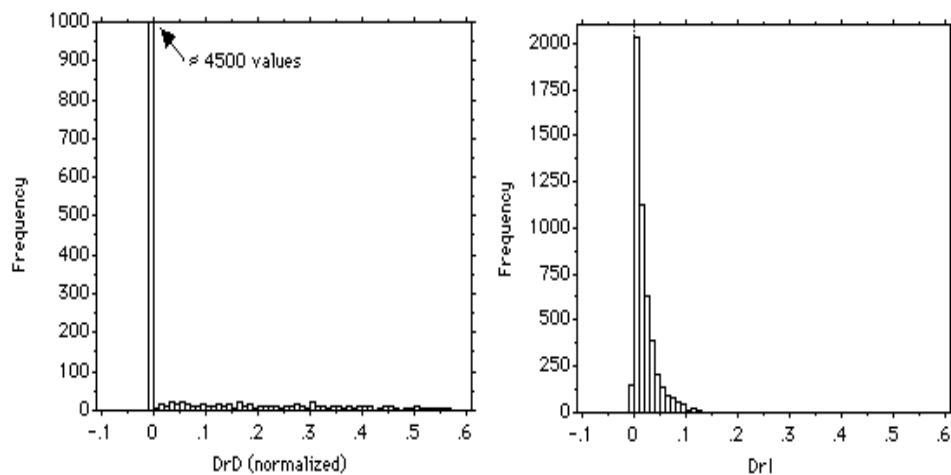


Sensitivity of a Forest Ecosystem Model to Climate Parametrization Schemes

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ABSTRACT

An analysis of the climate parametrization scheme adopted by conventional forest gap models revealed that most assume implicitly 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 e.g. General Circulation Model (GCM) based climate scenarios falls short relative to FORCLIM's sensitivity. A rehearsal of climate-dependent processes in forest gap models is advocated before these models are used in impact studies of climatic change.

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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). In the present study the following few aspects focusing on the influence of climate on ecosystems shall be addressed: First there is the problem to derive from a few measured realizations, i.e. local weather, the characteristics of the underlying stochastic process, the climate. Second there is a multitude of climatic parameters that allow to relate climate with ecologically relevant weather variables. Possible climatic parameters range for instance from mean air temperature to the variance of the monthly number of days without precipitation. Which are the relevant ones to pick in order to understand 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 shall 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 IGBP¹ core project "*Global Change and Terrestrial Ecosystems*" we split the bi-directional interaction between atmosphere and biosphere into its parts, i.e. we consider only the impact of climate on terrestrial ecosystems (IGBP, 1989, 1992). Feedbacks such as the carbon balance, surface roughness, albedo or evapotranspiration are deliberately left out, yet our approach does not preclude to add them later.

Within the last years, possible impacts of climatic change on terrestrial ecosystems and especially forests have attracted much public and scientific attention (SCHNEIDER, 1989; HOUGHTON *et al.*, 1990). The widely used forest gap models (BOTKIN *et al.*, 1972a,b;

¹ The International Geosphere-Biosphere Program: A Study of Global Change

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 originally have not been constructed 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 have to be modified by replacing static climate parametrizations with more flexible solutions. Thus, there arises the question to which extent conventional forest gap models make explicit or implicit assumptions on climate or treat climatic effects only marginally, and whether the models would still behave realistically if these assumptions were relaxed or removed.

In addition, the intrinsic variability within climatic parameters may also affect the behaviour of a forest gap model, but little is known about this kind of sensitivity. Since the parameter space of forest gap models is huge, spanning ca. 600 parameters for central Europe, and 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 & NISBET (1992) have studied the sensitivity of the JABOWA-II model in function of 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 us

that have investigated a forest gap model's structural sensitivity with respect to climate, i.e. its sensitivity to different parametrizations of climate dependent processes.

In this paper we will first analyze the climate parametrizations of the model FORCLIM I (BUGMANN, 1991), which we derived from the FORECE gap model (KIENAST, 1987). Both models use the same climate parametrizations but differ in the biotic processes considered. 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 raises the question how sensitive model behaviour is to such modifications. We present an approach to analyze 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.

Material and methods

Abbreviations

Mathematical notation and functions used are given in Tab. 1, symbols and abbreviations are listed in Tab. 2. Note that variables are subscripted according to the following convention: The subscript's 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 subscript's 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 $T_{m,l}$ (cf. Eq. 1), whereas the annual mean for a given year at a given site is simply denoted as T_l . On the other hand, an interannually varying, location-specific quantity X (X different from temperature or precipitation) is denoted as $X_{y,l}$.

$E[X_z]$	Expected value of random variable X_z (for meaning of subscripts see below)
$VAR[X_z]$	Variance of random variable X_z
$X_z \sim N(\mu, \sigma^2)$	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

Tab. 1: List of functions and mathematical notations.

