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Simulation modeling of the effects of site conditions and disturbance history on a boreal forest landscape

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Abstract. Computer simulations were used to elaborate hypotheses about controls on forest structure and composition in a $0.7 \text{ km} \le \text{area}$ of boreal forest in Central Sweden. DBH and species of all adult trees and stand conditions were recorded for 57 - 10 m radius plots. Ordination of these data suggested that nutrient-availability and time-since-disturbance were the main controls of forest composition and structure within the area.

The simulation model couples equations representing the effect of tree canopy structure and biomass on light and soil conditions with equations representing the effect of these conditions on reproduction, growth and mortality in height cohorts of trees on a 0.1 ha patch. Nitrogen-availability levels for each modeled plot were simulated by species-specific growth multipliers. The model was run for 400 simulated yr at six levels of N availability. Age and N status of each study plot were inferred by matching with the most similar model output. Inferred ages agreed with what is known of the disturbance history, and site factors related to soil fertility were correctly correlated with the inferred N status.

The consequences of size-selective disturbance were explored by model experiments. Biomass was removed from large or small size classes at 100 - 200 yr and the simulations were run for an additional 300 yr. Disturbed stands of high N status often became similar to undisturbed stands of different N status. Size-selective disturbances produced stands that were different from any in the undisturbed succession, but these differences disappeared within 50 - 100 yr, implying successional convergence in stand structure and composition. Plots of simulated basal area against time and nitrogen- availability for the four species illustrate the time dependence of species performance along a fertility gradient.

Keywords: Canopy structure; Central Sweden; Cohort; Forest dynamics; Gap model; Nitrogen availability; Ordination.

Nomenclature: Lid (1985).

Introduction

The 'special theory' of forest dynamics as articulated by Shugart (1984) has been widely applied to explain trends and patterns of forest structure and composition. This theory, based ultimately on the ideas of Watt (1947), considers forest dynamics over a time scale of decades to centuries to be a consequence of interactions between local populations of adult trees and the environment of a small (ca. 0.1 ha) patch of ground. Thus, the essential mechanisms included are those of neighborhood competition (Mack & Harper 1977). Differences between forest stands can be accounted for by variations in boundary conditions over time or space (e.g. disturbance history or soil conditions), or as a result of partially stochastic processes such as mortality and establishment. The theory has been embodied in simulation models of the 'gap model' type (Botkin, Janak & Wallis 1972; Shugart 1984) and successfully tested on a wide variety of forest types, including boreal forests (Bonan 1989; Prentice & Leemans 1990).

Because gap models incorporate autogenic processes, such as local competition for light, the response of species to a gradient of site conditions can be timedependent (Smith & Huston 1989). The physiological responses of the species to the gradient can be compared with the predicted species performance at any given time. This allows these models to predict differences between the fundamental niche and the realized niche - a fundamental issue in gradient analysis.

The purpose of this paper is to apply the 'special theory' to account for differences in species composition and size structure between sites in a boreal forest landscape in Central Sweden. Simulation exercises were carried out to elaborate hypotheses about the causes of forest compositional and structural variations observed within the study area today. The model was further used to clarify the possible role of size-selective disturbances on the accuracy of ecological calibration, and to illustrate the behavior of the major species over time in relation to a fertility gradient.

The study area and preliminary data analysis

The study area is located in a mixed-conifer forest in Tiveden National Park in South Central Sweden. The landscape consists of glacial till of variable thickness over granitic bedrock. Spruce (*Picea abies*) dominates in ravines with thick mineral soil and pine (*Pinus sylvestris*) dominates on bogs and rocky upland areas. Birch (mostly *Betula pubescens* with some *B. pendula*) and aspen (*Populus tremula*) are found in smaller amounts throughout. Much of the area has been periodically cut for charcoal from the 16th century through the 19th century (Bäck & Renström 1988).

