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MODELLING NUTRIENT DYNAMICS IN FORESTS, AND THE
INFLUENCE OF NITROGEN AND PHOSPHORUS ON GROWTH.

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ABSTRACT

A model is described which calculates the influence of nitrogen and phosphorus on growth of a forest stand over a period of several decades. The simulation is based on a carbon model in which stand increment is calculated from incoming photosynthetically active radiation, photosynthetic capacity of the foliage, and the availability of water. Nitrogen and phosphorus requirements are estimated from current and maximum concentrations in the main biomass components. Site nutrient availability is estimated with an elementary nutrient supply model that is based on a combination of fast- and slow-release nutrient pools in the soil. Current needle element content is the result of nutrient uptake together with redistribution of nutrients in the standing biomass. The influence on growth is estimated from the relation between needle content and growth. Nutrient uptake is estimated from maximum requirements or from soil availability whichever is smallest. Withdrawal of nutrients from dying biomass is taken into account also. The model is applied to even-aged stands of Douglas fir in the Netherlands, and the results are discussed against the background of high nitrogen deposition resulting from intensive live-stock farming in the Netherlands.

INTRODUCTION

Modelling of forest growth can take many forms. It is done here by employing a simulation model in which total stand growth is viewed as the result of a combination of physiological, physical, and chemical processes. Basic physiological processes as photosynthesis, respiration, and assimilate distribution, can be studied indepently, and subsequent integration in a stand-level model results in a prediction of overall stand dynamics and yield. The analysis of the nutrient status is limited to nitrogen and phosphorus only, as N and P are required in relatively large amounts, and nitrogen as well as phosphorus both have been shown to limit growth under various growing conditions in temperate coniferous forests (Fiedler et al., 1973, Gussone, 1974).

Growth limiting, growth determining, and growth reducing factors can be distinguished in the analysis of plant growth. Growth determining factors are the species and weather characteristics that determine the potential growth level for a particular crop or stand, they are independent of the soil conditions of a particular site. Most important species characteristics that determine potential growth are the maximum CO₂ assimilation rates under ambient temperature, and the efficiency with which the species uses incoming radiation in the photosynthetic process.

Growth limiting factors consist of soil characteristics as water- and nutrient availability, and determine the yield level that can be attained at a particular site. In addition, growth can also be influenced by growth reducing factors as pests, diseases and weeds, pollution, and wind- and frost damage. This third group of growth factors will not be discussed here, as its incorporation in forest growth models at this moment is still in its early days.

In order to separate the growth factors as described above, it is convenient to distinguish between production situations. Following De Wit and Penning de Vries (1982), distinction can be made between 1) a potential production situation where water- and nutrients are in ample supply; 2) the situation in which productivity is reduced by water shortage; 3) the situation where, in addition to water shortage, nitrogen and/or phosphorus are limiting growth; and 4) situations where nutrients other than nitrogen and phosphorus limit growth.

A complete description of the simulation model together with an evaluation of model performance in permanent field plots, will be published elsewhere (Mohren, 1986). A pilot version of the carbon model was described earlier by Mohren et al. (1984).

AN ELEMENTARY CARBON MODEL OF FOREST GROWTH.

Canopy assimilation can be calculated as the sum of the contributions of all individual leaf or needle surfaces in the canopy. Under optimal growing conditions, needle photosynthesis is directly related to the amount of Photosynthetically Active Radiation (PAR) absorbed. Using a description of the canopy light climate, the amount of PAR absorbed can be calculated, and from this total canopy photosynthesis. The amount of carbohydrates formed is used for maintenance and growth. Maintenance requirements depend to a large extent on protein content and overall metabolic activity, and can be estimated from biomass composition and average growth activity. Stemwood is thought of as consisting of two components: dead heartwood tissue, which has a supporting function only and does not require maintenance, and living sapwood, involved in the transport of water through the plant and consisting of conducting elements and living parenchymatous tissue. The latter requires assimilates for maintenance; a small amount per unit sapwood weight, but a considerable amount for the whole stand, in case large amounts of sapwood are present. Other biomass components considered explicitly, are needles, branches, and roots. Bark biomass is not accounted for separately.

