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Source: *Global Ecology and Biogeography Letters*, Vol. 1, No. 5 (Sep., 1991), pp. 129-135

Published by: Blackwell Publishing

Stable URL: <http://www.jstor.org/stable/2997426>

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RESEARCH LETTER

The possible dynamic response of northern forests to global warming

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Abstract. Increasing greenhouse-gas concentrations in the atmosphere are expected to produce maximum warming in high latitudes, displacing the potential boreal forest zone of the northern hemisphere far to the north. We analyse the implications of this shift for forest composition and biomass dynamics across the present-day boreonemoral zone in Scandinavia, using a forest succession model that includes a generalized disturbance regime and realistic climatic effects on species' regeneration and growth. Temperature increases in the range of 2–4 K in summer and 5–6 K in winter, typical of simulated CO₂ doubling effects, force the boreonemoral zone >1000 km northward from central Sweden where dominance passes from

Picea (spruce) to *Fagus* (beech), *Quercus* (oak) and *Pinus* (pine) over 150–200 years. Simulated increases of 175–250 mm in annual precipitation are required to counteract drought, which would otherwise reduce forest biomass and increase the representation of the more drought-tolerant species. The simulated forest dynamics are the net result of individualistic responses of species to different aspects of climate, modulated by successional processes that are on the same time scale as human impacts on climate.

Key words. Climate change, biomass, forest dynamics, individualism, landscape modelling, boreonemoral zone.

INTRODUCTION

The impacts of increasing greenhouse-gas concentrations on global and regional climates have been simulated with general circulation models (GCMs) (Schlesinger & Mitchell, 1985; Harrison, 1990; IPCC, 1990). GCMs differ in many details, but they agree (a) that the largest temperature increases will be in high latitudes, and (b) that maximum high-latitude warming will be in the winter months due to snow and sea-ice feedbacks (Manabe & Wetherald, 1975; Manabe & Stouffer, 1980; Gates, Cook & Schlesinger, 1981; Washington & Meehl, 1983; Hansen *et al.*, 1984, 1988; Wilson & Mitchell, 1987; Schlesinger & Zhao, 1989; Washington & Meehl, 1989). Climate changes simulated in these experiments are large enough to have affected vegetation at all spatial scales from global patterns down to individual stands.

The distribution of vegetation types in the high latitudes is strongly determined by temperature (Walter, 1979; Tuhkanen, 1984). High-latitude vegetation will thus probably show the largest response to global

warming (Shugart *et al.*, 1986). This is supported by applications of static vegetation models (Prentice & Solomon, 1991) which predict the *potential* distribution of vegetation formations. Emanuel, Shugart and Stevenson (1985) applied the Holdridge (1947) model to GCM-based estimates of regional changes in annual mean temperature due to doubling CO₂. The potential boreal forest was shifted northward, displacing the tundra; temperate forests encroached from the south. Broadly similar results have been obtained by Leemans (1990) using the Holdridge model with a variety of GCM scenarios, and by Woodward (1989) and R. Leemans (pers. comm., 1990) using ecophysiological based models (Woodward & Williams, 1987; Prentice *et al.*, 1991b).

The time scale of CO₂ increase is comparable to potentially rate-limiting ecological processes such as establishment and growth of new species and genotypes (Prentice, 1986; Prentice & Solomon, 1991). The dynamics of vegetation change in response to such rapid climate changes are expected to be more complex than a regular transition between different

potential vegetation types. The transient dynamics of vegetation changes can be simulated using ecological models that include these ecological processes, climate providing the boundary conditions (Solomon, 1986; Pastor & Post, 1988; Bonan, Shugart & Urban, 1990). Such models require species-specific data on characteristics affecting successional behaviour, as well as on climatic controls. The models are computationally demanding, particularly when applied to landscape-scale problems requiring large numbers of replicates, but such applications are feasible on medium- to large-sized computers.

The models are not global in scope, but there are several that apply to substantial regions, especially in the high latitudes where there are relatively few tree species. One such model is FORSKA 2 described by Prentice, Sykes & Cramer (1991a). We use this model to simulate the transient dynamics of forest vegetation under global warming, on a transect across the boreonemoral zone (Walter, 1979) that separates the boreal coniferous and temperate deciduous forests of northern Europe.

