Productivity of Scandinavian Forests

in relation to changes

in Management and Environment

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INTRODUCTION

The concept of limiting factors goes back to the work of Liebig in the 1840s, where he stated that plant growth was limited by the nutrient element in minimum, that is the element in least supply as compared with the demand of the plant. Liebig's way of looking upon plant growth relations was a very simplified one, and it has later been found that very often more than one factor limits plant growth and that the various limiting factors may interact in different ways. Often the interaction between growth factors can be expressed as multiplicative effects with positive interactions between factors. However, there are also cases described where one factor may act as a substitute for another factor to a larger or smaller extent.

In forestry we often find rather well established empirical relations between forest growth and some factor, although the relationship may be a very indirect one. A few cases of this type will be discussed in the present paper, because indirect relationships present difficulties in interpretation, when we apply the principle of limiting factors.

It is characteristic of the boreal forest that it shows distinct successional patterns (Fig. 1). A common cause of the start of a new succession in a natural forest is a forest fire, but extensive wind felling or insect attacks may sometimes replace the fire. In the succession there are gradual changes both in the forest stand and in the soil, and the factors limiting forest tree growth are not necessarily the same in different phases of the succession. At the

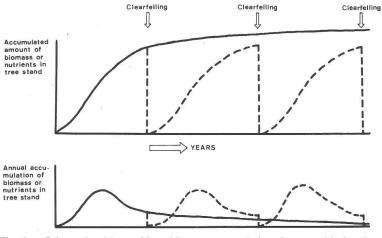


Fig. 1 — Schematic picture of how biomass accumulation changes with time in a boreal forest ecosystem. The assumption that subsequent tree crops show identical development is hypothetic.

start of a new succession, irrespective of its causes (natural or man-made), there is an intensive decomposition of most of the organic forest floor material (the Ao horizon) and also of slash remaining on the ground. For a few years there is a good supply of nutrients on the cleared area, better on good sites than on poor sites. In any case there are higher concentrations of available plant nutrients in the soil than at any time beneath a closed canopy. Pioneer vegetation takes advantage of this, as do tree seedlings, if seed sources are available or plants are put in by man. The rapid decomposition is a transient stage, and when the new saplings are 5, 10 or 15 years old (depending on site quality) most of the nutrients in the humus layer are gone. They have been leached from the site or washed into the mineral soil where some of them are bound in a form not easily available to plant roots. However, with the growth of the young trees, the soil beneath the trees is again supplied with litter, and a new humus layer starts to build up. Competition between trees and between the tree stand and lesser vegetation is severe, and most of the litter is decomposed already in the organic horizon (A_{Ω}) on top of the mineral soil, which is interwoven with fine roots and their mycorrhiza. Fungal hyphae, both of decomposing fungi and of mycorrhizal species, form a considerable part of the humus layer and there is some evidence that mycorrhizal roots may decrease the rate of litter decomposition (Gadgil and Gadgil 1974). The "Gadgil effect" has so far been conclusively shown only for Pinus radiata plantations in New Zealand, but ongoing research in Sweden has given preliminary results

qualitatively in agreement with the hypothesis (B. Berg, personal com). The physiological background for the assumed antagonism between mycorrhizal and decomposing fungi may be complex, but it is clear that mycorrhizal fungi are better off with regard to energy supply than are decomposers compelled to extract their metabolic energy from cellulose, lignin and other resistant materials. Ecologically, the delayed decomposition might give a certain degree of stability to the undisturbed ecosystem, where litter supply often changes by a factor of 1.5 or more from one year to the next. On the other hand, after a disturbance, such as clear-felling or thinning, the Gadgil effect would result in a more enhanced decomposition and faster nutrient mineralisation than accounted for only by the decrease in competition. Such an increase in nutrient availability after disturbance has long been observed, the "assart effect" (cf. Romell 1935, 1967). Of course the "assart effect" does occur also in other types of forests, but it is particularly striking in an environment characterised by a generally low availability of nutrients.

THE RÔLE OF NITROGEN

Numerous experiments have shown that a supply of nitrogen fertiliser increases growth in typical boreal forests (Table 1). Effects

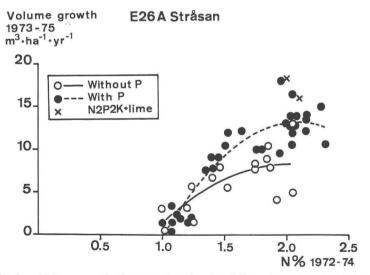


Fig. 2 — Volume growth of spruce plotted against foliage nitrogen concentrations. Nitrogen supplied as ammonium nitrate annually from 1967 onwards, phosphorus 1967, 1969 and 1970. Open dots represent plots without P, filled dots with P. Stand planted in 1958.

