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The use of a European forest model in North America: a study of ecosystem response to climate gradients

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Abstract. The forest gap model FORCLIM that originally was developed for central European conditions is applied to simulate the species composition of near-natural forests in eastern North America along a latitudinal transect from 60 to 30°N, covering the transition from the tundra to the boreal and deciduous forests.

The results show that FORCLIM provides plausible species compositions along this gradient; most of the divergences concern species that are of minor abundance. In the central part of the gradient, the simulated species composition is considerably more realistic than the one obtained in an earlier study with a model developed for these conditions. However, in the boreal forest the behaviour of some light-demanding species is anomalous. Along drought gradients in the south western part of the gradient, FORCLIM misrepresents the influence of increased drought on forest structure, thus pointing to further research needs.

The results are discussed within the context of model verification, the applicability of FORCLIM to study climatic change issues and the evolution of different tree species on the two continents. Prospects are outlined for developing a forest gap model that is applicable over a wide range of environmental conditions across several continents, thus contributing to the development of dynamic global vegetation models.

Key words. Gap model, forest ecology, ecosystems analysis, global change.

INTRODUCTION

During the past 20 years, several types of ecological models were developed to address the causes and implications of compositional changes of the tree layer in forests (e.g. Botkin, Janak & Wallis, 1972; Shugart, Crow & Hett, 1973; Ek & Monserud, 1975; Horn, 1975). Forest gap models (Botkin *et al.*, 1972; Shugart, 1984) turned out to be especially useful for this purpose and were subsequently adapted to a wide range of sites around the globe. Originally, these models were designed to project forest dynamics in a small geographical area, e.g. in the Hubbard Brook Forest (Botkin ., 1972) or in southern Appalachian forests (Shugart & West, 1977). Solomon (1986) provided the first example of an application of one single forest gap model across a wide range of climatic conditions, ranging from 30° to 60° northern latitude in eastern North America.

Modifications are often required to apply forest gap models under new ecological and climatic conditions (e.g. Kercher & Axelrod, 1984; Kienast, 1987; Kellomäki *et al.*, 1992). We know of no application of a single, unmodified gap model along climate gradients on several continents. The transfer of a model that was developed for central European conditions to eastern North America represents such an attempt, which we consider to be important for several reasons.

First, the large spatial and temporal scales (several hectares, several centuries) on which forest gap models operate make it difficult to provide adequate data for model validation (Shugart, 1984). There are high-quality descriptions of the near-natural forest vegetation of eastern North America (e.g. Rowe, 1972; Küchler, 1975). These descriptions are truly independent of the data that were used to structure a 'European' forest gap model (Shugart, 1984). In this sense, the comparison of eastern North American near-natural vegetation (Rowe, 1972; Küchler, 1975) with

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the output of a 'European' forest gap model is a contribution to model validation.

Secondly, the application of gap models to evaluate the impacts of climatic change on forests (e.g. Solomon, 1986; Pastor & Post, 1988; Kienast, 1991) requires that the models provide plausible descriptions of forest dynamics beyond current climatic conditions. The behaviour of a forest gap model on a different continent that is characterized by different ecological (i.e. different species) and different climatic conditions is a test of whether such applications are feasible.

Thirdly, such an exercise allows us to address fundamental ecological and evolutionary questions quantitatively: how much of the forest dynamics observed in eastern North America can be explained by the processes that were found to be important in central Europe (e.g. Huntley, Bartlein & Prentice, 1989)? Have the different climatic conditions brought about the dominance of different processes shaping competitive relations and, consequently, the species composition of near-natural forests?

Finally, the assessment of the impact of climatic change on forests on a global scale requires models that are applicable under the widest possible range of environmental conditions. Task 2.1.3 of the project 'Global Change and Terrestrial Ecosystems' (GCTE) states that it is necessary to '...develop patch models for global application...' (Steffen *et al.*, 1992). The application and evaluation of one single forest gap model across multiple continents is a contribution to this task.

