SIMULATING FOREST DYNAMICS IN A COMPLEX TOPOGRAPHY USING GRIDDED CLIMATIC DATA

HARALD BUGMANN
Department of Global Change and Natural Systems, Potsdam Institute for Climate Impact Research, P.O. Box 60 12 03, D-14412 Potsdam, Germany

ANDREAS FISCHLIN
Systems Ecology, Institute of Terrestrial Ecology, Swiss Federal Institute of Technology Zürich (ETHZ), Grabenstrasse 3, CH-8952 Schlieren, Switzerland

Abstract. The forest model FORCLIM was used to evaluate the applicability of gap models in complex topography when the climatic input data is provided by a global database of 0.5° resolution. The analysis was based on 12 grid cells along an altitudinal gradient in the European Alps. Forest dynamics were studied both under current climate as well as under four prescribed $2 \times CO_2$ scenarios of climatic change obtained from General Circulation Models, which allowed to assess the sensitivity of mountainous forests to climatic change.

Under current climate, FORCLIM produces plausible patterns of species composition in space and time, although the results for single grid cells sometimes are not representative of reality due to the limited precision of the climatic input data.

Under the scenarios of climatic change, three responses of the vegetation are observed, i.e., afforestation, gradual changes of the species composition, and dieback of today's forest. In some cases widely differing species compositions are obtained depending on the climate scenario used, suggesting that mountainous forests are quite sensitive to climatic change. Some of the new forests have analogs on the modern landscape, but in other cases non-analog communities are formed, pointing at the importance of the individualistic response of species to climate.

The applicability of gap models on a regular grid in a complex topography is discussed. It is concluded that for their application on a continental scale, it would be desirable to replace the species in the models by plant functional types. It is suggested that simulation studies like the present one must not be interpreted as predictions of the future fate of forests, but as means to assess their sensitivity to climatic change.

1. Introduction

Several forest gap models have been developed that are capable of simulating the species composition of near-natural forests at a wide range of sites and climates within mountainous terrain in the European Alps (Kienast, 1987; Kräuchi, 1994), and also along climate gradients in this area (Bugmann, 1994). In such studies forest dynamics are simulated under current and/or under changed climatic conditions, but at sites that are located typically in the bottom of valleys. They represent the state and future fate of forests as they are perceived by the local population, which may also be of relevance to forestry and tourism.

On the other hand, global models of vegetation cover such as BIOME (Prentice et al., 1992) or MAPPS (Neilson, 1995) are based on climatic input data on a grid that has a resolution of 0.5° or less. The results for mountainous areas from

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such models cannot be compared directly with site-specific simulation results of forest gap models because the average conditions assumed in the global models can be found only rarely in a complex topography, and they may be fairly atypical because the topography imposes steep environmental gradients. On the other hand, the site-based simulation results from gap models often are not representative of a larger forested area.

The present study addresses two questions: (1) Is a forest gap model capable of producing a realistic spatial pattern of forest types in a complex terrain like the European Alps when the climatic input data is provided at a spatial resolution of 0.5°, the one typically used in global models of vegetation cover? (2) How sensitive is the simulated species composition to a set of GCM-derived 2 × CO_2 scenarios of future climate which are defined on the same coarse spatial resolution?

2. Material and Methods

2.1. STUDY AREA AND INPUT DATA

Twelve grid cells in the European Alps were selected from the global database by Leemans and Cramer (1991; Figure 1). These cells cover an altitudinal gradient from above the current alpine (cold) timberline in the south (46° N) to low-elevation mixed deciduous forests in the north (47.5° N). The species composition of near-natural forests along this gradient is characterized as follows (cf. Schmid, 1949; Ellenberg and Klötzli, 1972; plant nomenclature follows Hess et al., 1980);

- 46 and 46.5° N: Mostly above the alpine (cold) timberline. In the valleys there are subalpine forests dominated by European larch (*Larix decidua* Miller) as the most abundant early successional species; the late successional dominants are Norway spruce (*Picea excelsa* [Lam.] Link) and Swiss stone pine (*Pinus cembra* L.).
- 47° N: Subalpine and montane sites with forests dominated by Norway spruce, silver fir (*Abies alba* Miller), European beech (*Fagus silvatica* L.), and maple species (mainly *Acer pseudoplatanus* L. and *Acer platanoides* L.).
- 47.5° N: Low-elevation mixed deciduous forests dominated by European beech, oaks (mainly *Quercus robus* L. and *Q. petraea* (Mattuschka) Lieblein), and several other deciduous species.

