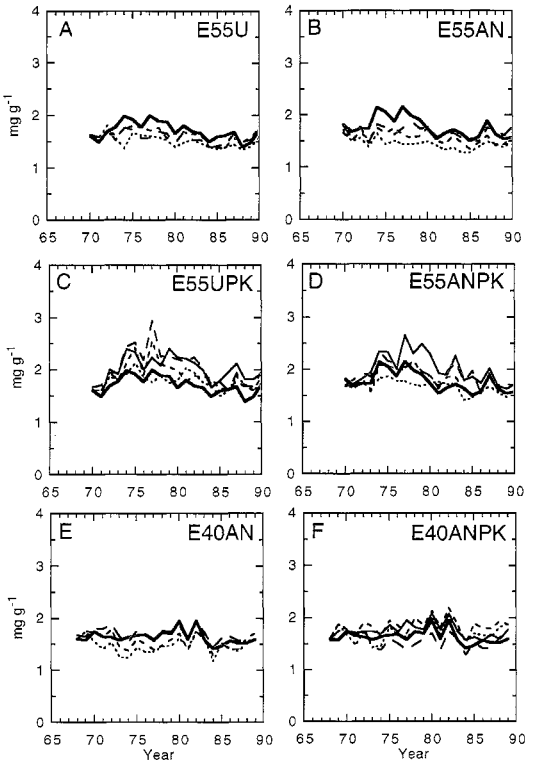

Fig. 4.2. P concentrations, mg g^{-1}, in the same samples as in Fig. 4.1. (See legend to Fig. 4.1).

Since one of the aims of our experiments was to study tree growth in relation to nutrient status, and since foliar analysis was used as a method for studying nutrient status (see Section 1), in Table 4.1 the data in Fig. 4.1 were condensed to a table with means for two growth periods (different periods for E55 and E40), coinciding with periods for which tree growth data are available. For individual plot data on all six elements analysed, see Aronsson *et al.* (1999).

In agreement with Ingestad (1987), we consider ratios of elements to N as often more

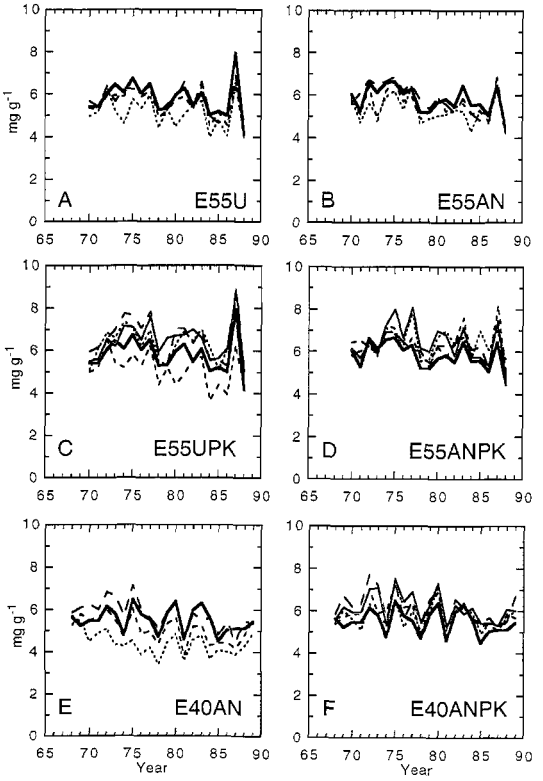

Fig. 4.3. K concentrations, mg g^{-1}, in the same samples as in Fig. 4.1. (See legend to Fig. 4.1).

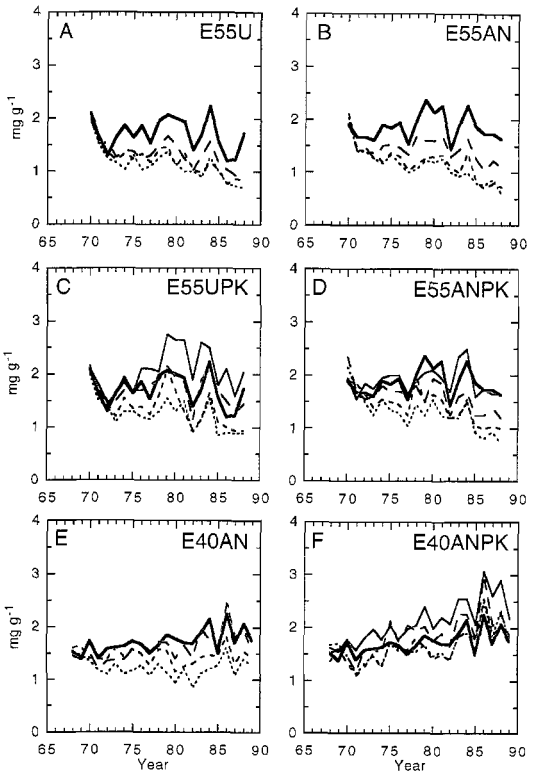

Fig. 4.4. Ca concentrations, mg g^{-1}, in the same samples as in Fig. 4.1. (See legend to Fig. 4.1).

informative than concentration data for elements, and therefore we present in Table 4.2 values for P/N, K/N and Mg/N for the same periods as those selected for Table 4.1, and for E55U, E55AN and E40. These three elements were considered the elements most likely to limit tree growth on our sites, had the N demand been satisfied. In Table 4.2 'target values', suggested by Linder (1995) are listed; these are a modification of Ingestad's ratios for use in field experiments.

To summarise the results of the foliar analyses as expressed in Figs. 4.1–4.6 and Tables 4.1 and 4.2, we may draw the following conclusions, element by element:

Nitrogen

N levels have been almost doubled in regime N3, N1 and N2 being intermediate. Compared with the first period, levels were slightly lower during the last period, a difference which can be related to the lower addition rates during the latter. Despite lower N additions at Lisselbo from 1977 onwards (Table 2.2), N concentrations tend to be higher there than in corresponding treatments at Norrliden. There is no sign that PK addition has influenced foliar N levels. The range of N levels created covers reasonably well the range from deficiency to sufficiency found in laboratory experiments with *Pinus sylvestris* (Ingestad, 1979; Ingestad & Kähr, 1985), although it is clear that conclusions based upon nutrient concentrations expressed as mg g^{-1} DM on one occasion during the year have a lower information content than those from a time series with seasonal samplings (Linder, 1995).

Phosphorus

High N additions tend to depress P levels and P/N ratios, but this is largely compensated for by the PK treatment. All P values exceed those described as deficiency levels for *Pinus sylvestris* (*cf.* Ingestad, 1979), even if the values for treatments N2, N3 and N3PK fall below Linder's target values.

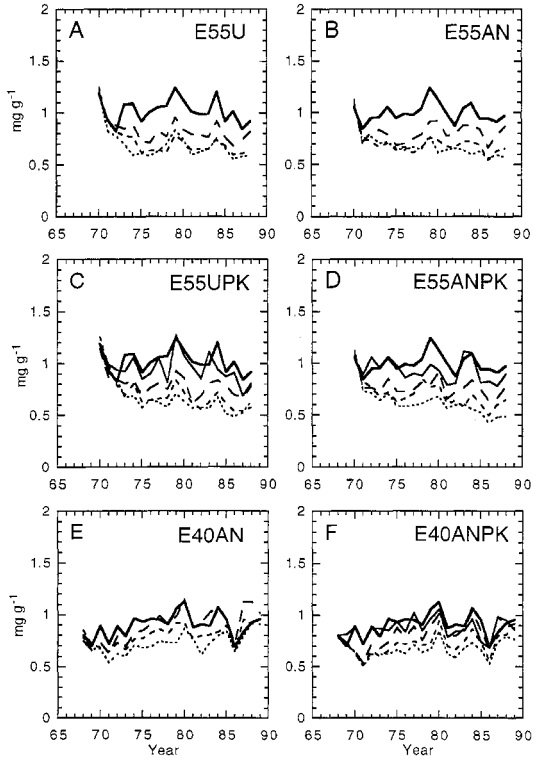

Fig. 4.5. Mg concentrations, mg g^{-1}, in the same samples as in Fig. 4.1. (See legend to Fig. 4.1.)

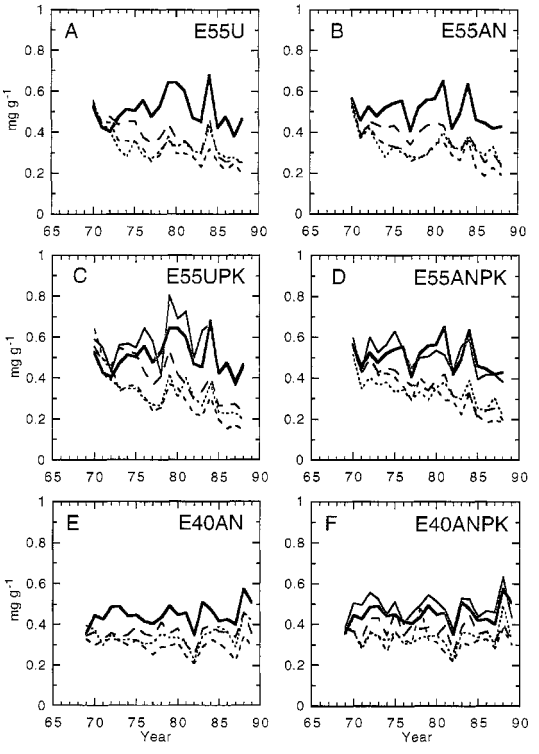

Fig. 4.6. Mn concentrations, mg g^{-1}, in the same samples as in Fig. 4.1. (See legend to Fig. 4.1.)

Potassium

This element behaved very similarly to P, except that the lowest level at Lisselbo, 4.2 mg K g^{-1} DM in regime N3, falls within the accepted deficiency range. The lowest mean value for a period is 4.9 mg g^{-1} DM at Norrliden and 4.2 at Lisselbo (Aronsson *et al.*, 1999). However, in some years, treatment means below 4.0 were found at Lisselbo and down to 4.2 at Norrliden. On both sites, treatments N2 and N3 fell clearly below the target values, and this was also found for N2PK and N3PK at Lisselbo, whereas the same treatments at Norrliden are closer to the target values but never exceed them. As with the P/N ratio, Lisselbo has somewhat lower K/N ratios than Norrliden, particularly during the first observation period (Table 4.2). It may seem surprising that visual symptoms of K deficiency were not observed on pine. However, twigs from the upper crown were not closely inspected, except at autumn samplings. At that season, the needles had usually already assumed the yellowish winter-colouring typical of northern provenances of Scots pine. Deficiency symptoms may have occurred on lower branches earlier in the season, but since most plots with a low K/N ratio were those which had grown well initially, and had dense crowns, visible symptoms, if they occurred, escaped us.

Table 4.1. *Nitrogen concentrations in exposed current needles in different nutrient regimes in Expts E40 Lisselbo and E55 U and AN Norrliden. Values are treatment averages over two periods, corresponding to stand measurement periods. All values given as mg g^{-1} DM*

Nutrient regime	E40 Lisselbo 1969–1976	E40 Lisselbo 1977–1988	E55U Norrliden 1971–1978	E55U Norrliden 1980–1988	E55AN Norrliden 1971–1978	E55AN Norrliden 1980–1988
N0	13.2	12.9	12.2	11.3	12.9	11.5
N0PK	13.2	12.8	12.6	11.2	12.3	10.8
N1	17.7	14.7	14.8	14.1	15.1	14.3
N1PK	17.3	14.9	14.3	13.3	15.5	13.9
N2	20.8	18.0	17.6	17.0	19.7	17.5
N2PK	21.0	17.3	17.2	16.6	18.7	17.1
N3	26.7	22.4	19.4	18.8	21.0	17.6
N3PK	25.3	19.3	18.9	18.0	21.6	17.9

Table 4.2. *Element-to-N ratios for P, K and Mg in Expts E40 Lisselbo and E55 Norrliden, compared with 'target values' recommended by Linder (1995) for Picea abies. The target value for N concentration used by Linder is 18 mg g^{-1} residual ('structural') dry mass, a figure which can be approximately converted to mg g^{-1} total dry mass by a decrease of 10% (for seasons without starch accumulation). Measuring periods as in Table 4.1*

Expt	E40		E55U		E55AN	
Treatment	1969–1976	1977–1988	1971–1978	1980–1988	1971–1978	1980–1988
			P/N ratio (Target value 10% of N)			
N0	12.4	12.6	14.8	14.2	14.9	14.3
N0PK	13.0	13.8	16.3	17.6	17.4	17.7
N1	9.7	11.4	11.2	11.8	11.3	11.4
N1PK	10.8	12.5	15.7	14.3	13.2	13.1
N2	7.7	8.4	9.7	9.1	8.3	8.6
N2PK	8.7	10.8	12.0	10.6	10.3	10.0
N3	5.4	6.6	8.3	7.5	7.1	7.9
N3PK	6.5	9.1	10.0	9.7	8.1	9.0
			K/N ratio (Target value 36% of N)			
N0	42	42	50	50	47	49
N0PK	48	47	52	58	55	58
N1	34	34	40	39	43	38
N1PK	38	40	49	48	41	45
N2	26	26	33	32	29	31
N2PK	30	34	32	36	34	36
N3	17	19	28	26	26	29
N3PK	23	30	35	36	30	36
			Mg/N ratio (Target value 4.1% of N)			
N0	6.5	7.2	8.1	8.9	7.5	8.6
N0PK	6.4	7.0	7.4	8.1	7.7	8.3
N1	4.3	6.7	5.6	5.6	5.0	5.7
N1PK	4.2	5.9	5.6	5.6	4.9	5.4
N2	3.5	4.7	4.2	3.9	3.5	3.8
N2PK	3.1	4.3	4.3	3.7	3.9	3.7
N3	2.4	3.4	3.5	3.4	3.3	3.5
N3PK	2.5	3.6	3.7	3.2	3.0	3.1

Calcium

Foliar concentrations are depressed by N additions and increased somewhat by PK fertilisation. In this case, the lowest levels occur in regimes N2 and N3 at Norrliden, 1.0 mg Ca g^{-1} DM. However, such low Ca concentrations in *Pinus sylvestris* needles are not uncommon.

Magnesium

Foliar concentrations were depressed by N fertilisation, particularly at Norrliden, where the values for regimes N2 and N3 suggest Mg limitation. The PK treatment does not appear to affect the Mg concentrations. Concentrations in treatments N2, N3 and N3PK are below the target values, together with some of the N2PK values. The difference between the two sites is small. We did not observe distinct symptoms of Mg deficiency on the pines, probably for the same reason as for K. However, in September 1992, several understorey spruce on plots under regimes N2PK and N3PK showed typical symptoms of Mg deficiency (Plates VII and VIII).

Manganese

As was the case with Mg concentrations, those of Mn were depressed by N fertilisation and unaffected by PK addition. There is little difference between Norrliden and Lisselbo. Concentrations of Mn are far above known deficiency levels (Ingestad, 1958).

Needle concentration data from the acidification experiments E57 Norrliden and E42 Lisselbo (Tamm & Popovic, 1989) confirm the results from E55 and E40, when controls and N2PK plots are compared.

Nutrient levels in other tree components

The selection and harvesting of sample trees are described in Section 2, where also the background to some assumptions in our estimates is described, unsuitable weather conditions having

led to the destruction of needle and branch samples intended for chemical analysis. There were also differences between E55U and AN in sample tree selection, sample trees being taken from more treatments in E55U (but only two trees from each plot were sampled), whereas more trees were sampled from fewer treatments in E55AN (sample trees representing four diameter classes on each plot).

The composition of the stem and wood samples was unaffected by the warm weather, and will be discussed first. Together with other samples from the optimum nutrition experiments, the stem samples are unique in that most of the wood and bark was formed during a long period of controlled nutrient regimes.

Estimated needle and branch values, calculated from the 'diagnostic needle values' (subsection above) and biomass data from a sampling in E57 in 1987, are then presented. Finally, results from an early biomass sampling in E40 Lisselbo are reviewed. In the last subsection, the chemical composition of vegetation other than trees is briefly discussed (data from Aronsson *et al.*, 1999).

Variation with treatment of element concentration in wood and bark in experiment E55

Nitrogen concentrations in the stems increase with increasing N regime (Table 4.3 and Fig. 4.7*a* and *b*) for wood and bark. No significant effect of PK on N concentrations is visible in these data, and the same applies to the form in which N was applied. Quadratic equations for wood and bark concentrations, as a function of N regime, give a better fit than a straight line, but the difference is small, especially for stemwood.

Bark concentrations are in most cases 6–8 times higher than wood concentrations, but run parallel to them, with a tendency to culminate in regime N2 (Table 4.3, Fig. 4.7*b*). We expected a good correlation between wood and bark concentrations of N, and the relationship is statistically significant; however, the linear regression explains less than 60% of the variation (Fig. 4.7*c*).

Phosphorus concentrations in both wood and bark increase almost parallel with N concentration in the N regimes and are slightly increased by the PK treatment, but appear unaffected by the form of N (Table 4.3).

Potassium concentrations vary similarly to those for P, even if there is little or no difference between N0 and N1, nor between N2 and N3 (Table 4.3).

Calcium concentrations in wood appear to be unaffected by the treatments, although bark values are slightly higher with both PK and AN. Since variation in Ca concentration with N regime appears to be rather irregular (Table 4.3), no firm conclusions can be drawn. Mn concentrations in stemwood are low in the rapidly growing trees from regimes N1 and N2, but apart from that, neither Mg nor Mn concentration appears to be related to the treatments (Table 4.3).

Chemical analyses of biomass fractions were mainly intended for calculating nutrient distribution in the stand, and ultimately, in the ecosystem, see Sections 6 and 7 below. However, simple multiplication of dry masses by concentrations could be misleading, if element concentrations depend on tree size. Mean tree sizes differ in different nutrient regimes (see Section 5). Because chemical variation with tree size is interesting in itself, and is seldom possible to study over a range of nutrient regimes, Aronsson *et al.* (1999) made a study of this possible source of error. Their conclusion was that only a minor part of the variation in wood and bark concentrations of nutrients could be accounted for by tree size. For wood, concentrations of N, P, K, Mg and S were positively related to tree diameter (r values between 0.26 and 0.38). At least for N, the 'size effect' can be considered a treatment effect, as N addition increased tree growth and N uptake at the same time. In a multiple regression analysis with wood N concentration as dependent variable, tree diameter gave no significant contribution, if (N *regime*) and (N *regime*)^2 were among the independent variables. In bark, where also microelements were analysed, all significant correlations (for Ca, Fe, Al and Cu) were negative, with r values values between -0.33 and -0.50.

To summarise the results of the wood and bark analyses, we consider that the concentration data (condensed in Table 4.3) form a good base for budget calculations (see Sections 6 and 7), without correction for concentration changes with tree size.

Table 4.3. *Element concentrations in stemwood and stembark from sample trees exposed to different nutrient regimes in Expt E55 1971–1984. In E55U, the tree of mean basal area was sampled from two plots from each treatment. Four trees were usually sampled from each of two E55AN plots, although some treatments were omitted. To give equal weight, as far as possible, to values from different treatments, the tree of mean basal area was used throughout, except for a few outlying values, where it was replaced by the mean of the next larger and smaller tree. −PK and +PK include plots with N regimes N0 to N3*

		Nutrient regimes							
		N0	N1	N2	N3	−PK	+PK	N as U	N as AN
		No. of plots							
Wood samples		8	6	8	6	16	12	12	8
Bark samples		8	8	7	7	16	14	11	11
		Concentration mg g^{-1} DM							
Element	Component								
N	Wood	0.68	0.90	1.09	1.20	0.97	0.94	1.04	1.10
N	Bark	4.48	5.78	7.72	6.86	6.24	6.19	6.85	6.74
P	Wood	0.06	0.08	0.10	0.11	0.09	0.09	0.09	0.11
P	Bark	0.71	0.72	0.80	0.72	0.69	0.79	0.76	0.74
K	Wood	0.58	0.58	0.66	0.63	0.56	0.68	0.62	0.63
K	Bark	2.72	2.50	2.86	2.78	2.44	2.98	2.77	2.66
Ca	Wood	0.62	0.62	0.63	0.64	0.61	0.65	0.62	0.64
Ca	Bark	3.80	3.02	3.68	3.16	3.33	3.47	3.20	3.46
Mg	Wood	0.16	0.17	0.18	0.17	0.17	0.17	0.17	0.18
Mg	Bark	0.62	0.61	0.64	0.65	0.66	0.61	0.63	0.64
Mn	Wood	0.12	0.09	0.09	0.14	0.11	0.10	0.10	0.12
Mn	Bark	0.26	0.20	0.23	0.27	0.24	0.23	0.22	0.24
S	Wood	0.06	0.08	0.10	0.09	0.08	0.08	0.08	0.10
S	Bark	0.40	0.44	0.56	0.45	0.44	0.49	0.49	0.47

Table 4.4. *Element concentrations in crown components (needles and branches) from different treatments of Expt E55 Norrliden. Values for needle concentrations were calculated from the regressions in Table 4.6, with the mean value 1982–1984 for diagnostic needle samples from different treatments as independent variable; branch concentrations were calculated in the same way, except that for P, where no significant regression was obtained in Table 4.6. Instead, P concentrations in Table 4.5 were used for treatments −PK and +PK; for the N levels, the mean of these two values was used. See text for details*

Element	Component	N0	N1	N2	N3	−PK	+PK
		Concentration, mg g^{-1} DM					
N	Needles	10.94	13.83	17.20	18.20	15.03	14.78
	Branches	2.47	3.04	3.71	3.91	3.33	3.23
P	Needles	1.51	1.48	1.45	1.42	1.42	1.49
	Branches	0.49	0.49	0.49	0.49	0.42	0.55
K	Needles	4.78	4.69	4.66	4.59	4.41	4.94
	Branches	1.86	1.83	1.82	1.80	1.74	1.91
Ca	Needles	3.81	2.65	1.84	1.72	2.25	2.77
	Branches	1.94	1.61	1.38	1.35	1.50	1.64
Mg	Needles	0.77	0.69	0.53	0.49	0.63	0.61
	Branches	0.40	0.38	0.33	0.31	0.36	0.35

Estimates of nutrient concentrations in crown components, using data from Expt E57

Chemical data for needles (other than the 'diagnostic samples' of current needles) and branches from E55 are lacking, due to weather conditions (see above). We therefore asked the question: To what extent can we use data from a tree sampling of E57 in 1987, partly from identical treat-

Table 4.5. *Nutrient concentrations (mg g^{-1} DM) in biomass fractions of N2PK fertilised trees (+) and control trees (−) from Expt E57 Norrliden, sampled in October 1987. Each vaue is the mean of five individual trees. Positive differences mean higher values in fertilised trees, negative differences lower values. Differences are also given in per cent of the control*

Treatment	Element	Needles C	All	Branches	Stembark	Stemwood
+	N	16.09	16.82	5.53	6.84	1.06
−		11.62	10.82	3.47	3.83	0.68
Difference		4.47	6.00	2.06	3.01	0.38
		***	***	***	**	***
%		**39**	**56**	**59**	**79**	**56**
+	P	1.750	1.604	0.547	0.682	0.098
−		1.921	1.416	0.424	0.548	0.068
Difference		−0.171	0.188	0.123	0.134	0.030
			*	**		***
%		**−9**	**13**	**29**	**24**	**44**
+	K	6.46	5.54	2.169	2.180	0.640
−		6.01	4.58	1.852	1.820	0.380
Difference		0.45	0.96	0.317	0.360	0.260
						**
%		**8**	**21**	**17**	**20**	**68**
+	Mg	0.636	0.539	0.483	0.430	0.164
−		1.049	0.851	0.461	0.498	0.170
Difference		−0.413	−0.312	0.022	−0.068	−0.006
		***	**	*		
%		**−39**	**−37**	**5**	**−14**	**−4**
+	Ca	1.27	2.26	1.469	2.580	0.620
−		1.79	3.45	1.826	2.760	0.600
Difference		−0.52	−1.19	−0.367	−0.180	0.020
		**	*			
%		**−29**	**−34**	**−20**	**−6**	**3**
+	Mn	0.262	0.450	0.169	0.176	0.098
−		0.418	0.828	0.232	0.172	0.102
Difference		−0.156	−0.378	−0.063	0.004	−0.004
		***	***	*		
%		**−37**	**−46**	**−27**	**2**	**−3**

Table 4.6. *Linear relations between nutrient concentration in biomass fractions and that in current needles in 22 sample trees from Expt E57, Norrliden, sampled in October 1987 from the treatments Control, N2PK, Acid 3, N2PKAcid 3, Lime and Lime + N2PK. Only statistically significant relationships are included*

Element	Biomass fraction	Intercept	Slope	r^2	*P* value
N	Needles	−0.95	1.052	0.89	0.0001
	Branches	1.20	0.208	0.38	0.0024
	Stembark	−1.76	0.508	0.74	0.0001
	Stemwood	−0.07	0.057	0.68	0.0001
P	Needles	0.92	0.323	0.20	0.038
K	Needles	1.22	0.608	0.68	0.0001
	Branches	0.64	0.213	0.29	0.0095
Ca	Needles	−0.71	2.319	0.79	0.0001
	Branches	0.66	0.664	0.46	0.0005
Mg	Needles	0.005	0.810	0.75	0.0001
	Branches	0.19	0.233	0.30	0.0064

Table 4.7. *Comparison of N concentrations in stemwood and stembark, analysed on sample trees from E55 (data in Table 4.3) and values of wood and bark concentrations estimated from regression on current needle concentrations in sample trees from E57 (Table 4.6). The treatment mean N concentration 1979–1989 in E55 was used as independent variable in the regression calculations. Values in mg g^{-1} DM*

	N0	N1	N2	N3
Wood N, analysed	0.68	0.90	1.09	1.20
Wood N, estimated	0.57	0.73	0.91	0.97
Difference, % of analysed	−16	−19	−16	−19
Bark N, analysed	4.48	5.73	7.73	6.86
Bark N, estimated	3.98	5.38	7.00	7.49
Difference, % of analysed	−11	−6	−9	9

Table 4.8. *Nitrogen concentration in aboveground stand fractions in Expt E40 at the sampling in spring 1975. All values in mg g^{-1} DM*

Fraction	Control	Nitrogen regime N1	N2	N3	N2PK
Stem wood	0.9	1.0	1.2	1.3	1.2
Stem bark	3.5	4.4	5.2	6.0	5.2
Branches	2.1	2.5	2.6	2.9	2.8
Needles	11.4	13.3	16.1	21.8	15.0
Dead branches	3.8	4.4	4.0	5.7	3.8

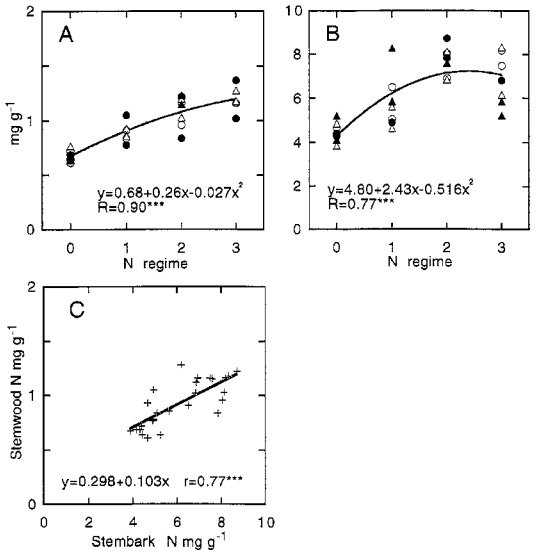

Fig. 4.7. N concentrations in stemwood and stembark from E55U and AN Norrliden. (A) Wood concentrations plotted against N regime. (B) Bark concentrations plotted against N regime. (C) Wood concentration plotted against bark concentration in the same tree. The regression lines were calculated for all analysed trees (28 for wood and 30 for bark), but in (A) and (B) different symbols have been used for different regimes: circles for U and triangles for AN; filled symbols for treatments with PK.

ments (Control and N2PK), first, to supplement missing data and secondly, to check the representativeness of our E55 results?

Aboveground biomass was sampled in October 1987, and comprised a large number of sample trees from six of the ten treatments in E57. The results were reported as component masses and amounts of seven elements per hectare by Popovic (1990/1991). He concluded that there were treatment effects (of acidification, liming and N2PK fertilisation) on element concentrations, but that the amounts of most elements mainly followed the dry masses. For N, the markedly higher concentrations in N2PK-treated plots contributed to the 'recovery' of fertiliser N (see Aronsson *et al.*, 1999).

From the concentration data underlying the diagrams published by Popovic, data for the two treatments identical with those occurring in experiment E55, *viz.* control and N2PK, were selected. Five sample trees were taken from each of these treatments, one mean basal area tree from each of three replicate plots, and from one of the plots, one smaller and one larger tree. The detailed data from these trees have been condensed in Table 4.5 to the same biomass components as used in the calculations for biomass in experiment E55.

These data confirm several of the conclusions drawn earlier, *e.g.* the generally positive effect of fertilisation on N concentrations in all studied components, and the depressive influence on foliage concentrations of elements not added (Mg, Mn) or with small additions with the fertiliser (Ca). For P and K there are two competing influences: a dilution, because of increasing growth, and a direct influence of the addition of these two elements. The direct fertiliser influence seems to dominate in older tissues—especially in P—while the differences between control and fertilised trees are smaller in the current needles.

The next step was to investigate relationships between the chemical composition of current foliage and the other components: all needles, branches, stembark, and stemwood. For this purpose we used all 22 sample trees from E57, *i.e.* also trees from some limed and acidified plots. The statistically significant correlations found are listed in Table 4.6. From scatter diagrams we concluded that there was no reason to test for curvilinear relationships.

For N, the relationships are significant ($p<0.01$) for all four fractions, but for branches only 38% of the variation in concentration can be explained from the variation in current needle concentrations (Table 4.6). In Scots pine, current needles make up a considerable proportion of the foliage during the dormant season (Flower-Ellis & Persson, 1980), so it is not surprising that between current needles and all needles there is a relationship close to 1 : 1, with a small intercept and an r^2 value of 0.89. We take this as indicating that variation in N concentrations in the crown is moderate, and that

we shall not be too far from the truth if we use the relationship in Table 4.6 for calculating the N concentration in the all-needle fraction of sample trees in E55, from our diagnostic needle samples (Table 4.4). Helmisaari (1992*a*) found little or no difference in concentration between top-branch needles and total needles, except in Al. The same author found little or no influence of needle age on the concentrations of mobile nutrients (N, P, K, Mg) in a mature pine stand, while these nutrients decreased with age in a sapling stand and a pole-stage stand. In this last stand, the N concentration in current needles of 1983 decreased from 13.1 mg $N\,g^{-1}$ DM in September 1983 to 10.1 in September 1984 and to 9.1 in September 1986. The other mobile nutrients behaved similarly, while immobile elements, such as Ca, Mn and Fe, increased with age, a well-known phenomenon. We take Helmisaari's results as supporting our approach of using regressions between current needles and total needles, but the 1 : 1 relationship discussed above should apparently not be generalised.

For P concentrations, only the relationship between total and current foliage was statistically significant ($p < 0.05$), and this regression explains only 20% of the variation (Table 4.6). Despite the low r^2 value, we have used the regression for calculating total foliage P concentrations, as we consider that the low r^2 is partly caused by the small range of variation between fertilised and unfertilised trees for P in Table 4.5, compared with other elements. Helmisaari (1992*a*) also found remarkably low variation in P concentrations between needles from different positions or of different ages. For branch P concentrations, we are limited to using the value 0.424 mg $P\,g^{-1}$ DM for trees not fertilised with P (Table 4.6) and 0.547 for trees fertilised with P. This procedure will probably give too high P concentrations for plots given high N but no PK, and too low values for plots given no N but PK, since no account is taken of the depressive effect of high N levels on P concentrations, visible in the current foliage (Fig. 4.2). However, the errors are probably not very large, considering the small effects of fertilisation with P on phosphorus concentrations in stemwood, and only slightly greater influence on stembark (Table 4.3). N addition appears to increase wood concentrations of P somewhat, but scarcely affects bark P concentrations (Table 4.3).

For the elements K, Ca and Mg there were statistically significant relationships between the concentrations in total needles or branches on the one hand, and current needles, although the degree of explanation varies between 19% (K in branches) and 79% (Ca in total needles, Table 4.6). We have therefore used the functions in Table 4.6 for calculating the element stores in needles and branches (Section 6).

The answer to the question posed on p. 43 is thus that regressions between concentrations in current needles and other crown components can be used for estimating amounts of elements in these components, although with an accuracy varying from relatively satisfactory for N, K, Ca and Mg in total needles, to poor for branches. For P in branches, no useful relationship could be established, so we have had to use a very simplified calculation.

Some tests on the comparability of wood and bark data from E55 and E57

Except for N, in Table 4.6 there is no statistically significant relationship between stemwood and stembark concentrations on the one hand and current foliage, either because of a genuine lack of relationship or because of the scatter in the data. However, two kinds of check can be made on the quality of the values for bark and wood. The one is a simple comparison between Tables 4.3 and Table 4.5, where the control and N2PK have received the same treatment. The main difference is time, *viz.* sampling in the spring of 1985 (E55) and in the autumn of 1987 (E57), a difference which is unlikely to affect the wood and bark concentrations greatly. Strict comparisons are not possible, as Table 4.3 shows the effects of N regime, PK regime and N source in separate columns, while Table 4.5 shows differences between five trees from two treatments, control and N2PK. However, for N in E55, neither PK nor N source appears to have affected N concentrations in wood and bark much. For P and K, the addition of PK has increased the concentrations of these elements, especially in the bark. In any case, differences between the two experiments with respect to N and P concentrations in wood and bark from similarly treated trees are not large. The answer to the second question on p. 43–5 is thus that trees within Expts E55 and E57 appear to have reacted fairly similarly to the fertiliser treatments.

The other possible check is presented in Table 4.7. Since N concentrations in stemwood and bark were reasonably well related to current needle concentrations (Table 4.6), we calculated wood and bark concentrations as described for needles and branches. The estimated values can then be compared with the analysed N concentrations in stemwood and bark (Table 4.7). Estimated wood concentrations were 15 to 20% lower than analysed concentrations, while the difference is less in bark. Considering all the errors that occur in biomass estimates, we conclude that our analysed wood and bark samples can be used for estimating biomass nutrient contents per unit area, although treatment means for components may have errors up to 20%.

Biomass concentrations in Expt E40 Lisselbo and in field vegetation

As mentioned above, biomass was sampled in the spring of 1975. The results have not been published in full (Albrektson, Aronsson & Tamm, 1977; Albrektson, 1980), but N concentration data are compiled in Table 4.8 (unpublished ms., Albrektson & Aronsson). The analyses were made on more detailed needle and shoot fractions than those shown in the table, hence the data presented here are weighted means for these fractions. The data in Table 4.8 do not differ greatly from those in Tables 4.3 and 4.4, and the differences, *e.g.* control levels of N, may have to do with the difference in age and size of the sample trees. There are also site differences between Lisselbo and Norrliden, as will be discussed later, and a small but consistent difference in N concentrations in needles on no-N plots (Table 4.1) may be related to the sites. The data in Table 4.8 will be further used in Section 6, where the recovery of fertiliser N in the tree stand is discussed.

Nutrient levels in field vegetation

A rapid and striking effect of fertilisation with N has been changes in field and bottom layer vegetation (van Dobben, Dirkse, ter Braak & Tamm, 1992; van Dobben, Dirkse & ter Braak 1999; see also Fig. 2.3 and Section 7, p. 67). The question whether these changes affect the nutrient budget of the ecosystem is discussed by Aronsson *et al.* (1991), and here briefly reviewed at the end of Section 6.

5. Changes in stem production with N and PK regimes

Measurements and results

Stem measurements

Stem diameter and height measurements have been made from the starting year (at Lisselbo two years later, but with retrospective measurements of tree height) at intervals of 3–5 years. Basic data on stand characteristics at the first and last measurements are shown in Tables 5.1–5.3. The data measured on standing trees are used for statistical tests of treatment effects in this section. They are also essential for calculating tree biomass and nutrient contents, discussed in Sections 6 and 7. In addition to these measurements, increment cores were measured, at E55–E57 Norrliden from trees removed in the thinning in April of 1985. At Lisselbo, cores were taken in 1988–1989, primarily from trees overthrown by wind or damaged by snow during that winter.

Stem volume is the integrated result of height and basal area growth and bears a close relation to stem biomass, a main component in our nutrient budget studies. We shall therefore discuss volume growth in most detail. However, tree height and height growth are of interest, not only for their contribution to stem volume, but also because tree height or height growth are key variables in most systems for silvicultural site classification. The site index, often defined as the height of the 100 largest trees per hectare at age 100 (or 50) years, is taken as expressing site fertility. Although fertility is a complex concept, including both edaphic and climatic factors, we might expect changes in tree height if the nutrient availability in the soil is maintained at a higher level for extended periods. That this holds true is common knowledge from fertiliser experiments on nutrient-deficient sites, in Sweden from peatland afforestation as well as from spruce plantations on mineral soil (Tamm, 1985; Tamm & Fu, 1985).

