

Improving the behaviour of forest gap models along drought gradients

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Abstract

Recent applications of forest gap models have shown weak performance along drought gradients. Using the gap model FORCLIM, we examine two possible explanations for this: (1) the parameters denoting the drought tolerance of the tree species need to be estimated more accurately, and (2) the soil water balance estimation schemes used in most gap models are not capable of tracking soil moisture content under dry conditions sufficiently well to reflect its influence on tree growth. The behaviour of the model along two drought gradients in Europe and eastern North America is used as a test case. Parameter adjustments alone turned out to be ineffective for improving the performance of FORCLIM. A theoretical analysis of the soil water balance model by Thornthwaite and Mather [Thornthwaite, C.W., Mather, J.R., 1957. Instructions and tables for computing potential evapotranspiration and the water balance. *Publ. Climatol.* 10, pp. 183–311.], which is used in FORCLIM and in many other gap models, showed that it yields inconsistent results when applied to simulate the year-to-year variability of drought occurrence. We therefore have developed a new water balance model with the goal of adequate performance in connection with a forest gap model, similar simplicity and low computational demand as in previous models. The new scheme uses a bucket approach and monthly time steps of temperature and precipitation alone. The performance of FORCLIM did not improve when the new water balance model was used together with the original estimates of the species' drought tolerance. However, when both a small number of drought tolerance parameters were adjusted and the new water balance model was incorporated, the performance of FORCLIM increased strongly along the drought gradients on both continents. In Europe, the transition from beech to oak forests could be simulated correctly, whereas in eastern North America the simulated pattern of aboveground biomass became much more realistic. We conclude that the Thornthwaite and Mather model of soil water balance should not be used in forest gap models any more. © 1998 Elsevier Science B.V.

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1. Introduction

Forest gap models (Botkin et al., 1972; Shugart, 1984) have been used successfully to simulate the tree species composition at a wide range of sites in

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many different parts of the world. However, there is increasing evidence that many of these models do not adequately portray the effects of drought on forest dynamics, thus preventing their application along drought gradients. This constitutes a significant problem for assessing the possible effects of anthropogenic climatic change on forests (Kirschbaum et al., 1996). In the future, although the regional pattern of rainfall and temperature changes is highly uncertain and the location of future drought-prone areas is still unknown, increasing drought is likely to occur in many now forested regions (Kattenberg et al., 1996).

For example, Solomon (1986) found that the FORENA model failed to simulate the influence of increased drought on forest structure in the south-western part of eastern North America. Similar difficulties were encountered with the LINKAGES model (Pastor and Post, 1985; W.M. Post, pers. commun. 1993). Bugmann (1994) tested the behaviour of the FORCLIM model systematically in a climatological parameter space spanned by the annual mean temperature and the annual precipitation sum in central Europe, and found that along drought gradients, the model performs only weakly. Finally, Lasch and Lindner (1995) adapted the FORSKA model (Prentice et al., 1993) for the conditions along a drought gradient in eastern Germany. They found that strong parameter tuning was necessary to obtain plausible results under these subcontinental conditions, but at the same time the performance of the model deteriorated for the area where it originally had been developed, i.e. Scandinavia.

As the dry timberline is approached, the interannual variability of moisture availability strongly determines the establishment and survival rates as well as the competitive ability of plants (e.g., Kozłowski et al., 1991). A model whose aim is to realistically simulate species composition along drought gradients, therefore, needs to incorporate this variability of weather conditions, as opposed to just long-term averages of climatic data, and it needs to accurately estimate the processes of evapotranspiration, infiltration and runoff.

Because FORSKA uses the long-term mean climatic data as input to determine successional processes, it is not surprising that this model is not able to simulate plausible species composition along

drought gradients. Most other gap models, however, incorporate stochastic weather generators or can be driven by time series of measured weather data (e.g., Pastor and Post, 1985; Solomon, 1986; Kienast, 1987; Botkin and Nisbet, 1992; Bugmann, 1994). Thus, the failure of these models must be related to other deficiencies.

The present analysis is based on the forest gap model FORCLIM (Bugmann, 1994, 1996a; Fischlin et al., 1995), which was developed for central European conditions (e.g., Bugmann and Fischlin, 1994) and has also been applied successfully in eastern North America (Bugmann and Solomon, 1995). Drought gradients in both of these areas will be used as test cases. Similar to many other gap models (e.g., Pastor and Post, 1985; Kienast, 1987; Kellomäki et al., 1992), FORCLIM contains the submodel of soil water balance of Thornthwaite and Mather (1957). The findings of the present analysis are therefore likely to be valid for those models as well.

Bugmann (1994) presented several hypotheses that could explain the weak performance of gap models along drought gradients. Here, two hypotheses are examined in more detail: (1) whether the parameters denoting the drought tolerance of the tree species may need to be estimated more accurately, and (2) whether the simple soil water balance models used in most gap models are not capable of tracking soil moisture content under dry conditions.

The first hypothesis is of interest because such a 'tuning' would provide a simple solution to improve the performance of the models, given that the parameter values do not exceed their plausibility range. On the other hand, several researchers have proposed that detailed biophysical submodels need to be added to forest gap models to adequately portray the soil moisture balance and the occurrence of drought (e.g., Martin, 1990, 1992; Bonan and van Cleve, 1992; Bonan, 1993; Kräuchi, 1994). FORCLIM is designed to run across large geographical areas, where only limited input data are available (Cramer and Fischer, 1996). Therefore, the principle of parsimony (Jefferys and Berger, 1992; Bugmann and Martin, 1995) will be used to examine the second hypothesis, i.e., we attempt to formulate and evaluate an alternative bucket model of soil moisture that is equally simple but realistically incorporates the processes determining water availability along drought gradients.

2. Material and Methods

2.1. Model description

The FORCLIM model (Bugmann, 1994, 1996a; Fischlin et al., 1995) was developed for central European conditions based on the model FORECE (Kienast, 1987). FORCLIM was designed to incorporate reliable yet simple formulations of climatic influences on ecological processes, using only a minimum number of ecological assumptions. FORCLIM consists of three modular submodels, each of which can be run independently, or combined: (1) FORCLIM-E, a submodel for the abiotic environment as modified from FORECE (Kienast, 1987), including a slightly modified version of the soil water balance model of Thornthwaite and Mather (1957) (cf. Fischlin et al., 1995); (2) FORCLIM-S, a submodel for soil carbon and nitrogen turnover, modified from Pastor and Post (1985); (3) FORCLIM-P, a submodel for tree population dynamics based on the gap dynamics hypothesis (Watt, 1947; Shugart, 1984).

In the following, a short overview of FORCLIM, version 2.4 is given. Then the soil moisture balance routine as incorporated in FORCLIM, version 2.4 is described and analysed in detail. Finally, an alternative formulation of the soil water balance model is proposed, giving rise to version 2.6 of FORCLIM.