The long-term monthly mean temperature and precipitation data for the simulation experiments were taken from Leemans and Cramer (1991; Table I). The monthly standard deviations of both variables as well as the monthly cross-correlation coefficients between mean temperature and precipitation sum were adopted from Bugmann (1994) based on data of the Swiss Meteorological Agency (SMA, 1901–1990).

Scenarios of future constant climate were obtained from 2 × CO_2 runs of the GFDL, GISS, OSU and UKMO General Circulation Models (for a detailed scenario

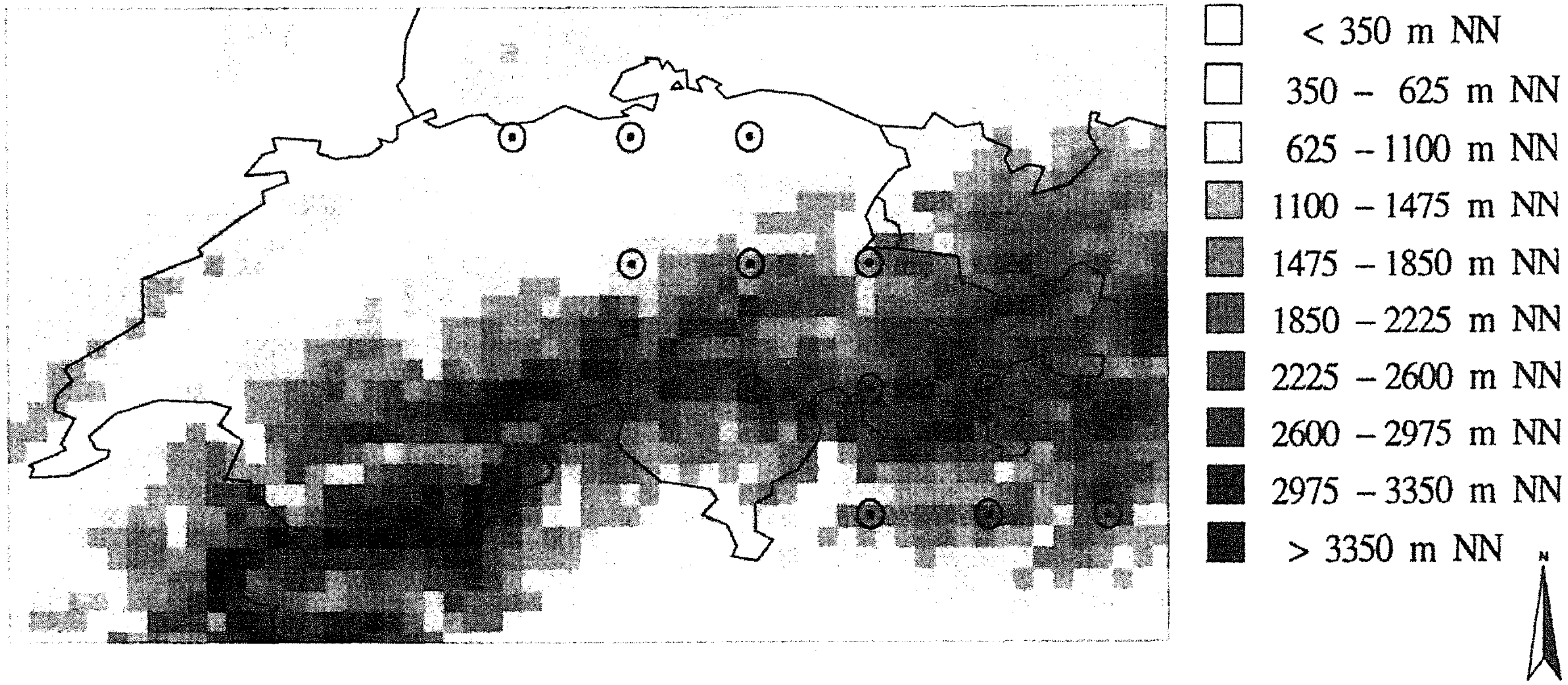

Figure 1. Map of the twelve grid cells used in the present study (cf. Table I, Figure 3). The symbols (⊙) mark the center of each grid cell. The digital elevation model shown here has a resolution of 0.083° (5′), whereas the climate database (Table I) has a reolution of 0.5° only, i.e. six times less.