Symbol	Explanation	Type	Unit/Value
a	Polynom value used to compute PET	<i>AV</i>	-
AET	Actual evapotranspiration	<i>AV</i>	cm
b	Biomass	<i>SV</i>	t/ha
c_0, \dots, c_6	Coefficients used to calculate PET	<i>EPS</i>	-
c_7, c_8	Coefficients used to calculate water deficit	<i>EPs</i>	-
DD	Degree days	<i>AV</i>	°C·d
DD _{min}	Minimum DD required by a species to exist	<i>EP</i>	°C·d
DD _{max}	Minimum DD tolerated by a species to exist	<i>EP</i>	°C·d
DrD	Number of dry days in a year	<i>AV</i>	d
DrI	Drought index	<i>AV</i>	0..1
DrTI	Number of dry days above which no growth occurs	<i>AV</i>	d
DrTol	Drought tolerance	<i>EP</i>	1,2,..5
DTT	Development threshold temperature	<i>EP</i>	°C
FC	Field capacity	<i>P</i>	cm
gDD	Degree day growth factor	<i>AV</i>	0..1
gDS	Drought stress growth factor	<i>AV</i>	0..1
gQ	Carrying capacity growth factor	<i>AV</i>	0..1
H	Heat index used to compute PET	<i>AV</i>	
h_1, h_2	Slope and intercept of degree day correction	<i>EPs</i>	-, °C·d
kDays	Average number of days per month	<i>P</i>	30.5
K_{sN}	Half saturation constant for NPP as a function of annual P	<i>EP</i>	700 mm
K_{sQ}	Half saturation constant for Q as a function of NPP	<i>EP</i>	1200 g/m ² /a
λ	Dependence of PET on latitude	<i>EP</i>	-
nDays	Number of days per month		28...31
NPP	Annual net primary production	<i>AV</i>	g/m ² /a
NPP _{max}	Maximum NPP	<i>EP</i>	3000 g/m ² /a
nYrs	Number of years with T or P measurements		-
η	Nutrient availability factor as a parameter of soil fertility	<i>EP</i>	1.0
P	Precipitation (input variable)	<i>IV</i>	mm
PET	Potential evapotranspiration	<i>AV</i>	cm
Q	Ecosystem carrying capacity	<i>EP</i>	t/ha
Q _{max}	Maximum carrying capacity as a function of NPP	<i>EP</i>	1000 t/ha
ρ	Slope of linear NPP/Temperature dependency	<i>EP</i>	100 g/m ² /a/°C
SM	Soil moisture	<i>AV</i>	cm
T	Mean air temperature (input variable)	<i>IV</i>	°C
T*	Temperature around which NPP varies linearly in function of temperature	<i>EP</i>	10.0 °C
Tw	Winter mean air temperature (parameter resp. auxiliary variable)	<i>AV</i>	°C
V_p	Vegetation period (growing season), see V_o and V_e	-	see below
V_o, V_e	Begin resp. end of the growing season as day numbers within the year	<i>EPs</i>	#, #
WD	Water deficit	<i>AV</i>	cm
WP	Wilting point	<i>P</i>	cm

Tab. 2: List of symbols and abbreviations, subscripts are mostly omitted. Legend: *IV* - input variable; *SV* - state variable; *AV* - auxiliary variable; *P* - model parameter and *EP* - empirical parameter(s).

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 (Tab. 3). They were selected to study forests at differing altitudes under various temperature and precipitation regimes. Besides them, some other Swiss locations (Basel, Davos, Locarno) along an ecological gradient from N to S across the Alps were included for special purposes (Tab. 5).

Location l	Longitude & Latitude	Elevation [m.a.s.l.]	Annual mean temperature $T'_{y,l}$ [°C]	Annual precipitation sum $P'_{y,l}$ [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

Tab. 3: Swiss test sites used to analyze the sensitivity of forest model behaviour to climate parametrizations.

Climatological parametrizations were based on daily mean, minimum and maximum temperatures and daily precipitation sums extracted from the data base of the Swiss Meteorological Agency (SMA), Zurich (BANTLE, 1989; SMA, 1901-1990). The climate stations considered correspond to the selected test sites (Tab. 3). Data are available from 1901-90, 1901-1980, and 1901-77 for Bern, Bever and Sion, respectively, but daily minimum and maximum temperatures for Sion are available only from 1965 to 1977. For each station long-term monthly temperature means $E[T'_{m,l}]$, precipitation sums $E[P'_{m,l}]$ and their variances were calculated (Eqs. 1, 2).

$$E[T'_{m,l}] \approx \frac{1}{nYrs_{m,l}} \cdot \sum_{y=1}^{nYrs_{m,l}} T'_{m,y,l} = \frac{1}{nYrs_{m,l}} \cdot \sum_{y=1}^{nYrs_{m,l}} \left(\frac{1}{nDays_m} \cdot \sum_{d=1}^{nDays_m} T'_{d,m,y,l} \right) \quad (1)$$

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

Annual degree-day sums $DD_{y,l}$ were calculated from monthly mean temperatures (Eqs. 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): By the year 2030 temperature is assumed to increase by +3 °C and +2 °C in the summer- and winter-half year relative to pre-industrial levels, respectively, corresponding to increases by +2.5 °C (summer-half year) and +1.5 °C (winter-half 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 preindustrial 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 $0.7 \pm 3^\circ\text{C}$ in summer (June to August) and $0.5 \pm 3.6^\circ\text{C}$ 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 $+2.0^{\circ}\text{C}$ (MITCHELL *et al.*, 1990). As all ranges listed above average to ca. 1°C the uncertainty bounds for temperature in our “reference climatic change” scenario were set to $\pm 1^{\circ}\text{C}$.

Relative to observations the mean error of all GCMs for precipitation in southern and central Europe amounts to at least $-9\pm 47\%$ in summer and $+18\pm 23\%$ in winter (GATES *et al.*, 1990). Under a doubling of atmospheric CO_2 the models predict for global precipitation an increase of $+9\pm 6\%$ (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 ca. 25%, but to be rather on the conservative side, the uncertainty bounds for precipitation in our “reference climatic change” scenario were set to $\pm 15\%$. Another reason for these low bounds is that due to the coarse spatial resolution of GCM's, errors in regional precipitation changes as projected by the models were considered to be poorer indicators of the true uncertainties as this is the case for the temperature.