There is thus a particular reason to study treatment effects on tree height in the present experiments. The other main component of stem growth, basal area growth, is known to be sensitive to fertiliser applications. Possible changes in stem form have not been as systematically studied in our pine experiments as in the spruce

Table 5.1. *Stand data for Expt E55AN, Norrliden. Measurement plot size 400 m². 'Total 1989' volume includes volume removed in 1984. The last column represents treatment means of total production in 1989, assuming that losses before 1971 can be neglected*

Treatment	Plot	No. trees/plot		Mean height m		Basal area o.b. m^2 ha^{-1}		Volume o.b. m^3 ha^{-1}		Removed		Total	Treatment
Year	No.	1971	1989	1971	1989	1971	1989	1971	1984	1984	1989	1989	mean
AN N0	37	74	59	4.8	12.6	7.8	21.0	25.9	120.3	24.3	135	160	192
	50	75	60	5.5	13.2	11.0	24.4	40.1	150.8	27.8	166	195	
	51	85	69	5.7	13.7	12.7	28.0	45.7	169.4	26.4	194	220	
AN N0PK	41	79	65	5.2	13.0	10.4	27.7	35.6	158.1	22.1	181	203	189
	59	83	57	4.7	11.8	9.3	22.2	30.9	139.9	32.9	140	176	
AN N1	38	84	61	5.0	13.2	10.1	31.1	34.1	183.2	38.3	208	248	243
	53	83	56	5.1	13.1	9.6	29.1	32.9	179.0	44.0	190	238	
	57	74	53	5.3	13.4	10.5	29.0	36.9	189.5	47.5	194	243	
An N1PK	40	75	54	5.4	13.5	10.1	29.4	35.2	180.1	38.1	199	242	223
	55	72	52	5.1	13.2	7.7	26.2	26.7	154.1	29.1	173	205	
AN N2	36	89	58	3.9	11.9	6.9	29.1	20.9	159.3	33.3	175	213	220
	42	86	67	5.2	12.2	12.0	32.6	41.3	197.4	39.4	204	244	
	52	70	50	5.1	11.9	9.1	27.8	31.2	161.2	32.2	168	203	
AN N2PK	43	72	51	4.9	11.8	8.6	26.4	29.5	158.2	36.2	157	195	206
	58	77	49	5.3	12.7	10.8	25.9	37.7	171.7	44.7	165	216	
AN N3	39	88	65	5.3	12.0	12.0	32.4	41.8	185.5	29.5	197	228	198
	44	69	48	5.0	12.0	9.6	26.6	33.6	157.1	33.1	163	200	
	56	79	52	4.9	11.0	9.9	20.3	33.8	141.3	45.3	120	166	
AN N3PK	45	72	44	5.2	11.5	9.8	24.1	33.8	139.6	28.6	141	183	173
	54	66	46	5.2	11.3	8.5	22.8	29.8	138.6	31.6	131	164	

Table 5.2. *Stand data for E55U Urea. See also Table 5.1*

Treatment Year	Plot No.	No. trees/plot 1971	1989	Mean height m 1971	1989	Basal area o.b. m^2 ha^{-1} 1971	1989	Volume o.b. m^3 ha^{-1} 1971	1984	Removed 1984	1989	Total 1989	Treatment mean
U N0	67	71	57	5.1	12.5	8.1	20.6	28.2	117.7	17.7	136	155	147
	80	79	61	4.3	12.2	6.6	21.8	21.4	111.5	13.5	140	154	
	83	77	60	4.7	12.0	6.9	18.6	22.6	98.2	16.2	116	133	
U N0PK	66	80	60	5.0	12.6	9.5	21.8	33.1	129.5	24.5	143	168	155
	87	80	63	4.2	12.0	5.7	19.8	18.9	104.3	16.3	125	142	
U N1	68	67	52	5.2	12.9	8.5	24.5	30.0	140.0	26.1	160	187	195
	81	75	59	4.5	12.7	7.2	28.8	24.0	147.3	22.3	184	206	
	86	81	60	4.9	12.2	8.3	26.1	28.7	148.3	28.3	164	193	
U N1PK	71	77	58	4.9	12.8	8.6	27.6	28.9	155.9	30.9	178	209	212
	89	80	60	4.7	12.8	7.4	28.0	24.1	159.8	32.8	182	215	
U N2	73	77	55	4.8	11.8	8.2	26.8	17.2	146.1	29.1	162	192	176
	74	68	46	4.9	12.4	7.6	24.3	26.0	136.0	25.0	153	185	
	82	79	56	3.8	10.8	5.0	23.3	15.5	109.1	18.1	132	152	
U N2PK	69	77	50	4.8	12.1	7.6	26.1	25.6	157.4	38.4	162	205	193
	88	71	50	4.3	11.9	5.8	24.5	18.2	136.1	31.1	149	181	
U N3	70	75	58	4.8	11.3	8.1	24.2	27.3	130.8	21.8	143	166	154
	72	76	49	4.4	11.2	6.4	21.2	20.4	113.7	23.7	122	147	
	84	73	50	4.4	10.9	6.0	20.5	19.4	116.3	32.3	116	150	
U N3PK	75	78	40	4.5	11.3	7.2	21.3	23.2	127.7	31.7	123	163	163
	85	79	53	4.8	11.3	7.3	23.2	24.6	125.3	28.3	135	164	

Table 5.3. *Stand data for Expt E40 Lisselbo. Measuring plot size 400 m². Plots 3 and 5 wee damaged by the removal of five sample trees (including stumps and coarse roots) from each plot in the spring of 1975; these plots have therefore been excluded from most calculations of growth relationships. 'Total 1988' volume includes the volume removed by thinning in 1985 and (for plots 3 and 5) in 1975. The last column represents treatment means of total production in 1988, assuming that losses before 1971 can be neglected*

		No. trees/plot		Mean height m		Basal area o.b. m^2 ha^{-1}			Volume o.b. m^3 ha^{-1}				
Treatment Year	Plot No.	1968	1988	1968	1988	1971	Removed 1985	1988	1971	Removed 1985	1988	Total 1988	Total 1988
N0	7	43	42	2.9	12.2	4.56	0.47	21.21	13.9	2.7	131.3	134.0	119.2
	28	44	41	2.9	11.2	3.78	1.23	18.93	10.9	7.6	110.9	118.5	
	40	48	44	3.1	10.7	4.43	0.66	17.96	14.0	3.5	102.7	106.2	
	45	45	41	3.1	11.3	4.41	1.47	18.70	13.6	7.7	110.4	118.1	
N0PK	20	48	47	3.2	12.8	6.11	0.20	27.28	19.7	0.9	175.5	176.4	135.9
	29	47	46	3.0	11.5	3.95	0.10	20.09	12.4	0.4	120.8	121.2	
	35	48	48	3.2	10.4	4.27	0.00	18.85	12.6	0.0	108.2	108.2	
	47	55	53	2.8	11.2	4.18	0.16	22.19	12.3	7.7	129.9	137.6	
N1	17	48	46	3.4	12.5	7.90	0.85	30.62	25.4	4.7	191.4	196.1	168.1
	23	49	44	3.3	12.6	6.95	2.31	26.18	22.3	13.4	165.0	178.4	
	33	48	46	3.4	11.0	5.56	0.71	22.50	17.1	3.6	127.5	131.1	
	48	46	42	2.9	11.9	5.32	0.90	25.83	16.5	10.0	156.7	166.7	
N1PK	11	53	49	2.6	11.0	5.17	0.92	24.14	15.6	3.8	137.7	141.5	160.0
	27	55	55	2.9	12.6	6.03	0.00	31.10	18.2	0.0	197.6	197.6	
	37	58	56	3.2	11.3	6.37	0.37	27.84	19.3	1.8	162.6	164.4	
	42	43	39	2.8	11.9	4.25	1.10	21.83	12.9	5.1	131.3	136.4	
N2	3	39	31	2.9	11.7	4.94	0.00	23.43	15.3	0.0	138.7	143.9	164.2
	24	62	56	3.4	12.3	9.06	2.25	31.97	29.0	11.8	200.1	211.9	
	39	46	42	2.8	10.3	4.28	0.97	22.41	12.4	4.2	120.2	124.4	
	44	51	47	2.9	11.9	5.47	1.44	28.08	16.0	7.0	169.8	176.8	
N2PK	5	42	32	2.8	11.9	5.26	0.00	24.67	16.1	0.0	147.4	151.3	140.0
	30	48	42	3.2	10.5	5.70	1.45	22.89	18.2	6.4	126.9	133.3	
	38	45	37	3.3	11.4	6.12	2.29	22.91	19.1	9.8	137.7	147.5	
	52	50	40	2.6	10.4	4.46	2.40	21.65	12.7	10.3	117.4	127.7	
N3	14	41	38	3.4	10.1	6.13	0.69	19.52	19.2	2.9	103.1	106.0	114.6
	32	61	45	3.0	8.4	5.17	2.52	17.22	15.8	8.2	79.3	87.5	
	36	46	41	2.7	10.2	4.25	0.66	23.34	12.4	2.7	125.1	127.8	
	41	58	52	2.6	10.0	5.27	1.84	24.91	15.1	7.2	129.8	137.0	
N3PK	9	46	35	2.6	10.3	4.53	2.56	16.79	13.6	10.4	90.2	100.6	121.6
	31	54	44	2.9	10.1	4.86	1.52	21.54	14.3	5.2	112.7	117.9	
	34	47	39	3.1	10.8	5.88	2.06	23.66	17.6	8.2	132.0	140.2	
	51	49	36	3.0	10.4	5.98	2.88	21.75	18.7	11.0	116.8	127.8	

experiment at Stråsan (Mead & Tamm, 1988), but some observations will be reported in connexion with top dieback and winter damage. We can also compare (Section 6) stemwood mass and stem volume, calculated from height and diameter, according to commonly used formulae (Näslund 1940–1941; 1947), which would reveal large aberrations in stem form, if these occurred.

Stand height and shoot elongation

Height did not differ greatly between treatments (Fig. 5.1*a–c*), but there is a tendency to decreasing height from regime N1 to N3, while height in N1 is possibly slightly greater than in the control. Addition of PK does not appear to have affected height growth on either site, nor is there much difference between E55AN and E55U at Norrliden.

The slightly taller trees in regime N1 compared with N0 might indicate a positive growth effect, but the decrease with further addition of N is at least partly a consequence of an increasing occurrence of dieback or other damage to leading shoots (*cf.* Plates V and VI). A relationship between top damage and B deficiency has been established (Aronsson, 1983), and since it is known that both N addition and liming decrease B status in plants, it is not surprising that the treatment NPK + Lime in E42 has caused a collapse of the pine stand (Tamm & Popovic, 1989). It is perhaps more surprising that for a long time the corresponding treatment at Norrliden (E57) did not cause significantly more damage than other treatments with high N supply. Although the fertilisation treatments in E57 were discontinued in 1991, needle sampling in 1993 revealed very low concentrations of B and Cu on all fertilised plots, with no difference between those with or without lime (Section 8).

Nitrogen additions with increased N concentration in tissues have been shown to change the growth pattern to production of larger needles and to increase shoot diameter more than shoot elongation in E40 Lisselbo (Albrektson *et al.*, 1977). The present data do not permit us to distinguish between the two components of reduced height growth at high N regimes, *viz.* direct meristem damage and a general reallocation of resources.

The conclusion from the height growth measurements is that the effects of addition of N and PK fertiliser have been rather small in Expts E55 and E40, much smaller than that observed in spruce on sites deficient in N (Tamm, 1985; Tamm & Fu, 1985) and in both species following the addition of PK or NPK on many drained peatlands (Paavilainen, 1972; *cf.* also Meschechok, 1968). However, a young pine stand at the N-limited Stråsan site showed a weak positive reaction in height growth after addition of 60 kg N ha^{-1} (Tamm, 1971).

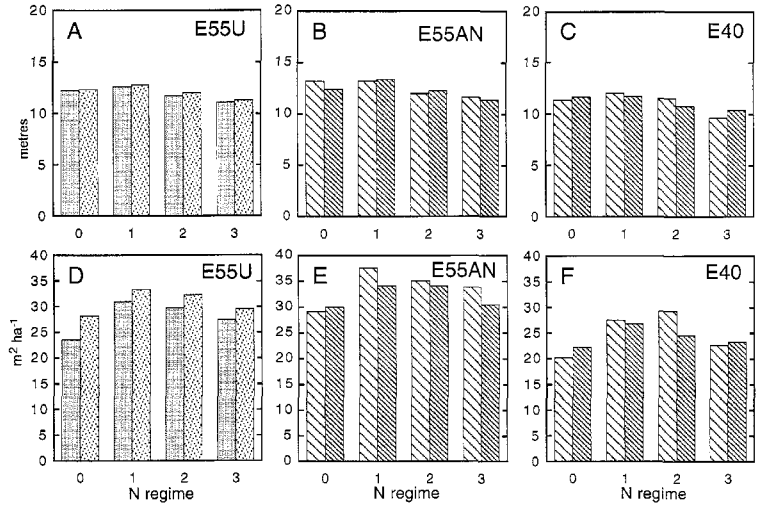

Fig. 5.1. Stand height and basal area in E55 Norrliden, 1989, and E40 Lisselbo, 1988 (measured values). (A), (B) Arithmetic mean height, E55 U and AN, in different nutrient regimes. (C) Arithmetic mean height, E40, in different nutrient regimes. (D), (E) Mean basal area, E55 U and AN, in different nutrient regimes. (F) Mean basal area, E40, in different nutrient regimes in 1988. Legend: Bars for each N regime in order from left: – PK; + PK.

Basal area

Basal area reacts much more strongly to improvement of the N nutrition from regime N0 to N1 at both Norrliden (Fig. 5.1*d–e*) and Lisselbo (Fig. 5.1*f*) than does height growth. The response curves for basal area are fairly similar within the different groups of treatment (U, AN, UPK, ANPK). Some of the differences occurring might be caused by differences in initial conditions, or by differences in site quality, as will be discussed later in connexion with statistical tests of differences in volume growth. In Fig. 5.1 and 5.7, the measured values are shown without adjustment for basal area before the onset of treatment (in contrast to Figs. 5.3–5.6).

Basal area increment

Basal area growth has been measured both from caliper data and from increment cores. Here only the measurements on cores are discussed, since the field measurements have given results very similar to the stem volume data discussed below. The merits of the two methods—calipering in the field and ring measurements on cores—were discussed in Section 2, as also the advantage of using covariates in the statistical analysis (ANOCOVA).

At Norrliden (E55), basal area before the start in 1971 was used as a covariate in the statistical analysis, to reduce variation caused by differences in growth of the sample trees before treatment. At Lisselbo, only one year's growth before treatment (1968) could be used, since many trees which had not attained breast height in 1967 would otherwise have been excluded. Nevertheless, the adjustment made by analysis of covariance reduced variation between plots considerably. The relationship between the dependent variable, basal area growth, and the adjustment variable (pretreatment basal area or area growth) is very close at the beginning of the observation period, but becomes weaker with time.

Curves for annual basal area growth at E55AN Norrliden and E40 Lisselbo are shown in Fig. 5.2. These diagrams will not be discussed in detail here; but note that they, like the diagrams on needle nutrient concentrations, show fairly good agreement between 'highs' and 'lows' in different treatments, including controls in both experiments.

The adjusted data from the cores have also been expressed as accumulated basal area as a

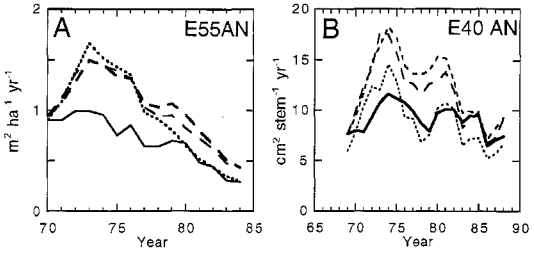

Fig. 5.2. Examples of between-year variation in basal area growth at Norrliden and Lisselbo. (A) E55AN plots without PK; (B) E40 plots without PK. For symbols, see Fig. 4.1.

percentage of the value for control plots (Fig. 5.3 E55U and AN and Fig. 5.4 E40). The use of relative basal area growth allows treatment effects to be examined separately from age effects.

The three N regimes showed an increasing, positive reaction in the first few years' treatment, before levelling off. The curves for the N regimes are fairly similar in E55U and AN (Fig. 5.3*a* and *b*), while PK addition appears to increase growth, at least in regimes N1UPK and N2UPK (Fig. 5.3*c*), whereas there is no positive

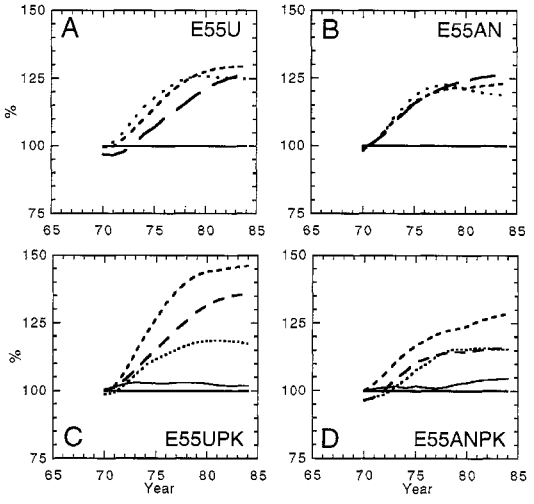

Fig. 5.3. Progression of basal area in different treatments in E55 Norrliden (U and AN treated separately), relative to that of control plots (mean of three control plots = 100 for each year). Measurements under bark, made on increment cores (normally from 25 trees per plot). Values for both treated plots and controls were adjusted by analysis of covariance for differences in mean basal area 1967–1969, prior to treatment. Subdiagrams for each treatment group: (A) U–PK, (B) AN–PK, (C) U + PK and (D) AN + PK. Legend: Horizontal solid line is the mean of control plots, long dashes N1, intermediate dashes N2 and short dashes N3. Thin solid line in (C) and (D) represents the mean of two N0PK plots.

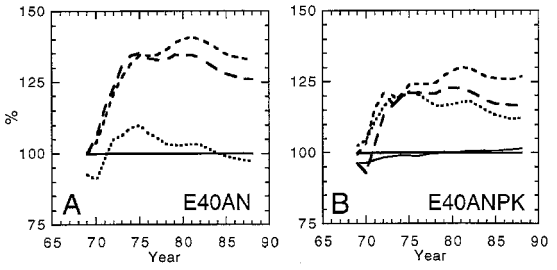

Fig. 5.4. Progression of basal area in different treatments in E40 Lisselbo, relative to that of control plots (mean of four control plots = 100 for each year). Measurements under bark made on 4–5 trees per plot; on some plots trees damaged in the winter of 1988–1989 were preferentially sampled (see text). Values for both treated and control plots were adjusted by analysis of covariance for differences in basal area growth in 1968, prior to treatment. (A) treatments without PK, (B) treatments with PK. See also Fig. 5.3.

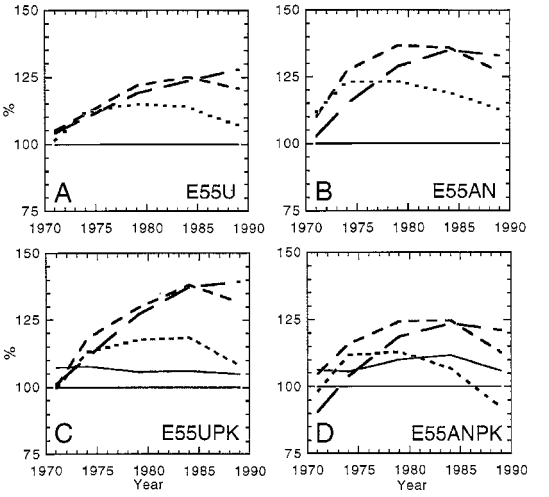

Fig. 5.5. Progression of stem volume over bark by treatment in E55U and AN, relative to that of control plots (mean of three control plots = 100 for each year). All values adjusted by analysis of covariance for differences in starting conditions, as expressed by the Bjørgung index $\sqrt{n \cdot h^2}$. The measured stem volume production, $m^3 ha^{-1}$, of the controls at each revision is given in Fig. 5.6(C). See text and Fig. 5.2 for further explanation. (A) Treatment group U–PK, (B) AN–PK, (C) U + PK, (D) AN + PK

PK effect in E55ANPK (Fig. 5.3*d*). At Lisselbo, responses are similar to those in E55AN, except in regime N3, which shows a poor response (Fig.5.4*a*). This deviation by regime N3 in both Fig. 5.3*b* and *d* and Fig. 5.4*b* can be explained at least in part by the low pre-treatment value for regime N3 in E40. A close examination of Fig. 5.3 and 5.4 suggests that the pretreatment situation may have influenced the response curves (N1 in Fig. 5.3*a*, N3 in Fig. 5.3*c*, N1 and N3 in Fig. 5.3*c*, N1 in Fig. 5.4*b*). Evidently, there are site or other differences between plots which have not been accounted for by the concomitant variable. It should also be recalled that the number of sample trees was lower, and less representative, in E40 than in E55U and AN (although there were four replicate plots in E40 instead of three or two in E55U and AN). Final conclusions will not be drawn until we have examined growth measures other than annual basal area growth.

Relative stem volume growth

Stem volume development is illustrated in Fig. 5.5 for E55U and AN and in Fig. 5.6 for E40. The values in the diagrams are relative (first adjusted for differences in the Bjørgung index by ANOCOVA). They can be transformed to absolute values by multiplying by the control values in Fig. 5.6*c* (see also Aronsson *et al.*, 1999). In E55U and AN, stem volumes on control plots increased about sixfold from 1971 to 1989. At Lisselbo, the annual volume growth

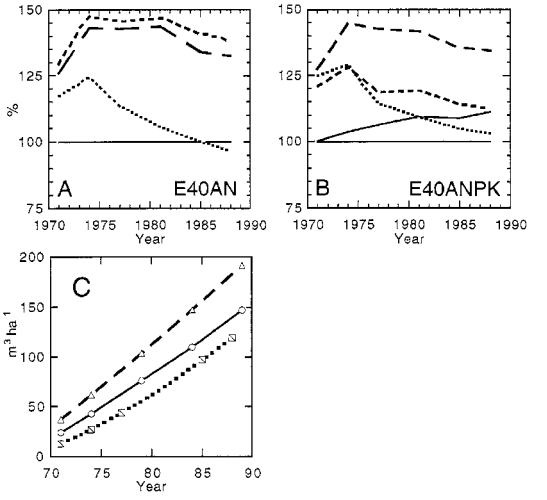

Fig. 5.6. Progression of stem volume over bark by treatment in E40 Lisselbo, relative to that of control plots (mean of four control plots = 100 for each year). All values adjusted for differences in starting conditions (Bjørgung index $\sqrt{n \cdot h^2}$: (A) Treatments without PK; (B) Treatments with PK; (C) Measured stem production on control plots at each revision in E40 (squares and short dashes), E55U (circles and solid lines) and E55AN (triangles and long dashes). See also text.

was lower than at Norrliden, as may be seen in Tables 5.1–5.3. However, the low initial volume gave an eightfold increase in volume on the control plots at E40 Lisselbo from 1971 to 1988.

There is no clear evidence for any effect of PK alone, either on relative basal area or on relative volume. In E55U and AN, the curves for N0PK run parallel to the corresponding N0 curves, although at a slightly elevated level (Fig. 5.5*c* and *d*, *cf.* also Fig. 5.3*c,d*). Evidently, this is a further example of differences in initial level persisting, to some extent at least, during the whole period. In E40, the curve for N0PK starts from the same point as the control line and rises slowly (Fig. 5.6*b*), eventually crossing the curve for N3PK. The corresponding curve for relative basal area (Fig. 5.4*b*) also shows a rising trend, starting from below the control line to end slightly above.

Considering that basal area growth is a main component of volume growth, especially on sites where height response to treatments is small, the generally good agreement between the curves in the diagrams of relative basal area and relative volume is not surprising (Fig. 5.3 compared with 5.5 and 5.4 compared with 5.6). However, relative values of this kind are not well suited for statistical tests; we shall therefore make such tests on stem volume data (Tables 5.4–5.7). On the other hand, the diagrams give a much better picture of growth changes over time. We may conclude that the initial growth response to N addition is rapid in all cases for regimes N1 and N2. A levelling-off occurred after about five years in E40 and after about ten years in E55 U and AN. Levelling-off means that the trees continue to grow at the same rate as the control trees, while a decreasing curve means lower growth-rates. It is evident in all diagrams, except Fig. 5.3*c,d*, that trees in regime N3, after an early growth culmination, are decreasing in growth, especially at Lisselbo (Fig. 5.4 and 5.6). Some growth decrease occurs in regime N2, most clearly in Fig. 5.6*b*. There is thus a time dependency in the response of tree growth to N regimes, a phenomenon to be discussed later in the context of optimum N nutrition.

Total stem production in different nutrient regimes

Total stem production is shown in Fig. 5.7*a* (E55U), Fig. 5.7*b* (E55AN) and Fig. 5.7*b* (E40).

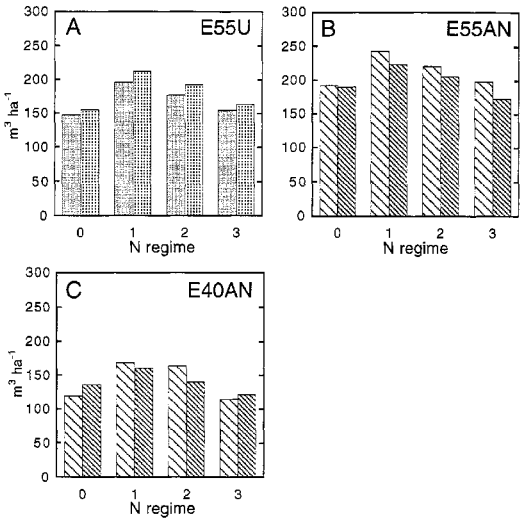

Fig. 5.7. Total stem volume production over bark in E55U (A) and E55AN (B) in 1989, and E40 (C) in 1988, by nutrient regimes. Measured (unadjusted) values. For symbols, see Fig. 5.1.

For our purpose, the main advantage of the volume diagrams over basal area diagrams, is that the results are presented in units more commonly used in forest management, and more directly related to economic terms. For this reason, we have made statistical analyses of the treatment effects on stem volume in 1979 and 1989 for E55 and in 1977 and 1988 for E40. These are presented in Tables 5.4–5.7, as noted above.

The general conclusion from Fig. 5.7*a,b* is that the response to N application is at most *ca.* 50 m^3 ha^{-1} in 1989 at Norrliden, from controls to regime N1, more or less independently of whether the N form is urea or ammonium nitrate. However, there are consistent differences between E55U and E55A in all N regimes. Plots with PK tend to have higher volume than plots without PK in E55U, while the opposite is true in E55AN. However, the response to N regime does not differ much between U and AN, particularly if N1 is compared with N0.

Several types of test may be used to discover whether the differences in accumulated tree growth, discussed here, are statistically significant. We have used a GLM procedure, in which the N regimes form four classes (N0, N1, N2 and N3) and the PK regimes two classes (0 and PK). The covariate, stem volume in 1971, is a continuous variable. In Section 7, tests will be

made with periodic stem volume growth as dependent variable, with foliar concentrations as the nutrition variables.

Table 5.4 demonstrates that all tested variables, PK, N level and stem volume in 1971, significantly influenced stem volume in 1979 and 1989, in both E55U and AN. The p value for N varied between 0.002 and 0.0001, while that for PK varied between 0.030 and 0.049. The covariate (*Volume* 1971) had p values below 0.001, except for E55U in 1989, where p was 0.045. The N regime with the highest volume in 1979 was N2, with a small difference between N1 and N2 but larger differences from N3 and N0 (Table 5.5). In 1989, the N1 regime had passed the N2 regime. The most interesting point in Table 5.5 is perhaps that the PK effect has a negative sign (+ PK < − PK) in E55AN in both years, and a positive sign in E55U in both years. Even if the p values for the PK effects are not far below the 5% level, this confirms a tendency visible in some of the diagrams, in particular Fig. 5.3 and 5.5.

Table 5.6 demonstrates the statistical test for the E40 treatments in the same way as Table 5.4 for E55U and AN, with the difference that no significant PK effect was found, and that stoniness index was introduced as a further covariate (without attaining statistical significance). The covariate BI (Bjørgung index) was used here, since stem volume in 1971 had already been affected by treatments (1969–1971). The N level was a significant variable in both years, with p values 0.0008 and 0.0011, respectively. Level N1 produced the highest volume in both years (*cf.* also Fig. 5.7).

Table 5.4. *Statistical tests of the treatment effects on stem volume production in Expts E55AN and U Norrliden. GLM Procedure: Class PK with values 0 and PK, Class N with values N0, N1, N2 and N3. Stem volume 1971 as covariate. Sums of squares given are of 'Type I'. For parameter estimates, see Table 5.5*

A. E55AN, stem volumes in 1979.

Source of variation	D.f.	Sum of squares	Mean square	F value	P value
Total	19	3606.05			
Model	5	3134.35	626.87	18.6	0.0001
Error	14	471.70	33.69		
PK	1	192.33	192.33	5.7	0.0315
N level	3	840.31	280.10	8.31	0.002
Vol. 1971	1	2101.70	2101.70	62.4	0.0001

B. E55U, stem volumes in 1979

Source of variation	D.f.	Sum of squares	Mean square	F value	P value
Total	19	2569.44			
Model	5	2077.23	415.45	11.8	0.0001
Error	14	492.21	35.16		
PK	1	163.52	163.52	4.6	0.049
N level	3	1128.70	376.23	10.7	0.0006
Vol. 1971	1	785.01	785.01	22.3	0.0003

C. E55AN, total volume production in 1989

Source of variation	D.f.	Sum of squares	Mean square	F value	P value
Total	19	14968.10			
Model	5	12338.21	2467.64	13.1	0.0001
Error	14	2629.89	187.85		
PK	1	1117.03	1117.03	6.0	0.029
N level	3	7281.72	2427.24	12.9	0.0003
Vol. 1971	1	3939.46	3939.46	21.0	0.0004

D. E55U, total volume production in 1989

Source of variation	D.f.	Sum of squares	Mean square	F value	P value
Total	19	11493.52			
Model	5	9760.04	1952.01	15.8	0.0001
Error	14	1733.49	123.82		
PK	1	726.04	726.04	5.9	0.030
N level	3	8435.70	2811.90	22.7	0.0001
Vol. 1971	1	598.29	598.29	4.8	0.045

Conclusions

The general conclusion of the stem growth measurements is that growth on both sites is

Table 5.5. *Mean values of stem volumes (V) in the four groups tested in Table 5.4 and parameter estimates within the groups. The volumes are given in m^3 ha^{-1} and the 1989 figures include volume removed by thinning*

	A. AN V1979	B. U V1979	C. AN V1989	D. U V1989
Mean value	113.07	88.73	206.99	173.28
Intercept	46.27	51.61	93.84	131.69
	± 8.43	± 8.73	± 19.90	± 16.38
No PK	1.76	−3.88	9.00	−10.59
	± 2.71	± 2.74	± 6.40	± 5.14
With PK	0.00	0.00	0.00	0.00
N level N0	−11.32	−11.74	0.06	−10.41
	± 3.68	± 3.80	± 8.69	± 7.14
N level N1	9.84	5.06	50.55	38.15
	± 3.69	± 4.01	± 8.70	± 7.53
N level N2	10.34	9.26	32.47	28.52
	± 3.72	± 3.85	± 8.77	± 7.22
N level N3	0.00	0.00	0.00	0.00
Regression coefficient for covariate (V1971)	1.876	1.627	2.57	1.42
	± 0.237	± 0.344	± 0.56	± 0.65

Table 5.6. *Statistical tests of the treatment effects on stem volume in Expt E40 Lisselbo. GLM Procedure: Class N with values N0, N1, N2 and N3. As no significant influence of PK was found in the first run, PK was excluded as a treatment factor. Two covariates were included although they did not attain full significance in all cases: Bjørgung index (BI_{1968}) and stoniness index (Si_{30cm}). The sums of squares given are of 'Type I'. For parameter estimates, see Table 5.7*

A. Stem volumes in 1977

Source of variation	D.f.	Sum of squares	Mean square	F value	P value
Total	31	5521.62			
Model	5	3280.24	656.05	7.61	0.0002
Error	26	2241.38	86.21		
N level	3	1973.75	657.91	7.63	0.0008
BI	1	1196.95	1196.95	13.88	0.0010
Si_{30cm}	1	109.54	109.54	1.27	0.27

B. Stem volumes in 1988

Source of variation	D.f.	Sum of squares	Mean square	F value	P value
Total	31	27568.54			
Model	5	14503.55	2900.71	5.77	0.0010
Error	26	13064.99	502.50		
N level	3	10846.28	3615.43	7.19	0.0011
BI	1	2076.13	2076.13	4.12	0.052
Si_{30cm}	1	1581.14	1581.14	3.15	0.088

Table 5.7. *Mean values of stem volumes 1977 and 1988 in E40, and parameter estimates from the statistical analysis*

	Volume 1977	Volume 1988
Mean value	55.68	140.41
Intercept	9.23 ± 11.40	47.79 ± 27.52
N level N0	-4.58 ± 4.68	9.23 ± 11.30
N level N1	13.17 ± 4.75	42.14 ± 11.46
N level N2	7.05 ± 4.74	28.53 ± 11.45
N level N3	0.00	0.00

primarily N-limited, but that the quantitative response is moderate, compared with what has been reported from other sites and especially with other tree species (Tamm, 1969, 1985; Raison & Myers 1992*a*; Pereira *et al.*, 1994; Linder, 1995; Bergh, Linder Lundmark & Elfving, 1999). It is generally agreed that Scots pine is a species well adapted to poor sites, and it is not surprising if the species has paid for its fitness on N-limited sites, and its fire resistance, with a reduced ability to compete on rich sites. On the other hand, the experiments started at a stage in stand development when responsiveness to nutrient supply should be near-maximum (Miller, 1981). The possibility that even regime N1 is supraoptimal can be rejected, since the response to N additions was initially positive at all N levels; it is only with time that negative effects have been observed, and it is not until the last measuring period (1985–1989) that N2 curves at Norrliden fall below those for level N1 (Fig. 5.4).

Another conclusion can be drawn from our comparisons between different growth measures: volume growth and annual ring growth lead to rather similar conclusions, and the choice of variable and time period can be based on criteria other than accuracy. Both types of measurement appear to be accurate enough for attempts to relate changes in stem growth, *e.g.* to changes in internal nutrient concentrations in the trees. Height measurements, on the contrary, tell us less about the reaction of Scots pine to fertilisation on the sites studied.

In Section 1 we discussed the possibility of maintaining both constant foliar concentrations (primarily of N) and constant growth-rates for extended periods. The foliar concentrations were discussed in Section 4. Here, we can conclude from the levelling-off of the curves in Fig. 5.3–5.6 that growth-rates (relative to the controls) have varied less during the latter part of the experimental period than earlier, for regimes N1 and N2. By contrast, growth-rates in regime N3 have decreased markedly in several cases. Addition of PK has accentuated the decrease, which can also be observed in regime N2PK in Fig. 5.6*b*. More detailed information on periodic volume growth may be found in Aronsson *et al.* (1999).

6. Effects of N and PK regimes on production and allocation of aboveground biomass and its nutrient content

Changes in biomass of aboveground tree components

Biomass samples were taken from the N dosage experiments in April, 1975, at Lisselbo (E40; associated stand measurements were made at the end of the 1974 growing season) and in the early spring of 1985 at Norrliden (E55; associated stand measurements were made in autumn

1984). Condensed data from the Lisselbo sampling have been published (Albrektson *et al.*, 1977; Albrektson, 1980). Norrliden data have, however, not been published, mainly because needle and branch samples for chemical analysis were spoiled by unsuitable weather conditions before they could be analysed. However, dry mass data are available for stemwood, stembark and dead branches from both E55U and AN. Living branches and needles were weighed in E55AN only. The data from E55 have been used here by permission of E. and B. Axelsson.

Allometric relationships between the fraction in question and stem diameter or basal area are customarily used to estimate biomass fractions for forest plots (Madgwick & Satoo, 1975). For stemwood, however, our graphs showed that there was little advantage in using logarithmic expressions, since linear regressions between wood DM and stem volume over bark gave a correlation coefficent of $r=0.963$, with a small intercept and no clear differences between treatments. The ratio of DM to stem volume, calculated according to Näslund (1940–41; 1947) gave similar values for all N regimes and a common factor, 0.336*(stem volume over bark), was used (Table 6.1*a*).

It is well known that increased N supply may negatively affect wood density. Ericsson (1974, 1985) reported changes in dry-matter content in wood formed after fertilisation of 21 pine stands, with decreases between 1 and 7%. It is evident that other sources of variation dominate at Norrliden.

For the biomass fractions stembark, branches and needles, the graphs showed that the relationships with stem diameter at breast height differed between N levels, and different equations were used (Table 6.2). Since nothing in our working diagrams—in which biomass fractions from individual trees were plotted with different symbols according to treatments—indicated systematic differences caused by the presence or absence of PK, the functions in Table 6.2 were not separated beyond N level. The mass of stem bark, living branches, and needles was calculated for each tree on the net plot and summed to form plot values.

Table 6.2. *Allometric relations between the dry mass (kg) of stem bark, living branches and needles (dependant) and stem diameter (mm) on bark at breast height. Expt E55*

Nutrient regime	Equation	Correlation coefficient	No. of trees
Stem bark			
0 + PK	$y=0.126x^{2.04}$	0.918***	25
N1 + N1PK	$y=0.171x^{1.98}$	0.951***	23
N2 + N2PK	$y=1.891x^{1.49}$	0.892***	23
N3 + N3PK	$y=1.828x^{1.50}$	0.892***	24
Living branches			
0 + PK	$y=0.0107x^{2.695}$	0.939***	16
N1 + N1PK	$y=0.0039x^{2.92}$	0.890***	16
N2 + N2PK	$y=0.00255x^{2.99}$	0.925***	16
N3 + N3PK	$y=0.0368x^{2.44}$	0.855***	16
Needles			
0 + PK	$y=0.0692x^{2.196}$	0.896***	16
N1 + N1PK	$y=0.0202x^{2.467}$	0.921***	16
N2 + N2PK	$y=0.0143x^{2.542}$	0.848***	16
N3 + N3PK	$y=2.7522x^{1.491}$	0.854***	16

As living branches and total needles were not measured in E55U, we had to assume that the allometric relationships for E55AN between mass and stem diameter were also valid for E55U.