MATERIAL AND METHODS

The forest model FORCLIM

In the present study, the forest gap model FORCLIM was used (Bugmann, 1994; Fischlin, Bugmann & Gyalistras, 1995). It was developed for central European conditions based on the model FORECE (Kienast, 1987). FORCLIM was designed to incorporate reliable yet simple formulations of climatic influences on ecological processes to produce plausible results when applied along climate gradients. Moreover, the model was scrutinized to include only a minimum number of ecological assumptions. FORCLIM was tested systematically in central Europe and was found to reproduce known tree species composition of unmanaged stands for a wide range of environmental conditions in this area (Bugmann, 1994).

FORCLIM consists of three modular submodels, each of which can be run independently or combined: (1) FORCLIM-E, a submodel for the abiotic environment as modified from FORECE (Kienast, 1987); (2) FORCLIM-S, a submodel for soil carbon and nitrogen turnover, modified from Pastor & Post (1985); (3) FORCLIM-P, a submodel for tree population dynamics based on the gap dynamics hypothesis (Watt, 1947; Shugart, 1984). In using FORCLIM-E/P, nutrient availability is kept constant. By also including the submodel FORCLIM-S as FORCLIM-E/P/S, nutrient availability as well as below-ground carbon storage are calculated explicitly.

FORCLIM-P simulates size cohorts, i.e. groups of trees that have the same diameter at breast height, instead of individual trees (Bugmann, 1994). Maximum tree growth in FORCLIM-P is constrained by light availability, soil nitrogen level, summer temperature and water stress. The influence of summer temperature on tree growth is calculated using a parabolic relationship between the annual sum of degree-days and the growth rate of the trees. The calculation of the degree-day sum was improved as compared to earlier models (e.g. Kienast, 1987). Water stress is expressed as the annual evapotranspiration deficit (Prentice, Sykes & Cramer, 1993), which is calculated using the Thornthwaite & Mather (1957) model of soil water balance as incorporated in Pastor & Post (1985), but without resetting soil moisture to field capacity at the beginning of every simulation year (cf. Fischlin *et al.*, 1995).

Tree establishment rates in FORCLIM are determined from light availability at the forest floor, browsing intensity and winter minimum temperature. The latter is assumed to be correlated with the minimum of the current mean temperatures of December, January and February (cf. Prentice *et al.*, 1992).

Tree mortality is modelled as a combination of an age-related and a stress-induced mortality rate (Shugart, 1984; Kienast, 1987; Solomon & Bartlein, 1992). There is no direct influence of weather on mortality rates; however, trees that grow slowly due to adverse environmental conditions are more likely to be subject to the stress-induced mortality rate, which thus provides a linkage between tree growth and mortality.

Estimates of the model parameters for the above environmental constraints were assembled from previous modelling studies (Kienast, 1987), compilations of silvics data for succession modelling (Prentice & Helmisaari, 1991) and a wide array of other published sources (cf. Bugmann, 1994). A more detailed description of the model, its calibration and testing is given in Bugmann (1994).

Tree species and climatic data of eastern North America

A tree species in FORCLIM is defined by fourteen species-specific parameter values (Bugmann, 1994). Since near-natural forests of Europe and eastern North America have no species in common, it was necessary to derive the FORCLIM parameters for the seventy-two eastern North American species used in previous studies (e.g. Solomon *et al.*, 1984; Pastor & Post, 1985; Solomon, 1986). Four of the fourteen FORCLIM parameters per species were adopted directly from the FORENA data (Solomon, 1986), seven of them had to be recalculated based on the FORENA parameters, and three could be derived using the species descriptors published for LINKAGES by Pastor & Post (1985). A detailed description of the transformation rules and a summary of all the species parameters are given in Bugmann (1994). These transformation rules were established *a priori*, i.e. no tuning of the species parameters was performed at all.

