

SENSITIVITY OF A FOREST ECOSYSTEM MODEL TO CLIMATE PARAMETRIZATION SCHEMES

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(Received 23 July 1992; accepted 3 March 1994)

Abstract

An analysis of the climate parametrization scheme adopted by conventional forest gap models revealed that most models assume a constant climate and are difficult to calibrate consistently. Tree growth showed unrealistically sensitive threshold effects along ecological gradients of temperature and precipitation. A new parametrization was compared with its predecessors in terms of the model's capability to predict realistic steady state species compositions at three test sites in the Alps. Applying the new model variant FORCLIM to some climate-change scenarios suggests that forest gap models are highly sensitive to climate parametrizations, regardless of the realism with which they simulate forests for the current climate. Moreover, the precision of climate scenarios based on General Circulation Models (GCM), for example, falls short of FORCLIM's sensitivity. Climate-dependent processes in forest gap models should be rehearsed before these models are used in impact studies of climatic change.

INTRODUCTION

Studies investigating climate-change impact on terrestrial ecosystems are confronted with a variety of problems (Bolin *et al.*, 1986; Shands & Hoffman, 1987; Parry *et al.*, 1988; IGBP, 1989; Houghton *et al.*, 1990). This study addresses the influence of climate on ecosystems in the following three ways. First, how is climate derived from a few measured realizations, i.e. local weather, the characteristics of the underlying stochastic process? Second, many different climatic parameters can be used to relate with ecologically relevant weather variables with climate. Possible climatic parameters range, for instance, from mean air temperature to the variance of the number of days per month without precipitation. Which are relevant to understanding a weather-dependent process, such as ecosystem net primary production or the extinction of a particular species? Third, once some climatic parameters have been identified, how will they be linked to ecosystem models; i.e. to which input variables, model parameters, or ecological processes shall they be coupled?

In the present analysis, forests were selected as case studies along an altitudinal transect through the European Alps, offering strongly varying environmental factors within a small region. For the sake of simplicity and according to the IGBP[†] core project *Global Change and Terrestrial Ecosystems*, the bi-directional interaction between atmosphere and biosphere was split into its parts, i.e. only the impact of climate on terrestrial ecosystems was considered (IGBP, 1989, 1992). Feedbacks such as the carbon balance, surface roughness, albedo or evapotranspiration were deliberately left out, yet this approach allows them to be added later as necessary.

Within recent years, possible impacts of climatic change on terrestrial ecosystems, especially forests, has attracted much public and scientific attention (Schneider, 1989; Houghton *et al.*, 1990). The widely used forest gap models (Botkin *et al.*, 1972a; Shugart & West, 1977; Shugart, 1984) are capable of producing realistic transient and climax forests for current climatic conditions and operate on a spatial and temporal scale that is of interest to climate-change impact studies. Hence, many gap models have already been applied to project future forests under scenarios of a changing climate (Solomon *et al.*, 1981, 1984; Solomon, 1986; Solomon & West, 1987; Pastor & Post, 1988; Overpeck *et al.*, 1990; Kienast, 1991). However, because gap models were not originally intended to be applied to such ends, most of them contain climatic parametrizations that assume a constant climate, such as the carrying capacity of above-ground biomass (Botkin *et al.*, 1972a,b) or the length of the growing season (Pastor & Post, 1985). To treat climatic influences more adequately, forest gap models and their climate parametrization schemes have to be carefully scrutinized, and the model equations modified by replacing static climate parametrizations with more flexible solutions. Thus, there arises the question, to what extent do conventional forest gap models make explicit or implicit assumptions on climate or treat climatic effects only marginally? Further, would the models still behave realistically if these assumptions were relaxed or removed?

The intrinsic variability within climatic parameters may also affect the behaviour of a forest gap model, but

[†]The International Geosphere-Biosphere Program: A Study Of Global Change

little is known about this kind of sensitivity. Since the parameter space of forest gap models is huge, e.g. spanning close to 600 parameters for central Europe, and since these models are stochastic, a systematic, all-inclusive sensitivity analysis is prohibitive. Therefore, it is not surprising that sensitivity studies have only been conducted for small subsets of parameters. Botkin and Nisbet (1992) have studied the sensitivity of the JABOWA-II model to sampling errors due to the time-window used to select measurements of temperature and precipitation. They found that the model generally is not sensitive to a 10% error in parameter estimation. Climate-dependent parameters whose sensitivities have been investigated are the minimum and maximum degree-day parameters (Kercher & Axelrod, 1984; Botkin & Nisbet, 1992) and a drought-tolerance parameter (Botkin & Nisbet, 1992); the others are biological or physical parameters (e.g. Leemans, 1991). However, no studies are known to have investigated a forest gap model's structural sensitivity with respect to climate, i.e. its sensitivity to different parametrizations of climate-dependent processes.

This paper will first analyse the climate parametrizations of the model FORCLIM I (Bugmann, 1991), derived from the gap model, FORECE (Kinast, 1987). Both models use the same climate parametrizations but consider different biotic processes. We then propose some improved climate parametrization schemes, leading to a new model variant (FORCLIM II) which parametrizes climate in an explicit and more flexible way. Again this questions how sensitive model behaviour is to such modifications. We present an approach to analyse efficiently the sensitivity of the steady state behaviour of FORCLIM II relative to uncertainties in the climatic input parameters and changes in the process formulations. Finally we discuss the consequences from these findings for FORCLIM's applicability to the temperate and boreal zone of the northern hemisphere.

MATERIALS AND METHODS

Abbreviations

Tables 1 and 2 show the mathematical notation and functions and the symbols and abbreviations used in this study. Variables are subscripted according to the

following convention: the subscripts y (year), m (month), d (day), l (location), or s (species) denote that the variable is specific in respect to the subscripted item. In case of temperature and precipitation, omission of one of the subscripts y, m, or d denotes an aggregation over the respective time resolution. Otherwise, it denotes that the quantity in question depends on a certain year, month, or day, respectively, but not directly on any of the parameters omitted. For instance, the long-term means for monthly mean temperatures as estimated from, say, 60 years are represented by the symbols $T_{Jan,l}$, $T_{Feb,l}$, or in general $T_{m,l}$, (see eqn 1), whereas the annual mean for a given year at a given site is simply denoted as T_j . On the other hand, an interannually varying, location-specific quantity X (X different from temperature or precipitation) is denoted as $X_{y,l}$.

Sites and climatic data

All test sites used in the present study are located in Switzerland and are in the vicinity of the European Alps (see Table 3). The sites allow forests to be studied at differing altitudes under various temperature and precipitation regimes. Some other Swiss locations (Basel, Davos, Locarno) along an ecological gradient from north to south across the Alps were included for special purposes (see Table 5).

Climatological parametrizations were based on daily mean, minimum, and maximum temperatures and daily precipitation sums extracted from the database of the Swiss Meteorological Agency (SMA), Zurich (Bantle, 1989; SMA, 1901–90). The climate stations considered correspond to the selected test sites listed in Table 3. Data are available from 1901–90, 1901–80, and 1901–77 for Bern, Bever, and Sion, respectively, but daily minimum and maximum temperatures for Sion are available only from 1965–77. For each station, long-term monthly temperature means $E[T_{m,l}]$, precipitation sums $E[P_{m,l}]$ and their variances were calculated (eqns 1 and 2).

$$E[T'_{m,l}] \approx \frac{1}{nYrs_{m,l}} \cdot \sum_{y=1}^{nYrs_{m,l}} T_{m,y,l}$$

$$= \frac{1}{nYrs_{m,l}} \cdot \sum_{y=1}^{nYrs_{m,l}} \left(\frac{1}{nDays_m} \cdot \sum_{d=1}^{nDays_m} T_{d,m,y,l} \right) \quad (1)$$

Table 1. List of functions and mathematical notations

$E[X_i]$	Expected value of random variable X_i (for meaning of subscripts see below)
$VAR[X_i]$	Variance of random variable X_i
$X_i \sim N(\mu, \sigma^2)$	Normally distributed random variable X with expected value μ and variance σ^2
$MAX(x_1, \dots, x_n)$	Maximum of n values x_1, x_2, \dots, x_n
$MIN(x_1, \dots, x_n)$	Minimum of n values x_1, x_2, \dots, x_n
$SIGN(q)$	Sign of quantity q (equal to +1 if $q > 0$, 0 if $q = 0$, -1 otherwise)
$f(x, y, \dots)$	A real function with arguments x, y, \dots not specified in detail
y	Subscript denoting a year
m	Subscript denoting a month [Jan–Dec]
d	Subscript denoting a day [1–28, 29, 30 or 31]
s	Subscript denoting dependency on species characteristics
l	Subscript denoting dependency on geographical location
'	Dash denotes observed resp. measured quantities

Table 2. List of symbols and abbreviations, subscripts are mostly omitted

Symbol	Explanation	Type	Unit/Value
a	Polynom value used to compute PET	AV	—
AET	Actual evapotranspiration	AV	cm
b	Biomass	SV	t/ha
c_0, \dots, c_6	Coefficients used to calculate PET	EPs	—
c_7, c_8	Coefficients used to calculate water deficit	EPs	—
DD	Degree days	AV	$^{\circ}C \cdot d$
DD_{min}	Minimum DD required by a species to exist	EP	$^{\circ}C \cdot d$
DD_{max}	Minimum DD tolerated by a species to exist	EP	$^{\circ}C \cdot d$
DrD	Number of dry days in a year	AV	d
DrI	Drought index	AV	0–1
$DrTI$	Number of dry days above which no growth occurs	AV	d
$DrTol$	Drought tolerance	EP	1–5
DTT	Development threshold temperature	EP	$^{\circ}C$
FC	Field capacity	P	cm
gDD	Degree day growth factor	AV	0–1
gDS	Drought stress growth factor	AV	0–1
gQ	Carrying capacity growth factor	AV	0–1
H	Heat index used to compute PET	AV	—
hk	Slope and intercept of degree day correction	EPs	—, $^{\circ}C \cdot d$
$kDays$	Average number of days per month	P	30.5
K_{sN}	Half saturation constant for NPP as a function of annual P	EP	700 mm
K_{sQ}	Half saturation constant for Q as a function of NPP	EP	1200 $g/m^2/a$
λ	Dependence of PET on latitude	EP	—
$nDays$	Number of days per month		28–31
NPP	Annual net primary production	AV	$g/m^2/a$
NPP_{max}	Maximum NPP	EP	3000 $g/m^2/a$
$nYrs$	Number of years with T or P measurements		—
η	Nutrient availability factor as a parameter of soil fertility	EP	1.0
P	Precipitation (input variable)	IV	mm
PET	Potential evapotranspiration	AV	cm
Q	Ecosystem carrying capacity	EP	t/ha
Q_{max}	Maximum carrying capacity as a function of NPP	EP	1000 t/ha
ρ	Slope of line where NPP varies linearly as a function of temperature	EP	100 $g/m^2/a/^{\circ}C$
SM	Soil moisture	AV	cm
T	Mean air temperature (input variable)	IV	$^{\circ}C$
T^*	Temperature around which NPP varies linearly as a function of temperature	EP	10.0 $^{\circ}C$
T_w	Winter mean air temperature (parameter resp. auxiliary variable)	AV	$^{\circ}C$
V_p	Vegetation period (growing season), see V_0 and V_e	—	see below
V_0, V_e	Begin and end resp., of the growing season as day numbers within the year	EPs	#, #
WD	Water deficit	AV	cm
WP	Wilting point	P	cm

Legend: IV —input variable; SV —state variable; AV —auxiliary variable; P —model parameter; EP —empirical parameter(s).