For the fraction dead branches, where DM data were available from both experiments, there was little benefit from using an exponential function. However, Fig. 6.1*a* suggests that, in E55AN, the ratio of dead branches to live branches increases in regime N3 and possibly N2, as does also the scatter around the regression lines. Absence or presence of PK does not affect the proportion of dead branches (Fig. 6.1*b*). As there were no living branch data

Table 6.1. *Some ratios used for calculation of biomass fractions (stemwood to stem volume o.b. and dead branches to live branches)*

Regime	N0	N1	N2	N3	All
A. Stemwood dry mass to stem volume					
No. of trees	25	15	34	24	97
Ratio	0.332 ± 0.005	0.334 ± 0.010	0.341 ± 0.005	0.327 ± 0.008	0.336 ± 0.003
B. Dead branch dry mass to live branch dry mass					
No. of trees	16	16	16	16	
Ratio	0.83 ± 0.07	0.78 ± 0.08	1.00 ± 0.15	1.24 ± 0.16	

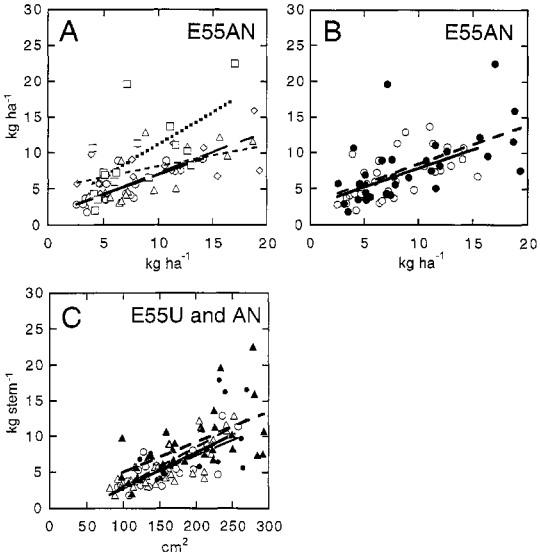

Fig. 6.1. Dry mass of dead branches on sample trees in E55AN, as related to mass of live branches and stem basal area. (A) Dead branch mass plotted against living branch mass, with different symbols for N regimes. Legend: N0 ○, N1 Δ, N2 ◇, N3 □. (B) The same data as in (A), but with open symbols and solid line for trees without PK, filled plots and broken line with PK. (C) Dead branch mass in E55U and AN, plotted against basal area of sample tree. Legend: open symbols denote low-N regime (N0 + N1), filled symbols high-N (N2 + N3), circles E55U, triangles E55AN.

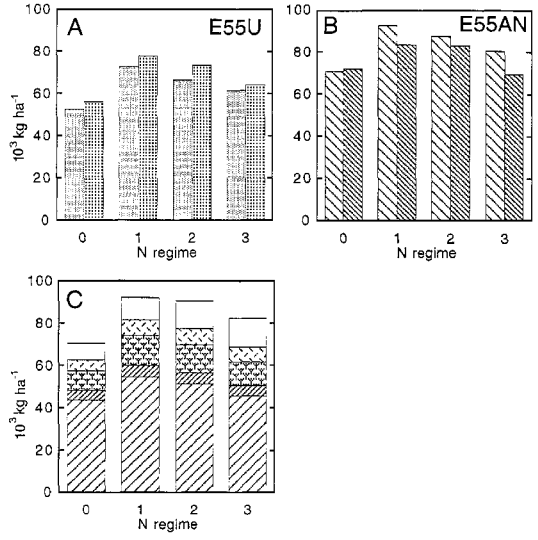

Fig. 6.2. Dry mass of aboveground biomass in different treatments of E55U (A) and AN (B) in the spring of 1985, and (C) the distribution of biomass components and dead branches in U and AN combined. For symbols in (A) and (B), see Fig. 5.1. For symbols in (C): column segments from below: stemwood, stembark, living branches, needles and dead branches. (See also text.).

from E55U, we could not test directly whether there was a difference in living branch DM per unit stem basal area between U and AN. However, Fig. 6.1*c* demonstrates that there is no great difference between N forms in dead branch DM, when the masses actually measured in E55 U and AN are plotted against the basal area of each sample tree. In any case, the very similar behaviour of the dead-branch fraction between E55U and AN lends some support to our assumption that the source of N *per se* has not disturbed the allocation of growth to branches and needles. On the other hand, it is evident that increasing N regime increases both the scatter around the regression lines and the ratio of dead to living branches. For calculating the dead-branch fraction, we used a simple calculation model, the ratio of dead to living branch mass, for each N regime (Table 6.1*b*), assuming little or no difference in allocation of growth between E55U and AN (Fig. 6.2*c*).

The results of the calculations of total aboveground biomass are shown in Fig. 6.2*a* and *b*, which, for natural reasons, is very similar to (but not identical with) Fig. 5.7.

The data underlying Fig. 6.2 are used in what follows for calculating the nutrient amounts in the tree stand.

Stand dry mass at Lisselbo in 1975 is illustrated in Fig. 6.3 (from Albrektson *et al.*, 1977, supplemented with unpublished belowground data from J.G.K. Flower-Ellis). The Lisselbo paper (Albrektson *et al.*, 1977) also contained detailed data on the mass per hectare of needles of different age (Table 6.3).

While current and one-year-old needles (C and C + 1) increase with N regime (up to N2), C + 2 needles and older needles have their maximum in regime N1 and decrease with higher regimes. This suggests premature needle-shedding in higher N regimes, which was confirmed by an inventory in April 1978. The number of stem internodes with more than 10% of the needles still green was counted from the top downwards (Fig. 6.4). Fig. 6.4*a* shows that in Expt E40, increasing N concentration in the diagnostic needle samples (= higher N regime) leads to shorter needle life. PK addition further

Table 6.3. *Needle dry mass (kg ha^{-1}) of pines in different nutrient regimes, Expt E40 Lisselbo, at the sampling in the early spring of 1975. From Albrektson* et al. *(1977)*

Needle age	Control	Treatment N1	N2	N3	N2PK
Current (C)	1191	2298	2495	2415	2531
C+1	1169	2454	2774	2464	2648
C+2	935	1962	1725	1146	1322
C+3−	318	604	278	188	131
All ages	3613	7318	7272	6213	6632

shortens needle life. In E42, where plots were separated only with respect to absence or presence of N2PK addition, needle longevity appears to be slightly higher than in E40, but the pattern is similar: fertilised trees shed needles earlier than unfertilised ones (Fig. 6.4*b*). In E41, where all plots received regime N2, means of plots with or without additions (P, K, Mg, S and 'Micro') form a dense cluster. There are certainly no significant differences, but the only visible deviations concern +Mg and +Micro, which are on top of the cluster, while their counterparts are within it or at the base.

It is known that conifers growing under harsh

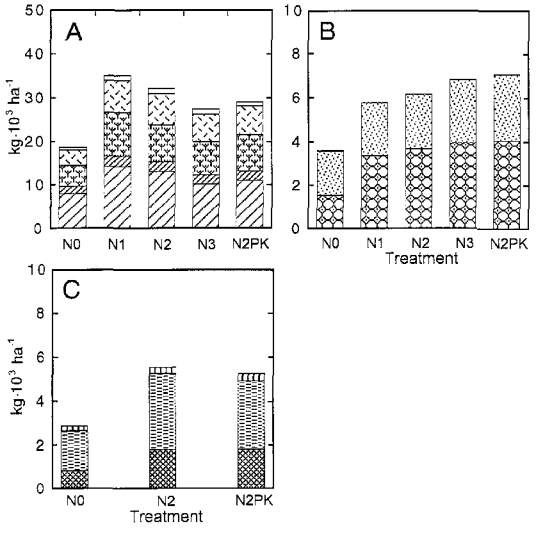

Fig. 6.3. Biomass fractions and dead branches in E40 Lisselbo in 1975 (from Albrektson *et al.* (1977), supplemented with belowground data, kg·10^3 ha^{-1}). (A) Aboveground biomass fractions: from the base, stemwood, stembark, live branches, live needles, dead branches. (B) Root biomass fractions: from the base, roots >2 mm, roots <2 mm (Flower-Ellis, unpubl.). (C) Stumps with attached roots: from the base, stumps only, roots >10 mm, roots <10 mm.

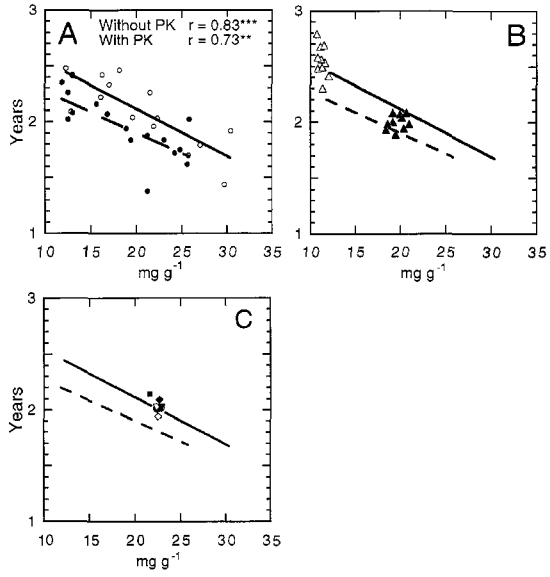

Fig. 6.4. Needle retention on different plots at Lisselbo in April 1978 as a function of needle N concentration (mean 1974–1977). Retention was visually estimated from the number of stem internodes with >10% green needles persisting. (A) E40 plots without PK (open rings and solid line) compared with plots with PK (filled rings and broken line). (B) E42 plots (without NPK open triangles, with NPK filled triangles), with the regression lines from (A) for comparison. (C) Means for plots in E41 with elements (filled symbols) or without (open symbols), with the regression lines from (A) for comparison. The only elements for which a small difference can be seen between + and − are Mg (diamonds) and Microelements (squares).

conditions may keep their needles for long periods, up to four or more decades (*e.g. Pinus longaeva* (D.K. Bailey); Ewers & Schmid, 1981; *cf.* also Waring & Franklin, 1979).

Changes in plant nutrient stores in aboveground tree components

Calculation of nutrient stores in crown components (needles and branches) from the biomass data given in the preceding section, and the nutrient concentrations for needles and branches, discussed earlier (Section 4) was fairly straightforward, if the method of replacing missing values is accepted. An exception is branch P, for which no significant relation with current needle P was established. Here, data from E57 were used more directly (see legend to Table 4.4). For the nutrient amounts in stemwood and stembark, measured data for samples from each regime were used, which are the basis of the data in Table 4.3.

Dead-branch data from other biomass samplings in Swedish stands of Scots pine (Tamm, 1963*a*; Popovic & Burgtorf, 1964; Albrektson & Aronsson, unpubl.) suggest that the N concentration in dead branches is about 80% of that in living branches of the same trees. For the less mobile element Ca, living and dead branches do not differ systematically. Dead branches contain only one-third the concentration of the mobile elements P and K of living branches. Half the Mg concentration of the dead branches is also lost. As dead branches constitute a relatively small fraction of the aboveground mass of the trees, we have found it acceptable to use the relationship with concentrations in living branches to calculate their nutrient stores. For N, the stores in all aboveground fractions, including dead branches, are presented in Fig. 6.5*c* (E55U and AN) and Tables 6.4 (E55) and 6.5 (E40). They are further discussed in Section 7.

Tables 6.4 and 6.5 both contain estimates of the 'formal recovery' of added N for different N regimes. The recovery figures are, not unexpectedly, highest in the lowest N regime (N1), and higher in Expt E40 than in E55. There is no clear difference in recovery between E55U and AN, despite a considerable difference in storage on N0 plots in the two experiments.

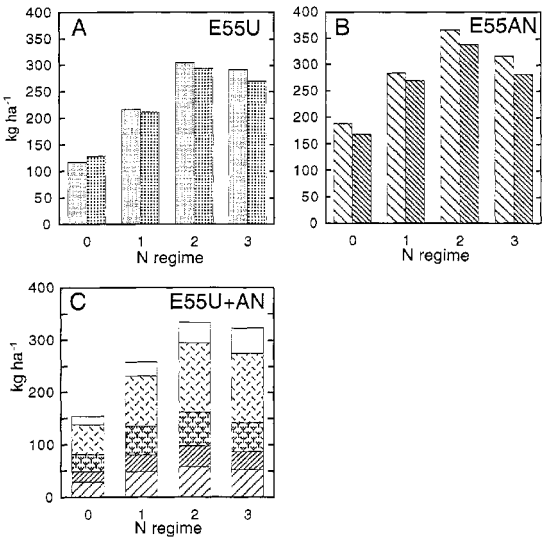

Fig. 6.5. (A) N in the tree stand aboveground in different treatments of E55U, (B) AN at the sampling in spring 1985; and (C) the distribution of N by tree components. For methods of calculation and symbols, see text and legend to Fig. 6.2. Amounts of N in dead branches are included in (C) but not in (A) and (B).

Stand stores were calculated for five elements in addition to N for E55 Norrliden, *viz.* C, P, K, Ca and Mg. Since the formal recovery, in terms of the percentage of that added, is either low (P, K, Ca) or irrelevant (C, Mg), the main interest centres on possible treatment effects on the distribution in the ecosystem, between stand and soil, and between soil compartments treated differently. Since this is dealt with in Section 7, the results are presented in Fig. 7.9–7.11 to avoid duplication.

Before leaving the subject of biomass and nutrient stores, the participation of lesser vegetation in the nutrient cycle of the forest should also be mentioned. Considerable changes in the composition of vegetation, related to the treatments, are described in the second subsection of Section 7. Although we lack complete biomass data, some estimates were made by Aronsson *et al.* (1999). From these it was concluded that the change in nutrient stores aboveground in lesser vegetation following N application, is rather small, because the main changes consist in the replacement of dwarf shrubs having a relatively tall, aboveground perennial biomass, by grasses and herbs with no perennial aboveground biomass. Even though the grasses have at least twice the summer concentration of N compared to the dwarf shrubs, this does not fully compensate for the disappearance of dwarf shrubs (together with most mosses and lichens). In any case, it was concluded that changes in storage were small, compared with changes in stand storage. N cycling may be expected to be faster in the grass, and it might have been of interest to study the belowground components of the field-layer plants.

7. Changes in ecosystem processes related to N and PK regimes

Introductory remarks

Strictly speaking, much of that discussed in earlier sections can be called ecosystem processes, soil acidification, nitrification, biomass production, *etc.* However, there has been little discussion of transfers of organic matter and nutrients between different ecosystem compartments, nor of other relations between compart-

ments, *e.g.* between organisms and their environment. This section deals with some of these relationships. The distribution of plant nutrients in the ecosystem, the effect of experimental nutrient regimes on this distribution and on losses from the site, will also be discussed. We shall also briefly review studies made on the soil and vegetation at Norrliden and Lisselbo by other researchers.

Changes in litterfall and litter nutrient concentrations

Studies of litter production have a long tradition in the Nordic countries (*e.g.* Romell, 1939; Mork, 1942; Viro, 1955) and studies of litter transformation in the soil an even longer history (Müller, 1887; Hesselman, 1926). However, it was not until the advent of the International Biological Programme (IBP; 1964–1974) that they came to be considered an essential part of ecosystem-oriented projects. Since both the first optimum nutrition experiments (E26A and E40–42), and the older N optimisation experiment E1 Hökaberg, at Remningstorp (Tamm, 1968), were incorporated into the Swedish section of the IBP, it was considered desirable to lay out litter traps in Expt E1. However, litter collection was soon interrupted by stand damage (by drought and bark-beetles), so only a brief series is available (November 1968–May 1970, Tamm, 1971). Moreover, litter traps in the ancillary experiment E2 showed that litterfall in 1969–1970 was higher than normal (Tamm, unpublished)

In the Stråsan and Lisselbo experiments, the canopy was not fully closed at the start of the experiments, but the trees were taller at Lisselbo than at Stråsan. The sandy soil at Lisselbo was also more suitable for soil studies; see Tamm & Popovic (1989) for incubation tests and Farrell, Nilsson, Tamm & Wiklander (1980); Farrell, Wiklander, Nilsson & Tamm (1984*a,b*) for lysimeter experiments. Since manipulation of the water regime was of interest in the litterfall studies, litter traps were laid out in E42, where irrigation was one of the treatments. Ten litter traps were laid out at random on each replicate of the ten treatments on 14 April 1971. The collecting area of each trap was 1207 cm^2 and they were emptied at monthly intervals at least until the first snowfall (mid-October to mid-November). Accumulated winter litter was collected in the spring (mid-April to early May), so our 'litter year' extended from about 1 May in one year to approximately the same date in the following year. After collection and drying, litter was separated into needles and 'other litter', and dry mass (105°C) was determined. The amount of 'other' litter (small twigs, male flowers, bud scales, occasional cones, *etc.*) was highly variable in time and between traps. For 19 of the samplings in 1974–1980, it made up on average 14.3 and 17.8% of the total litter collected on the two control plots and 14.1 and 16.5% on the two NPK plots. The fraction 'other litter' will not be discussed further here. Needle litter was analysed for N, P, K, Ca, Mg, and Mn. Before analysis, small samples (mostly summer collections) were pooled in most years.

Various sources of error may affect litter studies carried out as at Lisselbo. The first years' collections showed clearly that ten litter traps per plot were insufficient to give reliable estimates of litter amounts for individual treatments. However, variation could be expected to decrease with increasing canopy closure. It also soon became clear from the growth measurements that the main treatment response obtained in E42 was that for the addition of NPK, so comparisons could initially be made between 50 plots with, and 50 without, NPK. The plots with NPK + Lime had to be excluded because of damage after some years (Tamm & Popovic, 1989), so the number of fertilised plots was later reduced to 40. (*Cf.* also Plates V and VI.)

In 1973, the Swedish Coniferous Forest Ecosystem Project (SWECON) started field studies at Jädraås, 45 km NW of Lisselbo. The SWECON studies included detailed litter investigations in pine stands of different ages, situated on sandy soils similar to those at Lisselbo, although in a slightly colder climate (altitude 190 m compared with 80–85 m at Lisselbo). SWECON litterfall data were reported by Flower-Ellis & Olsson (1978) and Flower-Ellis (1985).

Despite the lack of accuracy in the early years' measurements at Lisselbo, we found it desirable to continue litter collection there for a longer period, to permit comparison with the Jädraås site. In 1977, several of the litter traps were damaged by European elk (*Alces alces*) after damage to the fence (in combination with a deep snow cover). Litter collections were later resumed, so that data for litter mass are available

I. Lisselbo, June 1971, with plot 73 receiving irrigation. (Photo S. Tamm).

II. Soil profile at Lisselbo, taken inside the almost 2-m deep lysimeter pit (hence the board at the top). (Photo COT).

for the period 1980–1983. However, the traps were emptied at somewhat longer intervals, and only the samples from the 'litter year' 1980 have been analysed chemically.

III. Soil profile at Norrliden. (Photo BP).

IV. Lisselbo, damaged field layer, June 1971. (Photo S. Tamm).

V. Boron deficiency symptoms, E42, June 1974. (Photo AA).

VI. Boron deficiency symptoms, E42, June 1977. (Photo AA).

VII. Mg deficiency, E55 spruce, Sept. 1992. (Photo COT).

VIII. Mg deficiency, E55 spruce; close-up, September 1992. (Photo COT).

From E40 Lisselbo and from the Norrliden site, litter was collected only to obtain material for decomposition studies (see below).

Results

There was strong seasonality in litterfall, with a maximum in autumn (Fig. 7.1*a*). Fertilised and unfertilised plots behaved very similarly, the only difference being that the amount of litter

Table 6.4. *Amounts of N found in aboveground stand biomass in Expt E55 in 1985, (A), and in dead branches (B), compared with the amounts added by fertilisation 1971–1984. For biomass, the formal recovery of fertiliser N was calculated for each treatment group separately by subtracting the mean for the no–N plots in the group. For calculation of N in dead branches, see text. The values are given both as kg ha^{-1} (italics) and in per cent of added (bold type)*

Nitrogen regime	N0	N1	N2	N3
Added N 1971–84	–	540	1080	1620
Plot group			A. Biomass	
U	122.1	225.3	285.3	285.6
recovered	–	*103.2*	*163.2*	*163.5*
% of added		**19.1**	**15.1**	**9.9**
AN	175.0	285.4	364.0	342.4
recovered	–	*110.4*	*189.0*	*167.4*
% of added		**20.4**	**17.5**	**10.3**
UNPK	128.4	211.4	293.4	274.4
recovered	–	*83.0*	*165.0*	*146.0*
% of added		**15.4**	**15.3**	**9.0**
ANPK	168.4	268.9	335.9	282.2
recovered	–	*100.5*	*167.5*	*113.8*
% of added		**18.6**	**15.5**	**7.0**
All groups	148.5	247.8	319.6	296.2
recovered	–	*99.3* $\pm$ *5.8*	*171.2* $\pm$ *6.0*	*147.7* $\pm$ *12.2*
% of added		**18.4** $\pm$ **1.1**	**15.8** $\pm$ **0.6**	**9.1** $\pm$ **0.8**
			B. Dead branches, all groups	
All groups	15.5	29.4	39.2	42.5
recovered	–	*13.9*	*23.7*	*27.0*
% of added		**2.6**	**2.2**	**1.7**
			All recovered aboveground	
% of added		**21.0**	**18.0**	**10.8**

Table 6.5. *N in aboveground components of the pine stand in Expt E40 Lisselbo at the sampling in spring 1975. Values in kg ha^{-1}*

	Treatment Control	N1	N2	N3	N2PK
Stemwood	7.2	14.2	15.7	13.3	13.3
Stembark	5.6	10.6	11.8	12.6	10.8
Branches	18.1	44.8	41.3	41.7	43.7
Needles	40.7	97.1	116.1	134.9	98.8
Dead branches	1.6	3.1	3.7	4.8	2.2
Aboveground, sum	73.2	169.8	188.6	207.3	168.8
Difference from control		96.6	115.4	134.1	95.6
Added	–	280	560	840	560
Formal recovery, %		**34.5**	**20.6**	**16.0**	**17.1**

was 2–3 times higher on fertilised plots from the autumn of 1972 until 1976. A similar, though smaller, difference in amount of litter was found during 1980–1983 (Fig. 7.3*a*).

Marked seasonality in litterfall has been reported by Viro (1955), and by Flower-Ellis (1985) from the SWECON series of measurements in 1973–1983. In the SWECON material, the short intervals between collections (weekly or biweekly) further emphasised that needle litterfall in pine on that site was almost as concentrated in season as leaf-fall in deciduous trees.

The small summer samples had higher N concentrations than the large autumn samples (Fig. 7.1*b*), but the difference in concentration only partly compensated for the difference in amount. As in Fig. 7.1*a*, the curves for fertilised and unfertilised treatments run parallel, with 30–50% higher values on fertilised plots. The difference between +NPK and −NPK per-

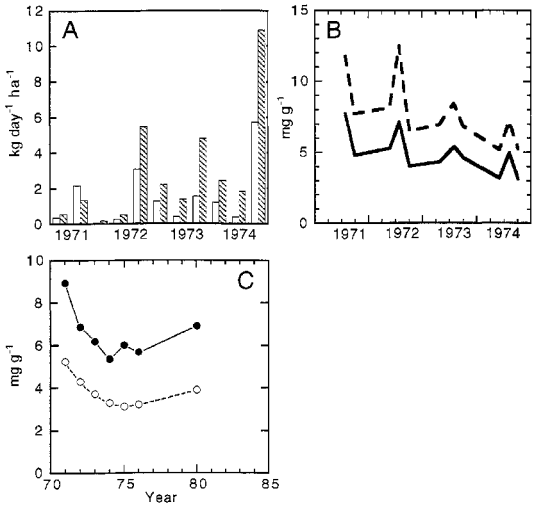

Fig. 7.1. Annual and seasonal variation in amounts of needle litter and its N concentration in E42 Lisselbo. (A) Litterfall 1971–1974. (B) N concentration 1971–1974. The usually small spring and summer collections were combined. (C) Annual means of N concentration 1971–1980 (values lacking for 1977–1979). Open rings: mean of 10 plots without NPK. Filled rings: mean of 8 plots with NPK.

sisted in the last samples analysed (1980, Fig. 7.1*c*). The N concentrations in the small samples from 1971 were much higher than in later years, although some of the needles shed in 1971 were formed before treatments began in June 1968.

The relation between the amounts of litterfall and the N concentrations is further explored in Fig. 7.2*a,b*. Data for individual plots and periods are presented by Aronsson *et al.* (1999).

There is probably a simple explanation of the higher concentrations in small samples collected

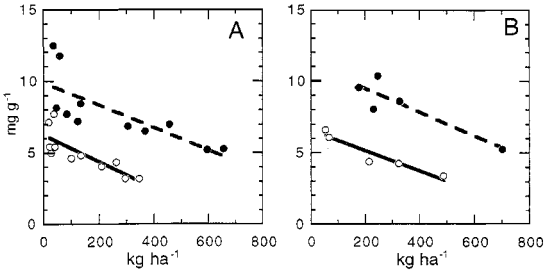

Fig. 7.2. Relations between needle litter N concentration and sample size in Expt E42. (A) Sampling period 1971–1974. (B) sampling period 1980. Block mean values for plots without and with NPK. Winter and summer samples from two blocks, autumn samples from one block only. For more detailed data, see Aronsson *et al.* (1999).

outside the normal needle-fall period. These samples consist to a large extent of needles prematurely shed because of some external agency. The trees have thus not been able to resorb as much of the needle N as needles shed by the normal process. Prematurely shed needles are also by definition younger, but the differences in N concentration between pine needle age-classes are usually smaller than the differences between small and large samples found here (*cf.* Helmisaari, 1992*a,b*; Finér, 1994).

The litter samples were analysed for the same elements as the needle samples, and variations similar to those for N also occurred in the concentrations of other elements. Some data are presented by Aronsson *et al.* (1999). However, since elements such as P, K and Mg may be leached from litter during the sometimes long collection periods, the results must be considered less accurate than those for N, which is not lost from *Pinus silvestris* needle litter during the early stages of breakdown (Berg & Staaf, 1981; *cf.* also Hesselman, 1926). Helmisaari & Mälkönen (1989) found no leaching of N and P from the canopy, in contrast to other mobile elements (K, Mg).

Seasonal variation in litterfall and chemical composition, although interesting, was not the main aim of the litter study. Annual trends in litter production and composition are more important in an ecosystem context, and it is also of interest to compare the amounts of needle litter, its between-year variation, and its relations to tree growth and biomass. Needle litterfall tended to increase from 1971 to 1976 (Fig. 7.3). Data for 1980–1983 indicate lower amounts of litterfall on fertilised plots than in 1976. On unfertilised plots there was a further increase from 1976 to the period 1980–1983, but not to the same level as on fertilised plots. Litterfall in the SWECON study showed a similar trend up to 1976 (Flower-Ellis & Olsson, 1978), which was later broken (Flower-Ellis, 1985). Similarities between the Lisselbo and Jädraås series may reflect a regional litterfall pattern.

The rapid increase in litterfall on fertilised plots follows from the initial reaction to treatment, which was an increase in shoot and needle masses and numbers (Albrektson *et al.*, 1977). Needle production on fertilised plots in E40 in 1973 and 1974 was more than double that on controls (Table 6.3). The difference in remaining needles formed in 1972 (C+2) was smaller, but

still considerable. The importance of differences in C+3 needles is more difficult to judge, as needle shedding has reduced needle numbers considerably. Needle shedding appears to start earlier in regimes N2, N3 and N2PK than on controls and in regime N1, and notably affects also the amount of C+2 needles (Fig. 6.4). Since the rate of needle shedding increases with needle age, especially after the second year, the small amounts collected in 1971 are easily explicable, as the C+2 needles in the autumn of 1971 were formed in buds in 1968, and grew out in 1969, the first year of treatment. Even if single-needle mass is influenced by conditions during the summer in which needles grow out (Romell & Malmström, 1945), needle numbers were predetermined in the buds, *i.e.* by conditions before fertilisation.

It should be recalled that needle biomass figures concern Expt E40, while litter figures relate to E42. This may affect the absolute values (amounts per hectare), but scarcely the temporal trends, since tree growth has run closely parallel in the two experiments, although E40 control plots had grown 20% more than E42 controls (see Fig. 4.9 in Tamm & Popovic, 1989, and comments in Section 8 below).

The slow, but steady increase in litterfall from 1971 to 1976 on unfertilised plots is to be expected in a stand not yet fully closed. A similar development was observed by Flower-Ellis (1985) for at least the first seven years in the youngest stand studied by him, initial age 18 years. Owing to the interruption of our observations in 1977–1979, we cannot identify when a balance between needle production and litterfall was established, but it seems safe to assume that this occurred before the second measuring period (1980–1983). There is evidently considerable between-year variation in litterfall, on both fertilised and unfertilised plots. The exceptionally high litterfall on fertilised plots in 1976 is likely to have been caused by some external factor, affecting fertilised more than unfertilised pines (*cf.* the remarks above, regarding possible regional patterns). Basal area growth at Lisselbo decreased markedly from 1974 to 1977, more so on N-fertilised plots than on controls (Fig. 5.2*b*). The summer of 1976 was dry, and that of 1975 also had lower precipitation than normal (Aronsson *et al.*, 1999). It is known from Australia that litterfall in *Pinus radiata* (D.Don.) is increased by drought, especially after fertilisation (Raison, Khanna, Benson, Myers, McMurtrie & Lang, 1992).

Litterfall measured in E42 (Fig. 7.3*a*) is lower than the biomass of either C or C+1 needles measured in the early spring of 1975 in E40. There are several possible explanations for this, all of which probably make some contribution: *(i)* Needles lose 25–40% of their dry matter during senescence according to Helmisaari (1992*b*) and needles in litter-traps lose further mass between shedding and collection (Flower-Ellis, pers.comm.). *(ii)* Needles falling in 1972–1977 were to some extent formed before 1974, well before canopy closure. *(iii)* Tree growth on controls was 20% higher in E40 (with biomass data) than in E42 (with litter data) during the whole period 1971–1985. Tree growth is related to needle biomass (Albrektson *et al.*, 1977).

Mean annual litterfall on individual plots for two periods, 1972–1977 and 1980–1983, has been presented by Aronsson *et al.* (1999), together with stem volume growth for the same plots for periods as close as possible to the litterfall periods. For fertilised plots they found no positive correlation between stem growth and litterfall. The interpretation of this may be that litter production (1575 ± 101 kg ha^{-1}yr^{-1} in the first period, 1722 ± 79 in the second period) had already reached a level at which moderate changes in needle production had little or no importance to tree growth. For unfertilised plots, the corresponding litter amounts were 564 ± 78 and 1082 ± 98 kg ha^{-1}yr^{-1}, and the correlation coefficient was $+0.66$ for both periods. This implies a formal p value of <0.05, under the somewhat dubious assumption that treatment effects other than that of NPK can be neglected. None of these other effects has been statistically confirmed in Expt E42; all that can be said is that there seems to be a limit to litter production at Lisselbo, close to the conditions on fertilised plots, and that the unfertilised plots were below this limit during the periods of litterfall measurent.

It remains to discuss whether long-term trends occur in chemical composition of litter. Fig. 7.1*b* demonstrated a downward trend in litter N concentrations during the first few years, but according to Fig. 7.1*c*, there were relatively small changes after 1974. Treatments with and

without NPK differed in N concentration even in 1980, when analyses were discontinued (Fig. 7.2*b*). For data on other nutrients (P, K, Ca, Mg and Mn), see Aronsson *et al.* (1999).

Fig. 7.3*b* demonstrates annual trends in amounts of N returned in needle litter on plots with and without fertilisation. Fig. 7.3*a* and *b* illustrate well the conclusion by Miller (1981) and others, that the role of fertilisation in young stands is to accelerate canopy closure and to establish nutrient cycling, in this case N, between stand and soil.

At the same time, the figure illustrates a difference in ecological behaviour between evergreen and deciduous species, which has been discussed by several authors (Waring & Schlesinger, 1985; Monk 1966; Chapin, Vitousek & van Cleve 1986; Flanagan & van Cleve, 1983). In both types of species, large amounts of nutrients are allocated to the photosynthesing organs, and some resorbed before shedding of leaves and needles—often more efficiently from leaves. However, in overwintering needles the same nutrients can be used during several seasons, which outweighs the possibly lower degree of resorbtion. The final result is that many evergreen conifers have a high nutrient-use efficiency (Waring & Franklin, 1979; Vitousek, 1982)

A further consequence is that pine has a competitive advantage on poor sites (as well as its ecological companions *Calluna vulgaris* (L.) Hull and *Vaccinium vitis-idaea* L.), *viz.* that during the phase of stand establishment, only a small fraction of the N taken up is returned to the soil in the same year, while deciduous species must return a much larger proportion of the annual uptake. The combination of internal nutrient economy with production of litter having a relatively slow decomposition rate, appears to be a fully sufficient explanation for the ability of pine to compete successfully on poor sites.

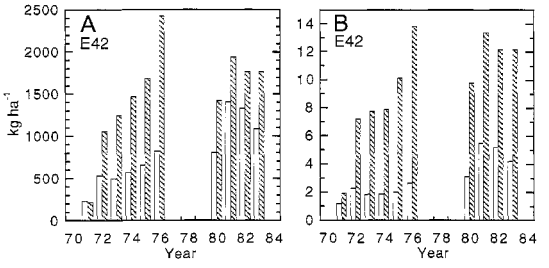

Fig. 7.3. Annual trends in dry mass of needle litter and corresponding N amount for treatments with and without NPK in E42, 1971–1983. (A) Dry mass of needle litter. (B) Amounts of N. Amounts of N for 1981–1983 were calculated under the assumption that concentration remained unchanged from 1980 (*cf.* Fig. 7.1(C)). Open bars: plots without NPK. Hatched bars: plots with NPK.

Studies in plant and soil biology at Norrliden and Lisselbo

Since the early 1970s, several individual scientists and research groups have used our experimental plots for sampling or experimentation, aimed at answering questions generated within their own projects. We welcomed this development, the only restriction being that such activities should not interfere with our own research. In some cases we changed the management to accomodate particularly important ancillary projects. Many of these activities have had a direct or indirect bearing on our project aims, and have then been quoted when discussing our own results, here or in previous publications (Tamm & Popovic, 1989; 1995). However, in some cases the scientific results of these ancillary projects are themselves of great interest, in addition to their relevance to the discussion of our results. Here, some of these activities are reviewed, which are covered briefly or not at all elsewhere in the text.

Vegetation changes

As is normal for experiments in which N is added to Swedish coniferous forests, the field vegetation responded rapidly, initially in the form of a luxuriant growth of *D. flexuosa*, which occurred sparsely and as small specimens before treatment. Dwarf shrubs and bottom-layer species mostly reacted in a negative direction, especially on plots with more intensive treatments (high N regimes, particularly if combined with PK or other elements, *cf.* Plate IV). However, most of our own observations have been qualitative only. Vegetation samples for determination of standing crop and nutrient content were collected in several treatments of E57 in 1980 and are discussed by Aronsson *et al.* (1999).

A very thorough inventory of the vegetation of the Lisselbo experiments was made by Dirkse in August 1987, and a corresponding inventory of Norrliden by van Dobben and Dirkse in August 1988 (van Dobben *et al.*, 1992; Lisselbo) and van Dobben *et al.* (1999; both sites).

The inventory comprised entire net plots (400 m^2), the percentage cover of each species being scored on a ten-point scale on each plot. The statistical analysis was made both at individual species level, using ANOVA and multiple regression analysis, and at vegetation level, using multivariate techniques such as least-squares redundancy analysis (RDA), a canonical form of principal-component analysis. Many of the results can be visualised in biplot diagrams, in which the most important axis (principal component) primarily reflects the N regime. Other treatments, such as acidification and liming, had some effect, but related to the next axis of importance. PK addition alone had little or no effect in E55, but possibly some effect, in the same direction as N, in E40. Given with N, PK appeared to reinforce the N effect. A comparison with Ellenberg's indicator values (Ellenberg, 1979; Ellenberg, Weber, Düll, Wirth, Werner & Paulissen, 1991) showed good agreement between conclusions based upon indicator plants and those based upon RDA. There were also many similarities between N-fertilised plots at Norrliden and Lisselbo on the one hand, and non-fertilised pine forest at Harderwijk in the Netherlands on the other; this forest has long been exposed to high atmospheric deposition of N. A number of interesting observations at species level may also be found in the references given.

Soil fauna

In recent years, a great part of the soil biology studies carried out in Swedish forest soils has been connected with acidification studies (Staaf & Tyler, 1995). This also applies to several studies carried out at the Norrliden and Lisselbo sites, references to which are given by Tamm & Popovic (1995). However, in the early 1970s it was known from Finnish and Norwegian studies, that several soil animals reacted to fertilisation containing N: in Finland, NPK (Huhta, Karppinen, Nurminen & Valpas, 1967; Huhta, Nurminen & Valpas, 1969) and in Norway, urea (Abrahamsen & Thompson, 1979). A soil biology group at Uppsala University, involved in planning the SWECON project, wished to obtain experience from a coniferous forest, and at the same time, to extend work done in Finland and Norway on more conventional forest fertilisation, to less 'unnatural' fertiliser regimes (repeated low additions). Pilot studies were therefore made at E40 Lisselbo in May and August 1971, followed by an extensive sampling of all N0, N1 and N3 plots in October (Axelsson, Lohm, Lundkvist, Persson, Skoglund & Wirén, 1973). Differences between N1 and control plots were usually not significant, but with fertilisation there was a trend towards lower numbers of many species, a trend even more pronounced when N3 was compared with N1 and the control. Several species of Collembola showed statistically significant decreases, as did the group of oribatid mites.

