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Abstract:

1

2 **Nitrogen budgets for Scots pine and Norway spruce ecosystems 12**
3 **and 7 years after the end of long-term fertilisation**

4

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22 **Abstract**

23 The magnitude of nitrogen storage and its temporal change in forest
24 ecosystems are important when analysing global change. For example,
25 the accelerated growth of European forests has been linked to increased
26 nitrogen deposition, but the changes in the N inputs that cause long-term
27 changes in ecosystems have not yet been identified.

28 We used two Swedish forest optimum nutrition experiments with Scots
29 pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* (L.) Karst.) to
30 study the long-term fate of N applied to these forest ecosystems. In the
31 pine experiment, in addition to fertiliser (NPK) application, soil acidity
32 was manipulated by application of lime and dilute sulphuric acid. From
33 the spruce experiment, we selected treatments with similar fertiliser doses
34 as in the pine experiment and with and without lime addition.

35 We quantified various terms in the N budget 12 years (pine) and 7 years
36 (spruce) after the last N addition. In the pine ecosystem, large losses of
37 added N occurred, whereas in the spruce ecosystem we recovered more N
38 than could be accounted for by inputs. In the pine ecosystem, increases in
39 N stocks were mainly in the soil, in contrast to the spruce ecosystem
40 where trees accumulated most of the added N. There was no clear pattern
41 in the interaction between acidification/liming and N deposition.

42

43

44

45 **Keywords:** Tree growth; Soil nitrogen; Nitrogen budget; *Pinus sylvestris*; *Picea*

46 *abies*; Long-term fertilisation; Nitrogen retention; Acidification; Liming.

47 **Introduction**

48

49 In a world of global change our society will not survive
50 unless the political decisions taken can be defended in a
51 holistic environmental perspective

52 Tamm, 1995

53

54

55 The fate of nutrients deposited to terrestrial ecosystems is a key to understanding their
56 impact. Since the early years of forestry, therefore, nutrient relationships in forest
57 ecosystems have been subjected to intensive investigations (e.g. Ebermayer, 1876,
58 1882; Tamm, 1964; Odén, 1968; Rennie, 1995). More recently, nutrients have been
59 studied in the context of air pollution, particularly the effects of sulphur (S) and
60 nitrogen (N) deposition on nutrient imbalances and leaching (e.g. Nilsson and
61 Wiklund, 1995; Wright et.al., 1995; Mälkönen et al., 1999). Today's urgent issues in
62 forest research are studies of the nutrient impact on tree growth induced by a
63 changing climate. The sequestration of C and N in forests is also a controversial issue
64 in the global change debate (e.g. Tamm et al., 1999; Janzen, 2004) because of the
65 strong coupling between C and N (e.g. Rastetter et al., 1992, 1997). The scope has
66 also been broadened to become a central goal of ecosystem ecology with
67 understanding of how the cycling of nutrients and the growth of organisms are linked
68 (Augustine and McNaughton, 2004). Thus, increased N deposition altering forest
69 nutrient cycling (Ågren and Bosatta, 1988; Aber et al., 1989, Peterjohn et al., 1996)
70 may have a positive or negative impact on forest ecosystems (Mund et al., 2002).
71 Accelerated growth of European forests (Spiecker, 1998) is suggested to be linked to

72 this increased nitrogen deposition (Karjalainen et al., 2006). However, the question is
73 whether this increased growth rate will also be sustained in the future if nitrogen
74 deposition declines.

75

76 It seems to be tacitly understood that changes in N inputs will cause long-lasting
77 ecosystem changes (Holland et al., 1997) and that forest ecosystems where nitrogen
78 cycling has been accelerated will be able to maintain an elevated level of biomass
79 production even when the external forcing in terms of N influx is decreased (Ingestad
80 et al., 1981; Ingestad 1987, 1991). However, this aspect has not been tested.

81

82 Nutrient budgeting, which indicates trends in resources at the ecosystem level
83 (Ranger and Turpault, 1999), has been widely used to generate quantitative ecological
84 data on ecosystem functions (Ranger et al., 2002) and as an accounting method to
85 elucidate complex nutrient cycles (Duvigneaud and Denaeyer-De Smet, 1970; Bonito
86 et al., 2003). An interest in resource balances in agricultural science dates back to the
87 1830s (Wild, 1988) and input-output analyses became a major focus of system
88 ecology in the 1950s (Odum, 1968). Many studies of the N budget at forest stand
89 level are available (e.g. Nihlgård, 1972; Helmisaari, 1995; Abrahamsen and Stuanes,
90 1998; Rolff and Ågren, 1999; Ukonmaanaho and Starr, 2002). However, forests are
91 likely to be heterogeneous in their response to N (Wilson and Emmet, 1999) and the
92 information obtained from budget calculations is site-specific (Ranger and Turpault,
93 1999) and species-specific (van Breemen, 1995). Furthermore, whereas N availability
94 can vary substantially from year to year, the nitrogen budget changes only on longer
95 time scales (Schimel et al., 1997). This means that the time factor is the greatest
96 obstacle in experimental research in forest ecosystems (Tamm et al., 1984) and short-

97 term studies can give a completely misleading picture of the long-term development
98 (e.g. Ågren and Hyvönen, 2003). Moreover, short-term and long-term results may
99 differ not only in degree but also in direction, but the literature concerning the long-
100 term fate of N applied to forest ecosystems is still rather limited (Aber et al., 1989;
101 Aber and Magill, 2004). Numerous experiments have been designed to address these
102 questions, but it will take years before they yield conclusive evidence.