All steady state estimates of forest species composition were made by assuming that climate has already reached equilibrium. Although this is an unrealistic assumption, it allows to study the sensitivity of an ecosystem model independently of the much more complex coupling of forests with climate models. Even if we coupled the output of a transient climate change run of a GCM 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 fixpoint 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.

Modeling and simulation tools

The FORCLIM models were implemented using the modelling and simulation software RAMSES (Research Aids for Modeling and Simulation of Environmental Systems; FISCHLIN *et al.*, 1990; FISCHLIN, 1991). This modeling technique allows to program the model equations in a simple yet structured and powerful way in the language Modula-2 (WIRTH, 1988). As an open system RAMSES allows the convenient usage of additional dialogue routines as provided by the underlying «Dialog Machine» (FISCHLIN, 1986). This allows to add easily problem specific program features within a 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, 1991) 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. However, 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 modeling 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 are relevant just two, i.e. FORCLIM-W, which parametrizes weather and climate dependent processes and links them to the plant growth sub-model FORCLIM-P. The latter is a gap dynamics model described elsewhere (BUGMANN & FISCHLIN, in prep.).

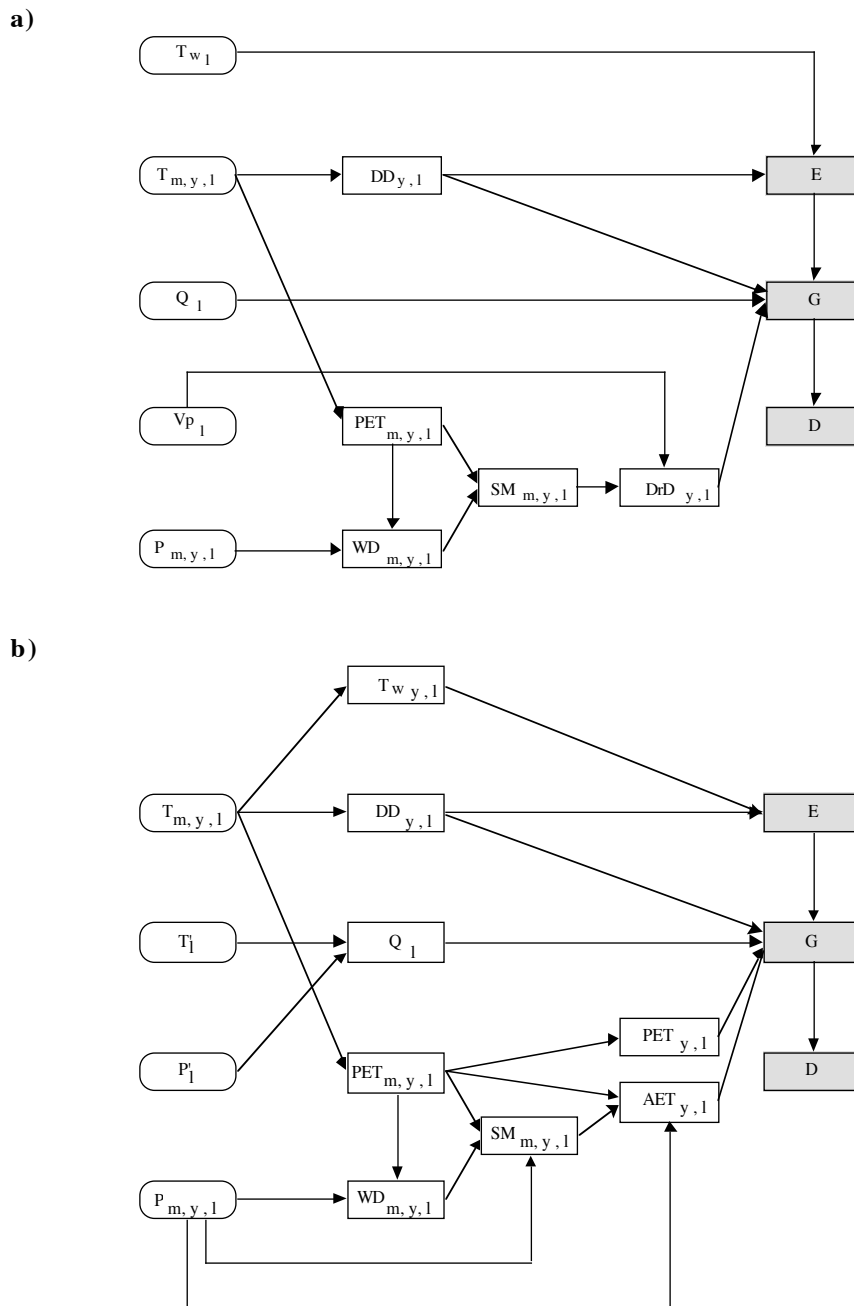


Fig. 1: Relational digraph (FISCHLIN, 1991) depicting functional dependencies between climate dependent input parameters and the ecosystem processes E (establishment of sapling cohorts), G (plant growth), and D (tree death). **a)** Model variant I (conventional, e.g. FORCLIM-W1, or FORECE by KIENAST, 1987), **b)** Model variant II (FORCLIM-W2). **Legend:** ○ - Climate dependent input or parameter; □ - Auxiliary variable; ▒ - 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 mean temperature and precipitation; T_w - Minimum winter temperature as a measure for winter severity; DD - Sum of degree days; Q - Ecosystem carrying capacity; V_p - Vegetation period; DrD - Number of drought days; PET and AET - Potential respectively actual evapotranspiration; WD - Water deficit; SM - Soil moisture (for indices see above).