Occurrence of fungal fruiting bodies

While determination of sterile fungal species has been extremely laborious until the recent introduction of DNA identification techniques, inventory of fruiting bodies is a convenient way of studying changes in the fungal flora, if it is borne in mind that such inventories give biased results. The effect of a certain treatment on fruiting body frequencies may differ from its effect on the mycelium and its function. Furthermore, ecologically important species may form fruiting bodies rarely or not at all.

At Lisselbo, two inventories were made, in September 1980 and 1981 (Wästerlund, 1982). He determined the total fresh mass of fruiting bodies of mycorrhizal fungi from transects comprising 120 m^2 from each net plot studied (400 m^2). Most studied plots belonged to E40, but some treatments of E41 and E42 were also sampled. More treatments were sampled in 1981 than in 1980, but plots sampled in both years (*e.g.* controls, N1 and N3PK) showed good agreement between years in species composition, even if fruiting-body mass was much higher in 1980. N addition decreased fruiting-body mass from regime N2 upwards, at the same time as species diversity decreased from level N1. *Lactarius rufus* was the dominant mycorrhizal species on fertilised plots, but *Paxillus involutus* also increased. Additions other than of N had small effects only.

Further inventories were made in 1986–1988 at Lisselbo and 1989–1990 at Norrliden, by B. Gahne. The results are only partly available in figures or tables, but Fig. 7.4 (from Persson, Wirén, Andersson & Gahne, 1989) demonstrates changes similar to those reported by Wästerlund, such as the sensitivity of mycorrhi-

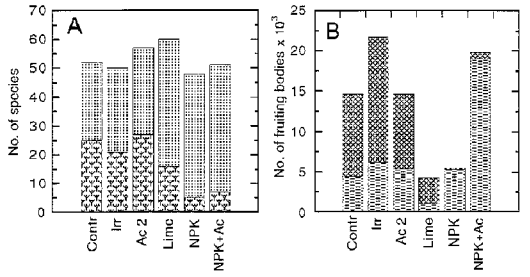

Fig. 7.4. Inventory of fungal fruiting bodies in E42 Lisselbo in the autumn of 1988. (A) Numbers of species; the upper part of the bars represents decomposer species and the lower, mycorrhizal species. (B) Numbers of fruiting bodies of mycorrhizal species, with the species *Lactarius rufus* at the base, the sum of other species above. Redrawn from Persson *et al.* (1989).

zal fungi to fertilisation, and the tolerance (or even positive reaction) of *Lactarius rufus* to acidification and fertilisation, but not to liming.

Fig. 7.4*a* demonstrates, in addition, that litter- and wood-decomposing fungi, as a group, tolerate fertilisation, acidification and liming much better than mycorrhizal species, and even appear to be favoured by some of these treatments, perhaps because more litter, both woody and needle, has been produced on the fertilised plots.

A decrease in the production of fruiting bodies by ectomycorrhizal species on regular N addition has been reported by Rühling & Tyler (1991) from an experiment in mature beech forest in southwestern Sweden. Several litter decomposers increased, while wood decomposers were little affected.

Amino acids in needles

In 1984, it had become increasingly clear that some of the treatments had caused unbalanced nutrition in spruce trees in another of the optimum nutrition experiments, E26A Stråsan. Because of this, needle samples were collected in two different seasons from some plots, for amino-acid analysis. The results of the first analyses were reported by Aronsson (1985), *viz.* that needles from high N regimes, but not supplied with P, contained remarkably high arginine levels, together with somewhat elevated levels of ornithine and lysine. The next sampling, comprising more plots, confirmed the results (see Fig. 5.2. in Tamm, 1991). Arginine accumulation in conifer needles following fertilisation with N had earlier been found by Durzan & Stewart (1967), and others.

Further analyses were made at the Forestry Faculty in Umeå. This work resulted in a series of publications, several of them using samples from the experiments at Norrliden and Lisselbo. Here we shall briefly review some of their results, to which we return in Section 10.

The first Norrliden sampling was a study of seasonal variation in several amino acids, protein and total N in pine needles from E55 controls, N2PK, N2 and N3 plots (Näsholm & Ericsson, 1990), extending from May 1987 to May 1988. Variation occurred in most of these constituents, except arginine on control plots, which occurred in traces only. Total N, protein N and arginine had less seasonal variability in concentration than did asparagine, glutamine, glutamic acid, γ-aminobutyric acid (*gaba*) and proline. Glutamine and proline had maxima during spring and early summer and low concentrations during the rest of the year, while glutamic acid, asparagine and *gaba* had longer periods with high concentrations and shorter with low concentrations. All of the variables studied differed between the investigated N regimes, the lowest level occurring in controls and the highest in N3. While total N varied between *ca.* 10 mg g^{-1} in controls to 20–25 mg g^{-1} on N3 plots, arginine concentrations varied from $<0.5\%$ of total N in controls, to 2–5% in N2PK and 7–16% in N2, and 10–27% in N3. The authors found relatively small differences in protein N between the different fertilised plots (but a considerable increase compared with the control). They conclude that a maximum level of needle protein had been attained before much arginine had accumulated, and that further N taken up remains in the needles as arginine.

The problem of the function of arginine in needles of fertilised trees is further discussed by Näsholm (1994), also using samples from E55 Norrliden. He compared total N, protein N and arginine N (μg $needle^{-1}$) between green and senescent needles of the same age from the control and N1 and N2 treatments. Senescent needles from control plots contained 50% less N and N1 senescent needles 65% less N than green needles from the same trees. N2 senescent needles differed from green needles by 44%, the difference from N1 being largely explicable as a retention of 77% of their arginine content (17% of total N in green needles). Neither control nor N1 needles contained large amounts of arginine. The conclusion was drawn that the function of

arginine in trees with a high uptake of N is more to bind surplus N (and ultimately to remove it in litterfall), rather than to store it for later metabolic use. There were also differences in ^{15}N concentrations between green and senescent N2 needles, possibly caused by volatilisation of ammonia during senescence.

The most recent publication on arginine concentrations in pine needles from the optimum nutrition experiments concerns the possibility to compensate for the nutritional imbalance caused by excessive N supply. It deals with a small, new experiment on some of the previously heavily fertilised plots of E40 Lisselbo (Edfast, Näsholm, Aronsson & Ericsson, 1996). It was shown that trees given 60 kg N $ha^{-1}yr^{-1}$ (=regime N3 resumed) maintained high arginine concentrations. Former N3 trees receiving PKMg or NPKMg returned rapidly to values close to the controls. The authors emphasise the possibility of using arginine concentration as an indicator of nutrient status in pine.

Litter decomposition

The first extensive soil biology studies at Norrliden (Bååth, Berg, Lohm, Lundgren, Lundkvist, Rosswall, Söderström & Wirén, 1980) also comprised decomposition studies by the litterbag technique, but concerned only the effects of soil acidification (E57), which retarded the decomposition rate, as was also found in some other experiments (Berg, 1986*a*)

New series of litterbags were, however, laid out on six occasions during 1983 to 1985 on three plots of E55 (Control, N1P2 and N2P2) and incubated for a year (Berg, Tamm & Aronsson, 1991). The litter was the standard 'unified needle litter', extensively used by Berg and collaborators, *e.g.* in transects across Europe, but local litter from some treatments was also analysed chemically. The litterbags lost mass slightly faster on fertilised plots during the the first year, but the between-year variation was large enough to cause overlaps between treatments. As in earlier experiments (Berg 1986*b*), lignin concentration strongly influenced the decomposition rate in the later stages.

The litterbag data from Norrliden were used by Berg and collaborators in the transect studies mentioned above (Berg, Berg, Bottner, Box, Breymeyer, Calvo de Anta, Couteaux, Gallardo, Escudero, Kratz, Madeira, Mälkönen, Meentemeyer, Muñoz, Piussi, Remacle & Virzo de Santo, 1993). Needle litter with different concentrations of N and of some other constituents, organic and inorganic, was collected from E40 plots at Lisselbo (Meentemayer & Berg, 1986). These samples were used in litterbag experiments (Berg & Staaf, 1980; 1981; Berg, Staaf & Wessén, 1987; Berg *et al.*, 1993).

Nitrogen and other plant nutrients as factors regulating primary production in young pine forest ecosystems

In most forest ecosystems, including those studied here, most of the primary production takes place in the trees. It is also clear that this production is affected by the N regime and, to a lesser extent, by additions of other plant nutrients. Some growth and biomass data were presented in Sections 5 and 6, respectively, and Tables 5.4–5.7 show statistical tests of treatment differences in stem volumes.

However, the mechanisms behind the differences found have not been discussed. Since physiological studies have been made on our sites to a very limited extent only, our discussion here will concentrate on the relationships between nutrient concentrations in needles, the amounts of needles, and the resulting production of aboveground biomass fractions. This is, of course, not a new approach, and has earlier been used on data from our experiments (Albrektson *et al.*, 1977). However, the unique feature is the long-term measurements of tree growth and foliage nutrient concentrations during controlled fertiliser regimes, supplemented with biomass data.

Some of the questions posed in the Introduction concerned the difference between the functions of forest ecosystems at optimum nutrient levels, as compared with those at higher or lower levels, and the possibility of defining tree nutritional status from foliar concentrations of nutrients. Here we discuss some of these questions. Further discussion of the topic follows in Sections 9 and 10 below, including the possibility that alternative ways of expressing nutritional status may offer advantages over concentrations per unit biomass.

Statistical tests of tree growth relationships with foliage nutrient concentrations

The statistical analyses in Table 7.1 report results of multiple regression analyses with stem

volume growth as depending on needle concentrations of six plant nutrients and two parameters describing initial stand or site conditions (Bjørgung index, BI, see Section 2) and soil stoniness (Si_{30cm}), respectively. As the experiments were designed to include both suboptimal and supraoptimal N levels, both N and N^2 were included in the tests, though there was no reason to suspect strongly supraoptimal values in other element concentrations. In Table 7.1, only variables are included which contribute markedly to the explanatory value of the regression function, the limit being set at $p=0.1$ (except that both N terms were included, even when the first-order term was not significant; see below). The choice of the high p value, 0.1, does not imply that the parameter in question is considered significant, but that it may facilitate detection of similarities between the three experiments (E55U, E55AN and E40), possibly also between the two periods studied. The R^2 values for the equations vary between 0.54 and 0.73.

From Table 7.1 it is clear that stem volume growth and foliar N concentration are significantly related in all six cases, although the importance of the linear and the quadratic N terms varies in the 'type I analysis'. Error estimates for the coefficients (Table 7.2) confirm that both terms contain information. The optimum N concentrations which can be derived from the regression equations are discussed below, together with Fig. 7.5, 7.6 and 7.8.

In all three experiments, the variable BI is important during the first period, which is logical, as initial stand conditions are more important before stand closure than later (Tamm & Popovic, 1989; see also Section 2). The stoniness index contributes significantly in E55U and E40 during the second period.

Nutrients other than N make, in most cases, a relatively small contribution, or no contribution, to statistical significance. In addition, nutrient concentrations are not fully indepen-

A. E55U 1972–1979 $R^2=0.779$

Source of variation	D.f.	Sum of squares (Type I)	F value	P value
Total	19	2088.03		
N	1	225.15	7.32	0.0163
N^2	1	712.89	23.17	0.0002
BI	1	540.02	17.55	0.0008
Mg	1	148.52	4.83	0.0441
Error	15	461.45		

B. E55U 1980–1989 $R^2=0.795$

Total	19	4498.06		
N	1	13.91	0.24	0.63
N^2	1	3247.10	56.31	0.0001
Si_{30cm}	1	314.45	5.45	0.0329
Error	16	922.60		

C. E55AN 1972–1979 $R^2=0.449$

Total	19	2195.99		
N	1	236.88	3.13	0.0958
N^2	1	479.76	6.58	0.0207
BI	1	251.46	3.33	0.0870
Error	16	1209.89		

D. E55AN 1980–1989 $R^2=0.526$

Total	19	5881.81		
N	1	330.29	1.89	0.1877
N^2	1	2222.67	12.75	0.0026
Mg	1	539.06	3.09	0.0978
Error	16	2789.79		

E. E40 1972–1977 $R^2=0.542$

Total	31	2247.21		
N	1	0.64	0.02	0.9860
N^2	1	764.94	20.88	0.0001
BI	1	448.66	12.20	0.0016
Error	28	1029.96		

F. E40. 1978–1988 $R^2=0.722$

Total	31	10103.31		
N	1	1831.90	16.28	0.0005
N^2	1	1958.18	17.40	0.0003
Si_{30cm}	1	1249.29	11.10	0.0027
Ca	1	2.78	0.02	0.88
P	1	863.12	7.67	0.010
Mg	1	1385.14	12.31	0.0017
Error	26	2812.90		

Table 7.1. *Statistical dependence of stem volume growth on foliage nutrient concentrations and two covariates, one related to initial stand vigour (Bjørgung index, BI), and one related to site quality (stoniness index, Si_{30cm}). The terms N and N^2 are always included but other variables only when they contribute significantly or almost significantly ($P \leq 0.1$) in either type I or type III tests (cf. also SE of parameter estimate in Table 7.2). A. Expt E55U, period I; B, E55U II; C. E55AN I; D. E55AN II; E. E40 I; F. E40 II*

Table 7.2. *Parameter estimates for the multiple regressions in Table 7.1. Estimates with the standard error of the estimate below. The dependent variable is the total stem volume growth in* $m^3\ ha^{-1}$ *during the period specified, and the concentrations are given in mg* g^{-1} *DW,* Si_{30cm} *is measured in cm, for BI see Section 2, Tree growth measurements. The column* N_{opt} *indicates the optimum nitrogen concentrations (other terms in the equation kept constant)*

Experiment	Intercept	BI	Si_{30cm}	N	N^2	P	Ca	Mg	N_{opt}
A. E55U	−74.6	2.77	–	19.5	−0.63	–	–	−62.2	15.4
1972–1979	±93.1	±0.59		±0.91	±0.26			±28.3	
B. E55U	−475.3	–	1.89	73.4	−2.46	–	–	–	14.9
1980–1989	±73.7		±0.81	±9.4	±0.31				
C. E55AN	−137.5	1.33	–	21.7	−0.59	–	–	–	18.4
1972–1979	±67.8	±0.73		±7.8	±0.23				
D. E55AN	−448.8	–	–	63.9	−2.08	–	–	90.0	15.3
1980–1989	±144.3			±17.2	±0.58			±51.2	
E. E40	−76.8	0.36	–	9.3	−0.23	–	–	–	20.2
1972–1977	±20.8	±0.10		±2.0	±0.05				
F. E40	−367	–	1.26	39.1	−1.06	−50.2	37.8	112.2	18.4
1978–1988	±88		±0.30	±7.5	±0.20	±24.3	±12.6	±32.0	

dent variables (*cf.* Section 4). The concentrations of most other nutrients are depressed by high N additions, leading to high N concentrations. Also, P, K and Ca were added together. For period I, Mg is the only nutrient besides N to show a significant relationship with growth ($p = 0.044$ in E55U). However, the regression coefficient has a negative sign in Table 7.2, which suggests that there is no direct causal relationship, rather an indirect N effect, as described above. The apparent negative effect of P (E40, period II) might be similarly explained. The positive 'effect' of Ca (E40, period II) is not significant in the 'Type I test', and perhaps needs no discussion, with regard to all the types of soil change in which Ca may participate. There is a single case of a positive 'effect' of a studied element (apart from N), where there is reason to believe in a more direct relationship with tree growth, *viz.* Mg in E40, period II. The p value is 0.0017 and the coefficient positive. It may be noted that in E55AN, period II, there is also a positive Mg coefficient, though the p value is non-significant (0.098). The likelihood that Mg limitation has been induced in our experiments, is further supported by the low Mg concentration at high N regimes, discussed in Section 4, and the observed symptoms of Mg deficiency (Plates VII, VIII).

Examples of correlation coefficients between the individual elements (expressed as r values) are found in Table 7.3. Bioelement concentrations are often intercorrelated in organisms, and the table illustrates the danger of drawing conclusions from simple correlations, apart from some obvious statements such as that the concentrations of P and K are intercorrelated (as they were added together). A similar correlation matrix for the Norrliden experiment is presented by Aronsson *et al.* (1999).

The relationships between tree growth and N concentrations illustrated in Tables 7.1 and 7.2 are in good agreement with general experience from experimentation with N addition in boreal forests (Tamm, 1991; Mälkönen, Derome & Kukkola, 1990; Pettersson, 1994). The influence of the covariates BI and Si_{30cm} is also easily understood. The lack of earlier Swedish evidence for the importance of Si_{30cm} may be due to the fact that stoniness may have both positive and negative effects on site quality; positive on soil physical properties, and negative by reducing the amount of 'fine earth'. These influences may balance each other in heterogeneous data sets.

Comparison with earlier attempts to use foliar analysis in forest research

As was noted in the Introduction, Mitchell & Chandler (1939) attempted to use foliar analysis as a tool for determining tree nutrient status, and performed N dosage experiments already in the 1930s, to obtain foliage concentration standards; our attempts to use the same approach led eventually to the experiments described here.

The problems of sampling technique in foliar analysis of trees were answered empirically in the 1950s (see Leyton, 1958; Tamm, 1964*a*, for references), when a consensus was reached that

Table 7.3. *Expt 40. Direct correlation coefficients (r) between foliar concentrations of six elements and stem volume growth and, below the r value, its probability value (italics), if ≤0.1. Values above and to the right of the empty diagonal concern the period 1972–1977; values below and to the left, the period 1978–1988. Element concentrations in mg g^{-1} DM. (A). Treatments with low nitrogen regimes (N0 and N1), 16 plots*

(A)	N	P	K	Ca	Mg	Mn	Stem growth
N		0.50	0.23	−0.58	−0.78	−0.42	0.66
		0.05		*0.02*	*0.0003*	*0.10*	*0.005*
P	0.41		0.65	0.10	−0.54	0.04	0.46
			0.006		*0.03*		*0.07*
K	−0.33	0.57		0.30	−0.23	0.25	0.46
		0.02					*0.07*
Ca	−0.27	0.63	0.71		0.55	0.44	−0.32
		0.01	*0.002*		*0.03*	*0.09*	
Mg	−0.14	−0.46	−0.55	−0.53		0.26	0.59
		0.07	*0.03*	*0.03*			*0.02*
Mn	−0.29	0.07	−0.06	0.38	−0.16		−0.50
							0.05
Stem growth	0.31	0.16	0.09	0.10	0.22	−0.49	
						0.06	

(B). Treatments with high nitrogen regimes (N2 and N3), 16 plots for inter-element correlations, 14 plots for relations with stem growth

(B)	N	P	K	Ca	Mg	Mn	Stem growth
N		−0.52	−0.67	−0.54	−0.38	0.28	−0.52
		0.04	*0.004*	*0.03*			*0.04*
P	−0.59		0.85	0.53	0.13	0.28	0.17
	0.02		*0.0001*	*0.03*			
K	−0.64	0.91		0.59	0.06	−0.02	0.21
	0.01	*0.0001*		*0.02*			
Ca	−0.66	0.87	0.89		0.37	0.25	0.61
	0.006	*0.0001*	*0.0001*				*0.01*
Mg	−0.19	−0.45	−0.50	−0.34		−0.07	0.72
		0.08	*0.05*				*0.002*
Mn	0.24	0.20	0.02	0.20	−0.30		−0.09
Stem growth	−0.72	0.07	0.22	0.22	0.47	−0.53	
	0.002				*0.07*	*0.03*	

sampling needles from well specified positions at the beginning of the dormant season gave the most reproducible data for temperate conifers. Nevertheless, there was a feeling that other sampling dates might give other, and perhaps more valuable, information (Waring & Youngberg, 1972; Linder, 1995). Some researchers have analysed organs other than needles, *e.g.* phloem (Hohenadl, Alcubilla & Rehfuess, 1978) or xylem sap (see Dambrine, Martin, Carisey, Granier, Hällgren & Bishop, 1995, with further references), to find out whether such components reflect tree nutrient status better than needles. However, some of these procedures are more destructive than needle sampling, and therefore less suited to monitor tree nutrient status for long periods. Moreover, there is usually a correlation between the concentrations of each nutrient in different organs of a tree (Section 4). We see no reason to prefer tissues other than needles from specified positions for sampling, in long-term studies on sites where N is in limited supply.

Several authors, *e.g.* Heinsdorf (1963), have found excellent relationships between stem growth and the content of N or other nutrients per 1000 needles. While such regressions may be of interest in certain cases, we consider that they add little information on how nutrient status affects growth. The reason is that in an individual tree, almost all expressions of tree vigour, such as height or basal area growth for the current or previous seasons, and the dry mass of needles from specified positions, are closely interrelated (Tamm, 1964*b*). Regressions of tree growth on 1000-needle mass or needle content in mg of element per needle, thus involve some circular reasoning.

Problems concerning the nature or even the existence of a defined optimum status with respect to one or more plant nutrients, are more difficult to solve than are sampling problems. In this section, we use a traditional empirical approach, relating tree growth to nutrient regimes, foliar N concentrations, and needle biomass. In Section 10 we briefly describe historical developments in forest nutrition, and compare our data with those from other studies, including studies based on Ingestad's concepts.

What follows here concerns results from Expts E55 and E40. Some interactions with other factors, *e.g.* water supply, are therefore omitted, but some are returned to in Section 8 and in the final discussion (Sections 9 and 10)

Tree growth in relation to N regime or foliar N concentration

As was discussed in the Introduction, meaningful relationships between nutrient status and growth reactions are difficult to establish, unless both nutrition and growth are reasonably constant over time. The growth-rate of a plant can be measured over different time-scales, for the entire plant or for some specific organ. In forest trees, it is common to measure stem volume periodically, and to present the results as annual volume growth, or to measure basal area growth on increment cores at the end of an experimental period. For ecological questions, continuous measurement of the production of biomass of the whole tree, or of crown fractions, would be preferable, but is not really feasible (*cf.*, however, Brix (1981, 1983). We therefore used conventional mensurational methods to measure tree growth, trusting that they reflect more fundamental production processes, without necessarily being linearly related to them. In young stands, stem volume or basal area growth can be expected to follow a sigmoid curve, first with an exponential rise, followed by a flattening-out. Tamm & Popovic (1989) concluded that even if E42 and E57 followed this general pattern, the deviations from linearity were moderate on unfertilised plots. This conclusion is confirmed in Fig. 5.6*c* for E55AN and U and E40. The effect of the different nutrient regimes has of course changed the shape of the curves, but most of the curves for regimes N1 and N2 in Fig. 5.5 and 5.6 do not deviate much from parallelism with the horizontal control line during the latter part of the experimental period, which implies a reasonably steady growth-rate. Growth-rate in regime N3 decreases in all cases after an early culmination. Data on stem growth for shorter periods between measurements are presented by Aronsson *et al.* (1999).

We have earlier found a large between-year variation in tree growth (Fig. 5.2), as well as in foliar nutrient concentrations (Fig. 4.1–4.6). However, these variations are to a large extent synchronous between controls and elevated N regimes. At least during the last measurement periods (1980–1989) in E55 in regimes N0, N1 and N2, the differences between N regimes in growth and foliar N level were relatively constant, while variation was larger in N3. Variation with time was also somewhat greater during 1978–1988 in E40, but still lower than at the beginning of the experiment. Growth and foliar N concentrations, at least, have been far more constant than usually is reported from conventional field fertiliser experiments.

It should also be recalled that increasing allocation of resources to stem growth is characteristic of the development of young stands (Möller, Müller & Nielsen, 1954). To the small extent that a curvature can be traced in Fig. 5.6*c*, *viz.* in the curve for E40 controls, this might be explained by increasing allocation of resources to stem growth, rather than by an increase in aboveground production.

The first test made is illustrated in Fig. 7.5, *viz.* a comparison between the dependence of stem volume growth in E55 on either foliar N concentrations (Fig. 7.5*a*) or N regime (Fig. 7.5*b*). The two curves are very similar, but

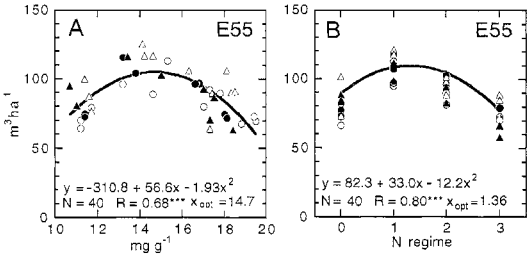

Fig. 7.5. Stem volume growth 1980–1989 in E55U and AN Norrliden, plotted (A) against mean foliar N concentration during the same period, and (B), against N regime. Symbols for treatment groups: dots U; triangles AN; open symbols without PK, filled symbols with PK. The regression line is common to all 40 plots; for equations for individual treatment groups, see Table 7.4.

the curve in *b* (regimes) has a somewhat better fit, possibly because the range in the *X*-variable is wider (0–3 in N regime) than in *a* (10–20 in mg $N\,g^{-1}$). The correlation coefficients are highly significant in both cases. There is no great difference between E55U and AN or between treatments with or without PK (shown by different symbols). It should also be observed that the curve in Fig. 7.5*b* is valid only under the specific experimental conditions in which it was obtained, whereas the curve in Fig. 7.5*a* is based upon a relationship between physiological characteristics—growth and nutrient status. As was shown by Mitchell & Chandler (1939), such a relationship may have a wider range of applicability.

Fig. 7.6*a* and *b* show curves from E40 Lisselbo, similar to the Norrliden curves in Fig 7.5. The scatter of points appears to be wider at Lisselbo, but the difference in fit between the alternative *X*-variables is small. The optimum N concentration, derived from the equation shown, is not very different between the two experiments, while the 'optimum N regime' is lower at Lisselbo compared with Norrliden, and the presence of PK tends to depress N_{opt} on both sites (Table 7.4). For Norrliden, the optimum N concentrations derived for E55U and AN in Table 7.2 (second period), are not very different from the combined value in Fig. 7.5*a*, while the E40 optimum in Table 7.2 is higher than that in Fig. 7.6*a*. We must then consider the fairly wide scatter in the figure, perhaps also that the function in Table 7.2*f* contains more 'independent' variables (P, Ca, Mg), which are in fact influenced by N additions. When comparing Fig. 7.6*b* with Fig. 7.5*b*, it should be borne in mind that the N additions at Lisselbo were

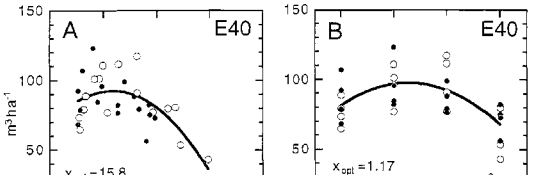

Fig. 7.6. Stem volume growth 1978–1988 in E40 Lisselbo, plotted (A) against mean foliar N during the same period and (B) against N regime. Legend: open dots without PK, filled dots with PK. For equations for treatments without or with PK, see Table 7.4.

reduced by 33% from 1977 onwards, while they were kept constant at Norrliden. It should also be mentioned that E40 needles (from control plots as well as from all plots before treatment) had slightly higher N concentrations than E55 needles (Fig. 4.1 and Table 4.1).

The discussion might have ended here, with the statement that tree growth is related to foliar N concentrations by an optimum-type curve, with optimum values near 15 mg $N\,g^{-1}$ DM. However, Fig. 7.5 and 7.6 do not tell us much about the range of condition in which this result may be valid. In addition, regressions such as those in Fig. 7.5 reveal little about the causal relationships between N status and tree growth. We already know, from Section 5, that the statistical analyses in several cases suggest an influence on tree growth of both the PK treatment and stand variables (BI or initial stem volume). Also, the site variable Si_{30cm}, which differs between and within E55U and AN at Norrliden, has a statistically significant influence at Lisselbo ($p=0.0027$) and in E55U ($p=0.033$) during the period in question (Table 7.1). The relatively few indications in Table 7.1 and 7.2 of the importance of plant nutrients other than N, have already been discussed.

To be able to go a step further than the simple statement above, we have examined in some detail the relationships within the various treatment groups in E55 and E40. For this purpose we have used some of the biomass data from Section 6 in connexion with the foliage N concentrations, and stem growth data, as well as some commonly accepted knowledge about the physiological background of tree growth.

Relations between N status, foliage production, and stem growth

It is a truism that plant primary production depends on the amount of photosynthetic tissues, often best expressed as leaf area index (LAI). However, neither total primary production nor LAI is easy to determine directly, so every means of simplifying the measurements, without loss of essential information, should be used.

The relations between stem growth and the amount of leaves (measured as leaf area) have been discussed in several papers (Waring, Gholz, Grier & Plummer, 1977; Waring, Thies &

Table 7.4. *Parameters for relationships within treatment groups between stem volume growth (m^3 ha^{-1}), needle N concentration (N mg g^{-1} DM), N regimes, and needle biomass (needle kg ha^{-1}) illustrated in Fig. 7.5–7.7. Multiple correlation coefficients, R, with asterisks for significance levels 5, 1, and 0.1%. For measuring periods, see the diagrams*

Expt	Fig. No.	Group	Variable X	Y	Intercept	Coefficient X	Coefficient X^2	No. of plots	R	X_{opt}
E55	7.5A	U	N mg g^{-1}	m^3ha^{-1}	−312	53.9	−1.77	12	0.85***	15.2
		AN			−330	60.0	−2.03	12	0.59*	14.8
		UPK			−652	104.4	−3.56	8	0.96***	14.7
		ANPK			−331	63.9	−2.31	8	0.88**	13.8
E55	7.5B	U	N regime	m^3ha^{-1}	72.9	32.5	−11.6	12	0.83***	1.40
		AN			90.6	34.0	−12.6	12	0.78**	1.35
		UPK			75.8	43.1	−14.9	8	0.94***	1.45
		ANPK			75.8	25.1	−11.3	8	0.90**	1.11
E40	7.6A	AN	N mg g^{-1}	m^3ha^{-1}	−230.0	38.7	−1.13	16	0.80***	17.1
		ANPK			−138.4	31.4	−1.06	16	0.54*	14.8
E40	7.6B	AN	N regime	m^3ha^{-1}	75.6	38.4	−14.0	16	0.72**	1.37
		ANPK			87.6	12.3	−5.9	16	0.56*	1.04
E55	7.7A	U	N mg g^{-1}	needles kg·10^3 ha^{-1}	−13.3	2.37	−0.069	12	0.87***	17.6
		AN			−23.0	3.90	−0.119	12	0.84***	16.4
		UPK			−25.1	4.11	−0.130	8	0.84*	15.8
		ANPK			−11.4	2.47	−0.079	8	0.77*	15.6
E55	7.7B	U	N regime	needles kg·10^3 ha^{-1}	4.62	2.29	−0.53	12	0.88***	2.16
		AN			6.05	3.01	−0.77	12	0.88***	1.95
		UPK			4.81	2.50	−0.61	8	0.86**	2.05
		ANPK			6.00	2.34	−0.69	8	0.93***	1.70

Muscato, 1980; Waring, 1983). The discussion is simplified by the finding that leaf area can be calculated by a conversion factor from leaf mass (within the same species and avoiding sites with strong environmental stresses). Waring *et al.* (1977, 1980) claim that there exists a further linear relationship between leaf area (and leaf biomass) and water-conducting area in the stem (sapwood area). This relationship, if proved, would greatly simplify the calculation of leaf area and biomass. The ratio of leaf area : sapwood area differs between species adapted to climates differing in the severity of water stress, but Waring (1983) presents a list of conversion factors for 14 conifer species, mainly North American.

If growth efficiency is then defined as stem growth per unit leaf area (alternatively, but often more difficult in practice, as total biomass production per unit leaf area), a convenient index is obtained, which, according to Waring (1983), reflects not only environmental stresses (water, nutrients) but also differences in genetic potential.

However, the general validity of the fixed conversion ratios has been questioned, in particular the leaf area : sapwood area ratios (Brix & Mitchell, 1983, Binkley, 1984). Albrektson (1984) tested the relationship between leaf biomass and sapwood area for 16 Scots pine stands in Sweden, including controls and some fertilised plots at Lisselbo. He concluded that a close linear relationship existed within each individual stand, but the scatter of points increased considerably if a combined equation for all the stands was used. Variation could be decreased by introducing ring width as an independent variable in the equation.

Since we have determined needle biomass directly (Section 6), we can test, without using conversion factors, whether leaf productivity (stem growth/leaf biomass) differs between nutrient regimes. However, methods which facilitate measurement of leaf area and leaf biomass are certainly desirable. In the early samplings at Lisselbo and Stråsan, we attempted to measure leaf area, but the device then available gave biased results, with errors increasing non-linearly from large to small needles, and the measurements were discontinued.

Figure 7.7*a* demonstrates the dependence of needle biomass on needle N concentration, and Fig. 7.7*b* that on N regime at Norrliden. Evidently, the relationships obtained resemble those earlier described for stem volume growth as depending on the same variables. The difference in statistical fit between the two *X* variables appears smaller than in Fig. 7.5. This also holds

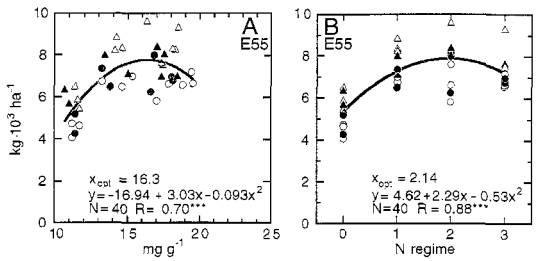

Fig. 7.7. Amount of needles in E55 in 1984, plotted (A) against mean foliar N concentration 1980–1989, (B) against N regime. For legend, see Fig. 7.5 and for equations for individual treatment groups, see Table 7.4.

true when the relations between stem growth and the X variables are tested separately within treatment groups (Table 7.4).

Derivation of an equation is the standard method for establishing optimum values. While the optimum X derived from groups of eight or twelve values may not be highly accurate, there is less variation in the value of optimum X between groups when X is N concentration, than when it represents the N regime (Table 7.4).

Fig. 7.8*a* demonstrates that the relationship

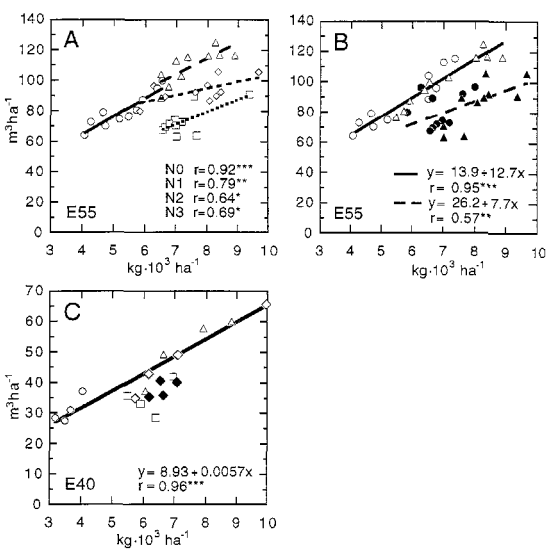

Fig. 7.8. Stem volume growth plotted against needle biomass. (A) E55U and AN, growth period 1980–1989 and biomass data from the spring of 1985, with individual symbols and regression lines for each N regime. Legend: N0 ○, N1 Δ, N2 ◇, N3 □. (B) Low-N regimes (N0 + N1), combined (solid line and open symbols). High-N regimes (N2 + N3), broken line and filled symbols. (C) E40, growth period 1972–1979, biomass data from the spring of 1975. Symbols: *cf.* (A). For regression lines and equations for individual treatments, see Aronsson *et al.* (1999).

between stem volume growth and needle biomass is indeed very close for regimes N0 and N1. For N2 and N3, the relationship is less close, and the same needle mass produces less stemwood in the high than in the low N regimes. Although N1 pine has a higher needle biomass, and produces more stemwood than N0 pine, the N1 regression line is almost a prolongation of that for N0. In Fig. 7.8*b*, N1 and N2 have therefore been grouped together, resulting in a common line with little dispersion of points ($r = 0.95$***). Regimes N2 and N3 form a heterogeneous group, in which single N2 plots fall near the 'low-N' line, but most N2 and N3 are far below it.

With the results from Fig. 7.8*a* and *b* in mind, we return to the Lisselbo material underlying Fig. 2*b* in Albrektson *et al.* (1977). This diagram, together with a similar one from E26 Stråsan, was used to demonstrate the linear relationship between tree growth and LAI in young stands in which self-shading was of little importance. However, when stem volume growth in the period 1972–1977 is plotted against needle biomass (Fig. 7.8*c*), a tendency to lower 'efficiency' appears in two of the treatments (N2PK and N3), while the behaviour of the N2 plots differs little from that of N1 plots during this early stage of the experiment. An increase in needle biomass (in the 'lower' regimes) increases stem growth by 5.5 dm^3kg^{-1}, *i.e.* slightly less than half the effect at 'low N' in E55 Norrliden. However, considering the lower site quality at Lisselbo, and the early stage of stand development, the figure is not unreasonable.

We agree with Waring (1983) that decreased apparent efficiency of a tree stand in producing stemwood can be considered a sign of disturbed tree growth processes, and thus indicates a decrease in vitality. Such changes should therefore be studied in the search for vitality indicators. However, in the case of supraoptimal N supply, lower efficiency is not necessarily evidence of lower photosynthetic efficiency: this is only one of several possible mechanisms. Allocation of photosynthetic products varies with nutrient and water supply, in both the SWECON experiment (Linder & Axelsson, 1982) in Australia (the BFG experiment; Raison & Myers, 1992*b*) and in New Zealand (Beets & Whitehead, 1996). The SWECON results demonstrated that young trees on poor sites allocated more resources to

root production and to new shoots than to stem growth, at least until the canopy was fully closed. An improvement in nutrient conditions may well change this pattern. In addition, Fig. 6.4 and Table 6.3 suggest that old needles are shed earlier in higher N regimes at Lisselbo. This may indicate a less efficient use of the resources allocated to needles, but the difference cannot be great, since the difference in needle longevity is moderate. Mineral soil leaching and acidification in regimes N2 and N3 may imply site deterioration, possibly interfering with root growth and root activity. On the other hand, a direct relationship with the water factor is not expected, since stem growth follows needle biomass virtually linearly over the whole range studied (Fig. 7.8, regimes N0 and N1). An increase in water stress with higher needle biomass would not be unexpected, since irrigation (Expt E58, Norrliden) gave positive growth effects (Aronsson & Tamm, 1982; see also Section 8 below). Similar results have been reported for irrigation even in a rather humid area of SW Sweden (Nilsson & Wiklund, 1992). However, had water availability been a major limiting factor, we should have expected curved regression lines in Fig. 7.8, since higher needle biomass is likely to cause greater water stress.