Ten of the twenty-one locations used by Solomon (1986) were selected for the present study (Fig. 1),

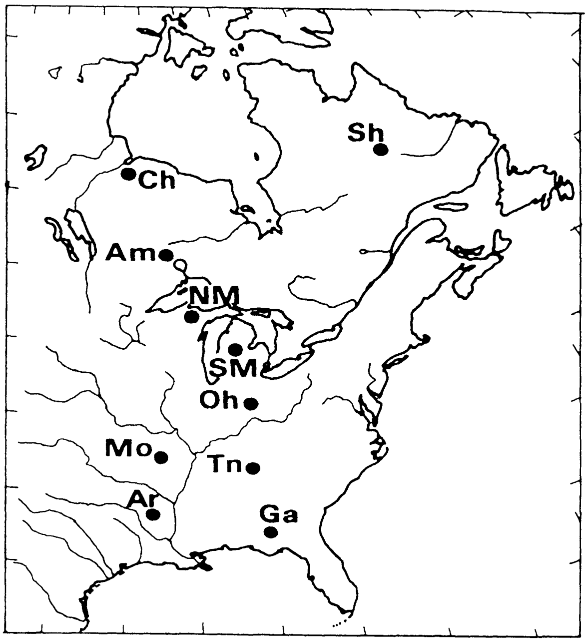

FIG. 1. Map of the ten locations in eastern North America used in the present study. Their climatic data are the same as the ones used by Solomon (1986). Ch: Churchill (Manitoba); Sh: Shefferville (Quebec); Am: Armstrong (Ontario); NM: West Upper Division, Michigan; SM: Central Lower Division, Michigan; Oh: West Central Division, Ohio; Mo: West Ozarks Division, Missouri; Ar: South Central Division, Arkansas; Tn: Cumberland Plateau Division, Tennessee; Ga: South Central Division, Georgia.

covering a latitudinal gradient from 58°N to 31°N, with annual mean temperatures ranging from -7.3°C (Churchill) to 19.6°C (Georgia), and annual precipitation sums from 396 mm yr^{-1} (Churchill) to 1378 mm yr^{-1} (Tennessee).

Simulation experiments

At each of the ten locations, 200 patches were simulated during 1200 years (Bugmann & Fischlin, 1992, 1994; Bugmann, 1994). This is a much larger sample size and a longer time span than the one used by Solomon (1986), who simulated only ten patches over 400 years under current climate. The ForClim model was run using the submodels ForClim-E (stochastic abiotic environment) and ForClim-P (gap dynamics model for tree establishment, growth and mortality). At all locations a mesic silt loam with a field capacity of 30 cm was simulated, assuming a fertile soil with a nitrogen availability of 100 kg/ha. No disturbances such as windthrow or fire were simulated. The steady-state species composition of the simulated forests was estimated by averaging the output from the years 1000–1200 of each patch.

RESULTS AND DISCUSSION

Tundra–woodland transition and northern boreal forest

Figure 2 summarizes the steady-state species compositions along the northern part of the gradient. Only few and stunted trees grow at Churchill and Shefferville, matching the stand structure of the tundra–forest transition zone typical of this area (Rowe, 1972). While the occurrence of *Picea glauca* and *Populus* spp. is realistic, the large fraction of *Larix laricina* appears to be unrealistic (Rowe, 1972). In eastern North America, *L. laricina* is characteristic of cold-air drainage situations and low peatlands, which are not simulated here. In reality, its establishment from seeds is strongly limited by light availability; this was accounted for in Forena (Solomon, 1986) by preventing its establishment when leaf area index (LAI) is above 0.05 $\mathrm{m^2m^{-2}}$, a factor that was not included in ForClim. The lack of *Pinus banksiana* on these mesic soils, and in the absence of fire, is also reasonable.

Species typical of closed forests at boreal sites like Armstrong are *Picea glauca*, *P. mariana*, and *Betula papyrifera* (Rowe, 1972). These species are correctly simulated as dominants (Fig. 2), but other species attain anomalous abundance: again, *L. laricina* should be of marginal importance. In reality, both *Populus* spp. and *P. banksiana* require abiotic disturbances to provide them with full sunlight. However, the simulation experiment is for undisturbed forests, and the large abundance of *Populus spp.* at Armstrong is thus unrealistic (Fig. 2). In Forena, *Populus* spp. did not occur because its establishment was prevented by the LAI requirement mentioned above. *Pinus banksiana* is not important in the model, however, because its degree-day requirements are not met, which may be due to erroneous parameter estimation (Rowe, 1972; Hare & Thomas, 1979). Thus *P. banksiana* appears to be absent for the wrong reasons.