103

104 To date, the focus in studies of element cycling has mainly been on single compounds
105 (Erisman et al., 2003) and despite the well-known role of multiple element
106 interactions in a number of biogeochemical processes, few ecosystem models include
107 them explicitly (Ollinger et al., 2003). Nevertheless, elements interact with each other
108 (e.g. Melillo et al., 2003; Ågren et al., 2003). Thus, interactions between N and S have
109 been documented (Matzner and Murach, 1995; Galloway, 1995, 2003). The N cycle is
110 also affected by liming (Persson et al., 1995; Kreutzer, 1995; Ventera et al., 2004),
111 but we are still lacking information about its long-term effects (Hüttl and Schneider,
112 1998). Moreover, deposition-induced acidity may in fact have enhanced the N cycle
113 in multiple ways and further studies are also needed to clarify the role of soil acidity
114 in N losses from temperate forest (e.g. Ventera et al., 2004).

115

116 The main objective of this study was to explore the long-term nitrogen redistribution
117 in a pine and a spruce boreal forest ecosystem. We used two Swedish long-term
118 optimum nutrition field experiments to quantify various terms in the N budget several
119 years after the last N addition and examined whether retention in different pools
120 varied between the two tree systems. The effects of simultaneous acidification and
121 liming were also investigated.

122

123

124 **Materials and methods**

125

126 Study areas

127 Two forest stands from the Swedish Forest Optimum Nutrition Experiments (Tamm,
128 1974a; 1974b), both located in Central Sweden, were studied: E42 with Scots pine
129 (*Pinus sylvestris* L.) at Lisselbo and E26A with Norway spruce (*Picea abies* (L.)
130 Karst.) at Stråsan. In the pine experiment, in addition to fertiliser application (NPK)
131 soil acidity was manipulated by application of lime (Ca) and dilute sulphuric acid in
132 low (Ac1) and high (Ac2) dosages. Only the plots with the intermediate (N2P2K2)
133 level of fertiliser applications were used for the budget calculations here.

134

135 From the spruce experiment, we selected treatments with similar fertiliser (N2P2K2)
136 dosage as in the pine experiment and with and without addition of lime. The sites,
137 experimental designs and methods have been described in detail elsewhere (Tamm,
138 1974a, 1974b; Tamm and Popovic, 1989; Tamm et al., 1999), and only a brief
139 summary of the general characteristics is given in Table 1.

140

141 **Insert Table 1 here**

142

143 The pine stand was damaged by heavy snow in late 1988, which caused the loss of an
144 unknown number of trees, and the stand was thinned in 2000. However, at most 2%
145 and 20% of trees on N and no-N plots, respectively, were damaged (Tamm et al.,
146 1999). The spruce stand was thinned in 1982 and 1988. However, the thinnings

147 removed the trees with the smallest diameter and thus only a small amount of nitrogen
148 was removed; in the spruce stand the increase in average tree diameter as a result of
149 the thinning was even large enough to make the allometric functions (see below)
150 predict larger tree biomasses. In our calculations of ecosystem level N budget, we
151 have therefore not included these events.

152

153 Nitrogen budgets

154 The nitrogen storage in the pine stand was estimated for 1971 and 1997, when the
155 first and last soil samplings, respectively, were made. The spruce stand was monitored
156 followed from 1972, when the first basal area measurement was made, until 2003,
157 when the last diameter measurement was made. When the experiments were started in
158 1969 and 1967 in the pine and spruce stands, respectively, the trees were too small to
159 allow basal area measurements.

160

161 We estimated the total content of N in the three most important compartments in the
162 ecosystem [i.e. whole tree biomass, humus layer, and mineral soil 0-20 cm (pine
163 stand) and 0-30 cm (spruce stand)]. The inputs of nitrogen that we included were
164 inorganic fertiliser, wet plus dry deposition, and biological N-fixation. The changes in
165 nitrogen pools were calculated as the differences in nitrogen amounts in trees, humus
166 layer, and mineral soil between the beginning and end of the investigation period.

167

168 Data acquisition, estimates and calculations

169 Most of the data for our calculations were taken from previously published data sets.
170 However, budget components were not always been measured at the same time, so we
171 were obliged to interpolate between observations in several cases.

172

173 An annual nitrogen fixation rate of 0.3 kg N ha^{-1} was estimated by Granhall and
174 Lindberg (1980) for a comparable pine stand in central Sweden. This gives inputs of
175 7.8 and 7.5 kg N ha^{-1} over the investigation periods for the pine and spruce stands,
176 respectively. Atmospheric inputs of oxidised and reduced nitrogen of 191 and 134 kg
177 ha^{-1} for the pine and spruce stand, respectively, were obtained from the MATCH
178 modelling system of SMHI (Swedish Meteorological and Hydrological Institute)
179 (Cecilia Akselsson, pers. comm.).

180

181 Biomass of tree components (needles, branches, stems, and coarse roots plus stumps)
182 was estimated from average tree diameter at breast height (dbh) using species-specific
183 regression functions (Marklund, 1988). Tree diameter in the pine stand in 1971 was
184 calculated from basal area (Tamm and Popovic, 1989), while in 1997 it was
185 interpolated from diameter measurements made in 1985 (Tamm and Popovic, 1989)
186 and our own diameter measurements made in 2003. Tree diameter data for the spruce
187 stand for the years 1971 and 1997 were taken from unpublished diameter
188 measurements made in 1972 and 1997 (Linder and Tamm, personal comm.).

189 Additional basal area information was taken from Gay et al. (1994). The N stocks in
190 the tree components were calculated by multiplying the biomass of each component
191 by published nitrogen concentrations (Table 2).