(From Albrektson, Aronsson and Tamm 1977)

Table 1 — Summary of more than ten-year-old fertiliser experiments including comparisons between nitrogen only and nitrogen + PK. The first six sites represent typical boreal forests in middle and north Sweden, while Experiment P 883 represents a highly productive spruce stand planted on former arable land in southwestern Sweden (the "beech region").

Experiment Designation	Tree Species	Observation Period — Years		0	
			No N	With N	With NPK
S 84, Siljansfors	Pine	15	1.3	3.2	3.3
P 731, Lövnäs	Pine	15	1.7	4.3	4.5
P 728, Själlarimsheden	Pine	15	2.3	5.0	4.4
S 85, Siljansfors	Pine	15	2.3	3.7	3.8
P 777, Rotnäset	Spruce	10	2.4	4.3	4.2
P 725, Ljusbergskilen	Spruce, pine (birch)	15	5.9	9.3	9.2
P 883, Frodeparken	Spruce	14	15.2	15.8	17.0
No. of plots measured			14	12	9

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of other nutrients (phosphorus, potassium etc.) are rare on mineral forest soils on the young glacial material prevalent in Scandinavia, although an additional effect of phosphorus has been obtained in young spruce forests fertilised with large amounts of nitrogen (Fig. 2), sometimes even in fast growing stands. (cf. Table 1). It can thus be considered a fact that nitrogen supply is a factor limiting tree growth in the boreal forest, and that this deficiency of nitrogen directly affects tree growth. The physiological mechanism may be either more intensive photosynthesis of needles well supplied with nitrogen or an increased amount of needles which can be formed if the nitrogen supply is good. Very probably both of these mechanisms operate simultaneously, but an experiment in young spruce forest in central Sweden has shown that the tree crowns and the amount of needles rapidly increase following nitrogen

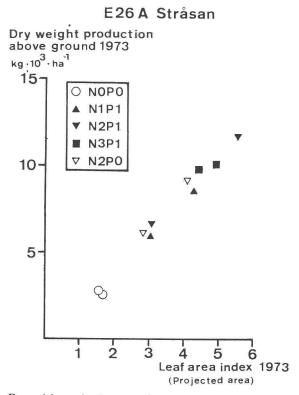


Fig. 3 — Dry weight production above ground as a function of leaf area index in the spruce experiment in Fig. 2. Each symbol represents one plot. (From Albrektson, Aronsson and Tamm 1977)

fertilisation, and that this increase explains most of the subsequent growth increase (Fig. 3, Tamm 1974). Similar studies in a young pine stand (Albrektsson et al. 1977) also show an increase in needle biomass after fertilisation and a close relationship between stand growth and leaf area index (Figs. 4, 5). This does not exclude a fertiliser response due to increased photosynthetic efficiency (cf. Brix and Ebell 1969, Miller 1976, Linder and Ingestad 1977), which may occur also in dense stands, where an increased needle biomass would result in increased self-shading. However, the typical boreal forest is not very dense and the dominating control mechanism for the primary production appears to be the amount of photosynthetic tissue.

Manipulations such as thinning affect leaf biomass directly, but the decrease in competition for nitrogen allows the remaining trees to increase their crowns. A leaf area index similar to that before the thinning may be attained within a few years, always supposing that no major soil changes occur. It is a general belief that during the life-time of a stand, more and more of the site's nitrogen store is immobilised in the tree biomass and in an "inactive" mor layer. On poor sites and where decomposition is slow, due to a cold climate, this may eventually hamper tree growth. There is not much firm evidence for this theory, even if it is in agreement with what we know at present (Tamm 1977). Yet in parts of Scandinavia and Finland there are environmental influences which may complicate

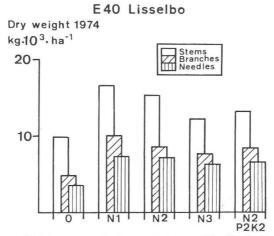
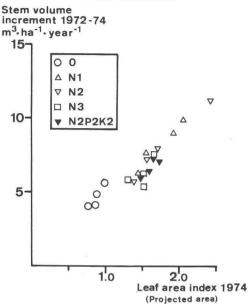
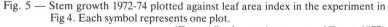


Fig. 4 — Dry weight above ground of a young pine stand fertilised with ammonium nitrate annually from 1969 onwards (see Tamm, Nilsson and Wiklander 1974). Each value mean for four plots. Stand established after windfellings in 1954.

