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Nitrogen cycling in undisturbed and manipulated boreal forest

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Like most forests and several other natural terrestrial ecosystems, the boreal forest accumulates N in biomass and soil organic matter, even although measured rates of biological N_2 fixation are normally low. The accumulation of N is disrupted if the forest canopy is removed by natural causes (fire, wind-felling or insect outbreaks) or by cutting. During the period after such a 'catastrophe' (in fact a common event in boreal forests, considered in a long-term perspective), the accumulation is discontinued or even changed into a loss of N from the site. Some losses are caused directly by fire or, in managed forests, by removal of biomass. These losses are usually small, except with whole-tree utilization. Nitrogen losses associated with nitrification processes (both leaching and denitrification) may be more serious on a cleared area, where uptake by vegetation is inconsiderable for some period. Nitrate formation may then take place both in the humus layer (the mor) and in the mineral soil, although the pH may be well below 4.5 in the mor layer. Scarcity of available N in the soil is a common cause of slow growth. Effects of fertilization on ecosystem functions are discussed.

NITROGEN ACCUMULATION AND MOBILIZATION

Like most other types of forest, and also several other ecosystem types, the boreal forest accumulates nutrients, N in particular, during the largest part of its life cycle. This accumulation can be illustrated by data from the Swedish coniferous forest ecosystem project with its main site located at a poor pine forest on outwash sand in middle Sweden (table 1). Both carbon and N are accumulated in the system, while 'cyclic' elements such as sodium and chlorine leave the profile in quantities that sometimes exceed the same year's input. The retention of hydrogen ions illustrates the buffering capacity of the soil. With carbon, the cause of accumulation is retarded or incomplete decomposition of the photosynthetic products; these of course also affect N retention. As the addition of N by N_2-fixing organisms is very small (about one-tenth of the supply of bound N from precipitation and dry fall-out) we believe that the main sources of the N are the relatively small amounts of fixed N supplied through the air and estimated at present to be about 0.4 g m^{-2} (4 kg ha^{-1}) annually. The measured leaching of soluble N from the profile is one to two orders of magnitude smaller.

In other cases when fresh soil is exposed and a primary succession takes place, the N and C accumulation can be several times, faster, as in the classical example of alder invasion on soil exposed upon the retreat of glaciers in Alaska, as described by Crocker & Major (1955) and Ugolini (1968). However, the rapid accumulation of N does not go on for ever. Also, with carbon there seems to be a point where some sort of steady state is established (Jenny 1941).

A very important point is that the amount of N accumulated in an ecosystem seems to depend on the ecological situation, the acid–base conditions in particular, as illustrated by Dahl *et al.* (1967). We do not know the quantitative role of the sources from which N is accumulated, i.e. N_2-fixing organisms (free living or symbiotic), rain and absorption from the air, and flushing of subsurface waters (in certain types of sloping site). It is therefore difficult to tell why sites with a good supply of mineral nutrients and water also tend to have large amounts of both total and available N.

TABLE 1. ANNUAL ION FLOW (MILLIMOLES PER SQUARE METRE) THROUGH A PINE FOREST ON A LOW-POTENTIAL SITE (JÄDRAÅS, MIDDLE SWEDEN)

	H^+	Na^+	NH_4^+	NO_3^-	Cl^-
incoming rain, 1976	14.1	2.5	12.2	11.6	3.9
6 cm depth, 1976	5.3	28.8	0.8	0.6	23.1
80 cm depth, 1976	7.0	71.2	0.7	0.3	38.9
80 cm depth, 1975	0.4	10.0	0.1	0.1	not det.

Microbial N_2 fixation *ca.* 2.5 mmol N m^{-2} annually.
Total store of N in soil (above 30 cm) 7900 mmol m^{-1} (111 g m^{-2}); total store of C in soil (above 30 cm) 317000 mmol m^{-1} (3800 g m^{-2}).
(Data from Bringmark (1980).)