In 1982, the National Swedish Environmental Protection Board (SNV) established a monitoring site in the western area of the park. Data on species composition and dbh of adult (>2 cm dbh) trees were collected by SNV workers for 57 10-m radius circular plots located on a grid in a 0.7 km² rectangular area. A description of the area and analysis of these data in terms of forest and ground vegetation types may be found in Bäck & Renström (1988). The data were compiled into a matrix of basal area (m^2/ha) of each species in 5 diameter classes (2.0-5.9 cm, 6.0-13.9 cm, 14.0-23.9 cm, 24.0-36.0 cm, >36.0 cm). Environmental data included soil texture class, soil type, mean depth of mineral soil, slope, aspect, and site moisture class. Age distributions of trees could not be collected because tree coring is prohibited in monitoring sites. but the historical information summarized in Bäck & Renström (1988) suggests that most stands are 100-200 yr old.

A two-dimensional ordination of the 57 plots was carried out by local non-metric multidimensional scaling on the basal area/size class data (Prentice 1980; Minchin 1987) using the Bray-Curtis dissimilarity measure:

$$d_{lk} = 1 - \frac{2\min(x_{ijl}, x_{ijk})}{x_{ijl} + x_{ijk}}$$
(1)

where d_{lk} is the dissimilarity between plots *l* and *k*, and x_{ijk} is the basal area of species *i* in size class *j* of plot *k*. Each size class of each species was treated as a separate 'species' so that the resulting ordination reflected both structural and compositional differences between plots. The Bray-Curtis measure has been recommended as a good general measure of ecological distance (Beals 1984; Faith, Minchin & Belbin 1987). A DECORANA ordination (Hill & Gauch 1980) was used for the initial configuration, as recommended by Minchin (1987). Patterns related to the recorded environmental variables

Table 1. Basic equation used in FLAM.

(1) Light intensity at depth z in canopy.

 $I_z = I_o \exp(-kF_z)$

 I_o = light intensity at top of canopy; k = extinction coefficient; F_z = cumulative leaf area index at depth z.

(2) Net photosynthesis/leaf area at depth z:

$$P_z = \frac{kI_z - c}{kI_z + \alpha - c}$$

c = compensation point; α = half-saturation point.

(3) Soil competition multiplier:

$$C = (W_{\max} - W) / W_{\max}$$

W = patch biomass; $W_{max} =$ maximum patch biomass.

(4) N-availability multiplier:

$$N = r \left[d + ae \left(1 - 10^{-c (b + 4AN - 170)} \right) \right]$$

AN = Available Nitrogen (kg ha⁻¹ yr⁻¹); *a*, *b*, *c*, *d*, *e* = parameters set according to N-defiency tolerance; r = factor to rescale N to 1 at AN = 65.

(5) Growth rate:

$$\frac{\Delta(D^2H)}{\text{year}} = \text{NC} \int_B^H S_l \left(\gamma P_z - \delta_z\right) dz$$

 D^2H = diameter squared × height; S_1 = vertical density of leaf area; γ = growth scaling constant for species; δ_z = maintenance cost of leaves at height z; B = bole height of tree (leafless trunk).

(6) Height as a function of diameter:

 $H = 1.3 + (H_{\text{max}} - 1.3) (1 - \exp(-aD))$

 H_{max} = maximum height for species; a = constant for species.

(7) Relative growth efficiency:

$$E_r = \frac{\Delta (D^2 H)}{\gamma L P_o}$$

 $L = \text{leaf area; } P_o = P_z \text{ evaluated at } I_z = I_o.$



Fig. 1. A non-metric multidimensional scaling ordination of the 57 field plots; showing overlays of pine basal area, spruce basal area, mean basal area/tree, and dominant soil type.

were found by graphical overlays, some of which are shown in Fig. 1.