After maintenance requirements have been met, the amounts of assimilates available for growth are distributed over the biomass components. Assimilate distribution over the plant organs is governed by the morphogenetic development pattern of the plant species, and depends on the development stage of the trees in the stand. Simulation of assimilate distribution is complicated by its dependence on growing conditions: Water- and nitrogen availability have been shown to influence development rate as well as the distribution of assimilates over the organs (Van Keulen et al., 1986). Distribution of growth over below- and above ground parts has been given considerable attention within a modelling context, already several years ago (e.g. Brouwer and De Wit, 1968). Despite much research, it still is not possible to simulate assimilate distribution in an explanatory fashion, and most models rely on the use of descriptive carbon-allocation keys that are based on field observations of distributions of dry weight increment over plant organs. This is done here also, the distribution keys employed being based

on published biomass data (compilations by Cannell, 1982, and Satoo & Madgwick, 1982). It amounts to allocation of 20 % of the assimilates available for growth to the roots in case of optimal growth, this fraction increases linearly to 50 % when productivity decreases to zero. Of the assimilates available for above-ground growth, 60 % is allocated to stem growth, 25-30 % goes into foliage mass, and 10-15 % is allocated to the branches. When the trees mature, both foliage and branch growth somewhat increase on account of stem growth.

Uptake of CO_2 through the stomata is coupled to a loss of water from the plant to the atmosphere. This water loss has to be replenished by root uptake of soil moisture. The influence of water availability can be modelled relatively easy by keeping track of soil moisture. A number of models are available to estimate transpiration in relation to weather variables and canopy parameters. When soil moisture becomes limiting, stomata close and transpiration as well as CO_2 assimilation is reduced, resulting in decreased growth. Soil moisture is replenished again by precipitation, run-on, or capillary rise. The stands concerned here are located on high sandy soils, and soil moisture is replenished as a result of precipitation only. More details on the simulation of the influence of hydrology on growth and yield can be found in the textbooks by Penning de Vries and Van Laar (1982), and Van Keulen and Wolf (1986).

The model operates with time steps of one day, allowing simulation of annual courses of assimilation, respiration and transpiration. The weather variables that are needed as input consist of total daily global radiation, air temperature, humidity, average daily windspeed, and daily precipitation. Precipitation data may vary over short distances, and have to be taken from recordings near to the site. To simulate total stand growth and yield, the model is allowed to run for periods of 40 to 60 years.

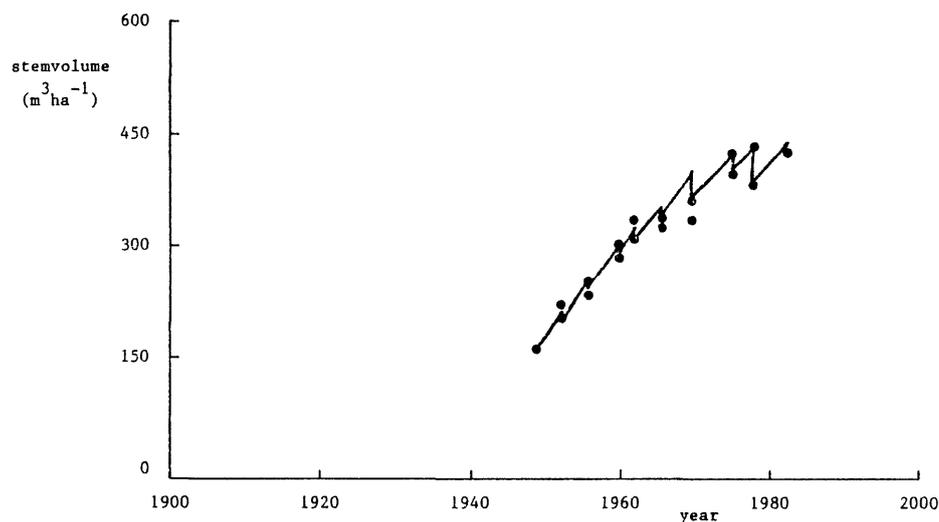


Figure 1: Model results for field plot D25. Drawn line: simulated total stem volume in $\text{m}^3 \text{ha}^{-1}$. Dots: field measurements.