Table I

Location, elevation, long-term annual means of current climate (CUR), and changes under the four climate scenarios (GFDL, GISS, OSU, and UKMO) at the 12 grid cells selected for the present study (data from Leemans and Cramer, 1991)

Location		Elev.	Temperature (° C)					Precipitation (cm)				
Lat (°N)	Lon (°E)	(m)	CUR	GFDL	GISS	OSU	UKMO	CUR	GFDL	GISS	OSU	UKMO
47.5	9.0	507	5.8	+5.1	+4.1	+2.9	+6.4	77.8	+7%	+18%	+5%	+21%
47.5	8.5	553	5.7	+5.1	+4.0	+2.9	+6.4	75.7	+7%	+17%	+4%	+22%
47.5	8.0	630	7.0	+5.1	+4.0	+2.9	+6.3	103.7	+7%	+17%	+4%	+22%
47.0	9.5	1190	2.5	+5.0	+4.0	+2.9	+6.4	124.9	+9%	+17%	+4%	+20%
47.0	9.0	873	11.1	+5.0	+4.0	+2.9	+6.4	247.7	+5%	+17%	+4%	+21%
47.0	8.5	680	8.3	+5.1	+4.0	+2.9	+6.3	140.8	+6%	+17%	+4%	+22%
46.5	10.0	2600	-5.4	+4.9	+4.0	+2.9	+6.4	92.9	+6%	+17%	+4%	+19%
46.5	9.5	1957	-1.8	+5.0	+4.0	+2.9	+6.3	107.5	+8%	+16%	+4%	+19%
46.5	9.0	2003	-2.9	+5.0	+3.9	+2.9	+6.2	87.4	+6%	+16%	+4%	+20%
46.0	10.5	2350	-1.5	+4.8	+3.8	+3.0	+6.3	83.3	+4%	+17%	+4%	+18%
46.0	10.0	2267	-1.9	+4.9	+3.8	+2.9	+6.2	94.1	+5%	+17%	+4%	+18%
46.0	9.5	2263	-1.8	+4.9	+3.8	+2.9	+6.1	118.9	+7%	+17%	+4%	+19%

description see Lauenroth, this issue). The variances of monthly mean temperatures and monthly precipitation sums were assumed not to change, and no direct effects of CO_2 on tree growth were modelled.

2.2. THE FOREST GAP MODEL FORCLIM

The FORCLIM model (Bugmann, 1994; Fischlin et al., 1995) was developed based on an earlier gap model, FORECE (Kienast, 1987): First, the model was scrutinized to include only a minimum number of ecological assumptions, showing that many factors included in FORECE could be omitted (Bugmann, 1994), such as the local feedback of seed production on establishment rates, and synecological indicator concepts. Second, the remaining factors were designed to incorporate reliable yet simple formulations of climatic influences (Bugmann, 1994; Fischlin et al., 1995) so as to produce realistic results when applied along climate gradients.

FORCLIM consists of three modular submodels, each of which can be run independently, or combined: (1) FORCLIM-E, a submodel for the abiotic environment containing a stochastic weather generator and a one-layer 'bucket' model of soil moisture balance with a monthly time step (Thornthwaite and Mather, 1957); (2) FORCLIM-S, a submodel for soil carbon and nitrogen turnover modified from Pastor and Post (1985); (3) FORCLIM-P, a submodel for tree population dynamics that is 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, nitrogen availability as well as belowground carbon storage are calculated explicitly. A complete description of the model is given in Bugmann (1994; FORCLIM-P and -S, plus part of FORCLIM-E) and Fischlin et al. (1995; part of FORCLIM-E).

The most important structural differences of FORCLIM as compared to the standard gap model approach (Shugart and Smith, this issue) are: (1) The equation to predict maximum tree growth is based on a simple carbon-balance approach (Moore, 1989), which is more mechanistic than the equation proposed by Botkin et al. (1972); (2) The 'dry days' drought index has been replaced by the evapotranspiration deficit approach (Prentice et al., 1993), and the accuracy of the calculation of the annual sum of degree-days has been increased (Bugmann, 1994); (3) The influence of nitrogen availability on tree growth according to Aber et al. (1979) has been included; (4) Sapling establishment rates are determined from light availability at the forest floor, browsing intensity, and winter minimum temperature (Prentice et al., 1992); (5) Size cohorts of trees are modelled instead of individuals, thus saving computer time; (6) All implicit dependencies of model parameters on climate, such as the length of the growing season, have either been removed or been replaced by explicit dependencies (Bugmann, 1994; Fischlin et al., 1995).