The analysis showed several patterns: (1) the sites on both bogs and rocky upland sites had sparse, pinedominated forests, (2) the environmental factors most clearly related to the species composition were soil type (podsol vs. peat soil) and depth of mineral soil, and (3) the remaining variation was related to the relative distribution of basal area in the different size classes. These patterns suggested that the main controls on the forest may be related to nutrient availability and stand age. A model exercise, including plots of different nitrogen availability, is used here to test the sufficiency (cf. Botkin 1981) of this hypothesis. Rocky upland sites and sites with peaty soils should resemble simulations with low nitrogen availability, and sites with thicker podsolic soils should resemble simulations with higher nitrogen availability.

Some parts of the forest may have been affected by size-selective removal of adult trees. Cutting for charcoal burning sometimes involved only removal of trees in the smaller size classes (S. Bråkenhielm pers. comm.); the large trees were left either as seed sources or because they are unsuitable for charcoal production. Wind storms may preferentially fell the larger trees in a stand. The accuracy of ecological calibration, where site conditions are inferred from the vegetation of the site (Jongman, ter Braak & van Tongeren 1987; ter Braak & Prentice 1988), can be affected by these kinds of disturbance. Simulation exercises were used to assess the possible effects of size-selective disturbances on the apparent age and N-status of stands, and to suggest some possible stability characteristics of forest succession in this system.

Methods

Simulation model

The model FLAM (Forest LAyer Model) simulates the numbers, leaf area and stem volume of trees in a small number of height classes on a small (ca 0.1 ha) patch (Fulton in press a). For these model runs, the patch was represented by ten 4 m-thick height cohorts from 1.3 m to 41.3 m. Equations representing the effect of the trees on the local light and soil environment are linked with equations governing the recruitment, growth



Fig. 2. The randomization test of model performance shown schematically as a Venn diagram. The test compares the data/ model overlap with the overlap between the model and randomly selected points within the test space.

and mortality of adult trees on the patch (Table 1). Recruitment and mortality are stochastic, so the behavior of a stand is simulated by the average of several replicate patches.

Adult trees affect the environment of the model patch and this environment in turn affects the trees by multipliers that decrease the growth rate from the species-specific maximum. The Beer-Lambert law (Monsi, Uchisima & Oikawa 1973) relates the decrease of light through the canopy to the vertical distribution of leaf area. The shading of leaves modifies growth through an asymptotic equation whose parameters are the photosynthetic compensation point and half-saturation point for the species. Prentice & Leemans (1990) discuss how these parameters may be derived or approximated for this modeling context. Symmetric competition (Weiner & Thomas 1986) for soil resources is simulated by specifying a maximum biomass for the patch, and tree growth is decreased as this maximum is approached.

A fixed nitrogen-availability (kg/ha/yr) was specified for each modeled stand. Each species was assigned a nitrogen tolerance class (Helmisaari & Nikolov 1989), and equations relating nitrogen availability to growth response (Aber & Melillo 1982) were applied to derive growth multipliers. These factors were re-scaled to equal 1.0 at a nitrogen-availability of 65 kg/ha/yr. The conjecture underlying this static N-availability is that the between-site variations in this parameter are more important than the within-site variations over time.

Simulated tree growth, as an increment of stem volume, is distributed according to a function relating height to diameter. In keeping with the pipe-model theory of tree function (Waring, Schroeder & Oren 1982), leaf area increases linearly with increasing basal

area, and is decreased by a fixed annual proportion (the sapwood turnover rate) and by pruning of leaf area shaded below the species compensation point. Fulton (in press a) describes the application of these relationships to a height-class structured model. The mortality rate is a step function of relative growth efficiency (Prentice & Leemans 1990); if the efficiency falls below a threshold the probability of mortality is considerably enhanced.

Trees are introduced at a height of 1.3 m by a stochastic function of the environment. The expected number of saplings is proportional to the growth multiplier for the species calculated for conditions under the canopy. The assumption implicit in this relationship, that the density of recruitment of small trees is positively correlated with their growth rate, was borne out by observations in the study area, although the exact relationship is not linear (Fulton in press b). A similar formulation for tree recruitment is used by Pastor & Post (1985).

To allow direct comparison with the field data, the model provided a description of each patch in terms of basal area (m^2/ha) in five diameter classes for each species.