The model is evaluated by comparison of model outcome with measurements from permanent field plots, used in growth and yield research. An evaluation showed good agreement of the model outcome with field measurements of stemvolume, and gave results for the other biomass components that were in

agreement with values reported in the literature. Figure 1 shows the model outcome together with stemvolume measurements from one of the field plots used.

A MODEL OF NITROGEN AND PHOSPHORUS DYNAMICS

For a given species, the nitrogen and phosphorus composition of the structural biomass components varies relatively little. Beyond a minimum concentration there is no further growth and at a maximum concentration, there is no further uptake. These minimum and maximum concentrations can be determined from fertilizer experiments with all other elements not limiting. Numerous of these experiments have been carried out, for the Netherlands e.g. by Blok et al. (1975). Table 1 gives minimum and maximum concentrations of nitrogen and phosphorus in Douglas fir for the main biomass components, based on published data. It should be remarked however, that the maximum concentrations in a particular situation may be lower because the N/P ratio in these biomass components cannot be higher than 30 and lower than 4.

Table 1.

Minimum and maximum concentrations in needles, branches, stems and roots as used in the model. Data from Blok et al. (1975), Turner et al. (1979), Foerst (1980), Mead (1984), and Van den Burg (1986).

	\underline{N}_{\min}	\underline{N}_{\max}	\underline{P}_{\min}	\underline{P}_{\max}
needles	0.80	2.00	0.08	0.30
branches	0.15	0.50	0.02	0.05
stemwood	0.05	0.15	0.01	0.02
roots	0.15	0.50	0.02	0.08

Nitrogen and phosphorus content in the needles is related to total stand growth. A suggested relation between growth reduction (F_G) and the N or P content of the needles is given in Figure 2.

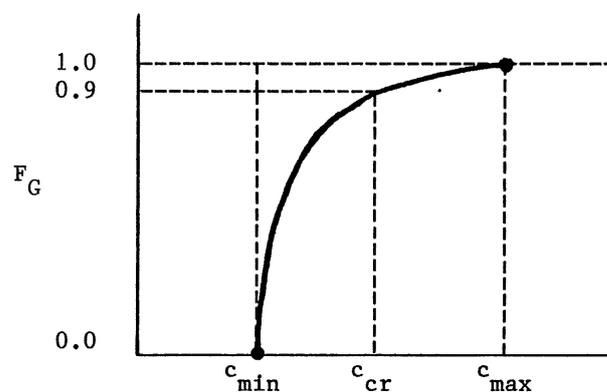


Figure 2: Relationship between element content in the needles and the reduction on total stand growth.

At the maximum concentration the growth is as simulated with the carbon model described in the previous paragraph and at the minimum concentration, the growth is zero. The form of the curve is based on the observation that at a nitrogen content of about 1.5 %, or at a phosphorus content of 0.15 %, growth is reduced by 10 % (Bengtson & Holstener-Jørgensen, 1971; Van den Burg, 1986).

Taking into account only the nitrogen content and the needle biomass, the calculation of growth and uptake proceeds now as follows. Let the needle biomass in the year t be W_t and the amount of nitrogen in this biomass N_t . The nitrogen fraction in the biomass is then:

$$c_t = N_t / W_t \quad (\text{kg kg}^{-1}) \quad (1)$$

The weight of the biomass in the year $t+1$ is now

$$W_{t+1} = W_t + I_t - L_t \quad (\text{kg ha}^{-1}) \quad (2)$$

The yearly needle increment equals

$$I_t = F_G \times (\text{simulated increase}) \quad (\text{kg ha}^{-1} \text{yr}^{-1}) \quad (3)$$

in which F_G is read from the graph in Figure 2.