2.1.1. The core structure of FORCLIM

In FORCLIM-P, size cohorts are simulated, i.e., groups of trees that have the same diameter at breast height, instead of individual trees (Bugmann, 1994, 1996a). Maximum tree growth is constrained by light availability, soil nitrogen level, summer temperature, and water stress. Light availability through the canopy is calculated using the Beer–Lambert law. For the influence of nitrogen availability on tree growth, the approach by Aber et al. (1979) is used. The effect of summer temperature on tree growth is calculated using a parabolic relationship between the annual sum of degree-days and the growth rate of the trees. The calculation of the degree-day sum was improved as compared to earlier models (e.g., Kienast, 1987). Drought is expressed as the annual evapotranspiration deficit, $1 - \text{AET}/\text{PET}$ (Prentice et al.,

1993), where AET and PET are the annual sums of actual and potential evapotranspiration, respectively.

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

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

Estimates of the model parameters for these environmental constraints were assembled from compilations of silvics data for succession modelling (Prentice and Helmisaari, 1991) and from other published sources listed in Bugmann (1994). A detailed description of the model, its calibration and testing is given by Bugmann (1994, 1996a).

2.1.2. The Thornthwaite and Mather model of soil water balance (FORCLIM, version 2.4)

The model of soil water balance of Thornthwaite and Mather (1957) is a simple empirical scheme that requires only few input data, i.e., monthly mean temperatures and monthly precipitation sums. It has been used for a wide variety of applications on both the global (e.g., Meentemeyer et al., 1985, cf. the review by Mintz and Serafini, 1992) and the local scale, e.g., in many forest gap models (Pastor and Post, 1985; Kienast, 1987; Fischlin et al., 1995). Thornthwaite and Mather (1957) developed the model to predict the climatological water balance, i.e., the long-term average water balance based on the long-term averages of monthly mean temperature and monthly precipitation sum. Typically, these variables show rather smooth seasonal cycles. In this mode of application, the Thornthwaite and Mather model seems to provide plausible results for a wide range of conditions (e.g., Müller, 1982; Mintz and Serafini, 1992).

Assessing the water balance of a specific year based on the measured weather data of that year is likely to pose additional problems because of the short-term, within-season fluctuations of temperature and precipitation, but this has not been addressed yet. In the first gap model that incorporated the bucket model of Thornthwaite and Mather (1957) (LINKAGES; Pastor and Post, 1985), the water balance of each simulation year is determined based on stochastically generated weather data. Pastor and Post (1985) implicitly assumed that the model did not require any modification, although it was used in a different mode than the one intended by its developers. The validity of this assumption is evaluated below.

The basic assumption of the model by Thornthwaite and Mather (1957), which operates on a monthly time step, is that the evaporative demand is satisfied by precipitation in the first place, and soil moisture is drawn upon only when there is insufficient precipitation. According to this model, under conditions of high evaporative demand, 100% of the precipitation is intercepted by the canopy, which is not realistic. Formally, this can be written as

$$\Omega_{m+1} = \min(\Omega_m + P_{s,m} - E_m, \Omega_{\max}) \quad (1)$$

where Ω_m is soil moisture, $P_{s,m}$ is surplus precipitation that infiltrates into the soil, E_m is the amount of water drawn additionally from the soil by both transpiration and evaporation, Ω_{\max} is the water holding capacity of the soil, and m denotes the month.

Surplus precipitation ($P_{s,m}$) is calculated as

$$P_{s,m} = \begin{cases} P_m - \text{PET}_m & , P_m \geq \text{PET}_m \\ 0 & , \text{else} \end{cases} \quad (2)$$

where P_m is the monthly precipitation sum, and PET_m is an estimate of potential evapotranspiration as a function of monthly mean temperature and geographical latitude. It is well known that potential evapotranspiration is mainly a function of net radiation; Thornthwaite and Hare (1965) noted that the success of the estimate of PET by Thornthwaite and Mather (1957) “depends on the fact that the mean air temperature does, to a considerable extent, serve as a parameter of the net radiation.”

The amount of water drawn from the soil (E_m) is calculated as

$$E_m = \begin{cases} 0 & , P_m \geq \text{PET}_m \\ -\Delta\Omega_m & , \text{else} \end{cases} \quad (3)$$

The quantity $\Delta\Omega_m$, i.e., the amount of water drawn from the soil when precipitation does not satisfy evaporative demand, is calculated via an empirical relationship where the amount of water retained in the soil ($w_{r,m}$) is calculated:

$$\Delta\Omega_m = w_{r,m} - \Omega_m \quad (4)$$

$w_{r,m}$ then is determined based on the amount of ‘accumulated potential water loss,’ i.e., the running sum of unsatisfied evaporative demand (Eq. (5)).

$$w_{r,m} = \Omega_{\max} \cdot e^{(k_i - \frac{k_s}{\Omega_{\max}}) \text{PWL}_m} \quad (5)$$

where PWL_m is accumulated potential water loss (Eq. (6)), and the k_i are empirical parameters.

$$\text{PWL}_m = \begin{cases} \text{PWL}_{m-1} + P_m - \text{PET}_m & , \Omega_{m-1} < \Omega_{\max} \\ 0 & , \text{else} \end{cases} \quad (6)$$

Actual evapotranspiration (AET_m) is an output variable in the model of Thornthwaite and Mather (1957); it is calculated as

$$\text{AET}_m = \begin{cases} \text{PET}_m & , P_m \geq \text{PET}_m \\ P_m - \Delta\Omega_m & , \text{else} \end{cases} \quad (7)$$

In FORCLIM, version 2.4, the following annual index was used to model drought occurrence (Bugmann, 1994):

$$u\text{Dr} = 1 - \frac{\sum_m \text{AET}_m}{\sum_m \text{PET}_m} \quad (8)$$

A theoretical analysis of Eqs. (1)–(8) and simulation studies with the model revealed that two undesirable conditions may occur when the model is driven with (annually varying) weather data instead of long-term climatic means:

(1) Because the model lacks an explicit constraint of potential evapotranspiration (PET_m) on actual evapotranspiration (AET_m), it is possible that AET_m exceeds PET_m (if $P_m < \text{PET}_m$, Eq. (7)). In this case, the model simulates too much drought.

(2) When there is not enough rain to satisfy potential evaporation, i.e., under dry conditions ($PET_m > P_m$), it happens that the amount of water retained in the soil (Eq. (5)) is larger than the current soil water storage, thus resulting in a net flux of water from the atmosphere into the soil, i.e., a positive $\Delta\Omega_m$ in Eq. (4). Hence under dry conditions, the model may generate additional precipitation instead of simulating a depletion of soil moisture; the result is too little drought.