192

193

Insert Table 2 here

194

195 Initial soil data were missing for the spruce stand and only unpublished soil nitrogen
196 from 1994 were available (T. Persson & M. Sjöberg, pers. comm.). Soil nitrogen data

197 for the pine stands for 1997 were from our own measurements. In each plot, eight
198 sampling points were systematically distributed in a rectangular grid > 5 m from the
199 plot border. The L, F, and H layers (organic layers) were sampled using frames (361
200 cm²). The mineral soil was sampled with cores 4.4 cm in diameter in 5-cm increments
201 to a depth of 20 cm. Samples were pooled to one composite sample per plot and soil
202 horizon. After removal of living plant residue, twigs, etc., soil samples were well
203 mixed and sieved fresh: screen mesh 5 mm for organic layers and 2 mm for mineral
204 soil. Bulk density values from the samplings were used for L, F, and H layers, while
205 the bulk density of mineral soil was estimated from the stoniness index (Tamm and
206 Popovic, 1989). Soil N concentrations were determined using dry combustion (NA
207 1500, Carlo-Erbe Strumentazione, Milan). In 1971, Tamm and Popovic (1989)
208 measured soil nitrogen in the humus layer, which we assumed to correspond to our
209 F+H layer. No mineral soil N data were available from 1971 and were replaced by
210 samplings from 1985 (Tamm and Popovic, 1989; Hallbäcken and Popovic, 1985).

211

212 Statistics

213 For each stand, the effects of treatments were evaluated using analysis of variance
214 (ANOVA). Tukey's test for post-hoc comparisons of means and least significant
215 difference (LSD) multiple comparison, with sub-plot measurements considered as
216 treatment replicates, were used for cases in which ANOVA revealed significant
217 treatments effects. The results are given as treatment means. The level of significance
218 was set to 5%.

219

220

221 **Results**

222

223 Basal area development

224 The basal area development for the two stands and different treatments is shown in
225 Figure 1. There was a small but consistent increase in basal area in all the fertilised
226 pine treatments compared to the non-fertilised during the period when fertilisation
227 was taking place (up to 1985). After that, all treatments had similar rates of basal area
228 growth except the NPK treatment, which had a somewhat more rapid development
229 and the untreated, Ca, and Ac1 treatments, which fell behind. In the spruce stand, the
230 growth stimulation was so strong in all fertilised plots that by the end of the
231 fertilisation period (1990), the basal area in the fertilised plots was about three times
232 that in the unfertilised plots. Once fertilisation had ceased, the growth rate on the
233 fertilised plots dropped to that of the unfertilised ones.

234

Insert Figure 1 here

235

236 Nitrogen inputs

237 The nitrogen budgets for the pine and spruce ecosystems are summarised in Tables 3
238 and 4, respectively. The total inputs of N (fertilisation, deposition, and biological
239 fixation) to the pine ecosystem over the period 1971-1997 varied from 199 kg N ha⁻¹
240 in unfertilised plots to 999 kg N ha⁻¹ in fertilised plots (Table 3). In the spruce
241 ecosystem, the corresponding inputs of N over the period 1972-1997 varied from 142
242 kg N ha⁻¹ to 1382 kg N ha⁻¹ (Table 4).

243

244

Insert Table 3 and 4 here

245

246 N pools in ecosystem compartments

247 The distribution of N in 1997 between ecosystem compartments in the pine and
248 spruce stands for the various treatments is shown in Figure 2. In both stands the
249 effects of the N additions could still be observed 12 (pine) and 7 (spruce) years after
250 the N additions had ceased. However, there were differences in response. In the pine
251 stand, the NPK-treatment was the only treatment that produced a significant increase
252 in N in the tree biomass (96% above control). The other fertilised plots also had larger
253 amounts of N in the tree biomass, but not significantly so. In the spruce stand, the N
254 additions increased tree biomass N in all treatment combinations (207% above control
255 in both NPK and NPKCa treatments). In addition, the effect of treatments on N stock
256 in spruce biomass was significant already in 1972, four years after the start of
257 fertilisation, when the first biomass estimates were made.

258

259  Insert Figure 2 here

260

261 As a result of a significant increase in humus N, the N applications caused significant
262 changes in ecosystem N content in three (NPK, NPKAc1 and NPKAc2) of the four
263 treatments in the pine experiment (Fig. 2). The increases in humus N for the NPK,
264 NPKAc1 and NPKAc2 treatments were also large enough to cause a significant
265 increase in total soil N. There was also a significant increase in mineral soil N in the
266 NPK and NPKAc2 treatments. In spite of the changes in amounts of N in individual
267 compartments, the relative distribution of nitrogen between trees and soil did not vary
268 across treatments, with trees containing around 12% of pine ecosystem N (Fig. 3).
269 The relative distribution of N between humus layer and mineral soil (0-20 cm depth)
270 varied between treatments but there seemed to be no systematic variation with

271 treatment; the humus contained around 46% of soil N (down to a depth of 20 cm in
272 the mineral soil).

273

274 In the spruce stand, the N fertilisation increased N pools in both the trees and the soil
275 but the increase in the soil was restricted to the humus layer, whereas the mineral soil
276 N pool might rather have decreased (Fig. 3). The uptake of the N fertiliser was
277 proportionally larger in the trees such that in the fertilised spruce stands (Table 4), in
278 contrast to the pine stand (Fig. 3), the distribution of N shifted in favour of the trees.
279 The humus layer also seemed to contain a lower share of the N stock in the spruce
280 stand (around 37% of soil N to a depth of 30 cm in the mineral soil) relative to the
281 pine stand.

282

283 Insert Figure 3 here

284

285 In 1997, we found more N in the spruce ecosystem than could be explained by the
286 sum of inputs and initial amounts in 1972 (Table 4). The same was true for the
287 unfertilised pine plots, whereas some N was unaccounted for in the fertilised plots
288 (Fig. 4). The budget for soil N in the spruce stand was based on a comparison between
289 control and treated plots in 1997 because initial data were lacking. When we
290 compared the pine stand in the same way, the values in the soil N components
291 changed only slightly and without consequences for the interpretation.

292

293 Acidification and liming also affected N accumulation. In both fertilised and
294 unfertilised plots in the pine stand, liming led to a smaller increase in the humus N
295 pool. The amount of N unaccounted for in the pine stand in the NPKCa treatment was

296 also larger than in the NPK treatment. Furthermore, there was a difference in the soil
297 in the pine stand between high and low doses of acidification, with a higher build-up
298 of humus N in the high dosage. There was also an indication that NPK and NPKAc2
299 led to a larger increase in mineral soil N than NPKAc1 and NPKCa.

