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Edaphic controls on the boreonemoral forest mosaic

Mark R. Fulton and I. Colin Prentice

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Field data and simulations were used to investigate possible edaphic causes of patchy dominance by conifers and temperate deciduous trees in the boreonemoral transition zone of east-central Sweden. Tree species, basal area and soil conditions were recorded for 39 plots of 10 m radius on a ca 30-ha uninhabited island in Lake Mälaren. Canonical correspondence analysis produced a single dominant axis of variation in species composition related to soil depth, pH, organic matter and texture. The forests on the island included most types found in the surrounding region. The simulation model links patch-scale tree demography to the effects of trees on the light environment, with tree growth rates further influenced by climatic variables, soil moisture and nitrogen availability. Soil water holding capacity and nitrogen availability were varied systematically in a model experiment. The simulated response surfaces of tree species accord with reality. When each field site was matched to the most similar model treatment, the observed soil conditions of the field sites were strongly correlated with the modelled nitrogen-availability gradient. These results are consistent with a systems approach to vegetation dynamics that incorporates interactions between species composition and nitrogen-availability with climate, soil conditions and landscape position as external constraints.

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Climate is the main control on vegetation over broad spatial and long temporal scales. As the time periods and areas under consideration become smaller, climate recedes into the constant background and other (edaphic and biotic) processes become important (Prentice 1986). A transition between biomes, such as the boreonemoral zone in which temperate deciduous forest and boreal forest intergrade, provides opportunities to study these finer scale controls. Such transitional areas are also likely to be sensitive to climate change (Prentice et al. 1991); a full understanding of the local factors determining the distribution of the species representing the different biomes will help ecologists to predict the dynamic consequences of climate change.

The boreonemoral zone of southern Sweden consists of a mosaic of pine (*Pinus sylvestris*) and spruce (*Picea abies*) forests, interrupted with patches of deciduous

species of typically more southern distribution (Sjörs 1965a). In the area of Lake Mälaren, west of Stockholm, these species include oak (*Quercus robur*), lime (*Tilia cordata*), elm (*Ulmus glabra*) and ash (*Fraxinus excelsior*). In general, the incidence of the deciduous forests increases to the south as the climate becomes more favourable to their growth. Regional pollen diagrams show the decline of deciduous forests in this area over the last 2000 yr (Fries 1962), the continuation of a process that began after ca 6000 yr ago when both summers and winters in northern Europe were warmer than today (Huntley and Prentice 1993).

Descriptive studies have generated several hypotheses to explain the local distribution of deciduous forests in the boreonemoral zone. Soil conditions clearly play some role: *Ulmus* and *Fraxinus* forests are generally confined to moist calcareous soils, *Pinus* dominates on

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well-drained sandy ridges, and *Quercus* is limited to the shores of lakes and rivers in the northern part of its range (Sjörs 1965a). Disturbance history may be important in some cases; the persistence of some deciduous forests may be related to a long period without fire or other large disturbances that allow new species to invade (Bradshaw and Hannon 1989). Also, Sjörs (1965a) has noted that some *Quercus* forests date from periods of grazing that reduced the cover of competing vegetation.

Simulations provide another approach to the understanding of controls on vegetation. Simulation models embody a systems approach to vegetation, where interactions within the vegetation and the effects of independent variables are considered simultaneously (Roberts 1987). Forest succession models (Botkin et al. 1972, Shugart 1984, Prentice and Leemans 1990) represent the effects of tree growth on the local light environment in the context of external factors such as climate (Solomon 1986, Prentice et al. 1991, 1993), disturbance regime (Doyle 1981), altitude (Shugart and Noble 1981) and nitrogen availability (Fulton 1991a). Pastor and Post (1986) developed one of the more comprehensive of such models, in which the interactions of litter decay, nitrogen availability and the tree canopy are included (Fig. 1). The primary independent variables considered by Pastor and Post are climate and soil texture. These in turn lead to characteristic species compositions and nitrogen availabilities. Drought tolerant species generally have poor litter quality, so dry soil conditions are generally correlated with low nitrogen availability. An interesting consequence of the model is a positive feedback between initial species composition and nitrogen-availability. N-deficiency tolerant species usually also produce "low quality" litter with a high lignin content and slow decomposition rate, so an initial abundance of such species could drive the system toward low N-availability and dominance by the tolerant species. Given slight differences in initial conditions, such a

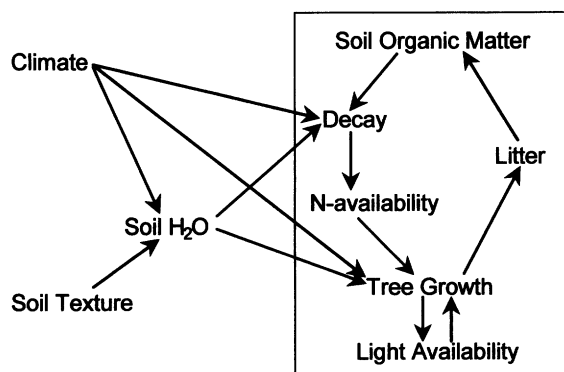


Fig. 1. The main interactions in the model of Pastor and Post (simplified and re-drawn from Pastor and Post 1986).