Table 3. Swiss test sites used to analyse the sensitivity of forest model behaviour to climate parametrizations

Location	Longitude and latitude	Elevation [m.a.s.l.]	Annual mean temperature $T_{y,j}$ [$^{\circ}C$]	Annual precipitation sum $P'_{y,j}$ [mm]	Site description and forest type
Sion	7.3°E 46.2°N	491	10.0	592	Pronounced valley location, central alpine climate, close to arid treeline; mixed coniferous
Bern	7.4°E 46.9°N	540	8.4	1001	Valley location at the north slope of the Alps; mixed deciduous
Bever	9.9°E 46.6°N	1708	1.5	838	Upper Engadine valley, representative of central- and south-alpine climate; subalpine softwood

$$\begin{aligned}
 E[P'_{m,l}] &\approx \frac{1}{nYr_{S_{m,l}}} \cdot \sum_{y=1}^{nYr_{S_{m,l}}} P'_{m,y,l} \\
 &= \frac{1}{nYr_{S_{m,l}}} \cdot \sum_{y=1}^{nYr_{S_{m,l}}} \left(\sum_{d=1}^{nDays_m} P'_{d,m,y,l} \right) \quad (2)
 \end{aligned}$$

Annual degree-day sums $DD_{y,l}$ were calculated from monthly mean temperatures (eqns 4 and 4*) or alternatively from daily minimum and maximum temperatures as required by the sine wave method by Allen (1976). Climatic parameters were calculated from observations by means of FORTRAN 77 programs run on the CDC mainframe computer at the Computing Centre of the Swiss Federal Institute of Technology, Zurich. For further statistical analyses we used the SYSTAT 5.0 (Wilkinson, 1989) and StatView 1.03 (Feldman *et al.*, 1987) commercial software packages on Macintosh personal computers.

Forest ecosystem model runs were performed for climate parametrized from the data sets described above and for a possible future climate for southern and central Europe derived from a scenario by Houghton *et al.* (1990). This scenario states that by the year 2030 temperature is assumed to increase by +3°C and +2°C in the summer and winter halves of the year relative to pre-industrial levels, respectively, and corresponding to increases by +2.5°C (summer half of the year) and +1.5°C (winter half of the year) relative to the observed mean temperatures of this century. Summer precipitation is reduced by 15%, and winter precipitation does not change; variances of both variables are assumed not to change either. This scenario is referred to as 'reference climatic change'.

To assess the sensitivity of forest models with respect to the intrinsic uncertainties in the reference climatic change scenario, we determined conservative deviations from it according to the following reasoning: based on a business-as-usual scenario for greenhouse gas emissions, Houghton *et al.* (1990) give a best-estimate for the change in global mean surface air temperature relative to pre-industrial times of +2.0°C for the year 2030 and of +3.3°C for 2070. Uncertainties in those projections are given by low and high estimates deviating from the best-estimates for 2030 by -0.7 and +0.8°C, and for 2070 by -1.1 and +1.5°C, respectively. An intercomparison of eight General Circulation Models (GCMs), at present the most reliable tools to study the entire global climate system (Dickinson, 1986), showed that compared with observations the models reproduce regionally averaged mean temperature of southern and central Europe with a mean error of 0.7±3°C in summer (June to August) and 0.5±3.6°C in winter (December to February) (Gates *et al.*, 1990). Under a doubling of atmospheric CO₂, the model results suggest an increase of annual global mean surface temperature by 2.5°C with an uncertainty of -1.0 and +2.0°C (Mitchell *et al.*, 1990). As all ranges listed above average to around 1°C the uncertainty bounds for temperature in our reference climatic change scenario were set to ±1°C.

Relative to observations, the mean error of all GCMs for precipitation in southern and central Europe amounts to at least -9±47% in summer and +18±23% in winter (Gates *et al.*, 1990). Under a doubling of atmospheric CO₂, the models predict an increase of +9±6% for global precipitation (Mitchell *et al.*, 1990). For precipitation, regional model-to-model standard deviations of projected changes are in contrast to temperature frequently in the same order of magnitude as the average change in precipitation (Santer *et al.*, 1990). The listed ranges average to around 25%, but the uncertainty bounds for precipitation in our reference climatic change scenario were set to ±15%. Another reason for these low bounds is that, due to the coarse spatial resolution of GCMs, errors in regional precipitation changes as projected by the models were considered to be poorer indicators of the true uncertainties, than in the case of temperature.

All steady-state estimates of forest species composition were made by assuming that climate has already reached equilibrium. Although unrealistic, this assumption allows the sensitivity of an ecosystem model to be studied independently of the much more complex coupling of forests with climate models. Even if we coupled the GCM output of a transient climate-change run to a model like FORCLIM, there would arise the currently unresolved problem of an exactly determined initial state of the forest model. Since all gap models use the least interesting situation of an unforested area as the initial state, the best defined point in the state space of a gap model appears to be the steady state. Thus, for the time being, we focus on the steady state and assume that significant changes in the forest's climax are also indicative of the system's reaction to the forcings of a transient climatic change.

Modelling and simulation tools

The FORCLIM models were implemented using the modelling and simulation software RAMSES (Research Aids for Modelling and Simulation of Environmental Systems; (Fischlin *et al.*, 1990; Fischlin, 1991)). This modelling technique allows model equations to be programmed in a simple yet structured and powerful way in the language Modula-2 (Wirth, 1988). As an open system, RAMSES can use additional dialogue routines as provided by the underlying Dialog Machine (Fischlin, 1986). This means that problem-specific program features can be added to the robust user interface, e.g. extra dialogue windows for changing sites or the climate, editing species parameters, graphic visualization of model behaviour, or estimating a steady state by adding a particular post-simulation procedure.

The equilibrium states of species composition and total above-ground biomass were estimated as the arithmetic means of 200 sampled state variates (Bugmann & Fischlin, 1992) from one single simulation run. Sampling starts after 1000 simulation years to discard the transient behaviour. Samples are then repeatedly taken every 150 years, although there is still a detectable autocorrelation between these points. How-

ever, the method yields standard errors generally smaller than 10% of the resulting means for all common species in the steady state, which was considered to be an acceptable compromise between precision and the efficiency of equilibrium state estimation.

CLIMATE PARAMETRIZATION SCHEMES

The climate parametrization schemes studied within this work form part of a more general forest ecosystem modelling effort geared towards the study of the impacts of climatic change on terrestrial ecosystems. The resulting model is called FORCLIM and consists of several submodels. In this context only two are used: FORCLIM-W parametrizes weather and climate dependent processes and links them to the plant growth submodel FORCLIM-P. The latter is a gap-dynamics model described elsewhere (Bugmann, 1994).

Abiotic ecological factors

In terrestrial ecosystems the fundamental ecoprocesses like primary production are primarily limited by precipitation and temperature, and only secondly by nutrients (Whittaker, 1975). Since forest gap models are constructed as discrete-time models with an annual time step, it is desirable to use climatic data of similar resolution for developing parametrization schemes. This means that annual weather data are to be coupled to the biotic processes, sapling establishment, growth, or death (Fig. 1). However, the coupling equations are preferably derived and interpreted on a higher temporal resolution. Typically this is achieved by computing year-specific auxiliary variables from monthly or, exceptionally, even daily weather values (e.g. eqns 1–5). Therefore the present analysis will adhere to the gap model tradition (Botkin *et al.*, 1972a,b; Shugart, 1984) of using monthly weather data to compute the weather-dependent ecological processes, sapling establishment and tree growth (Fig. 1).

We will now analyse the conventional parametrization scheme adopted by most forest gap models (FORCLIM-W1, Fig. 1(a)). Then we will contrast it with a scheme used by a new forest model (FORCLIM-W2) developed by the authors as shown in Fig. 1(b). Equation numbers followed by an asterisk refer specifically to FORCLIM-W2. All other parts of the two forest models are described elsewhere (Bugmann, 1994).

Temperature

The distribution of the monthly temperature means

$T_{m,y,l}$ at the sites investigated does not significantly ($\alpha = 5\%$) depart from normality (Kolmogorov–Smirnov test). Hence, monthly mean temperatures are generated for each month m and year y by sampling the variates $T_{m,y,l}$ according to eqn 3.

$$T_{m,y,l} \in T_{m,l} \sim N(E[T'_{m,l}], \text{VAR}[T'_{m,l}]) \quad (3)$$

Within FORCLIM-W1, the annual sum of degree-days is calculated conventionally using an approximation based on mean monthly temperature $T_{m,y,l}$ (Botkin *et al.*, 1972a,b; eqn 4). The results obtained from this approximation can be used to infer, by means of a linear regression, the degree-day sum as calculated by the much more precise sine wave method by Allen (1976), based on daily measurements. A perfect approximation of Allen's method would have the regression slope $h_1 = 1$ and the intercept $k_1 = 0$ (Table 4).

$$DD_{y,l} = \sum_{m=Jan}^{Dec} DD_{m,y,l} = \sum_{m=Jan}^{Dec} \text{MAX}(T_{m,y,l} - DTT, 0) \cdot k \text{Days} \quad (4)$$

At all test sites the conventional gap model approximation method (eqn 4) is biased by a significant underestimation of degree-day sums. The closer the mean temperature $T_{m,y,l}$ is to the development threshold temperature DTT of 5.5°C and the more the temperature varies within that month, the more is $DD_{y,l}$ underestimated (Fig. 2, left, and Table 4). Since the variability of monthly temperature and the number of months with realized temperatures $T_{m,y,l}$ close to DTT varies from site to site, the approximation method error is site-specific (Fig. 2, right, and Table 4). FORCLIM-W2 first computes the annual sum of degree-days $DD_{y,l}$ conventionally (eqn 4), but then uses their site-specific linear regression coefficients (Table 4) in eqn 4* to correct for the bias produced by eqn 4.

$$DD'_{y,l} = h_1 DD_{y,l} - k_1 \quad (4^*)$$

Precipitation

The distribution of monthly precipitation sums $P_{m,y,l}$ for the months November to April deviates, often significantly, from a normal distribution, whereas precipitation sums of all other months ($m \in [\text{May–Oct}]$) appear to be normally distributed (Kolmogorov–Smirnov test, $\alpha = 5\%$). This result is consistent with findings by Fliri (1974, p. 38), who has found generally moderate positive skewness for precipitation data in the European