300

301 Insert Figure 4 here

302

303 *N unaccounted for*

304

305 The N budgets did not match. In the pine ecosystem, we found between 16 and 219 kg
306 ha⁻¹ more N in the unfertilised plots in 1997 than in 1971 (Table 3). In the fertilised
307 plots, on the contrary, between 254 and 738 kg ha⁻¹ was unaccounted for. This
308 unaccounted for N can be represented by the following series:

309

310 (NPKAc1, NPKCa) > (NPK, NPKAc2) > (Ca, Ac1, Control, Ac2)

311

312 The NPKAc1 and NPKCa treatments were the only treatments with a significant
313 increase in the amount of unaccounted for N compared not only to the control, but
314 also to all other unfertilised plots (Ca, Ac1, Control, Ac2). The other fertilised plots
315 (NPK and NPKAc2) also had higher amount of unaccounted for N than unfertilised
316 plots, but the differences were not significant (5% level).

317

318 In the spruce stand at the end of the observation period in 1997, there was between
319 517 and 591 kg ha⁻¹ more N in fertilised plots compared to control plots and the trees
320 in control plots had taken up 250 kg ha⁻¹ more N than our estimated input (Table 4).

321

322 **.1 Discussion**

323

324 One of the most striking observations from our calculations was the great difference
325 in response between Scots pine at Lisselbo and Norway spruce at Stråsan. Long-term
326 N additions, alone or in combination with sulphuric acid or lime, must therefore be
327 expected to modify N pools in boreal coniferous forest ecosystems in a species-
328 specific and/or site-specific way. The response is also time-dependent. In both stands
329 investigated, the fertilisation increased biomass but this biomass increase was
330 sustained only in the NPK-fertilised plots in the pine forest when the fertilisation had
331 ceased. However, there was a strong tendency for higher biomass in all fertilised
332 spruce plots.

333

334 The increased biomass in the spruce stand as a result of fertilisation was accompanied
335 by an increased N concentration in the needles (Table 2). This led to increases of
336 about 1100 kg ha⁻¹ in spruce tree N in all plots, with no differences between
337 treatments. Simultaneously, soil N increased by more than 800 kg ha⁻¹ but with the
338 extra N concentrated to the humus layer, while the mineral soil N was likely to even
339 have decreased. These increases in spruce ecosystem N pools were larger than the
340 estimated inputs. However, the increase in spruce tree N in the unfertilised plots was
341 250 kg ha⁻¹ more than estimated from deposition and N fixation. Nevertheless, if this
342 extra N is included in the balances for the fertilised plots, there still remains about 300
343 kg N ha⁻¹ to be accounted for.

344

345 In the unfertilised plots in the pine stand, the N content in the stand was 120 kg ha^{-1}
346 higher in 1997 than in 1971. If this extra N is included in the N budget for the
347 fertilised stands, the NPKAc1 and NPKCa plots then would have lost as much N as
348 had been added with the fertiliser, whereas the NPK and NPKAc2 plots retained
349 about half the fertiliser added. The allocation of the increases in N differed between
350 stands; the pine stand retained more in the soil than in the trees (about 2/3 in the NPK
351 and NPKAc2 plots) whereas the spruce stand retained somewhat more in the trees
352 than in the soil.

353

354 The effects of acidification or liming in addition to the fertilisation had no consistent
355 pattern. There was no growth and N uptake effect of liming in the fertilised pine and
356 spruce stands. With only NPK and NPK in combination with the high acid dosage,
357 there was some increase in N stocks in the pine stand. However, in the low
358 acidification and lime treatments in the pine stand, fertilisation did not increase the N
359 stock. Acidification and liming did not seem to have the same effect without fertiliser
360 as with fertiliser. Without fertiliser, acidification and liming seem to be almost
361 without long-term effects, although it is possible that the high acid dosage increased
362 N stocks somewhat more.

363

364 The differences in response between the pine and spruce stands are probably
365 attributable to species differences. The potential of spruce to increase its needle
366 biomass is much larger than that of pine; Ågren (1983) estimated the maximum
367 needle biomasses for pine and spruce to be $20\,000 \text{ kg DW ha}^{-1}$ and $49\,000 \text{ kg DW ha}^{-1}$,
368 respectively. Another aspect is the difference in soil texture, since the pine stand

369 was growing on a coarse sandy soil with lower nutrient retention capacity than the
370 more fine-textured soil in the spruce stand.

371

372 We found more nitrogen than could be explained by inputs and initial values in all
373 plots except the fertilised pine plots, where large losses occurred. The losses of N in
374 the fertilised pine plots can be explained as leaching losses. The extra N in the pine
375 stands corresponded only to an extra inflow of 1 to 8 kg ha⁻¹ yr⁻¹ but was between 10
376 and 23 kg ha⁻¹ yr⁻¹ in the spruce stand. There are two potential sources for the extra N
377 in the other stands. First of all, it is likely that some of the nitrogen derived from
378 mineralisation in deeper soil horizons than those included in the budgets. Root
379 activity and nutrient availability in deeper soil layers, which remain poorly explored,
380 may play an important role in ecosystem functioning (e.g. Richter and Markewitz
381 1995, Jackson, 1999; Jobbagy and Jackson, 2001, 2004). Indications exist that
382 considerable amounts of plant available nitrogen and other nutrients below 20-30 cm
383 depth can be an important resource of nutrients for trees (e.g. Stone and Comerford,
384 1994; Kowalenko, 1996). Over decade time scales and longer, the release of N from
385 the mineral soil may be a key process for long-term accumulation in both vegetation
386 and the organic horizon (e.g. Ross et al., 2002; Ritter et al., 2003; Finzi and
387 Schlesinger, 2003; Currie et al., 2004). It is also possible that the spruce control plots
388 received N through lateral transport as a result of site topography. In addition, lateral
389 root development and soil mining by roots outside the unfertilised plots is a possible
390 factor of unexplained N accretion in the unfertilised plots (e.g. Högberg, 1991).

