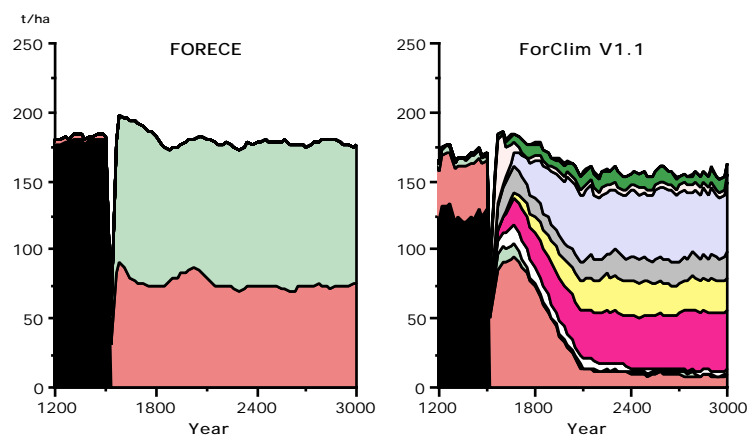


Comparing the Behaviour of Mountainous Forest Succession Models in a Changing Climate

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by

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Abstract

The temporal behaviour of three forest gap models built to simulate species succession in central Europe is compared in the current as well as future climates. The first model, FORECE, represents a conventional forest gap model, the second, FORCLIM 1.1, is an ecologically simplified descendant of the first, and the third model, FORCLIM 1.3, was derived from the second by avoiding any implicit climate dependencies. The species compositions produced by the three models were studied along an altitudinal gradient in the European Alps while manipulating climatic parameters. First, the equilibrium states of the models were calculated for the present climate. Second, starting from the equilibrium states, the step responses of the models were explored by imposing an instantaneous climatic change based on regional projections, which have been statistically downscaled from transient GCM simulations for the next century. According to similarity coefficients all three models produce similar equilibrium species compositions in the present climate. In a changed climate the results suggest that central European forests at high altitudes are more susceptible to temperature changes and that lower forests are more susceptible to precipitation changes. However, some models produce a markedly differing behaviour in a changed climate. Hence, contrary to wide-held expectations, this type of models needs to be thoroughly revised before forest gap models may be applied to assess in details the impacts of climatic change impacts on forests.

INTRODUCTION

In mountainous regions forests fulfil a multitude of functions. They protect settlements from avalanches or landslides; they regulate runoff, thereby helping to prevent erosion; forests and meadows make a varied mountain landscape and provide the environment necessary for various recreational activities; they hold a large fraction of the world's terrestrial carbon, and are also important carbon sequestering systems; finally, and not least, forests are exploited for fuel, pulpwood, and timber. Climatic changes may impact on all these functions (e.g. BOLIN *et al.*, 1986; DAVIS, 1990). However, the complex topography in mountains leads to a large spatial

variability of climate, soil, and other site factors, which makes it difficult to assess their influence on forest dynamics. Moreover, via the tree species composition edaphic factors such as soil organic matter and nutrient availability may have large effects on above functions (PASTOR & POST, 1985; SHUGART *et al.*, 1986; DAVIS, 1990; SHUGART, 1990). Therefore, in mountains it is more important to study the processes involved explicitly and in more details than in flat terrain.

Models of forest succession which are based on the gap dynamics hypothesis (BOTKIN *et al.*, 1972a,b; SHUGART, 1984) operate on similar temporal and spatial scales. These "gap models" simulate the establishment, growth, and death of individual trees partly as a deterministic, partly as a stochastic process confined within small, often $1/12$ ha, plots. The actual forest succession on the ecosystem level is then averaged from the successional patterns simulated for many plots. These models offer the following advantages for studying the impact of climatic change: First, they are based on a well documented ecological theory of tree growth and plant competition (WATT, 1947; BRAY, 1956; CURTIS, 1959; FORMAN & GODRON, 1981). Second, it has been shown that these models incorporate many essential mechanisms and exhibit realistic features of species succession in forest ecosystems (BOTKIN *et al.*, 1972a,b; SHUGART, 1984). Moreover, since forest gap models operate on small spatial scales from 10 m to 1 km, it appears particularly feasible to apply such models to mountainous forests in a complex topography.

Many authors have constructed forest gap models for a wide range of test sites, but all have assumed a constant climate (BOTKIN *et al.*, 1972a,b; SHUGART & WEST, 1977; DOYLE, 1981; PASTOR & POST, 1985; KIENAST, 1987; LEEMANS & PRENTICE, 1989; BONAN, 1992). From the realistic behaviour of forest gap models under current climates some authors have inferred that the models can be used to simulate the impacts of future climatic changes on species composition (e.g. PASTOR & POST, 1988; KIENAST, 1991). Other authors have tried to enhance the trustworthiness of these models by applying them for past constant climates (e.g. SOLOMON *et al.*, 1981; LOTTER & KIENAST, 1992) or for scenarios of past climatic change (e.g. SOLOMON *et al.*, 1980, 1981; SOLOMON & THARP, 1985). However, there remains still a considerable uncertainty concerning the appropriateness of the "facts and concepts" incorporated in gap models, a view shared by some authors such as SOLOMON (1986, p. 568): "*...the errors become amplified (...), generating flaws that are large enough to preclude direct application of the model...*". Moreover, applying these models to a changing climate we found evidence pointing at a considerable input and structural sensitivity of forest gap models in terms of their temporal behaviour (FISCHLIN *et al.*, 1993). Yet, we are not aware of any previous study that explicitly explores the applicability of these models for assessing the impact of climatic change.