Very little of the N in a forest profile is immediately available to the trees. Most is bound as organic N, often in a form that is not readily decomposed. However, even the apparently very stable organic matter in the mineral soil in a podzol profile seems to decompose slowly. Radiocarbon datings (Tamm & Holmen 1967) have shown that the ^{14}C age in typical profiles from middle and north Sweden range in age from 300 to about 1000 years for the organic matter in the B horizon. As these sites are around 10000 years old, there must be a slow decomposition of the organic matter, even if much of the N seems to be conserved on site. Radiocarbon dating of organic matter from podzol profiles in Germany have given higher apparent ages (Scharpenseel *et al.* 1968; Scharpenseel 1971).

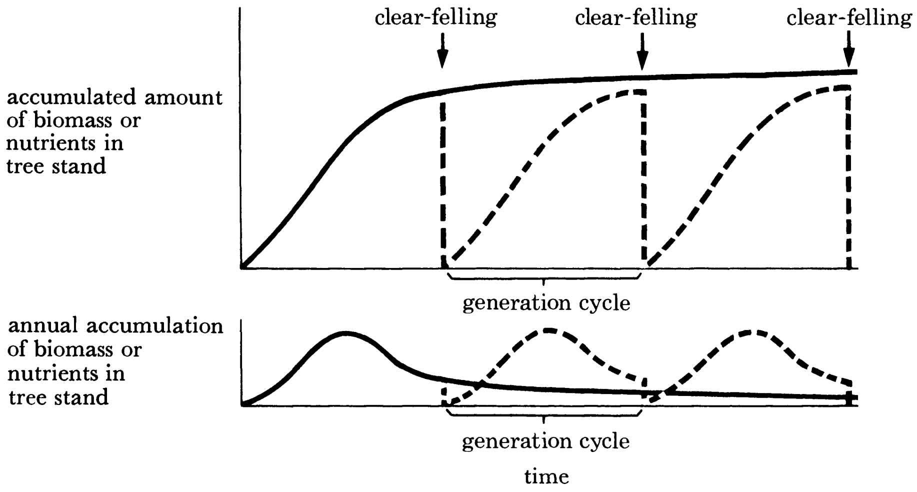

FIGURE 1. Schematic picture of the accumulation of biomass and nutrients in the tree stand in a forest established on open land (e.g. after a forest fire). Solid line, undisturbed forest; broken line, the development interrupted by cutting (or natural causes, such as fire). The assumption of similar size and nutrient content of subsequent crops is highly hypothetical.

The process of accumulation of N, however, is interrupted occasionally in the boreal forest by the occurrence of forest fire or other catastrophes such as wind-felling or insect outbreaks (see figure 1). The frequency of fire differs with climate and with the condition of the forest. Poor sites in European boreal forest are characterized by pine with a ground layer rich in lichens. In North America, black spruce occurs with this type of lesser vegetation. Medium and good sites often have spruce or fir forests with a lesser vegetation rich in feather mosses and dwarf shrubs, with the number of herbs increasing with increasing site index. Sites with poor drainage are characterized by the occurrence or even dominance of *Sphagnum* species.