Table 4. Linear regressions between the two methods for degree-day calculation (Eqns 4 resp. 4*). The null hypothesis $h_1 = 1$ and $k_1 = 0$ is rejected at the 5% level for all sites ($\alpha = 5\%$, critical F -values are 3.98, 3.1 and 3.1 for Sion, Bern, and Bever, respectively; F -test according to Riedwyl, 1980). The far-right column contains the long-term mean values of annual degree-day sums for comparison with regression intercepts

Site	Sample size (years)	h_1 (slope)	k_1 (intercept, $^\circ\text{C}\cdot\text{d}$)	$F_{2,n-2}$	Expl. variance (%)	Period mean of $DD_{y,l}$ ($^\circ\text{C}\cdot\text{d}$)
Sion	13	0.87	592	405	88.1	2411
Bern	90	0.89	391	1362	93.5	1900
Bever	80	0.92	293	875	77.0	816

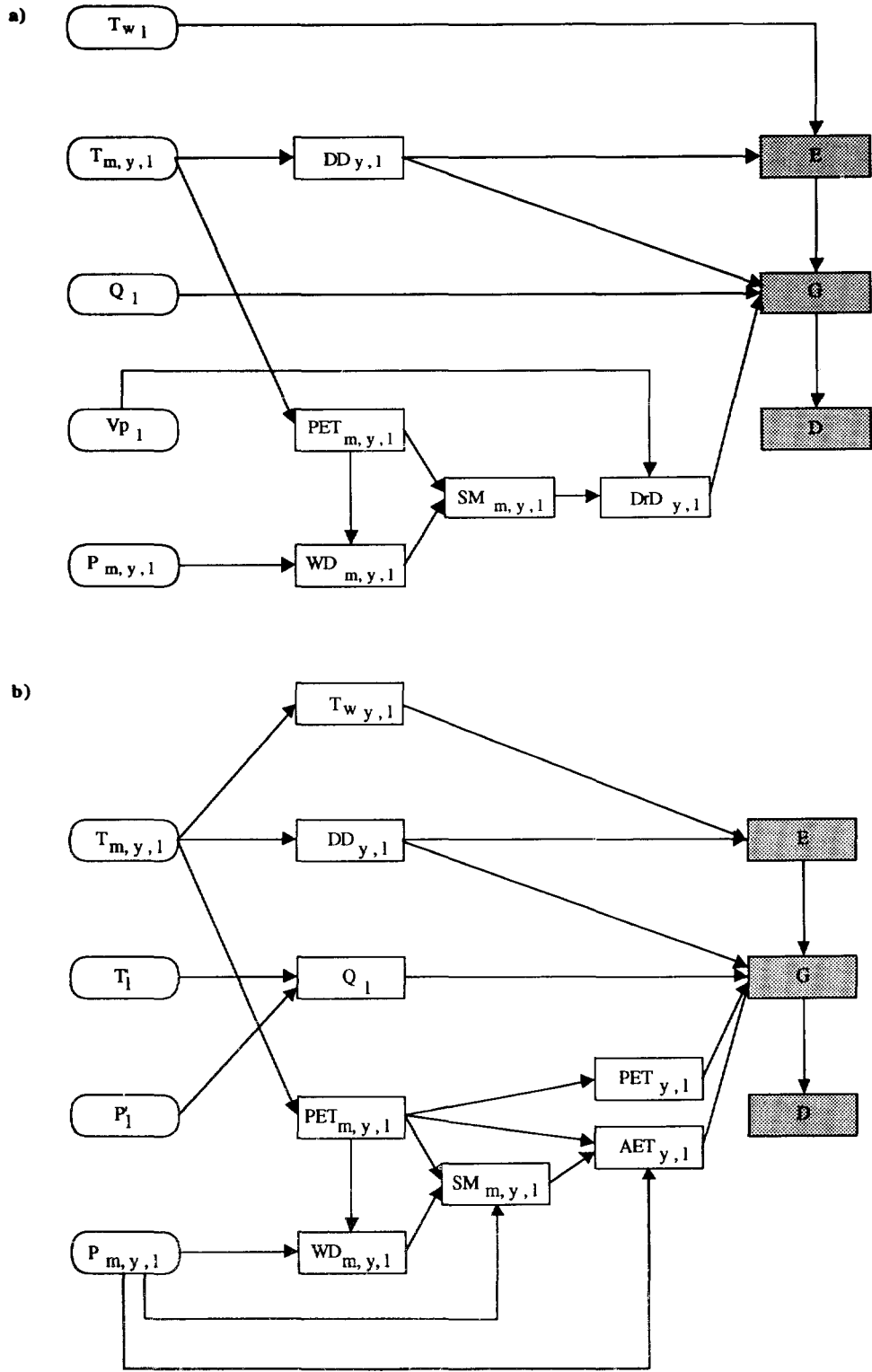


Fig. 1. Relational digraph (Fischlin, 1991) depicting functional dependencies between climate dependent input parameters and the ecosystem processes E (establishment of sapling cohorts), G (plant growth), and D (tree death). (a) Model variant I (conventional and gap model, e.g. FORCLIM-W1, or FORECE by Kienast, 1987) (b) Model variant II (FORCLIM-W2). Legend: \square — Climate dependent input or parameter; \blacksquare — Auxiliary variable; \circ — Ecoprocess; $T_{m,y,l}$ and $P_{m,y,l}$ — Temperature and precipitation for month m of year y at location l ; T' and P' — Expected value (or long-term mean) of annual temperature and precipitation; T_w — Minimum winter temperature as a measure for winter severity; DD — Sum of degree-days; Q — Ecosystem carrying capacity; Vp — Vegetation period; DrD — Number of drought days; PET and AET — Potential respectively actual evapotranspiration; WD — Water deficit; SM — Soil moisture (for indices see above).

Alps. Attempts to increase the normality of winter precipitation by means of a log-normal transformation resulted only in a little improvement of normality. Since

winter weather is generally less important than that of the vegetation period, we approximated $P_{m,l}$ by a normally distributed random variable with expected value

$E[P'_{m,l}]$ and variance $VAR[P'_{m,l}]$. Hence, in both model variants precipitation is generated by sampling variates $P_{y,m,l}$ according to eqn 5.

$$P_{m,y,l} \in P_{m,l} \sim N(E[P'_{m,l}], VAR[P'_{m,l}]) \quad (5)$$

Temperature and tree establishment

The following climatic effects influence the stochastic ecoprocess sapling establishment. First, winter temperatures affect vulnerable saplings; mild winters allow, severe frosts prevent, sapling establishment. Second, the physiological suitability of the temperature regime is considered by testing whether the annual degree-days $DD_{y,l}$ (eqn 4 and eqn 4*, resp.) fall within the species-specific range in which establishment may occur. The probability to be established is always 0·1, given establishment is not prevented by these climatic effects.

Winter temperature

Woodward (1988) has shown that distribution boundaries of perennial species depend on absolute minimum winter temperatures. The latter are well correlated with the corresponding monthly temperature means (Prentice & Helmisaari, 1991). Therefore Pastor and Post (1985) have used mean January temperature $T'_{Jan,y,l}$ to modify the probability of establishment. Even simpler, Kienast (1987) has used the long-term average January temperature $T'_{Jan,l}$. The latter approach is also used in FORCLIM-W1 (eqn 6) and leads to abrupt changes in species composition under transient climatic change as soon as January temperature $T'_{Jan,l}$ exceeds the threshold value Tw_s of a species whose occurrence is disabled via this establishment factor (eqn 7), a behaviour which contrasts strongly with reality.

$$Tw_1 = E[T'_{Jan,l}] \quad (6)$$

establish saplings of species *s* with probability 0·1 only if

$$Tw_1 > Tw_s \quad (7)$$

Moreover, since actual mean temperatures of the months December $T_{Dec,y,l}$ and February $T_{Feb,y,l}$ are often

lower than January temperatures $T_{Jan,y,l}$ the latter may be a poor indicator for winters containing exceptional cold events. As an alternative to eqn 6, we used in FORCLIM-W2 the smallest value of subsequently realized mean temperatures for the months December through February to calculate the occurrence of severe winters (eqn 6*). Sapling establishment is again formulated as a simple random event (eqn 7*)

$$Tw_{y,l} = \text{MIN}(T_{Dec,y-1,l}, T_{Jan,y,l}, T_{Feb,y,l}) \quad (6^*)$$

establish saplings of species *s* with probability 0·1 only if

$$Tw_{y,l} > Tw_s \quad (7^*)$$

Equations 7 and 7* couple FORCLIM-W1 and FORCLIM-W2, resp. to FORCLIM-P.

Degree-days

Both model variants assume that establishment of a species is not possible in a given year if the current annual sum of degree-days $DD_{y,l}$ lies outside the interval defined by the species parameters DD_{min_s} and DD_{max_s} (eqn 8). These parameters are usually estimated by comparing species range maps with maps of degree-day isolines (e.g. Kienast, 1987). Typically, degree-day maps are calculated from monthly climatic data (e.g. Walter & Lieth, 1967). Thus, it is probable that degree-day parameters in gap models are also subject to systematic errors. Consequently, a meaningful rehearsal of degree-day calculations in gap models should include the definition of a method for calculating the species parameters anew. For the present analysis, we used the regression equations obtained for the three sites (Table 4) to estimate true degree-days, and increased all species-specific degree-day parameters by 15%. The latter value corresponds to the average error of annual degree-day estimation over the three test sites and three additional locations within Switzerland (Basel, Davos, and Locarno; see also Table 5). Therefore, the two model variants differ only in the way arguments and parameters are computed (eqn 4 vs eqn 4*). A Boolean expression (eqn 8) couples FORCLIM-W to FORCLIM-P.