Comparing the consistency and robustness of the results produced by several models applied to the same climate might be a means to explore the strengths and limits of forest gap models. This approach requires us to compare closely related members of the same family of models; from a viewpoint of systems theory, each of these models has the same base model and the same experimental frame (ZEIGLER, 1976; FISCHLIN, 1991). Such a study is especially interesting if we do not have unanimously accepted reasons for favouring *a priori* one of the models over the others. These prerequisites are met exactly by the family of models used in this study. The three forest gap models FORECE (KIENAST, 1987), FORCLIM 1.1, and FORCLIM 1.3 (FISCHLIN *et al.*, 1993) can all simulate forest succession for European conditions. The models are built for the same experimental frame, i.e. the same degree of resolution and the same temporal and spatial scales, and differ from each other only in the formulation of climatic influences and with respect to the modelling of some ecological processes.

Models of this type usually require climatic input parameters, such as monthly temperature plus precipitation means and variances. For exploring the applicability of such a model to climatic change, the models should be scrutinized under current and future climates. For the current

climate within the Swiss Alps it is easy to derive these parameters from long-term measurements of weather. However, future climates must be estimated by additional means, for instance by the new methods of downscaling (GYALISTRAS *et al.*, submitted). They allow us to scale down global climates as projected by General Circulation Models (GCM) to a particular weather station. Not only does this downscaling allow for "best estimates" of a future changed climate, e.g. based on the scenarios for greenhouse gas emissions (HOUGHTON *et al.*, 1990), but also to quantify its variability.

Such comparisons have to concentrate on the most interesting impacts of climatic change, i.e. those on which the listed functions of mountainous forests obviously depend strongest. Among those falls the temporal behaviour of the species-specific biomasses, which must not differ beyond certain ranges from model to model if the models are to be considered reliable and applicable to climate change. In case the projected forests should differ substantially from model to model, it may at least be necessary to understand the reasons. Are the differences due to the location, the number of factors incorporated in the model, or the climate parametrization?

In this paper we compare and evaluate the behaviour of the chosen family of models with respect to the following questions: how similar – or how different – are the species compositions simulated by the three models (1) under present climates, (2) under future "best estimate" climates downscaled from GCM results, and (3) under the variability of the downscaled best estimates? Since the downscaling yields site-specific data, we chose several representative test sites along an altitudinal gradient within the European Alps. We found that some models yield similar and consistent results, in particular for current climates, but that they can disagree considerably in other situations.

MATERIAL AND METHODS

The following three forest gap models were used:

The first model, FORECE (KIENAST, 1987), is a conventional gap model derived from LINKAGES (PASTOR & POST, 1985) to accommodate European conditions and species.

The second model, FORCLIM 1.1, is a simplified descendant of FORECE and comprises fewer, i.e. only the most fundamental, ecological processes (BUGMANN, 1991; BUGMANN & FISCHLIN, 1992). Based on a structural sensitivity analysis under the current climate the following processes were dropped: The modification of the rates of sapling establishment by (1) the annual mean and annual amplitude of monthly temperatures (temperature indicators after ELLENBERG, 1986); (2) degree-days; (3) the influence of frost; (4) sprouting from tree stumps, a factor often of little importance in unmanaged forests; (5) the positive feedback of the presence of adult trees on seed availability ("scoring system" after KIENAST, 1987). Moreover, instead of tracking individual trees FORCLIM 1.1 simulates only size cohorts. The parametrization of the climate is done in the same way as in FORECE.

The third model, ForClim 1.3, was developed from ForClim 1.1 by altering the mathematical formulations of the climatic factors (FISCHLIN *et al.*, 1993). The only difference to FORCLIM 1.1 is that it adopts a more reliable parametrization of climate by avoiding any implicit temperature and precipitation dependencies: (1) The calculation of the annual sum of degree-days is corrected for site-specific bias by linear regression; (2) sapling establishment is limited by the minimum of the actual mean temperatures of December, January, and February instead of the long-term mean January temperature, which avoids unrealistic threshold effects when climate changes; (3) the carrying capacity for above-ground biomass (parameter SOILQ in

conventional gap models) is not assumed to be constant but is calculated based on long-term temperature and precipitation data to allow for simulations of climatic change (O'NEILL & DEANGELIS, 1981); (4) drought stress is calculated according to the outlines by PRENTICE & HELMISAARI (1991) instead of using the "dry days" approach (PASTOR & POST, 1985), again avoiding threshold effects. FISCHLIN *et al.* (1993) have described the exact mathematical formulations fully.

Tab. 1: Characteristics and major current climate parameters of the test sites used to simulate the three forest succession models.

Site	Location	Elevation [m above sea level]	annual mean temperature [°C]	annual preci- pitation sum [cm]	potential natural vegetation (ELLENBERG & KLÖTZLI, 1972)
Bern	Swiss Plateau	540	8.4	100.1	mixed deciduous forests dominated by beech (<i>Fagus sylvatica</i> L.) and silver fir (<i>Abies alba</i> Miller)
Davos	Northern Alps	1560	3.0	101.1	coniferous forests dominated by larch (<i>Larix decidua</i> Miller) and spruce (<i>Picea abies</i> L.)
Bever	Central Alps	1708	1.5	83.8	coniferous forests dominated by larch (<i>Larix decidua</i> Miller) and Swiss Stone pine (<i>Pinus cembra</i> L.)

The following reasons lead to the selection of the test sites Bern, Davos, and Bever (Tab. 1): These three sites represent three dominant belts of vegetation determined by altitude (Tab. 1; plant nomenclature according to HESS *et al.*, 1980), and long term climate records have been compiled by the Swiss Meteorological Agency (BANTLE, 1989; SMA, 1901-1990), which allow us to calculate reliable long-term means and standard deviations of monthly temperatures and precipitation sums (FISCHLIN *et al.*, 1993).