Traditional optimum curves for tree nutrition: concluding remarks

When Mitscherlich (1909) presented the 'law of diminishing returns', he formulated his equation from theoretical considerations. More recently, Ingestad (1982) described the Mitscherlich curve as a special case of more fundamental principles established in well controlled laboratory experiments. However, there are no generally accepted formulae for plant response to supraoptimal nutrient supply. For field experiments, with many sources of variation except treatment, we have found it acceptable to use simple 2nd degree equations, when they fit the experimental data.

Much of the variation in stem growth between plots in the pine experiments discussed here can be accounted for either by foliage N concentrations or by N regimes. We interpret the relationship as a consequence of increased needle biomass when the N status of the stand is increased up to a certain optimum range, above which either needle function or carbon allocation is disturbed. The relationship between the amount of foliage and N concentration is as good as that between stem growth and N concentration, and the curves are of similar form. For a given N regime, stem growth and amount of foliage are linearly related, although the slope of the regression line decreases with increasing N regime, especially when regimes N0 and N1 are compared with regimes N2 or N3. The dispersion of points around the regression line increases with increasing N regime. The poorer stem growth at higher N regimes cannot be explained by self-shading, as there is no consistent difference in amount of needles between regime N1, and regimes N2 and N3 (Fig. 7.8*a,b*).

As regards the possible characterisation of an optimum range for N in pine needles, sampled as in our experiments, we may note that there is less variation in optimum value when foliage concentration is the independent variable, than with N regime, and that the concentration range 14–17 mg N g^{-1} DM seems to be valid at both Norrliden and Lisselbo, irrespective of whether PK is added or not, or—at Norrliden—whether the source of N is urea or ammonium nitrate (Table 7.4).

If it is asked whether there is a defined optimum point for foliar N concentration with respect to pine growth in the field, our answer must be negative. Optima of empirical curves based on a limited number of plots are not very accurately determined, but the differences between the two sites appear to have a real background. Despite a lower growth-rate, E40 control plots have higher N concentration than E55U and AN controls in almost all years. Before the first treatment, some of the Lisselbo plots had N concentrations close to some of the optimum values in Table 7.4. However, our experiments have not 'falsified' the assumption that an optimum range can be defined for N concentrations, if some variation between both sites and years is allowed for. It must be admitted that our tests were made in young stands on two sites only, albeit with different climates and soils. It should also be noted that the selection of earlier periods in the history of the experiments results in somewhat higher optimum values. This does not really contradict the statement just made, since it is clear from both foliar analyses and from stem growth curves, that the stands were not in anything resembling

steady-state conditions during the early years after the start of the treatments.

Concerning nutrients other than N, the evidence for growth stimulation at increased concentrations is meagre in the data from E55U and AN and E40. Several of the statistically significant relationships found are negative, and probably indicate indirect relations, such as biological dilution or increased leaching, induced by N additions.

The positive correlation between stem growth and Mg at E40 Lisselbo (period II) may indicate a real causal relationship, as suggested by the occurrence of very low Mg concentrations. Nutrient ratios are discussed in greater detail below (Section 10), but the low Mg/N ratios at high N levels at both Lisselbo and Norrliden (Table 4.2) provide some support for the hypothesis of Mg as a growth-limiting element under these conditions (see also Table 7.1*f*). However, the P/N and K/N ratios are also low at high N levels. The addition of PK partly compensates these low ratios, but growth stimulation following addition of PK could be established only when urea was the N source (Table 5.4). With ammonium nitrate the PK effect was negative.

Distribution of native and added plant nutrients in the ecosystem

Distribution patterns

Fig. 7.9–7.14 show the stores of the six bioelements C, N, P, K, Ca and Mg, in the three most important pools in the ecosystem at Norrliden: stand aboveground, humus layer, and upper mineral soil (for P, in the stand only; for the three base cations, the soil data refer to the fraction extractable with 1 M ammonium acetate solution).

We shall first deal with general traits in the diagrams, and their possible causes, which for the soil data includes a brief review of information already presented (Section 3). Aboveground biomass and N pools have also been dealt with earlier (Section 6), but for nutrients other than N, only the concentrations, not the amounts, in biomass components have so far been discussed. Some element-specific characteristics in the diagrams are also indicated.

The diagrams all follow the same pattern, except that soil data for P are lacking. The

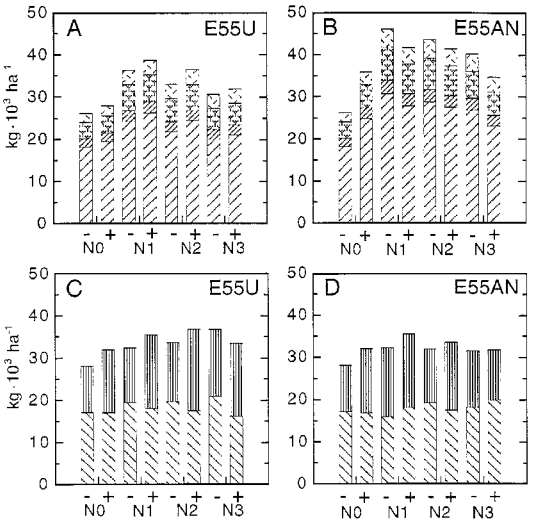

Fig. 7.9. Distribution of carbon in different nutrient regimes in E55U and AN Norrliden. Stand data concern conditions at the biomass sampling in the spring of 1985, and soil data conditions at the sampling in June 1988. Each column is the mean value for three plots without PK (marked −) or two plots with PK (marked +). Individual plot values for soils can be calcultated from mass and concentration data in Aronsson *et al.* (1999). Carbon data for the stand are derived from the biomass data presented in section 6, by multiplying by 0.5. Symbols: bar segments in (A) and (B) represent, from below, stemwood, stembark, living branches and needles; in (C) and (D) mineral soil 0–20 cm and humus layer, respectively.

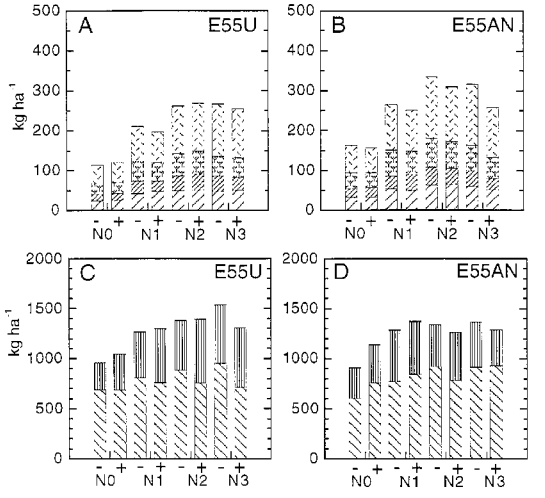

Fig. 7.10. Distribution of N by nutrient regimes in E55U and AN. For explanations and symbols, see Fig. 7.9. (See also text.).

columns are means of three plots (without PK addition) or two (with PK), arranged pairwise for each N regime. For the elements C, K and

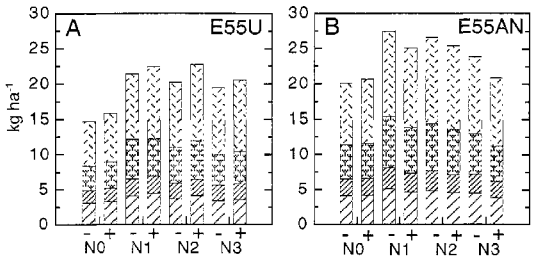

Fig. 7.11. Distribution of total P in the stand in E55U and AN. For explanations and symbols, see Fig. 7.9. All PK plots had received 200 kg P ha^{-1} in 1985, when the stand was sampled.

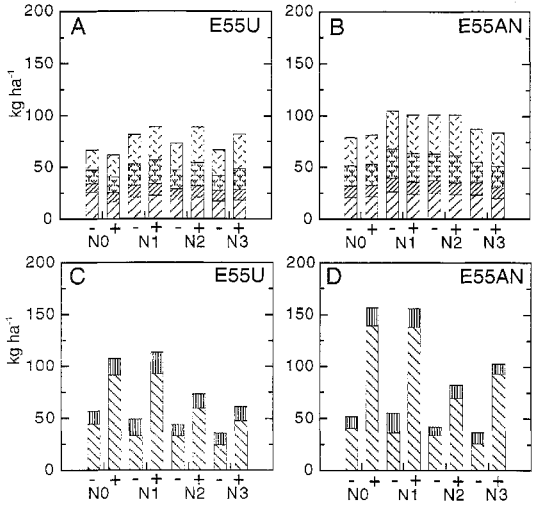

Fig. 7.12. Distribution of total K in the stand and exchangeable K in the soil, E55U and AN. For explanations and symbols, see Fig. 7.9. All PK plots had received 384 kg K ha^{-1} in 1985, when the stand was sampled, and 462 kg K ha^{-1} in 1988, when the soil was sampled. See also Fig. 7.9 and 7.10.

Mg, the same vertical scale has been used for stand and soil data, whereas the soil scale for N is four times the stand scale, and for Ca twice the stand scale.

For C (Fig. 7.9), the diagrams reflect trends already discussed (Sections 3 and 6), *viz.* that stand C increases in regime N1 and may then decrease, while soil C, particularly mineral soil C, is much less affected by the treatments.

The figures for N (Fig. 7.10) also repeat information discussed earlier, but permit comparison between stand and soil. Most of the figures show that both stand and soil accumulate N up to regime N2, but that in E55AN, the pool in the humus layer appears to reach its maximum in N1.

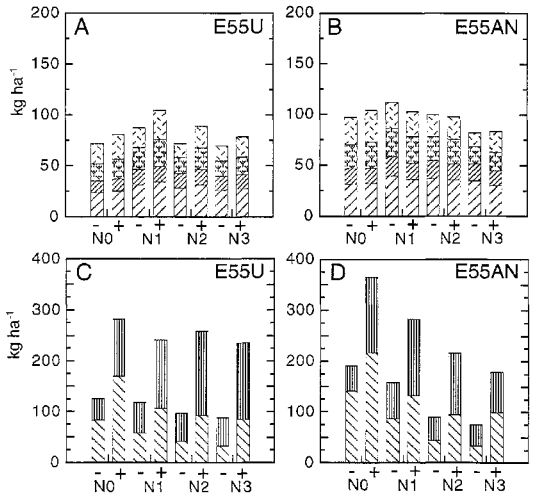

Fig. 7.13. Distribution of total Ca in the stand, and exchangeable Ca in the soil, in Expt E55U and AN. For explanations and symbols, see Fig. 7.9. All PK plots had received 471 kg Ca ha^{-1} in 1985 and 566 kg Ca ha^{-1} (in the PK fertiliser) in 1988. See also Fig. 7.9 and 7.10.

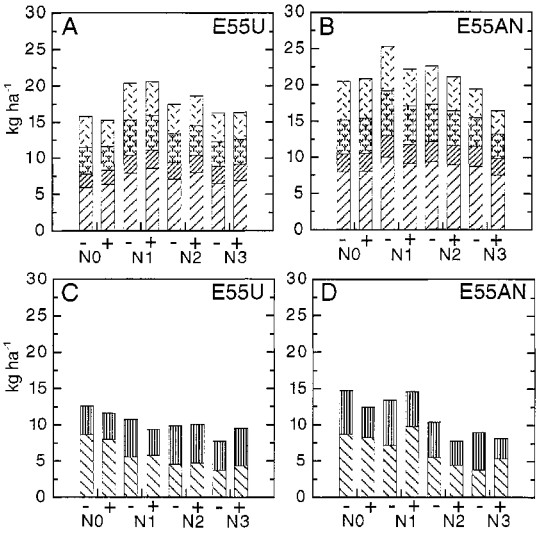

Fig. 7.14. Distribution of total Mg in the stand, and exchangeable Mg in the soil, in Expt E55U and AN. For explanations and symbols, see Fig. 7.9.

Phosphorus in the stand (Fig. 7.11) follows a pattern similar to that for N, almost half the P pool being in the needles. In E55U, the PK treatments have a few kg ha^{-1} more than treatments without PK, while this is not the case in E55AN.

On the control plots of E55U, the amount of K in the stand is approximately the same as the exchangeable amount in the soil, most of which

is in the mineral soil (Fig. 7.12). In the controls of E55AN, there is 50% more K in the stand than in the soil. In the stand, K is more evenly distributed among tree components than are N and P. The pool of K in the stand is little affected by the N regime; a small increase appears to accompany the increase in biomass from no-N, to regimes N1 to N3. In E55U (but not AN), there is a tendency to a PK effect, as in the case of P. In paired comparisons between +PK and −PK for both N sources, however, the amount of exchangeable K in the mineral soil has at least doubled. At the same time, it is evident that much K_{exch} has disappeared from the mineral soil in regimes N2 and N3. On the other hand, K_{exch} in the humus layer is far less affected by the treatments than is that in the mineral soil.

Calcium in the stand is also rather uniformly distributed between tree components, the fraction in the needles being even lower than that for K (Fig. 7.13). In the soil, where there is about twice as much Ca as in the stand, the addition of Ca with the PK fertiliser shows clear effects in both humus layer and mineral soil. Both strata show decreasing amounts in higher N regimes.

The distribution of Mg between stand and soil differs from that of the other elements studied (Fig. 7.14). In all cases, and particularly after N application, there is more Mg in the stand than Mg_{exch} in the soil. The decrease in Mg with increasing N regime affects the mineral soil more than the humus layer, as was the case with K.

Conclusions

Since the recovery of fertiliser N will be discussed below, in connexion with Table 7.5, the discussion here concentrates on differences in the distribution of bioelements in the ecosystem, and on the sensitivity of the distribution of elements to disturbances, such as increased supply of N and other elements. The actual distribution between stand and soil of course changes with time, since both the stand and the humus layer change during a rotation. Changes in the mineral soil, particularly in C and N content, are normally slower, since C has a long residence time in the mineral soil (Tamm & Holmen, 1967) and N mineralisation is much slower in mineral horizons than in the humus layer (Tamm & Pettersson, 1969; Persson & Wirén, 1995).

There are relatively small changes with treatment of P, K, Ca and Mg in the stand, especially as compared with the strong treatment effects on K, Ca and Mg in the soil. We assume that most of the observed decreases in these elements are due to leaching. The alternatives to leaching would be uptake by vegetation or fixation in clay minerals. Uptake by the tree stand can be ruled out, since there is no corresponding increase there. The glacial till at Norrliden has a low clay content (< 5%, Tamm & Popovic, 1989; Melkerud, 1989), and it seems unlikely that heavy N fertilisation should stimulate fixation not only of K, but also of Ca and Mg. Biological and chemical immobilisation is a possibility for P; however, we have no data for soil P.

The most likely explanation of the small differences between stand pools of the elements P, K, Ca and Mg, is that growth has not been limited by the supply of these elements, at least not during the period before the biomass sampling in 1985. The uptake of these elements has been largely determined by the demands of the stand, with marginal increases in P, K and Ca following PK additions.

A more detailed soil study, with consideration of pedological horizons, and samples from deeper horizons, would have been desirable. Use of extractants other than ammonium acetate might have provided information on nutrients less accessible than exchangeable cations. However, even the results reported here have a clear bearing on the function of forest ecosystems in regions with high N deposition. The low retention of added mineral nutrients in the tree stand, the somewhat better retention of K and Ca in the soil, and the increased losses of all three base cations with excessive N supply, are examples of processes of a more general applicability, at least to sites where N has long been a limiting element. The leachability of Mg, together with the uneven partitioning between the exchangeable pool in the soil and the amounts taken up by the stand, is in good agreement with the widespread occurrences of Mg deficiency in areas with high N deposition in Central Europe.

Apparent recovery of added N

Since the fate of the added N is of prime importance in studies of atmospheric deposition, as well as in experiments simulating deposition, we have paid particular attention to N budgets,

even if our resources have not admitted direct measurement of leaching from the system, except in model studies in lysimeters. Such studies were initiated at Lisselbo at an early stage, with both lysimeter containers ('zero tension') and ceramic suction plates. The results from the zero-tension lysimeters have been published (see Tamm, Wiklander & Popovic, 1977; Farrell, Nilsson, Tamm & Wiklander, 1980; Farrell, Nilsson, Wiklander & Tamm, 1984*a,b*; Nilsson, Wiklander & Farrell, 1983). They confirmed a rapid leaching of K, Ca, Mg and S upon addition of fertiliser or acid in the coarse-textured soil, but since tree roots were cut off, they were not suitable for providing data for ecosystem budgets. The early versions of tension lysimeters available at that time did not work well in the medium sand at Lisselbo, and sampling was discontinued. Instead, we have used the indirect approach of estimating the total content of N in the main compartments of the ecosystem after a long period of annual N additions. As will be discussed later, Högberg and his co-workers have confirmed some of our conclusions by studies of N isotope ratios in needle samples from E55 Norrliden (Högberg 1990, 1991; Högberg & Johannisson, 1993), as well from as the spruce experiment E26A Stråsan (Högberg, Tamm & Högberg, 1992). In the latter experiment, Berdén, Nilsson & Nyman (1997) made lysimeter studies of leaching and soil changes, which will also be discussed below (Sections 9 and 10). Our observation of nitrate in the mineral soil, especially in the horizon 0–20 cm, at the sampling in June 1988 in E55 Norrliden (Fig. 3.11), shows the possibility of nitrate leaching from plots fertilised with large amounts of urea or with ammonium nitrate, but does not provide quantitative information.

The retention of N in the soil has been discussed in some detail above (Section 3): we shall therefore concentrate here on N in the stand aboveground. In Table 6.4, recovery was calculated in both kg ha^{-1} and in per cent of added amounts, separately for treatment groups. The total amounts of N were consistently larger in the AN blocks than in the U blocks, but the recovery figures were fairly similar in the four treatment groups. Total recovery increased from regime N1 to N2, but differences between N2 and N3 were small and mostly negative. The percentage recovery figures declined regularly with increasing N regime, as expected. The regularity in the recovery figures makes it meaningful to calculate standard deviations for the means of the treatment groups, as is done in Table 6.4. In Table 7.5, the data for percentage recoveries in Table 6.4 have been combined with those for the soil in Table 3.5. For dead branches, we had to make some simplifying assumptions, as described above (Section 6), and have therefore refrained from estimating a confidence interval. The same applies to the bottom line in Table 7.5, where the data for stand and soil differ by three growing seasons. However, the standard deviations of the means for the main compartments give an idea of the reliability of the estimates for the combined figures.

It is evident that we have not accounted for all N added in the experiment up to 1985 (stand) and 1988 (soil). It should, however, be borne in mind that data for some compartments are lacking. The most important unknown compartments are tree roots (including stumps below 1% of tree height), and mineral soil below 20 cm.

The ground vegetation is also a compartment with a poorly known biomass and N store, *cf.* Section 6. As discussed by Aronsson *et al.* (1999) and Mäkipää (1994), the changes in the understorey of a young pine stand upon fertilisation cannot be expected to lead to much accumulation of N, but possibly to some loss.

The omission of the root compartment prob-

Table 7.5. *Amounts of N recovered in stand biomass, dead branches and soil in different N regimes, Expt E55 Norrliden, per cent of amounts added. The amounts, kg ha^{-1}, are given in Tables 3.5 and 6.4, respectively, but no fully correct error estimates can be made for dead branches and for the total sum. The standard errors are derived from data given in the tables mentioned*

	N1	N2	N3
Stand biomass aboveground	18.4 ± 1.1	15.8 ± 0.6	9.1 ± 0.8
Dead branches	2.65	2.2	1.7
Humus layer Ao	27.8 ± 6.8	13.3 ± 3.5	9.0 ± 2.6
Mineral soil 0–20 cm	18.9 ± 5.8	13.8 ± 3.0	11.3 ± 2.4
Humus layer + mineral soil	46.7 ± 9.1	27.1 ± 4.7	20.2 ± 3.2
Stand and soil	69	45	31

ably leads to larger errors than does the omission of the field and moss layers. Aronsson *et al.* (1999) made some rough calculations on the possible content of stumps and roots, based on data available for boreal stands of Scots pine (Mälkönen, 1973; Albrektson, 1980; Helmisaari, 1991; Finér, 1991; Laiho & Finér, 1996). Some assumptions were made, *e.g.* that wood and bark of coarse roots and stumps had similar N concentrations as the same fractions in stems, and that these fractions increased in proportion to stem DM in unthinned stands, regardless of the cause of the increase (age or fertilisation). Concerning fine roots (< 2 mm), most data show that the increase with increasing N supply is moderate, and that relative allocation of resources to root growth decreases (Linder & Axelsson, 1982; Axelsson & Axelsson, 1986). N concentration in fine roots can be asssumed to increase, but Aronsson *et al.* (1999) found only one study in Scots pine with a fertiliser supply comparable with our N regimes, *viz.* Ahlström, Persson & Börjessson (1988). Liquid fertilisation with complete nutrient solution had supplied 340 kg ha^{-1} by the end of the third treatment year, which was also the sampling year. The treatment did not dramatically change fine root DM or length (measured in ingrowth cores), but the N concentration increased from 9.8 to 16.0 mg N g^{-1}.

Aronsson *et al.* (1999) concluded that to the figures in Table 6.4 should be added 10 kg N ha^{-1} for the control figures and 20 kg N ha^{-1} in regime N2, to account for stumps and roots > 30 mm. If we use the figure for roots < 5 mm from Clemensson-Lindell & Persson (1993) for the control plots at Expt E57 Norrliden, $5.7 \cdot 10^3$ kg DM ha^{-1} and the N concentration 9 g kg^{-1}, the amount of N in this fraction should correspond to 51 kg ha^{-1}. Assuming the same DM for regime N2, and the concentration 16 g N kg^{-1}, the amount should be 91 kg N ha^{-1}. There are several question-marks to be commented on, *e.g.* that the root fraction 5–30 mm has been omitted, but it is evident that the figures for apparent recovery of added N would be increased by several percentage units, had N accumulation in belowground tree compartments been considered.

The other possibly serious omission from our data concerns mineral soil strata below 20 cm. Quantitative data on the amounts of C and N in the deeper horizons of podzol profiles in the boreal regions are not common, and even less is known about mineralisation rates in these horizons. Persson & Sjöberg (in prep.) took new samples in 1994 from 12 plots in E55, four from plots without N (controls and PK), eight from regime N2 (with and without PK. This sampling went down to 50 cm depth. We have compared our data for C and N with theirs for the same plots. Although the sampling methods and the horizon boundaries differed, there are correlations between our plot estimates and theirs. A few deviant values can probably be explained by the different methods for dealing with the variation in stoniness in the two samplings. While it is difficult to say whether changes have occurred during the eight years between the samplings (with more fertiliser added), the preliminary data from Persson and Sjöberg at least do not suggest lower recoveries than our data. Some information about how N is distributed in the profile has also been provided, which is discussed below.

Persson & Wirén (1995) report data from nine sites in south Sweden and eastern Denmark, most of which now carry Norway spruce stands but which have a history of beech or other hardwoods in the past. All sites were podzolised, but to a variable extent. The soil C pool averaged $117 \cdot 10^3$ kg ha^{-1}, of which 25% was in the LFH horizon, 45% in the mineral soil 0–20 cm, 13% in 20–30 cm and 18% in 30–50 cm. The corresponding figures for soil N were 22, 46, 14 and 19%. However, the rates of N mineralisation in laboratory incubations decreased rapidly with depth. In the samples from 20–50 cm, the average rate was only one-third of that in upper mineral horizons. If, for the moment, we disregard the objections which can be made to laboratory incubation as a quantitative measure of N availability, but consider it as a general expression for biological activity, the data of Persson and Wirén suggest that the horizon 30–50 cm may account for about one-tenth of the N turnover in these soils.

However, results from North-European forests must not be generalised—not even to other temperate forests—if they have another climate and history. Studies in the Pacific Northwest of North America (Gessel, Cole & Steinbrenner, 1973) indicate that in these ecosystems, often dominated by Douglas fir (*Pseudotsuga menziesii*

(Mirb.) Franco), the N pool in the soil is usually higher than in boreal forest, and a considerable part of it is in the mineral soil below 30 cm depth. Estimates of recovered fertiliser N indicate that the mineral soil participates actively in N cycling, at least down to the horizon 15–30 cm (Gessel *et al.*, 1973, Heilman & Gessel, 1963*a,b*). If these results are compared with European conditions, it should be borne in mind that human landuse has depleted most European forests for centuries—or even millennia—by grazing, litter-raking and shifting cultivation, and that the generally higher humidity in the Douglas fir region has permitted a long-term accumulation of organic matter and N, partly from symbiotic N fixation.

The preliminary data from the sampling at E55 Norrliden in 1994 by T. Persson & M. Sjöberg (pers.comm.) provide opportunities for comparing the distribution of N (and C) with depth at Norrliden with the data from Persson & Wirén (1995). The horizon 30–50 cm accounted for 17–20% of the N pool in the soil (LFH layer + 0–50 cm mineral soil). No separation was made between the horizons 10–20 cm and 20–30 cm, which together contained 33–36% of the N pool. If we assume that half of this figure refers to the horizon 20–30 cm (probably an overestimate), we arrive at a figure of *ca.* 35% for the horizon 20–50 cm, omitted from our study. The figure 35% is not much different from the average 33% for the more southern sites studied by Persson & Wirén (1995).

According to Persson (pers. comm.), the contribution of deeper horizons to the organic matter turnover and N mineralisation is probably lower in typical boreal podzol profiles than on more southern sites, which often have a history of beech or oak generations before the present conifer stand.

The incubation experiments by Tamm & Pettersson (1969) also speak for a low N mineralisation rate in the B horizon of podsol profiles. The ^{14}C datings of soil humus by Tamm & Holmen (1967) indicated a considerable ^{14}C age of the organic matter in the B and B/C horizons of boreal podzol profiles. The result was considered to indicate that the organic matter in these horizons, or at least most of it, was fairly stable, decomposing slowly and releasing N slowly, in comparison both with the humus layer and with the uppermost mineral soil.

Another site of interest in this context is experiment P777 Norråker, sampled in 1992 and 1994 (Hallbäcken & Bergholm, 1998). L. Hallbäcken has kindly supplied more detailed information. This fertiliser experiment is situated in an old spruce forest on glacial till at Norråker (64°27′N, 15°34′E, 280 m a.s.l.). The amount of N in the soil profile down to 70 cm was estimated. The fertiliser additions were comparable with those in regime N1 at Norrliden in total amount, 960 kg N ha^{-1}, added on nine occasions between 1963 and1986. The estimated mean store of N in the horizon 0–20 cm was 782 kg on the two control plots, while the mean for six fertilised plots amounted to 830 kg. The difference, 48 kg ha^{-1}, corresponds to 5% of the amount added. For the horizon 20–70 cm, the control figure was 428 kg and the fertiliser mean 442 kg. The difference, 14 kg N ha^{-1}, corresponds to 1.5% of the amount added. Since these figures are based on an experiment with two control plots only, the accuracy of the results may be debatable. However, Hallbäcken's results suggest that the error caused by omission of horizons deeper than 20 cm is of moderate importance on this site. The Norrliden soil and climate are not very different from those at Norråker.

In the ecosystem compartments included in Table 7.5, we accounted for about two-thirds of the N added at regime N1. In higher N regimes, less than half could be accounted for. In the discussion above, we found reason to expect a limited further recovery, mainly from stumps, roots and mineral soil deeper than 20 cm.

The three main pathways for losses of N from a forest ecosystem are: *(i)* tree harvesting (which did not occur at Norrliden from 1971 to the biomass sampling in 1985), *(ii)* volatilisation, and *(iii)* leaching. We shall discuss pathways *(ii)* and *(iii)*.

It is well known that ammonia formed by hydrolysis can evaporate from urea used for fertilisation as pellets or grains (Nömmik, 1973; Overrein, 1969). These losses vary with weather conditions after spreading, being highest when pellets remain on top of moist humus during a period without rain. With rain immediately after spreading, losses would be very low, so the range of variation would be 0–30% of the fertiliser N.

During a period of 14 or 17 years, as at Norrliden, it is likely that some years have been favourable for ammonia evaporation, others unfavourable. No reliable estimate can be made, but it is evident that the difference between 100% recovery of added N and that found for regime N1, leaves room for some ammonia evaporation. With this process at work, another type of experimental error would arise, *viz.* underestimation of the treatment effects, since some of the added N may have been captured as ammonia by the humus layer and aboveground biomass on plots other than those where the fertiliser was spread. As mentioned earlier, Högberg *et al.* (1995), in their isotope studies in our experiments, found evidence of border effects between plots; ammonia capture may be a contributing factor, but is hardly the complete explanation, since the border effect has also been observed on plots with ammonium nitrate additions.

Another pathway for gaseous losses to the atmosphere is associated with denitrification and nitrification, where N compounds may be transformed to N_2 and N_2O. These processes require the presence or formation of nitrate in the soil, a condition satisfied in higher N regimes and during short periods on N1 AN plots. According to Nohrstedt, Ring, Klemedsson & Nilsson (1994), denitrification should not play an important part in normal well-drained forest soil, but it can scarcely be said that the nitrogen-saturated plots at regime N2, and particularly N3, have 'normal forest soils', so some losses may be possible.

As regards leaching losses, it is well known that added nitrate is lost from forest soils (Nõmmik & Popovic; 1971, Tamm *et al.*, 1974*a*). After conventional forest fertilisation, with rates around 150 kg N ha^{-1}, losses approaching 20% of the added N may appear as nitrate in the groundwater (Wiklander, 1980). With higher additions, leaching losses increase more than proportionately (Nohrstedt *et al.*, 1994). At the present rate of fertilisation at Norrliden (N1 = 30 kg N $ha^{-1}yr^{-1}$), little nitrate leaching from AN plots is to be expected, and almost none from U plots, since nitrification was unimportant there, at least before the soil sampling in 1988 (Högberg *et al.*, 1986). However, N rates on N1 plots were higher in the period 1971–1973 (60 kg $ha^{-1}yr^{-1}$) and 1974–1976 (40 kg $ha^{-1}yr^{-1}$), so we cannot exclude the possibility that some nitrate may have leached from AN N1 plots during snowmelt or periods of heavy rain in the early years.

We conclude that so much of the applied N was accounted for on N1 plots at the 1988 sampling, that these plots did not then satisfy the definition of N saturation as 'the availability of ammonium and nitrate in excess of total combined plant and microbial demand' (Aber, Nadelhoffer, Steudler & Melillo, 1989). On the other hand, regimes N2 and N3 are classified as N-saturated because of the large deficit in N recovered.

The question whether N1 plots have later become N-saturated cannot be answered without new studies. So far, there are no indications of saturation. Högbom & Högberg (1991) reported nitrate concentrations in leaves of *D. flexuosa* in E55U N1 in 1989, not much different from control leaves. Leaves from E55AN N1 had elevated concentrations, especially in July (after fertilisation in June). Needle N concentrations in regime N1 stayed well below those in N2 and N3 during the years after 1988, even if they are higher than those on no-N plots (Fig. 4.1). The ratios P/N, K/N and Mg/N (Table 4.2) are in no way alarming in regime N1, if the 'target values' of Linder (1995), *cf.* Section 10, are considered to indicate balanced nutrition.

8. Interactions between tree nutrition and factors other than N and PK regimes

Effects of variation in elements other than N and combined PK fertilisation

The working hypothesis in our experiments was that growth in boreal forests was primarily limited by N supply. Expts E55 Norrliden and E40 Lisselbo were designed to test the effects of different N levels. However, as we aimed at adding N to a level optimal for the trees, the question arose: what would be the next limiting element? Previous experimentation had not given much guidance concerning the nutrition of pine stands on mineral soils, in contrast to organic soils, where the elements P and K normally are low, and where growth is often limited

by the supply of either P or K, or both. Since the plan for field experiments must necessarily be limited as regards the number of treatment combinations, we took advice from Bertil Matérn, then professor of Biometry at the College of Forestry. For the main experiments with N levels, it was natural to include a PK treatment in a factorial mixture with the N levels.

However, we were also interested in the effect of adding or omitting the single elements P and K, as well as others such as Mg and microelements. Since we were supplying S in considerable amounts in the acidification experiments E57 and E42, we decided to include in the design the macronutrient S, in a form which should not acidify the soil. The remaining macroelements Ca and Fe were considered very unlikely to limit tree growth in normal Swedish soils, even at optimum N supply.

The final design of experiments E56 and E41 is illustrated in Table 2.6 (Section 2). It contains four incomplete balanced blocks, with four plots each, where all plots received N (regime N2), but other elements in different combinations, selected so that each block had two plots with, and two plots without, each of the four elements P, K, Mg and S.

Superimposed on this design is a smaller experiment, where a fifth plot in each block received the most complete combination of elements occurring in that block, together with the treatment Micro (see Table 2.3). The reason for this design was the risk that one or more of the micronutrients might have an adverse effect. It is known that the range from deficiency to supraoptimal concentrations can be narrow, *e.g.* in B.

When discussing the results, each of the experiments E56 and E41 has been treated as two experiments, the one where eight plots with each macroelement are compared with eight plots without the element, the other in which four plots with 'micro' and four without 'micro' are compared, pairwise fertilised with the same macronutrients.

The results from stem volume measurements in E56 and E41 are presented in Table 8.1. Fig. 8.1 shows results of basal area measurements in E56. Volume growth values were obtained directly from the measured values (for data for individual plots, see Aronsson *et al.*, 1999), except that the last line in the table presents volume growth data for E41, adjusted for differences in stoniness index, Si_{30cm}, a variable with a significant influence on tree growth on both sites (Table 7.1), which unfortunately was not measured in E56. The other covariate used in our statistical analyses, the Bjørgung index (BI), is also listed. The basal area data in Fig. 8.1 are adjusted for initial basal area, as described above (Section 5) and expressed as mean accumulated growth of plots with the element specified, in per cent of the mean for plots without the element.

The differences between + and − treatments are small in all cases in both Table 8.1 and Fig. 8.1. There is only one situation in which all three data series give similar results, *viz.* Mg addition gives positive differences, not related to differences in the covariates. Additions of P have no effect according to Fig. 8.1*b*, and in Table 8.1 the difference is negative for +P in E56 and positive in E41. The same applies to K and S. Microelement additions (B, Cu, Mn, Mo and Zn) show a positive difference in volume growth at Norrliden but a negative one in basal area trends, while the positive difference in volume growth at Lisselbo can largely be explained by differences in stoniness index.

Needle analyses were made according to our normal routines at E56 and E41; the results are reported by Aronsson *et al.* (1999). They concluded *(i)* that pretreatment differences in element concentrations were small between means of groups with and without each element(s); *(ii)* that there were consistent differences during the treatment periods between 'with' and 'without' for the elements P, K and Mg; *(iii)* that the addition of an element little affected concentrations of other elements. Aronsson (1984) reported increased uptake of B in E41, while there were small, and not fully consistent, increases in Mn, Cu and Zn on +Micro plots.

The small differences in growth between + and − treatments in the three data series (stem growth in two independent experiments and basal area growth measured on increment cores in one of the experiments), suggest that the treatments had little or no effect on growth under the circumstances obtaining, with the possible exception of Mg, for which the three data series all show positive differences for +Mg. The decrease with time of the Mg/N ratios in E55 and

Table 8.1. *Periodic annual stem growth (VG, $m^3ha^{-1}yr^{-1}$) in Expts E56 Norrliden and E41 Lisselbo, and total stem production during the whole experimental period (VG total, m^3ha^{-1}). Plots are grouped according to presence (+) or absence (−) of each element varied in the experimental plan (see Table 2.6). Two covariates used in statistical analyses are listed, in Expt E56 the Bjørgung index (BI, see text), which normally is positively related to stem growth (but is not here fully statistically significant); and in Expt E41 stoniness index (Si_{30cm}) and BI, which correlate positively with stem growth (highly significantly for Si_{30cm}). For E41 the total VG values are given both as measured values (meas.) and corrected for the differences in Si_{30cm} (adj.)*

	P		K		Mg		S		Micro	
	−	+	−	+	−	+	−	+	−	+
E56 Norrliden										
BI	174	158	167	164	171	161	169	162	159	148
VG 1972–79	10.8	10.5	10.8	10.5	10.6	10.7	10.8	10.6	10.2	10.4
1980–84	10.8	10.8	10.9	10.7	10.6	11.0	11.2	10.4	10.6	11.2
1985–89	8.8	8.4	8.6	8.6	8.4	8.8	8.4	8.8	8.3	9.6
VG1972–89 total	184.1	178.8	182.8	180.0	178.3	184.6	182.6	180.2	176.6	190.2
E41 Lisselbo										
Si_{30cm}	14.4	14.6	16.4	12.6	13.8	15.2	15.6	13.4	11.5	13.5
BI	47.8	44.8	46.9	45.7	44.8	47.8	44.1	48.5	44.1	46.3
VG 1972–77	6.4	6.7	7.0	6.0	6.3	6.8	6.7	6.4	6.1	6.6
1978–85	6.7	7.3	7.5	6.5	6.7	7.3	7.4	6.6	6.8	7.4
1986–88	7.1	7.9	8.1	7.0	7.4	7.7	7.9	7.1	7.5	7.3
VG 1972–85 total (meas.)	113.3	122.3	126.4	108.9	113.2	122.2	122.7	112.7	113.7	120.2
VG 1972–85 total (Si_{30cm} adj.)	113.6	122.0	121.2	114.1	115.4	120.3	119.7	115.7	116.4	117.4

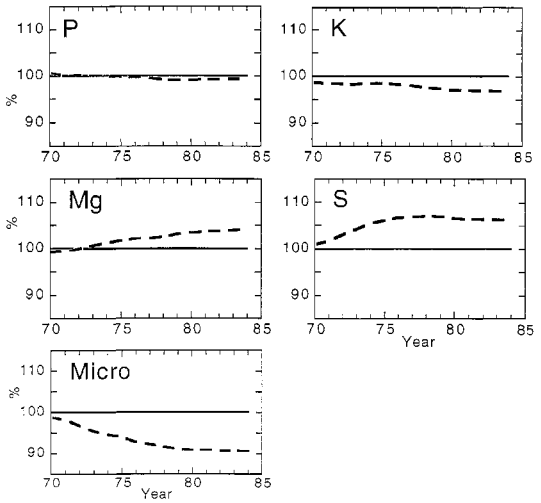

Fig. 8.1. Expt E56. Relative accumulated basal area u.b. 1970–1984 for plots with the element(s) specified added, in per cent of the value for the plots without the element in question. Values adjusted for differences in pretreatment basal area as in Fig. 5.2. Legend: broken line denotes mean of plots with element(s), solid line 100% (mean of plots without element(s).