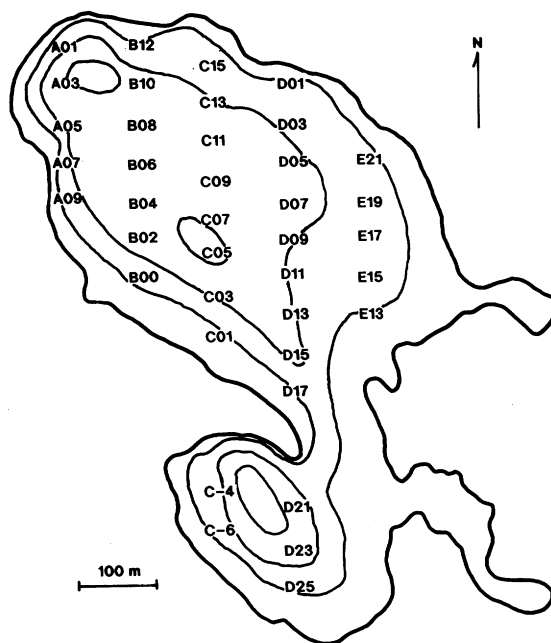


Fig. 2. Map of Prästholmen showing locations of study plots. Elevation contour interval is 5 m.

feedback could lead to patchiness in forest types that is not directly related to underlying soil conditions. There is also evidence that litter decay rates and N cycling vary with site conditions even with identical litter on similar soil types, implying that factors other than soil moisture may play a role (Berg and Staaf 1981).

In this study, field observations and simulation experiments were carried out to investigate the possible role of edaphic factors in determining the local dominance of boreal conifers versus temperate deciduous trees in east-central Sweden. Forest composition and soil conditions were observed on a small (ca 30 ha) uninhabited island, to minimize the effect of variations in local climate or land use. Simulation experiments using a fast forest succession model were run under the current climate around Mälaren with a range of soil moisture holding capacities and N-availabilities. A reasonable range of these variables was expected to reproduce the qualitative features of forests in the region. The field data and model results were compared in an attempt to determine the mechanism behind observed relationships between tree species composition and the local site environment.

Site description

Prästholmen is a small (ca 30 ha) island (Fig. 2) in Lake Mälaren ca 40 km west of Stockholm, Sweden. Now a nature reserve, it is uninhabited and has been relatively

undisturbed since the beginning of the century or before (U. Westerlind pers. comm.). Some large *Quercus* and *Tilia* trees with a distinctive spreading growth form remain from after an earlier open period with some livestock grazing. The island is somewhat isolated; the nearest mainland is >2 km away, and the nearest larger island >1 km away. The dominant trees range from *Pinus*, to *Tilia/Picea*, to *Ulmus/Tilia*.

Methods

Field data

Thirty-nine circular plots (10 m radius) were laid out at 50-m intervals along five parallel transects spaced 100 m apart (Fig. 2). At each plot, the dbh and species were noted for all trees with dbh >2 cm. These data were compiled into a matrix of basal area (m²/ha) for each species on each plot. Soil depth was estimated by driving a 0.8-cm diameter steel rod into the ground (until solid rock was encountered or 25 cm was reached) at 9 regularly spaced points. A soil sample (5 × 5 cm area, 10 cm depth) was taken at a randomly located point within a 4 × 4 m square in the centre of each plot. The soil samples were analysed for pH (water: fresh soil 4:1), percentage organic matter by weight loss on ignition, and percentage fines (particles <0.05 mm) by the Bouyocous method (Ball 1986). Soils with >70% organic matter were not analysed for texture; for these samples the fines were recorded as 0.0 for numerical analysis.

Relationships between the four soil factors and tree species composition were analysed using canonical correspondence analysis (ter Braak 1986, ter Braak and Prentice 1988). Canonical correspondence analysis (CCA) is a form of correspondence analysis in which the species and site scores are constrained to be a linear combination of a set of environmental variables. A correspondence analysis was also run directly on the species data, for comparison with the constrained ordination.

Model description

The model FLAM (Forest LAYER Model) is a computationally efficient forest succession model which simulates the growth and demography of trees in a small number of height classes on a 0.1-ha patch (Fulton 1991b). Recruitment and growth are stochastic, so the stand behaviour is simulated by averaging replicate patches.