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. Eqs. 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).

In the following, we will analyze the conventional parametrization scheme adopted by most forest gap models (FORCLIM-W1, Fig. 1a). Then we will contrast it with a scheme used by a new forest model (FORCLIM-W2) developed by the authors as shown in Fig. 1b. Equation numbers followed by a dash refer specifically to FORCLIM-W2. All other parts of the two forest models are described elsewhere (BUGMANN & FISCHLIN, in prep.).

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 Eq. 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; Eq. 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 $h_{1,l} = 1$ and the intercept $h_{2,l} = 0$ (Tab. 4).

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

Site	Sample size (years)	$h_{1,l}$ (slope)	$h_{2,l}$ (intercept, °C·d)	$F_{2,n-2}$	Expl. variance (%)	Period mean of $DD_{y,l}$ (°C·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

Tab. 4: Linear regressions between the two methods for degree-day calculation (Eqs. 4 resp. 4'). The null hypothesis $h_{1,l} = 1$ and $h_{2,l} = 0$ 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 rightmost column contains the long-term mean values of annual degree-day sums for comparison with regression intercepts.

At all test sites the conventional gap model approximation method (Eq. 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, Tab. 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, Tab. 4). FORCLIM-W2 computes first the annual sum of degree-days $DD_{y,l}$ conventionally (Eq. 4), but then uses the site site-specific linear regression coefficients (Tab. 4) in Eq. 4' to correct for the bias produced by Eq. 4.

$$DD'_{y,l} = h_{1,l} \cdot DD_{y,l} - h_{2,l} \quad (4')$$

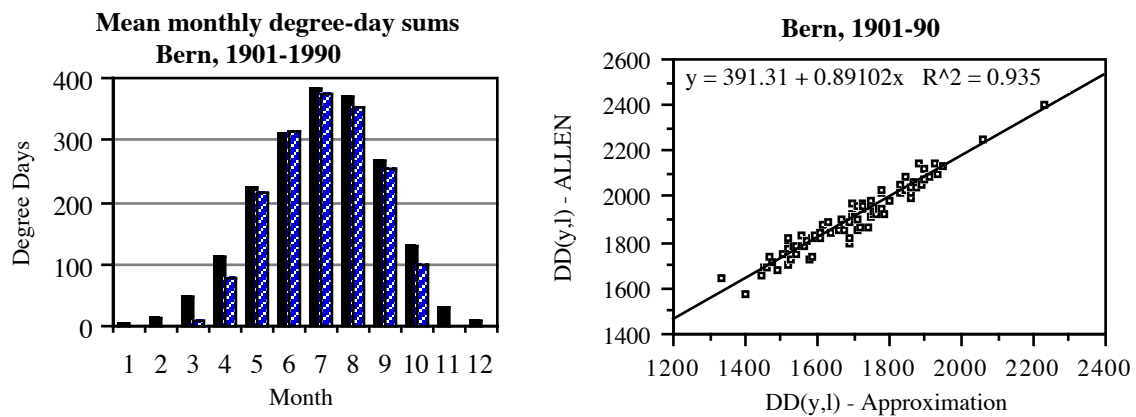


Fig. 2: Comparison between the conventional gap model method for monthly degree-day calculations (e.g. FORCLIM-W1, Eq. 4) and the sine-wave method by ALLEN (1976) based on daily temperatures for the site Bern. *Left*: The systematic and site-specific error results mainly from an underestimation in spring 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, Eq. 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 $h_{1,l} = 1$ and intercept $h_{2,l} = 0$ (cf. Tab. 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. 38f.) who has found generally moderate positive skewness for precipitation data in the European Alps. Attempts to increase the normality of winter precipitation by means of a log-normal transformation resulted only in 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 $\text{VAR}[P'_{m,l}]$. Hence, in both model variants precipitation is generated by sampling variates $P_{y,m,l}$ according to Eq. 5.

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

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 $DD_{y,l}$ (Eq. 4 resp. 4') 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 & 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 (Eq. 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 (Eq. 7), a behaviour which is in contrast to reality.

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

$$\text{establish saplings of species } s \text{ with probability } 0.1 \text{ only if } Tw_1 > Tw_s \quad (7)$$

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 Eq. 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 (Eq. 6'). Sapling establishment is again formulated as a simple random event (Eq. 7')

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

$$\text{establish saplings of species } s \text{ with probability } 0.1 \text{ only if } Tw_{y,l} > Tw_s \quad (7')$$

Eqs. 7 and 7' couple FORCLIM-W1 resp. FORCLIM-W2 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} (Eq. 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 (Tab. 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 tests sites and three additional locations within Switzerland (Basel, Davos and Locarno, see also Tab. 5).

Therefore, the two model variants differ only in the way arguments and parameters are computed (Eq. 4 vs. 4'). A boolean expression (Eq. 8) couples FORCLIM-W to FORCLIM-P.

$$\text{establish saplings of species } s \text{ with probability } 0.1 \text{ only if } DD_{\min_s} \leq DD_{y,l} \leq DD_{\max_s} \quad (8)$$

Temperature, precipitation and tree growth

The ecoprocess growth is modelled as a deterministic, species and site specific, complex process (BUGMANN & FISCHLIN, in prep.). 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 Eq. 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 analyzed 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 (Eq. 4 vs. 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 (Eq. 10, Fig. 1a).