E41 at regimes N2 and N3 has earlier been noted, as has the occurrence of symptoms of Mg deficiency in the understorey (Plate VII and VIII) in E55. The statistical analysis in Table 7.1*f* suggested, furthermore, a significant, positive influence of foliar Mg concentration on stem growth in E40 (period II), and a tendency in the same direction in E55AN (Table 7.1*d*). It should also be noted that deficiency in Mg is widespread in central Europe, where forests at high altitudes and on poor soils have been exposed to elevated levels of N deposition for long periods (Hüttl, 1991).

Considering the observed occurrences of B deficiency (Aronsson, 1983; Plate V and VI), and the low needle concentrations of some of the microelements on fertilised plots in E57 (see below, Table 8.4), it may seem strange that our results are so inconclusive in this respect. The reasons are probably twofold: *(i)* the test of microelements comprised only four plots with, and four without, and *(ii)* the level N2 was already supraoptimal. The combinations of different elements, in addition to the standard ammonium nitrate application, may create a variety of interactions, as is shown by the negative interaction AN*PK at Norrliden (Table 5.4), and the tendency to increased mineral soil acidification with PK (Fig. 3.2 and 3.3).

Effects of irrigation

Analysis of the effect of the water supply was included in the primary aims of the project (see Section 1). On the pine sites, two experiments were designed to address this problem, *viz.* E58

Norrliden and eight plots within E42 Lisselbo. Both experiments were factorial, with a control and the treatments irrigation, NPK and NPK + irrigation, at Norrliden with three replicates, at Lisselbo with two only. The aim of these experiments was not to optimise water supply, as was later attempted in the SWECON experiment at Jädraås (Aronsson *et al.*, 1977) and in more recent experiments in spruce plantations (Linder, 1995; Bergh *et al.*, 1999). Instead, the aim was to mitigate the effect of summer drought. This was done by measuring the local precipitation over each ten-day period between June and September, then supplying the deficit as compared with the normal period 1931–1960 at the nearest meteorological station (for Norrliden, Hällnäs-Lund, 7 km SW). Although the amount of water reaching the ground from the sprinklers (placed above the stand or at tree-top level, Plate I) was checked, it is evident that irrigation was less even and probably less accurate than the fertiliser distribution. Some data are also missing (June 1971 at E58, as irrigation did not begin until July 1971; data for June 1972 are unfortunately also missing).

However, as reported earlier (Aronsson & Tamm, 1982), statistically significant effects of irrigation on tree growth were observed at Norrliden, effects supported by similar observations, both at Lisselbo and in the SWECON experiment (Flower-Ellis, 1982), although not statistically significant on the latter two sites. Basal area measurements are now available from increment cores collected in 1984 from Norrliden, as well as a longer series of observations of tree volume growth (until 1994). There are also data on foliar nutrient concentrations from annual samplings at both Norrliden and Lisselbo. However, since the effects of irrigation on foliar concentrations were small, these data are not discussed here, although some are dealt with below (p. 91–2, concerning the after-effects of our treatments, fertilisation in particular).

The tree volume data presented in Fig. 8.2, show (Fig. 8.2*a*) that stem volume increased more on irrigated and irrigated + fertilised plots than on controls during the first phase (1972–1979). After 1979, when both irrigation and fertilisation had been discontinued (1977 and 1978, respectively), stem growth was approximately linear on time in non-fertilised treatments. Fig. 8.2*b* demonstrates that the treatment effects appeared already in the first measurement period. After the treatment period, the fertiliser response ($m^3\ ha^{-1}$) remained at an elevated level during at least the period 1980–1989. The response to irrigation was smaller, and its persistance cannot be judged from Fig. 8.2, because of differences in initial volume.

Expressed in relative terms (per cent of control, Fig. 8.3*a*) the responses to NPK and NPK + Irr decreased in 1979–1994. The small increase in relative volume (Fig. 8.3*a*) for the irrigation-only treatment in the period 1979–1994, is not statistically significant.

Increment cores collected in 1985 made it possible to measure basal-area development for a period from before the treatments started until 1984. The results are shown in Fig. 8.3*b*, in a

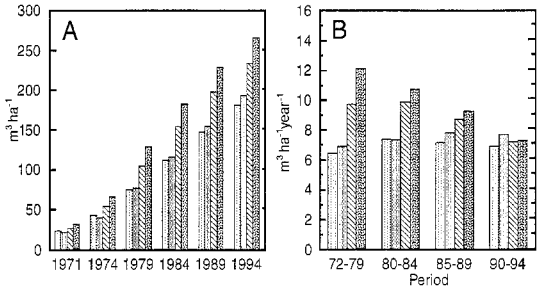

Fig. 8.2. Stem volume growth in Expt E58 Norrliden. (A) Total production measured at different revisions. (B) Annual mean production measured during different periods. Each bar represents the mean of three plots. Bars in order: Control, irrigated, fertilised, fertilised + irrigated.

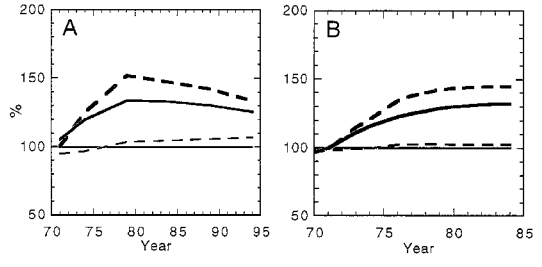

Fig. 8.3. Relative accumulated stem production in Expt E58, per cent of control. (A) Stem volume 1971–1994, adjusted for differences in Bjørgung index 1970. (B) Basal area 1970–1984, measured on increment cores and adjusted for differences in basal area 1967–1969. Legend: Control, solid thin line; irrigation only (1971–1977); broken thin line; fertilisation only (1971–1978), heavy solid line; irrigation + fertilisation, heavy broken line.

diagram which illustrates relative basal-area changes and which uses the basal area for 1967–1969 as covariate, as described above for E55 (Section 5, Fig. 5.5). The general growth pattern agrees reasonably well for basal area and volume. The more accurate basal area data seem to indicate a more persistent effect of fertilisation, than do the volume data (up to 1984).

The higher time resolution in the basal-area data can be used to relate the treatment responses to conditions in individual years, to the amounts of irrigation in particular. Fig. 8.4*a* shows measured irrigation for June, July and August 1973–1977, years in which there are data for all three summer months. As most of the annual ring is formed in June and July (Jonsson, 1969), it seems unlikely that August and September precipitation should influence the current annual ring much (but possibly the following year's ring). Since the time series for Norrliden is very short, we also refer to the longer series of precipitation data for Hällnäs-Lund, (Fig. 8.4*b*). As summer rain often comes in showers, no complete agreement can be expected, but it can be noted that 1973, and especially 1974, with low amounts of irrigation, were also wet years at Hällnäs-Lund, while either June or July was dry there in 1975 and 1976, when more irrigation was given. As precipitation (and irrigation) data are missing from Norrliden for 1971 and 1972, it should be noted that Hällnäs-Lund had somewhat lower June precipitation than normal in both years, and that July 1972 was dry.

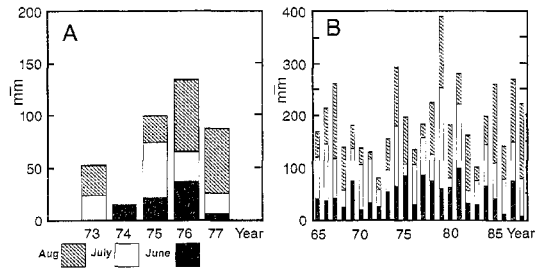

Fig. 8.4. (A) Amounts of irrigation in Expt E58 June-August 1973–1977, the years for which full records are available (irrigation started in July 1971 and ended with August 1977; for 1972, only a figure for the combined July and August irrigation is available). (B) Summer precipitation for the meteorological station Hällnäs-Lund, 7 km SW of Norrliden, altitude 181 m. Each bar contains monthly data, from the base upwards for June, July and August, respectively.

Fig. 8.5*a–d* are based upon the same increment core measurements as Fig. 8.3*b*, but better demonstrate annual growth variations. Fig. 8.5*a* shows annual basal-area growth, without any other transformation than the ANOCOVA adjustment for differences in previous growth. In Fig.8.5*b* the control figures are normalised to 100%, showing maxima for the curves for Irrigation and for NPK + Irrigation in 1976, the year with maximum June irrigation. In Fig. 8.5*c*, the percentage differences between Irrigation and Control, and between NPK + Irr and NPK alone, are compared, in both cases as percentages of the non-irrigated alternative. Fig. 8.5*d* deals similarly with the fertiliser response.

The next step in the analysis was to plot the deviation from the 100% line in Fig. 8.5*c* against the amount of irrigation in June-July in the same year. The result is shown in Fig. 8.6*a*. Although there are only five years with measured data, each group (irrigation minus control and NPK + irr minus NPK) demonstrates a statistically significant relationship between basal area growth and amount of irrigation. The *p* value is less than 0.01 for the first group and less than

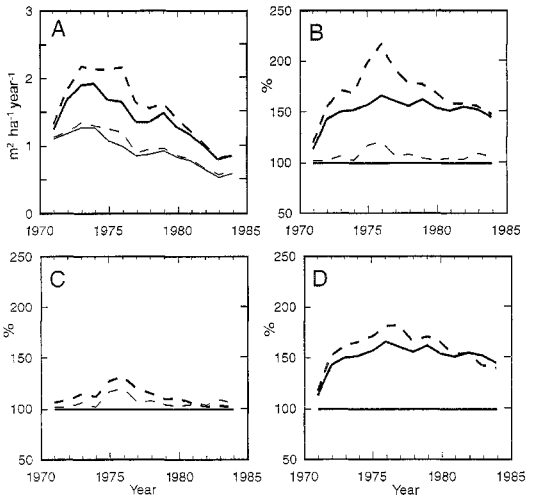

Fig. 8.5. Effects of irrigation and fertilisation on basal area growth 1971–1984 in E58. (A) Annual basal area growth 1971–1984. Values are means for triplicate plots and adjusted as in Fig. 8.3. (B) The values in Fig. 8.5(A) expressed in per cent of the control. (C) Values for irrigated plots as in (B), values for NPK + Irrigation expressed in per cent of values for NPK only. (D) Values for NPK plots in per cent of the control, values for NPK + Irrigation in per cent of values for irrigation only. Symbols as in Fig. 8.3.

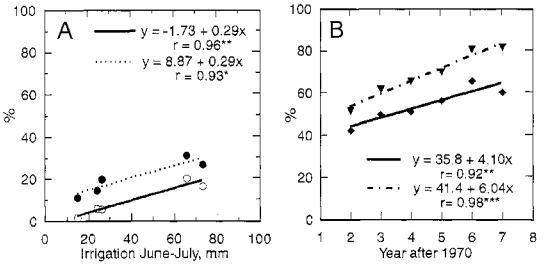

Fig. 8.6. Expt E58. Treatment effects on basal area growth in single years. (A) Differences in annual basal area growth between irrigated and non-irrigated plots, expressed as percentages of non-irrigated plots, and plotted against the June-July irrigation for the year in question. Open dots without NPK, filled dots with NPK. (B) Difference between fertilised and non-fertilised plots, percentages of non-fertilised. Diamonds without irrigation, triangles with irrigation.

0.02 for the second group. Moreover, the regression lines are practically parallel, suggesting that the addition of water in June-July, corresponding to an increase in precipitation from 20 mm in a very dry summer, to 70 mm in a very wet one, should be expected to increase basal-area growth by about 14 percentage units for both fertilised and unfertilised trees.

For comparison, the fertilisation effects (percentage units) from Fig. 8.5*d* for the irrigation period are plotted against time. As noted above, the fertiliser effect is far stronger than the irrigation effect, but the irrigation data also fit significant or highly significant regression lines. The difference in level in Fig. 8.6*a* and in both slope and level in Fig. 8.6*b*, can be taken as indicating a positive interaction NPK*Irrigation, *viz.* that fertilised trees produce more basal area for a given amount of irrigation than do unfertilised trees. The analysis of variance of stem volume growth in E58 (Aronsson & Tamm, 1982) suggested a similar tendency for volume growth ($p<0.08$).

For E42 Lisselbo, basal-area data to illustrate the annual variation in irrigation effects are lacking; we can only repeat that stem volume development, as shown in Aronsson & Tamm (1982), is very similar to Fig. 8.3*b*, even if the small number of replicates precludes statistical confirmation.

In summary, the conclusions from the earlier publication (Aronsson & Tamm, 1982) are confirmed, *viz.* that irrigation during dry summer periods increases tree growth in a young pine forest on glacial till, a very common type of inland site in N. Sweden. The irrigation response is, however, much lower than the response to the fertiliser rates applied.

The good correlation between basal-area growth and irrigation in June + July in the same year, suggests a direct influence on primary production. However, our tests do not exclude the possibility that indirect influences also exist, such as a stimulation of the soil microorganisms, releasing N and other nutrients in a form available to the roots. Better moisture conditions in the soil may also favour root growth and thereby increase nutrient uptake. Other climatic variables are also correlated with precipitation (solar radiation, air temperature).

The conclusion drawn here regarding the response of growth to irrigation is by no means remarkable. A negative influence of low summer precipitation on tree growth is normal over large areas of Europe (*e.g.* Holmsgaard, 1955), but has been considered to be less common in N. Sweden. However, Jonsson (1969) concluded, from extensive annual ring measurements, that the growth decrease due to drought in May–July varied between one and nine per cent. A moderate, positive effect of irrigation on basal area growth was also found in the SWECON experiment, in the southern part of the boreal region (Linder, 1987). Bergh *et al.* (1999) found no effect of irrigation on stem-volume production in the Flakaliden spruce experiment (35 km SW of Norrliden), but a clear response in a similar spruce experiment at Asa in S. Sweden (Bergh *et al.*, 1999).

Effect of interrupted fertilisation

When large-scale N fertilisation was introduced in Swedish silviculture during the 1960s, and some forest companies drew up plans for repeated fertilisation over much of the rotation, concern was expressed about what might happen if forests regularly fertilised no longer received N additions. This was of course before the discussion of the increasing atmospheric deposition of N arose.

It would necessarily take a very long time to obtain answers from more applied studies, with fertilisation after the first thinning, repeated at seven-year intervals until shortly before final felling at age 70 years or more. Since the possibly harmful effects of supplying fertiliser to the forest

ecosystem were already included in our project aims (Section 1), it seemed natural also to include the consequences of discontinued heavy fertilisation. Our early experiments had shown a temporary depression of height growth in spruce some years after the positive effect of single applications of N had ceased (Tamm, 1971; Tamm & Fu, 1985). Some adverse consequences of high N additions, including soil acidification of unknown duration, had also been observed (Tamm & Popovic, 1974). Compared with repeated practical forest fertilisation, our nutrient regimes could be expected to 'load' the ecosystem with N in a much shorter time.

However, the original aim, to ascertain whether repeated N additions in practical forestry did harm the ecosystem, lost some of its topicality, since it was discovered that atmospheric deposition had supplied amounts of N comparable to those so far distributed over Swedish forests as fertiliser. In consequence, the Swedish authorities (the Swedish Board of Forestry and the Environmental Protection Board) issued recommendations (Anon., 1984, 1991) that forest owners should refrain totally from forest fertilisation with N in S. Sweden, and restrict its use in middle and N. Sweden.

On the other hand, interest in the behaviour of N-loaded ecosystems, and their responses to further changes in supply, has by no means decreased, so all existing information, however meagre, should be used.

It is also of interest, particularly in regions with low atmospheric loads of N, to test a hypothesis advanced by Ingestad (1985, 1987): That it should be possible to create, by repeated nutrient additions, new steady-state conditions in a formerly N-limited ecosystem, where high productivity was maintained with nutrient additions corresponding to nutrient losses in harvested material only.

The information at present available on the persistence of improvement in pine growth after fertilisation has ended, is derived from the same experiment as discussed in the previous subsection, E58 Norrliden, where NPK fertiliser was given annually in the interval 1971–1978, amounting to 720 kg ha^{-1} (Table 2.5).

On several of our sites (see Sections 9 and 11) there are experiments in which fertilisation was discontinued completely or in some treatments during the period 1985–1991. From these, further information could be obtained by new measurements. Both changes in tree growth and recovery by the ecosystem from supra-optimal nutritional stress, are of interest.

Growth data for E58 were presented earlier in this section (Fig. 8.2 and 8.3). It may be concluded that both volume growth (recorded until 1994) and basal-area growth (recorded until 1984) continue at a high rate for some time on fertilised plots, even if the relative lead over controls—in volume growth at least—decreases. During the latest measuring period for volume growth, 1990–1994, there was little difference between fertilised and unfertilised plots (Fig. 8.2*b*). For stand data in E58, see Aronsson *et al.* (1999).

Two further types of evidence can be used in the discussion of long-term changes related to the treatments: soil changes and needle nutrient concentrations.

Soil was sampled in E58 in September 1986, but only concentration data are available, and are reported by Aronsson *et al.* (1999). They show no clear effect of irrigation, but there is a consistent *p*H decrease in the mineral soil from control to NPK, and from irrigation to NPK + irrigation. The results agree with those reported above (Section 3) from E55, where regime N1, at the time of soil sampling, had received slightly lower amounts of N than fertilised plots in E58 at the sampling in 1988 (630 kg ha^{-1} in E55 compared with 720 kg ha^{-1} in E58). However, differences within each soil stratum are seldom statistically significant in E58.

The chemical data most relevant regarding the duration of the fertilisation effect are: *(i)* the C/N ratios in soil, and *(ii)* needle concentrations of nutrients, N in particular. The C/N ratios are lower on fertilised than on unfertilised plots independently of irrigation (Table 8.2). However, in that table, no differences exceed the least significant difference (LSD) at the 5% level. Consequently, no firm conclusions can be drawn, other than that a new sampling would be needed to establish whether the changes in the C/N ratio and other soil variables can be confirmed.

The initial changes in needle concentrations of nutrients are similar to those in the other Norrliden experiments, *viz.* sharp rises in N con-

Table 8.2. *Carbon/nitrogen ratios in different treatments of Expt E58 Norrliden, sampled in September 1986. Each value is the mean of three replicate plots. LSD = the least significant level at $p < 0.05$*

Treatment	Humus	Mineral soil 0–5 cm	5–10 cm	10–20 cm
Control	40.0	32.9	28.6	30.0
Irrigation	39.5	33.9	30.9	29.3
NPK	35.0	30.8	28.9	27.6
NPK + Irrigation	33.9	29.5	27.2	27.3
LSD	6.5	5.0	3.6	4.8

centration and 'dilution effects' on Ca, Mg, and Mn on NPK-fertilised plots (Fig. 8.7).

There are very small, if any, effects of irrigation *per se*, on foliar concentrations. However, of greater interest to the discussion of the after-effects of fertilisation is the development of needle N concentrations after the last fertiliser addition in 1978. ANOVA-tests were made on the needle N concentrations, using the data available (1987–1991). Significant differences between +NPK and −NPK plots were found for the years 1987 and 1991, and tendencies in the same direction in 1988 and 1989 (Table 8.3; no data for 1990).

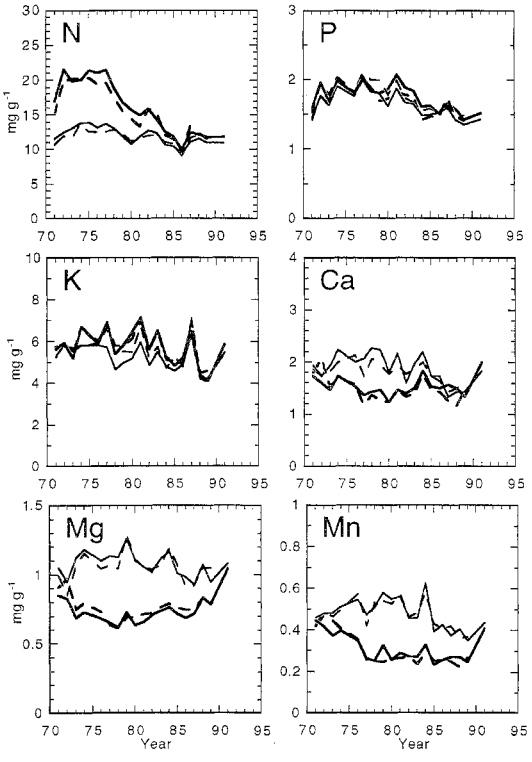

Fig. 8.7. Foliar nutrient concentrations in E58, 1971–1989 (for control and NPK treatment, also 1991). Symbols as in Fig. 8.3.

Similar needle N concentrations do not necessarily imply similar production, since stem biomass is still higher on fertilised plots in 1994 (Fig. 8.2*a*), and the same may be valid for needle biomass. However, the stem growth data (Fig. 8.2*b*) demonstrate that any growth differences between treatments must be small during the last period, 12–17 years after the last application. On the other hand, no negative after-effect has been observed.

As regards Ingestad's hypothesis of a more permanent productivity rise in an ecosystem loaded with nutrients, we can only conclude that 720 kg N ha^{-1} in eight annual applications, together with 120 kg P and 225 kg K (in three applications), did not suffice to bring about this change.

Our results may be compared with those of Miller (1981), who followed the growth of Corsican pine (*Pinus nigra* var. *maritima* (Ait.) Melville) to age 52 years, with fertilisation at age 36, 37 and 38 years with a total of 252, 504, 1008, or 1512 kg N ha^{-1}. The N pool on the site was slightly lower than that at Norrliden (198 kg N ha^{-1} in the stand, 884 in the soil on controls). Growth rates returned to that of controls at age 44–47 at the two lower rates, but persisted at an elevated level even at age 52 at the two highest rates. Miller concluded that fertilisation in the first place affects the stand rather than the soil, but when additions approach the size of the soil store, a more persistent site improvement may result.

Binkley & Reid (1985) reported a case of increased N availability in a Douglas fir stand fertilised 18 years earlier with 470 kg N ha^{-1}. The stem growth response also persisted longer (at least 15 years) than usual, but it was noted that the results deviated from those of several other studies.

Further discussion of this topic follows below (Section 10), where the recovery of added fertiliser N is dealt with in greater detail.

Effects of soil acidity manipulation

In addition to the changes in soil acidity caused by addition of N fertilisers (Section 3), sites were more directly manipulated by the addition of

Table 8.3. *Foliar nitrogen concentrations in Expt E58 Norrliden 1987–1991 and ANOVA tests of the differences between plots with and without NPK addition 1971–1978. nd: no data*

Treatment	Mean concentration mg g^{-1} − NPK	+ NPK	Treatment	Error	F-value	Signf.
1987	11.40	12.90	1	10	8.34	$P<0.05$
1988	11.80	12.27	1	10	1.64	$P>0.2$
1989	11.30	11.67	1	10	2.18	$0.2>P>0.05$
1990	nd	nd				
1991	11.00	11.83	1	4	10.78	$P<0.05$

acidifying compounds (sulphuric acid) or acid-counteracting substances (lime). The two experiments in question, E57 Norrliden (30 plots) and E42 Lisselbo (16 of 20 plots), and their results have been described in two publications (Tamm & Popovic, 1989, 1995). Here we shall first briefly review the main results, then add new information on stem growth after 1984 (E57) and 1985 (E42), and needle element concentrations from a sampling in 1993 (E57), in which both macro- and microelements were analysed. In addition, in Aronsson *et al.* (1999) some of the soil data on C and N in Tamm & Popovic (1989) and stand data in Popovic (1990/1991) have been recalculated, for comparison with material presented here (in Section 7, *e.g.* Fig. 7.9–7.10), which illustrates the distribution of C and N in the ecosystem.

The original aim of the acidification experiments was to establish whether, and how, a limited amount of acid affects soil acidity and tree growth. Since the project began as a low-budget extension of the larger project, 'Optimum nutrition experiments', a simple, and rather crude method was used, *viz.* irrigation with dilute but still relatively strong, sulphuric acid during six (E57) or eight (E42) years, and as an acidity countermeasure, a single addition of calcium carbonate.

The addition of acid might be expected to cause both acute and chronic effects; this certainly happened, although visible shock effects on trees were absent, and effects on field and bottom-layer vegetation were delayed for some time (Plate IV). At the higher acidification rates at least, the desired soil acidification was established, though it turned out that the annual NPK addition resulted in stronger acidification of the mineral soil than did the heaviest acid application. Acidification by sulphuric acid made it possible to study the after-effects of the treatments in both soil and stand (see Tamm & Popovic, 1989, 1995, and references to microbiological studies therein). We concluded that an unexpected increase in tree growth during the period of active acidification, can be explained as resulting from acute damage to field-layer vegetation and other organisms more sensitive to acid, than are the trees. In consequence, competition was reduced and nutrients released from killed organisms.

Long-term, chronic effects of acid supply alone are fewer, but there are clear indications of losses of 'basic' cations (Ca, Mg) from the soil, replaced by Al and hydrogen ions. There is also a tendency towards decreased needle concentrations of Mg.

As noted above (p. 82), a lysimeter experiment was in operation at Lisselbo between 1972 and 1978, with the treatments Control, Irrigation, Acid 2, NPK, NPK + irrigation, and NPK + Acid 2, with annual additions similar to those in Expt E42. The results confirmed that the acid treatment induced leaching, of Mg in particular, while Ca and K were retained better. In irrigated lysimeters, there was even an increase in Ca, ascribed to the low but measurable Ca concentration in the irrigation water from a nearby oligotrophic lake (Farrell *et al.*, 1980; Nilsson, Wiklander & Farrell, 1983).

The combination of acid and NPK fertiliser aggravated the soil changes described, and NPK itself lowered needle concentrations of Ca and Mg, an effect lasting several years after application ceased (Table 8.4). As can be seen from that table, NPK application also decreases needle concentrations of the microelements Mn, B and Cu, and to a lesser extent, those of Zn and Al. The values for B are particularly low on all plots with NPK, and may be the main cause of the growth decline from 1979 onwards on all NPK plots in E57 (Fig. 8.8*b,c*). However, Cu

Table 8.4. *Concentrations of 13 elements in current needles from Expt E57 Norrliden, collected in autumn 1993. Each value is the mean for triplicate plots, with its standard deviation. Data by courtesy of J. Bergholm (unpublished)*

Element	Without NPK					With NPK			
	Control	Acid1	Acid2	Acid3	Lime	No Acid	Acid1	Acid2	Acid3	Lime
						mg g^{-1}				
N	11.5 ± 0.5	11.4 ± 0.2	11.5 ± 0.4	11.7 ± 0.5	11.7 ± 0.8	15.7 ± 1.0	14.7 ± 0.8	15.1 ± 0.6	15.1 ± 0.1	14.8 ± 1.0
P	1.64 ± 0.12	1.60 ± 0.10	1.61 ± 0.02	1.66 ± 0.04	1.70 ± 0.02	1.87 ± 0.08	1.79 ± 0.16	1.76 ± 0.14	1.70 ± 0.11	1.72 ± 0.10
K	5.5 ± 0.5	5.7 ± 0.4	5.5 ± 0.2	5.4 ± 0.2	5.9 ± 0.5	6.0 ± 0.3	5.9 ± 0.5	5.9 ± 0.2	5.9 ± 0.2	5.3 ± 0.3
Ca	2.03 ± 0.15	2.13 ± 0.23	1.83 ± 0.31	2.07 ± 0.25	1.57 ± 0.21	2.57 ± 0.15	1.73 ± 0.32	1.47 ± 0.12	1.60 ± 0.36	1.77 ± 0.31
Mg	1.01 ± 0.08	0.93 ± 0.04	0.88 ± 0.08	0.92 ± 0.11	0.92 ± 0.12	0.67 ± 0.03	0.77 ± 0.05	0.76 ± 0.13	0.71 ± 0.05	0.70 ± 0.03
Mn	0.45 ± 0.03	0.51 ± 0.05	0.43 ± 0.05	0.50 ± 0.11	0.30 ± 0.02	0.40 ± 0.02	0.39 ± 0.01	0.39 ± 0.01	0.41 ± 0.10	0.19 ± 0.01
S	0.78 ± 0.05	0.78 ± 0.02	0.77 ± 0.02	0.78 ± 0.04	0.80 ± 0.10	0.92 ± 0.03	0.92 ± 0.06	0.84 ± 0.05	0.84 ± 0.04	0.86 ± 0.10
						µg g^{-1}				
Zn	49.9 ± 3.4	48.3 ± 1.9	48.2 ± 3.9	47.9 ± 0.4	50.4 ± 4.0	48.4 ± 0.6	46.3 ± 0.6	43.6 ± 1.7	45.6 ± 0.9	42.1 ± 3.2
B	7.3 ± 0.9	5.7 ± 1.7	6.9 ± 1.4	5.0 ± 2.0	5.8 ± 1.7	1.6 ± 0.2	1.5 ± 0.3	1.2 ± 0.3	1.2 ± 0.4	1.7 ± 0.2
Cu	2.7 ± 0.2	2.8 ± 0.3	2.6 ± 0.5	2.6 ± 0.2	2.7 ± 0.2	1.4 ± 0.5	1.3 ± 0.4	1.3 ± 0.4	1.4 ± 0.3	1.2 ± 0.2
Fe	26.3 ± 1.5	24.4 ± 1.6	23.0 ± 2.3	22.4 ± 2.3	21.6 ± 1.4	27.8 ± 1.1	27.2 ± 0.8	22.1 ± 1.1	24.4 ± 2.4	23.4 ± 4.1
Al	178 ± 35	191 ± 29	192 ± 8	160 ± 28	141 ± 24	157 ± 15	138 ± 11	125 ± 11	129 ± 29	134 ± 46
Na	2.4 ± 0.4	4.0 ± 1.6	2.1 ± 0.8	2.5 ± 0.6	3.3 ± 1.2	3.1 ± 1.0	3.6 ± 1.9	2.1 ± 0.5	3.5 ± 1.2	1.7 ± 0.2

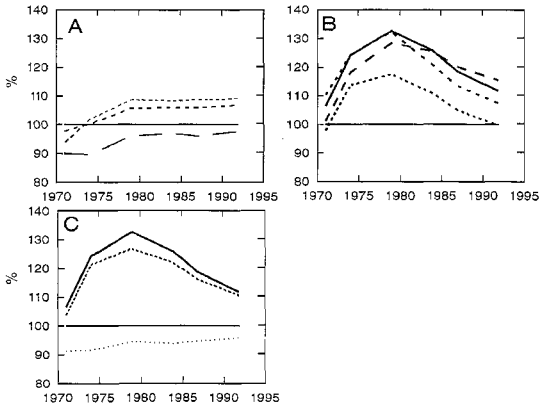

Fig. 8.8. Progression of stem volume over bark in different treatments of E57 relative to that of control plots (mean of three control plots = 100 for each year). All values adjusted by analysis of covariance for differences in starting conditions, as expressed by the Bjørgung index $\sqrt{n \cdot h^2}$ (A) Acidified plots; length of dashes decreasing from Acid 1 to Acid 3. (B) Fertilised and acidified plots; heavy lines, otherwise as (A). (C) Fertilised and limed plots; liming marked by very short dashes.

and Mg concentrations are also in the range within which deficiencies may be suspected. Unlike E55 and E40, the acidification experiments did not receive B additions (Section 2, Table 2.2).

With one exception, Lime combined with NPK at Lisselbo (Section 7; see also Aronsson, 1983; Tamm & Popovic 1989), treatments other than NPK (Acid levels and Lime) had small effects, if any, on growth after the active treatment phase. The curves for treatments without NPK are roughly parallel both in E57 (Fig. 8*a* and *c*) and E42 (Fig. 8.9*b,c,d*). The curves for NPK + other treatments in E57 and E42 (Fig. 8.8–8.9) do not differ much from Fig. 5.5*d* and 5.6*b*, respectively. Further support for the absence of measurable, long-term effects of the acid treatments in E57 can be found in the needle concentration data in Table 8.4. The only clear effects in the table, apart from that of NPK, concern the liming treatment, which increases Ca concentrations slightly but depresses Mn concentrations considerably. There may also be a depressive effect of acid on B concentration on fertilised plots. Horticultural experience suggests a depressive influence of liming on B concentrations, which indeed happened early on NPK + Lime plots at Lisselbo (Aronsson, 1983).

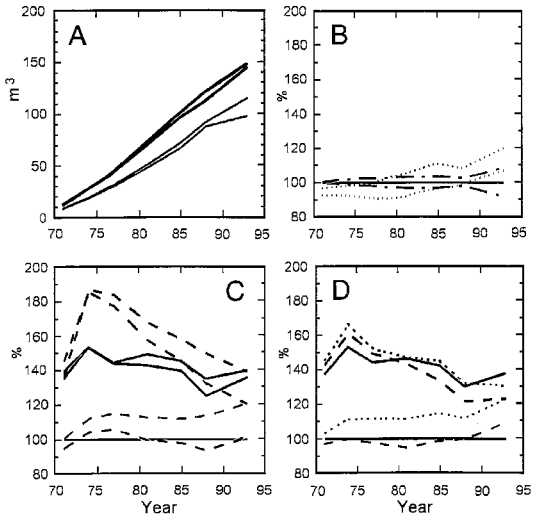

Fig. 8.9. Progression of stem volume over bark in different treatments of Expt E42 Lisselbo, 1971–1993. Values adjusted as in Fig. 8.8. (A) Volume development on the individual control plots (thin lines) and NPK plots (heavy lines). (B) Relative values (control mean = 100) for the two controls and the two limed plots (very short dashes). (C) Relative values for the individual irrigation plots (thin broken lines), NPK plots (heavy solid lines) and NPK + irrigation plots (heavy broken lines). (D) Relative values for Acid and Acid + NPK plots (means of duplicate plots). Thin lines without NPK, heavy lines with NPK. Long dashes Acid 1; short dashes Acid 2. Note that there was snow damage in November 1988 (Fig. 8.10), especially on unfertilised plots, and that the shape of curves in 1988–1993 may have been affected by this.

At Norrliden, B concentrations were low in 1992 on all fertilised plots in E57.

Retention of S in the soil at Norrliden was studied by Gustafsson & Jacks (1993). Samples were collected in 1991, 15 years after the last application of acid. Comparisons were made between Acid 3 and Control plots in E57, and with both recent (1989) and old (1951) samples from a site in Halland, SW Sweden, exposed to considerable atmospheric deposition of S in the period between samplings. The retention of added S in organic form was low at both sites, while retention by adsorption to iron-aluminium oxide complexes was important in the B horizon at Norrliden but not in Halland. The difference is ascribed to a higher organic matter concentrations in Halland, which blocks the adsorbtion sites for sulphate ions. The results have obvious consequences for models which simulate soil recovery after a decrease in S emission.

Distribution of soil C and N in Expts E57 and E42

The soil data from E57 and E42, published earlier (Tamm & Popovic, 1989), were recalculated by Aronsson *et al.* (1999), to permit comparison with the budget calculations for E55 (Table 3.5 and Section 7). Some of their results for N and C are presented in Table 8.5 (for details, see Aronsson *et al.* (1999)). The store of N on no-N plots is not very different in E57 from that in E55U and AN. The increase with fertilisation ('apparent recovery') at level N2 is somewhat lower in E57, but the difference falls within the confidence interval.

A comparison between E57 and E42 also shows similar amounts of N on no-N plots, a little more N in the humus layer and somewhat less in the mineral soil on E42. The E42 data have lower precision, as they are based on six pairs of plots, compared with 15 pairs in E57. The tendency, however, is that recovery of fertiliser N is higher in E42 than in E57. Some support is given by the C data, which suggest an increase in the upper soil strata on fertilised plots in E42, more than twice that in E57. There are also differences in C/N ratios, both between E42 and E55, and in the way in which the ratio is changed by fertilisation. Although the data are not conclusive, they call for further study, as the sequestration of C and N in forests is a controversial issue in the 'Global Change' debate.

Effects of nutrient regimes on snow-damage frequency

In November 1988, there were heavy snowstorms in the Lisselbo area at temperatures around and just below 0°C. Some of the experimental plots were damaged, to the extent that further observations were considered to be of limited value. The damage frequency varied with the N regimes in an unexpected way, which called for closer examination. On the worst damaged plot (No. 45: control), 39% of the trees were destroyed, while several N1 and N2 plots had zero damage (Fig. 8.10).