Model exercises

Three model exercises were carried out. Parameters for pine, spruce, birch (*B. pubescens*) and aspen were the same as in Prentice & Leemans (1990), except that the maximum recruitment rates of birch and aspen were lowered to 5/ha/yr and 0.5/ha/yr respectively because these species are heavily affected by browsing by moose and roe deer in Tiveden (Bäck & Renström 1988 and pers. obs.).

The first exercise was run for comparison with the field data. The protocol for data-model comparison closely resembles that described by Harrison & Shugart (1990). First, the model was run to produce a set of stands varying in age and N-availability. The age and N-status of each of the 57 field plots was inferred by matching to the most similar model stands; a form of ecological calibration. The resulting distributions of inferred N-status and age were then compared to the available information about the field plots as a test for the adequacy of the model.

The specifics of the comparison were as follows. 20 replicate patches were run for 400 yr at each of six levels of N-availability, from 10 to 78 kg/ha/yr. Ellenberg (1971) reports N-mineralization rates of 13-79 kg /ha/yr for cold-temperate spruce forests. The diameter-class distributions (averages for the 20 replicate patches) were output every 20 yr. The Bray-Curtis similarity index was used for matching field plots with model stands. Each

size class of each species was treated as a separate 'species' so that both structure and species composition were matched. The inferred age and inferred N-status of each field plot were then compared with the environmental field data using Kendall's τ correlation coefficient. The distribution of inferred ages could only be informally compared to the disturbance history of the area due to the lack of precise stand histories.

Because of the indirect nature of the data-model comparisons, an additional measure of model performance was applied. The test described here was designed to determine whether the model output is more similar to the field data than to a randomly generated set of configurations. Given that the model output and the field data each comprise a subset of all 'possible' stands, one reasonable measure of model performance is to compare the data-model similarity with the similarity between the model and a random sample of 'possible' stands. The outcome of such a test is affected by the range of stands considered to be possible; the larger the range, the more significant the data-model similarity is made to appear (unless the model has no similarity to the field data at all). A fairly rigorous criterion was chosen for this study, using the limits of the field data alone. A test space was delimited between the maximum and minimum basal areas for each species in each diameter class from the field data (Fig. 2). With 4 species and 5 diameter classes, the resulting space has 20 dimensions. 1000 samples were drawn at random from this space and the Bray-Curtis similarity to the nearest model stand was noted for each. The resulting distribution of similarities was compared with the distribution of field datamodel similarities.

The second exercise simulated the effects of partial disturbances on the development of stands. The patch descriptions from the first model exercise were retained from 100 and 200 yr. Each set of patches (at each of the six levels of N-availability) was subjected to two types of disturbance: (1) 'low-grading' where 80% of the total biomass was removed starting with the small size classes, and (2) 'high grading' where 80% of the total biomass was removed starting with the large size classes. The resulting four treatments were run for an additional 300 yr, and the diameter class distributions from every 20 yr were matched with stands from the first model exercise as in the comparison of field and model data above. One additional N-availability, 92 kg/ha/yr, was added to the first model exercise to extend the range of possible calibrations. The Bray-Curtis similarity of the disturbed stands to the nearest stand from the first exercise was noted, as well as the inferred age and N-status of the disturbed stands.

The third exercise was performed to examine the time-dependence of species' responses to the fertility

gradient. 100 replicates at each of 16 levels of N-availability, from 5 to 80 kg/ha/yr, were run for 400 yr. Total basal area (m²/ha) was recorded for each species at 20 yr intervals. To further illustrate how the model distributes the species along the fertility gradient, the correlation between the values of the N-availability growth response multipliers and the basal area of each species was calculated for each recorded year.