Needle loss depends on the total amount of needle biomass and needle retention time, and is simulated with the carbon model.

The amount of nitrogen in the needles in the year $t+1$ is equal to

$$N_{t+1} = N_t + U_t - LN_t \quad (\text{kg ha}^{-1}) \quad (4)$$

Using f_w for the fraction of the total amount of nitrogen, that is withdrawn before abscission, the loss of nitrogen (LN_t) can be calculated as:

$$LN_t = (1 - f_w) \times c_t \times L_t \quad (\text{kg ha}^{-1} \text{yr}^{-1}) \quad (5)$$

The uptake of nitrogen is the minimum of the potential uptake (U_p) of the nitrogen in the soil and the maximum of the nitrogen that can be taken up by the needles:

$$U_t = \text{Min} (U_p, W_{t+1} \times c_{\text{max}} - (W_t \times c_t - LN_t)) \quad (\text{kg ha}^{-1} \text{yr}^{-1}) \quad (6)$$

The presence of branches, roots and stems can be taken into account by assuming a proportionality between their relative element contents and that of the needle biomass. For branches and roots, litter loss and turnover are estimated in the carbon model. Sapwood is assumed to have a life-span of 15 years, after which conversion to heartwood occurs.

Similar calculations can be performed for phosphorus, the largest reduction rate on increment (F_G) resulting from either nitrogen or phosphorus limitations is used in the model. It is then also taken into account that the N/P ratio is limited between the two extremes given above. The withdrawal before abscission of dead biomass is assumed to be equal to 25 % for nitrogen, and 35 % for phosphorus.

The problem is now to estimate the potential uptake (U_p) of nitrogen and phosphorus in the soil. Using the approach described above, the influence of nutrient availability on potential uptake and hence on growth, can be assessed when site nutrient supply is known. Nutrient availability depends on the soil volume that is rooted by the trees, on the concentration of

nutrients in the soil solution, and on the rates of release from the nutrient pools in the soil together with the input of nutrients to the rooted soil compartment.

Both nitrogen and phosphorus in the soil are not only taken up by the plants, but are subject to other processes as well, which in addition to the input processes mentioned previously, further complicate their chemistry in the soil. Deterministic simulation approaches are difficult under these circumstances, and so far only complex, comprehensive models have been developed (Van Veen, 1977; Penning de Vries, 1981).

These models can be used to study detail-processes, but lack of quantitative knowledge prevents them from being implemented in general primary production models. In case of a perennial crop as a forest however, only an average value for nutrient availability is needed, and as the exact nature and magnitude of the underlying processes are of no great explanatory value here, an elementary model as e.g. described by De Wit and Wolf (1984a,b), suffices to evaluate the effects of N and P on growth.

In their models, two nutrient pools in the soil are considered (for N and P independently), a stable slow-release pool, and an unstable fast-release pool, both of which relate to the amounts of nutrients in the rooted zone of the soil profile only. All input into the soil compartment, either through atmospheric input, litter decomposition, biological fixation or fertilization, are either taken up by the trees, lost through denitrification and leaching, or added to the stable or unstable pools.

Table 2.

Transfer coefficients used to calculate nutrient supply. All coefficients are dimensionless fractions. Loss covers both leaching and denitrification.