The damage was of two kinds: *(i)* entire trees overturned (uprooted) and *(ii)* the stem was broken in the mid- or lower part. Type *(i)* was more common than *(ii)*. For example, on plot

Table 8.5. *Stores of N and C in topsoil of Expts. E57 Norrliden and E42 Lisselbo, sampled in June 1985. Fertiliser additions before June 1985 contained, in kg N* ha^{-1}, *1180 kg in E57 and 1000 in E42. The data in the table are based on 15 pairs of plots (with and without NPK) in E57 and six pairs in E42. N stores in kg* ha^{-1}; *C stores in* 10^3 kg ha^{-1}

	E57 Norrliden		E42 Lisselbo	
	−NPK	+NPK	−NPK	+NPK
N store in humus layer	302±14	409±21	347±30	502±48
N store in mineral soil, 0–20 cm	733±20	858±23	511±25	634±38
N store in topsoil	1036±28	1268±26	858±32	1156±71
Mean of differences in topsoil N	231.9±30.5		298±62	
C store in humus layer	11.16±0.47	13.66±0.65	11.72±1.06	16.70±1.68
C store in mineral soil	19.46±0.59	21.36±0.48	17.13±0.96	21.55±1.57
C store in top soil	30.62±0.88	35.02±0.73	28.86±0.96	38.25±2.62
Mean of differences in topsoil C	4.4±0.9		9.4±2.4	
C/N ratio	29.6±0.4	27.7±0.4	33.8±0.5	33.6±0.9
C/N ratio of mean differences	19.0		31.5	
N recovery				
% of added	19.7		29.8	
% of no-N mean	22.4		34.7	
C increase				
% of no-N mean	14.4		32.6	

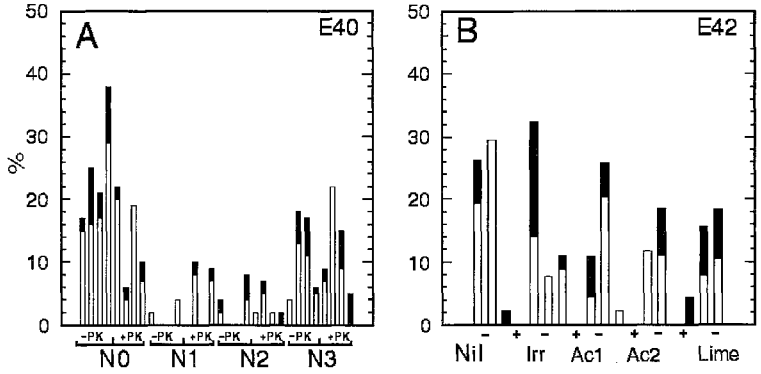

Fig. 8.10. Frequencies of snow damage in the Lisselbo experiments E40 (A) and E42 (B) in November 1988. Individual plot values, arranged by treatments, and within treatments in block order. In (A) there are four replicates of each treatment (some plots with regimes N1 and N2 having no damaged trees). In (B) there were two replicates only, damage having occurred on all plots without NPK (marked −), while four plots with NPK (marked +) had no damage. The lower part of each bar (empty) shows uprooted trees and the upper part (dark), broken stems.

45 there were 16 uprooted trees and four broken stems, of a total of 41 trees. Both types of damage appeared to be similarly distributed, both by treatments, and throughout the experimental area (Fig. 8.10). The two types were therefore not separated in the statistical treatment. However, as is often the case with storm damage, the spatial distribution on the experimental area was uneven, with clusters of plots with high frequencies. The uneven distribution of the damage caused difficulties in the statistical analysis, since the standard deviations of the original data (proportions of damaged trees) deviated much between treatments.

This could largely be overcome by an arcsin transformation of the original data, suggested by B. Matérn, who also made the ANOVA analyses (Tables 8.6–8.7).

The results of the calculations are shown for all three Lisselbo experiments in Table 8.6, both (A) with untransformed values (proportions of damage) and (B) with transformed values, the latter with standard errors. It is clear that the highest frequencies of damage occur on no-N plots (with similar levels within E40 and E42), and that the frequencies are much lower in N regimes N1 and N2. Plots within E40 with N3 again have high frequencies, well separated from

Table 8.6. *Means of snow-damaged trees at different N levels. in the Lisselbo experiments, November 1988. Sum of overturned trees and broken stems divided by total number of trees. Values shown both directly calculated (A) and transformed for the ANOVA operations (B). B = arcsin* $\sqrt{A}$

Exp No.	Nitrogen level N0 A	N0 B	N1 A	N1 B	N2 A	N2 B	N3 A	N3 B
E40	0.207	0.462 ± 0.045	0.034	0.127 ± 0.045	0.036	0.160 ± 0.045	0.129	0.357 ± 0.045
E41					0.030	0.118 ± 0.035		
E42	0.195	0.447 ± 0.052			0.021	0.100 ± 0.052		

Table 8.7. *ANOVA-test of variations in snow-damage (transformed dependent variable)*

Experiment and source of variation	Sum of squares	D.f.	Mean square	F ratio
E40				
Block	0.028953	3	0.009651	
N	0.612641	3	0.204214	12.71***
PK	0.000052	1	0.000052	
N*PK	0.061552	3	0.020517	
Error	0.337493	21	0.016071	
Total variation	1.040691	31		
E42				
Block	0.009526	1	0.009526	
NPK	0.482428	1	0.482428	22.74**
Other treatments	0.011526	3	0.003842	
Interaction	0.029445	3	0.009815	
Error	0.148507	7	0.021215	
Total variation	0.681432	15		

N1 and N2, but approaching the level for the no-N plots. In regime N2, all three experiments have similarly low frequencies of damage, despite large variations in other treatments.

Considering that practical forest fertilisation has caused concern about an increased risk of storm damage (Laiho, 1987), the data presented here should be reassuring. However, our results should not be over-interpreted. The Lisselbo stands consisted of young pines, which had reacted to N fertilisation with increased needle, branch, and basal area production, but not with increased height growth. The trees had thus become more sturdy. An even more important factor may be that they had a long period in which to adapt to the increase in crown mass, unlike trees shortly after a single fertilisation.

The time of year in which the storm occurred may also be important. Soil freezing is at a maximum in late winter, except in years with very deep snow cover. This may at least affect the ratio between overturned trees and broken stems.

9. Results in relation to the original aims

Scientific problems change with time, as the scientific frontier moves on. It therefore seems appropriate to discuss the results of a long-term project, both in relation to the original aims, and with respect to the contribution they may give to problems now considered urgent. This section deals with problem areas (1) to (7) in the early grant applications (Section 1). The following section discusses some of the results in the context of what now seems to be at the forefront of research.

Area 1. Primary production of forest ecosystems at nutrient levels for optimum growth.

The meaning of the term 'optimum' will be further discussed below (Section 10). Here the term will be used in the sense common in the 1960s and earlier, *i.e.* the maximum point of conventional yield curves.

To determine the total primary production of our experimental ecosystems above- and belowground was a task beyond the available resources. However, the dynamics of the most important soil compartments and aboveground biomass fractions were studied.

Thus stem production was determined at different levels of nutrition, which permitted estimation of empirical 'optimum' N regimes and 'optimum' N foliar concentration under given climatic conditions (Fig. 7.5, 7.6). The size of aboveground (at Lisselbo also belowground) biomass fractions was determined on one occasion for each of the experiments E55 Norrliden and E40 Lisselbo. These data permit an assessment of how the nutrient regimes affect the above ground biomass fractions.

Gas-exchange studies of trees at different levels of nutrition, considered initially, were not realised, both for lack of resources and to avoid duplication of activities within the SWECON project, started in 1973.

Area 2. Importance of different nutrients, of canopy density, and of water supply for actual and potential production at selected sites.

The results confirmed that the supply of N is the dominant growth-limiting factor for tree growth on the experimental sites. An optimum range of N concentrations in current needles (14–17 mg N g^{-1} DM, sampled in autumn) seems to be valid for both sites, irrespective of whether PK is added or not. There is no evidence that any element, other than N, stimulates tree growth on our sites when given alone. As regards a possible N*PK interaction on tree growth, the evidence is somewhat confusing: it is positive with urea as the source of N, negative with ammonium nitrate. Although both interactions are statistically significant for some periods, none of them explains more than a small fraction of the variation in growth.

Effects of B and Mg, as well as changes in element proportions in the plant, will be discussed below under problem areas 3 and 5.

Tree growth is also influenced by factors other than nutrient supply, even if climatic factors are more difficult to vary experimentally. A clear influence of pre-experimental stand conditions—previous growth or the 'Bjørgung index', expressing the combined influence of stand density and tree height (Bjørgung, 1968)—has been found, especially in the early experimental phases. Site variation between plots, as expressed by the stoniness index (Viro, 1952), has also been found to be of importance. The stoniness index is related to the water-holding capacity of the soil, as well as to the particle surface exposed to weathering; our irrigation experiments, E58 Norrliden in particular, showed a direct, positive growth effect of irrigation during dry summers.

The curves obtained by plotting needle biomass against needle N concentrations (or N regime), Fig. 7.7, may be interpreted as evidence for the existence of a site-specific optimum needle biomass. The observation that optimum needle biomass appears to be higher in ammonium nitrate blocks than in urea blocks, fits in with a difference in site quality between these groups of blocks.

The interaction between nutrition and soil acidification will be dealt with under problem areas 3 and 5.

Area 3. Disturbances in ecosystem functions at optimum and supra-optimal nutrient regimes.

Originally, study of this problem area was motivated by the increasing use of N fertilisers in Swedish forestry in the 1960s, when some companies planned regular refertilisation during a large part of the rotation. However, from the middle 1960s we were aware of Odén's discovery of the increase, from 1950–1965, in the atmospheric deposition of N (and S), with possible ecological consequences (Odén, 1968; Tamm & Popovic, 1995).

This problem area should have been restricted to optimal and supraoptimal N regimes only, since the regimes in the pine experiments consisted of 'yes' or 'no' alternatives with respect to other elements. There have certainly been variations in the nutritional status of other elements, measured as concentrations in needles or other organs, but not to the extent that we can define supraoptimal concentrations.

Given this restriction, we can enumerate a number of disturbances observed, some expected, such as nutritional imbalances, others less self-evident, such as an N-induced acidification of the upper mineral soil (in spite of an opposite effect in in the humus layer).

The first signs of harmful effects of N additions were observed at Lisselbo in the early 1970s, and consisted in shoot and needle damage on fertilised trees. A decrease in cold resistance of needle tissue was also established (Aronsson, 1980). However, somewhat similar symptoms had been described from both Finland (Kolari, 1979) and Norway (Braekke, 1979), and had there been assumed to be caused by deficiency in micronutrients, presumably B. Our chemical analyses confirmed that the B concentrations were very low in N-fertilised trees, and lowest on the plots with NPK + Lime at Lisselbo. However, this result does not exclude the possibility of frost damage. Some of the early damage, with frost rings in the branch cambium, was associated with specific spring frosts

(Aronsson, 1980). Similar symptoms were also induced by freezing single branches in the field. This is not the place to discuss a relationship between low B concentrations and sensitivity to frost, but such a connexion is a possibility.

Other nutrient imbalances concern the ratios between some other elements and N, and will be discussed under problem area 5.

Some of our treatments, high N regimes in particular, have strongly changed the chemical status of the soil. Normal boreal forest soils efficiently retain most nutrients and metal cations, and do not nitrify the ammonium ions produced by decomposing organisms, except after serious disturbances (forest fire, clearfelling). The addition of N in excess of plant and microorganism demand leads to nitrification, and leakage of nitrate ions (added or formed from urea or organic compounds). With nitrate ions, cations from the exchangeable pool leave the profile, as described below. Addition of sulphuric acid has similar effects, and addition of PK fertiliser increases the leaching of Mg, while the losses of K and Ca are compensated for.

Acidification of podzol soils occurs as a natural phenomenon, both as a slow geological process since the end of the latest glaciation, and as a largely reversible acidification of the organic layer with stand age (Hesselman, 1937; Tamm & Hallbäcken, 1988). The acidification observed in our experiments following addition of fertilisers and sulphuric acid, is a much faster process, as is the acidification observed when old samplings have been repeated in areas with high atmospheric deposition of S and N (Nilsson & Tyler, 1995). Such changes are clearly disturbances of the soil conditions, and much has been written about possible adverse effects on tree roots and soil organisms.

Before we discuss biological effects, it should be noted that acidification processes differ, depending on the active agent. Sulphuric acid reduces *p*H and base saturation in all soil horizons, even if the effects are not always statistically significant at the lower rates (Tamm & Popovic, 1989). The counteracting processes (plant uptake and absorption of sulphate on soil particles) are too weak to delay the process more than slightly (at the rates discussed here). Removal of hydrogen ions by sulphate reduction would not be of importance in well-drained soils.

Acidification by N is more complicated, since this element occurs in large amounts and in different forms both in the forest ecosystem and in air pollutants. N-induced acidification will be further discussed (Section 10) in connexion with the 'N-saturation problem'.

Our studies have quantified the acidity changes and changes in mineral nutrients in the biologically most important pools, the living trees and the exchangeable pools in the upper soil strata, the main rooting zone.

Further disturbances studied by collaborating research groups are the changes that occur in field and bottom layer composition, in frequency of mycorrhizal and decomposer fungal species (reviewed in Section 7), and acid-induced changes in both organisms and soil biological processes, reported by Tamm & Popovic (1989, 1995).

Area 4. Between-year variation in growth and foliage nutrient concentrations of trees at different nutrient regimes.

The first problem addressed was the question whether between-year variation in needle N concentrations, known from earlier studies, depended on variations in tree processes, *e.g.* nutrient uptake by roots, or in soil processes, such as weather-dependent variations in N mineralisation in the soil. The needle variations in N concentration proved to be synchronous in both controls and N regimes, as was also the case in the early spruce experiment E1 at Remningstorp (Tamm, 1968), and in the spruce optimum nutrition experiment E26B Stråsan (Tamm, 1991). Weetman & Fournier (1984) found a similar synchronous variation between regimes in their optimum nutrition experiment in *Pinus banksiana* Lamb.

Since an increased or even excessive supply of N to the soil did not decrease between-year variation in needle N concentrations, we should look for the direct causes of the variation in within-tree processes. Climate-induced between-year and between-tree variation in growth and biomass production appear to be more important factors than the access of the roots to N. However, to address the complicated interactions between climatic factors, annual tree growth, and the variations in concentrations of both growth-limiting and non-limiting nutrients, long time series are needed, and it is not until

now that series comprising 20–25 years have become available in our experiments.

Our time series of current-needle concentrations of elements other than N clearly demonstrate between-year variation in P, K, Ca, Mg and Mn, also synchronised, to a considerable extent, between controls and the various treatments.

Area 5. Interactions between added nutrients, lime, and other factors.

Nitrogen supply tends to depress plant concentrations of other elements, as is evident in concentration ratios (K/N, P/N, Mg/N, *etc.*) in needles. Mg deficiency is a likely cause of decreased growth at high rates of N addition. In the case of B, the concentrations have decreased below the limit for deficiency, first on the NPK + Lime plots in E42 Lisselbo. The associated growth disturbances and B applications in E40 and E55 have already been mentioned. Visual deficiency symptoms, associated with the low ratios K/N and P/N, were not observed in our pine experiments, as distinct from the spruce experiment E26A Stråsan. The question of possible growth retardation at low K/N and P/N has to do with the interpretation of our optimum curves, which is discussed below (Section 10). At the start of the experiments, more interactions were expected than were actually observed, *e.g.* between liming and N addition.

Simultaneous addition of acid and NPK decreased tree growth more than was expected from the effect of either treatment alone. An unexpected, temporary stimulation of tree growth by acid supply alone was observed. The explanation seems to lie in an interaction between different ecosystem components, where the trees are more resistant to acidification than other organisms. They are therefore favoured by decreased competition, and by increased release of ammonium-N from killed or damaged soil organisms.

Area 6. Effects of interrupted fertilisation on forest plots maintained at elevated nutrient levels (N regimes in particular) for extended periods.

Since it took longer than planned to ascertain that a *quasi* steady-state nutrient situation had been established, we were able to follow the development in one case only, (E58, fertilised annually 1971–1978). There the tree stand (stem growth and needle nutrient levels) was observed for *ca.* 15 years after the end of treatment, and the soil was sampled after ten years. We conclude that the added 720 kg N ha^{-1} was insufficient to raise site quality significantly, but that the return to normal growth rate has been slow, and no negative after-effects of the NPK additions have been observed.

Area 7. Long-term effects of often repeated N additions, comparable with the loads of N compounds in atmospheric deposition in polluted areas.

This is often referred to as 'N saturation', although this term had not been invented when problem area 7 was formulated in the 1970s. We accept here the definition of N saturation as 'a supply of N in excess of the combined demand for N by primary producers and soil organisms' (Aber *et al.*, 1989), even if it is sometimes necessary to use further characteristics of saturation (elevated concentrations of nitrate, Al and hydrogen, leaching losses, physiological functions in trees, *etc.*) to decide whether an ecosystem is N-saturated or not (Aber *et al.*, 1989; Aber, 1992).

In particular, it is difficult to decide how the definition should be applied to ecosystems from which nitrate is leached during short periods only, *e.g.* during the season when roots and soil organisms are more or less inactive, or shortly after a disturbance, when biological uptake is temporarily reduced. In such cases, we consider it necessary to pay attention mainly to the size of leaching losses over a longer period (> one year), and to the physiological health of the vegetation.

We conclude that the highest N regime (N3) in our experiments has saturated the ecosystem according to all suggested definitions. In our opinion, regime N2 has also led to saturation, as evidenced by large losses from the ecosystem. Tree growth is still relatively good, but regime N1 plots are catching up with N2. Regime N1 can be considered as unsaturated at the time of our final revision, since losses from the ecosystem are small, but probably not negligible.

Our results have thus given at least approximate figures for how much N a pine forest ecosystem can absorb without the deleterious effects

associated with the term 'N saturation'. Further aspects of this problem are discussed below (Section 10).

10. Results in relation to some problem areas of current interest

In this section we review briefly research development since about 1960 in some areas of current interest, and discuss to what extent our results may contribute to the solution of urgent problems.

Three topics will be dealt with here:

(i) The meaning of nutrient optimum and the shape of curves describing plant growth as a function of nutrient supply.

(ii) Do optimum nutrient ranges change with developmental stage, stand age in particular?

(iii) The fate of N added to forest ecosystems by fertilisation or deposition.

The meaning of nutrient optimum and the shape of curves describing plant growth as a function of nutrient supply

The Introduction (Section 1) described in some detail the approach used by Mitchell & Chandler (1939), and our attempts to apply a similar approach to boreal conifer species, as well as the need felt for a means of avoiding the arbitrariness associated with pairing data from two highly dynamic time developments, *viz.* that of foliar nutrient concentrations and that of annual tree growth. The obvious solution was to create stable conditions in both of these parameters, and to measure relationships between growth and concentrations under steady-state conditions, something which is overlooked in most publications and textbooks dealing with Liebig's Law of the Minimum and Mitscherlich's formula (see, however, Odum, 1971).

We began the new approach in 1957, with a field experiment E1 Hökaberg, in a young spruce plantation on an abandoned field in SW Sweden. Experience from the experiments at Remningstorp, described above (Section 1), was a spur to the establishment of new and better experiments with similar basic aims.

Parallel with the field experiments at Remningstorp and elsewhere (Tamm, 1965), Torsten Ingestad studied the nutrition of tree seedlings in our laboratory. He found that the growth rate of the seedlings increased markedly when the traditional method—weekly change of solutions—was replaced by flowing solution culture (Ingestad, 1962). He concluded that the decisive factor for seedling growth was the rate of nutrient supply, not the concentration in the solution. He went on to adapt nutrient supply to growth, hence to the demand of the seedlings, using methods which automatically adjusted the addition of three basic solutions according to signals from *p*H and conductivity sensors. The results were first presented in congress papers (*e.g.* Ingestad, 1967) and in greater detail later (*e.g.* Ingestad, 1977, 1982; Ingestad & Ågren, 1992).

An important feature of Ingestad's experiments was the accurate maintenance of a constant chemical composition of plants during test periods of several weeks. He found a linear relationship between relative growth rate and internal concentration of, in the first place, N, until the plants became large enough for self-shading to become important. By plotting the logarithm of plant mass against time for his experiments with varied N addition rates, he obtained a number of straight lines (r^2 values >0.99). A plot of relative growth rate against seedling N concentration (constant during each experiment for each growth-rate) gave a new set of straight lines with very high correlation coefficients. The steepest line marked optimum growth-rate, in the case of *Betula pendula*, 22% mass increase per day during the experimental period (Ingestad, 1977). For other species or growing conditions, other values were obtained.

However, at N addition rates above the optimum rate as defined above, seedling growth decreased. In some cases the system appeared to break down suddenly (Ingestad, 1977); in others, the seedlings appeared to tolerate some luxury consumption before serious growth disturbances occurred (Ingestad, 1982). The negative effects of high N addition rates could sometimes be explained by excessive salt concentrations, but were more often assumed to

depend on an unfavourable balance between N and other nutrients.

It became clear that the old models for plant responses to nutrients were inadequate, based as they were upon experiments with regular exchange of standard nutrient solutions or, in the field, massive applications of fertilisers and measurements of cumulative growth. They should be replaced by models using more dynamic concepts, such as nutrient flux density and nutrient productivity (Ingestad & Ågren, 1992). The relations between relative growth rate, rate of N addition, and internal plant N concentration are simple, accurate and in agreement with accepted physiological principles, *viz.* that plant growth is directly related to the amount of protein in the living cell, which depends primarily on the supply of N. This is a good starting point for a mechanistic model.

An alternative approach is based upon the concept of nutrient-use efficiency (Chapin, 1980; Vitousek, 1982), the amount of organic matter produced per unit of nutrient taken up, which in annual plants is simply taken as the inverse of nutrient concentration. In perennial plants, where at least part of the nutrients once taken up, is used repeatedly, the definition becomes more complicated (Vitousek, 1982), and the use of the concept requires data on litterfall (amount and nutrient concentration) and on organic matter and nutrients permanently immobilised in woody tissues. Nutrient productivity, which for practical purposes is equal to the proportionality between growth-rate and plant nutrient concentration, does not have this weakness, but is founded on the linear relationships found in Ingestad's seedling experiments, but not, *e.g.*, in Fig. 7.5*a* here.

Evidently, there is a need for more research on what happens when the N addition rate exceeds Ingestad's saturation point, or an 'optimum' as here in Fig. 7.5*a*. So far, research has been very empirical, and the results are much more difficult to generalise than in the suboptimal range. Concerning the optimum point, Ingestad (1987) has shown that there is remarkably little variation in optimum composition within a wide range of life-forms and species.

Ingestad and his group determined nutrient productivity relations for several elements besides N, and effects on the allocation of growth of a varied supply of several elements (Ingestad, 1979, 1981; Ericsson, 1995; Ericsson & Ingestad, 1988; Ericsson & Kähr, 1992, 1993). Self-shading and ageing have been introduced into some models (Ingestad *et al.*, 1981; Ingestad & Ågren, 1992), but more work is needed before we have a fully mechanistic model for tree growth in the field, valid also for conditions in which N is no longer limiting.

Several field experiments using Ingestad's concepts as guidelines have been laid out since the mid-1970s, but for chronological reasons we shall now return to our optimum nutrition experiments with annual additions of N at different dosages. These experiments were laid out 1967 (Stråsan), 1969 (Lisselbo), and 1971 (Norrliden). We acknowledge the encouragement obtained from Ingestad's success in keeping constant internal concentrations of N in the test plants during the periods occurring in the laboratory experiments. As was mentioned above, we did not fully succeed in establishing steady-state conditions in the Remningstorp experiments in 1957–1969.

Some difficulties are evident in the transition from short-term experiments in a controlled environment, to field conditions. There is seasonal variation in chemical composition, as well as between-year variation. Element concentrations, even in specified organs (needles), may vary with age and position in the crown. Total biomass cannot be determined without destructive sampling. However, several of these sources of variation can be minimised by standardised sampling. Between-year variation in both concentrations and ring growth can only be offset by using means for several years, but this is, in any event, desirable in this type of experiment, not least because the growth of Scots pine and Norway spruce in any year is largely predetermined by conditions in the previous year. Additionally, the causes of between-year variation offer another challenge (*cf.* Item 4 on the list of problem areas in Sections 1 and 9).

In the series of optimum nutrition experiments established in 1967–1971, the first experiment (Stråsan) was laid out in a young spruce stand, the other two in young pine stands. The experimental design was almost the same for the two pine experiments, as described here, while the Stråsan experiment was a factorial N (four levels) * P (3 levels) * K + Mg + micronutrients (2 levels), in all cases including a zero level. A

further spruce experiment (E63 Åseda, Tamm & Popovic, 1995) lacked variation in N level, as it was believed that the relatively high N deposition in south Sweden would relatively quickly decrease the role of N as a limiting factor, and that interactions between soil acidification and the supply of mineral nutrients would therefore gain in importance. The experiment was thus a factorial N*PK*S (elemental S). As has been described for the pine sites, the spruce sites also had ancillary experiments, to study the effect of other factors (irrigation, liming).

The results of the pine experiments have been reported in this publication, and those from Stråsan by Tamm (1991) and in references therein. Recent soil and biomass studies at Stråsan have been reported by Berdén, Nilsson & Nyman (1997) and Eriksson, Berdén, Rosén & Nilsson (1996). Results from Åseda were reported by Tamm & Popovic (1995), with some emphasis on the acidification problem. In the three experiments with varied N regimes, 'optimum curves' have been fitted to the data, even if a period of some years was required before we could observe a decline in growth at the highest N regime(s), and still longer was required to confirm statistically this decline from the observed 'optimum' (see Tables 5.5 and 5.7). The positive growth response could largely be explained by increased needle biomass (*cf.* Brix, 1983; Ericsson, Rytter & Linder, 1992). Stem growth first increased linearly with needle biomass (Albrektson *et al.*, 1977), with the curve flattening out towards canopy closure (Tamm, 1991). As we have little or no data on light interception, nor data for growth allocation below-/aboveground, we can not decide in detail what happens when the curve maximum is approached; only that our results fit in with traditional optimum curves. Nor is there a large discrepancy between the rising branch of our curve and an Ingestad model that includes a factor for self-shading (Ingestad *et al.*, 1981; Ingestad & Ågren, 1992), even if our 'optimum' N concentrations tend to be lower than his.

Concerning the supraoptimal part of the growth curve, the empirical character of the curve has already been emphasised; this certainly makes it site-specific, if the independent variable is N regime. Moreover, the maximum point and the declining branch appear to be time-dependent, *i.e.* the curve maximum is displaced to the left with time, both when N regimes and concentrations are on the *X*-axis.

Several further results from our pine experiments were summarised above (Section 9). One of the most striking observations from our experiments—not discussed above—is the great difference in response between Norway spruce at Stråsan and Scots pine at Lisselbo and Norrliden. While stem growth in pine at optimum may increase by about 40% over that of the control, growth of spruce increased from 5–6 $m^3\ ha^{-1}yr^{-1}$ to well over 20, *i.e.* by 300%. Some of the differences may be explained by an interaction between fertiliser effects and inherent differences in rates of development. Spruce is a climax species, retarded more than pine by being planted after clearfelling and burning. Repeated biomass samplings at Stråsan demonstrated that a maximum needle biomass had been attained on some fertilised plots already in 1978 (*ca.* $22{\cdot}10^3$ kg ha^{-1}; Axelsson 1985). The maximum pine needle biomass at Norrliden is much lower. Average figures (1985) are $5{\cdot}10^3$ kg ha^{-1} for plots without N and $7–8{\cdot}10^3$ kg ha^{-1} with N (Fig. 7.7). In addition, needle biomass at Norrliden seems to vary with treatment group, with higher values for AN plots than for U. It is not clear whether this difference is due to the source of N, since both site differences and differences in sample tree selection between AN and U may interfere. In any case, maximum needle biomass at Norrliden is less than half that at Stråsan. At Lisselbo, it amounted to $4–7{\cdot}10^3$ kg ha^{-1} in 1975 (Table 6.3), but probably did not rise much further, since litterfall was less than $2{\cdot}10^3$ kg $ha^{-1}yr^{-1}$ in 1980–1983 (Fig. 7.3) and only some of the needles live more than three years (Table 6.3).

Standard values for N concentrations for 'optimum' ranges were established in our dosage experiments, which are presumably also valid for a range of similar sites, sampled in the same way (Section 9). However, before we attach any deeper significance to these values, it is necessary to discuss some results from the new generation of experiments guided by Ingestad's concepts.

The first of these experiments, at Jädraås, middle Sweden, was begun in 1974 as part of the SWECON project. The aim was to maximise biomass production by removing the constraints due to suboptimal supply of water and nutrients (Aronsson, Elowson & Ingestad, 1977; Aronsson

& Elowson, 1980). The treatments were four: control (C), irrigation (I), fertilisation (F), and irrigation + fertilisation (IF).

As in our experiments, needle N concentrations tended to decline with time after the first two years, in spite of increased additions in the IF treatment (Aronsson & Elowson, 1980). The concentrations were initially highest in the F treatment, where the annual additions were the same as those used in 1971–1974 in regime N2 at Lisselbo. N concentrations were followed by sampling needles of different age at short intervals, and the curves for all treatments were parallel, reflecting seasonal variation in needle dry mass (Tamm, 1955) and starch content (Ericsson, 1979) but also reallocation within the tree. Basal-area growth for the period 1974–1984 was highest in treatment IF, the basal area in 1984 being almost three times that of the control (Linder, 1987). IF was closely followed by F. Treatment I was only slightly better than the control. Volume growth data have been published for the period 1984–1988 (Linder, 1990; Linder & Flower-Ellis, 1992). The treatment values were as follows: C 5, I 6, F 11 and IF 12 $m^3\ ha^{-1}\ yr^{-1}$.

The SWECON growth data for the F and C treatments are clearly higher than the Lisselbo data. The differences are smaller compared with E55 Norrliden, where controls grew better in 1980–1984 (*ca.* 8 $m^3 ha^{-1} yr^{-1}$) and the best regime, N1, grew at a similar rate as the SWECON F plots, *ca.* 11 $m^3\ ha^{-1}\ yr^{-1}$. Needle N concentrations in 1974–1988 in the SWECON treatments (Linder, 1990) fall within the lower part of Ingestad's optimum range (1.7–2.5% DM) for both of the treatments IF and F, in spite of a much higher N addition to IF plots. Compared with E40 and E55 data, the SWECON N concentrations (for F and IF) correspond to values between those for regimes N1 and N2 in most years, while C and I concentrations were fully comparable with those on our controls. So far, there is no major discrepancy between the SWECON results and ours.

However, there is more to be said. First, there was a marked difference in the reaction of the lesser vegetation between IF and F plots, where the former were invaded by *Epilobium (Chamaerion) angustifolium* and *Rubus idaeus* L., while the latter differed much less from the C and I plots. This might explain why IF plots initially had lower N concentrations than F plots, in spite of higher total additions in the IF treatment. Secondly, the IF treatment, with other nutrients added simultaneously with N and in fixed proportion to N ('the Ingestad solution') led to a less unbalanced nutrition than the F treatment in 1975, the first year with full data for nutrient concentrations, reported by Aronsson & Elowson (1980). However, in 1977 damage to apical buds and shoots was observed, which, somewhat later, was identified as B deficiency, and led to an increase in the amount of B added in the nutrient solution. The growth increase was somewhat higher than in our experiments with the same tree species, and might have been higher still, had the N addition levels been slightly lower. Later experience from both laboratory and field studies suggests that the optimum N concentration for field-grown trees may be lower than the 1.7–2.5% DM originally suggested for seedlings with much juvenile tissue (Ingestad, 1962; Ingestad & Kähr, 1985). As mentioned above (Section 7, Table 7.4), our results indicate a N optimum at 1.4–1.7% DM.

Further field experiments with fertilisation according to Ingestad's principles, are the Biology of Forest Growth experiment (BFG) in Australia (Linder, Benson, Myers & Raison, 1987; Raison & Myers, 1992*a*) and an experiment in a eucalypt plantation in Portugal (Pereira, Linder, Araújo, Tomé, Madeira & Ericsson, 1994). However, for a more detailed comparison with our results, we shall mainly use one of two Swedish experiments, Flakaliden, where the tree species is different (Norway spruce) but where the climate and soil are similar to the Norrliden site. Much experience, from both SWECON and from the experiments with other tree species mentioned, was used in designing the Flakaliden experiment (Linder, 1995; Bergh *et al.*, 1999). The distance from Norrliden is about 35 km, and the altitude 310 m a.s.l.

The Flakaliden experiment differs from the three growth optimisation experiments mentioned above, by a more rigid control of the internal concentrations of both macro- and micronutrients, with a possibility to correct from year to year any deviations from the set 'target values' for each nutrient, not only N as in our experiments. The target values at the start in 1987 were a version of Ingestad's optimum values, modified with the help of experience from

earlier field trials. Further adjustments were made in 1990 and 1993, based on recent laboratory experiments and on experience from the first years. N additions were decreased from 100 kg ha^{-1} yr^{-1} to 75 kg ha^{-1} yr^{-1}. Modifications to other elements were mostly adjustments downwards. Other improvements were in the monitoring of leaching by a large number of tension lysimeters, and the use of residual ('structural') dry mass (Table 4.2) as a base for the element concentrations. The new base eliminated much of the seasonal variation in concentrations due to starch accumulation in the needles in spring and early summer, and made it possible to follow nutrient status during the entire growing season (using the C + 1 needles, or older). Concentrations and additions for elements other than N were expressed in per cent of those for N.

Tree growth data have been published by Bergh *et al.* (1999). Both height and volume growth increased dramatically at Flakaliden for treatments Irrigation + Fertilisation (IL) and Fertilisation (F), height growth in the second summer from the beginning of the treatments being more than doubled, compared with Irrigation only (I) and Control (C). Volume growth at the start of the treatments was small, because of the small size of the trees, but increased fourfold, compared with the control, during the period. For 1994–1996, the annual volume growth for IL was 13.4 m^3 ha^{-1} yr^{-1}, for F 12.6, for C 3.4 and for I 3.2. For the sister experiment of Flakaliden, Asa in south Sweden, on a climatically much better site, the corresponding figures were: IL 25.7, F 16.7, I 13.5 and C 10.4 m^3 ha^{-1} yr^{-1} (Bergh *et al.*, 1999).

Compared with the Stråsan experiment, the production of the IL treatment in 1995 at Asa clearly exceeds our peak values. If volume growth at Stråsan for the period 1973–1975 (6–8 years from the start of fertilisation) is compared with the Flakaliden data for 1995–1997, the differences are small, with *ca.* 3 m^3 ha^{-1} yr^{-1} on controls at both sites, and best performances 16 and 14 m^3 ha^{-1} yr^{-1}, respectively. Later, peak production at Stråsan increased to 22–23 m^3 ha^{-1} yr^{-1} (1979–1986), with control values of 5–6 m^3 ha^{-1} yr^{-1}. A similar increase is expected at Flakaliden, and it will not be surprising if growth there exceeds the Stråsan peak values, in spite of a somewhat colder climate.

Pinus radiata D.Don (Raison & Myers, 1992*a,b*) and *Eucalyptus globulus* Labill. (Pereira *et al.*, 1994) may have a higher potential growth than Scots pine and Norway spruce, but to our knowledge, Flakaliden is the most successful growth optimisation experiment existing, judging from the difference between the control and the best treatment. Needle concentrations of almost all nutrients have been at or slightly above the target values, at least for the period after the redefinition of some of the values (Linder, 1995 and pers. comm.). The largest deviation from target concerns Ca, where concentrations have been far above the target value, presumably due to large supplies in the soil and to the well-known Ca accumulation with needle age (the samples were C + 1 needles). There were also some difficulties in keeping Mg constantly at target level. In the case of the micronutrients Cu and B, it is not clear that the experiments from which the target values were taken were accurate enough.

In conclusion, the revised target values from Flakaliden have proved their value as the best estimates existing for optimum nutrient concentrations in a boreal conifer. Since nutrient-to-N ratios are very similar for a wide variety of species, including Scots pine and Norway spruce (Ingestad, 1987), the corresponding ratios should not differ much for Scots pine.

However, in the case of N concentrations, there is room for comment (see also the next subsection). As noted earlier, the differences between conclusions drawn from values on the rising branch of our empirical curves, and from target values, appear small. Much of the difference can be explained by the selection of sample positions (C (current) or C + 1 (previous year's) needles) and the choice of base for calculation (total DM or residual DM). Our choice of current needles was based on systematic comparisons between element concentrations in the current and C + 1 needles on the same branches, sampled in October (Tamm, 1956) and a desire to avoid unnecessary damage when shooting down samples with a shotgun from the tops of trees too tall for the use of pole secateurs.

For concentrations above the optimum N values, neither the old curves nor the target values give other than purely empirical infor-

mation. It is hoped that arginine analyses might be helpful, since N values around or above 20 mg g^{-1} DM are associated with marked increases in arginine, according to Aronsson (1985) and Näsholm & Ericsson (1990). A later inventory of concentrations of arginine and N, P and K in spruce needles from south Sweden (Ericsson, Walheim, Nordén & Näsholm, 1995) suggests that arginine accumulation may occur also at somewhat lower N concentrations, but the authors still consider it related to nutritional imbalances. Näsholm & Ericsson (1990) suggested that their fertilised trees (N2, N2PK and N3 at Norrliden) had reached a maximum concentration of foliar protein, and that the addition of more N led to accumulation of arginine. As mentioned earlier, Edfast *et al.* (1996) found a decrease in arginine at Lisselbo when former N3 trees were fertilised with either PKMg or N3PKMg, resulting in a more balanced nutrition. It may also be pointed out that all our N values at or above 20 mg g^{-1} in Table 4.1 are associated with below-target values in one or more of the ratios P/N, K/N and Mg/N (Table 4.2).