Scenarios for future climates at the test sites (Tab. 2) were obtained by statistical downscaling which relates large-scale temperature and pressure anomalies (North Atlantic, Europe) to local weather anomalies by means of principal component analysis and canonical correlation analysis (GYALISTRAS *et al.*, submitted). The data for this downscaling were provided by a 100 year (1986-2085) uncorrected transient run of the ECHAM General Circulation Model (CUBASCH *et al.*, 1992) for the IPCC "Business As Usual" Scenario A (HOUGHTON *et al.*, 1990). Using the downscaled trends (Tab. 2) we computed the anomalies of the mean winter (Dec-Feb) and summer (Jun-Aug) temperature (T) and precipitation (P). The values obtained were added to the site specific current monthly means and applied during 6 months each (summer - Apr-Sep, winter - Oct-Mar). Since any scenario of climatic change is based on essentially unknown assumptions about the future (HOUGHTON *et al.*, 1990), we compared the behaviour of each model within the range of ca. 95% (± 2) of those 84 downscaling models which performed best in the validation period (GYALISTRAS *et al.*, submitted). Fig. 1 (centre) gives an example of typical simulation results as obtained with the three models for the best estimate of climatic change, whereas the effect of varying this estimate by ± 2 is shown in the corners (Fig. 1).

At each site, the equilibrium states of the gap models were calculated for the present climate during the first 1500 simulation years. Second, starting from the equilibrium states, the step response of the models was explored by imposing an instant climatic change based on the downscaled projections described above, and the simulations ended after 3000 years (Fig. 1). Average species biomasses were calculated from 200 stochastic runs (BUGMANN & FISCHLIN, 1992). The equilibrium states were estimated by averaging the results over the periods 1000-1500 and 2500-3000 simulation years for current and future climates, respectively. The

ForClim models were simulated on an Apple Macintosh IIfx computer using the simulation software ModelWorks and RAMSES (FISCHLIN *et al.*, 1990; FISCHLIN, 1991). Simulations with the model FORECE are less efficient and were thus executed on a SUN SS630 workstation.

Tab. 2: Site specific winter and summer temperature (T) resp. precipitation (P) changes projected for the year 2100 relative to current climatic conditions (1901-1990 for Bern and Davos, 1901-1980 for Bever). These climatic scenarios are based on downscaled trends from a "Business As Usual" transient ECHAM GCM run (CUBASCH *et al.*, 1992; GYALISTRAS *et al.*, submitted). **Trend(μ)**: linear trend of the mean (1986 to 2085); **Mean(s)**: standard deviation in 2036 (= average of period 1986-2085); **Trend(s)**: linear trend of the standard deviation (1986 to 2085). **T₀P₀**: "best estimate" of changes for year 2100 extrapolated from Trend(μ). **X \pm** : lower/upper end of confidence interval for variable X, $X_{\pm} = X_0 \pm 2 \cdot s_{2100}$, where s_{2100} is the standard deviation for 2100 extrapolated from Trend(s) and Mean(s).

Site		Winter (Dec-Feb)		Summer (Jun-Aug)	
		T [°C]	P [cm · month ⁻¹]	T [°C]	P [cm · month ⁻¹]
Bern	Trend(μ)	3.27	2.73	2.30	3.46
	Mean(s)	0.37	0.57	0.30	1.06
	Trend(s)	0.46	0.44	0.48	1.42
	T ₀ P ₀	3.76	3.13	2.64	3.98
	T+P+	5.09	4.85	3.85	7.94
	T+P-	5.09	1.42	3.85	0.02
	T-P+	2.43	4.85	1.43	7.94
	T-P-	2.43	1.42	1.43	0.02
	Davos	Trend(μ)	2.61	1.86	2.85
Mean(s)		0.35	0.96	0.20	0.58
Trend(s)		0.43	0.96	0.27	0.60
T ₀ P ₀		3.00	2.14	3.28	0.91
T+P+		4.26	5.32	4.02	2.86
T+P-		4.26	-1.03	4.02	-1.05
T-P+		1.74	5.32	2.53	2.86
T-P-		1.74	-1.03	2.53	-1.05
Bever		Trend(μ)	1.28	2.21	3.62
	Mean(s)	0.27	0.35	0.36	0.64
	Trend(s)	0.32	0.38	0.67	0.86
	T ₀ P ₀	1.48	2.54	4.16	3.82
	T+P+	2.42	3.74	5.75	6.21
	T+P-	2.42	1.35	5.75	1.43
	T-P+	0.53	3.74	2.57	6.21
	T-P-	0.53	1.35	2.57	1.43