From:	to:	trees	loss	unstable	stable
nitrogen:					
litter:		0.4	0.2	0.3	0.1
fertilizer:		0.4	0.3	0.2	0.1
atm. input:		0.2	0.3	0.4	0.1
biol. fix.:		0.2	-	0.6	0.2
unstable pool ($R_{LP,t}$):		0.67	0.33	-	-
phosphorus:					
litter:		0.05	-	0.75	0.2
fertilizer:		0.05	-	0.85	0.1
atm. input:		-	-	-	-
biol. fix.:		-	-	-	-
unstable pool ($R_{LP,t}$):		1.0	-	-	-

From Table 2, it can be seen that even in this simple model, some 20 transfer coefficients have to be estimated for each nutrient. The estimation can however, be simplified by lumping of relatively unknown but comparable input processes. If detailed information is lacking, it does not make sense to treat industrial fertilizer input, input from decomposition, and atmospheric background input separately. Instead, the same estimate for the transfer

coefficients can be used, which simplifies the matrix of coefficients to a large extent. Also, in case of phosphorus, atmospheric deposition and biological fixation do not occur, and leaching of soluble phosphate out of the profile is negligible. Reducing the number of coefficients to be estimated in that way, the remainder has to be estimated from the behaviour of applied fertilizer in soils. It must be stressed that the parameter values that are used here, are based on rough estimates from general knowledge only, and have to be re-estimated when using the model under different growing conditions and for different soils.

Stable and unstable pools are in dynamic equilibrium, and transfer rates between the two can be represented by first-order equations, in which the stable pool (SP) acts as a slow-release pool with all nutrients that are released, are added to the unstable pool (LP).

The stable pool can be represented as follows:

$$SP_{t+1} = SP_t - SP_t/T_{SL} + LP_t/T_{LS} + I_{SP,t} \quad (\text{kg ha}^{-1}) \quad (7)$$

SP_t/T_{SL} and LP_t/T_{LS} represent the transfer rates from the stable pool to the unstable pool, and vice versa. The transfer coefficient describing the release to the unstable pool (T_{SL} , in yr.), is of the order of magnitude of 150 years for nitrogen, and 60 years for phosphorus. The coefficient used to describe the transfer from unstable to stable (T_{LS} , in yr.) is estimated to be 8 for nitrogen and 5 for phosphorus. All depend on the soil type involved. $I_{SP,t}$ represents the amount added to the stable pool as a result of fertilizer use, atmospheric input, biological fixation, and litter fall. $I_{SP,t}$ is calculated from total input rates in year t, using the coefficients in Table 2. For the unstable pool, the equation reads:

$$LP_{t+1} = LP_t - LP_t/T_{LS} + SP_t/T_{SL} + I_{LP,t} - R_{LP,t} \quad (\text{kg ha}^{-1}) \quad (8)$$

in which $R_{LP,t}$ is the release from the unstable pool, and $I_{LP,t}$ the amount added as a result of fertilizer use etc. In case of nitrogen, the amount released by the unstable pool is either taken up by the trees, or lost by processes as denitrification and leaching. The distribution of $R_{LP,t}$ over tree uptake and loss will be comparable to the distribution of the amount of nitrogen in the litter over these two. The resulting coefficients are given in Table 2. The loss is among others a result of the fact that part of the release takes place during the dormant season, when little or no root uptake takes place. Phosphorus is much less mobile in the soil, and leaching losses are negligible. All phosphorus released from the unstable pool is therefore assumed to be available for uptake. In case availability exceeds nutrient demands, it is assumed that the surplus is retained in the unstable pool.

Potential uptake (U_p) used in equation 6, equals the amount of nutrients that can be taken up immediately by the trees from the inputs by fertilizer use, atmospheric deposition, biological fixation, and litter fall, together with the maximum amount available from release by the unstable pool. The total amount released by the unstable pool can be estimated from known fertilizer recovery fraction, assuming that the availability of fertilizer is the same as the availability of the nutrients in the unstable pool. This is based on the observation that e.g. phosphate fertilizer is indistinguishable from unstable phosphate in the soil, already a few days after fertilizer application. The model is essentially the same for nitrogen and phosphorus, differences occur only in the parameter values (Table 2).