CLIMATIC SETTING

The boreonemoral zone shows a gradual latitudinal shift of dominance from boreal evergreen conifers such as *Picea* (spruce) to temperate deciduous broad-leaved trees including species of *Fagus* (beech) and *Quercus* (oak). The poleward limits of these genera are related to growing-season warmth, whereas the equatorward limits of the boreal conifers are determined by drought, winters that are too mild to satisfy chilling requirements for regeneration or budburst (Cannell & Smith, 1986), increasingly effective competition from temperate species (Neilson *et al.*, 1989; Woodward, 1987; Woodward & Williams, 1987), or a combination of these factors.

The temperate species disappear towards the continental interior where boreal forests grade directly into steppe. The boreal conifers disappear towards the oceanic margins where birch (*Betula*) species form the treeline. The boreonemoral zone thus occupies a region of intermediate oceanicity with mean coldest-month temperatures *c.* -20 to 0°C , accumulated annual temperatures above 5°C *c.* 1200–1700 day $^{\circ}\text{C}$, and sufficient soil moisture to support closed forest. In northern Europe these conditions are met in a narrow zone in southern Norway that broadens eastward, extending from close to the southern and western coasts of Sweden northward to

the *limes norrlandicus* in central Sweden (Sjörs, 1967), and continuing eastward through the Baltic region and Russia to the Urals.

THE MODEL

Forest and landscape dynamics

FORSKA 2 uses a computer-intensive approach to bridge the gap between static models that predict the potential natural vegetation of areas (*c.* 10^9 m²) and forest succession models that simulate transient dynamics of patches (*c.* 10^3 m²) or stands. The landscape is treated as an array of patches, each simulated as in the FORSKA 1 forest succession model (Prentice & Leemans, 1990). The patches are subject to a Weibull disturbance regime, a stochastic process whereby the hazard increases as a power function of time since disturbance (Johnson & Van Wagner, 1985; Clark, 1989). The result is a simulation of a *generalized landscape*. Some disturbance regime is assumed to be present, whether natural (e.g. wildfire) or artificial (primarily logging), and susceptibility to disturbance is assumed to increase with time in either case.

Twenty species were included: all the important north European species that occur in Scandinavia today, or that could occur in the changed climate. Data on the silvics (including shade tolerance, dimensional relationships and optimal growth rates) of these species were taken from Prentice & Helmisaari (1991).

Climatic controls on tree regeneration and growth

Previous applications of forest succession models to climate impact assessment have used unrealistic formulations of the responses of tree regeneration and growth to climate. Most seriously, earlier models have used a parabolic response of growth to annual accumulated temperature (Botkin, Janak & Wallis, 1972). According to this function, an increase in the length of the growing season for a species near its equatorward range limit (such as *Picea abies* (L.) Karst., Norway spruce, in southern Scandinavia) will produce a reduction in growth. The climate response functions in FORSKA 2 represent a first attempt to incorporate the relevant mechanisms, as far as they are known.

Tree growth is altered by species-specific functions describing the effects of the seasonal temperature and drought regimes on annual net assimilation. The response of net assimilation to daily temperature is par-

abolic, with temperature compensation points of -4 and 36°C for the conifers *Pinus sylvestris* L. (Scots pine) and *Picea abies* and -4 and 42°C for the other species (Larcher, 1969, 1983). Drought is indexed by the Priestley-Taylor coefficient (Hare, 1980: ratio of total actual to equilibrium evapotranspiration) computed for the assimilation period by the method of Cramer & Prentice (1988). The drought response is a parabola, ranging from unity when soil moisture is always adequate, to zero at the species' limit. Species' limits are estimated from their occurrence on soils of different water capacity.