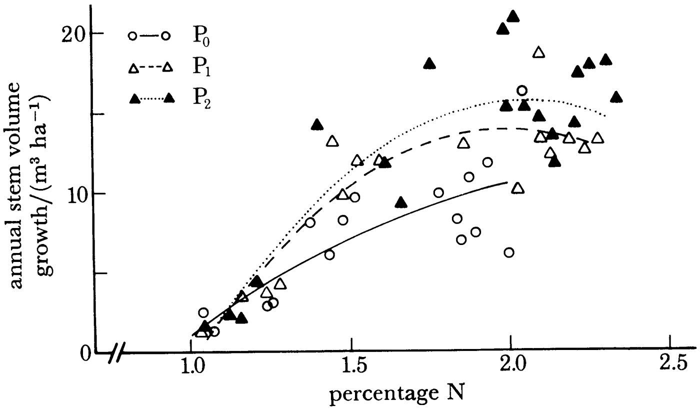

FIGURE 2. Volume growth (1973–8) of young spruce planted in 1958 in the optimum nutrition experiments at Stråsan plotted against foliage nitrogen concentrations (representing nitrogen régimes N_0, 1.04–1.26% N; N_1, 1.38–1.76% N; N_2, 1.78–2.10% N; and N_3, 1.90–2.28% N, maintained by annual fertilization from 1967 onwards (see Tamm 1980, Albrektson *et al.* 1977)). Each dot represents a plot 20 m × 20 m.

The lichen pine forests catch fire much more easily than the more moist moss-rich forests, but on medium sites there seems to be a switch in ecological development: where a site is frequently burnt (either for purely climatic reasons or because of man's interference) the development goes in the direction of a lichen–pine forest, while other similar sites, which for topographical reasons, or by chance, rarely burn, develop towards moss-rich spruce forest. In both cases there is an intensive decomposition of the organic matter after clear-felling or a new fire; this leads to mobilization of the N in plant-available form as ammonium or nitrate. Even if the relative rate of decomposition were the same in poor lichen–pine forest as in moss-rich spruce forest, which is probably an overestimate (Tamm & Pettersson 1969), the amount of organic material is usually much higher in the spruce forest.

There seems to be another switch in the system regulating the occurrence of nitrification, although we do not quite know the reasons why nitrification occurs on certain sites but not on others. The pattern of loss of N from the site due to leaching or denitrification, or both, is thus something that we cannot fully explain at present. The concentration of nitrate in spring water originating from cleared areas varies considerably between individual springs, but on the whole fertile sites seem to leak more nitrate than low site classes, as demonstrated by Wiklander (1981) (see also Tamm *et al.* 1974).

Decomposition is enhanced by mechanical disturbances of the soil profile such as those now used in site preparation for planting. Studies have also shown that the amount of N in the profile decreases in sites subject to intensive soil disturbance in the past (Lundmark 1977). Nitrification, and thus also leaching of nitrate, is much stimulated by liming the forest soil (Nömmik 1979), an operation not yet done on a practical scale but possible as a counter-measure to the effects of the acid rain in the future.

NITROGEN AS A LIMITING FACTOR

It has long been known that much of the boreal forest suffers from a deficiency of N, or, in other words, the application of N fertilizer increases forest growth considerably. In the typical case, at least in Sweden, there is little effect of elements other than N on mineral ground, unless N has been applied in large amounts (table 2, figure 2).

The foliage phosphorus level in the case reported in figure 2 is well above reported deficiency levels in spruce, and the phosphorus effect is probably an indirect one, by stimulation of soil processes. This hypothesis is supported by an increase in N foliage concentrations in NP treatments compared with N only (Tamm 1980).

TABLE 2. EFFECTS OF FERTILIZATION WITH N AND NPK ON SWEDISH CONIFEROUS FORESTS

(Only experiments conducted over a minimum of 10 years are included. All experiments except P883 are middle-aged to old stands situated in north Sweden. P883 represents planted spruce in southwest Sweden.)

site	tree species	number of years	stem growth annually m^3 ha^{-1} no N	with N	with NPK
S84, Siljansfors	pine	15	1.3	3.2	3.3
P731, Lövnäs	pine	15	1.7	4.3	4.5
P728, Själlarimsheden	pine	15	2.3	5.0	4.4
S85, Siljansfors	pine	15	2.3	3.7	3.8
P777, Rotnäset	spruce	10	2.4	4.3	4.2
P725, Ljusbergskilen	spruce (pine, birch)	15	5.9	9.3	9.2
P883, Frodeparken	spruce	14	15.2	15.8	17.0

Drained peatlands respond to phosphorus and potassium, and sometimes N and other elements such as boron.