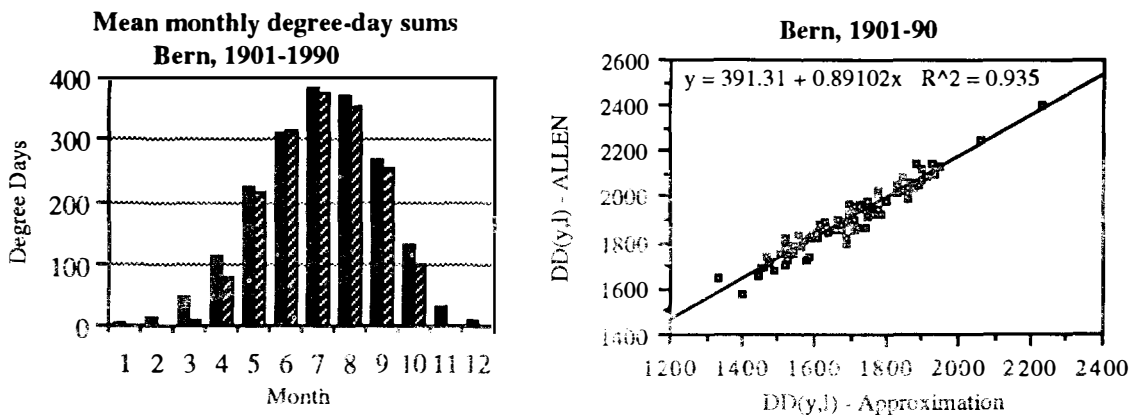


Fig. 2. Comparison between the conventional gap model method degree-day calculations (e.g. FORCLIM-W1, eqn 4) and the sine wave method by Allen (1976) based on daily temperatures for Bern. *Left:* The systematic and site-specific error results mainly from an underestimation in spring and autumn, where temperatures are close to the threshold temperature DTT (black bars—long-term means according to Allen (1976); striped bars—gap model approximation, eqn 4). *Right:* Linear regression of Allen's annual degree-days $DD_{y,l}$ from the conventional gap model approximation ($n = 90$ years) showing large deviations from the ideal regression line with slope $h_1 = 1$ and intercept $k_1 = 0$ (see Table 4).

establish saplings of species s with probability 0.1 only if

$$DD_{\min_s} \leq DD_{y,l} \leq DD_{\max_s} \quad (8)$$

Temperature, precipitation, and tree growth

The ecoprocess growth is modelled as a deterministic, species- and site-specific, complex process (Bugmann, 1994). Climate and weather influence this process only by modification of the following climate-dependent growth factors: the influence of temperature through degree-days, $gDD_{y,l,s}$; the influence of the carrying capacity through temperature and precipitation regime, $gQ_{y,l,s}$; and the influence of temperature and precipitation through drought stress, $gDS_{y,l,s}$. Those growth factors take values between 0 and 1 and are used to calculate realized growth rates from theoretical maximum potential tree growth.

Degree-days

Forest gap models use annual degree-days $DD_{y,l}$ to model the direct influence of temperature on species-specific tree growth $gDD_{y,l,s}$ according to a parabolic relationship as defined in eqn 9:

$$gDD_{y,l,s} = 4 \frac{(DD_{\max_s} - DD_{y,l}) \cdot (DD_{y,l} - DD_{\min_s})}{(DD_{\max_s} - DD_{\min_s})^2} \quad (9)$$

Both model variants analysed use this approach to couple degree-days to tree growth; they differ only in the way the annual degree-day sum and the species-specific parameters DD_{\min_s} and DD_{\max_s} are calculated (eqn 4 vs eqn 4*). This difference propagates through the degree-day growth factor $gDD_{y,l,s}$.

Carrying capacity

Many conventional forest gap models, e.g. FORCLIM variant I, use site-specific, constant values for the carrying capacity Q_1 (eqn 10, Fig. 1(a)).

$$Q_1 = \text{const}_1 \quad (10)$$

The parameter Q_1 implicitly aggregates average edaphic factors (Botkin *et al.*, 1972_{a,b}) for a particular temperature and precipitation regime (Walter & Breckle, 1986). In impact studies Q_1 would have to be adjusted accordingly.

For FORCLIM-W2 we fitted the parameters in the eqns 10* and 11 to the upper range of the net primary productivity and total standing crop data by O'Neill and DeAngelis (1981). These data have been collected for the International Woodlands Data Set of the International Biological Programme (IBP) (O'Neill & DeAngelis, 1981) and cover a wide range of forest ecosystems. Since climate dependencies are the focus of this study, we assumed hereby an average soil fertility factor η_1 of 1.

$$Q_1 = Q_{\max} \cdot \frac{NPP_1}{K_{sQ} + NPP_1} \quad (10^*)$$

where

$$NPP_1 = [NPP_{\max} \cdot \frac{E[P'_{y,l}]}{K_{sN} + E[P'_{y,l}]} + \rho \cdot (ET'_{y,l} - T^*)] \cdot \eta_1 \quad (11)$$

By using annual mean temperatures and precipitations for many sites in Switzerland, plus averaging soils by setting $\eta_1 = 1$, the new eqns 10* and 11 yielded plausible ecosystem carrying capacities (Table 5, Fig. 1(b)). For the three stations, Basel, Bern, and Sion, the carrying capacities are similar to those used in the FORECE model (Kienast, 1987), whereas higher values resulted for the high-elevation sites, Davos, Bever, and the sub-Mediterranean site Locarno (Table 5).

Most gap models represent nutrient competition by modifying growth through the carrying capacity growth factor $gQ_{y,l}$. The closer the total biomass of all species approaches the ecosystem carrying capacity Q_1 , the smaller $gQ_{y,l}$ becomes (eqn 12).

$$gQ_{y,l} = \text{MAX} \left(1 - \frac{1}{Q_1} \sum_s b_{y,l,s}, 0 \right) \quad (12)$$

Both FORCLIM model variants use eqn 12; they differ only in the way Q_1 is computed.

Drought stress

The models presented here calculate soil moisture content $SM_{m,l}$ from a single layer soil model solved at monthly intervals based on the approach used in the forest gap model by Pastor and Post (1985), which has been derived from an empirical water balance model by Thornthwaite and Mather (1957).

Conventional gap models (Pastor & Post, 1985; Solomon, 1986; Kienast, 1987; Kellomäki *et al.*, 1992) and FORCLIM variant I assess drought stress by calculating the number of drought days $DrD_{y,l}$ (eqn 13). This number is a function of the parameters determining the start and end of the growing season (V_0 , V_c) which implicitly depend on climatic parameters (Fig. 1(a)).

$$DrD_{y,l} = \sum_{d=V_0}^{V_c} \text{SIGN}(\text{MAX}(WP_1 - SM_{d,y,l}, 0)) \quad (13)$$

Table 5. Comparison of the ecosystem carrying capacities Q_1 along an ecological gradient across the Alps from North to South, as used by the conventional FORCLIM model variant I or FORECE (Kienast, 1987) with those used in FORCLIM variant II. The latter were calculated by assuming average soil fertilities modified by the site-specific annual means of temperature and precipitation

Site	Elevation (m a.s.l.)	Constant Q_1 FORCLIM I [t/ha]	Calculated Q_1 FORCLIM II [t/ha]
Basel	306	540	556
Bern	540	540	572
Davos	1560	300	472
Bever	1708	260	395
Sion	491	540	534
Locarno	198	540	661

where

$$SM_{d,y,l} = f(SM_{m-1,y,l}, SM_{m,y,l}) \quad (13.1)$$

where $m-1, m =$ months adjacent to day d

The auxiliary variable $DrD_{y,l}$ corresponds to the accumulated number of days during the growing season where soil moisture is below the wilting point WP_i . Its value depends on daily soil moistures $SM_{d,y,l}$ which are determined via a piecewise linear interpolation between preceding and following monthly soil moisture contents $SM_{m,y,l}$ (eqn 13.1)

The required monthly soil moistures $SM_{m,y,l}$ are calculated according to eqns 14 and 14.1.

$$\text{for } SM_{m,y,l} = \begin{cases} \text{MIN}(FC_1, SM_{m-1,y,l} + P_{m,y,l} - PET_{m,y,l}) & \text{otherwise} \\ FC_1 e^{\frac{(c_7 - c_8)}{FC_1} \cdot WD_{m,y,l}} \cdot P_{m,y,l} \geq PET_{m,y,l} \end{cases} \quad (14)$$

where

$$WD_{m,y,l} = \begin{cases} 0 & SM_{m-1,y,l} = FC_1 \\ WD_{m-1,y,l} + P_{m,y,l} - PET_{m,y,l} & SM_{m-1,y,l} < FC_1 \end{cases} \quad (14.1)$$

Potential and actual evapotranspiration are given by eqns 15 and 16.

$$PET_{y,l} = \sum_{m = \text{Jan}}^{\text{Dec}} PET_{m,y,l} \quad (15)$$

where

$$PET_{m,y,l} = \lambda_{m,l} \cdot c_0 \cdot \left(\frac{10 \cdot \text{MAX}(T_{m,y,l}, 0)}{H_{y,l}} \right)^{a_{y,l}} \quad (15.1)$$

$$H_{y,l} = \sum_{m = \text{Jan}}^{\text{Dec}} \text{MAX}(c_1 \cdot T_{m,y,l}, 0)^{c_2} \quad (15.2)$$

$$a_{y,l} = c_3 \cdot (H_{y,l})^3 + c_4 \cdot (H_{y,l})^2 + c_5 \cdot H_{y,l} + c_6 \quad (15.3)$$

$$AET_{y,l} = \sum_{m = \text{Jan}}^{\text{Dec}} AET_{m,y,l} \quad (16)$$

where

$$AET_{m,y,l} = \begin{cases} PET_{m,y,l} & P_{m,y,l} \geq PET_{m,y,l} \\ P_{m,y,l} + SM_{m-1,y,l} - SM_{m,y,l} & P_{m,y,l} \leq PET_{m,y,l} \end{cases} \quad (16.1)$$

In FORCLIM-W1 the number of drought days $DrTl_{y,l,s}$ beyond which species s ceases to grow is computed from $DrD_{y,l}$ (eqn 13) and the species' drought tolerance $DrTol_s$ according to eqn 17.

$$DrT_{0y,l,s} = \text{MAX} \left(\frac{DrTol_s}{10} \cdot (V_{c1} - V_{0l}), DrD_{y,l} \right) \quad (17)$$

Finally, based on experimental evidence by Bassett (1964), the drought day growth factor $gDS_{y,l,s}$ used in FORCLIM-P is calculated by FORCLIM-W1 according to eqn 18.

$$gDS_{y,l,s} = \sqrt[2]{1 - \frac{DrD_{y,l}}{DrTl_{y,l,s}}} \quad (18)$$

The calculation of $DrD_{y,l}$ (eqn 13) appears to produce an extremely discontinuous distribution (Fig. 3, top): according to eqn 13, a soil moisture always slightly above the permanent wilting point, WP_i , results in zero drought days or no drought stress (eqn 18). This contrasts strongly with reality where such conditions represent severe drought. This approach seems appropriate at very moist or xeric locations; however, it seems less appropriate for transitions between mesic and xeric conditions.