Growth and regeneration are suppressed if these temperature and drought functions are zero or negative, or if coldest-month temperature or daily accumulated temperature over 5°C are below limits determined by comparing species' present distributions with bioclimatic maps (Prentice & Helmisaari, 1991). Regeneration is suppressed if warmest-month temperature is below 16.0°C for *Tilia cordata* Miller (lime; Piggott & Huntley, 1981), 16.5°C for *Fagus sylvatica* L. (beech) and 17.0°C for *Carpinus betulus* L. (hornbeam), or if coldest-month temperature is above -1.5°C for *Picea abies* (Skre, 1972; Dahl, 1990) or -2.5°C for *Alnus incana* (L.) Moench (grey alder). No cold-winter requirement is imposed on *Pinus sylvestris*, which is not native in climates with coldest-month temperatures above $c. -0.5^{\circ}\text{C}$ (Prentice & Helmisaari, 1991) but regenerates freely west of this limit, suggesting that the limit is proximately due to competition rather than directly caused by climate (Bennett, 1984).

Finally, temperature affects growth through sapwood respiration, which increases exponentially with daily temperature ($Q_{10} = 2.3$) (Landsberg, 1986).

MODEL VALIDATION AND EXPERIMENTAL DESIGN

Baseline climate data (mean monthly temperature, precipitation and proportion of possible sunshine hours) were extracted for Pajala in northern Sweden ($67^{\circ}20'\text{N}$, $23^{\circ}42'\text{E}$), Stockholm in central Sweden ($59^{\circ}35'\text{N}$, $18^{\circ}07'\text{E}$) and Malmö in southern Sweden ($55^{\circ}43'\text{N}$, $13^{\circ}05'\text{E}$). These sites are located today in the boreal, boreonemoral and temperate deciduous (nemoral) forest zones. Each site was represented by three soil types with 90 mm, 150 mm and 180 mm water capacity. 200 patches were simulated on each soil type. The disturbance hazard was allowed to increase linearly with time, with an average (r.m.s.) return time of 100 years. Each set of patches was run

under present climate for 400 years. This was sufficient to achieve approximate equilibrium in species composition and biomass.

The results obtained at the end of 400 years of simulation can be compared with published averages for forest land within the relevant forestry districts (Table 1). These districts include an unquantified range of climate and soil variation, and a variety of management regimes. Nevertheless, the generalized landscape simulations correctly predicted which species are dominant in each district, and their approximate biomass.

Monthly temperature and/or precipitation were then increased linearly over 100 years, a middle-range estimate of the time to CO_2 doubling (Bolin, 1986; IPCC, 1990). The magnitudes of the increases were derived from the GCM simulation of CO_2 doubling by Hansen *et al.* (1984) (Table 2). These increases are typical of the values obtained for Scandinavia in GCM experiments of this type. The model was allowed to equilibrate in the new climate for a further 300 years.

RESULTS

With increases in both temperature and precipitation (Fig. 1), the northern (boreal forest) site changes to a boreonemoral forest composition, with small amounts of *Quercus robur* (Mattuschka) Liebl. (pedunculate oak) and other temperate species. The central (boreonemoral forest) site shows a larger change: from dominance by *Picea abies* to a forest with *Fagus sylvatica*, *Quercus robur*, *Q. petraea* (sessile oak) and *Pinus sylvestris*, lacking *Picea abies*, and with somewhat increased biomass. The southern (temperate deciduous forest) site shows no such large change, although the abundance of *Fagus* increases.

Increasing precipitation alone has no effect at the northern site but increases biomass further south, favouring *Picea* and *Fagus*, implying that drought limits the growth of these species in the boreonemoral zone even today. Increasing temperature alone causes drought at the central and southern sites, reducing or reversing the simulated increase in biomass, and favouring *Pinus*. Thus, the GCM-simulated increases in precipitation are needed to offset the increase in evapotranspiration caused by the warming.