While the first problem could be fixed rather easily, the second exhibits more fundamental difficulties of applying this equilibrium method to time series data. It should be noted that many forest gap models (e.g., Pastor and Post, 1985; Kienast, 1987; Kellomäki et al., 1992; Bugmann, 1994) use this submodel in the implementation of Pastor and Post (1985), and are likely to produce inconsistent results when simulating forest dynamics under dry conditions. We conclude that a more reliable model than Eq. (5) needs to be found to calculate the quantity $\Delta\Omega_m$, or that a different approach should be developed altogether. We favour the second alternative and present an improved bucket model in Section 2.1.3.

2.1.3. An alternative formulation of the soil water balance model (FORCLIM, version 2.6)

We use the simple model of Thornthwaite and Mather (1957) as a baseline and modify it where required. We consider only one soil layer ('bucket'). For each process in the new soil water balance model, we attempt to find the simplest formulation that can be expected to yield a plausible parameterization of drought influence on long-term successional processes. The resulting model thus represents a hypothesis on the minimum number of factors and the lowest level of detail to be included in such model. If this model fails to provide the basis for simulating realistic changes of tree species composition along drought gradients, then additional factors must be incorporated, or the formulation of the factors must be refined (cf. Bonan, 1993; Bugmann and Martin, 1995).

The new water balance model incorporates the following features:

(1) It incorporates essential concepts that were lacking in the model of Thornthwaite and Mather

(1957), such as the distinction between supply and demand. The logic for this part is based on the model of soil water balance by Cramer and Prentice (1988). The new model also includes an explicit parameterization of canopy interception. Models that operate at a daily time step may assume that all the precipitation infiltrates into the soil, i.e., they may neglect interception (e.g., Cramer and Prentice, 1988). At a monthly time step, however, this assumption is unreasonable, especially when soil moisture is already depleted. Hence, interception must be treated either implicitly (e.g., Thornthwaite and Mather, 1957), or, preferably, it must be considered explicitly.

(2) For the sake of simplicity, it is based on a monthly time step. Monthly mean input data are available with a global coverage (Leemans and Cramer, 1991), whereas data at a higher temporal resolution are available at few weather stations only. In the latter case, the application of a model over whole regions, let alone in remote areas, would be difficult. In addition, the calculations of a model that is based on a monthly time step are quite efficient. Alternatively, monthly weather data could be interpolated smoothly to daily values (e.g., Prentice et al., 1993), or a weather generator could be used to provide daily data (e.g., Friend, 1997).

(3) As input variables, it uses the mean temperature and the precipitation sum only. For both variables, not only the long-term means, but also their distributions are obtained rather easily. On the other hand, although the long-term means of incident radiation are widely available, the quantification of its distribution is possible for few weather stations only. Therefore, this variable is not used in the model.

Following the rationale of the model by Thornthwaite and Mather (1957), we formulate the balance equation of soil moisture (Ω_m) of a one-layer water store in the soil as

$$\Omega_{m+1} = \min(\Omega_m + P_{s,m} - E_m, \Omega_{\max}) \quad (9)$$

Evapotranspiration from the soil, E_m , is assumed to be equivalent to the lesser of a supply function and a demand function (Federer, 1982), which is adopted here as an analog of the instantaneous formulation used by Prentice et al. (1993):

$$E_m = \min(S_m, D_m) \quad (10)$$

where D_m is the monthly evaporative demand from the soil, and S_m is the monthly supply of water from the soil. The demand function is approximated by an estimate of potential evapotranspiration (Eqs. (12)–(14)) modified from Thornthwaite and Mather (1957) and Pastor and Post (1985), from which intercepted water is subtracted (Eq. (11)); the latter is used to satisfy the evaporative demand in the first place. Note that Thornthwaite and Mather assumed that the full monthly precipitation sum can evaporate without infiltrating into the soil.

$$D_m = PET_m - P_{i,m} \quad (11)$$

where PET_m is potential evapotranspiration (Eq. (12)), and $P_{i,m}$ is intercepted precipitation.

$$PET_m = lp \left(\frac{10}{hi} \cdot \max[T_m, 0] \right)^a = g(T_m, lat) \quad (12)$$

where lp is a correction function for sun angle and day length depending on latitude (lat), hi is a 'heat index' calculated from the long-term monthly mean temperatures $T_{c,m}$ (Eq. (13)), and a is an empirical function (Eq. (14)).

$$hi = \sum_{m=Jan}^{Dec} \max(k_1 \cdot T_{c,m}, 0)^{k_2} \quad (13)$$

$$a = k_3 \cdot hi^3 + k_4 \cdot hi^2 + k_5 \cdot hi + k_6 \quad (14)$$

where the k_i are parameters. Note that the values of k_3 and k_4 are very small; hence over the range of realistic hi values, a can be approximated excellently by a linear function. For the sake of consistency with the original model, we retained the form of Eq. (14), though.

Intercepted and infiltrating precipitation ($P_{i,m}$ and $P_{s,m}$, respectively) are calculated according to Eqs. (15) and (16). We assume that a constant fraction of the monthly precipitation is intercepted by the canopy, based on data compiled by Mitscherlich (1971), which show that this relationship holds well at the broad scale.

$$P_{i,m} = \min(f_i \cdot P_m, PET_m) \quad (15)$$

$$P_{s,m} = P_m - P_{i,m} \quad (16)$$

where f_i is a parameter denoting the fraction of precipitation that is intercepted. The supply function S_m is formulated according to Federer (1982):

$$S_m = c_w \cdot \frac{\Omega_m}{\Omega_{max}} \quad (17)$$

where c_w is a parameter denoting the maximum evapotranspiration rate from saturated soil under conditions of high demand (Prentice et al., 1993).

The drought index (uDr' , cf. Eq. (8)) is modified as follows:

$$uDr' = 1 - \frac{\sum_m E_m}{\sum_m D_m} \quad (18)$$

The index of Eq. (18) explicitly considers the amount of water transpired by the trees (as approximated by the quantity E_m) relative to the evaporative demand drawing on soil water (D_m). Therefore, we expect the formulation of Eq. (18) to be a better proxy of drought stress as experienced by the trees than Eq. (8).