FORCLIM was tested systematically in central Europe (Bugmann, 1994) and in eastern North America (Bugmann and Solomon, 1995). It was found to reproduce known tree species composition of unmanaged stands for a wide range of environmental conditions on both continents.

2.3. SIMULATION EXPERIMENTS

At each grid cell, forest dynamics were simulated during 1800 years on 200 patches (Bugmann and Fischlin, 1992; Bugmann et al., 1996; Figure 2). Patch size was set to $\frac{1}{12}$ ha (Bugmann, 1994). During the first 800 years, the model is allowed to reach its steady-state species composition under current climatic conditions. From the year 800–900, a linear change of climatic parameters takes place, and from the year 900 to 1800 climate is kept constant at the level obtained from each of the four GCMs. The steady-state species composition under current and future climate was estimated by averaging the output from 200 patches over the years 600–800 and 1600–1800, respectively.

3. Results and Discussion

Under current climatic conditions, FORCLIM produces a plausible pattern of species composition across the 12 grid cells (Figures 2 and 3):

At the highest elevations ($\leq$ 46.5° N), temperatures are so low (Table I) that FORCLIM correctly simulates no forest.

In the subalpine/montane area (47° N), the simulated forests do not always correspond to observed patterns (cf. Ellenberg and Klötzli, 1972). For example, the *Larix–Picea* forest at 9.5° E is quite typical of subalpine forests in this area, but the *Fagus–Quercus* forest at 9° E is typical of lower elevations and is hardly characteristic of the area. The mixed deciduous forests simulated at 8.5 and 9° E are due to the anomalously high temperatures in the climate database (Table I). In a more recent version of this database that includes more ground-base data from climate stations and that was derived using a more precise digital elevation model and improved interpolation algorithms, the quality of the predicted climate in the Alps has increased substantially (results not shown here).

At 47.5° N, FORCLIM simulates mixed deciduous forest, which is plausible. At this latitude, beech (*F. silvatica*) should dominate strongly (e.g., Ellenberg and Klötzli, 1972), but the simulation yield an anomalously large abundance of coniferous genera (*Abies, Picea* and *Larix*), which are more characteristic of higher elevations. In reality, the climate at this latitude and longitudes is warmer than the database suggests (especially at 8.5 and 9° E, Table I), thus favouring deciduous species.

Under the four scenarios of climatic change, we found three types of forest response (Figure 2): (1) afforestation of areas that are presently above the alpine timberline; (2) gradual changes occurring on the timescale of a few centuries; (3) dieback of the current forest shortly after the onset of climatic change and a