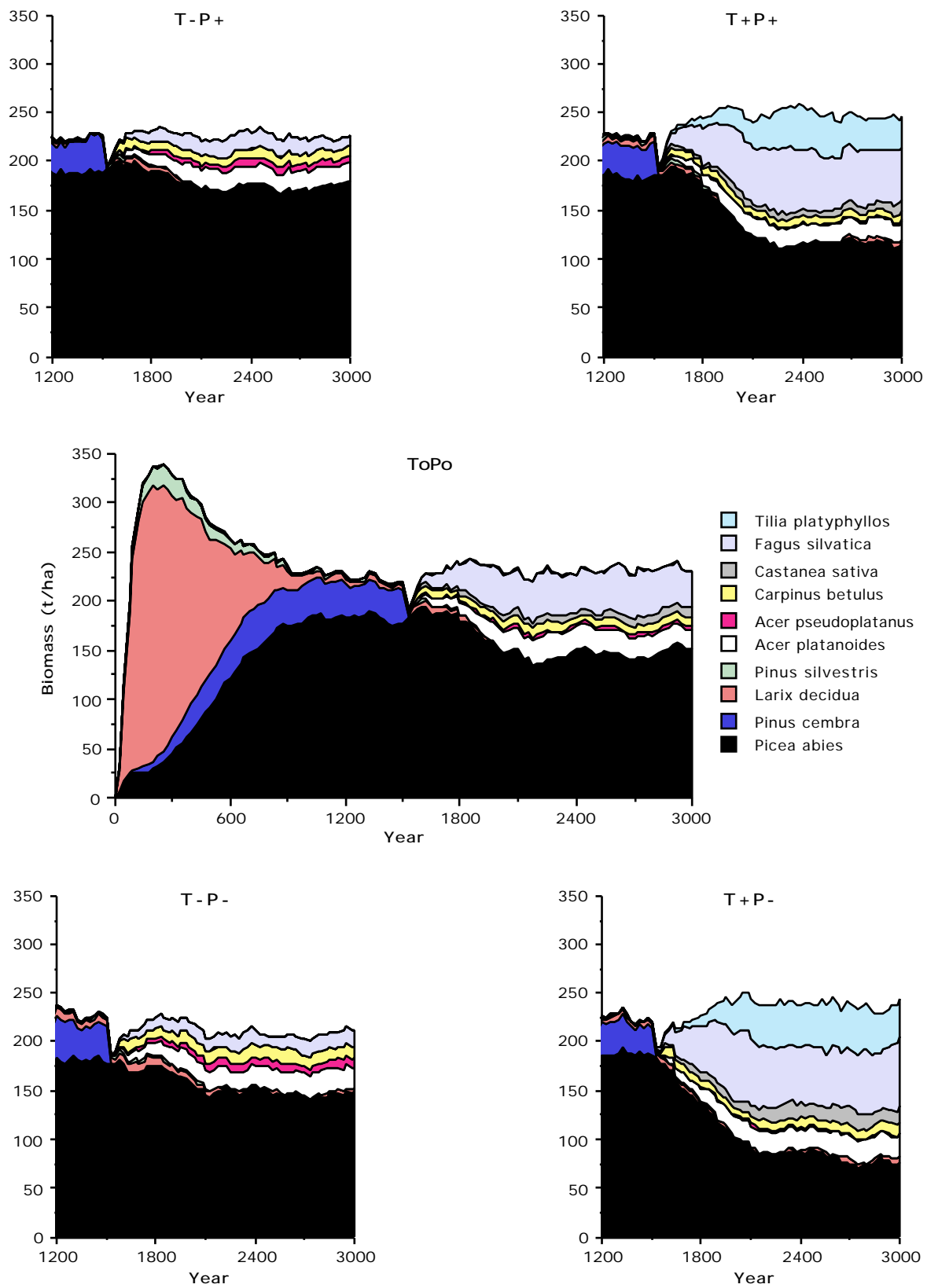


Fig. 1: Species compositions simulated by FORCLIM model version 1.3 at Davos (Tab. 1): First 1500 years of primary forest succession in the current climate, second 1500 years of secondary forest succession in response to a downscaled best estimate (T_0P_0) step change in the global climate (centre). The panels in the corners show the model's secondary successional step responses (corners) to the uncertainties inherent in the climatic change scenarios (Tab. 2).

The differences between the equilibrium states of species biomasses produced by the various models and climate scenarios were quantified using a percentage similarity coefficient (PS) (e.g. PRENTICE & HELMISAARI, 1991), which relates any two sets of data $X = \{x_1, x_2, \dots, x_n\}$ and $Y = \{y_1, y_2, \dots, y_n\}$ as follows:

$$PS = 1 - \frac{\sum_{i=1}^n |x_i - y_i|}{\sum_{i=1}^n (x_i + y_i)} \quad (1)$$

where $0 \leq PS \leq 1$. This coefficient can be interpreted as the fraction of values common to both sets of data. It offers the following advantage: not only does it track differences in the relative distributions of the x_i and y_i values (e.g. species-specific biomasses), but it also declines the larger the difference between the sums $\sum x_i$ and $\sum y_i$ (e.g. total biomass) becomes.

RESULTS

In this study we focused on the comparison among steady states of biomasses computed as t/ha per tree species. All three models can reach a singular steady state. Simulation experiments showed that the equilibrium biomasses calculated from 200 simulation runs have a standard error smaller than 10% of their mean. These steady states are reached after a rather long transient behaviour lasting between 400 (Fig. 3 left) and more than 700 years (Fig. 1, Fig. 3 right).

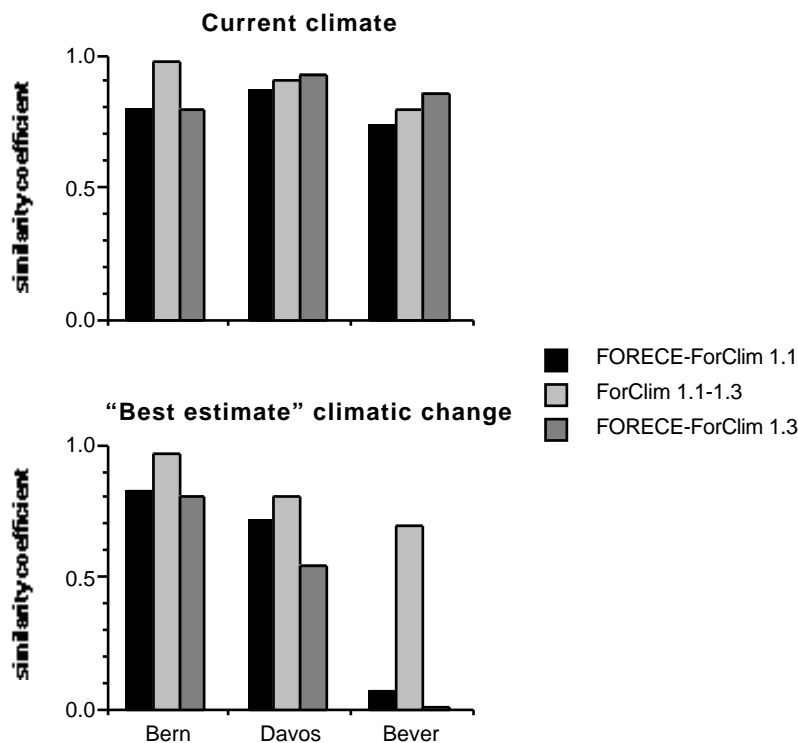


Fig. 2: Similarity coefficients computed for all possible pairs of the three model versions at the three test sites: (top) under current climate, (bottom) under the downscaled best estimate (T_0P_0) of the changed climate projected by the ECHAM GCM for the end of the next century (Tab. 2).