The current model differs from previous versions (Fulton 1991a,b) in that it includes routines for simulating the effect of climate and soil moisture holding capacity on the growth of the trees, as described by

Prentice et al. (1993). Within the climatically determined distribution limits of each species (Sykes et al. 1996), the potential stem volume growth rate for that species is reduced from an observed maximum rate by non-dimensional multipliers that are proportional to the modelled responses of net assimilation to daily temperatures and drought. The temperature response function is parabolic and symmetrical between -4°C and 36°C for *Pinus sylvestris* and *Picea abies* and between -4°C and 42°C for the other species (Larcher 1969, 1983). It is summed over the period with daily temperatures greater than 5°C (deciduous trees) or -4°C (evergreen trees). Sapwood maintenance respiration depends exponentially with a Q_{10} of 2.3 on daily temperatures and is summed over the year, converted to equivalent stem volume units, then subtracted from stem volume growth.

The drought response function is parabolic, with a maximum for no drought and curves downwards increasingly steeply (as a function of an annual drought index) towards the species' drought-tolerance limit. The drought index is $1 - \text{AET}/\text{EET}$ where AET is the annual actual evapotranspiration and EET is the annual equilibrium evapotranspiration (a function of daily net radiation and temperature). A physically based soil-moisture accounting model (fully described in Prentice et al. 1993) is used to generate estimates of the seasonal course of EET, soil moisture, runoff (excess soil water that is lost from the ecosystem) and AET. The resulting drought index value depends not only on the input climate variables (monthly temperature, precipitation and sunshine) but also on the (plant available) soil water-holding capacity, i.e. the difference between field capacity and wilting point multiplied by the root zone depth. In central Sweden there is an excess of moisture in winter and a slight deficit in summer which can limit tree growth. Soils with higher water-holding capacity retain more of the winter excess into the dry period, producing a lower drought index.

Adult trees affect the environment of the model patch and this environment in turn affects the growth of the trees. The decrease of light through the successive height layers is related to the simulated vertical distribution of leaf area by the Beer-Lambert Law (Monsi et al. 1973). An equation of Michaelis-Menten type relates the contribution to growth rate from each leaf layer to the profile of available light. Competition for soil resources is simulated by reducing all trees' growth rate by a factor dependent on total patch biomass.

Nitrogen availability was specified as an external condition for these experiments, on the assumption that differences between sites are more important than changes within sites over time. Each species was assigned a nitrogen deficiency tolerance class using silvical data from Prentice and Helmisaari (1991). Equations relating nitrogen availability to growth response (Aber

and Melillo 1982) were used to derive growth multipliers appropriate to each tolerance class (Fulton 1991a). These factors were re-scaled to equal 1.0 at a nitrogen-availability of $65 \text{ kg ha}^{-1} \text{ yr}^{-1}$.

Tree growth is allocated according to a species-specific function relating height to diameter. In keeping with the pipe-model theory of tree function (Waring et al. 1982), leaf area increases at first linearly with increasing basal area, but is progressively decreased by a fixed annual proportion (sapwood turnover rate) and (where required) by pruning of leaf area that would be shaded to below the species compensation point. Fulton (1991b) described how these relationships are applied to a height-class structured model. The mortality rate is a step function of relative growth efficiency (Prentice and 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 soil, light and climatic conditions at the base of the lowest layer.

Model runs

The model was run for a range of soil water-holding capacities and N-availabilities under a constant climate taken from the 30-yr average at Stockholm. Soil water-holding capacity was varied between 90 and 190 mm at 20-mm intervals, with an additional arbitrarily high value (500 mm) to represent soils in parts of the landscape with a shallow water table or concave land surfaces where water would seldom be limiting in this climate. N-availabilities were set at 7 levels between 40 and $160 \text{ kg ha}^{-1} \text{ yr}^{-1}$, representing values between those typical of cool temperate *Picea* forests and temperate riverside deciduous forests (Ellenberg 1971). In all, the model was run under 49 combinations of soil water-holding capacity and N-availability.

Thirteen tree species native to the Stockholm area were included in the simulations. Values for the most important parameters for each species are given in the Appendix.

Each 0.1-ha patch was represented by 8 height classes (5 m thick) between 1.3 m and 41.3 m. The results, expressed in basal area (m^2/ha) for each species, are averages of 50 replicate patches. The model was run for 200 simulated yr for each treatment, and output recorded at 50-yr intervals.

Data-model comparison

The model results constitute a set of hypothetical stand compositions to which the field plots may be matched. Each of the 39 field plots was matched with the most similar of the 196 "model stands" (7 levels of N-availability \times 7 levels of soil moisture holding capacity

\times 4 times since disturbance). Similarity was defined by the percentage similarity coefficient:

$$\text{Similarity} = \frac{200 \sum \min(m_i, f_i)}{\sum(m_i + f_i)}$$

where m_i and f_i are the basal area (m^2/ha) of species i in the model output and field data respectively. The resulting distributions of field plots within the model gradient surface can be compared with what is known about the environmental factors and history of the area.