Results

Comparison with field data

The inferred ages of the field plots were mostly from 100 to 200 yr. Inferred N-status was generally from 24 to 65 kg/ha/yr (Table 2). The matched model stands from 200-380 yr were of mostly of low Nstatus. As expected, soil texture class and podsol soil type were positively correlated with the inferred Nstatus (Table 3). Peat soil and bare rock were negatively correlated with inferred N-status, but the latter correlation was not significant. No site factors were significantly correlated with inferred age. The mean similarity of the field plots to the nearest model stand was 62.7%, compared to 56.3% for the 1000 randomly generated plots (difference significant at p < 0.001). The similarity of field plots to the nearest model stand was correlated with the inferred age (Kendall's τ = 0.288, p < 0.005).

Table 2. Number of field plots matched to models stands of different age and N-availability.

			Darr					
		10	24	37	51	65	78	totals
	80				2	•	2	2
	100				2	2	2	6
	120				3	23	3	9
	140		1	2	1	2	1	7
	180		1	1			1	3
	200		1	3	1	2		7
Model	220			2	1			3
Year	240		2					2
	260		1					
	280		3					3
	300		I				2	
	320						2	2
	340							
	360		I					
	380	1						
Colu	mn totals:	1	11	11	16	11	7	



Fig. 3. Structural profiles for simulation output at 160 yr, and matching field plots. Profiles show the basal area ha^{-1} for each size class and species. The top, middle and bottom simulated stands have N-availabilities of 24, 51 and 78 kg ha^{-1} yr⁻¹ respectively.

Diagrams of model stands from simulated year 160 matched with field plots (Fig. 3) illustrate predicted stand structures at different N-availabilities and the degree of residual variation not captured by the model. General qualitative and quantitative agreement is high, but the model tends to overestimate the presence of birch and aspen. In a few cases, a field plot with spruce present was matched to a model plot with lower N-status

Table 3. Non-parametric correlations (Kendall's τ) of inferred stand age and N-availability with site variables recorded in the field.

	Model	Year	Model	N-availab.
Soil texture class	-0.134	(n.s.*)	0.439	(<i>p</i> < 0.001)
Podsol soil type	-0.152	(n.s.)	0.406	(p < 0.001)
Peat soil type	0.127	(n.s.)	-0.359	(p < 0.005)
Abundant bare rock	-0.089	(n.s.)	-0.150	(n.s.)
$n.s.^* = implies p > 0.1$	l.			

than the tolerance limit of spruce. This was apparently due to a close match between the size structures of pine in the model and field plot.

Partial disturbance

The response of stands to partial disturbance depended in a complex fashion on the N-status and the specific type of disturbance. The time for disturbed stands to become indistinguishable from undisturbed stands was 100-150 yr for the low grading disturbances and 50-100 yr for the high grading disturbances (Fig. 4). The low grading disturbances produced more atypical structures and compositions, and the stands took longer to re-converge to the 'normal' course of succession. High graded stands of low N-status (< 51 kg/ha/yr) were generally indistinguishable from undisturbed stands.

Disturbed stands with N-status higher than 24 kg/ha/ yr were frequently matched with undisturbed stands of different N-status. The low grading at 100 yr caused the more fertile disturbed stands to have a lower inferred



Fig. 4. Comparisons between stand simulations with size-selective disturbances and the original undisturbed model succession, obtained by calibrating the disturbed stands against the original model succession as for the field data. Each row of boxes gives the results from a single disturbance experiment, and each column of boxes presents a type of comparison.

N-status for as long as 300 yr, due to the selective removal of slower growing spruce in the understory. The same effect occurred in stands of intermediate N-status that were low graded at 200 yr. High grading selectively removed faster growing pines from the more fertile stands, making the inferred N-status higher in some cases. The stands with N-status of 24-10 kg/ha/yr were little affected in this way. In general the more fertile stands have more contrasting overstory and understory species composition, so size-selective thinning has a more noticeable effect on the inferred N-status.

The inferred age of the disturbed stands was usually lowered by disturbance, particularly high grading. For some of the more fertile stands, the inferred age was raised by low grading because this disturbance mimics the thinning of the understory characteristic of a mature stand. After re-convergence to a 'normal' stand structure, the inferred age generally increased in even steps.