The estimated steady states appear not to depend on the initial states. This allows us to compare the results obtained with species compositions observed in real forests, although there exist no precise field data on the true initial states at the three test sites.

For the current climate the steady states simulated by the three models show realistic species compositions at all three sites: The mixed deciduous forest at Bern is dominated by common beech (*Fagus sylvatica* L.) and silver fir (*Abies alba* Mill.); subalpine coniferous forests at Davos are composed mainly of Norway spruce (*Picea abies* L.) and European larch (*Larix decidua* Miller) (Fig. 1 centre); simulated forests at Bever are dominated by European larch and Swiss stone pine (*Pinus cembra* L.) (Fig. 3). Moreover, the simulated species compositions compare well with phytosociological descriptions by ELLENBERG & KLÖTZLI (1972) and ELLENBERG (1986). For the FORECE model, this has been discussed in detail by KIENAST & KUHN (1989). The large percentage similarity coefficients (Fig. 2 top) show the good agreement among all three models for the current climate.

Depending on the test site, we observed diverging similarity coefficients among projected steady states under the best estimate scenario for the climate at the end of the next century: The smallest differences between the models were found at Bern (540 m a.s.l.), medium ones at Davos (1560 m a.s.l.), and marked differences were found at Bever (1708 m a.s.l.; Fig. 2 bottom). Thus, the degree of divergence among the three models correlates positively with elevation. Moreover, the similarity coefficients between the species compositions in the current climate and those in the future best estimate climate also decrease with increasing altitudes (Fig. 4, column BE), i.e. the higher the site the more different the communities might become due to the climatic change.

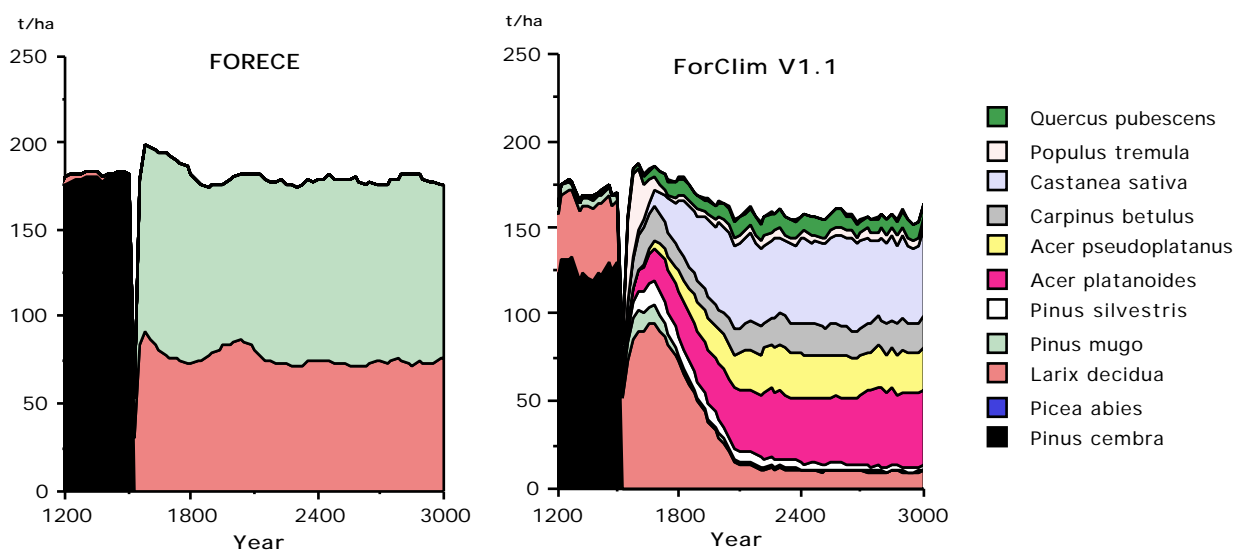


Fig. 3: Species compositions simulated by the forest succession model FORECE (left) respectively FORCLIM model version 1.1 (right) at Bever (Tab. 1). Both simulations represent step responses to the downscaled best estimate (T_0P_0) of the changed climate as projected by the ECHAM GCM for the end of the next century (Tab. 2).

Not only is the downscaled variability in the input data of the same order of magnitude as the estimates of the uncertainty inherent in GCM simulations, but the response of the forest models remains within a similar range (FISCHLIN *et al.*, 1993). The simulations with each model performed at each test site along the borders of the scenario ranges showed the following. The higher the site, the less similar are a model's steady states, which were generated while the climatic scenario was modified (Fig. 1, Fig. 4):

Precipitation changes appear to influence species composition mainly at lower elevations (Fig. 4, column P). Only at Bern do the similarity coefficients diverge. This behaviour can be explained by a threshold effect associated with the way drought effects are modelled (FISCHLIN *et al.*, 1993). Moreover, since we found in other studies that low dry sites are sensitive to changes of precipitation, we expect that the response of the models at Basel or Sion to changing precipitation sums could be even stronger than that found at Bern (Fig. 4, P top).