To have more continuous measures for drought

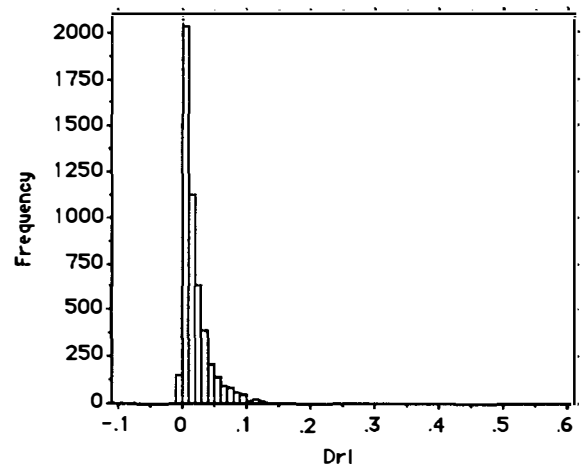
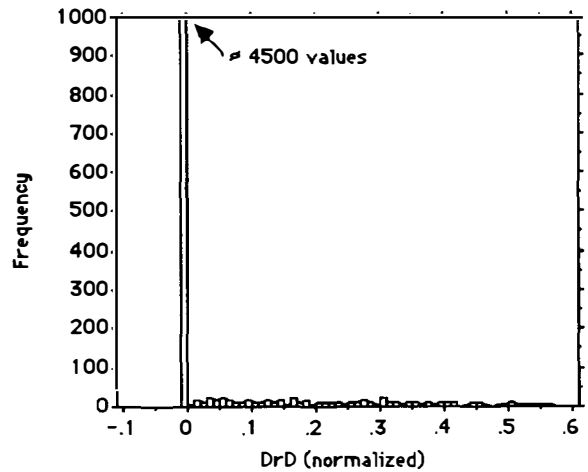


Fig. 3. Histograms of the two variants to compute drought conditions for Bern ($n = 5000$). *Top*: Conventional dry days $DrD_{y,l}$ (FORCLIM-W1, eqn 13) computed according to the method by Pastor and Post (1985). *Bottom*: Drought index $DrI_{y,l}$ (eqn 19) proposed by Prentice and Helmisaari (1991) used in FORCLIM-W2. The first bar in each graph represents the zero values. Note the different scales on the ordinates.

stress in FORCLIM-W2, we used an alternative growth factor formulation (eqn 18*) based on a drought index (eqn 19) proposed by Prentice and Helmisaari (1991).

$$gDS_{y,l,s} = \text{MAX} \left(1 - \frac{DrI_{y,l}}{0.06 \cdot DrTol_s}, 0 \right) \quad (18^*)$$

Equation 19 (below) produces smoother distributions and results in considerably more drought at low-elevation sites like Bern, a behaviour which appears to be more realistic (Fig. 3, bottom). Moreover, this formulation does not depend on the length of the vegetation period (Fig. 1(b)).

$$DrI_{y,l} = \frac{PET_{y,l} - AET_{y,l}}{PET_{y,l}} \quad (19)$$

Model variants

The climate parametrization scheme adopted by FORCLIM-W1 consists of eqns 1–7, 10, 13–15, and 17. FORCLIM-W1 represents a particular climate parametrization scheme similar to the ones adopted in conventional forest gap models such as JABOWA (Botkin *et al.*, 1972*a,b*), FORET (Shugart & West, 1977), Pastor and Post (1985), FORENA (Solomon, 1986), FORECE (Kienast, 1987) and SIMA (Kellomäki *et al.*, 1992). Equations 8, 9, 12, and 18 couple FORCLIM-W1 to FORCLIM-P. The combination of the submodels FORCLIM-W1 linked to FORCLIM-P is called FORCLIM model variant I.

FORCLIM-W2 consists of eqns 1–4, 4*, 5, 6*, 7*, 10*, 11, 14–16, and 19. FORCLIM-W2 represents a new climate parametrization scheme that avoids assumptions on a constant climate and allows for more flexible parametrization if climate changes. The coupling between FORCLIM-W2 and FORCLIM-P is done via the eqns 8, 9, 12, and 18*. The combination of the submodels FORCLIM-W2 linked to FORCLIM-P is called FORCLIM model variant II.

RESULTS AND DISCUSSION

First we compared the overall behaviour of the FORCLIM-P plant submodel in response to the exchange of the two submodel versions FORCLIM-W1 and FORCLIM-W2, resp. at the three test sites. Then the contribution of the various processes and the effects of the modifications in the climate parametrizations (represented by FORCLIM-W1 and FORCLIM-W2, resp.), on the steady state of the two model variants under a climatic-change scenario were studied. Most simulation results are shown only as equilibrium estimates instead of the averaged species biomasses vs time, as is the case in Fig. 5. For instance, the far-left bar in Fig. 4 shows the equilibrium estimate that corresponds to the steady state forest composition reached towards the end of the simulation as depicted in Fig. 5 (left).

Sion

For current climatic conditions, both model variants project a forest dominated by *Pinus silvestris* with fewer *Castanea sativa* and *Quercus pubescens* (species names are according to Hess *et al.*, 1980). Total biomass amounts to some 70–75 t/ha. However, in a warmer, drier climate, both model variants predict a complete forest breakdown. The regular occurrence of strong summer droughts causes all forest growth to cease. Both model variants project such severe drought stress that the final effect becomes independent of the details in which drought is actually modelled. Generally, no differential response to any of the model modifications is visible at this site, and we conclude that both model variants respond to extreme xeric conditions in an equally realistic way.

Bern

For today's climate, both model variants produce steady states that largely match current forests (Fig. 4, left). The formulation of the effects of low winter tem-

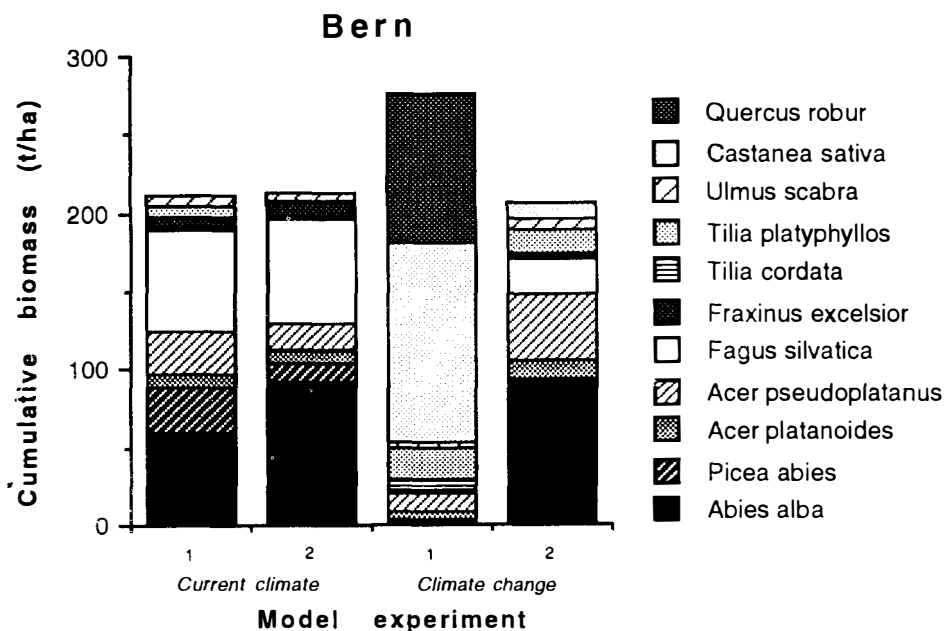


Fig. 4. FORCLIM-P steady state estimates of species composition at Bern (Table 3) for the two climate parametrizations FORCLIM-W1 (bar 1) and FORCLIM-W2 (bar 2), resp. and for the current climate (left), the reference climate change scenario (right), resp.

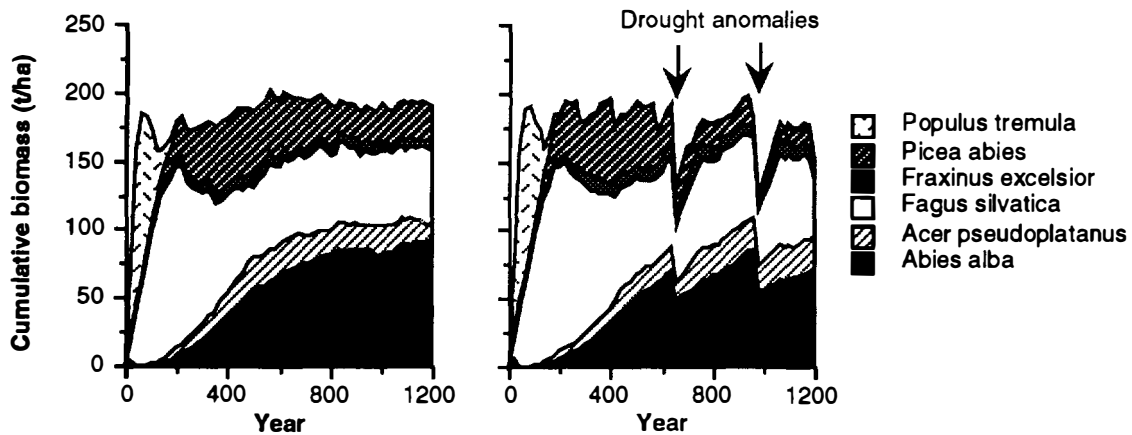


Fig. 5. Forest succession at the low-elevation site Bern (Table 3), as simulated by model variant I (FORCLIM-W1 linked to FORCLIM-P). *Left*: Newly sampled weather sequence for each individual gap (conventional approach). *Right*: Simulation of a forest by using a particular time series. Applying the same weather sequence in every gap leads to several unrealistic forest breakdowns (drought anomalies). The data are averages from 200 simulation runs with no climate change and show the dominating species only.

peratures T_{w_i} versus $T_{w_{y,i}}$ (eqns 6, 7 vs eqns 6*, 7*) has no effect on the final species composition. Mean January temperature, $T_{w_i} = E[T'_{Jan,Bern}] = -1.1^\circ\text{C}$, is much higher than the threshold temperature of -3°C tolerated by the species most susceptible to winter frost (*Quercus* sp.). In FORCLIM-W1, the establishment of oak saplings is never limited by winter temperatures (eqn 6), whereas in FORCLIM-W2 due to the variable, year-specific winter temperature, $T_{w_{y,i}}$ (eqn 6*), oak saplings often cannot become established. Yet this difference between the model variants has no effect on the presence or absence of oaks in the final forest, because restricted light availability actually prevents the growth of oak trees.

Different methods for degree-day calculations (eqns 4 vs 4*) do not influence species composition. In agreement with ecological theory, degree-days have little influence at this low-elevation site, a result that is also corroborated by findings from tree-ring investigations (e.g. Kienast & Schweingruber, 1986).

For current climatic conditions eqn 10* predicts an above-ground carrying capacity similar to the value assigned in model variant I (Table 5). Generally, at sites as fertile as Bern with high Q_1 values, changes in Q_1 up to $\approx 10\%$ show almost no effect on species composition.

The lower biomass of *Picea abies* in FORCLIM-W2 is attributable to the higher drought occurrence predicted by eqn 18* versus the conventional dry days approach of eqn 18. As a consequence, another coniferous species, *Abies alba*, replaces *P. abies*; the rest of the community is almost identical.