2.2. Adjustment of European species-specific drought response parameters

In FORCLIM, each tree species is characterized by its drought tolerance (parameter $kDrT_s$) as one of 14 species-specific parameters (Bugmann, 1994). The $kDrT_s$ parameter denotes the value of the drought index (Eq. (8)) where the growth of species s comes to a halt. Since detailed physiological observations for a large number of tree species are lacking, values of $kDrT_s$ in FORCLIM, version 2.4 (Bugmann, 1994, 1996a) were estimated based on Ellenberg (1986). It is important to note that the values we used are different from the so-called indicator values, which represent the realized niche of the species. The data base used for FORCLIM refers to the species' drought tolerance in the autecological sense (p. 82 of Ellenberg, 1986). These autecological data allowed to assign each species to one out of five classes (1 = very intolerant, 5 = very tolerant), which then were translated into values of the drought index, uDr (Eq. (8)). In the present analysis, the readjustment of parameters was restricted to $kDrT_s$, and to tree species dominating in the potential natural vegetation of central Europe (Ellenberg, 1986) because

Table 1

Original and adjusted drought tolerance parameters^a of five major tree species of central Europe

Species	Original value	Adjusted value
<i>Larix decidua</i>	2	3
<i>Picea excelsa</i>	1	2
<i>Pinus cembra</i>	5	4
<i>Fagus sylvatica</i>	2	3
<i>Quercus robur</i>	5	4

^a 1 = very intolerant; 5 = very tolerant.

Plant nomenclature follows Hess et al. (1980).

the drought tolerance of these species is known best. The plausibility interval of the $kDrT_s$ parameter was estimated to be not more than ± 1 class.

Given these constraints, we compared the autecological descriptions by Ellenberg (1986) with those of Landolt (1977), Prentice and Helmisaari (1991) and Jahn (1991). Five species were identified where a modification of the original drought tolerance parameter probably is realistic and could lead to significant changes of the simulated species composition along drought gradients in central Europe (Table 1).

2.3. Estimation of model parameters for the new water balance model

The new drought index, uDr' (Eq. (18)), was found to be always larger than uDr (Eq. (8)). To be able to run FORCLIM version 2.6 without having to reestimate all species-specific drought tolerance parameters individually, all the $kDrT_s$ parameters of all

species were adjusted uniformly to accommodate the new drought index. To this end, an extensive simulation study was conducted over a wide range of climatic conditions in Europe, and a simple relationship between the two indices was determined (Eq. (19)). Consequently, the $kDrT_s$ parameters were recalculated for all species. The simulation results obtained based on these recalculated parameters have to be interpreted as sensitivity tests; undisputedly it would be desirable to derive independent estimates of the new values of the $kDrT_s$ parameters.

$$kDrT_s = kDrT_s \cdot 1.67 \quad (19)$$

Moreover, there are two parameters in the new soil moisture balance model that were not present in the model of Thornthwaite and Mather (1957): f_i , the fraction of precipitation that is intercepted by the canopy, and c_w , the maximum rate of evapotranspiration of a saturated soil under conditions of high demand. They were assumed to have the following values: $f_i = 0.3$ (Lyr et al., 1992), and $c_w = 12$ cm/month (Waring and Schlesinger, 1985; Cramer and Prentice, 1988). It is acknowledged that in reality f_i is not a constant but a function of rainfall intensity and frequency, and is further influenced by the composition and the phenological status of the canopy. In spite of these complicating factors, f_i varies typically between 0.2 and 0.4 in temperate forests (e.g., Mitscherlich, 1971), depending on the season and the species. Hence we consider a value of

Table 2

European test sites used in the present study, their location, long-term annual mean temperature (T), long-term annual precipitation sum (P), bucket size (BS), and dominating tree species of the potential natural vegetation (PNV) according to Ellenberg and Klötzli (1972), Ellenberg (1986) and Krausch (1992)

Site	Location			T (°C)	P (mm)	BS (cm)	PNV
	Latitude (°N)	Longitude (°E)	Elevation (m)				
Bever S	46.6	9.9	1712	1.5	841	10	<i>P. cembra</i>
Bever N	46.6	9.9	1712	1.5	841	10	<i>P. excelsa</i>
Davos	46.8	9.8	1590	3	1007	10	<i>P. excelsa</i>
Adelboden	46.5	7.6	1325	5.5	1351	15	<i>P. excelsa</i> , <i>F. sylvatica</i> , <i>A. alba</i>
Bern	46.9	7.4	570	8.4	1006	20	<i>F. sylvatica</i>
Basel	47.5	7.6	317	9.2	784	15	<i>F. sylvatica</i> , <i>Quercus</i> spp.
Schwerin	53.6	11.4	45	8.2	625	24	<i>F. sylvatica</i> , <i>Quercus</i> spp.
Cottbus	51.8	14.3	76	8.8	573	24	<i>Quercus</i> spp., <i>Tilia</i> spp., <i>Carpinus betulus</i>
Sion	46.2	8.6	542	9.7	597	15	<i>P. silvestris</i> , <i>Quercus</i> spp.

Tree nomenclature is according to Hess et al. (1980).

N = steep north-facing slope (parameter $kSIAsp = -2$); S = steep south-facing slope (parameter $kSIAsp = +2$).

Table 3
 Eastern North American test sites (Canada) and climatic divisions (US) used in the present study, their location, long-term annual mean temperature (T), long-term annual precipitation sum (P), number of the vegetation type (Küchler, 1975), and dominating tree species of the potential natural vegetation (PNV) according to Rowe (1972) and Küchler (1975)

Site/division	Location	Latitude (°N)		Longitude (°W)		T (°C)	P (mm)	No.	PNV
Shefferville	55	67		-4.6	724	-			<i>Picea glauca</i> , <i>P. mariana</i> , <i>Populus</i> spp., <i>Pinus banksiana</i> , <i>Larix laricina</i>
Armstrong	50	90		-0.8	739	-			<i>P. banksiana</i> , <i>P. resinosa</i> , <i>P. glauca</i> , <i>Picea mariana</i> , <i>Betula papyrifera</i>
W.U. Michigan	47	89		4.9	817	106/107			<i>Pinus strobus</i> , <i>P. resinosa</i> , <i>Thuja occidentalis</i> , <i>Acer saccharum</i> , <i>Tsuga canadensis</i> , <i>F. grandifolia</i> , <i>Tilia americana</i>
C.L. Michigan	44	85		8.3	760	100			<i>Acer</i> spp., <i>F. grandifolia</i> , <i>Fraxinus</i> spp., <i>Tilia</i> , <i>Carya</i> spp., <i>Quercus</i> spp.
W.C. Ohio	40	84		10.9	930	100			<i>Carya</i> spp., <i>Quercus</i> spp., <i>Acer</i> spp., <i>Fraxinus</i> spp., <i>F. grandifolia</i>
C.P. Tennessee	36	85		14.2	1378	103			<i>Quercus</i> spp., <i>F. grandifolia</i> , <i>Liriodendron tulipifera</i> , <i>Acer</i> spp., <i>Castanea dentata</i> ^a
S.W. Georgia	31	85		19.6	1290	111/112			<i>Carya</i> spp., <i>Quercus</i> spp., <i>Liquidambar styraciflua</i> , <i>Pinus</i> spp.
W. Missouri	37	91		13.8	1095	111			<i>Carya</i> spp., <i>Quercus</i> spp., <i>Pinus</i> spp.
S.S.C. Arkansas	34	93		17.9	1312	111			<i>Carya</i> spp., <i>Quercus</i> spp., <i>Pinus</i> spp.