391

392 Another possible explanation for the N deficit is the uncertainty in the total input.

393 Nitrogen fixation is one uncertain component in the total input because measuring it

394 in natural systems is difficult (Vitousek et al., 2002). There are few studies of
395 nitrogen-fixing root surface bacteria on coniferous trees (Timonen et al., 1998;
396 Chanway et al., 1994). However, non-symbiotic N fixation can be an important input
397 to coniferous forests (Wei and Kimmins, 1998; DeLuca et. al., 2002; Chen and Hicks,
398 2003; Brunner and Kimmins, 2003) with an observed range for terrestrial
399 cyanobacteria of 1 to 41 kg N ha⁻¹ yr⁻¹ and with the majority of studies ranging
400 between 1-10 kg ha⁻¹ yr⁻¹ (West, 1990; Boring et al., 1998; Cleveland et al., 1999).
401 Since liming may affect N fixation negatively by reducing the abundance of
402 bryophytes (mosses) (Motta et al., 1994; Duliere et al., 2000), which are a major
403 nitrogen-fixing component of boreal forests (e.g. Solheim et al., 1996), the
404 underestimation of nitrogen fixation could be higher in the non-limed plots than in the
405 limed plots.

406

407 On average, 56% of the N applied, added alone or in combination with acid in high
408 doses, still remained in the soil, which is considerably more than the 30% reported
409 previously (Tamm et al., 1999). On the other hand, when N was added in combination
410 with low acid or lime, only 13% remained in the soil. As a result of the heterogeneity
411 of the soil, one has to be cautious with regard to the reliability of these values.

412 However, it is possible that the N retention capacity of an ecosystem is also
413 determined by interactions with acidity, which complicates the use of the critical load
414 concept (e.g. Pardo and Driscoll, 1996; Emmett and Reynolds, 1996; Augustin and
415 Bolte, 2005).

416

417 **Artikel II. Conclusions**

418 .1 1. The response of boreal coniferous forest ecosystems to long-term nitrogen
419 addition is time-dependent and modifies N pools in a species-specific and site-specific
420 way.

421

422 2. When N additions decline or are terminated, some ecosystems are likely to revert to
423 pre-treatment N stocks.

424

425 3. In pine ecosystems, the soil is the major sink for N. In contrast, in spruce
426 ecosystems trees conserve a large proportion of added N.

427

428 .2 4. Our results support the statement in the introduction that ‘the accelerated
429 growth of European forests is probably linked to increased nitrogen availability’.

430 However, the differences in growth responses across fertiliser combinations indicate
431 that factors other than nitrogen are of significance.

432

433 5. The interaction between N deposition and acidification remains a controversial
434 issue.

435

436 6. The risk of nitrogen leaching cannot be assessed only on the basis of nitrogen
437 deposition, since the ability of the ecosystem to retain N also has to be taken into
438 account.

439

440 7. Nitrogen budgets for boreal coniferous forest need to include deep mineral soil
441 horizons.

442

443

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449

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451

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711

1 Table 1. Site characteristics and overview of treatments in the experiments.

2

Site	Lisselbo	Stråsan
Latitude, Longitude, Altitude ^b	60°28'N; 16°57'E; 80 m	60°55'N; 16°01'E; 350 m
Experiment # ^a	E42	E26A
Tree species ^b	Scots pine (<i>Pinus sylvestris</i> L.)	Norway spruce (<i>Picea abies</i> (L.) Karst.)
Treatment period ^a	1969-1985	1967-1990
Soil material ^b	Sediment	Till
Soil ^b	Sandy, iron podzol	Glacial till, iron podzol
Mean annual temperature, °C ^b	4.8	3.1
Mean annual precipitation, mm ^b	593	745
Stand age at start of treatment ^b	14	9
Form of N added ^b	Ammonium nitrate (NH ₄ NO ₃)	Ammonium nitrate (NH ₄ NO ₃)
Amount of fertiliser N (kg ha ⁻¹) added ^a	240 during 1969-1970 800 during 1971-1985	520 during 1967-1971 1240 during 1972-1990

3

4 ^aTamm and Popovic (1995)

5 ^bGay et. al. (1994)

1 Table 2. N concentration (mg g^{-1}) in biomass components for Scots pine and Norway
 2 spruce and various treatments and years. In the spruce experiment needle N
 3 concentrations are given also at the individual plot level.

4

	<i>Scots pine</i>		<i>Norway spruce</i>	
	1971	1997	1972	1997
Stem wood	0.9 ^a	0.9 ^a	0.94 ^g	0.94 ^g
Stem bark	3.5 ^a	3.5 ^a	5.58 ^g	5.58 ^g
Branches	2.1 ^a	2.1 ^a	4.94 ^g	4.94 ^g
Needles	13.4 ^b	11.8 ^c Control 11.8 ^d Ac1 11.8 ^d Ac2 11.9 ^c Ca 17.8 ^c NPK 17.8 ^e NPKAc1 17.8 ^e NPKAc2 19.0 ^c NPKCa	13.1; 11.5; 9.5 ^f Control 20.4 ^f NPK 20.4; 20.5 ^f NPKCa	15.0; 13; 1 ^f Control 17.0; 19.0; 20.0; 21.0 ^f NPK 19.8; 18.6 ^f NPKCa

5

6 ^a measured in 1975 (Tamm et al., 1999)

7 ^b measured in 1968 (Aronsson, 1982)

8 ^c measured in 1987 (Nihlgård et al., 1996) and assumed unchanged (Tamm et al.,
 9 1999)

10 ^d assumed to be the same as for control plots

11 ^e assumed to be the same as for NPK plots

12 ^f S. Linder and C.O. Tamm (pers. comm.)