Species responses to time and N-availability

Each species had different quantitative and qualitative responses to the time and N-status gradients (Fig. 5). Spruce dominated in the fertile end of the gradient and uniformly increased with time. Pine had attained peak biomass in the middle of the gradient by the end of the simulation; it was decreasing in the fertile end. Aspen was most abundant between 100 and 200 yr in the most fertile part of the N-gradient. Birch was most abundant at about 100 yr and persisted only in the intermediate part of the gradient. The basal area of all four species was well correlated with the nitrogen growth response curves for the first 100 yr (Fig. 6); the correlation of the shade intolerant species began to decrease rapidly after this time. This decreased correlation was most pronounced for the N-deficiency tolerant species pine and birch; the latter species had a negative correlation by 260 yr.



Fig. 5. Total basal area (z-axis) of each species in relation to time and N-status during 400 yr of simulation.



Fig. 6. Correlations between simulated total basal area and N growth response curves for each species at 20 yr intervals.

Discussion

In general, the model appears to account well for the range of forest structures and compositions in the Tiveden study area. Inferred age and N-status are clearly distinguished due to the use of size classes in the data model comparison, and the site factors are correctly correlated with the inferred N-status. The modal inferred N-status falls in the middle of the range reported by Ellenberg (1971). The distribution of inferred ages is essentially as expected, except that there may be too many stands with a high inferred age; the historical data (Bäck & Renström 1988) suggest that most of the area has been cut or otherwise disturbed more recently than 200 yr. However, the results of the size-selective disturbance exercises imply that the exact age and Nstatus calibration of any particular stand should be interpreted with caution.

The model leaves out several potentially important mechanisms that may account for some of the variations observed. The possible effects of size-selective disturbances were indicated by the simulation exercises. Seed rain does not limit regeneration in the model, but the distribution of habitats in the study area is sufficiently coarse-grained that mass effects (Shmida & Ellner 1984) could be important. Pine is comparatively drought-tolerant, as well as nutrient stress-tolerant, so the dominance of pine on some of the rocky upland sites may be partly due to seasonal drought stress. Finally, casual sowing of tree seeds was sometimes carried out after cutting (Bäck & Renström 1988), particularly in the later 19th century, which may have biased the species composition of the resulting stands.

In their simplest forms, both gradient analysis and calibration imply some form of static mapping between vegetation and site factors. The results of these modeling exercises indicate several sources of complications for this traditional mapping. These include the time-dependent nature of the major species responses to the fertility gradient and the effect of size-selective disturbances on inferred age and N-status. In general, the dependence of vegetation on site factors is not functional but relational (Roberts 1987); site factors constrain what is possible but do not determine what vegetation actually occurs.

The changes in the correlations between the direct species responses to the simulated N-status gradient and the simulated basal area were largely as expected. The interesting feature was the fairly sharp transition at 100-120 yr. Light competition influences the overall stand composition only after the trees are fairly large, and the onset of this effect seems to be rapid. I. C. Prentice (pers. comm.) pointed out that this may partly explain some of the contrasting concerns of pure and applied forest ecologists. Foresters are usually concerned with young stands where the growth (and possibly species composition) are more closely determined by the nutrient status. Forest ecologists have been more concerned with species replacements that occur over longer periods of time; light competition is crucial in determining the longer term pattern (Prentice & Leemans 1990).

Prentice & Leemans (1990) predicted that directional succession would be the norm for undisturbed boreal forest, and any other forest in which narrowcrowned trees predominate. Two results presented here indicate that forest stand structures in this system also converge over time: (1) stand simulations affected by size-selective disturbances were different from the 'normal' course of succession at first, but later became indistinguishable from undisturbed stands; (2) the inferred age of the field plots was positively correlated with the similarity to the matched model stands. Adult tree interactions, if allowed to proceed uninterrupted, increasingly constrain the range of possible structures and species compositions in this system.

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