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

The parameter Q_1 implicitly aggregates average edaphic factors (BOTKIN *et al.*, 1972a,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 Eqs. 10' and 11 to the upper range of the net primary productivity and total standing crop data by O'NEILL & 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 in 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

$$NPP_1 = \left[NPP_{\max} \cdot \frac{E[P'_{y,1}]}{K_{sN} + E[P'_{y,1}]} + \rho \cdot (E[T'_{y,1}] - T^*) \right] \cdot \eta_1 \quad (11)$$

By using annual mean temperatures and precipitations for many sites in Switzerland, plus averaging soils by setting $\eta_1 = 1$, the new Eqs. 10' and 11 yielded plausible ecosystem carrying capacities (Tab. 5, Fig. 1b). 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 (Tab. 5).

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

Tab. 5: Comparison of the ecosystem carrying capacities Q_1 along an ecological gradient across the Alps from N to S 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.

Most gap models represent nutrient competition by modifying growth through the carrying capacity growth factor $g_{Q_y,1}$. The closer the total biomass of all species approaches the ecosystem carrying capacity Q_1 , the smaller becomes $g_{Q_y,1}$ (Eq. 12).

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

Both FORCLIM model variants use Eq. 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 & POST (1985), which has been derived from an empirical water balance model by THORNTWHAITE & 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 $DrD_{y,l}$ (Eq. 13). This number is a function of the parameters determining the start and end of the growing season (V_o , V_e), which implicitly depend on climatic parameters (Fig. 1a).

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

where

$$SM_{d,y,l} = f(SM_{m-1,y,l}, SM_{m,y,l}) \quad \text{where } m-1, m = \text{months adjacent to day } d \quad (13.1)$$

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_1 . Its value depends on daily soil moistures $SM_{d,y,l}$ which are determined via a piece wise linear interpolation between preceding and following monthly soil moisture contents $SM_{m,y,l}$ (Eq. 13.1).

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

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

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 Eqs. 15 and 16.

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

where

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

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

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

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

where

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

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

$$DrTl_{y,l,s} = \text{MAX} \left(\frac{DrTol_s}{10} \cdot (V_{e1} - V_{o1}), DrD_{y,l} \right) \quad (17)$$

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 Eq. 18.

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

The calculation of $DrD_{y,l}$ (Eq. 13) appears to produce an extremely discontinuous distribution (Fig. 3 left): According to Eq. 13, a soil moisture always slightly above the permanent wilting point WP_1 results in zero drought days or no drought stress (Eq. 18). This contrasts strongly with reality where such conditions represent severe drought. This approach seems appropriate at very moist or xeric locations, however less for transitions between mesic and xeric conditions.

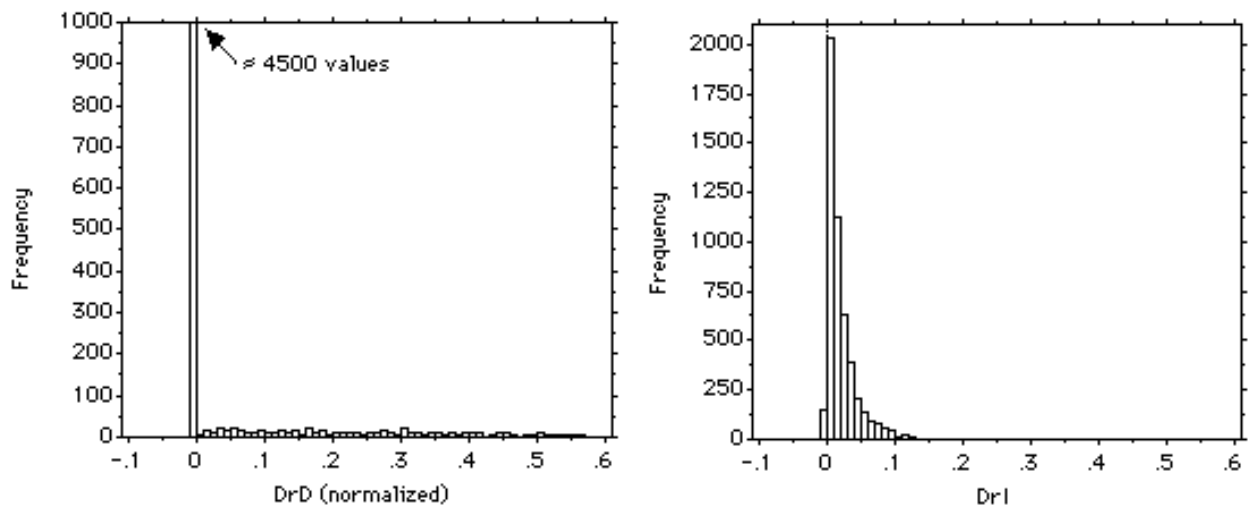


Fig. 3: Histograms of the two variants to compute drought conditions for the site Bern ($n = 5000$). Left: Conventional "Dry days" $DrD_{y,l}$ (FORCLIM-W1, Eq. 13) computed according to the method by PASTOR & POST (1985). Right: Drought index $DrI_{y,l}$ (Eq. 19) proposed by PRENTICE & HELMISAARI (1991) used in FORCLIM-W2. The first bar in each graph represents the zero values. Note the different scales on the ordinates.

To have more continuous measures for drought stress in FORCLIM-W2, we used an alternative growth factor formulation (Eq. 18') based on a drought index (Eq. 19) proposed by PRENTICE & HELMISAARI (1991).

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

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

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

Model variants

The climate parametrization scheme adopted by FORCLIM-W1 consists of the Eqs. 1, 2, 3, 4, 5, 6, 7, 10, 13, 14, 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.*, 1972a,b), FORET (SHUGART & WEST, 1977), PASTOR & POST (1985), FORENA (SOLOMON, 1986), FORECE (KIENAST, 1987) and SIMA (KELLOMÄKI *et al.*, 1992). The Eqs. 8, 9, 12, and 18 couple FORCLIM-W1 to FORCLIM-P. The combination of the sub-models FORCLIM-W1 linked to FORCLIM-P is called FORCLIM model variant I.