In case of phosphorus an additional, virtually inert pool may be distinguished apart from the stable and unstable pool described above. From this

inert pool, nutrients are only very slowly released. In the model it is assumed that this pool contains half of the total amount of phosphorus in the rooted zone (about 1 m), and that this amount is mineralizing at a rate of 0.05 % per year. In case of 2000 kg P per hectare in the rooted zone, this amounts to a mineralization rate of $0.5 \text{ kg ha}^{-1} \text{ yr}^{-1}$. The rest of the total amount of phosphorus is distributed over the stable and unstable pools. Initial distribution over the stable and unstable pools is done by assuming equilibrium between the two, neglecting again all other transfer rates ($LP_t/T_{LS} = SP_t/T_{SL}$).

NITROGEN AND PHOSPHORUS STATUS OF DOUGLAS FIR IN THE NETHERLANDS

An important reason for studying the dynamics of nitrogen and phosphorus in the Netherlands, is the change in atmospheric input of nitrogen in recent years: Resulting from a considerable increase in intensive live-stock farming since the sixties ammonia volatilization and emission from manure have increased preposterously, leading to average nitrogen input rates in the forested areas of over $50 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ (Van Aalst, 1984; Van Breemen et al., 1983). Compared to presumed nitrogen input rates of 10 to 20 $\text{kg ha}^{-1} \text{ yr}^{-1}$ at the beginning of the century, this increase can be expected to lead to nutrient imbalances and disturbances on former nitrogen-poor sites. This is the case for coniferous forests, that are mainly located on the higher sandy soils. Considering the coupling between nitrogen and phosphorus in the plant (Bengtson & Holstener-Jørgensen, 1971), phosphorus may well become limiting as a consequence of the increased nitrogen input.

This can be illustrated using the same field plot as in Figure 1, by comparing estimated soil availability and uptake by the stand at the beginning, and at the end of the measurement period for both phosphorus and nitrogen. Fertilizer input of both nitrogen and phosphorus is zero, as is biological fixation of nitrogen, and atmospheric input of phosphorus. Total nitrogen within the rooted soil volume amounts to about 4000 kg ha^{-1} , total phosphorus is about 2000 kg ha^{-1} . Figure 3 contains the simulation results.

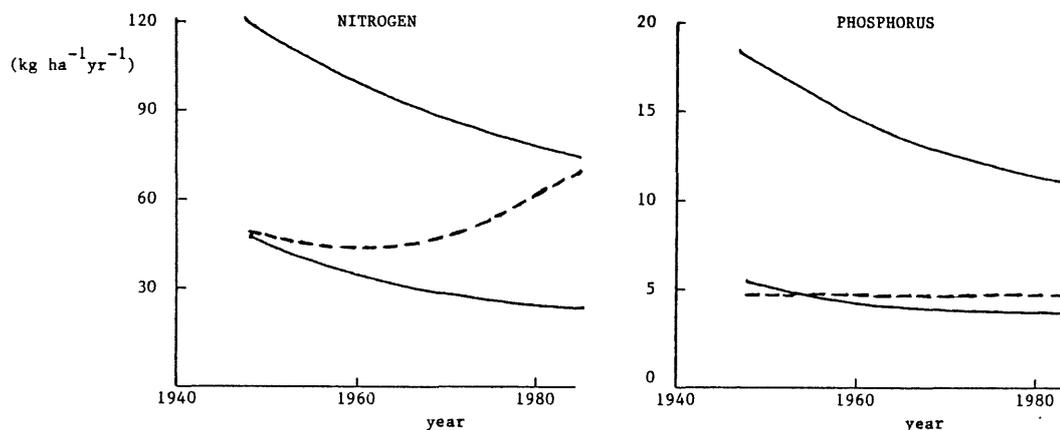


Figure 3: Gross maximum and minimum N and P requirements by the growing stand (drawn line) and estimated supply (dotted line) in field plot D25. Gross requirements calculated as maximum and minimum concentrations times calculated increment rates (redistribution before litter fall not yet taken into account).