The mechanism of the N effect has been discussed at length. Recent measurements by Linder & Troeng (1980) have shown that there is a slight increase in photosynthetic efficiency in fertilized trees compared with unfertilized ones. However, the big difference in yield seems to be due to a reallocation of the photosynthetic products to form new needles and then more stemwood, probably at the expense of fine root production. In young stands not yet fully closed, there is a linear relation between needle biomass (or leaf area index) and stem production (or total above-ground production) (Albrektson *et al.* 1977). When the stand becomes dense, either on good sites or after fertilization, the straight line seems to change into a diminishing-return type of curve (figure 3). As the typical boreal forest is fairly open, there is usually room for more needles and consequently the relative growth increases after N fertilization can be larger in the boreal forest than in, for instance, middle European or Japanese forests, which are dense even without fertilization.

This experience has led to extensive forest fertilization in Scandinavia, particularly in Sweden and Finland. So far the fertilization of mineral soils uses mainly N fertilizer, in Sweden ammonium nitrate in particular. There is very little evidence that phosphorus, potassium, magnesium, or other macronutrients would increase the fertilizer response beyond that obtained with the fertilizer régimes used at present (additions of around 150 kg N per hectare at intervals of 7 years). A possible deficiency in sulphur has been considered in the northwestern United States (Turner *et al.* 1977). Nitrogen fertilization seems to have induced a boron deficiency in some areas in Scandinavia and Finland on both peat and mineral soil (Huikari 1977; Albrektson *et al.* 1977; Braekke 1977). Further use of fertilization on a practical scale may lead to other disturbances, such as reduced winter hardiness or increased palatability for browsing animals. Such phenomena can usually be avoided if only stands of the less sensitive ages are fertilized.

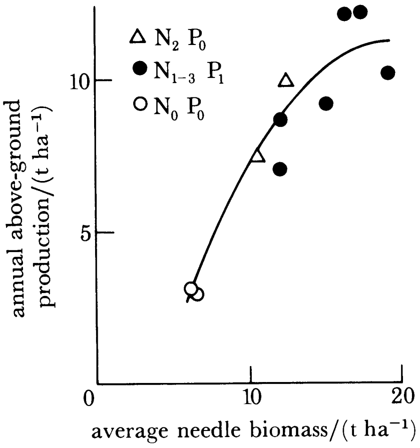

FIGURE 3. Above-ground production (1973–8) of the spruce in figure 2 plotted against needle biomass.

FUTURE PROSPECTS

In the long term, other factors have to be considered that affect the N economy of the manipulated boreal forest. First, there is a removal of nitrogen and other nutrients on harvesting. If stems only are removed, there is probably not much to worry about, but whole-tree harvest is increasing and stumps are also being removed. With stump removal (as with deep soil cultivation as a site-preparing measure) we may risk a decrease in soil organic matter and in the total store of N in the site; this may cause damage to poor sites. On the other hand this negative influence may be compensated for by the addition of fertilizer even if considerable amounts of added ammonium nitrate N (and to a lesser extent urea N) seem to be lost rapidly from the forest ecosystem by leaching and denitrification (Nömmik & Popović 1971; Tamm *et al.* 1974; Wiklander 1981) and only a small part goes into the trees (table 3). In addition to the intentionally added fertilizer, Scandinavian boreal forests, like most European forests, now receive more N from the air than during the pre-industrial era. In south Sweden, annual N additions may well exceed 10–15 kg ha^{-1}. This is a fairly large amount over a rotation period of 70–100 years, especially when the ability of the forest to hold back N is considered. The result of this development may be a more productive, but perhaps less stable, forest, with intensive nitrate production and leaching after clear-felling.

Another new influence is the acidity in precipitation and dry fall-out caused both by N compounds and by sulphur compounds. Nitrogen acidification is probably less serious in the boreal forest than further south because of the limited nitrification that occurs. It is only during the clear-felling phase, when there is intensive nitrification, that temporary soil acidification may occur. The acidity caused by sulphur compounds may be serious in the long run. The immediate effect on the soil seems to be an increase in apparent N mobilization, probably because of less competition for the N between microorganisms and roots. The trees may even grow better temporarily, if acid is applied experimentally (Tamm & Wiklander 1980).