13 ^g data from the Skogaby Norway spruce stand (G. Ågren, pers. comm.)

14

1 Table 3. Nitrogen stocks in the Scots pine stand in experiment E42 at Lisselbo in
 2 1971 and 1997. Data are averaged over plots. A significant difference ($P < 0.05$)
 3 between control and treatments is marked with (*).
 4

Budget items		Treatments							
		Control	Ac1	Ac2	Ca	NPK	NPKAc1	NPKAc2	NPKCa
Plots		55, 60	63,72	69, 57	62, 58	66, 61	70, 64	67, 56	68, 71
Line	N inputs, kg/ha								
1	<i>Fertilizer</i>					800	800	800	800
2	<i>Fixation</i>	8	8	8	8	8	8	8	8
3	<i>Total deposition</i>	191	191	191	191	191	191	191	191
4	Σ Input (1+2+3)	199	199	199	199	999	999	999	999
	N pools in ecosystem compartments, kg/ha								
5	<i>Trees 1971</i>	31	23	27	20	35	32	29	34
6	<i>Trees 1997</i>	126	129	148	127	247**	173	181	167
7	<i>Humus 1971^a</i>	346	338	373	407	392	564	311	495
8	<i>Humus 1997</i>	548	418	557	433	795**	754**	751**	596
9	<i>Mineral 0-20 cm 1985^a</i>	380	511	493	513	702	611	649	540
10	<i>Mineral 0-20 cm 1997</i>	409	645	606	595	829**	558	802**	567
11	<i>Total soil 1971 (7+9)</i>	726	849	866	920	1094	1175	960	1035
12	<i>Total soil 1997 (8+10)</i>	957	1062	1162	1028	1624**	1312**	1553**	1163
13	<i>Ecosystem 1971 (5+11)</i>	757	872	893	940	1129	1207	989	1069
14	<i>Ecosystem 1997 (6+12)</i>	1082	1192	1311	1155	1871**	1485**	1734**	1330
	Pool changes of N, kg/ha								
15	<i>In trees (6-5)</i>	95	106	121	107	212**	141	152	133
16	<i>In humus (8-7)</i>	202	80	184	26	403	190	440	101
17	<i>In mineral soil (10-9)</i>	29	134	113	82	127	-53	153	27
18	<i>In total soil (12-11)</i>	231	214	297	108	530	137	593	128

19	<i>In ecosystem (14-13)</i>	326	320	418	215	742	278	745	261
	Pool changes of N, % of Σ input								
20	<i>In trees (15/4*100)</i>	48	53	61	54	21	14	15	13
21	<i>In humus (16/4*100)</i>	102	40	92	13	40	19	44	10
22	<i>In mineral soil (17/4*100)</i>	15	67	57	41	13	-5	15	3
23	<i>In total soil (18/4*100)</i>	116	108	149	54	53	14	59	13
24	<i>In ecosystem (17/4*100)</i>	164	161	210	108	74	28	75	26
	Unaccounted N , kg/ha								
25	(4-19)	-127	-121	-219	-16	257	721**	254	738**

5

6 ^a Tamm, C.O., Popovic, B. (1989)

7

8

1 Table 4. Nitrogen stocks in the Norway spruce stand in experiment E26A at Stråsan in
 2 1972 and 1997. Data are averaged over plots. Only plots 13, 46, 19, 39, 4, and 48 are
 3 included in soil data. Pool changes and recovery in soil in N treated plots are by
 4 difference with control plots. A significant difference ($P<0.05$) between control and
 5 treatments is marked with (*).

6

Budget items		Treatments		
		Control	NPK	NPKCa
Plots		13, 46, 8	4, 38, 22, 48	19, 39
Line	N inputs, kg/ha			
1	<i>Fertiliser</i>		1240	1240
2	<i>Fixation</i>	8	8	8
3	<i>Total deposition</i>	134	134	134
4	Σ Input (1+2+3)	142	1382	1382
N pools in ecosystem compartments, kg/ha				
5	<i>Trees, 1972</i>	53	273**	247**
6	<i>Trees, 1997</i>	444	1366**	1364**
7	<i>Humus, 1997^a</i>	663	1621	1629
8	<i>Mineral soil 0-10 cm, 1997^a</i>	373	387	386
9	<i>Mineral soil 10-30 cm, 1997^a</i>	920	754	797
10	<i>Total soil (7+8+9), 1997</i>	1956	2762	2812
11	<i>Ecosystem (6+10), 1997</i>	2400	4128	4176
Pool changes of N, kg/ha				
12	<i>Trees (6-5)</i>	391	1093**	1117**
13	<i>Humus</i>		958	966
14	<i>Mineral soil 0-10 cm</i>		14	13
15	<i>Mineral soil 10-30 cm</i>		-166	-123
16	<i>Total soil</i>		806	856
17	<i>Ecosystem (12+16)</i>		1899	1973

	Pool changes of N, % of Σ inputs			
18	<i>Trees</i> (12/4*100)	276	79**	81**
19	<i>Soil</i> (16/4*100)		58	62
20	<i>Ecosystem</i> (17/4*100)		137	143
	Unaccounted N, kg/ha			
21	(4-12) Control, (4-17) Treated	- 250	- 517	- 591