Similar protocols for comparison between data and model output were developed by Harrison and Shugart (1990) and Fulton (1991a). The underlying principle of this approach is that one does not know a priori precisely what environmental measurements would best correspond to the soil water and nitrogen availability variables *experienced by the plants*, since these would depend on hard-to-measure factors like the vertical profile of root water and nutrient uptake capacity and the ability of the root systems of different species with mycorrhizal associations to take up nitrogen in different forms. Thus, instead of driving simulations with environmental measurements, one attempts to show simply that the prescribed variations of model parameters are sufficient to a generate a variation of vegetation states that is comparable with the variation seen in the field. Comparisons with general measurements such as soil texture and organic content then merely provide a check on the plausibility of the mapping between actual and simulated vegetation states.

Results

Field data

The measured soil properties were intercorrelated. The deeper soils tended to have high pH, low organic matter and a high percentage of fines. All these variables were strongly correlated with the first CCA axis. The first axis eigenvalue was 0.43 as compared with 0.14, 0.02 and 0.01 for the following three axes. This first axis accounted for 20.4% of the variance in the species data and the additional axes contributed little explanatory power. The implied high noise level may be a consequence of the relatively small plot size; in any case it does not detract from the ability of CCA to characterize the main signal. The first CCA axis was also highly correlated with the first axis of the unconstrained correspondence analysis (Kendall's $\tau = 0.546$, $p < 0.0001$), indicating that the main pattern of systematic variation in the tree composition data is captured by the constrained ordination and is therefore related to soil properties.

Ordering the sites and main species according to their first-axis scores (Fig. 3) exposes a diagonal structure in