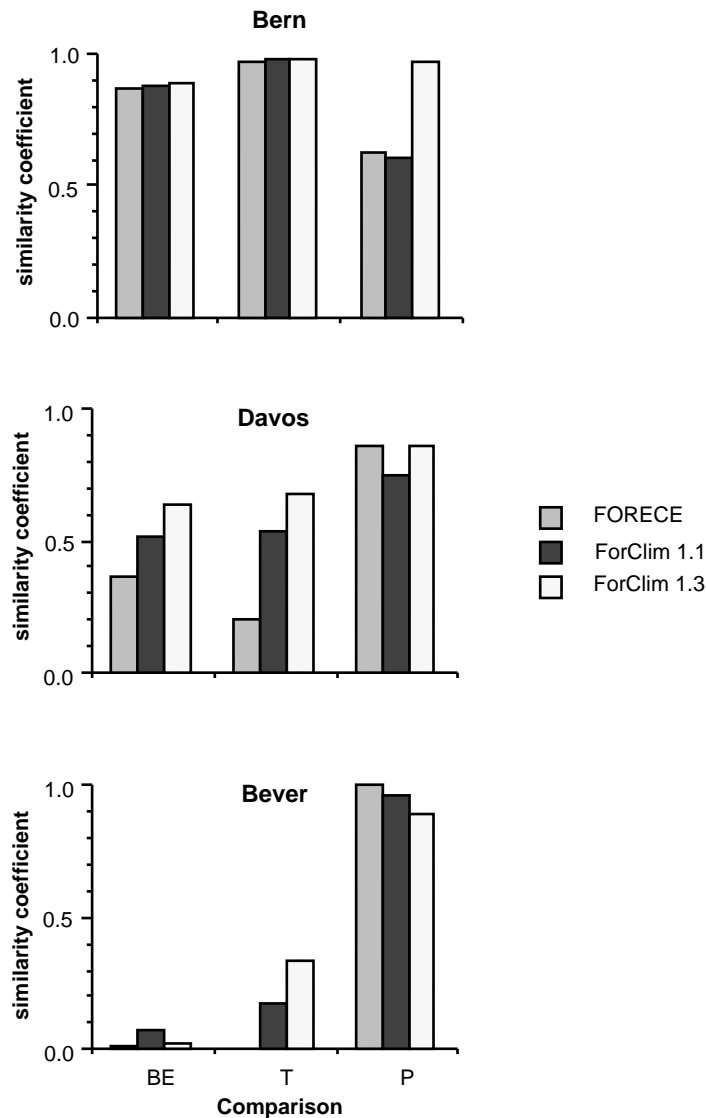


Fig. 4: Similarity coefficients computed between pairs of species steady states simulated by the same model while modifying climatic conditions: BE: Similarity between current climate and downscaled best estimate (T_0P_0). T: Similarity between T-P+ and T+P+ scenarios (temperature gradient). P: Similarity between T+P+ and T+P- scenarios (precipitation gradient) (Tab. 2).

Temperature changes have strong influences on species composition at higher elevations (Fig. 4, column T). The similarity coefficients are large and differ little at low altitudes (Fig. 4, top). They become smaller and diverge more with increasing elevation of the test sites. This augmented temperature sensitivity was found in all models, and it corroborates the expected temperature dependency of the alpine treeline. At these elevations the different formulations of degree-days and winter temperature are responsible for model divergence, whereas they are of little significance at lower elevations.

Discussion

Not only do the three models produce in 8 out of 9 comparisons for current climate (89%) consistent results with large inter-model similarity coefficients ($PS > 0.75$; Fig. 2 top), but their behaviour appears also to be in good accordance with field data wherever they are available and have been produced by model equations which conform with the current ecological theory of the processes governing the species composition of a forest stand. These findings corroborate the results and expectations of many other authors (BOTKIN *et al.*, 1972a,b; SHUGART & WEST, 1977; DOYLE, 1981; SHUGART, 1984; PASTOR & POST, 1985; KIENAST, 1987; LEEMANS & PRENTICE, 1989; BONAN, 1992). On this basis alone it would not be possible to favour one model over another, especially since they all have been built for similar purposes and are all applicable to central European forests.

On the other hand, the comparisons among the three models did reveal that their response to climatic change differ markedly in 23 out of 45 cases (51%). Thus, their application to assessing the impact of climatic change might not be as easy as some authors have thought.

What were the causes for the different behaviours? Under a changed climate the models respond more strongly to the complete elimination of factors that depend on the ecology or the climate (FORCLIM 1.1) than to slight modifications of model equations (FORCLIM 1.3). Especially the elimination of the temperature indicators after ELLENBERG (1986) in the model FORCLIM 1.1 has strong effects at the sites Davos and Bever. The use of these indicators in FORECE may be questioned: First, many species are excluded arbitrarily because of the indicators' discrete nature. Second, it is the current weather which really influences the establishment of saplings, not the long-term mean difference of the temperature between the warmest and the coldest month. FORCLIM 1.1 does not require us to assume such statistical relations, and is based to a larger extent on plausible, causal mechanisms.

Moreover, the steady state species compositions for current climate as simulated by the FORCLIM models are often more realistic (ELLENBERG & KLÖTZLI, 1972; ELLENBERG, 1986), e.g. for *Acer platanoides* L. at Bern and *Larix decidua* L. at Bever. The behaviour of the FORCLIM 1.3 model at sites closer to the precipitation limited treeline simulates the climatic influences more realistically. It avoids threshold effects due to discrete functions (FISCHLIN *et al.*, 1993), which are responsible for some of the observed strong dissimilarities (Fig. 4) and appear rather to be artefacts. Based on these findings we favour FORCLIM 1.3 over the other two models.

Although some results are contradictory and the exact species compositions might not always be predictable, it is possible to draw several conclusions from the results. As a consequence of assessed climatic changes strong responses in species composition can not be ruled out, and in certain environmental conditions they are even likely. This conforms again with the findings from earlier studies, although they have not been able to use GCM downscaled climate scenarios (SOLOMON, 1986; PASTOR & POST, 1988; OVERPECK *et al.*, 1990; KIENAST, 1991; FISCHLIN *et al.*, 1993).

In particular, as expressed by the sequence of sites Bever, Davos, and Bern (Fig. 4 left), the high forests appear to be more susceptible than the lower ones. This pattern supports findings by IPCC that subalpine forests might be especially susceptible (IZRAEL *et al.*, 1990) and also corroborates the climatological interpretation of tree-rings from subalpine zones (e.g. KIENAST & SCHWEINGRUBER, 1986).