Generally speaking, the characteristics of the transition zone from tundra to boreal forests, such as low tree species diversity, small tree stature and low total biomass, are simulated plausibly by the ForClim model (Fig. 2).

Southern boreal forest

The simulation results for Western Upper Michigan, the transition zone between boreal and deciduous forests, appear to be quite realistic (Rowe, 1972; Frelich & Lorimer, 1991; Fig. 3) and exhibit several features not present in the Forena results (Solomon, 1986). The sugar maple (*Acer saccharum*)—eastern hemlock (*Tsuga canadensis*) forest simulated by ForClim is typical of rich, undisturbed sites (Rowe, 1972; Küchler, 1975; Frelich & Lorimer, 1991). In this area, *T. canadensis* is a dominant species although it approaches its western boundary. The forest simulated by Forena (Solomon, 1986) was dominated by *Thuja occidentalis*, which is of low importance in ForClim chiefly because leaf area is calculated more accurately. In ForClim, the *T. occidentalis* trees generally are suppressed and do not come to dominance. Moreover, in reality *T. occidentalis* is competitive on calcareous soils only, a differentiation modelled neither in Forena nor in ForClim.

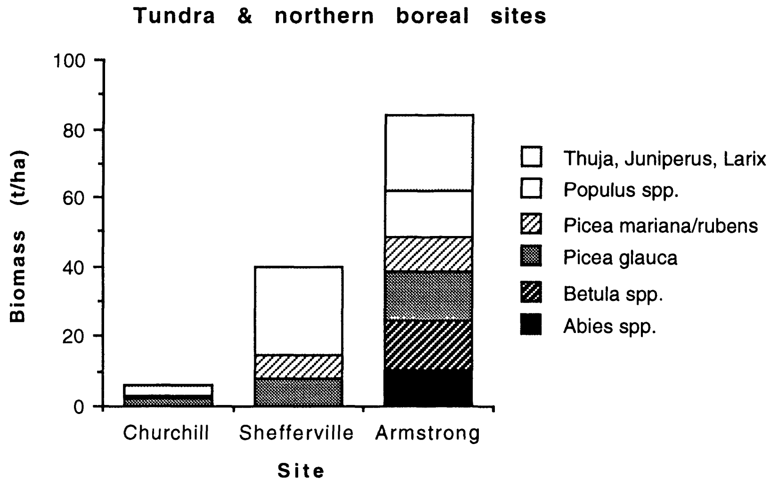

FIG. 2. Species-specific cumulative biomass in the steady state under current climate at tundra and northern boreal sites in eastern North America (cf. Fig. 1) as estimated by the ForClim-E/P model.

As soils become coarser, lower in organic matter and poorer in moisture capacity pines take over, first *Pinus strobus* then *P. resinosa* and finally, in pure stands, *P. banksiana*. With disturbance such as fire or windthrow, *Populus tremuloides*, which occurred in the ForClim simulation peaking at about 10 t/ha in the year 100, and *Betula papyrifera* dominate for periods of 50–100 years. The occurrence of these species during the first 400 years of the simulation thus appear to be realistic. Two species may be simulated with too high biomass: *Picea rubens*, which requires too much moisture to be present in the Michigan area, and *Quercus macrocarpa* (making up most of the northern oaks in Fig. 3), a very fire resistant and relatively shade intolerant species which is more typical of the oak savanna towards the prairie–forest border of Minnesota and Wisconsin. The more typical *Quercus rubra* must be treated as two species including a northern, shade intolerant *Quercus borealis* variant (Britton & Brown, 1913) for realistic quantities of this species to appear in simulations (Solomon & Bartlein, 1992).

The increase of both species diversity and total above-ground biomass simulated by ForClim appears to be realistic (DeAngelis, Gardner & Shugart, 1981), and the species composition simulated by this model agrees more with the descriptions of near-natural forests of the area (Rowe, 1972; Küchler, 1975; Frelich & Lorimer, 1991) than do the Forena simulations (Solomon, 1986).