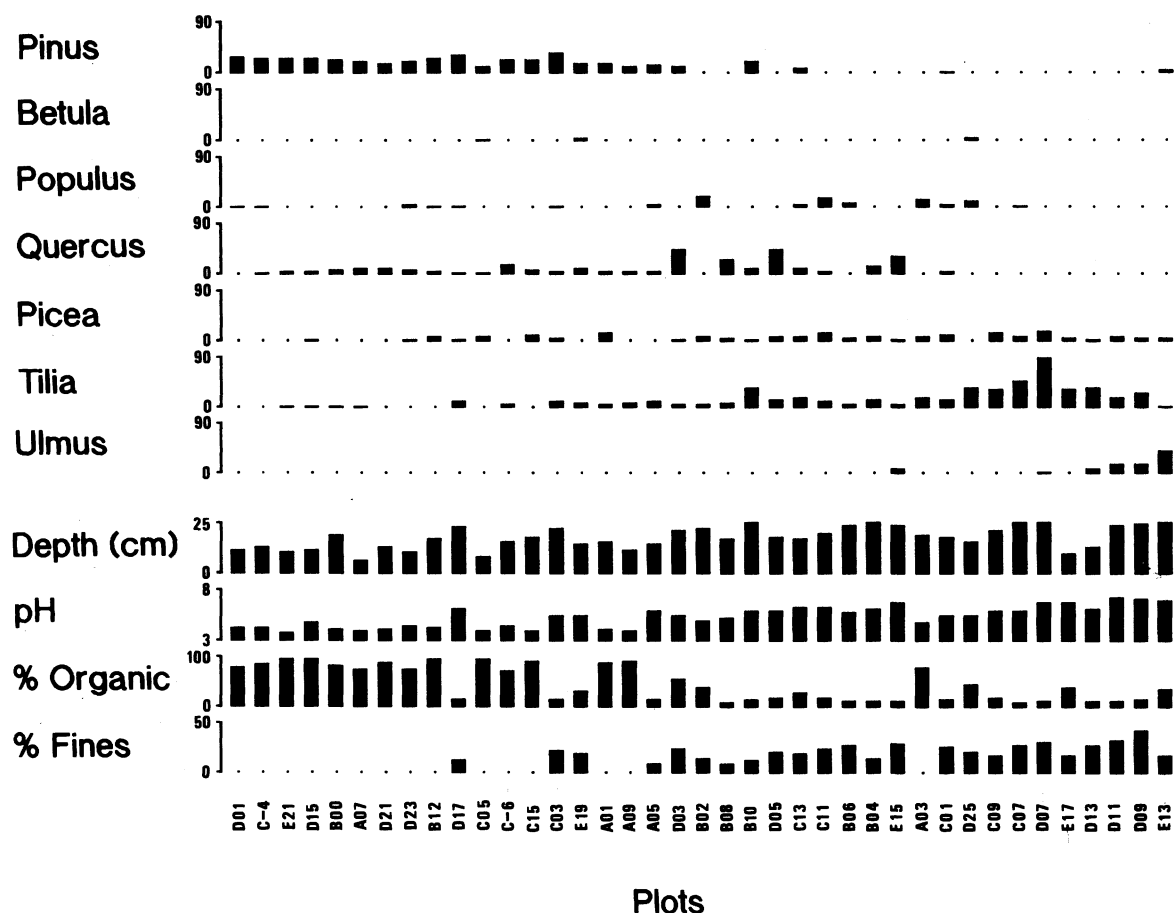


Fig. 3. Basal area (m^2/ha) of most abundant species and soil conditions for the 39 study plots. Plots and species are ordered by scores on the first CCA axis. Organic matter is plotted as percent weight loss on ignition.

the species data and provides a useful summary. *Pinus* is most abundant on sites with thin soil; *Tilia* and *Picea* dominate at the other end of the gradient. *Ulmus* is found in only a few sites at relatively low elevation with fine textured soils and in a concave landscape position. With the exception of a single small sapling, no *Fraxinus* was found growing on the island. *Fraxinus* is almost always found growing with *Ulmus* elsewhere in this region (M. Diekmann pers. comm.); possibly the isolation of the island has limited the dispersal of this species. The large basal area figures for *Quercus* are generally from old open-grown trees. The main difference between the range of forests on the island and the mainland is that the island has very few sites dominated by *Picea*. In this region, *Picea* usually completely dominates any site with reasonably good soil and water availability (Sjörs 1965a). In summary, the data show a clear edaphic gradient from shallow, acidic, high organic matter soils to deeper, more basic mineral soils. Soil parent materials range from poorly decayed organic matter and moraine deposits, to fine-textured lake sediments. The edaphic gradient is strongly correlated

with tree species composition. When a large change of species composition was observed across a plot, the change was usually associated with a sharp change in soil depth.

Model runs

The qualitative responses (relative dominance) of the major tree species to soil water-holding capacity and N-availability are summarized in Figs 3 and 4. *Juniperus* and *Pinus* dominate at the dry, low-N portion of the gradient, with *Juniperus* rapidly being outcompeted by *Pinus*. *Betula* (*B. pubescens*) is found throughout early in the succession, but persists only in the dry or low-N sites. *Quercus* achieves dominance only in the low-N, wet part of the gradient. *Picea* is found in all the sites, and dominates in all but the driest and lowest-N sites. *Tilia* grows best on dry sites with high-N, and in some sites actually increases its dominance over time at the expense of *Picea*. This is consistent with the occurrence of *Tilia* forests on rocky bluffs and scree (Sjörs 1965a)

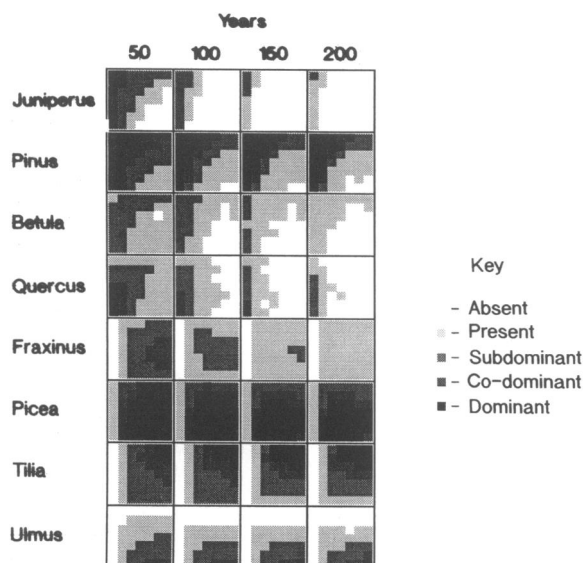


Fig. 4. Relative dominance of the major tree species over 200 yr of succession in the model stands. Within each box, the moisture gradient runs from top (dry) to bottom (wet) and the N-availability gradient from left (low N) to right (high N). The dominant species has highest basal area for that year and environment, co-dominants have basal area >0.5 of dominant, subdominants have basal area >0.1 of dominant.

but apparently not with the fact that many *Tilia* forests occur very close to lakeshores (but see discussion below). As expected, *Ulmus* dominates only in the very wettest and richest sites. *Fraxinus* is abundant only in the early part of succession on richer sites of intermediate soil water-holding capacity.

Data-model comparison

Most of the field sites were placed at the dry end of the model gradient, and covered the whole range of N-availability (Table 1). The mean similarity between field plot and matched model stand was 69%. The sites with high basal areas for *Quercus* were placed in the low-N,

Table 1. Number of field plots matched to each model 'treatment'

	N-availability (kg ha ⁻¹ yr ⁻¹)						
	40	60	80	100	120	140	160
Soil water-holding capacity (mm)	90	3	1	2	2		5
	110			1		2	6
	130	1	1		1	1	1
	150	1	2				
	170						
	190						
	500	(7)*				1	1

* Plots with large old oaks have been located here but do not occur on particularly moist soils – see text.