Under a changed climate the simulation results at Bern differ vastly between model variants I and II (Fig. 4, right). Model variant I projects a high occurrence of large numbers of dry days (eqn 18), which leads to the elimination of less drought-resistant tree species and an ultimate dominance of *C. sativa* and *Quercus robur*. On the other hand, in model variant II drought stress affects species composition gradually. Thus, climatic change does not affect the spectrum of the dominating

species, but only species abundances. In both model variants Norway spruce (*P. abies*) disappears because its degree-day range is exceeded.

Detailed investigations revealed that drought anomalies may occur in model variant I: two or more subsequent years with large numbers of dry days lead to strong growth reduction and subsequent forest die-off. This effect is most conspicuous when the model variant I is driven with a particular weather realization, i.e. the identical sequence of input data is fed into each individual simulation. Since this situation corresponds exactly to the situation in the field, the episodic large-scale forest breakdown as produced by FORCLIM-W1 (Fig. 5, right) is unrealistic and is rather to be interpreted as a model artefact. This behaviour is to be expected in every case where a forest simulation ought to be driven by actual measurements or by deterministic simulations of transient climate change, as performed by means of General Circulation Models (e.g. Dickinson, 1986). As such, this may pose an additional problem for the application of conventional gap models in climate-change studies. Ultimately realistic impact studies should analyse transient responses of forest ecosystems to transient climatic change. Therefore, we favour drought parametrizations according to eqn 18* over those of eqn 18. In any case, apart from questioning which parametrization scheme may be more realistic, the model behaviour in Bern is very sensitive to the mathematical formulation of drought stress.

Bever

For current climatic conditions, both model variants simulate similar species compositions (Fig. 6, left). Favourable growth conditions exist for *P. abies*, but this species is excluded in both model variants by its unrealistically low winter temperature tolerance of -7°C (eqns 6, 7 and eqns 6*, 7*) (Kienast, 1987). Prentice and Helmisaari (1991) have suggested that spruce actually tolerates much lower winter temperatures. If this parameter is lowered to at least -10°C , simulation results

for both model variants change drastically: the typical larch–cembran pine forest (*Larici–Pinetum cembrae*) as observed in reality is in the model replaced by a larch–spruce forest (*Larici–Piceetum*) (Ellenberg & Klötzli, 1972). We conclude that factors other than low winter temperatures must limit the spread of spruce in the upper subalpine zone (Bugmann, 1994), a fact which is not properly mimicked by any of the model variants described here.

Under today's climate, degree-days do not have a differential influence between the model variants, and hardly any drought occurs, irrespective of its formulation (Eqns 18 and 18*). A sensitivity-analysis of the Q_1 parameter in FORCLIM-W1 revealed that total above-ground biomass is linearly related to values of Q_1 between 100 and 500 t/ha at Bever, whereas for higher Q_1 values, saturation is reached. Equations 10 and 10*, respectively, lead to large differences of Q_1 values between the two model variants (Table 5), which strongly influences total simulated biomass (Fig. 6, left).

Both model variants also consistently project large changes in a warmer and drier climate (reference scenario), but they differ considerably from each other (Fig. 6, right). Winter temperature in both models excludes *P. abies* as under current climatic conditions. The new model variant II projects that a maple species (*Acer platanoides*) not present in the model variant I may become abundant. This difference, as well as the increased biomass of *Carpinus betulus* in variant II, are due to different responses to degree-day calculations (eqns 4 vs 4*). Since the variant II adjustment of the species' degree-day parameters DD_{max_s} and DD_{min_s} is only a first approximation, these findings suggest that the formulation of temperature effects are critical if the gap model is to be applied for studying climatic change impacts. Furthermore, the parameters h_1 and k_1 used in eqn 4* have to be reformulated so that they become in-

dependent from the site-specific climate, e.g. by finding an explicit functional relationship between temperature measurements and these parameters. To avoid any site-specific bias and implicit climate dependencies, we propose that the sum of degree-days be calculated using new, more accurate approximation methods.

In the climate-change scenario, the model variant II also predicts that *Larix decidua* will disappear. This is because in FORCLIM-W2 summer drought stress becomes gradually effective (eqn 18*, Fig. 3, bottom) earlier than in FORCLIM-W1 (eqn 18, Fig. 3, top). With the traditional parametrization of FORCLIM-W1, drought is not yet capable of tipping the drought stress factor $gDS_{y,Bever,s}$ over the threshold. Therefore, at Bever, model variant I, not II, shows little influence of drought stress on species composition; this is just the opposite of the situation at Bern.

The parametrization of carrying capacity Q_1 (eqns 10* and 11) is best calculated from long-term means of temperature and precipitation sums. This poses no problem as a long-term record of a changed climate is available. However, a transient climatic change Q_1 would have to be computed differently. Since Q_1 can be interpreted as a nutrient competition parameter (Botkin *et al.*, 1972a,b), explicit modelling of nutrient availability along the outlines by Aber and Melillo (1982), Weinstein *et al.* (1982), or Pastor and Post (1985) could be preferable and would provide a greater model flexibility.

Sensitivity of model projections to uncertainty in climatic inputs

Generally, current state-of-the-art approaches attempting to relate global climatic changes to local climates cannot make reliable estimates at a particular locality (Gyalistras *et al.*, 1994). This is true especially for sites within a complex topography such as the Alps, where our test sites are located. Instead, it is possible to assess

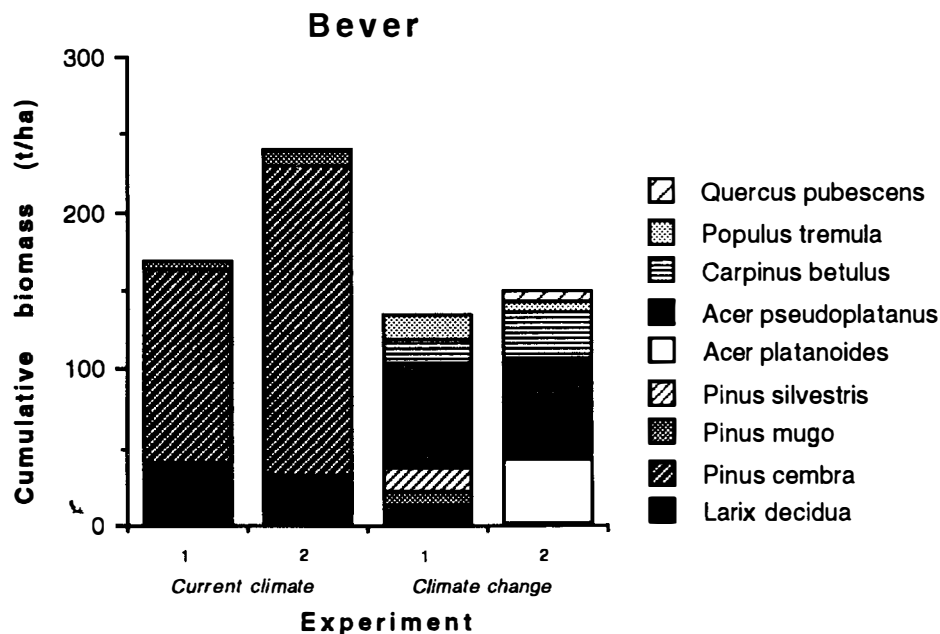


Fig. 6. FORCLIM-P steady state estimates of species composition at Bever (Table 3) for the two climate parametrizations FORCLIM-W1 (bar 1) and FORCLIM-W2 (bar 2), resp. and for the current climate (left), and the reference climate change scenario (right), resp.

the sensitivity of forest models with respect to the intrinsic uncertainties of climate forecasts within the parameter space of T_1 by P_1 . We explored the sensitivity of the more trustworthy FORCLIM variant II behaviour to the conservative deviations from the 'reference climate change' scenario at the subalpine test site Bever (Fig. 7).

The decreased temperature simulations, result in forests with a considerable amount of maple (*A. pseudoplatanus*) and pine (*P. silvestris*, *P. mugo*), but the relative abundances of these species differ (Fig. 7, left). Forests dominated by pine, as simulated under the additionally decreased precipitation, are typical of infertile sites; those under increased precipitation are dominated by maple, which is more typical for today's lower subalpine zone (Ellenberg & Klötzli, 1972). Note that both forest types differ markedly from the forest as simulated in the reference climatic change scenario.

Increased temperature relative to the reference scenario leads to forests dominated by chestnut (*C. sativa*) and maple (*A. platanoides* and *A. pseudoplatanus*) typical for warm, dry sites (Fig. 7). Again, the relative species abundances differ between the two simulations, and the two forests do not resemble the one of the reference climatic change scenario. Chestnut and maple dominate because other tree species, such as beech, fir, spruce, and oak (except for *Q. pubescens*), fail to grow

completely under these environmental conditions. Note also that total above-ground biomasses in these simulations (Fig. 7) lie in the low range of 160–230 t/ha (see Table 5). This might be of considerable importance for the carbon balance of these forests.

All simulations show a remarkable sensitivity of the FORCLIM-P model to rather small deviations from the reference climatic change scenario. Findings from other parameter sensitivity analyses indicate that forest gap models are not highly sensitive to changes in climate related parameters (Kercher & Axelrod, 1984; Botkin & Nisbet, 1992). The robustness of gap models to parameter changes is frequently stated and judged to be a general property of gap models (Shugart, 1984). However, the sensitivity studies by other authors do not cover the same changes or regimes of the climatic parameters covered by our investigations.