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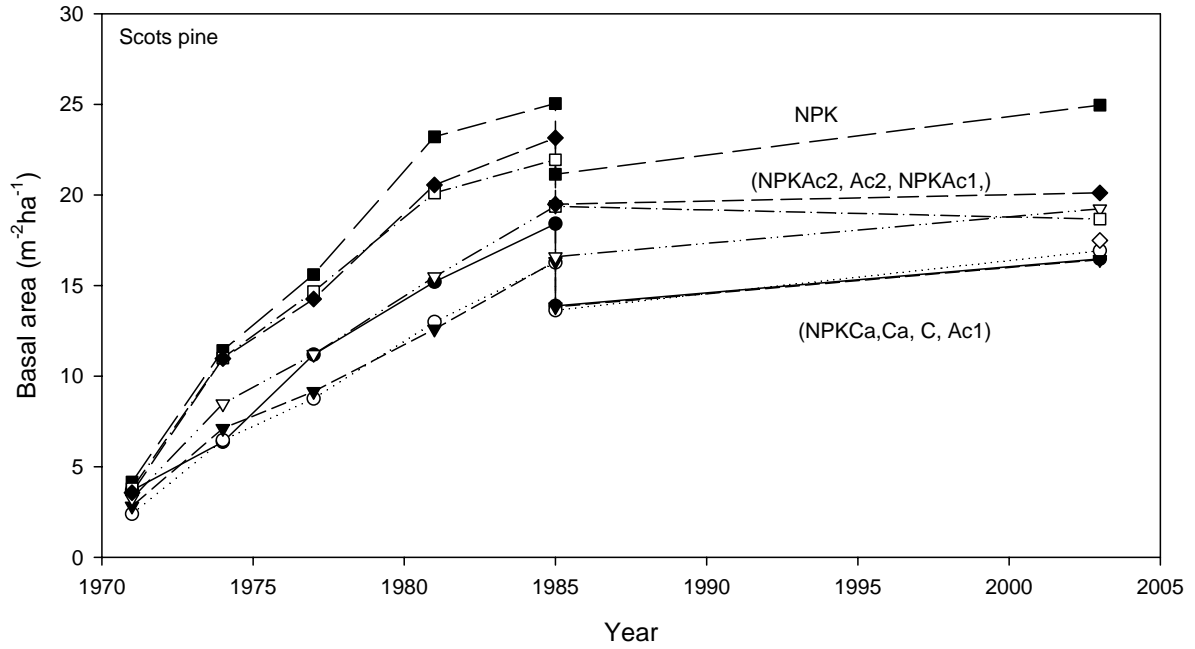
8 ^a data from the Stråsan Norway spruce stand in 1994 (T. Persson, pers. comm.)

9

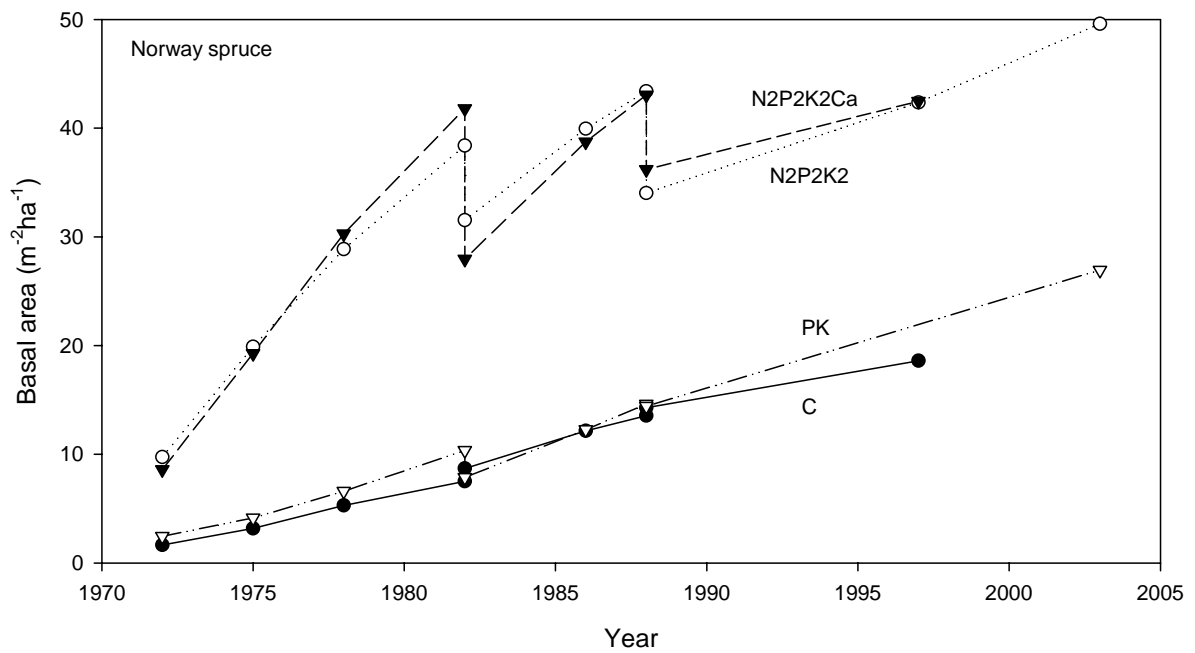
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1 Figure 1. Basal area development for pine and spruce stands and different treatments.