In our experiments, the difference in N concentration at curve maximum, with and without PK addition at both Norrliden and Lisselbo (Table 7.4), is small. We have no information whether the curve maximum is influenced by variations in addition of other elements, but according to Aronsson *et al.* (1999), data from E56 suggest that foliar N concentrations are influenced by the addition of P, K, Mg or S to a very limited extent, if at all.

Do optimum nutrient ranges vary with developmental stage, stand age in particular?

Comparisons have often been made between results from experiments with seedlings and those made with larger trees, most systematically by Miller, Miller & Cooper, (1981). They found a linear relationship between logarithmic tree mass and optimum needle N concentrations, from seedlings weighing 1 to 10 g DM, grown in solution culture in the greenhouse with 3% foliar N up to 13-year-old or older, field-grown young trees, weighing 5 to 10 kg DM with 1.5% N. However, there were no data for trees aged between 3 and 12 years and there was no further decrease in N optimum concentrations in still larger trees, fertilised at age 36, 37, and 38 years.

The causes of differences between seedlings and field-grown trees may be fairly trivial. Seedlings contain a large proportion of juvenile tissue, and the conditions in the greenhouse, especially in solution culture, are very different from those in the field, with respect to light intensity and water stress. Daylength and temperature regimes may also differ. The use of residual instead of total dry mass, or of element ratios, may reduce some, but by no means all, of the difference. Since the composition of the solution, with respect to nutrients other than N, was constant in the solution-culture experiments of Miller *et al.* (1981) and in their drip-feed sand cultures, the balance between N and other elements presumably varied considerably between N levels. As has been emphasised by Ingestad (1977), solution-culture experiments with periodic change of solutions give a poor control of the nutrient addition rate, which is a more important factor for plant growth than foliar concentrations *per se*. However, the results of Miller *et al.* (1981) agree with our experiences at one important point, *viz.* that optimum N concentrations derived from laboratory experiments tend to give higher optimum N concentrations than those derived from field experiments. As discussed earlier, our optimum value for Scots pine is 14–17 mg N g^{-1}, as compared with 15 as a standard value accepted in Britain (Miller *et al.*, 1981). While this figure is at variance with the value 20–25 reported from the first Swedish dosage experiment (Tamm, 1956), doubts concerning the traditional use of single additions in optimum experiments eventually led to the new generation of optimum nutrition experiments presented here.

If we disregard differences that can be explained by different morphology and environment, there is still justification for asking whether the optimum concentrations differ between standardised samples from saplings, pole-stage trees and old trees. Fiedler, Czerney, Höhne, Hofmann & Müller (1969) have demonstrated that needle N concentrations (%DM) did not vary systematically with stand age of Scots pine in three site groups in eastern Germany. What changed with age was needle length and mass, hence the amount of N in 100 needles. In P and K, however, there was some

decrease in element concentration in the oldest stands (>80 years old). The authors comment that further systematic experimentation would be desirable, as earlier-established standard values for pine nutrition are unsatisfactory.

Several authors, in particular Switzer, Nelson & Smith (1966) and Miller (1981, 1995), have shown that the net uptake of nutrients differs between these stages, with a maximum at canopy closure, after which recycling provides an increasing proportion of the nutrient demand of the tree. Recycling then takes place both internally, within the tree, and by litterfall and new uptake. Chapin *et al.* (1986) are critical of the use of the concepts nutrient optimum and limitation applied to ecosystems, but they agree with Miller and others that plant nutrient demand changes with age.

It seems clear that, on poor soils especially, there is a difference in growth and survival between adult trees and recently established young saplings, to the disadvantage of the latter. The 'lichen-pine forest' of northern Scandinavia is an example for which it is clear that competition is not primarily for light, but for N, although large and small trees grow on the same soil (Romell & Malmström, 1945; Björkman, 1945). The annual nutrient demand of a large, healthy tree is only a small proportion of its total store of more or less mobile elements, while a small sapling has a poor chance of surviving unless it can increase its size considerably from year to year. Yet the nutrient concentrations of exposed current needles may be similar, showing that both suffer from N deficiency.

Ericsson (1994) reviewed data on nutrient uptake and biomass production, and concluded that evergreen conifers have slightly higher N use efficiency than broadleaved deciduous trees, and that in trees, nutrient-use efficiency increases with age, at least until internal nutrient cycling is fully operative.

We conclude that the evidence is not very strong that foliar concentrations of N from well-specified positions follow different 'optimum curves' (*sensu* Mitchell & Chandler, 1939) between field-grown saplings and old trees.

For elements other than N, the successful use of 'target values' (Linder, 1995) in field experiments, derived from seedlings cultivated in the laboratory and expressed as element-to-N ratios, speaks against major shifts in optimum values for these elements with age.

We see no contradiction in the possibility that similar relationships may exist in saplings and adult trees, between growth-rate and needle concentrations of the growth-limiting element N. As stated above, the entire difference may lie in the fact that small, young trees need a higher growth-rate than adult trees (and hence a higher needle N concentration) for survival. A somewhat similar situation is that described by Miller (1995) between Sitka spruce (*Picea sitchensis* (Bong.) Carr) on the one hand and Scots and Corsican pine on the other, where the spruce has a higher growth-rate and larger uptake rate than the pines, but differs little from them in foliar nutrient concentrations for satisfactory growth.

The fate of N added to forest ecosystems by fertilisation or deposition

The fate of nutrients, N in particular, added to a forest ecosystem, has become an urgent problem in the discussion of ecological consequences of human impacts on the chemical climate, with increased deposition of N compounds in many regions. We shall describe how our research in the field has developed, but also compare with other studies of N input to ecosystems, where either N sequestration or output (or both) has been measured.

Although site differences in nutrient supply had been studied in Sweden since early this century, and Hesselman had begun field experiments with N additions in the 1920s (Linder, 1990), there was little discussion of practical forest fertilisation in Sweden or elsewhere until the late 1950s, despite the existence of several examples in which addition of one or more mineral nutrients had increased site productivity from very low to an economically feasible level. Hesselman's and Romell's early experiments, and a great deal of other information, had suggested N supply as a key factor for tree growth in Sweden (Linder, 1990). Mitchell & Chandler (1939) had shown that this was also the case in the north-eastern United States.

Our first attempt to study what happened with added fertilisers was made at the Mölna site (see Tamm, 1956). From the beginning in 1951, the N dosage experiment was associated with a small leaching study which, however,

concerned cations only (see Troedsson, 1955). The leaching induced by a small amount of ammonium nitrate appeared to be unimportant.

In the period 1958–1960, we began to sample biomass on fertilised and unfertilised plots at four different sites, including Mölna and Remningstorp (Tamm, 1963*a,b*; 1968). Our general conclusion was that stands with a closed canopy sequestered limited amounts of N aboveground (20% or less) when fertilised at rates of 200–300 kg N ha^{-1}. In contrast, young stands without fully closed canopies might account for one-third to more than half the added N, if it had been given as moderate annual additions for 4–6 years (Tamm, 1982).

Until the mid-1960s, there were few published studies on the recovery of nutrients added to forest stands. Wittich (1958) reported observations from a forest plantation in northwestern Germany, planted in 1950 and fertilised four times between 1950–1955. The main tree species was Scots pine, and at a sampling in 1956 the pine biomass (roots included) contained 42 kg ha^{-1} more N in the treatment NPKCa than on the control plots. This corresponds to 20% of the added N, but to this figure should be added the amounts in the admixed tree species (larch (*Larix kaempferi* (Lamb.) Carrière), Red oak (*Quercus rubra* L.), and spruce) which together made up nearly half the number of stems, but a smaller fraction of the volume and biomass.

In the Pacific Northwest, Heilman & Gessel (1963*a,b*) made five pairwise comparisons between fertilised and unfertilised stands of Douglas fir, aged 30 to 52 years, studying both stand and soil. In their study, between 64 and 138% of the N addition was accounted for in the entire ecosystem, and 13 to 61% in the vegetation (tree stand, lesser vegetation, and roots) The large variation between the sites was probably caused by pre-treatment differences between plots, since apparent recoveries far above 100% appear unlikely. It is interesting that the recovery in the soil was higher in the mineral soil than in the forest floor. Three of the five experimental stands had been fertilised annually for 4–7 years with 106–140 kg ha^{-1} yr^{-1} N each time, but the data do not permit conclusions to be drawn about differences between single or repeated additions.

Later, Miller, Miller & Pauline (1976) reported a high recovery of added N in a young stand of *Pinus nigra* in Scotland, with a larger part of the added N in the tree stand than in the forest floor.

The recovery of added N in the soil was studied in Norway by Overrein (1969, 1971) in model experiments using ^{15}N and by Nõmmik in the Forest Soils department of the College of Forestry, both by the ^{15}N technique (Nõmmik & Popovic, 1971) and by mass-balance calculations in field experiments (Nõmmik & Möller, 1981). It was concluded that normal forest soils had a large capacity to immobilise single additions of ammonium N, and even more of urea. Added nitrate disappeared from the root zone rapidly (within a year), to a large extent by leaching. For further references on N leaching and recovery, see Johnson (1992).

When our experiments demonstrated dramatic growth responses to annually repeated, moderate annual N additions, it became a pertinent question whether such additions changed soil conditions from the normal pattern of low leaching losses to a steady leaching, one of the assumed consequences of 'N saturation'. This problem could not be addressed in our experiments until the treatments had been maintained long enough to create N saturation. Our first case was the N optimisation experiment E1 Hökaberg (1957–1969), where biomass and soil were sampled after 13 years' fertilisation. The soil data indicated a low recovery in the top 20 cm soil of the large amounts of N added (a figure around 10% can be derived from data in Tamm & Popovic, 1974), and the total sequestration in the stand had fallen from high values (30–58%) at the time of stand closure to *ca.* 10% (Tamm, 1982).

In 1988, a large soil sampling of E55 was organised, with the results reported above (Section 3, Table 3.5), and compared with the biomass data from 1985 (Section 7, Table 7.5). Tree growth measurements showed that the growth optimum had fallen with time to below regime N2. Soil changes (strong mineral soil acidification, losses of N according to both mass-balance calculations and N isotope studies) also suggested N saturation in regimes N2 and N3. Thanks to these results, we could also consider regime NPK in the acidification experiments E57 and E42 (with the same N additions as regime N2 in E55 and E40, respectively) as

N-saturated, and use soil sampling data from 1985 (Tamm & Popovic, 1989) as further material (Aronsson *et al.*, 1999). We can then compare in the first place NPK with controls both at Norrliden and Lisselbo. Most treatments other than N had a small effect only, so with some reservations, further plots can also be discussed in the comparisons.

As shown by Aronsson *et al.* (1999), the apparent soil recovery of added N is somewhat lower in E57 (plots with NPK, irrespective of other treatments, compared with their counterparts without NPK) than in the main experiment E55 at Norrliden in regime N2. This is not surprising, since there was an interaction between NPK and some of the additional treatments, negative on tree growth and increasing leaching and mineral soil acidification. In E42 Lisselbo, the N recovery in the soil is comparable with that in E55U (30% in regime N2, Table 3.5) and higher than in E55AN (24%), but the differences are not statistically significant.

Since the soil sampling at Norrliden in 1988 was carried out, an exponentially increasing number of publications has discussed the consequences of N saturation, not all of which can be reviewed here. Our discussion will concentrate on comparisons with cases with large or often repeated N additions, which may elucidate the representativeness of our results. The emphasis will be laid on the processes around the 'point of N saturation'. First, we shall review Swedish studies, some of which are more or less connected with the Norrliden and Lisselbo experiments.

The oldest of the nutrient optimisation experiments, Stråsan, has been sampled for biomass several times, first after seven years' treatment (Tamm, 1974, 1982), when the N recovery aboveground was 18–25%. Because of the very stony soil, no comprehensive soil sampling was done until 1989 (Eriksson *et al.*, 1996), and even then only ten of the 52 plots were sampled, representing the treatments Control, N1P1 (addition 700 kg N ha^{-1}), N2P2 (addition 1700), and N3P2 (addition 2550). Biomass was also sampled on the same occasion. Not unexpectedly, there were large differences between some duplicate plots in estimated N recovery, both in stand and soil. The trend to decreased recovery with increasing additions found at Norrliden did not appear, according to Tables II and III in Eriksson *et al.* (1996), regime N2P2 having had a better recovery than both N1P1 and N3P2. On average, 67% of the added N could be accounted for in the ecosystem, which is considerably more than the figure 45% in regime N2 at Norrliden (Table 7.5). The proportion of the excess N found in the stand (on average 26%) did not vary much between regimes, neither at Stråsan (24–28%) nor at Norrliden (28–37%).

A further, as yet unpublished, soil sampling of five treatments at Stråsan (Control, PK, N2, N2PK and CaN2PK) was made in 1994 by M. Sjöberg and T. Persson (pers. comm.), from which preliminary data suggest a recovery of about 50% of the added N in the soil (LFH layer + mineral soil down to 30 cm).

The SWECON experiment at Jädraås has been mentioned as being subject to very detailed studies. However, concerning nutrient budgets, the only published report is a comparison between controls and IF plots, sampled in May, 1979, when 670 kg N ha^{-1} had been added (Ingestad *et al.*, 1981). The estimated recovery of fertiliser N above- and belowground (mineral soil down to 40 cm) was 76%, but the authors emphasise that the figure is not very accurate. However, it does not differ very much from our estimate for regime N1 at Norrliden, which in 1984 had received a somewhat higher N addition, without showing signs of N saturation.

There are also some experiments in 85- to 130-year-old pine stands, first fertilised in 1959. There are four experiments with the same design on poor soils in a severe climate, Expts P728 and 728A situated in Lapland, N. Sweden and P731 and 731A in Dalarna, middle Sweden (Burgtorf, 1981). There are no replications within sites, but since sites and stands are fairly similar, they are capable of being treated as four blocks of the same experiment. The plots were fertilised with ammonium nitrate, PK and lime in factorial combinations.

The original aim was to reveal the relative role of N and other nutrients on a common type of poor site, but when the optimum nutrition experiments were started, the N additions were adjusted to give total additions similar to regime N1 in Expts E55 and E26A. It was thought to be of interest to compare the effect of a similar total addition to young and old stands. The N

additions were then repeated, first every other year, later every third year. The PK addition was repeated once, in 1978, while lime was added in 1959 only. Tree growth during the period 1959–1978 was approximately doubled by N addition, but little affected by the other treatments. The total amount of N added up to 1978 was 780 kg N ha^{-1}, as compared with 630 kg added in regime N1 at Norrliden. These experiments were sampled in 1980 by Hallbäcken & Popovic (1985) as part of an inventory of old liming experiments in Sweden. Fortunately their samples (humus layer and 0–20 cm mineral soil) were analysed for N, so we have calculated recovery values for the soil. There were only moderate between-site differences in recovery. The recovery values differed between the four treatment comparisons possible (N–control), 18%, (NPK–PK), 37%, (NLime–Lime), 25%, and (NPKLime–PKLime), 58%. Only the difference NPKLime–PKLime differed significantly from the other three differences. The total recovery in the ecosystem is not known, but both tree stand and field layer look very different on plots with N, as compared with plots without N. The lower soil recovery (on plots without PKLime) compared with Norrliden, can at least partly be explained by the size of the individual N additions, 120 kg N ha^{-1}, as it is known that ammonium nitrate additions of this size lead to immediate leaching losses (Tamm *et al.*, 1974*a*; Wiklander, 1980).

There is also an experiment, P777 Norråker (see also Section 7, last subsection) in old spruce forest, 153 years old at the start of of the treatments in 1963, and fertilised with N similarly to the old pine stands until 1986 (Hallbäcken & Bergholm, 1998). There were eight plots, two controls, two given N as ammonium nitrate and two as urea. The two remaining plots received NPK, one ammonium nitrate and one urea. The PK fertiliser was given at the start and on three further occasions. The total N addition amounted to 960 kg ha^{-1}. Tree growth in the period 1963–1991 more than doubled on fertilised plots, from 2.5 to 5.7 m^3 ha^{-1} yr^{-1}. A preliminary N budget for the control and urea plots, calculated from soil samplings in 1990 and biomass samplings in 1993, shows a total N recovery of 75%, with 14% in the trees, 46% in the humus layer and 15% in the mineral soil, most of which is in the 0–20 cm horizon (L. Hallbäcken, pers. comm.).

Nohrstedt (1990) and Nohrstedt *et al.* (1994) have reported results from an old N dosage experiment in a 80-year-old, slow-growing pine stand, with ammonium nitrate additions from 120 to 600 kg N ha^{-1} in 1967, and refertilised in 1974 and 1981 with the same amounts. There were considerable differences in N recovery between the two experimental blocks, but recovery in the field layer, humus layer and mineral soil 0–10 cm ranged between 40 and 70%, except for the highest addition (1800 kg ha^{-1}), where it was <30%. In absolute figures, the losses increased continuously with addition up to about 1300 kg (of 1800) at the highest level. Of course, some of this N may have been taken up by the trees or have remained in the soil below 10 cm depth, but judging from our experience, these amounts should be limited. Presumably, considerable parts of at least the higher additions were lost shortly after fertilisation, but not later, since tension lysimeters installed in 1987 failed to show nitrate in the lysimeter water, except for a slightly elevated level at the highest fertiliser dose. The trees were felled in the autumn of 1987, and it is interesting to note that an increase in lysimeter nitrate occurred at the two highest N levels, but it was not as dramatic as those found at Stråsan after felling of recently fertilised N2P2 plots, with a total addition of 1700 kg ha^{-1} (Berdén *et al.*, 1997). However, at Stråsan nitrate leaching was much lower from N1P1 plots, with 730 kg N added, but no further additions were given after 1985, six years before clearfelling.

Further Swedish experiments with several repeated N additions have been described, in which the N losses have been checked with the help of lysimeters or budget calculations. The total additions have, however, not exceeded 1000 kg N ha^{-1}: Farabol 1976–1991, 600 kg (Andersson, Bergholm, Hallbäcken, Möller, Pettersson & Popovic, 1995), Skogaby 100 kg annually from 1988 (Nilsson & Wiklund, 1995), Västanbäcksmon 1968–1988, 810 kg (Nohrstedt, 1992). There has been a good retention of N in all these cases, and this is most remarkable concerning the two first examples, which are situated in S. Sweden and which have been exposed to a high atmospheric deposition of N for a long period.

In contrast, an experiment in mature beech forest (*Fagus silvatica* L.) in southernmost Sweden, with a bulk deposition of 24 kg ha^{-1} yr^{-1} inorganic N, responded to ammonium nitrate additions amounting to 60 and 180 kg N ha^{-1} yr^{-1} during five years, with several symptoms of N saturation (Tyler, Balsberg-Påhlsson, Bergkvist, Falkengren-Grerup, Folkesson, Nihlgård, Rühling & Stjernquist, 1992). Nitrate concentrations in the soil solution increased dramatically after fertilisation, and acidity increased. Ecosystem budgets indicate considerable losses of nitrate N, while some ammonium N was still sequestered in the system. Total amounts of N in the horizon 0–10 cm decreased significantly with fertilisation, and the C/N ratio increased. Increased concentrations of most metal cations in the soil solution suggested ongoing leaching of (among others) Ca, K, Mg and Mn. Tree growth was not affected much by the treatment, if at all.

From Finland, Mälkönen, Derome & Kukkola (1990) have reported soil retention (humus layer and 0–10 cm mineral soil) of N in 40 experiments fertilised several times during a 20-year period, with, on average, 315 kg N ha^{-1}. Their retention values were on average 43% for the humus layer and 42% for the mineral soil 0–10 cm, although the latter figure was not statistically significant because of the wide scatter in the values. However, there must have been sequestration in the trees, as fertilised pine stands had increased their stem growth by an average of 1.5 m^3 ha^{-1} yr^{-1}, and spruce stands by 0.8 m^3 ha^{-1} yr^{-1}. It thus seems likely that most of the added N still remains in the ecosystem.

Some publications by Stanturf and collaborators (Stanturf, Stone & McKittrick, 1989; Stanturf & Stone, 1994) are of particular interest, as they set out to investigate whether mixed hardwood stands on good sites in New York State still responded to N addition as they had done in the 1930s (Mitchell & Chandler, 1939). Their treatments started in 1967–1969 on various sites, which were fertilised twice with, in total, 672 and 1344 kg N ha^{-1}. A significant growth response was obtained for one species only, *Prunus serotina* Ehrh. Responses in *Acer saccharum* Marsh. and *Fraxinus americana* L. were small. Soil samplings after 10–11 years failed to demonstrate consistent N enrichment in the organic layer or in the mineral soil (0–10 cm). Neither N amounts nor C/N ratios were changed. However, the soil had lost base cations, although not in amounts equivalent to the lost and presumably leached N. In the mineral soil, *p*H had decreased significantly, while the decrease in the organic layer was smaller and non-significant.

Other experiments of great interest have been laid out more recently in New England. The first study (McNulty & Aber, 1993) was laid out in 1988 in high-elevation stands dominated by *Picea rubens* Sargent, already subject to moderately elevated N deposition. Further small additions of N (15–30 kg N ha^{-1} yr^{-1}) affected several ecosystem processes, including tree growth, where the mostly positive N response was difficult to quantify, due to high variation between plots, both during a pre-treatment period and later. Most evident was an increase in N mineralisation and mobility, suggesting potential losses of nitrate from the site. A second study (Aber, Magill, McNulty, Boone, Nadelhoffer, Downs & Halett, 1995) added three further experiments, two in mixed hardwood forest and one in Red pine (*Pinus resinosa* Ait.). They proposed that the different sites were in different positions on a four-stage scale from 0 (strictly N-limited with high retention) to 3 (N-saturation with leaching losses), and suggested that fertilised plots on the site earlier described (McNulty & Aber, 1993), and in the Red pine stand, were on the verge of stage 3. The two hardwood sites were not yet N-saturated. The most N-limited ecosystem (oak-maple at Harvard Forest) had retained 900 kg N ha^{-1} without significant nitrification.

Several catchment experiments with manipulations of the input of N (and S) have been installed during the past decade, *e.g.*, within the NITREX project (see Tietema, Wright, Blanck, Boxman, Bredemeier, Emmet, Gundersen, Hultberg, Kjønaas, Moldan, Roelofs, Schleppi, Stuanes & van Breemen, 1995). We cannot discuss them all here. However, the ARINUS project in the Black Forest (Feger, 1993) merits special attention, since it provides an opportunity to compare the effects of N addition to sites with similar deposition (14–16 kg N ha^{-1} yr^{-1}) but different bedrock and history. On one of the catchments, with 100-year-old spruce forest and a bedrock low in Mg, 28% of the

first N addition was leached out. The other catchment carried 50-year-old spruce, and had been exposed to N depletion (litter-raking). It lost only 4% of the added N. Apparently, the project has been successful in finding the point at which extensive leaching starts, and future results will show when a similar situation will arise also in the, as yet, non-saturated catchment.

In addition to the experiments by Stanturf *et al.* (1989) and Aber *et al.* (1995), several other recent plot experiments utilise intensive nutrient regimes to maximise tree production or to study ecosystem behaviour at conditions close to N saturation. Examples are BFG in Australia (Linder, Benson, Myers & Raison, 1987; Raison & Myers, 1992*a*), Skogaby (Nilsson, 1992; Nilsson & Wiklund, 1995), Flakaliden and Asa in Sweden (Linder, 1995; Bergh *et al.* 1999), Klosterhede in Denmark (Beier, Rasmussen, de Visser, Kreutzer, Schierl, Zuleger, Steinberg, Bredemeier, Farrell, Collins & Cummins, 1993; Hansen, Beier, Gundersen & Rasmussen, 1995). However, while most of these experiments have fulfilled their purpose—whether this was growth stimulation or revealing nitrate leakage—so far relatively little seems to have been published on the amounts of N needed to saturate an ecosystem, and on what happens when this point is exceeded.

Evidently, there is a need for efficient use of existing experiments where N saturation has been produced by controlled treatments, as will be further discussed in the next section. Here, we shall briefly mention resamplings so far made in our experiments, which, among other things, make it clear that resampling of a substrate as heterogeneous as a forest soil is not an easy task.

In their survey of Swedish liming experiments, mentioned earlier, Hallbäcken & Popovic (1985) sampled controls, Ca, NPK, and NPKCa plots in E42 and E57 in 1980–1982. The differences they observed between N stores on fertilised and non-fertilised plots do not differ much from ours, but the N concentrations in the humus layer differed systematically between the two samplings; higher values in our 1985 sampling also occurring on plots without N addition. This suggests that there may be systematic differences between the two samplings, not uncommon in samples from forest soils. The differences are likely to be found in the separation of the humus layer from litter, mineral soil, or both. As mentioned earlier, we await publication of data from a limited resampling of E55 by T. Persson and M. Sjöberg in 1994, where similar differences may also occur, but where the preliminary data seem to indicate better comparability.

Apparently, we should also look for other types of evidence of a possible accumulation of N in saturated forest ecosystems. The concentrations of N in biomass fractions appear to increase also in supra-optimal N regimes, according to the data cited above (Section 4, Tables 4.3, 4.4, 4.5, 4.8) and in earlier biomass studies (including some sequential samplings; Tamm, 1968, 1982). However, the decrease in vigour, and eventual breakdown of the tree stand at high N regimes, imply that higher concentrations do not necessarily lead to more N in the standing crop. On the other hand, the higher N concentrations in the litter (both above- and belowground) might lead to increased N concentrations in the soil organic matter, especially since decomposition studies seem to indicate retarded decomposition of litter at higher concentrations of N (Berg, 1986*b*), at least in some phases of the process.

A possible indicator of a potential retention of N in soil organic matter, under conditions of high N supply, might be the C/N ratio, either when comparing plots or sites with different N input, or when resampling sites with high N input. Since the C/N ratio is an intensity variable, like *p*H or base saturation, it should be easier to find statistically significant differences between plots or sites, than is the case with 'capacity variables', such as the amounts of elements per unit area (Troedsson & Tamm, 1969). Hokkanen *et al.* (1995) found a coefficient of variation of 14.9% for the C/N ratio, as compared with 40.2% for humus layer thickness, the only 'capacity variable' in their study that reflected total amounts. However, great care should always be taken over the distinction and separation of the different soil horizons.

Examples of C/N ratios have been given above (Section 3, Fig. 3.4 and Section 8, Tables 8.2 and 8.5). Fig. 3.4 is particularly informative, as it compares the different N regimes in E55, separately for the humus layer and the top mineral soil. It is evident that, in the humus layer, most of the reduction of the C/N ratio with N

addition has already taken place in regime N1. There is a tendency to further decrease with higher N regimes, but these changes are barely significant. Urea addition appears to give higher immobilisation than does ammonium nitrate—which agrees with other studies—and if there is an effect of PK addition, it is negative. In the mineral soil (0–20 cm), there are more gradual decreases in C/N with increasing N regimes, *i.e.* N accumulation continues from N1 to N2 and N3, unless we assume that carbon concentrations decrease with increasing N regimes, an assumption without support in Fig. 3.5. Nor does common knowledge of the stability of soil humus speak for such changes. We may thus conclude that there is some retention of N in the mineral soil also at high N supply. This conclusion is in agreement with the mass balance data (Table 3.5) which, in addition, give the (non-significant) difference in mineral soil N between N1 and N2 as 55 ± 39 kg N ha^{-1}.

Further data for C/N ratios for E57 at Norrliden and E42 at Lisselbo were presented by Aronsson *et al.* (1999). They found in all profiles at Norrliden a trend from a high C/N ratio in the humus to a much lower ratio in the mineral soil (which is normal in Swedish podsol profiles), while at Lisselbo this trend was weaker and more irregular, with values around 33 occurring in all horizons, and with small differences between fertilised and unfertilised. Judging from Table 8.5, part of the explanation may be a stronger C accumulation after fertilisation at Lisselbo than at Norrliden. Evidently, more work is needed to decide whether we may use changes in C/N as an indicator of N retention. We must also take into account the observation of an increase in C/N when more N was added to an already saturated beech forest (Tyler *et al.*, 1992). The stability and amounts of organic C fractions should also be considered.

In any case, on our sites there seems to be little hope that a substantial fraction of future high N additions will be immobilised in the relatively inert organic matter in the mineral soil. The humus layer has a larger initial capacity for N immobilisation, as illustrated both by C/N ratios (Fig. 3.4) and mass balances (Table 3.5), but even here, the changes in the C/N ratio are moderate, at most from 41 to 29 (treatment group UPK) or from 37 to 27 (U). Even the lower figures are well above the ratios on very fertile sites. If we consider the C/N ratio a measure of the 'quality' of soil organic matter on a site fertility scale, our treatments have evidently changed the quality, but it is still a long way from the situation on very good sites. It should also be noted that the treatments have barely decreased the initial differences in C/N between treatments. It is possible that some part of these differences is caused by small amounts of charcoal in some samples, mainly in those from the humus layer. In any case, changes in humus quality appear to be slow processes, not only in the mineral soil, but also in the humus layer. It should also be noted that there is little or no evidence that the N additions have decreased the initial differences in C/N between treatment groups (Fig. 3.4). It is possible that some part of these differences are not only chemical and physical, but also biological, with all manner of interactions between organisms and their environment.

We conclude from the foregoing that forest ecosystems have a large, but variable, capacity to retain added N. Depending on the site, the largest retention may take place in the humus layer or, less often, in the mineral soil. Retention in the tree stand and other vegetation is normally limited, but young stands, before canopy closure, may sequestrate half to one-third of N added annually in moderate amounts. When single, high doses of ammonium nitrate or urea are added, there are losses in the first season by leaching (ammonium nitrate treatments) or volatilisation (urea), which may lower the retention figures, but which may also facilitate the return of the soil biological community to more normal conditions. At least, the nitrification following clearfelling, in Nohrstedt's experiment (Nohrstedt, 1990; Nohrstedt *et al.*, 1994) with high doses at long intervals, has remained much lower than in the corresponding situation at Stråsan. And at Norrliden, both nitrification and N losses are already high in high-N regimes without clearfelling.

We agree with Nohrstedt (and Johnson, 1992) that such differences in results may be caused by the timing of the N additions. Heavy applications at long intervals are better suited to answer questions on environmental effects of practical forest fertilisation, while small additions at frequent intervals are less 'unnatu-

ral', if the purpose is to study effects of atmospheric N deposition.

Knowledge of the rates of many soil processes is unsatisfactory. This certainly applies to the accumulation of N and C in soil organic matter. Our results suggest that even experimental periods of decades (17 years at Norrliden) may be insufficient to measure ecosystem process rates, as well as the end result. If so, some of the currently used models for acidification and N saturation should be reconsidered. Even the most elaborate mechanistic models may fail to produce useful results, if they are run over periods of 50 to 100 years and if processes are neglected which are too slow to appear in the basic data used to build the model, but are still important in the longer perspective.

As the present atmospheric deposition has already led to (or very close to) N-saturation in some regions of Europe and North America, it is regrettable that we have found very few instances in which N-saturation has been created in reasonably well controlled experiments, and no other instance in which the experimental period has been as long as in our optimum nutrition experiments. We sincerely hope that present and future research will soon provide more material for comparison with our data and conclusions. So far, we have not found evidence questioning the validity of our results for large areas of boreal forest.

11. Suggestions for further research on experimental sites with controlled nutrient regimes

Together with positive results, we have reported (Section 9) cases in which our aims have not been fully achieved. Some unsolved problems have also been mentioned in the comparisons we make with other projects with different methodologies.

We do not argue that our approach is the only one or that it is able to solve all kinds of problems in forest nutrition. What we would emphasise is that 'longitudinal' studies, in which the same ecosystem is followed over a long period, have a value in themselves, especially when the long-term study contains meaningful experimental treatments. Long-term experiments are common in silvicultural research, when the issue is thinning practice, but not in the case of nutrient regimes. A rare exception are the combined thinning and fertilisation experiments started in Sweden between 1966 and 1975, and described by Eriksson & Karlsson (1997).

Most existing long-term experiments involving soil amendments consist of liming at planting or addition of phosphate to soil low in P. Both cases represent situations where single additions may have effects over many decades. Such experiments are relatively simple and inexpensive to maintain for long periods. Experiments with N additions require frequently repeated treatments, if the intention is to study changes in ecosystem functions at defined N levels. Experiments with easily leached mineral nutrients, such as K and Mg, require treatment regimes of intermediate intensity, if the objectives extend beyond the diagnosis of deficiences.

A problem of great interest from an environmental viewpoint concerns the functioning of N-saturated ecosystems. Such systems can be studied on agricultural sites, receiving much fertiliser, but excess N is not common in more natural terrestrial ecosystems, such as forests, except in two situations: *(i)* when some other nutrient is in poor supply, and *(ii)* after clearfelling or other serious disturbances on good sites. Both of these situations are well worth studying, but we may encounter still worse problems over large forest areas in Europe and some other parts of the world, unless atmospheric N deposition is drastically reduced.

Some regions in Europe, with intensive agriculture, much traffic and polluting industries, have already many N-saturated forest ecosystems, *e.g.* parts of the Netherlands, Belgium, Germany and France. The effects of N saturation are much studied there (van Breemen & van Dijk, 1988; Arnold, 1993; de Vries, Leeters, Hendriks, van Dobben, van den Burg & Bonmans, 1995; Landmann & Bonneau, 1995; Matzner & Murach, 1995), but there are no unaffected control plots available in these regions, and it is difficult to establish dose/response relationships, as the accumulated N input is only vaguely known, as are also leaching losses in the past. The same may also apply to situations in which the N input is calculated by

regional models (McNulty, Aber, McLellan & Katt, 1990), which may give excellent dose/effect relationships on a regional scale, but not necessarily for specific sites.

Our first recommendation is thus that existing long-term fertiliser experiments with known N additions, such as our N optimisation experiments, be sampled (or resampled) to determine N sequestration in different compartments of the ecosystem, if possible at different levels of N input. Resampling of sites earlier examined is particularly desirable, as they may provide a picture of how leaching and other ecosystem functions change over time when the input exceeds a saturation point or range (*cf.* stage 3 described by Aber *et al.*, 1989, 1995).

The soil samplings described in this paper give, with few exceptions, only the accumulated result of all additions up to the sampling date. Also, our biomass samplings refer to one point in time only, in contrast to the tree-growth measurements, which make it possible to study current increments for intervals of one to five years.

However, we have already noted that sampling of a substrate as heterogeneous as a forest soil, is a difficult task (Troedsson & Tamm, 1969; Nykvist & Skyllberg, 1989), especially in soils formed in stony till. If the same person is responsible for the sampling of an entire experiment, the data will probably be mutually comparable. Such continuity is seldom possible to achieve in samplings at an interval of a decade or more. It is therefore very important not only that the samplings are carefully done and well described, but also that all means of checking the results by other methods are used. We have earlier suggested that C/N ratios may offer one possibility, since, in soil sampling, concentration variables have a much lower coefficient of variation than amounts per unit area (Troedsson & Tamm, 1969). Högberg *et al.* (1992, 1995) have used the variation in the ratio $^{15}N/^{14}N$ as at least a semi-quantitative measure of N losses from our experimental plots.

A second recommendation is to use experimental plots, exposed to controlled nutrient regimes over long periods, for new experimental manipulations. The experiments may be at different scales, entire plots, microplots, or model experiments with material from field plots. Such activities have been realised in the Stråsan experimental area, where several plots have been cleared in order to study leaching conditions without, or with a long history of annual N additions (Berdén *et al.* 1997; Eriksson *et al.*, 1996). In this case, tension lysimeters were installed some years before felling and soil solutions were analysed before and after stand removal. Unfortunately, the Stråsan site has an even more stony till than Norrliden, which makes soil studies very laborious (Eriksson *et al.*, 1996). The analyses of lysimeter samples have, however, demonstrated striking differences between, *e.g.*, regimes N1 and N2. The earlier mentioned arginine-related experiment at Lisselbo (Edfast *et al.*, 1996) is another example of a new use of old experimental plots.

Our third recommendation is that the recovery of N-saturated ecosystems after interrupted N additions should be studied. This is done in the NITREX project (Tietema *et al.*, 1995) by means of expensive roof constructions and by spraying purified rainwater. Some spectacular results have already been obtained in this way, but it is evident that the cost of such experiments almost precludes statistically satisfactory replication. Our intention is not to criticise the NITREX project, where the scarcity of replications is partly compensated by the use of pretreatment calibration periods, which works well for integrated measuring parameters, such as runoff concentrations for mini-catchments. However, for measuring parameters with a high spatial variation, such as tree growth or soil acidity, it should be considered whether it would be possible to supplement catchment and lysimeter studies by sampling earlier N-enriched experimental plots.

A fourth recommendation for further studies relates to problem area 4 in the Introduction, the relationships between annual tree ring growth, internal concentrations of nutrients, and weather conditions. Our results were negative, in so far as differences in N supply did not affect the between-year variation in needle concentrations, only their levels. However, it is now possible to sample increment cores from several experiments with long series of needle samples from plots with different nutrient regimes. Situations in which only the water regime has been manipulated are also of interest. The between-year variation of needle concentrations of elements other than N, well illustrated

(Section 4, Fig. 4.2–4.6) gives further encouragement to such studies. Experimental data on the growth effect of water regimes can be compared with the survey data used by Jonsson (1969). The effect of environmental factors on nutrient concentrations—apart from their indirect influence by changing tree growth—can be compared between elements with different uptake mechanisms, possibly also with carbon isotope data, using the ratio $^{13}C/^{12}C$ as an indicator of water stress in the past (Högberg *et al.*, 1995).

Finally, we hope that the new generation of forest nutrition experiments laid out during the 1980s and 1990s will provide answers to questions requiring more interdisciplinary cooperation than we have been able to organise. However, with regard to the time factor, so important in environmental studies, we hope that the lessons learnt from the Swedish Optimum Nutrition Experiments in Forest Stands, will be used, both for comparisons and for planning new activities.

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