FORCLIM-W2 consists of the Eqs. 1, 2, 3, 4, 4', 5, 6', 7', 10', 11, 14, 15, 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 Eqs. 8, 9, 12, and 18'. The combination of the sub-models 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 respectively FORCLIM-W2 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 resp. FORCLIM-W2) on the steady state of the two model variants under a climatic change scenario were studied. Most simulation results are only shown as equilibrium estimates instead of the averaged species biomasses vs. time as it is the case in Fig. 5. For instance the leftmost 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).

Site Sion

For current climatic conditions, both model variants project a forest dominated by *Pinus silvestris* with little *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. Due to the regular occurrence of strong summer droughts, all forest growth ceases. 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.

Site 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 temperatures T_{w1} versus $T_{wy,1}$ (Eq. 6,7 vs. 6',7') has no effect on the final species composition. Since mean January temperature $T_{w1} = E[T'_{Jan,Bern}] = -1.1^{\circ}\text{C}$ 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 (Eq. 6), whereas in FORCLIM-W2 due to the variable, year specific winter temperature $T_{wy,1}$ (Eq. 6') oak saplings can often not establish. Yet this difference between the model variants has no effect on the presence or absence of oaks in the final forest because it is the restricted light availability that actually prevents the growth of oak trees.

Different methods for degree-day calculations (Eq. 4, 4') do neither 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 Eq. 10' predicts an above-ground carrying capacity similar to the value assigned in model variant I (Tab. 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 Eq. 18' versus the conventional "dry days" approach of Eq. 18. As a consequence another coniferous species, i.e. *Abies alba*, replaces *P. abies*; the rest of the community is almost identical.

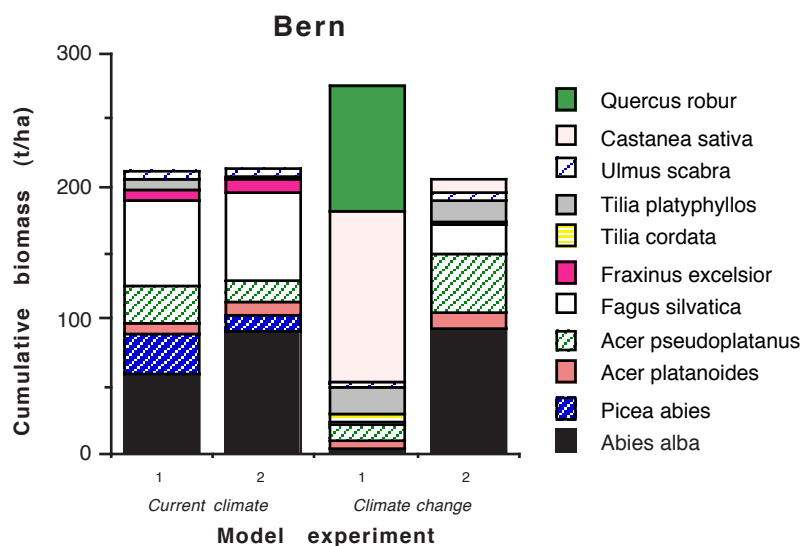


Fig. 4: FORCLIM-P steady state estimates of species composition at the site Bern for the two climate parametrizations FORCLIM-W1 (bars 1) respectively FORCLIM-W2 (bars 2) and for the current climate (left) respectively the reference climate change scenario (right).

Under a changed climate the simulation results at the site 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" (Eq. 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.

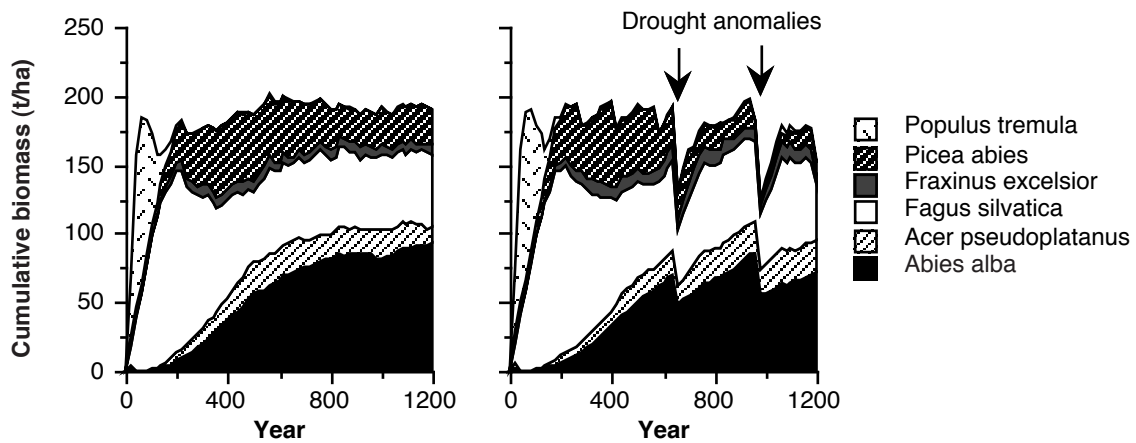


Fig. 5: Forest succession at the low-elevation site Bern, Switzerland, as simulated by model variant I (FORCLIM-W1 linked to FORCLIM-P). Left: Newly sampled weather sequence for each individual gap (conventional approach). Right: Simulation of a forest by using a particular time series. Applying the 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.