^aExtinct today due to the chestnut blight (cf. Shugart and West, 1977).

The bucket size of the soil was assumed to be 17 cm at all sites and divisions, respectively (Solomon, 1986). The abbreviations used for the climatic divisions and a map may be found in Bugmann and Solomon (1995).

0.3 to be a reasonable first approximation for the whole canopy.

2.4. Simulation experiments

In the present paper, we use the ecological (plant demography) part of the FORCLIM model as a diagnostic tool for assessing the ecological effects of the two soil moisture submodels, although a more conclusive test of the behaviour of the two soil moisture balance models would involve assessing their predictions of soil moisture content, AET, and runoff as a function of the interannual variability of weather along drought gradients. To this effect, fairly long (say, 10 yrs or more) continuous measurements of these water balance components would be required at a number of sites. To our knowledge, such data do not exist or at least are not accessible.

For central Europe, a factorial design was used to evaluate the importance of parameter adjustment vs. exchanging the water balance submodel. To study the behaviour of FORCLIM, sites along a combined gradient of increasing temperature and at the same time increasing drought from cool-moist to warm-dry conditions were selected. Bugmann (1996b) showed that such a gradient is largely representative of the terrestrial land area of central and northern Europe. Four sets of simulations were conducted to determine the species composition along this gradient (Table 2).

(1) FORCLIM, version 2.4, which contains the water balance model of Thornthwaite and Mather (1957), with the original set of $kDrT_s$ parameters (Bugmann, 1994).

(2) FORCLIM, version 2.4 with the set of revised $kDrT_s$ parameters (Table 1).

(3) FORCLIM, version 2.6, which contains the new water balance model presented in this paper, with the original set of $kDrT_s$ parameters recalculated according to Eq. (19).

(4) FORCLIM, version 2.6 with the set of $kDrT_s$ parameters recalculated according to Eq. (19), plus revised estimates of individual $kDrT_s$ parameters (Table 1).

Preliminary simulation results of the FORCLIM model at sites in eastern Germany were characterized by a strong codominance of chestnut (*Castanea sativa*). However, in the drier parts of eastern Ger-

many, chestnut is probably absent for phyto-geographical reasons, not because it would not be competitive enough. Therefore, at the eastern German sites Schwerin and Cottbus (Table 2), chestnut was removed from the array of species available for establishment.

To test whether the new water balance model leads to plausible effects on the simulated species composition in areas outside central Europe, a combined temperature–drought gradient in eastern North America was studied as well (Table 3; cf. Bugmann and Solomon, 1995). Since the $kDrT_s$ parameters for the eastern North American species had been estimated directly from their distribution limits (Solomon, 1986), only two simulation experiments were performed, one with FORCLIM, version 2.4, and one with FORCLIM, version 2.6. For both sets of simulations, no adjustments of individual $kDrT_s$ parameters were made.

All simulation studies on both continents were conducted with the model setup FORCLIM-E/P, thus excluding the effects of belowground nutrient limitations (Bugmann, 1994). The analysis concentrated on the equilibrium species composition, which was estimated using a new, efficient simulation method described by Bugmann (1997). It derives the equilibrium species composition from averaging the simulated dynamics over 31 000 yrs on one single forest patch, discarding the first 1000 yrs, instead of averaging the behaviour over 200 patches after, say, 1200 yrs (cf. Bugmann et al., 1996a).

3. Results and Discussion

3.1. Species composition along a drought gradient in Europe

3.1.1. FORCLIM, version 2.4 without parameter changes

Along the European drought gradient, this experimental setup of FORCLIM results in a general pattern of species composition (Fig. 1) that corresponds by and large to expectations (Ellenberg and Klötzli, 1972; Ellenberg, 1986; Krausch, 1992). Forests close to the alpine timberline, such as at Bever and Davos, are characterized by evergreen species, predominantly Norway spruce (*Picea excelsa*), and in central

alpine valleys on south-facing slopes, Swiss Stone pine (*Pinus cembra*). Then, there is a transition zone where spruce, silver fir (*Abies alba*) and beech (*Fagus sylvatica*) are codominant (Adelboden), followed by forests dominated by beech and silver fir (Bern). The reasons for the (unrealistic) codominance of silver fir in the model was discussed by Kienast and Kuhn (1989) and Bugmann (1994). As drought occurrence increases, the abundance of beech decreases (Basel), and beech is replaced by oak (*Quercus* spp.) towards the dry end of the gradient (Schwerin, Cottbus, Sion).

While this broad pattern is simulated correctly, the results at individual sites are increasingly questionable as drought increases. Specifically, at Basel and Schwerin, beech should still be a dominant species, but in FORCLIM, version 2.4 with the original parameter values, it is outcompeted by silver fir, chestnut (*C. sativa*) and oak. According to Krausch (1992), the transition from beech to oak-lime (*Tilia* spp.) forests should occur between the east German sites Schwerin and Cottbus (cf. Table 2). The model, however, projects that the transition is located at a much higher precipitation sum (Fig. 1). According to FORCLIM, both east German sites would be dominated by oak, which is unrealistic (Krausch, 1992). As far as the species composition at Sion is concerned, Bugmann (1994, 1996a) noted that slight changes of the drought tolerance parameter $kDrT_i$ of oak and Scots pine (*Pinus silvestris*) may lead to strong changes in the simulated species composition. Hence, although the simulated oak forest at Sion probably is not realistic (Ellenberg and Klötzli, 1972), it reflects primarily the uncertainty of accurately estimating $kDrT_i$ and less a structural flaw of the model. The adjustments of the $kDrT_i$ parameters (Table 1) in Section 3.1.2 will highlight this in more detail.

3.1.2. FORCLIM, version 2.4 with parameter changes

When the drought tolerance parameters of five major species are adjusted to reflect their drought tolerance more accurately (Table 1), the simulation results along the gradient change significantly. The broad pattern of spruce forests in cold climate, beech at warm, mesic sites, and oak at warm, dry sites is still visible, but Scots pine is now simulated to be a

dominant species as the dry timberline is approached, which is quite realistic (Fig. 1). However, at some sites, the simulation results deteriorate, and at most of the sites where they had already been unsatisfactory, they do not improve.

While the model with the original parameter set captured the effect of varying slope and aspect on the species composition in central alpine valleys (Bever, Fig. 1), the increase of the drought tolerance of *P. excelsa* (Table 1) allows this species to out-compete Stone pine (*P. cembra*) on south-facing slopes, which does not correspond to the observed vegetation pattern, e.g., in the Upper Engadine Valley in Switzerland and elsewhere (Ellenberg and Klötzli, 1972).