(From Albrektson and Aronsson, in prep.)



E40 Lisselbo



(From Albrektson, Aronsson and Tamm 1977)

the picture. Nitrogen immobilisation in old forest stands may be compensated for by increasing atmospheric deposition of ammonia and nitrate (at present estimated at 2-20 kg N ha⁻¹ yr⁻¹). The increasing acidity of the rain, caused by both sulfur and nitrogen compounds might work in the opposite direction by slowing down decomposition.

PRIMARY AND SECONDARY FACTORS

Even if it is proven beyond doubt that nitrogen is the most directly growth-limiting factor among the plant nutrients in most Scandinavian forests, it is somewhat difficult to consider nitrogen as a primary factor. All nitrogen present in the Scandinavian forest soils has been added to the soil during the 8000 — 12000 years since the Pleistocene glaciation, which left Sweden covered with virtually nitrogen-free mineral soil (glacial till and various sediments). There must be some mechanism accounting for the large differences occurring in nitrogen supply (amounts and concentrations).

Dahl et al. (1967) have observed that there is a close relationship

between the amount of nitrogen in the humus layer and the base saturation in this layer and also that the poorer forest types are low in both nitrogen concentration and base saturation, while more fertile forest types are high in both properties (Fig. 6). A similar relationship holds true on Swedish peatlands (Holmen 1964, Dahl et al., l.c.), There are several mechanisms possible to explain this relationship. One is the preference of nitrogen-fixing organisms for higher pH and better base saturation conditions. Another one is the possibility that more stable humus, rich in nitrogen, is formed, if the base saturation is higher. Also the water regime interacts with this relationship between nitrogen and base saturation. Slopes with more or less regular supply of surface or subsurface water trickling down them are usually good sites (cf. Hägglund and Lundmark 1977) and apparently higher than the surroundings in both nitrogen and base saturation.

PRACTICAL IMPLICATIONS

There are many problems still to be solved with respect to the

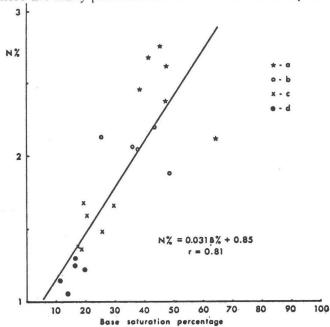


Fig. 6 — Nitrogen concentration in humus (A_O) samples (% of loss on ignition) plotted against base saturation in the same samples. The symbols stand for forest vegetation types with their productivity decreasing in the series a »b »c »d. Southern Norway.

(From Dahl, Gjems and Kielland-Lund 1967)

relationship between forest growth and site properties. The evaluation of site quality is also complicated by the fact that only a small part of the nitrogen in the forest soil is available for trees at a given time. We have no commonly accepted method for assessing the active fraction of the soil nitrogen supply, even if a method suggested by Nömmik (1976) offers some promise. A better insight into these relations is urgently needed, and particularly into how man's operations affect soil nitrogen availability. Man-made forest is now rapidly replacing the old, natural or at least self-sown forest in North Sweden. In this man-made forest there is often a change of tree species. Widely spaced pine is replacing old-growth spruce or a mixed hardwood-coniferous forest. Wide spacing between trees (2 x 2m and wider have been used extensively on poor sites) in the earlier phase of the succession prolongs the time during which there is no regular circulation of nutrients between soil and tree stand. Fertilisation is used as a silvicultural tool to improve yield. Changes in the negative direction are due to increased attacks of insects on the forest and to the acid rain, mentioned already, which has increased considerably in Europe during the past decade, due to combustion and processing in Europe's industrial and urbanised areas.

Some of the factors affecting forest production in a long-term perspective are listed below:

Positive Factors

Replacement of self-sown stands, often unmanaged in earlier days, with new stands planted in regular spacing with proper site treatment and genetically better material (genotypes or even species).