The transitions described for the combined temperature and precipitation change take place over $c. 150$ – 200 years and a substantial fraction of the changes takes place after the climate change is complete. There is a significant lag due to ecological processes, such that the effects of such a change would not be

Table 1. Forest biomass (Mg ha⁻¹) from data* and simulations.†

Data

	North	Central	South‡
<i>Pinus</i>	19.0	25.3	2.9
<i>Picea</i>	6.6	21.6	18.1
<i>Quercus</i>		2.4	10.6
<i>Fagus</i>			34.9

Simulations

	North			Central			South			
	Soil (mm):	90	150	180	90	150	180	90	150	180
<i>Pinus</i>		5.3	4.2	3.8	16.3	9.9	5.7	19.5	17.1	19.6
<i>Picea</i>		17.5	17.7	16.2	3.9	26.2	35.8			
<i>Quercus</i>					0.2	1.1	1.6	11.7	10.1	8.6
<i>Fagus</i>								1.3	10.8	20.1

* Average stem biomass on forest land for Norrbottens kustland (North), Stockholm (Central) and Malmö (South) forestry districts, 1989/90 (Skogsdata, 1990).

† Simulated average stem biomass based on climate data for Pajala (North), Stockholm (Central) and Malmö (South).

‡ Most of the extant forests in the Malmö district are within the native range of *Picea abies*, whilst the potential area of temperate deciduous forest is mostly farmed; hence the discrepancy between data and simulations for *Picea* in the south.

Table 2. Climate changes in Sweden produced by a CO₂ doubling, according to the GISS GCM. Values are differences between experiment and control (normal CO₂).

	Temperature change (K)				Precipitation change (mm day ⁻¹)			
	DJF	MAM	JJA	SON	DJF	MAM	JJA	SON
North	5.5	4.7	3.3	4.8	0.4	0.8	0.8	0.7
Central	5.1	4.0	2.2	3.8	0.4	0.6	0.7	0.5
South	5.4	3.5	2.7	3.9	0.4	0.7	0.4	0.4

registered immediately but would continue even after climate had stabilized.

DISCUSSION

The simulations illustrate how changes in forest composition can have multiple climatic causes. The expansion of *Quercus* is a response to warmer summers and a longer growing season, the expansion of *Fagus* is permitted by warmer summers and winters, and the contraction of *Picea* is due to warmer winters. *Picea* disappears from central Sweden not because of poor growth, but because of regeneration failure in a more oceanic climate. Existing stands remain productive, but are not replaced after felling.

There is thus no simple spatial shift of vegetation boundaries; rather, a complex response due to the different climatic tolerances of different species and their interactions. This is consistent with evidence from the Holocene of northern Europe and many other regions, where different tree species showed individualistic patterns of range expansion and contraction in response to differential changes of summer and winter temperatures and drought (Huntley & Webb, 1988; Prentice, 1991). The climate change assumed in Fig. 1 is comparable in magnitude to the difference between the mid-Holocene and present (Huntley & Prentice, 1988), but the change takes place over 100 years. Ecological processes cause a lag in the response of the forest that is substantial compared with the time scale