Conclusion

Within a large range of altitudes the models of forest succession studied respond to a climatic change by adapting their species compositions. The response of the models to climates downscaled from transient GCM simulations (CUBASCH *et al.*, 1992; GYALISTRAS *et al.*, submitted) for the end of the next century based on the IPCC "Business As Usual" scenario contrasts in some cases sharply with the steady states for current climatic conditions. Since the steady states of all the models appear to be globally stable, this statement can be made independently of the exact course of the primary succession in a constant climate (Fig. 1) as well as of the secondary succession following climatic changes. The successional transient response to a step in the climate abates only after about 400 up to a maximum of 700 years (Fig. 1, Fig. 2 right). This is of the same order of magnitude as abyssal oceans respond (FLOHN & FANTECHI, 1984; CUBASCH *et al.*, 1992).

The results suggest for forests within the European Alps that those at lower altitudes might be most susceptible to a drier climate, whereas at higher altitudes, especially in the subalpine zone, species compositions might be more susceptible to a warmer climate (Fig. 4). In general we tentatively conclude that the forests least susceptible to climatic change are at mid altitudes, i.e. in the montane zone. However, these findings may not generally hold in other climates, since the three test sites represent only a small fraction of possible climates in the parameter space of temperature and precipitation. More thorough and systematic sensitivity analysis would be necessary before general conclusions could be drawn (FISCHLIN *et al.*, 1993).

The members of our family of forest gap models show similar results under present climate (Fig. 3), but may produce markedly diverging steady state species compositions under a changed future climate. The observed differences depend partly on the exact mathematical formulations of the climate parametrization, the kind of ecological processes encapsulated in the models, and the assumed climatic scenarios plus their range of uncertainty (Fig. 1, scenario T-P+ vs. scenario T+P-). Thus, the fact that a gap model performs well in the present climate is not sufficient to furnish it equally applicable for a detailed study of the impact of climatic change on forests.

Sound criteria are needed to select the best performing member from a model family; this is particularly important if the members' behaviour diverge substantially in some conditions. Besides judging the validity of a model by comparing its behaviour with site specific field data under the current climate, the following additional criteria could be advanced: We favour the youngest member of the family over the other two models because FORCLIM 1.3 exhibits a realistic behaviour at more sites, its mathematical formulation is more rigorous, and it depends to a larger extent on causal relationships (FISCHLIN *et al.*, 1993).

From the observed discrepancies among models and their explanations, we surmise that many conventional forest gap models are not robust and sound enough to be used for detailed assessments of the impact of climatic change. Yet, it appears promising to improve and revise them by first analyzing the causes of inconsistencies, secondly reformulating their equations, and thirdly validating them against various, e.g. past, changing climates before they are applied in future impact studies of climatic change.

References

- Bantle, H., 1989. *Programmdokumentation Klima-Datenbank am RZ-ETH Zürich*. Swiss Meteorological Agency, Zürich.
- Bolin, B., Döös, B.R., Jäger, J. & Warrick, R.A., 1986. *The greenhouse effect, climatic change and ecosystems*. Wiley, Chichester a.o. (SCOPE Vol. 29), 541 pp.
- Bonan, G.B., 1992. *A simulation analysis of environmental factors and ecological processes in North American boreal forests*. In: Shugart, H.H., Leemans, R. & Bonan, G.B. (eds.), *A systems analysis of the global boreal forest*. Cambridge Univ. Press, Cambridge a.o., 404-427.
- Botkin, D.B., Janak, J.F. & Wallis, J.R., 1972a. *Some ecological consequences of a computer model of forest growth*. *J. Ecol.*, **60**: 849-872.
- Botkin, D.B., Janak, J.F. & Wallis, J.R., 1972b. *Rationale, limitations and assumptions of a northeastern forest growth simulator*. *IBM J. Res. Develop.*, **16**: 101-116.
- Bray, J.R., 1956. *Gap-phase replacement in a maple-basswood forest*. *Ecology*, **37**: 598-600.
- Bugmann, H., 1991. *Development of FORCLIM-P, a simplified forest gap model for workstations and personal computers*. Internal paper, Systems Ecology Group, ETHZ, 8092 Zürich, 60 pp.
- Bugmann, H. & Fischlin, A., 1992. *Ecological processes in forest gap models – analysis and improvement*. In: Teller, A., Mathy, P. & Jeffers, J.N.R. (eds.), *Responses of forest ecosystems to environmental changes*. Elsevier Applied Science, London & New York, 953-954.
- Cubasch, U., Hasselmann, K., Höck, H., Maier-Reimer, E., Mikolajewicz, U., Santer, B. & Sausen, R., 1992. *Time-dependent greenhouse warming computations with a coupled ocean-atmosphere model*. *Climate Dynamics*, **8**: 55-69.
- Curtis, J.T., 1959. *The vegetation of Wisconsin*. Univ. of Wisconsin Press, Madison.
- Davis, M.B., 1990. *Biology and palaeobiology of global climate change: Introduction*. *Trends in ecol. and evol.*, **5**: 269-270.
- 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. & Botkin, D.B. (eds.), *Forest succession: concepts and application*, Springer, New York a.o., 56-73.
- Ellenberg, H., 1986. *Vegetation Mitteleuropas mit den Alpen in ökologischer Sicht*. Verlag Eugen Ulmer, Stuttgart. 4th ed., 989 pp.
- Ellenberg, H. & Klötzli, F., 1972. *Waldgesellschaften und Waldstandorte der Schweiz*. Eidg. Anst. Forstl. Versuchswes., Mitt., **48**: 587-930.
- Fischlin, A., 1991. *Interactive modeling and simulation of environmental systems on workstations*. In: Möller, D.P.F. (ed.), *Proc. of the 4th Ebernburger Working Conference on the analysis of dynamic systems in medicine, biology, and ecology*, April, 5-7, 1990, Ebernburg, Bad Münster, BRD. Informatik-Fachberichte 275, Springer, Berlin a.o., 131-145.
- Fischlin, A., Bugmann, H. & Gyalistras, D., 1993. *Sensitivity of a forest ecosystem model to climate parametrization schemes*. *Env. Pollution*, submitted.
- Fischlin, A., Roth, O., Gyalistras, D., Ulrich, M. & Nemecek, T., 1990. *ModelWorks: An interactive simulation environment for work stations and personal computers*. Internal Report No. 8, Systems Ecology Group, ETH Zurich, 200 pp.