However, in the long run we can expect increased leaching of cations from acidified profiles, increased availability of aluminium, which is a poison for many organisms, and a decreased turnover rate of N on the site (Tamm 1976; Drabløs & Tollan (eds) 1980).

Table 3. Apparent recovery of fertilizer N in tree stand above ground

(All stands with 'excess N' above 20% are young, not fully closed.)

experiment	number of fertilizations	total N added kg ha^{-1}	'excess N' (% of added)
871, spruce	2	200	19
883, spruce	2	200	18
E1, young spruce N1	4	175	58
E1, young spruce N2	4	350	41
E1, young spruce N4	4	700	30
E1, young spruce N1	13	625	8
E1, young spruce N2–N4	13	1550	12
E1, young spruce N4–N8	13	3900	8
E26A, young spruce N1P1	7	340	25
young spruce N2P1	7	680	22
young spruce N3P1	7	1020	20
young spruce N2P0	7	680	18
872, pine	8	800	12
873, pine	2	300	8
728, pine	2	120	15
E40, young pine N1	6	280	33
E40, young pine N2	6	560	20
E40, young pine N3	6	840	15

References (Tamm)

Albrektson, A., Aronsson, A. & Tamm, C. O. 1977 The effect of forest fertilization on primary production and nutrient cycling in the forest ecosystem. *Silva fenn.* **11**, 233–239.

Braekke, F. H. 1977 Fertilization for balanced mineral nutrition of forests on nutrient-poor peatland. *Suo* **28**, 53–61.

Bringmark, L. 1980 Ion leaching through a podsol in a Scots pine stand. *Ecol. Bull., Stockh.* **32**, 341–361.

Crocker, R. L. & Major, J. 1955 Soil development in relation to vegetation and surface age at Glacier Bay, Alaska. *J. Ecol.* **43**, 427–448.

Dahl, E., Gjems, O. & Kielland-Lund, J., Jr 1967 On the vegetation types of Norwegian conifer forests in relation to the chemical properties of the humus layer. *Meddr norske Skogfors Ves.* **23**, 503–531.

Drabløs, D. & Tollan, A. (eds) 1980 *Ecological impact of acid precipitation.* (*Proceedings of an International Conference*, Sandefjord, Norway, 11–14 March.) S.N.S.F. project. Oslo: Ås.

Huikari, O. 1977 Micro-nutrient deficiencies cause growth-disturbances in trees. *Silva fenn.* **11**, 251–255.

Jenny, H. 1941 *Factors of soil formation. A system of quantitative pedology.* (281 pages.) New York: McGraw-Hill.

Linder, S. & Troeng, E. 1980 Photosynthesis and transpiration of 20-year-old Scots pine. *Ecol. Bull., Stockh.* **32**, 165–181.

Lundmark, J.-E. 1977 Marken som del av det skogliga ekosystemet. [The soil as part of the forest ecosystem.] *Svenska Skogsv. För. Tidskr.* **75**, 109–122. [In Swedish.]

Nömmik, H. 1979 Vilken roll kan kalken spela i framtidens skogsbruk? [The future role of liming in forestry.] *K. Skogs- o. LantbrAkad. Tidskr. Suppl.* **13**, 31–37. [In Swedish, with English summary.]

Nömmik, H. & Popović, B. 1971 Recovery and vertical distribution of ^{15}N labelled fertilizer nitrogen in forest soil. *Studia for. suec.* **92**, 1–20.

Scharpenseel, H. W. 1971 Radiocarbon dating of soils – problems, troubles, hopes. In *Paleopedology – origin, nature and datings of paleosols* (ed. D. H. Yaalon), pp. 77–88. Jerusalem: Israel Universities Press.