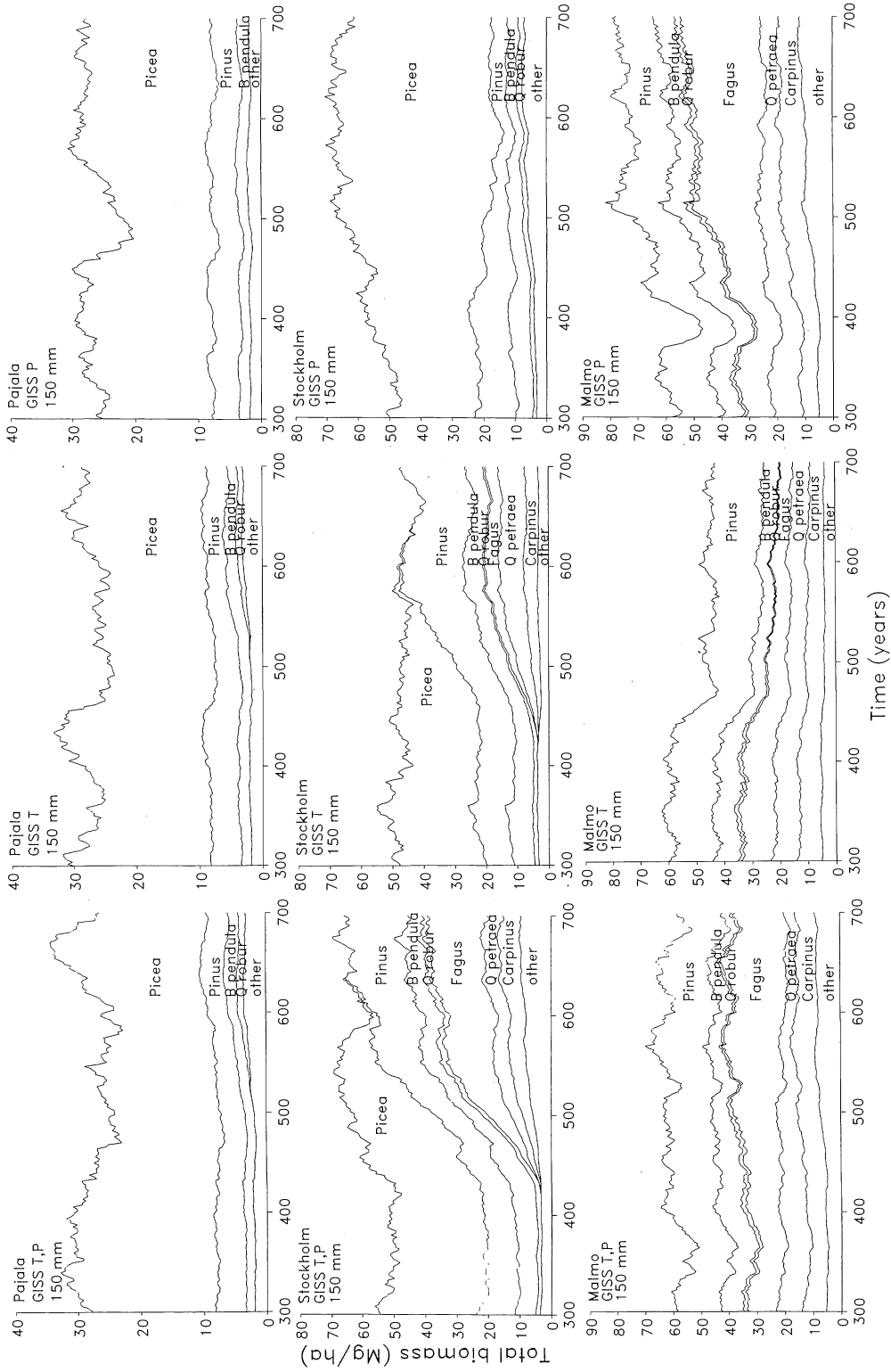


Fig. 1. Simulations of the transient response of forest composition to climate change on soils of 150 mm water capacity in north, central and south Sweden. Climate change took place during years 400–500. T, temperature changed; P, precipitation changed; T, P, both variables changed.

of the climate change, and the time course of the transition is affected by the species' life-history characteristics (such as growth rates and shade tolerance) and interactions as well as by direct responses to climate.

The simulated changes have major implications for forestry and nature conservation practice, that we do not consider here (see e.g. Boer, Koster & Lundberg, 1990; Dahl, 1990; Liljelund, 1990). Yet the simulations are conservative. Propagules of new species are assumed available wherever the changing climate selects them; on the other hand the results imply major range extensions of temperate deciduous species, which may imply additional (migration) lags (Davis, 1989). Also, the simulations assume stabilization of CO₂ at twice its pre-industrial level. This is probably unrealistic, and if CO₂ continues to increase, large areas of forest may become dominated by early-successional species with wide climatic tolerance.

Direct effects of raised CO₂ on tree growth (Eamus & Jarvis, 1989; Woodward, 1990) have been disregarded. Other, unpublished model experiments have indicated an increase in the growth rate and biomass of (especially) *Picea* and *Fagus* due to CO₂ fertilization, but the effects of the climate change remained paramount.

ACKNOWLEDGMENTS

Research supported by the Swedish Natural Science Research Council (NFR), through grants to the project 'Simulation modelling of natural forest dynamics' and the Alliant computer system at Uppsala.

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