Northern and south western deciduous forest

Figure 4 gives an overview of the steady-state species composition along a gradient from the northern to the south western deciduous forests. The climate along this gradient is characterized by both greatly increasing temperature and moderately increasing precipitation with the result that drought stress also increases. The forest simulated at Central Lower Michigan (Fig. 4) is in the transition zone from the sugar maple–eastern hemlock forests typical of locations in the north (Fig. 3) to the oak–hickory forests characteristic of locations further south (Figs 4 and 5). Comparing these results to those from Western Upper Michigan (Fig. 3), major differences are (1) the disappearance of *Thuja*, *Picea*, and *Abies* species; (2) a strong decrease of *Acer saccharum*; (3) an increase in the biomass of *Fagus grandifolia* and northern oaks; (4) the appearance of southern genera, such as *Carya*, *Fraxinus*, *Juglans* and *Tilia*. The ForClim model succeeds well simulating these transition forests (Küchler, 1975).

The forest simulated for West Central Division, Ohio, is dominated by northern oaks and hickory species (Fig. 4). The now extinct chestnut (*Castanea dentata*) attains some importance on this edge of its former range (Shugart & West, 1977), whereas the abundance of hemlock decreases with decreasing latitude; in fact, it should be less abundant here than simulated by ForClim, if not absent entirely. Forena and ForClim agree to a large extent on the composition of near-natural forests of this area (cf. Solomon, 1986).

The Western Missouri area is characterized by open, almost woodland structured forests, a feature that is due to moisture stress, which is not simulated with the generous assumption of 30 cm field capacity (Fig. 4). Thus, total biomass increases compared to that in the Ohio area, which is not realistic. Possibly for the same reason ForClim simulates *Fagus grandifolia*, which is absent from this area. Moreover, ForClim produces small amounts of *Tsuga canadensis* although the species should be absent at these latitudes and longitudes. However, the dominance of oak, hickory and chestnut, including the exact species among many in the former two genera, agrees well with descriptions of the near-natural forests of the area. The overall performance of ForClim thus is fairly good.

Major differences between the two models become evident with the Arkansas climate (Fig. 4): while the Forena simulation is dominated by southern oaks (Solomon, 1986), ForClim produces stands dominated by *Carya* spp. and northern oaks. However, the most

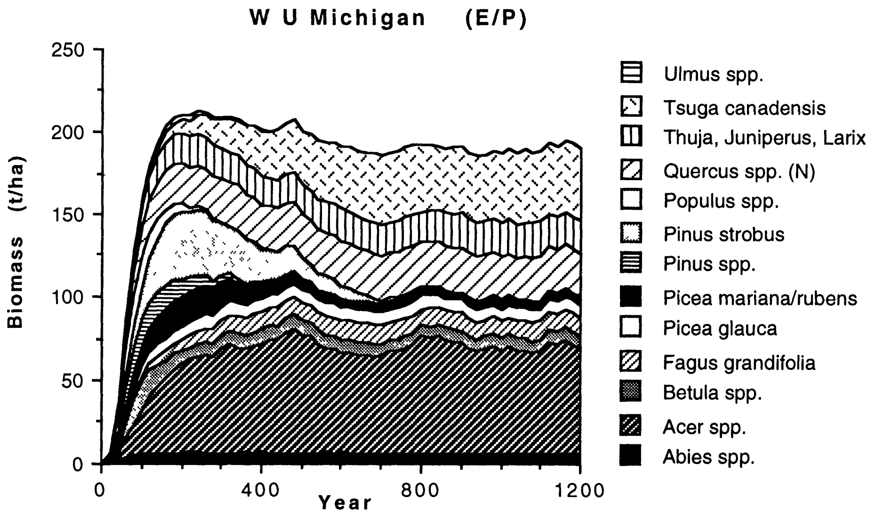

FIG. 3. Transient dynamics of species-specific cumulative biomass under current climate for West Upper Division, Michigan (cf. Fig. 1). The graph shows the average from 200 patches simulated by the FORCLIM-E/P model.

important oak species simulated by FORCLIM are also prominent on the landscape: *Q. alba* and *Q. velutina* (Küchler, 1975). *Carya* spp. is a warmth and drought-adapted genus, as are many of the oak species, which makes the FORCLIM simulation results quite realistic. The decrease of total above-ground biomass as compared to that in Missouri (Fig. 4) is due to drought stress; indeed, real forests of the area are also less dense, but the simulated biomass should be still lower (DeAngelis *et al.*, 1981). Experiments performed with lower values of the field capacity (10–15 cm) in the FORCLIM model showed that total aboveground biomass decreases below 200 t/ha, which may be more plausible.