There is little change of the simulated species composition at Davos, Adelboden, and Bern, but there is a strong increase in the performance of the model at Basel: There, the dominating species is beech (*F. sylvatica*), whereas oak and chestnut attain only minor abundance, which is quite realistic. However, the transition from beech to oak forests now is simulated to occur between the climates of the sites Basel and Schwerin (Table 2), still not corresponding to expectations (Krausch, 1992). The forest at Schwerin is dominated by oak and lime species, and the performance of the model is not better than without parameter adjustments.

Finally, model performance deteriorates at Cottbus and Sion, where low-biomass forests dominated by Scots pine are simulated. In eastern Germany, pine forests are restricted to the poorest, sandy soils, which are not represented by the simulation conditions (Table 2). Moreover, the drastic reduction of total aboveground biomass at Cottbus relative to the one simulated at Schwerin is highly unrealistic, and forests at Sion should also have higher biomass than the woodlands simulated here.

In conclusion, the revised estimates of the drought response parameters (Table 1) lead to contradictory results (Fig. 1). While the increased drought tolerance of beech shifts the transition zone from beech to oak forests towards drier conditions (i.e., between Basel and Schwerin), it does not succeed in projecting the transition zone between Schwerin and Cottbus. Moreover, with the modified parameter set Scots pine comes to dominance towards the dry timberline, which is realistic, but at the expense of unrealistic

values of aboveground biomass. Therefore, parameter adjustments alone do not at all yield plausible species compositions along the gradient.

3.1.3. FORCLIM, version 2.6 without parameter changes

Changing the water balance model alone leads to considerable, but not always plausible changes of the simulated species composition at the four driest sites along the gradient (Basel, Schwerin, Cottbus, Sion; Fig. 1). At Basel, beech is reduced to a negligible share of the aboveground biomass if the original

drought tolerance parameters are used, whereas chestnut and silver fir are too abundant (Ellenberg and Klötzli, 1972). The dominance of silver fir and oak at Schwerin is anomalous as well (Krausch, 1992), and Sion is still dominated by oak species. On the other hand, the species composition at Cottbus is more realistic now, although hornbeam (*Carpinus betulus*) should be present as well (Krausch, 1992).

We conclude that the replacement of the soil moisture balance model of Thornthwaite and Mather (1957) by the modified formulation developed in this paper does not in itself lead to a clear improvement

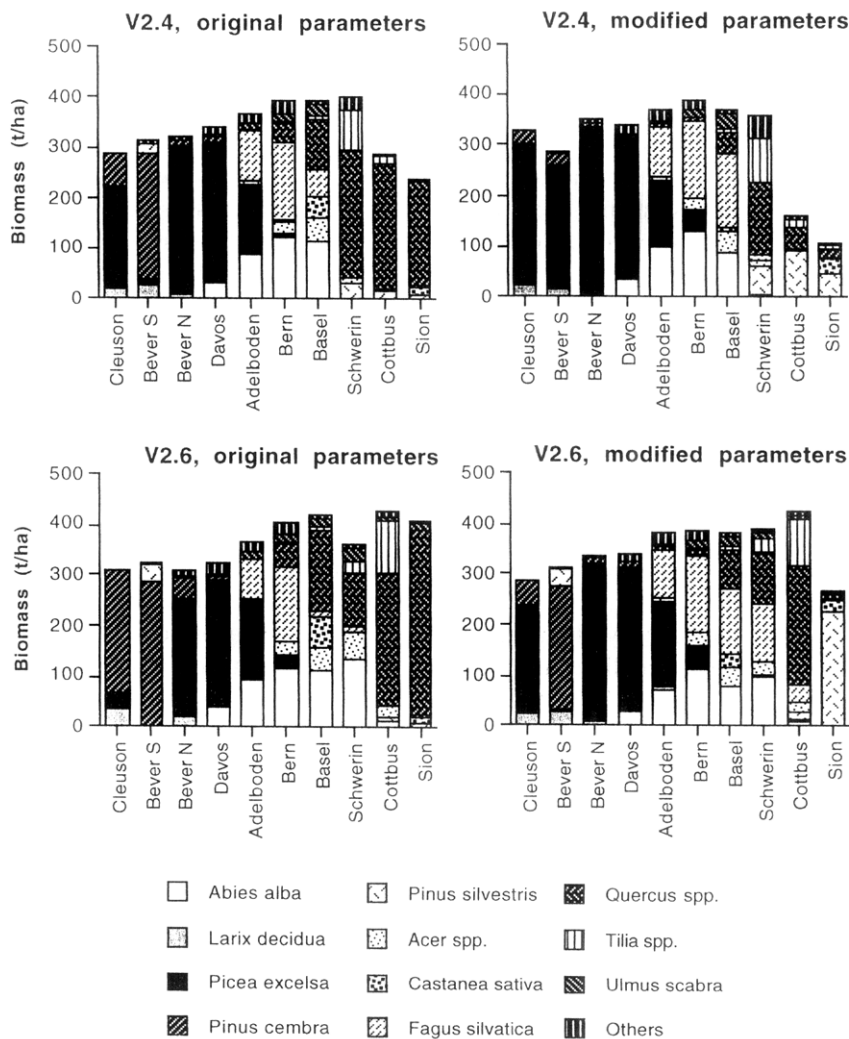


Fig. 1. Equilibrium species composition along an environmental gradient from the cold timberline (left) to the dry timberline (right) in central Europe as simulated by the forest gap model FORCLIM-E/P, version 2.4 (top row) and version 2.6 (bottom row).

of model performance along the European drought gradient. Most importantly, the transition from beech to oak forests still is not simulated realistically (cf. Basel, Fig. 1).

3.1.4. FORCLIM, version 2.6 with parameter changes

The simulation results of FORCLIM along the European drought gradient become markedly more plausible when the water balance submodel is exchanged, and the drought tolerance parameters of five species are adjusted (Fig. 1). While there is little change of the simulated species composition in the cool half of the gradient, i.e., from the sites Bever through Bern, there are significant changes at the sites Basel, Schwerin, and Sion (Fig. 1).

At Basel, beech is the most abundant species, followed by silver fir, which is still anomalous (cf. Kienast and Kuhn, 1989, Bugmann, 1994), and oak species. Maple (*Acer* spp.) and chestnut also have a considerable share. Generally speaking, the simulated forest is a beech–oak forest, which is realistic for this site (Ellenberg and Klötzli, 1972).