Scharpenseel, H. W., Tamers, M. A. & Pietig, F. 1968 Altersbestimmung von Böden durch die Radiokohlenstoff-datierungsmethode. *Trans. 9th Int. Congr. Soil Sci.*, Adelaide vol. **3**, pp. 577–589.

Tamm, C. O. 1976 Acid precipitation: biological effects in soil and on forest vegetation. *Ambio* **5**, 235–238.

Tamm, C. O. 1980 Response of spruce forest ecosystems to controlled changes in nutrient regime, maintained over periods up to 13 years. In *Stability of spruce forest ecosystems* (*International Symposium*, University of Agriculture, Brno) (ed. E. Klimo), pp. 423–433.

Tamm, C. O. & Holmen, H. 1967 Some remarks on soil organic matter turn-over in Swedish podzol profiles. *Meddr norske Skog fors Ves.* **23**, 67–88.

Tamm, C. O., Holmen, H., Popóvić, B. & Wiklander, G. 1974 Leaching of plant nutrients from soils as a consequence of forestry operations. *Ambio* **3**, 211–221.

Tamm, C. O. & Pettersson, A. 1969 Studies on nitrogen mobilisation in forest soils. *Studia for. suec.* **75**, 1–39.

Tamm, C. O. & Wiklander, G. 1980 Effects of artificial acidification with sulphuric acid on tree growth in Scots pine forest. In *Ecological impact of acid precipitation.* (*Proceedings of an International Conference*, Sandefjord, Norway, 11–14 March) (ed. D. Drabløs & T. Tollan), pp. 188–189. S.N.S.F. project. Oslo: Ås.

Turner, J., Lambert, M. J. & Gessel, S. P. 1977 Use of foliage sulphate concentrations to predict response to urea application by Douglas fir. *Can. J. For. Res.* **7**, 476.

Ugolini, F. C. 1968 Soil development and alder invasion in a recently deglaciated area of Glacier Bay, Alaska. In *Biology of alder* (ed J. M. Trappe, J. F. Franklin, R. F. Tarrant & G. M. Hansen), pp. 115–140. Portland, Oregon: Pacific NW Forest & Range Experiment Station.

Wiklander, G. 1981 Clear-cutting and the nitrogen cycle. Heterogeneous nitrogen leaching after clear-cutting. *Ecol. Bull., Stockh.* **33**, 642–647.

Discussion

J. V. Lake (*Agricultural Research Council Letcombe Laboratory, Wantage, U.K.*). Professor Tamm mentioned that the main effect of nitrogen fertilizer on spruce was to increase growth, but net photosynthesis was also increased somewhat. Was this photosynthesis calculated on a unit needle area basis, i.e. the added nitrogen somehow enhanced the activity of the photosynthetic apparatus, or could the result have been an indirect consequence of the increased growth?

H. G. Miller (*Macaulay Institute for Soil Research, Aberdeen, U.K.*). Dr Lake was puzzled by the claim of Professor Tamm that N fertilizer has increased the photosynthetic efficiency of pine foliage in Sweden. This may seem rather surprising but I can confirm that we have made a similar observation at Culbin (H. G. Miller & J. D. Miller (1976) *J. appl. Ecol.* **13**, 249–256). However, an increase in net assimilation rate was only observed as the N level in top-whorl foliage was raised from about 0.8% to a little under 1.0%; thereafter all further increase in net primary production was solely due to an increasing leaf area ratio. A response through an effect on net assimilation rate is therefore only likely in extremely deficient trees and is probably not a significant factor in most experiments.

C. O. Tamm. It is quite true that the pines on unfertilized plots where Linder & Troeng (1980) studied photosynthesis were extremely deficient in nitrogen, as shown by the dramatic response to fertilizer. The physiological mechanism for the increase in photosynthetic rate is not known, but it is clear that addition of nutrients causes sinks for the photosynthetic products by promotion of new growth.