South eastern deciduous forests

The simulation results from Georgia, the southernmost location along the transect, are given in Fig. 5. Southern oaks and *Carya* spp. dominate this forest. However, there is a large discrepancy between real and simulated forests both in FORCLIM and in FORENA: on the landscape, southern pines (*Pinus* spp. in Fig. 5) dominate the forests, which is due to the occurrence of disturbances such as fire and the droughtiness of the sandy soils prevailing in that area. However, on the clay soils of the piedmont, for which the simulation results are more representative, oaks and hickories dominate. Thus, as a statement about the potential natural forest vegetation in the absence of disturbance, the FORCLIM model is quite successful.

Similar simulation results are obtained for Cumberland Plateau, Tennessee (not shown). Although the annual precipitation sum is high, the area is subject to considerable drought because of the sandy soils, leading to low-biomass forests. However, at Cumberland Plateau FORCLIM

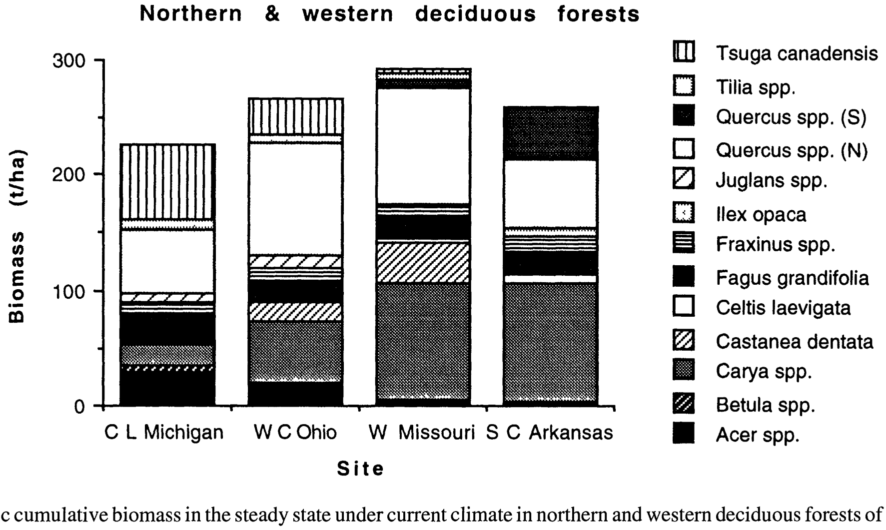

FIG. 4. Species-specific cumulative biomass in the steady state under current climate in northern and western deciduous forests of eastern North America (cf. Fig. 1) as estimated by the FORCLIM-E/P model.