Table 2. Rank correlations (Kendall's tau) between environment of matched model stands and the soil conditions and 1st axis CANOCO scores of the field plots. N is model N-availability, FCP is model soil moisture holding capacity. P-values are given in parentheses under the correlations.

	Depth	pH	% Organic	% Fines	CANOCO
FCP	-0.077 (0.53)	-0.272 (0.03)	0.201 (0.10)	-0.165 (0.20)	-0.272 (0.03)
N	0.464 (0.0001)	0.557 (0.0001)	-0.473 (0.0001)	0.510 (0.0001)	0.560 (0.0001)

high moisture end of the gradient. This placement is not consistent with the nature of these sites in the field; these are generally well-drained upland sites with intermediate soil depth and percentage fines. However, as noted previously, these oaks were probably established well before the current succession was initiated and grew for many years in an open environment.

The *Ulmus*-dominated sites are placed in the wettest and richest end of the gradient, as expected. These sites have a deep, fine-textured soil, and they are located at relatively low elevations in a concave part of the landscape.

Twenty-three of the sites were matched with 200-yr simulation results, the remainder were more or less evenly distributed among the younger ages. This is consistent with the fact that the island has been relatively undisturbed for more than a century.

The similarity between the field plots and matched model stands increases with the age of the model stand (Kendall's tau = 0.42, $p < 0.001$). This result implies a form of successional convergence; a similar result was obtained in a boreal forest landscape (Fulton 1991a).

Model N-availability was significantly correlated with all the soil factors as well as the first CCA axis (Table 2). Only pH and the CCA axis were correlated with model soil water-holding capacity, and neither of these correlations were significant beyond the 5% level. Deletion of the seven sites with high *Quercus* basal area did not improve the correlations with soil water-holding capacity.

Discussion

Prästhölmén has examples of most of the forest types found in the lake Mälaren area, except *Picea* forests. It may be that the soils, as indicated by the analogues found for the field plots in the model output, are generally too dry to support *Picea* as a dominant. Most sites are well drained with fairly light-textured soil. Historical factors may also play a part; *Picea* may have been introduced relatively late in the history of the island, after the other species had better established seed sources, and seed source limitation is the likely explanation of the almost complete lack of *Fraxinus* in

the *Ulmus*-dominated forests. Simulation studies (Ribbens et al. 1994) indicate the likely importance of spatial limitations of recruitment in the long term dynamics of forests.

The somewhat low explanatory power of the first CCA axis (20.4% of the variance in the species data explained) is probably due to the small plot size used in the field study. In general, correlations between vegetation and environment are expected to be lower for small plots than large plots due to the dominance of chance effects in small plots (Reed et al. 1993). Spatial limitations of seedling recruitment can also lead to patchiness of species distribution that is not accounted for by environmental variations alone (Pacala 1987, Ribbens et al. 1994).

With some caveats, the distribution of forest types across the simulated gradients corresponds with the range of forest types and environments found in the lake Mälaren area. Historical effects not included in the simulations, such as the persistence of *Quercus* in formerly grazed parklands, may have altered the observed patterns to some extent.

The results are consistent with the Pastor and Post (1986) theory of N-cycling coupled with species litter production, with external forcing by climate and soil moisture. Because the model used here prescribes N-availability as an external variable, this study leaves open the question of whether present differences in N-availability among sites were enhanced by the positive feedback mechanism implied by that theory. Soil parent materials varied widely within the study area, and these variations may be sufficient to account for most of the differences in species composition observed. However, the fact that the full range of soil water-holding capacity and N-availability seems to be needed to produce the whole range of forests in the area suggests that some other soil factors than soil moisture and litter quality might also affect the rate of N-cycling. Pastor et al. (1984) found high correlations between humus phosphate content and the rates of mineralization and nitrification in a study of an island in the midwestern U.S. with a range of evergreen and deciduous forest types. N-cycling is typically more rapid on base-rich soils (Gosz 1981); base-rich lacustrine and marine-deposited clays in the lake Mälaren area are often found in valleys or along lakeshores (Sjörs 1965b). We speculate that this could be part of the explanation for the occurrence of *Tilia* forests near lakeshores; the critical factor might be a base-rich soil favourable to rapid N-cycling, rather than the moisture regime itself.