CONCLUSION

Forest gap models and climate change

Forest gap models (Shugart, 1984) allow the study of climate-change impact on a spatial and temporal scale that has economic and ecological significance. These models seem to simulate the behaviour of today's forests realistically (Shugart, 1984; Leemans & Prentice, 1989; Kienast & Kuhn, 1989). However, they have

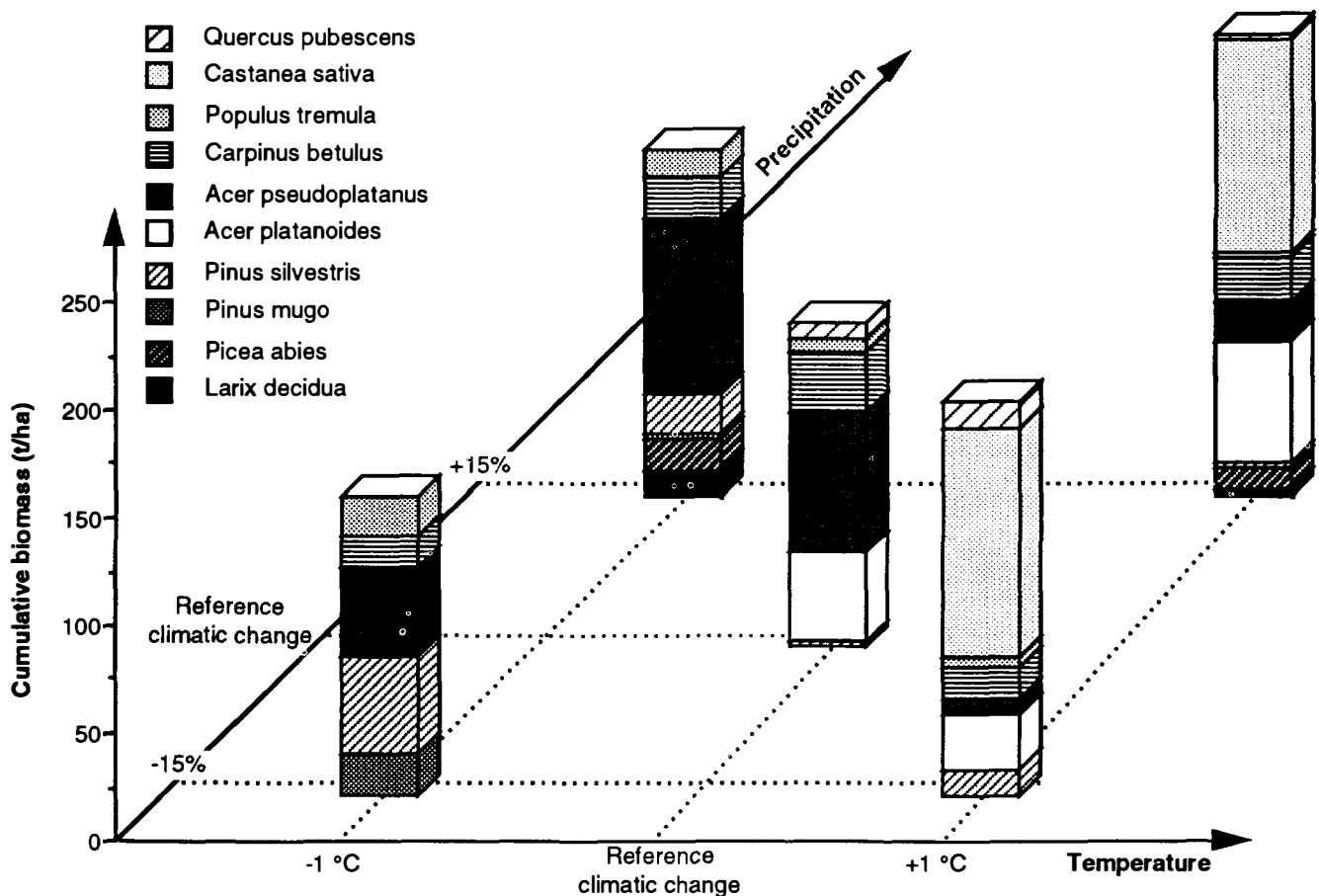


Fig. 7. FORCLIM variant II (FORCLIM-W2 linked to FORCLIM-P) steady state estimates of species composition at Bever (Table 3) for the reference climate change scenario (centre) and for four deviations from this scenario within the annual mean precipitation vs temperature parameter space. These deviations were chosen as rough representations of the uncertainties in the GCM projections of next century climatic change in central-southern Europe.

originally been constructed to study forest dynamics for a particular location with a given, non-changing climate (Botkin *et al.*, 1972a,b; Pastor & Post, 1985). Thus, the application of conventional gap models to climate change scenarios has more consequences than previously recognized, some of which are discussed below (Solomon *et al.*, 1981, 1984; Solomon, 1986; Solomon & West, 1987; Pastor & Post, 1988; Overpeck *et al.*, 1990; Kienast, 1991).

Our results indicate that the species composition of the studied forests is affected by the assumption of a constant climate, and that any switching to alternative formulations of the climatic parametrizations significantly affects the steady state behaviour of the system. Hence, to obtain reliable results, the climate parametrization must account for possible climatic changes more consistently.

Under current climate conditions, the simulations of model variant I are similar to those of variant II; however, if climate changes, the two model variants produce markedly different forest compositions. Thus, it seems that models suitable for simulating the behaviour of today's forests are not necessarily equally useful for projecting future forests in a globally changing climate.

Conventional gap models similar to model variant I contain sensitive parametrizations of degree-days and drought stress. The latter mechanism, especially, appears to be unrealistic, again regardless of the model's capability to produce realistic species compositions for the current climate. The few authors studying gap models along a drought stress gradient (Solomon, 1986; Kienast & Kuhn, 1989) have not encountered the threshold effect we detected when the climate changes. This is partly because they have looked only at situations far below (Bern, current climate) or far beyond, (Sion, current climate) the threshold. However, in a changing climate, at some locations and at some time, some forests are likely to come across exactly that sensitive threshold of drought stress as was the case in this study at Bern.

Generally, we conclude that gap models are sensitive to the specific mathematical parametrizations of climate. At the very least it can be concluded that conventional gap models are not as robust to modifications in parameters and mathematical structure as had been found in earlier studies (Shugart, 1984). Because of the detected sensitivities we advocate careful scrutinization of the mathematical structure, in particular the functional dependencies of model parameters, auxiliary variables, and equations, so that they adequately and explicitly reflect the influence of climatic parameters on the ecoprocesses (Fig. 1 (a) vs (b)).

Improving forest gap models

The development of our model variant II served as a first step towards a more flexible and reliable climate parametrization scheme in forest gap models. First, we tried to understand clearly the limitations of the climate parametrization in conventional gap models such as FORCLIM variant I. Secondly, we analysed systemat-

ically all explicitly and implicitly climate-dependent model elements, and reformulated the implicit dependencies so that they no longer assume a constant climate (Fig. 1), thus deriving FORCLIM variant II.

The following elements are best reformulated to depend explicitly only on measurable climate parameters: degree-days $DD_{y,l}$, DD_{min_s} and DD_{max_s} , resp. the carrying capacity Q_i and the vegetation period $V_{p,i}$. Furthermore, all climate-dependent processes, especially drought stress, should be formulated so that they become continuously valid over a large gradient of environmental conditions. Replacing the sensitive drought stress parametrization by a formulation that reacts more smoothly along drought gradients may serve as an example for this type of model improvement.

Although the present study demonstrates the feasibility of improving the climate parametrization scheme of a conventional gap model such as FORCLIM-W1 into a more useful version such as FORCLIM-W2, we feel that there are still several problem areas deserving efforts beyond that of just reformulations:

- (a) The salient nature of forest gap models, being partly deterministic and partly stochastic, may easily produce artefacts like an episodic forest breakdown over large areas. This principally threatens the validation and application of forest gap models by means of particular records of climatic input data, available either as time series from transient GCM runs or as a unique proxy data series (e.g. Pfister, 1988).
- (b) Winter temperature proved to be of marginal significance for forests under current environmental conditions in the European Alps, but in more continental regions it may become more important (Woodward, 1988; Kellomäki *et al.*, 1992). Moreover, climatic change might possibly lead to higher frequencies of thermal inversions at valley locations within the Alps, thus increasing the importance of winter temperature (Gyalistras *et al.*, 1994). Therefore, although the approach chosen in FORCLIM-W2 appears to be an improvement, it requires further study.
- (c) Since species composition was found to be sensitive to the method of degree-day calculations, better approximations are needed for degree-day sums based on monthly mean temperatures. Thus, the individual species' degree-day parameters must be re-estimated. More objective and better documented methods are needed for the consistent identification of species-specific parameters. This would allow more flexible addition or removal of species from a particular gap model than is currently possible.
- (d) The calculation of the carrying capacity as a function of nutrient availability under a given temperature and precipitation regime is such a simple approximation that it poses severe problems for the simulation of forests under the impact of transient climatic change. In particular, soil characteristics determined by processes such

as nutrient dynamics should be included more explicitly in the formulation of the carrying capacity.

Sensitivity of forests and the precision of future climate scenarios

The analysis of the steady state behaviour of the model variant II with respect to deviations from the reference climatic change scenario suggests the following points. Forests might differ substantially within the range of the inherent variability remaining in scenarios of future climate. Since FORCLIM-W2 parametrizes climate more reliably than FORCLIM-W1, we surmise that these findings are trustworthy and ascribe this sensitivity to inherent properties of forest gap models. Not only does this mean that the expected changes in temperature and precipitation have the potential to affect forests drastically, but also that GCM simulations have to forecast future climates more precisely than is currently the case (Wilson & Mitchell, 1987; Santer *et al.*, 1990; Giorgi & Mearns, 1991). Provided that the forest models are generally as sensitive as FORCLIM and as long as climate predictions do not become more precise spatially as well as numerically, climate impact studies based on forest gap models serve only as tools to study sensitivities and to identify potential adaptation difficulties. Such studies must not be confused with predictions; at best, they can outline the range of conditions within which our forests are most vulnerable to major changes.

These sensitivity studies show that at least some of the existing terrestrial ecosystem models derived for constant climate conditions are likely to be sensitive to these underlying assumptions. Once new model formulations are developed and validated, we are confident that forest models such as FORCLIM may be applied successfully to climate-change impact studies at least within the temperate and boreal zone of the northern hemisphere. However, to assess climate-change impacts on terrestrial ecosystems, e.g. by closer linking of climate and ecoprocesses, future bioclimatic scenarios must also match the surprisingly high precision called for by the sensitivity of the ecosystems.

ACKNOWLEDGEMENTS

Part of this research was sponsored by the Swiss National Science Foundation under grants Nos 3100-31142.91, 21-31134.91, 5001-35172, and by the Swiss Federal Institute of Technology, Zürich (ETHZ). The authors thank Dr F. Kienast for the many valuable discussions and not least for his generous disclosure of the code of his FORECE model. Thanks to D. Perruchoud for his unhesitating willingness to help in the drawing of a figure.