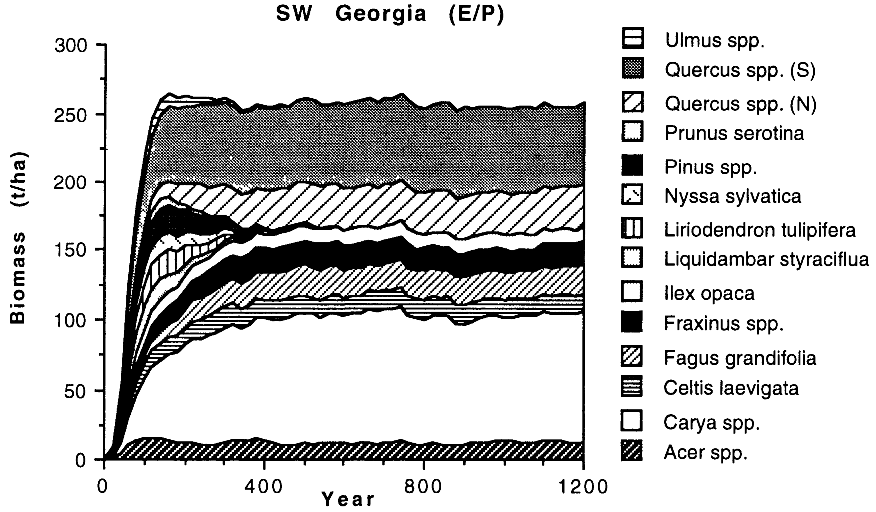

FIG. 5. Transient dynamics of species-specific cumulative biomass under current climate for Southwest Division, Georgia (cf. Fig. 1). The graph shows the average from 200 patches simulated by the FORCLIM-E/P model.

produces the largest amount of above-ground biomass along the transect. The FORENA model also misrepresents the effects of drought at this site. The assumption of 30 cm water at field capacity clearly does not represent sandy soils; however, the large amount of above-ground biomass simulated by FORCLIM is by and large independent of the value of the field capacity parameter used in the simulations. Hence, these anomalies may constitute a serious problem for both models.

Conclusions

The application of the 'European' forest gap model FORCLIM along a latitudinal gradient in eastern North America and the comparison of the results with those obtained from the FORENA model (Solomon, 1986) and with descriptions of near-natural forests of the area (Rowe, 1972; Küchler, 1975) revealed several interesting features.

First, FORCLIM successfully simulates the transition from tundra to boreal and deciduous forests. The simulated species composition agrees quite well with the descriptions of near-natural forests, and most of the divergences concern species that are of minor abundance. FORCLIM performs best in the central part of the climate gradient explored in this study, where the simulated species composition is even more realistic than the one obtained from FORENA. In the northern part, an anomalous behaviour of some light-demanding species becomes evident, whereas both FORENA and—even more pronounced—FORCLIM misrepresent the influence of increased drought on forest structure when approaching the south western edge of the simulated geographical range. Neither model appears capable of reproducing the open woodlands and savannas that characterize the forest–steppe transition here. These results point to the need of improved modelling of drought influences on tree growth.

Secondly, it is encouraging that FORCLIM produces plausible simulation results with a different set of tree species and under climatic conditions characterized by a wider span of annual mean temperatures, annual precipitation sums and much higher annual temperature amplitudes than in Europe. The eastern North American example shows that FORCLIM has some predictive power also when extrapolating beyond the ecological and climatic conditions for which it was developed. In fact, FORCLIM behaves as well as or better than other models developed for eastern North American conditions (e.g. Solomon *et al.*, 1984; Pastor & Post 1985; Solomon, 1986). Hence we may conclude that FORCLIM is a valid candidate for assessing the impact of climatic change on the species composition of near-natural forests both in Europe and in eastern North America.

Thirdly, it is interesting to note that the same small number of ecological factors—four factors for tree growth, three factors for sapling establishment and two factors for tree mortality—and even the same formulation of these factors is sufficient to model forest dynamics in central Europe and in eastern North America. Both study areas are located by and large within the temperate zone, but there are marked climatic differences between them (Bugmann, 1994). Of course, these differences have contributed to the evolution of different tree species on the two continents. However, assuming that the FORCLIM model represents reality sufficiently well, we may conclude that the same processes govern competition in forests on both continents. Hence the present study suggests quantitatively that the different evolution of tree species on the two continents is rather due to geographical separation than to any significant differences in the importance of ecological processes.

Finally, the experience gained from the present study shows that there is the potential for developing one single forest gap model that is applicable over a wide range of environmental conditions across several continents. Future studies should be conducted to test the behaviour of

FORCLIM in other areas of the temperate and boreal zone, e.g. in western North America and in Asia, as well as in other forest biomes such as in the tropics. The development of a single or a small number of forest gap models that can be used on a global scale would provide a link to the development of dynamic global vegetation models (GVM, Prentice *et al.*, 1989; or DGVM, Woodward *et al.*, in press). For example, the dynamics simulated by the forest gap model could be compared to the output of the DGVM; in this sense, forest gap models could contribute to the assessment of the biospheric impact of climatic change not only on the local and regional, but also on the global scale.

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