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 dieback. 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) is unrealistic and is rather to be interpreted as a model artefact. Since 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 (GCM, e.g. DICKINSON, 1986), this may pose an additional problem for the application of conventional gap models in climate change studies. Ultimately realistic impact studies should analyze transient responses of forest ecosystems to transient climatic change. Therefore, we favour drought parametrizations according to Eq. 18' over those of Eq. 18. In any case, apart from the question which parametrization scheme may be more realistic, at the site Bern model behaviour is very sensitive to the mathematical formulation of drought stress.

Site 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 $-7\text{ }^{\circ}\text{C}$ (Eq. 6,7 and 6,7') (KIENAST, 1987). PRENTICE AND HELMISAARI (1991) have suggested that spruce tolerates actually much lower winter temperatures. If this parameter is lowered to at least $-10\text{ }^{\circ}\text{C}$, simulation results for both model variants change drastically: The typical larch-cembra pine forest (*Larici-Pinetum cembrae* ELLENBERG & KLÖTZLI, 1972) 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 & FISCHLIN, in prep.), a fact which is not properly mimicked by any of the here described model variants.

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 (Eq. 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 the site Bever, whereas for higher Q_1 values, saturation is reached. Eq. 10 and 10', respectively, lead to large differences of Q_1 values between the two model variants (Tab. 5), which strongly influences total simulated biomass (Fig. 6).

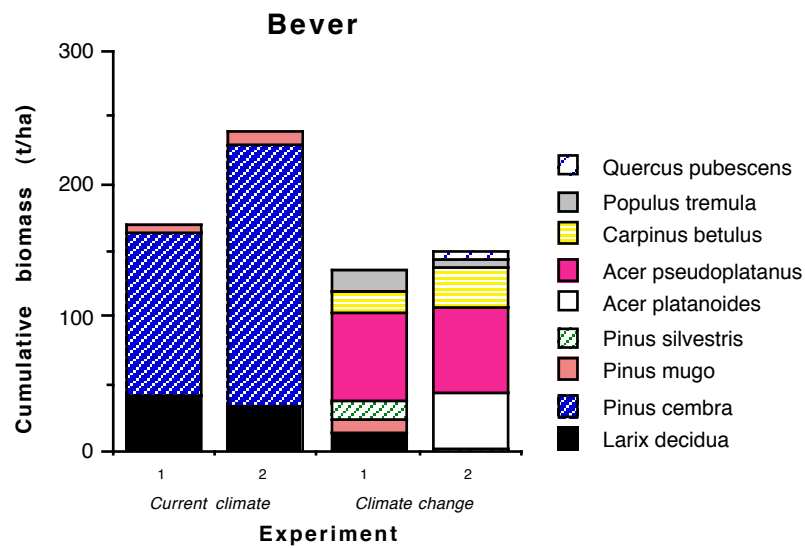


Fig. 6: FORCLIM-P steady state estimates of species composition at the site Bever for the two climate parametrizations FORCLIM-W1 (bars 1) respectively FORCLIM-W2 (bars 2) and for the current climate (left) respectively the reference climate change scenario (right).

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 (Eq. 4 and 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 $h_{1,l}$ and $h_{2,l}$ used in Eq. 4' have to be reformulated so that they become independent 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 predicts that also *Larix decidua* will disappear. This is because in FORCLIM-W2 summer drought stress becomes gradually earlier effective (Eq. 18', Fig. 3 Right) than in FORCLIM-W1 (Eq. 18, Fig. 3 left). 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; note that this is just the opposite of the situation at the site Bern.

The parametrization of carrying capacity Q_I (Eq. 10') ought to be calculated best from long-term means of temperature and precipitation sums. This poses no problem, given there is a long-term record of a changed climate available. However, in case of a transient climatic change Q_I would have to be computed differently. Since Q_I can be interpreted as a nutrient competition parameter (BOTKIN *et al.*, 1972a,b), explicit modelling of nutrient availability along the outlines by ABER & MELILLO (1982), WEINSTEIN *et al.* (1982) or PASTOR & 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 can not make reliable estimates at a particular locality (GYALISTRAS *et al.*, in prep.). This is of course true especially for sites within a complex topography such as the Alps, where our test sites are located. Instead, it is possible to assess the sensitivity of forest models with respect to the intrinsic uncertainties of climate forecasts within the parameter space of T_I by P_I . We explored the sensitivity of the here more trust-worthy FORCLIM variant II behaviour to the conservative deviations from the "reference climate change" scenario at the subalpine test site Bever (Fig. 7).

The simulations with decreased temperature 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.