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References

- Aber, J. D. and Melillo, J. M. 1982. FORTNITE: A computer model of organic matter and nitrogen dynamics in forest ecosystems. – Univ. of Wisconsin Research Bulletin R3130.
- Ball, D. F. 1986. Site and soils. – In: Moore, P. D. and Chapman, S. B. (eds), *Methods in plant ecology*, 2nd ed. Blackwell, Oxford, pp. 215–284.
- Berg, B. and Staaf, H. 1981. Leaching, accumulation and release of nitrogen in decomposing forest litter. – In: Clark, F. E. and Rosswall, T. (eds), *Terrestrial nitrogen cycles*. Ecol. Bull. (Stockholm) 33: 163–178.
- Botkin, D. B., Janak, J. F. and Wallis, J. R. 1972. Some ecological consequences of a computer model of forest growth. – *J. Ecol.* 60: 849–872.
- Bradshaw, R. and Hannon, G. 1989. The influence of disturbance on long-term successional processes in Swedish boreal forest. – In: Sjögren, E. (ed.), *Forests of the world: diversity and dynamics*. Studies in Plant Ecology 18. Uppsala.
- Doyle, T. W. 1981. The role of disturbance in the gap dynamics of a montane rain forest: an application of a tropical forest succession model. – In: West, D. C., Shugart, H. H. and Botkin, D. B. (eds), *Forest succession: concepts and application*. Springer-Verlag, New York, pp. 56–73.
- Ellenberg, H. 1971. Nitrogen content, mineralization and cycling. – In: *Productivity of forest ecosystems*, Proceedings Brussels Symposium 1969, UNESCO.
- 1978. *Vegetation Mitteleuropas mit den Alpen in ökologischer Sicht*. – Ulmer, Stuttgart.
- Fries, M. 1962. Studies of the sediments and the vegetational history in the Ösbysjö basin, north of Stockholm. – *Oikos* 13: 76–96.
- Fulton, M. R. 1991a. Simulation modelling of the effects of site conditions and disturbance history on a boreal forest landscape. – *J. Veg. Sci.* 2: 603–612.
- 1991b. A computationally efficient forest succession model: design and initial tests. – *For. Ecol. Manage.* 42: 23–34.
- Gosz, J. R. 1981. Nitrogen cycling in coniferous ecosystems. – In: Clark, F. E. and Rosswall, T. (eds), *Terrestrial nitrogen cycles*. Ecol. Bull. (Stockholm) 33: 405–426.
- Harrison, E. A. and Shugart, H. H. 1990. Evaluating performance of an Appalachian oak forest dynamics model. – *Vegetatio* 86: 1–13.
- Huntley, B. and Prentice, I. C. 1993. Holocene climates and vegetation of Europe. – In: Kutzbach, J. E., Street-Perrott, S. A., Ruddiman, W. F., Webb III, T. and Wright Jr., H. E. (eds), *Global climate for 9000 and 6000 yr B. P. in the perspective of glacial-interglacial climatic change*. Univ. of Minnesota Press, Minneapolis.
- Larcher, W. 1969. The effect of environmental and physiological variables on the carbon dioxide gas exchange of trees. – *Photosynthetica* 3: 167–198.
- 1983. *Physiological plant ecology*, 2nd ed. – Springer, Berlin.
- Monsi, M., Uchijima, Z. and Oikawa, T. 1973. Structure of foliage canopies and photosynthesis. – *Annu. Rev. Ecol. Syst.* 4: 301–327.
- Pacala, S. W. 1987. Neighborhood models of plant population dynamics. 3. Models with spatial heterogeneity in the physical environment. – *Theor. Popul. Biol.* 31: 359–392.
- Pastor, J. and Post, W. M. 1986. Influence of climate, soil moisture and succession on forest carbon and nitrogen cycles. – *Biogeochemistry* 2: 3–27.
- Aber, J. D. and McLaugherty, C. A. 1984. Aboveground production and N and P cycling along a nitrogen mineralization gradient on Blackhawk Island, Wisconsin. – *Ecology* 65: 256–268.
- Prentice, I. C. 1986. Vegetation response to past climatic variation. – *Vegetatio* 67: 131–141.
- and Leemans, R. 1990. Pattern and process and the dynamics of forest structure: A simulation approach. – *J. Ecol.* 78: 340–355.