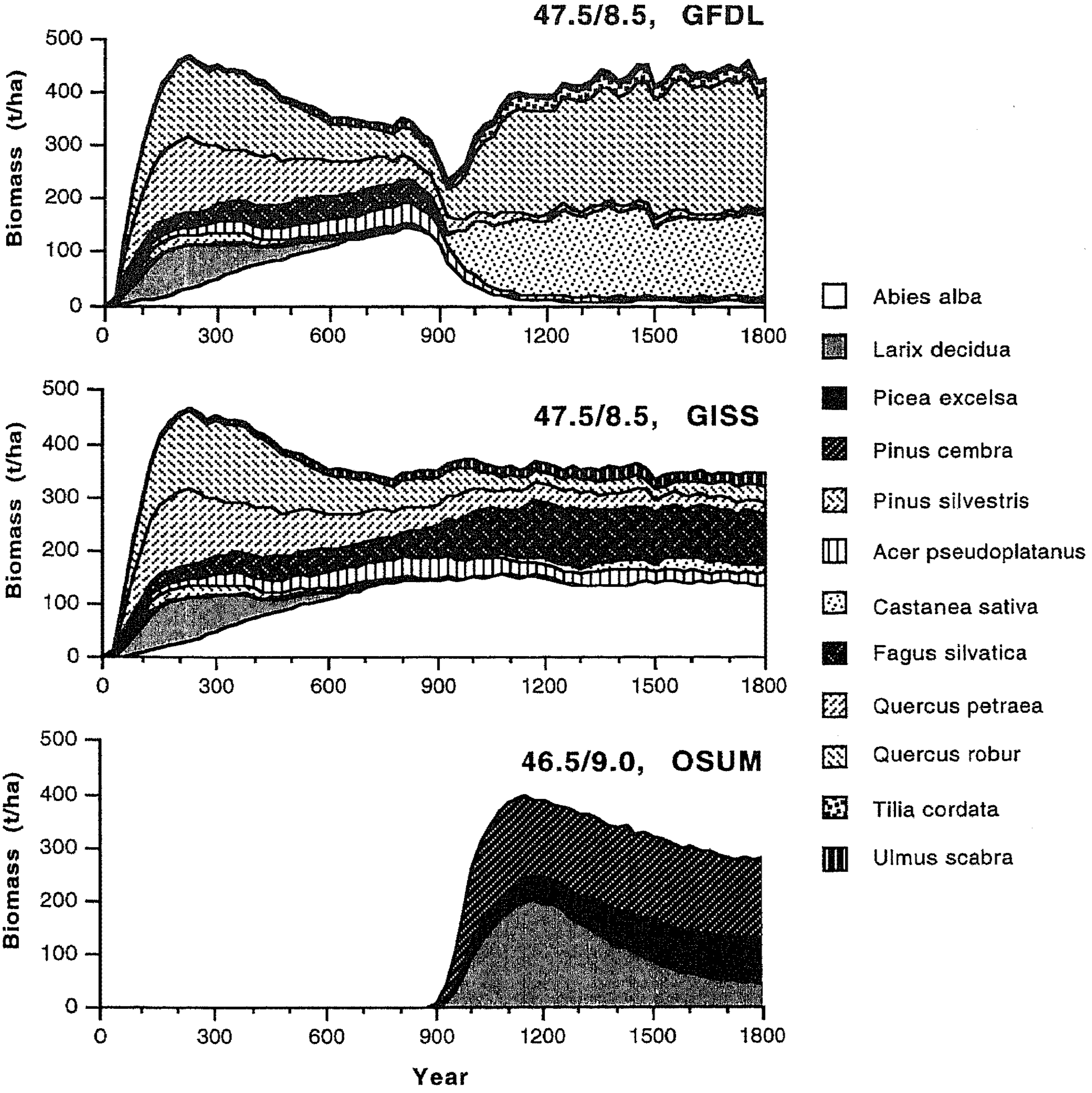

Figure 2. Types of forest change simulated by ForClim-E/P (Bugmann, 1994; Fischlin et al., 1995) when climate changes (years 0–800: current climate, starting from a bare patch; years 800–900: linearly interpolated change of climatic parameters; years 900–1800: constant new climate according to the 2 × CO_2 scenario as simulated by the corresponding GCM). Top: Rapid forest dieback and subsequent replacement by a different community. Centre: Gradual changes of the species composition occurring over several centuries. Botton: Afforestation of areas currently above the alpine (cold) timberline. Each panel shows the average cumulative biomass from 200 runs of a Monte Carlo simulation.

subsequent replacement by another forest type. Note that a fourth type of change, i.e. the dieback of the current forest and its replacement by non-forest vegetation, did not occur in this experiment. This is due to the increase of the annual precipitation sum under all four scenarios, which compensates for the increased evaporative demand under the elevated temperature (Table I). Even in those cases where summer drought increases, it does not become so large that the dry timberline would be