Supply rates (U_p) calculated with the model amount to around $4 \text{ kg ha}^{-1} \text{ yr}^{-1}$ for phosphorus, staying virtually constant during the period simulated, whereas for nitrogen the supply increases from some $40 \text{ kg ha}^{-1} \text{ yr}^{-1}$, due to increased atmospheric input of nitrogen. From the graph, it can be seen that in 1949, gross minimum requirements about equaled soil supply for both nitrogen and phosphorus. This remains the case at the end of the period for phosphorus, whereas nitrogen availability at the end of the period almost equals gross maximum requirements. This points to limiting availability of both nitrogen and phosphorus in 1949, but entirely phosphorus limited growth at the end of the simulation period. Nitrogen content of the needles, sampled in January 1984 revealed values of around 2.0 % of needle dry weight, with phosphorus concentrations of 0.10 to 0.12 %. On comparable soils, nitrogen and phosphorus concentrations of around 1.5 % and 0.12-0.20 % respectively would be expected on the basis of old fertilization experiments carried out in the fifties and early sixties (Blok et al., 1975).

The same phenomena apparent in the simulation were found also in a resampling of one of the old fertilizer experiments by Blok et al. (1975). The stands were sampled again in 1984 to investigate possible changes in nutrient content resulting from the increase in nitrogen deposition in Dutch forests. Table 3 gives some of the results taken from Mohren et al. (1986).

Table 3.

Nitrogen and phosphorus concentrations of current needles in the Kootwijk fertilization experiment, 1, 2, respectively 28 years after fertilizer application. Soils contained a total of 18 mg P/100 g soil, and 0.1 % of soil dry weight nitrogen, both in the top soil layer. Fertilizer treatments consisted of 35 kg ha^{-1} phosphorus, applied as basic slag at the beginning of 1956, and 100 kg ha^{-1} of nitrogen in the form of calcium ammonium nitrate at the beginning of 1957. For further details, see Mohren et al. (1986).

	Nitrogen			Phosphorus			N/P ratio		
	'57	'58	'84	'57	'58	'84	'57	'58	'84
Treatment:									
O	1.04	0.91	2.01	0.12	0.11	0.09	9	8	22
N	1.46	1.02	1.96	0.10	0.10	0.11	15	10	18
P	1.01	0.98	1.76	0.19	0.17	0.10	5	6	18
NP	1.54	1.03	1.87	0.13	0.14	0.10	12	7	19

The data from 1957 and 1958 show a response to both nitrogen and phosphorus fertilization. In 1984, all treatments appear to be saturated with nitrogen, and exhibit minimum concentrations of phosphorus. This is reflected very clearly in the nitrogen to phosphorus ratios of the needles.

This change in nutrient status due to the increase in nitrogen input, can be considered typical for the majority of Douglas fir stands in the Netherlands on sandy soils. To investigate the possibilities for improvement, e.g. through fertilization with phosphates a nutrient model as described in the previous paragraph can be very helpful. Phosphorus fertilization has already been shown to result in a positive growth response under comparable conditions (Smilde, 1973; Gussone & Reemtsma, 1981).

CONCLUDING REMARKS

For nitrogen and phosphorus, the main plant related aspects of stand nutrition can be handled, when an estimate of growth is available together with minimum and maximum concentrations of nitrogen and phosphorus in the plant tissue. Large uncertainties remain on the supply side of the model, concerning soil supply and root uptake of nutrients. In case root uptake capacity is related to root growth and root turnover, assimilate distribution and growth interfere with nutrient uptake capacity. In case improved nitrogen supply leads to less root growth, as has been shown for annual species (Brouwer & de Wit, 1968), this means that the phosphorus deficiency under high nitrogen deposition rates might be caused by reduced root growth. This remains to be investigated. A modelling approach as described here can be used to point to relevant or crucial processes or phenomena to concentrate on.

The advantage of using an elaborate carbon model to begin with, lies in the ability to quantify the influence of other growth limiting factors besides nutrients (notably radiation, temperature, and water availability). This facilitates comparison of different forest ecosystems under varying growing conditions. In case productivity is limited by e.g. nitrogen only, total stand growth can be described effectively with a nutrient flux density model (Ingstad et al., 1981; Ågren, 1986).

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