The simulated species composition at Schwerin now is similar to the one at Basel, which is plausible (Ellenberg, 1986). The abundance of oak is somewhat larger than at Basel, whereas the abundance of beech has decreased, and there is a considerable share of lime. The decreased abundance of beech points at the fact that at Schwerin this species gets close to its drought-induced distribution limit, which is to be found between the sites Schwerin and Cottbus (Krausch, 1992).

At Cottbus, beech has practically disappeared. The dominating species are oaks and lime, and these features are quite realistic (Krausch, 1992). Whether the slight increase of the total aboveground biomass simulated at Cottbus as compared to Schwerin is plausible requires further quantitative testing. Since one may expect the biomass to decline monotonically towards the dry timberline, this model feature may represent an anomaly.

Finally, at Sion, there is a drastic change of both the simulated species composition and the amount of aboveground biomass. The forest is composed of three tree species only: Scots pine dominates heavily, whereas oak and chestnut are of minor abundance. More importantly, the simulated biomass is much

lower than at Cottbus, but the model still simulates a closed forest (≈ 260 t/ha of aboveground biomass), not the low-biomass woodland as in model version 2.4 when the drought parameters were adjusted (Fig. 1). Again, both the simulated biomass of this forest as well as its composition are plausible (Ellenberg and Klötzli, 1972; Ellenberg, 1986).

Therefore, with the new soil moisture submodel and revised estimates of five species' drought tolerance parameters, the composition of the potential natural vegetation along the whole gradient from cool-moist to warm-dry conditions is captured quite realistically by FORCLIM, version 2.6.

3.2. Species composition along a drought gradient in eastern North America

3.2.1. FORCLIM, version 2.4

The behaviour of version 2.4 of FORCLIM along the latitudinal gradient used in the present study (Table 3) was discussed in detail by Bugmann and Solomon (1995). They found that, in general, the model captures the pattern of species composition along the northern part of the gradient quite well. Here, we review the problems encountered by the model as the dry timberline is approached in the southern part of the gradient (i.e., from Tennessee to Arkansas; Fig. 2).

The simulation for Cumberland Plateau, Tennessee represents rich soils due to the large value of the water-holding capacity (cf. Table 3). Consequently, FORCLIM produces the largest amount of aboveground biomass along the transect (Fig. 2) and a species composition that is characteristic of the mixed mesophytic forest (Küchler, 1975), which occurs in the area. However, although the annual precipitation sum is high, many forests in the area are subject to considerable drought because of the sandy soils, leading to low-biomass forests. Unfortunately, both the amount of aboveground biomass and the species composition at this test site are, by and large, independent of the water-holding capacity in the model, which is unrealistic.

The simulation results from Georgia, the southernmost location along the transect, are characterized by southern oak species (*Quercus* spp.) and hickory (*Carya* spp.). However, on the real landscape, southern pines dominate the forests, which is due to the

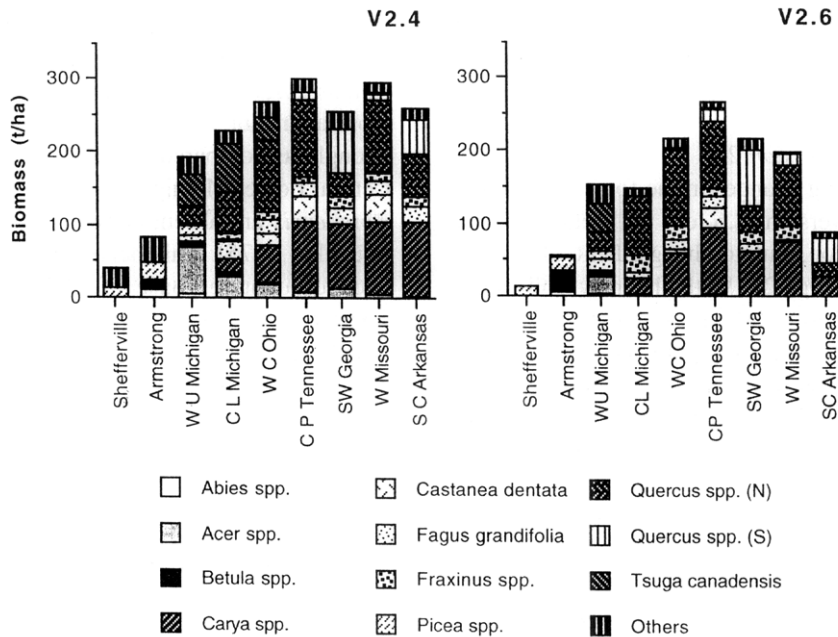


Fig. 2. Equilibrium species composition along an environmental gradient from the cold timberline (left) to the dry timberline (right) in eastern North America as simulated by the forest gap model FORCLIM-E/P, version 2.4 (left) and version 2.6 (right). The assignment of the 17 oak species to the two groups of northern ('N') and southern ('S') oaks is according to Solomon (1986).

occurrence of disturbances such as fire, and the drought sensitivity of the sandy soils. On the clay soils of the piedmont, for which the simulation results are more representative, oak and hickory dominate. Thus, as a statement about the potential natural forest vegetation in the absence of disturbance, the FORCLIM model is quite successful.

The western Missouri area is characterized by open, almost woodland structured forests, a feature that is due to moisture limitation. While the model succeeds in simulating the correct oak and hickory species as dominant, the amount of simulated aboveground biomass is larger than in the more mesic test area of Georgia, which is not plausible at all. As in the Tennessee case, simulation studies showed that the amount of aboveground biomass is only slightly sensitive to the value of the soil water-holding capacity. This certainly constitutes a deficiency of this model version.

In south central Arkansas, FORCLIM, version 2.4 yields stands dominated by *Carya* spp. and northern oaks. The most important oak species simulated by the model are also prominent on the landscape: *Q. alba* and *Q. velutina* (Küchler, 1975). *Carya* spp. is

a warmth- and drought-adapted genus, as are many of the oak species, which makes the species composition simulated by FORCLIM realistic. There is a small decrease of total aboveground biomass as compared to the value in Missouri (Fig. 2), which is due to increased drought occurrence. However, real forests of the area, which is close to the dry timberline (Küchler, 1975), have still lower biomass (DeAngelis et al., 1981), but the simulated value does not decrease much below 200 t/ha even if the water-holding capacity is reduced strongly (Bugmann and Solomon, 1995).

In conclusion, the simulation results of FORCLIM, version 2.4 along the gradient in eastern North America, by and large, yield the correct species composition (Bugmann and Solomon, 1995). However, the model fails to simulate the presence of pines (*Pinus* spp.) as the dry timberline is approached. Probably this failure is due to the lack of disturbance in the simulations, most importantly fire (Bugmann and Solomon, 1995). Moreover, the simulated aboveground biomass is hardly constrained by drought as the dry timberline is approached (Fig. 2). Although this may partly be explained by the fact

that disturbance is lacking in the model, it probably also points at a misrepresentation of drought occurrence in this model version.