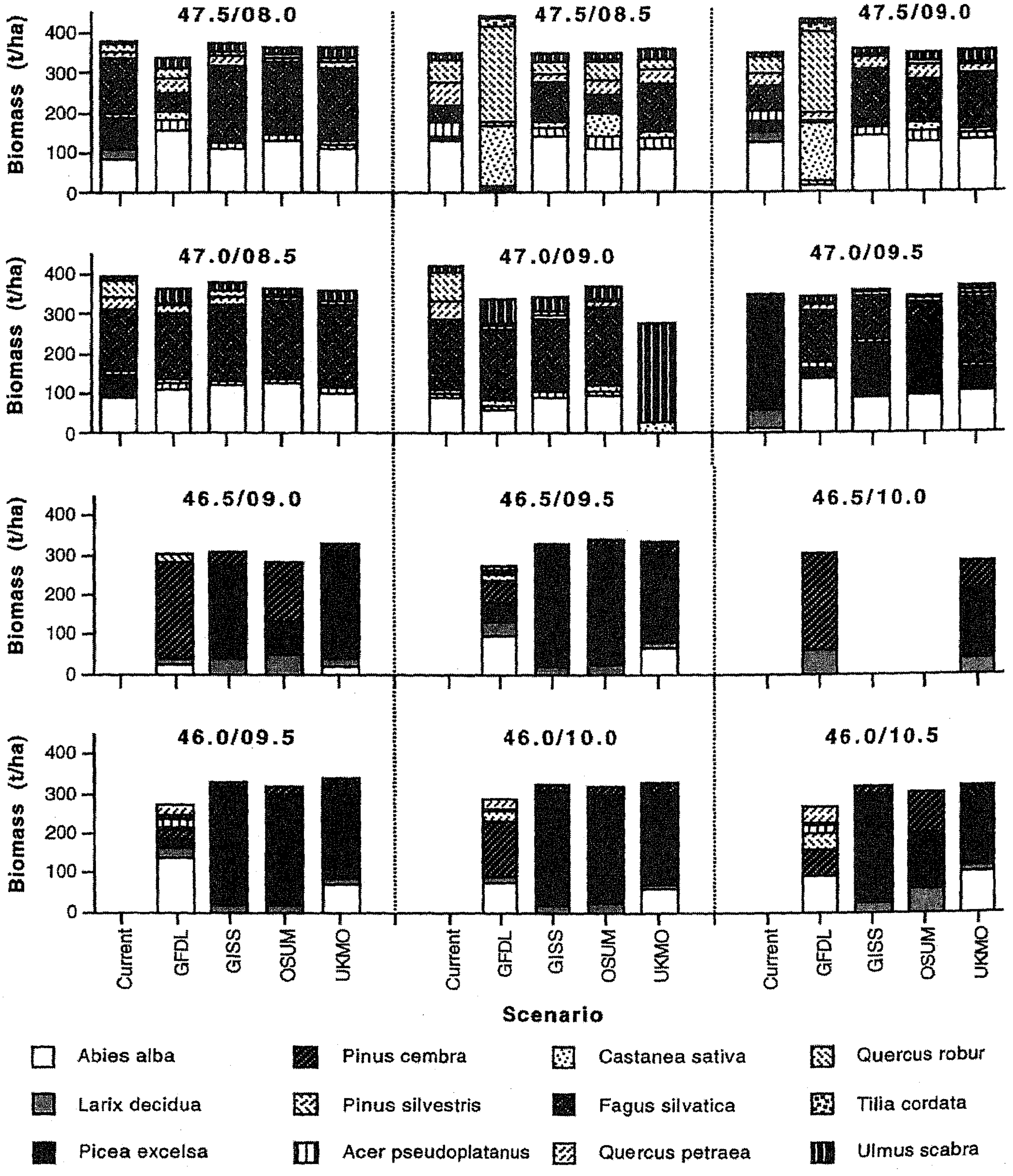

Figure 3. Steady-state species composition simulated by the model FORCLIM-E/P (Bugmann, 1994; Fischlin et al., 1995) at the 12 grid points under current climate (leftmost bar of each subpanel) and under the four scenarios of climatic change given by 2 × CO_2 simulations of four different GCMs.

reached. However, other studies using other climate scenarios suggest that this type of change could occur also in the European Alps (Kienast, 1991; Bugmann, 1994).

In many cases, the equilibrium species composition simulated under the climate scenarios has analogs in the modern European landscape, e.g., the spruce and Swiss stone pine–larch forests simulated at 46 and 46.5° N, the spruce–fir–beech forests at 47° N, and the oak–chestnut forests at 47.5° N (cf. Ellenberg and Klötzli, 1972; Ellenberg, 1986). However, in some cases communities are simulated that are clearly not present anywhere today, such as the fir–pine–oak stands under the GFDL scenario at 46° N (Figure 3). These results underline that the species respond to a changing climate individualistically; hence currently not existing species assemblages may be formed under a changed climate (cf. Davis, 1981).

At the grid cell 47° N/9° E, where the climate database predicts the highest annual mean temperature of the 12 grid cells under current conditions, the annual mean temperature under the UKMO scenario is 17.4 °C, and annual precipitation amounts to 300 cm (Table I). In the model, this leads to the dominance of *Ulmus scabra*, which is quite unrealistic (Figure 3). Under these conditions, the species included in FORCLIM probably would not be competitive compared to subtropical and tropical species, suggesting that species other than those considered in the current model may come to dominate.

The equilibrium species composition simulated under the GISS and OSU scenarios generally agree to a large extent (Figure 3), whereas the results obtained under the GFDL and the UKMO scenario often diverge strongly from the other scenarios. The reason for the divergence is that, unlike the other models, the GFDL model predicts a drastic decrease of summer precipitation (e.g., a 63% reduction of current values for July) and at the same time an increase of the summer temperature (up to +7 °C in July), thus leading to considerable drought. On the other hand, the UKMO model predicts the largest year-round increase of temperature of the four scenarios (Table I).