- and Helmisaari, H. 1991. Silvics of north European trees: Compilation, comparisons and implications for forest succession modelling. – *For. Ecol. Manage.* 42: 79–93.
- , Sykes, M. T. and Cramer, W. 1991. The possible dynamic response of northern forests to global warming. – *Global Ecol. Biogeogr. Lett.* 1: 129–135.
- , Sykes, M. T. and Cramer, W. 1993. A simulation model for the transient effects of climate change on forest landscapes. – *Ecolog. Model.* 65: 51–70.
- Reed, R. A., Peet, R. K., Palmer, M. W. and White, P. S. 1993. Scale dependence of vegetation-environment correlations: A case study of a North Carolina piedmont woodland. – *J. Veg. Sci.* 4: 329–340.
- Ribbens, E., Silander, J. A. and Pacala, S. W. 1994. Seedling recruitment in forests: calibrating models to predict patterns of tree seedling dispersion. – *Ecology* 75: 1794–1806.
- Roberts, D. W. 1987. A dynamical systems perspective on vegetation theory. – *Vegetatio* 69: 27–33.
- Sjörs, H. 1965a. For. regions. – *Acta Phytogeogr. Suec.* 50: 48–63.
- 1965b. Features of land and climate. – *Acta Phytogeogr. Suec.* 50: 1–12. Uppsala.
- Shugart, H. H. 1984. A theory of forest dynamics. – Springer-Verlag, New York.
- and Noble, I. R. 1981. A computer model of succession and fire response of the high-altitude *Eucalyptus* forest of the Brindabella Range, Australian Capital Territory. – *Aust. J. Ecol.* 6: 149–164.
- Solomon, A. M. 1986. Transient response of forests to CO₂-induced climate change: simulation modelling experiments in eastern North America – *Oecologia* 68: 567–579.
- Sykes, M. T., Prentice, I. C. and Cramer, W. 1996. A bioclimatic model for the potential distributions of north European tree species under present and future climates. – *J. Biogeogr.* 23: 203–233.
- ter Braak, C. J. F. 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. – *Ecology* 67: 1167–1179.
- and Prentice, I. C. 1988. A theory of gradient analysis. – *Adv. Ecol. Res.* 18: 271–317.
- Waring, R. H., Schroeder, P. E. and Oren, R. 1982. Application of the pipe model theory to predict canopy leaf area. – *Can. J. For. Res.* 12: 556–560.

Appendix

The most important species parameters.*

	HGRO	HMAX	STOL	NTOL	DROUGHT
<i>Picea abies</i>	0.90	51.0	1	2	0.35
<i>Pinus sylvestris</i>	0.90	48.0	3	1	0.50
<i>Juniperus communis</i>	0.14	15.0	3	1	0.50
<i>Acer platanoides</i>	0.63	27.0	2	3	0.35
<i>Betula pendula</i>	1.00	25.0	3	1	0.50
<i>Betula pubescens</i>	0.85	20.0	3	2	0.25
<i>Corylus avellana</i>	0.50	12.0	3	2	0.35
<i>Fraxinus excelsior</i>	0.75	30.0	2	3	0.35
<i>Populus tremula</i>	1.00	27.0	3	1	0.35
<i>Quercus robur</i>	0.85	45.0	3	1	0.35
<i>Sorbus aucuparia</i>	0.25	17.0	2	1	0.50
<i>Tilia cordata</i>	0.54	22.0	1	3	0.50
<i>Ulmus glabra</i>	0.85	35.0	1	3	0.25

* Other parameters follow Prentice et al. (1991).

HGRO: Maximum recorded height growth rate in m yr⁻¹. From observations compiled by Prentice and Helmisaari (1991) except for *Tilia* (where a more recent figure was used) and *Ulmus* (which can grow at a rate similar to *Quercus* and was set equal to *Quercus* in the absence of recent figures). Growth scaling constants are derived from HGRO by a method similar to that used by Prentice and Leemans (1990) to estimate growth scaling constants from maximum diameter increments.

HMAX: Maximum recorded height in m (Prentice and Helmisaari 1991).

STOL: Shade tolerance class. 1 = tolerant, 2 = intermediate, 3 = intolerant. as Prentice and Helmisaari (1991), but they distinguished only two classes. We transfer *Acer*, *Fraxinus* and *Sorbus* from the intolerant class to an intermediate class, based on field observations. Note that the assignments differ from the indicator values given by Ellenberg (1978) because the latter apply to species presence, including saplings and a number of species are more shade tolerant as saplings. Shade-tolerant species were assigned half-saturation points of 100 µmol m⁻² s⁻¹ and compensation points of 10 µmol m⁻² s⁻¹; intolerants, 330 and 60 µmol m⁻² s⁻²; intermediates were assigned intermediate values.

NTOL: N-deficiency tolerance class (Prentice and Helmisaari 1991). 1 = tolerant, 2 = intermediate, 3 = intolerant. Typical response curves for N-availability were assigned to each class (see text).

DROUGHT: Maximum tolerated value of drought index, based on an assessment of published descriptions of species' relative drought tolerances in Scandinavia and central Europe. Numerical values were assigned to each drought-tolerance class by comparing drought index values simulated for soils of different water-holding capacity with the observed edaphic distributions of representative species in each class. Note that these values differ from the estimates by Prentice and Helmisaari (1991) based on an interpretation of range limits according to the method of Pastor and Post (1986). The method based on silvical data is considered more reliable.