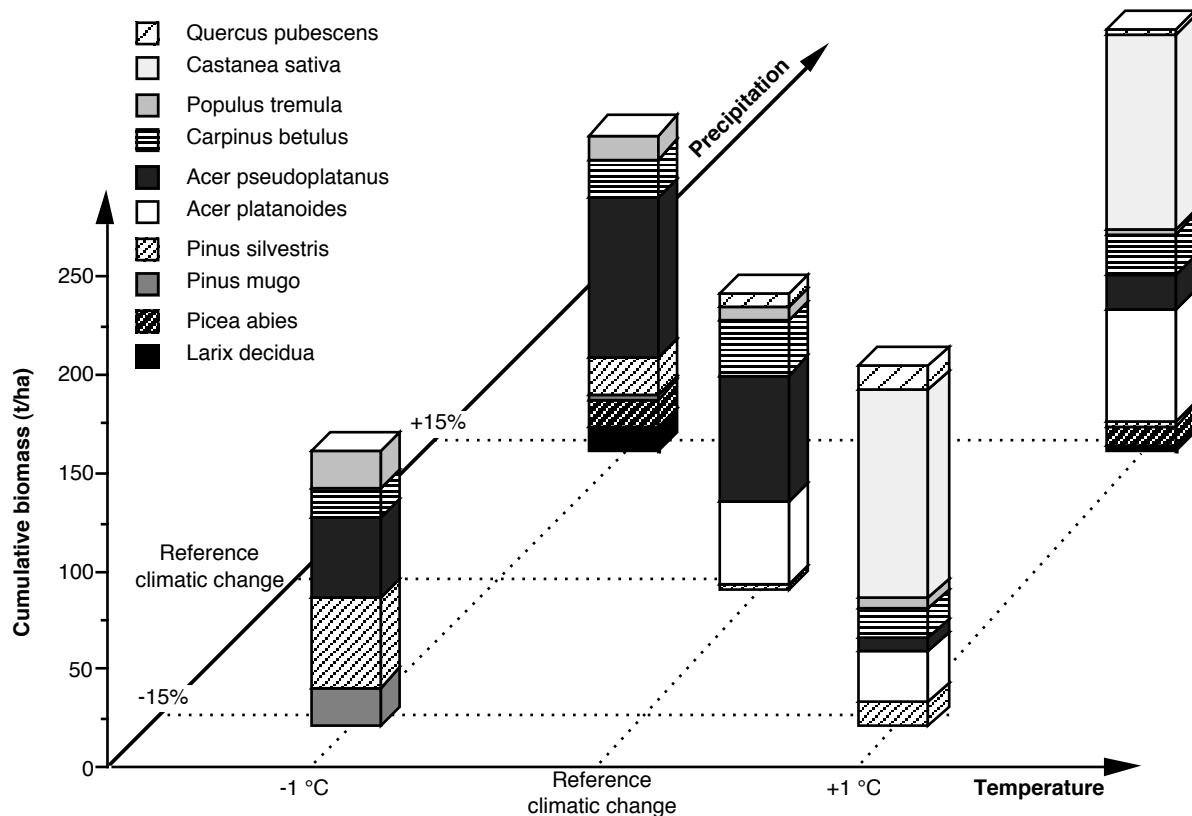


Fig. 7: FORCLIM variant II (FORCLIM-W2 linked to FORCLIM-P) steady state estimates of species composition at the site Bever for the "reference climatic change" scenario (centre) and for four deviations from this scenario within the annual mean precipitation vs. temperature parameter space. These deviations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

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, mainly 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 to 230 t/ha (cf. Tab. 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 known to us cover not the same changes nor the same regimes of the climatic parameters as our investigations.

Conclusion

Forest gap models and climate change

Forest gap models (SHUGART, 1984) allow to study climate change impact on a spatial and temporal scale that is of economical 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 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). Based on the following arguments this fact has more consequences than previously recognized in the studies that apply conventional gap models to climate change scenarios (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 sensitive to dropping the assumption of a constant climate and that any switching to alternative formulations of the climatic parametrizations affects the steady state behaviour of the system significantly. 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 differ not much from 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. Especially the latter mechanism 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 only looked at situations far before (Bern, current climate) or far beyond the threshold (Sion, current climate). 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 this was the case in our study for the site Bern.

Generally we conclude that gap models are sensitive to the specific mathematical parametrizations of climate. At least it can be concluded that conventional gap models are not as robust to modifications in parameters and mathematical structure as has been expressed in earlier studies (SHUGART, 1984). Because of the detected sensitivities we advocate to carefully scrutinize 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).

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

From this analysis we conclude that the following elements should be reformulated such that they depend explicitly only on measurable climate parameters: degree days $DD_{y,l}$ resp. DD_{\min_s} and DD_{\max_s} , the carrying capacity Q_l , and the vegetation period V_{pl} . Furthermore, all climate dependent processes, especially drought stress, should be formulated so that they become continuously valid over a large gradient of environmental conditions. The replacement of the sensitive drought stress parametrization by a formulation that reacts smoother 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 a forest gap models, being to one part deterministic and to the other stochastic, may easily produce artefacts like an episodic forest breakdown over large areas. This threatens principally the validation and application of forest gap models by means of particular records of climatic input data, either available as time series from transient GCM runs or in form of 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.*, in prep.). Therefore, the approach chosen in FORCLIM-W2 appears to be an improvement, but requires further studies.

c) Since species composition was found to be sensitive to the method of degree-day calculations, we advocate better approximations for degree-day sums still based on monthly mean temperatures. This requires also that the individual species' degree-day parameters are estimated anew. Hereby more objective and better documented methods are needed, which allow to

identify the species specific parameters in a consistent way. This would allow to add or remove species from a particular gap model more flexibly than this 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 if one wants to simulate 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: Within the range of the inherent variability remaining in scenarios of future climate, forests might differ substantially. Since FORCLIM-W2 parametrizes climate more reliably than FORCLIM-W1, we surmise that these findings are trust-worthy 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 our forests drastically, but also that GCM simulations have to forecast future climates at a higher precision than currently available (WILSON & MITCHELL, 1987; SANTER *et al.*, 1990; GIORGI & MEARN, 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 confounded with predictions; at best can they outline the range of conditions within which our forests are most vulnerable to major changes.

As a main result from these sensitivity studies we concluded 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.

Yet, to assess climate change impacts on terrestrial ecosystems, e.g. by linking climate and ecoprocesses closer, future bioclimatic scenarios must also match the surprisingly high precision called for by the sensitivity of the ecosystems.

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