4. Conclusions

Due to the limited availability of climatic input data, previous studies using forest gap models typically were restricted to simulate forest dynamics at single sites along transects (e.g., Solomon, 1986). The present simulation study shows that experiments with the gap model FORCLIM on a grid that is comparably coarse from the point of view of traditional applications of those models produce a plausible spatial pattern of forest communities even in a complex terrain such as the European Alps. Our study thus suggests that forest gap models can be applied to evaluate the large-scale spatial and temporal patterns of forest dynamics when the climatic input data is provided at the rather coarse resolution of 0.5°.

In complex mountainous terrain the precision of the gridded climatic input data (Leemans and Cramer, 1991) appears to be rather limited (Table I). In the meantime, this has improved considerably (Cramer, personal communication). For the present application, however, we conclude that simulation studies and interpretations must not rely on single grid cells. Only when many grid cells are used does the FORCLIM model capture the typical spatical pattern of forests in the European Alps under the present climate.

The estimation of the steady-state species composition at one grid cell with the FORCLIM model requires few computer resources (e.g., one minute on an IBM RS/6000 workstation). Thus systematic simulation studies on a regular grid covering large areas up to whole continents appear to become feasible as well. However, such applications are hampered by the limited array of species included in these models and the difficulty to obtain the required species data for several regions, let alone several continents. A solution to this problem would be to replace the species-based approach in gap models by functional types of plants (Smith et al., 1996). Although this is not a new idea, its implications for the application of gap models have been addressed only recently (Bugmann, 1996).

The simulation results show that in some instances the four scenarios of climatic change lead to drastic differences of the species composition (Figure 3; cf. Bugmann and Fischlin, 1994; Bugmann, 1994). Since none of these scenarios can be unequivocally identified as the 'Best Estimate', we conclude that such studies must not be interpreted as predictions of some future state of forest ecosystems. Instead, they should be viewed as means to assess the sensitivity of the simulated forests to changes of climatic parameters. Moreover, we should not forget that there is also considerable uncertainty concerning the formulation of the ecological factors included in the models (e.g., Bugmann and Martin, 1995), which corroborates this conclusion even further.

References

Aber, J. D., Botkin, D. B., and Melillo, J. M.: 1979, 'Predicting the Effects of Different Harvesting Regimes on Productivity and Yield in Northern Hardwoods', *Can. J. For. Res.* **9**, 10–14.

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.

Bugmann, H.: 1994, *On the Ecology of Mountainous Forests in a Changing Climate: A Simulation Study*, Ph.D. Thesis No. 10638. Swiss Federal Institute of Technology Zürich, Switzerland, 258 pp.

Bugmann, H.: 1996, 'Functional Types of Trees in Temperate and Boreal Forests: Classification and Testing', *J. Veg. Sci.* **7** (3), in press.

Bugmann, H. and Fischlin, A.: 1992, 'Ecological Processes in Forest Gap Models–Analysis and Improvement', in Teller, A., Mathy, P., and Jeffers J. N. R. (eds), *Responses of Forest Ecosystems to Environmental Changes*, Elsevier Applied Science, London, pp. 953–954.

Bugmann, H. and Fischlin, A.: 1994, 'Comparing the Behaviour of Mountainous Forest Succession Models in a Changing Climate', in Beniston, M. (ed), *Mountain Environments in Changing Climates*, Routledge, London, pp. 204–219.

Bugmann, H. and Martin, Ph.: 1995, 'How Physics and Biology Matter in Forest Gap Models', *Clim. Change* **29**, 251–257.

Bugmann, H. K. M. and Solomon, A. M.: 1995, 'The Use of a European Forest Model in North America: A Study of Ecosystem Response to Climate Gradients', *J. Biogeogr.* **22**, 477–484.

Bugmann, H., Fischlin, A., and Kienast, F.: 1996, 'Model Convergence and State Variable Update in Forest Gap Models', *Ecol. Modelling*, in press.

Davis, M. B.: 1981, 'Quaternary History and the Stability of Forest Communities', in West, D. C., Shugart, H. H., and Botkin, D. B. (eds), *Forest Succession: Concepts and Application*, Springer, New York, pp. 132–153.