- Flohn, H. & Fantechi, R. (eds.), 1984. *The climate of Europe: Past, present and future*. Reidel, Dordrecht a.o., 355 pp.
- Forman, R.T.T. & Godron, M., 1981. *Patches and structural components for a landscape ecology*. *Bioscience*, **31**: 733-740.
- Gyalistras, D., von Storch, H., Fischlin, A. & Beniston, M., 1993. *How to link GCM generated climate scenarios to ecosystems? Case studies of statistical downscaling in the Alps*. Climate Research, submitted.
- Hess, H.E., Landolt, E. & Hirzel, R., 1980. *Flora der Schweiz*. Birkhäuser, Basel & Stuttgart, 4 Vol., 2nd ed.
- Houghton, J.T., Jenkins, G.J. & Ephraums, J.J. (eds.), 1990. *Climate change - the IPCC scientific assessment*. Report prepared for IPCC by Working Group 1. Cambridge Univ. Press, Cambridge a.o.
- Izrael, Y.A., Hashimoto, M. & Tegart, W.J.M. (eds.), 1990. *Climate change - the IPCC impact assessment*. Report prepared for IPCC by Working Group 2. Cambridge Univ. Press, Cambridge a.o.
- Kienast, F., 1987. *FORECE - A forest succession model for southern central Europe*. Oak Ridge National Laboratory, Oak Ridge, Tennessee, ORNL/TM-10575, 69 pp.
- Kienast, F., 1991. *Simulated effects of increasing CO₂ on the successional characteristics of Alpine forest ecosystems*. *Landscape Ecology*, **5**: 225-238.
- Kienast, F. & Schweingruber, F.H., 1986. *Dendroecological studies in the Front Range, Colorado, U.S.A.*. *Arctic and Alpine Research*, **18**: 277-288.
- Kienast, F. & Kuhn, N., 1989. *Simulating forest succession along ecological gradients in southern Central Europe*. *Vegetatio*, **79**: 7-20.
- Lotter, A. & Kienast, F., 1992. *Validation of a forest succession model by means of annually laminated sediments*. In: Saarnisto, M. & Kahra, A. (eds.), *Proceedings of the INQUA workshop on laminated sediments, June 4-6, 1990, Lammi, Finland*. Geological Survey of Finland, Special paper series, **14**: 25-31.
- O'Neill, R.V. & DeAngelis, D.L., 1981. *Comparative productivity and biomass relations of forest ecosystems*. In: Reichle, D.E. (ed.), *Dynamic properties of forest ecosystems*. IBP publication no. 23, Cambridge Univ. Press, Cambridge a.o., 411-449.
- Overpeck, J.T., Rind, D. & Goldberg, R., 1990. *Climate-induced changes in forest disturbance and vegetation*. *Nature*, **343**: 51-53.
- Pastor, J. & Post, W.M., 1985. *Development of a linked forest productivity-soil process model*. U.S. Dept. of energy, ORNL/TM-9519.
- Pastor, J. & Post, W.M., 1988. *Response of northern forests to CO₂-induced climate change*. *Nature*, **334**: 55-58.
- Prentice, I.C. & Helmisaari, H., 1991. *Silvics of north European trees: Compilation, comparisons and implications for forest succession modelling*. *For. Ecol. Manage.*, **42**: 79-93.
- Shugart, H.H., 1984. *A theory of forest dynamics. The ecological implications of forest succession models*. Springer, New York a.o., 278 pp.
- Shugart, H.H., 1990. *Using ecosystem models to assess potential consequences of global climatic change*. *Trends in ecol. and evol.*, **5**: 303-307.

-
- Shugart, H.H. & West, D.C., 1977. *Development of an Appalachian deciduous forest succession model and its application to assessment of the impact of the chestnut blight*. *J. Env. Mgmt.*, **5**: 161-179.
- Shugart, H.H., Antonovsky, M. Ya., Jarvis, P.G. & Sandford, A.P., 1986. *CO₂, climatic change, and forest ecosystems*. In: Bolin, B., Döös, B.R., Jäger, J. & Warrick, R.A. (eds.), *The greenhouse effect, climatic change and ecosystems*. Wiley, Chichester a.o. (SCOPE Vol. 29), 475-522.
- SMA (Swiss Meteorological Agency), 1901-90. *Annalen der Schweizerischen Meteorologischen Anstalt*. Swiss Meteorological Agency, Zürich.
- Solomon, A.M., 1986. *Transient response of forests to CO₂-induced climate change: simulation modeling experiments in eastern North America*. *Oecologia*, **68**: 567-579.
- Solomon, A.M. & Tharp, M.L., 1985. *Simulation experiments with late quaternary carbon storage in mid-latitude forest communities*. In: Sundquist, E.T. & Broecker, W.S. (eds.), *The carbon cycle and atmospheric CO₂: natural variations archean to present*. American Geophysical Union, Washington D.C. Geophysical Monograph Vol. 32, 235-250.
- Solomon, A.M., West, D.C. & Solomon, J.A., 1981. *Simulating the role of climate change and species immigration in forest succession*. in: West, D.C., Shugart, H.H. & Botkin, D.B. (eds.), *Forest succession: concepts and application*, Springer, New York a.o., 154-177.
- Solomon, A.M., Delcourt, H.R., West, D.C. & Blasing, T.J., 1980. *Testing a simulation model for reconstruction of prehistoric forest-stand dynamics*. *Quat. Res.*, **14**: 275-293.
- Watt, A.S., 1947. *Pattern and process in the plant community*. *J. Ecol.*, **35**: 1-22.
- Zeigler, B.P., 1976. *Theory of modelling and simulation*. John Wiley, New York a.o., 435 pp.

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