Space regulation and brush control in young forest, thinning in middle-age stands.

Fertilisation.

Increase in atmospheric supply of ammonia and nitrate nitrogen.

Growth improvement and increase in forest area by draining peatlands.

Negative Factors

Too wide spacing in planting.

Too little attention to local site conditions because of increased mechanisation.

Increasing number of injurious insects (partly inadvertent side-effects of management operations).

Extended intervals between thinnings (as compared with conditions 2-3 decades ago).

Increase in rain acidity and in absorption of acid substances from the air.

Forest fires, especially on dry sites.

Factors with Slow or Uncertain Effects

Climatic changes, mineral weathering, increased carbine dioxide concentration in air, increased proportion of coniferous monocultures.

It is difficult to forecast the combined effects of all these changes, but it has caused alarm that the last reports from the Forest Survey of Sweden indicate a decrease in forest growth, at the same time as wood consumption continues to increase. We must use all scientific information available in order to optimise forest growth, with due attention to economic considerations and possible environmental restrictions. Some of the proposed forest programmes have been criticised for the last reason (intensive fertilisation, extensive drainage operations, herbicide use, etc.).

REFERENCES

- ALBREKTSON, A., ARONSSON, A. and TAMM, C. O. 1977. The effect of forest fertilisation on primary production and nutrient cycling in the forest ecosystem — Silva Fenn., Vol. 11(3): 233-239.
- BRIX, H. and EBELL, L. F. 1969. Effects of nitrogen fertilisation on growth, leaf area, and photosynthesis rate in Douglas-fir — Forest Science 15(2): 189-196.
- DAHL, E., GJEMS, O. and KIELLAND—LUND, J. 1967. On the vegetation types of Norwegian conifer forests in relation to the chemical properties of the humus layer—Meddelelser fra Det Norske Skogsforsøksvesen 23(85); 505-531.
- GADGIL, R. L. and GADGIL, P. D. 1974. Suppression of litter decomposition by mycorrhizal roots of *Pinus radiata* N. Z. Jl. For. Sci. 5(1): 33-41.
- HÄGGLUND, B. and LUNDMARK, J. E. 1977. Site index estimation by means of site properties. Scots pine and Norway spruce in Sweden. — Stud. For. Suec. No. 138.
- LINDER, S. and INGESTAD, T. 1977. Ecophysiological experiments under limiting and non-limiting conditions of mineral nutrition in field and laboratory — Bicentenary celebration of C. P. Thunberg's visit to Japan. Tokyo, Kyoto and Nagasaki, 17-25th May 1976. pp. 69-76.
- MILLER, H. G. and MILLER, J. D. 1976. Effect of nitrogen supply on net primary production in Corsican pine — J. Appl. Ecol. 13: 249-256.
- NÖMMIK, H. 1976. Predicting the nitrogen-supplying power of acid forest soils from data on the release of CO2 and NH3 on partial oxidation — Commun. Soil Sci. and Plant Analysis 7(6): 569-584.
- ROMELL, L. G. 1935. Ecological problems of the humus layer in the forest Cornell Univ. Agric. Expt. Sta. p. 3-28. Ithaca, New York.
- ROMELL, L. G. 1967. Die Reutbetriebe und ihr Geheimnis Studium Generale 20(6): 362-369.
- TAMM, C. O. 1974. Experiments to analyse the behaviour of young spruce forest at different nutrient levels — Proceedings of the First International Congress of Ecology. The Hague, Netherlands. p. 266-272.
- TAMM, C. O. 1977. Factors limiting primary production in the boreal forest long-term and short-term considerations — Bicentenary celebration of C. P. Thunberg's visit to Japan. Tokyo, Kyoto and Nagasaki, 17-25th May 1976. pp. 53-59.
- TAMM, C. O., ARONSSON, A. and BURGTORF, H. 1974. The optimum nutrition experiment Strasan. A brief description of an experiment in a young stand of Norway spruce (*Picea abies* Karst.) — Research Notes, Department of Forest Ecology and Forest Soils, Royal College of Forestry No. 17. Stockholm.
- TAMM, C. O. NILSSON, A. and WIKLANDER, G. 1974. The optimum nutrition experiment Lisselbo. A brief description of an experiment in a young stand of Scots pine (*Pinus silvestris* L:) — Research Notes, Department of Forest Ecology and Forest Soils, Royal College of Forestry No. 18. Stockholm.