3.2.2. FORCLIM, version 2.6

The most striking changes in the forests simulated by FORCLIM, version 2.6 do not relate to the species composition, but to the gradient of above-ground biomass (Fig. 2). With the new soil water balance model, FORCLIM yields a strong decrease of the aboveground biomass from the mixed mesophytic forest (Tennessee) to the driest location (Arkansas; Fig. 2). This pattern is quite realistic and much closer to reality than the one simulated by FORCLIM, version 2.4.

It is beyond the scope of the present paper to discuss the changes in the abundance of all 72 tree species as simulated by FORCLIM, version 2.6 along the gradient. Instead, only the major features will be outlined here. In some cases, the plausibility of the model results increases. For example, in the new model version, beech (*Fagus grandifolia*) is simulated to be absent in Arkansas and attains only low biomass at Missouri. These features are more realistic than the rather strong presence of the species close to the dry timberline in model version 2.4 (Fig. 2). Similarly, the abundance of chestnut (*Castanea dentata*), which formerly was simulated to be a codominant species at Ohio and Missouri, decreases to negligible values in these two areas (cf. Küchler, 1975).

In other cases, e.g., with the simulated distribution and abundance of the six hickory (*Carya* spp.) and 17 oak species (*Quercus* spp.) included in the model (Bugmann, 1994), there are some changes but the overall picture remains similar. For example, the setup of the simulation experiment provided $9 \cdot 17 = 153$ opportunities for the model to simulate the presence of an oak species where it should not occur, and vice versa. While in FORCLIM, version 2.4 this misbehaviour was observed in 33 cases (22%), in FORCLIM, version 2.6 it occurs in 36 cases (24%).

Finally, there is also a number of cases where the performance of the model deteriorated. An obvious example for this are the northern hardwoods in Western Upper Michigan, and the transition to oak–hickory forests in Central Lower Michigan (Fig. 2). In Upper Michigan, FORCLIM, version 2.6 still

simulates a northern hardwood forest dominated by *Acer saccharum*, *F. grandifolia*, and *Tsuga canadensis*, but the biomass of the species that is most abundant in reality, *A. saccharum*, decreases strongly as compared to version 2.4 of the model. In Central Lower Michigan, *A. saccharum* as well as *T. canadensis* are absent entirely, which is not realistic (Küchler, 1975). This behaviour is due to the simulated drought response of FORCLIM, version 2.6. Therefore, in-depth analyses are required to determine whether, similar to central Europe, these anomalies are due to an inaccurate estimation of the drought response parameters of the tree species ($kDrT$), or whether the new soil water balance model needs to be improved further.

4. Summary and Conclusions

In this paper, we focused on the analysis of the weak performance along drought gradients of many forest gap models. Specifically, we tested two hypotheses that were brought forward to explain this behaviour: (1) whether the species-specific drought tolerance parameters need to be estimated more accurately, and (2) whether the simple soil water balance models used in most gap models are not capable of tracking soil moisture content under dry conditions.

Using the gap model FORCLIM as a case study, we found on the one hand that simple parameter adjustments do not lead to clear improvements of the model behaviour along a drought gradient in central Europe, although these adjustments are ecologically motivated and based on the literature.

On the other hand, the analysis of the soil water balance model of Thornthwaite and Mather (1957), which is used in many gap models (e.g., Pastor and Post, 1985; Kienast, 1987; Kellomäki et al., 1992; Bugmann, 1994, 1996a), revealed that the empirical formulation of this model renders it inappropriate for simulating the year-to-year variability of drought. As an alternative, we developed a simple, but more consistent submodel of soil water balance. Including this model alone into FORCLIM did not improve the pattern of the simulated species composition along the European drought gradient.

Only when both some species' drought tolerance parameters were estimated more accurately and the

new soil moisture submodel was used in FORCLIM did the performance of the model increase considerably. A number of things are notable in this respect.

First, the response of FORCLIM to adjustments of the drought tolerance parameters is both encouraging and discouraging: encouraging, because the model version that includes the Thornthwaite and Mather (1957) formulation of soil water balance can not be ‘tuned’ to yield a plausible species composition along drought gradients, which would only hide the real reasons for the model failure; discouraging, because the model version that includes the improved soil moisture routine appears to be quite sensitive to the values of the species-specific drought tolerance parameters. This is probably not a model flaw, but reflects the fact that drought gradients in the landscape are quite steep. Therefore, it would be highly desirable to derive more accurate estimates of the drought tolerance of the tree species that are based directly on field data and physiological experimentation, and not merely on qualitative autecological descriptions.

Second, the performance of the FORCLIM model does not deteriorate under those conditions for which it originally has been developed (i.e., at moist to moderately dry sites in Switzerland, Bugmann, 1994, 1996a). Quite on the contrary, the simulated species composition agrees to a larger extent with descriptions of the potential natural vegetation at some sites, for example Basel (Ellenberg and Klötzli, 1972). The present study suggests that the adaptation of a gap model for a new region does not mean that its performance in other regions necessarily deteriorates (cf. Bugmann et al., 1996b). We conclude that the new soil moisture submodel expands the range of applicability of the FORCLIM model considerably.

Finally, in the present study, only the simulated species composition was used to assess the realism of the soil moisture submodel; the variables of the soil moisture model themselves were not considered except from a theoretical point of view. Rigorous tests should be conducted to evaluate the behaviour of the new soil moisture submodel, regarding specifically the simulated time series of soil moisture storage and actual evapotranspiration. A major problem in this context is to obtain long (> 5–10 yrs) time series of these variables for several test sites along drought gradients.

By using the new soil moisture submodel on another continent, i.e. in eastern North America, we showed that its applicability is not restricted to central Europe. As a matter of fact, the pattern of aboveground biomass simulated along a drought gradient in eastern North America is considerably more realistic with the new model than with the Thornthwaite and Mather (1957) formulation (cf. Bugmann and Solomon, 1995). Moreover, with the new bucket model it is also possible to simulate the species composition along a drought gradient from temperate rainforests to steppe in the Pacific Northwest of the United States (Bugmann, 1996c), which is characterized by a strongly different climate and different forests (Franklin and Dyrness, 1973; Waring and Franklin, 1979).

The present analysis was based on only one gap model, FORCLIM (Bugmann, 1994, 1996a). Since the model by Thornthwaite and Mather (1957) is used in many gap models (e.g., Pastor and Post, 1985; Kienast, 1987; Kellomäki et al., 1992), we surmise that the results of our study are representative of these other gap models also. We therefore suggest to abandon the usage of the soil water balance model of Thornthwaite and Mather (1957) in forest gap models where the annual water balance is to be simulated based on weather data as opposed to long-term mean climatic input data.

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