Ellenberg, H.: 1986, *Vegetation Mitteleuropas mit den Alpen in ökologischer Sicht*, Verlag Eugen Ulmer, Stuttgart, 4th edn., 989 pp.

Ellenberg, H. and Klötzli, F.: 1972, 'Waldgesellschaften under Waldstandorte der Schweiz', *Eidg. Anst. Forstl. Versuchswes., Mitt.* **48**, 587–930.

Fischlin, A., Bugmann, H., and Gyalistras, D.: 1995, 'Sensitivity of a Forest Ecosystem Model to Climate Parametrization Schemes', *Environ. Pollut.* **87**, 267–282.

Hess, H. E., Landolt, E., and Hirzel, R.: 1980, *Flora der Schweiz*, Birkhäuser, Basel, 4 Vols., 2nd edn.

Kienast, F.: 1987, *FORECE – A Forest Succession Model for Southern Central Europe*, Oak Ridge National Laboratory, Oak Ridge, TN, ORNL/TM-10575, 69 pp.

Kienast, F.: 1991, 'Simulated Effects of Increasing CO_2 on the Successional Characteristics of Alpine Forest Ecosystems', *Landscape Ecol.* **5**, 225–238.

Kräuchi, N.: 1994, 'Modelling Forest Succession as Influenced by a Changing Environment', Diss. ETH No. 10479, *Mitt. Eidgenöss. Forsch.anst. Wald Schnee Landsch.* **69**, 143–271.

Lauenroth, W. K., 1996: 'Application of Patch Models to Examine Regional Sensitivity to Climate Change', *Clim. Change* **34**, 155–160 (this issue).

Leemans, R. and Cramer, W.: 1991, *The IIASA Climate Database for Land Area on a Grid of 0.5° Resolution*, RR-91-18, International Institute of Applied Systems Analysis, Laxenburg, Austria.

Moore, A. D.: 1989, 'On the Maximum Growth Equation Used in Forest Gap Simulation Models', *Ecol. Modelling* **45**, 63–67.

Neilson, R. P.: 1995, 'A Model for Predicting Continental-Scale Vegetation Distribution and Water Balance', *Ecol. Appl.* **5**, 362–385.

Pastor, J. and Post, W. M.: 1985, *Development of a Linked Forest Productivity–Soil Process Model*, U.S. Dept. of Energy, ORNL/TM-9519.

Prentice, I. C., Sykes, M. T., and Cramer, W.: 1993, 'A Simulation Model for the Transient Effects of Climate Change on Forest Landscapes', *Ecol. Modelling* **65**, 51–70.

Prentice, I. C., Cramer, W., Harrison, S. P., Leemans, R., Monserud, R. A. and Solomon, A. M.: 1992, 'A Global Biome Model Based on Plant Physiology and Dominance, Soil Properties and Climate', *J. Biogeogr.* **19**, 117–134.

Schmid, E.: 1949, *Vegetationskarte der Schwiez*, Atlas der Schweiz, ETH Zürich, Switzerland.

Shugart, H. H.: 1984, *A Theory of Forest Dynamics, The Ecological Implications of Forest Succession Models*, Springer, New York, 278 pp.

Shugart, H. H. and Smith, T. M.: 1996, 'A Review of Forest Patch Models and their Application to Global Change Research', *Clim. Change* **34**, 131–153 (this issue).

SMA (Swiss Meteorological Agency): 1901–90, *Annalen der Schweizerischen Meteorologischen Anstalt*, Swiss Meteorological Agency, Zürich, Switzerland.

Smith, T. M., Leemans, R., and Shugart, H. H.: 1992, 'Sensitivity of Terrestrial Carbon Storage to CO_2-Induced Climate Change: Comparison of Four Scenarios Based on General Circulation Models', *Clim. Change* **21**, 367–384.

Smith, T. M., Shugart, H. H., and Woodward, F. I. (eds): 1996, *Plant Functional Types*, Cambridge Univ. Press, Cambridge.

Solomon, A. M.: 1986, 'Transient Response of Forests to CO_2-Induced Climate Change: Simulation Modeling Experiments in Eastern North America', *Oecologia* **68**, 567–579.

Thornthwaite, C. W. and Mather, J. R.: 1957, 'Instructions and Tables for Computing Potential Evapotranspiration and the Water Balance', *Publ. Climatol.* **10**, 183–311.

Watt, A. S.: 1947, 'Pattern and Process in the Plant Community', *J. Ecol.* **35**, 1–22.

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