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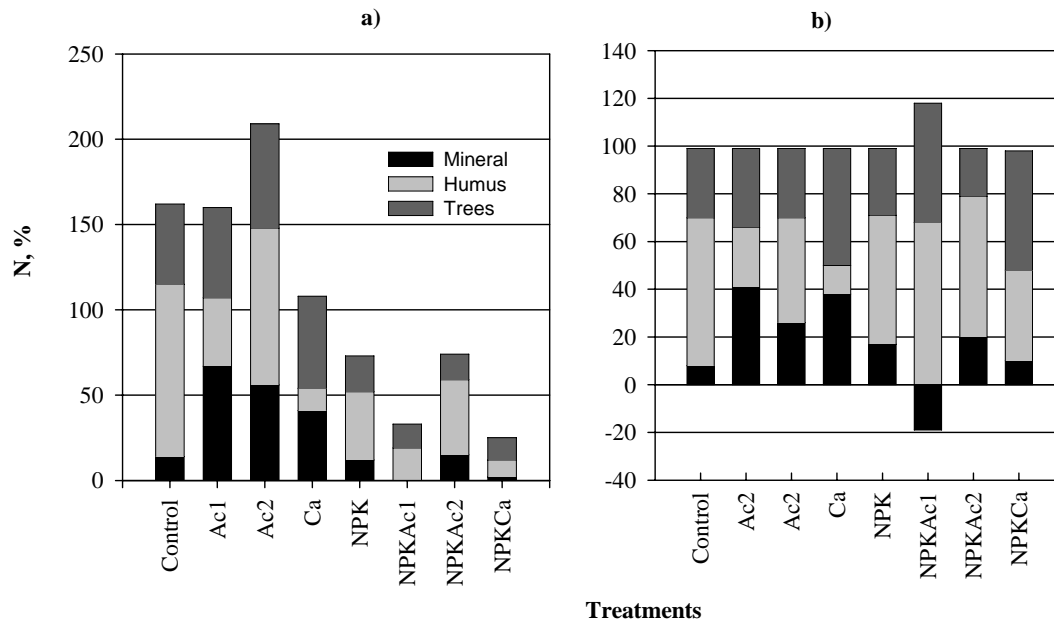
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1 Figure 2. Partitioning of N stores in 1997 between compartments in the pine and
 2 spruce ecosystem. Significant differences ($P < 0.05$) between control and treatments
 3 are marked with (*).

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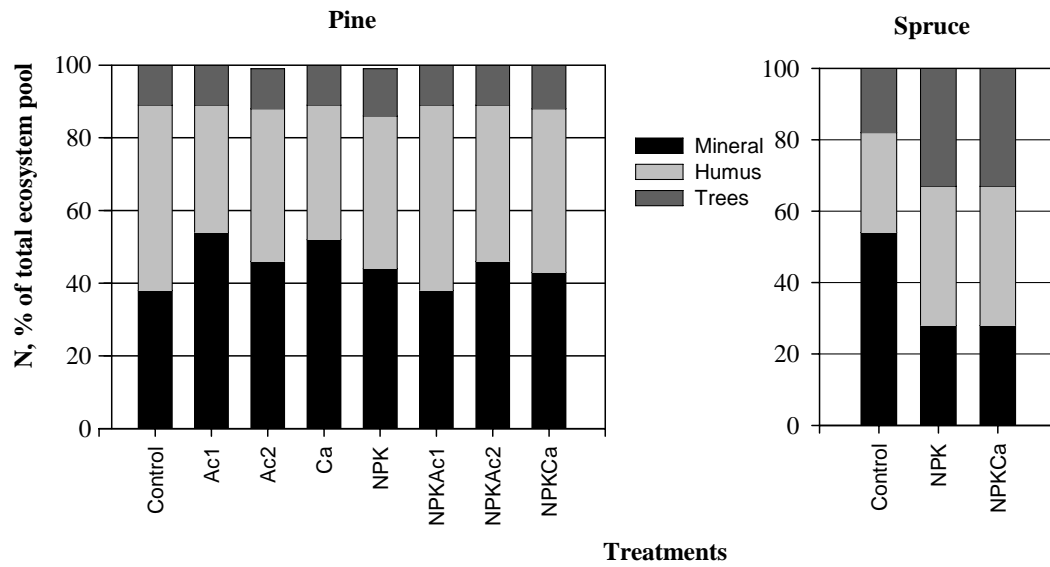
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1 Figure 3. Relative distribution of N in 1997 in the pine and spruce ecosystems.

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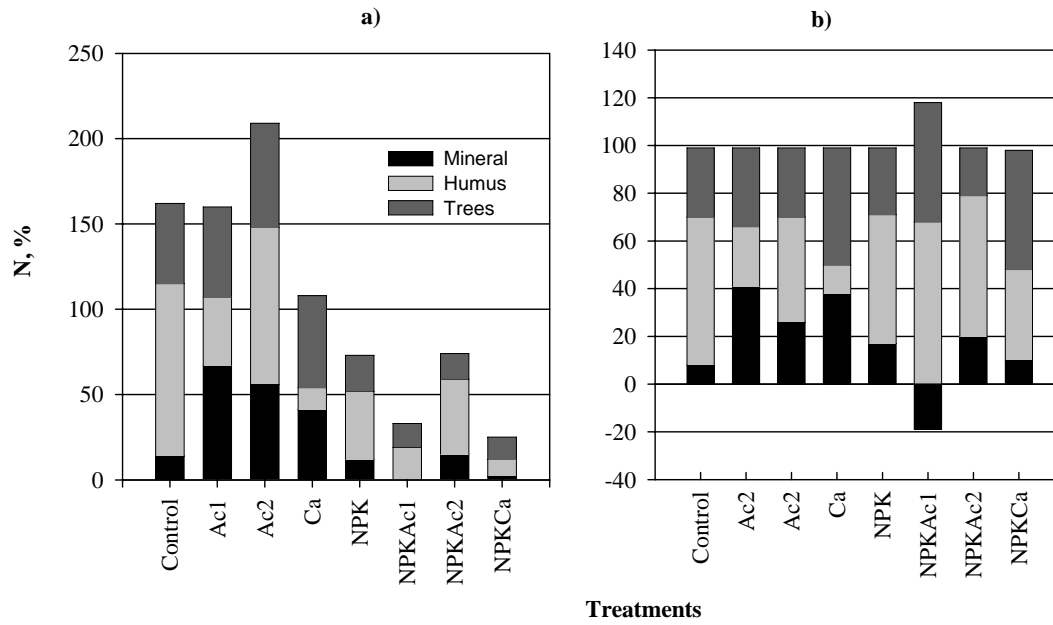
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1 Figure 4. Pool changes of N in pine ecosystem compartments: a) Relative to total
 2 inputs; b) Relative to change in ecosystem.

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