REFERENCES

- Aber, J. D. & Melillo, J. M. (1982). FORTNITE: A Computer Model of Organic Matter and Nitrogen Dynamics in Forest Ecosystems. Univ. of Wisconsin Res. Bull. R3130, WI, USA.
- Allen, J. C. (1976). A modified sine wave method for calculating degree days. *Environ. Ent.*, **5**, 388–96.
- Bantle, H. (1989). Programmdokumentation Klima-Datenbank am RZ-ETH Zürich, Schweiz. Meteorol. Anstalt, Zürich.
- Bassett, J. R. (1964). Tree growth as affected by soil moisture availability. *Soil Sci. Proc.*, **28**, 436–8.
- 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.
- Botkin, D. B., Janak, J. F. & Wallis, J. R. (1972a). Rationale, limitations and assumptions of a northeastern forest growth simulator. *IBM J. Res. Develop.*, **16**, 101–16.
- Botkin, D. B., Janak, J. F. & Wallis, J. R. (1972b). Some ecological consequences of a computer model of forest growth. *J. Ecol.*, **60**, 849–72.
- Botkin, D. B. & Nisbet, R. A. (1992). Forest response to climatic change: Effects of parameter estimation and choice of weather patterns on the reliability of projections. *Climatic Change*, **20**, 87–111.
- Bugmann, H. (1991). Development of FORCLIM, a Simplified Forest Gap Model for Workstations and Personal Computers. Internal report, Systems Ecology Group, ETHZ, 8092 Zürich, 60 pp.
- Bugmann, H. & Fischlin, A. (1992). Ecological Processes in Forest Gap Models — Analysis and Improvement. In *Responses of Forest Ecosystems to Environmental Changes*, ed. A. Teller, P. Mathy & J. N. R. Jeffers, Elsevier Applied Science, London, New York, pp. 953–4.
- Bugmann, H. (1994). On the Ecology of Mountainous Forests in a changing climate: A Simulation Study. PhD Thesis No. 10638, Swiss Federal Institute of Technology, Zürich, Switzerland. 258 pp.
- Dickinson, R. E. (1986). How will climate change? The climate system and modelling of future climate. In *The Greenhouse Effect, Climatic Change and Ecosystems*, ed. B. Bolin, B. R. Doos, J. Jäger & R. A. Warrick, Wiley, Chichester a.o. (SCOPE Vol. 29), pp. 206–70.
- Ellenberg, H. & Klötzli, F. (1972). Waldgesellschaften-und Waldstandorte der Schweiz. *Eidg. Anst. Forstl. Versuchswes., Mitt.*, **48**, 587–930.
- Feldman, D. S., Gagnon, J., Hofman, R. & Simpson, J. (1987). *StatView II: The Solution for Data Analysis and Presentation Graphics (v1. 03)*. Abacus Concepts Inc., Berkeley, CA, 278 pp.
- Fischlin, A. (1986). Simplifying the Usage and the Programming of Modern Working Stations with Modula-2: The 'Dialog Machine'. Internal report, Project-Centre IDA/CELTIA, Swiss Federal Institute of Technology, Zürich (ETHZ), 13 pp.
- Fischlin, A. (1991). Interactive Modelling and Simulation of Environmental Systems on Workstations. In *Dynamic Systems in Medicine, Biology, and Ecology*, ed. D. P. F. Möller & O. Richter. Springer, Berlin a.o., Informatik-Fachberichte 275, pp. 131–45.
- Fischlin, A., Roth, O., Gyalistras, D., Ulrich, M. & Nemecek, T. (1990). MODELWORKS, an Interactive Simulation Environment for Personal Computers and Workstations. Internal Report No. 8, Systems Ecology Group, ETH Zurich, Switzerland, 185 pp.
- Fliri, F. (1974). *Niederschlag und Lufttemperatur im Alpenraum*. Wissenschaftl. Alpenvereinshefte, Innsbruck, **24**, 110 pp.
- Gates, W. L., Rowntree, P. R. & Zeng, Q.-C. (1990). Validation of climate models. In *Climate Change — the IPCC Scientific Assessment*, Report prepared for IPCC by working Group I ed. J. T. Houghton, G. J. Jenkins & J. J. Ephraums. Cambridge University Press, Cambridge, UK, pp. 99–137.
- Giorgi, F. & Mearns, L. O. (1991). Approaches to the simulation of regional climate change: A review. *Rev. Geophys.*, **29**, 191–216.
- Gyalistras, D., Von Storch, H., Fischlin, A. & Beniston, M. Linking GCM generated climate scenarios to ecosystems:

- Case studies of statistical downscaling in the Alps. *Climate Res.* 4(9), (in press).
- Hess, H. E., Landolt, E. & Hirzel, R., (1980). *Flora der Schweiz*. 2nd edn, 3 Volumes. Birkhäuser, Basel & Stuttgart.
- Houghton, J. T., Jenkins, G. J. & Ephraums, J. J. (ed.) (1990). *Climate Change — the IPCC Scientific Assessment*. Report prepared for IPCC by Working Group I. Cambridge Univ. Press, Cambridge, UK, 365 pp.
- IGBP (1989). Effects of Atmospheric and Climate Change on Terrestrial Ecosystems. IGBP Report No. 5, Stockholm, 61 pp.
- IGBP (1992). Global Change and Terrestrial Ecosystems. The Operational Plan. IGBP Report No. 21, Stockholm, 95 pp.
- Kellomäki, S., Väisänen, H., Hänninen, H., Kolstrom, T., Lauhanen, R., Mattila, U. & Pajari, B. (1992). SIMA: A model for forest succession based on the carbon and nitrogen cycles with application to silvicultural management of the forest ecosystem. *Silva Carelica*, **22**, 91 pp.
- Kercher, J. R. & Axelrod, M. C. (1984). Analysis of SILVA: a model for forecasting the effects of SO₂ pollution and fire on western coniferous forests. *Ecol. Model.*, **23**, 165–84.
- 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 CO₂ on the successional characteristics of Alpine forest ecosystems. *Landscape Ecol.* **5**, 225–38.
- Kienast, F. & Kuhn, N. (1989). Simulating forest succession along ecological gradients in southern Central Europe. *Vegetatio*, **79**, 7–20.
- Kienast, F. & Schweingruber, F. H. (1986). Dendroecological studies in the Front Range, Colorado, U.S.A.. *Arctic and Alpine Res.* **18**, 277–88.
- Leemans, R. (1991). Sensitivity analysis of a forest succession model. *Ecol. Model.* **53**, 247–262.
- Leemans, R. & Prentice, I. C. (1989). FORSKA, a general forest succession model. Institute of Ecological Botany, Uppsala, Sweden, 70 pp.
- Mitchell, J. F. B., Manabe, S., Meleshko, V. & Tokioka, T. (1990). Equilibrium climate change and its implications for the future. In: *Climate change — the IPCC Scientific Assessment*, Report prepared for IPCC by Working Group I, ed. J. T. Houghton, G. J. Jenkins & J. J. Ephraums, Cambridge University Press, Cambridge, UK, pp. 139–73.
- O'Neill, R. V. & DeAngelis, D. L. (1981). Comparative productivity and biomass relations of forest ecosystems. In: *Dynamic Properties of Forest Ecosystems*. IBP publication no. 23, ed. D. E. Reichle. Cambridge Univ. Press, Cambridge, UK, 411–49.
- Overpeck, J. T., Rind, D. & Goldberg, R. (1990). Climate-induced changes in forest disturbance and vegetation. *Nature*, **343**, 51–3.
- Parry, M. L., Carter, T. R. & Konijn, N. T. (eds.) (1988). *The Impact of Climatic Variations on Agriculture, Volume I: Assessments in Cool Temperate and Cold Regions*. Kluwer Academic Publishers, Dordrecht, 876 pp.
- Pastor, J. & Post, W. M. (1985). Development of a Linked Forest Productivity-Soil Process Model. US Dept. of Energy, ORNL/TM-9519.
- Pastor, J. & Post, W. M. (1988). Response of northern forests to CO₂-induced climate change. *Nature*, **334**, 55–8.
- Pfister, C. (1988). *Klimageschichte der Schweiz 1525–1860: Das Klima der Schweiz von 1525–1860 und seine Bedeutung in der Geschichte von Bevölkerung und Landwirtschaft*, Haupt, Bern, 163 pp.
- 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.
- Riedwyl, H. (1980). *Regressionsgerade und Verwandtes*. Uni-Taschenbücher 923, Paul Haupt, Bern & Stuttgart, 141 pp.
- Santer, B. D., Wigley, T. M. L., Schlesinger, M. E. & Mitchell, J. F. B. (1990). Developing Climate Scenarios from Equilibrium GCM-results. Max-Planck-Institut für Meteorologie, Report No. 47, Hamburg, 29 pp.
- Schneider, S. H. (1989). The greenhouse effect: Science and policy. *Science*, **243**, 771–81.
- Shands, W. E. & Hoffman, J. S. (eds.) (1987). *The Greenhouse Effect, Climate Change, and U.S. Forests*. The Conservation Foundation, Washington, DC, 304 pp.
- Shugart, H. H. (1984). *A Theory of Forest Dynamics. The Ecological Implications of Forest Succession Models*. Springer, New York, 278 pp.
- 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. Environ. Manage.* **5**, 161–79.
- SMA (1901–90). *Annalen der Schweizerischen Meteorologischen Anstalt*. Schweiz. Meteorol. Anstalt, Zürich.
- Solomon, A. M. (1986). Transient response of forests to CO₂-induced climate change: Simulation modelling experiments in eastern North America. *Oecologia*, **68**, 567–79.
- Solomon, A. M., Tharp, M. L., West, D. C., Taylot, G. E., Webb, J. W. & Trimble, J. L. (1984). *Response of Unmanaged Forests to CO₂-induced Climate Change: Available Information, Initial Tests and Data Requirements*. DOE/NBB-0053, National Technical Information Service, US Dept. Comm., Springfield, VA, 93 pp.
- Solomon, A. M. & West, D. C. (1987). Simulating forest ecosystem responses to expected climate change in eastern North America: Applications to decision making in the forest industry. In *The Greenhouse Effect, Climate Change, and US Forests*, ed. W. E. Shands & J. S. Hoffman, The Conservation Foundation, Washington, DC, pp. 189–217.
- Solomon, A. M., West, D. C. & Solomon, J. A. (1981). Simulating the role of climate change and species immigration in forest succession. In *Forest Succession; Concepts and Application*, ed. D. C. West, H. H. Shugart, D. B. Botkin, Springer, New York, pp. 154–77.
- Thornthwaite, C. W. & Mather, J. R. (1957). Instructions and Tables for Computing Potential Evapotranspiration and the Water Balance. *Publ. Climatol.*, **10**, 183–311.
- Walter, H. & Breckle, S. W. (1986). *Ökologie der Erde*. Gustav Fischer, UTB Grosse Reihe.
- Walter, H. & Lieth, H. (1967). *Klimadiagramm-Weltatlas*. Fischer, Jena.
- Weinstein, D. A., Shugart, H. H. & West, D. C. (1982). The Long-term Nutrient Retention Properties of Forest Ecosystems: A Simulation Investigation. ORNL/TM-8472, Oak Ridge National Laboratory, Oak Ridge, TN.
- Wilkinson, L. (1989). SYSTAT: *The System for Statistics (v5.0)*. SYSTAT Inc., Evanston, IL, 638 pp.
- Wilson, C. A. & Mitchell, J. F. B. (1987). Simulated climate and CO₂-induced climate change over Western Europe. *Climate Change*, **10**, 11–42.
- Wirth, N. (1988). *Programming in Modula-2*. 4th edn. Springer, Berlin, 180 pp.
- Whittaker, R. H. (1975). *Communities and Ecosystems*. Macmillan, New York, 385 pp.
- Woodward, F. L. (1988). Temperature and the distribution of plant species. In *Plants and Temperature. Proc. Meet. held at the Univ. of Essex, 8–10 Sept. 1987*, ed. S. P. Long & F. I. Woodward. Symposia of the society for experimental biology, The Company of Biologists Limited, Univ. of Cambridge, Cambridge, **42**, 59–75.