

EXPLAINING FOREST COMPOSITION AND BIOMASS ACROSS MULTIPLE BIOGEOGRAPHICAL REGIONS

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Abstract. Current scientific concerns regarding the impacts of global change include the responses of forest composition and biomass to rapid changes in climate, and forest gap models have often been used to address this issue. These models reflect the concept that forest composition and biomass in the absence of large-scale disturbance are explained by competition among species for light and other resources in canopy gaps formed when dominant trees die. Since their initiation 25 yr ago, a wide variety of gap models have been developed that are applicable to different forest ecosystems all over the world. Few gap models, however, have proved to be equally valid over a wide range of environmental conditions, a problem on which our work is focused.

We previously developed a gap model that is capable of simulating forest composition and biomass in temperate forests of Europe and eastern North America based on a single model structure. In the present study, we extend the model to simulate individual tree species response to strong moisture seasonality and low temperature seasonality, and we modify the widespread parabolic temperature response function to mimic nonlinear increases in growth with increased temperature up to species-specific optimal values.

The resulting gap model, FORCLIM V2.9, generates realistic projections of tree species composition and biomass across a complex gradient of temperature and moisture in the Pacific Northwest of the United States. The model is evaluated against measured basal area and stand structure data at three elevations of the H. J. Andrews LTER site, yielding satisfactory results. The very same model also provides improved estimates of species composition and stand biomass in eastern North America and central Europe, where it originated. This suggests that the model modifications we introduced are indeed generic.

Temperate forests other than those we studied here are characterized by climates that are quite similar to the ones in the three study regions. Therefore we are confident that it is possible to explain forest composition and biomass of all major temperate forests by means of a single hypothesis as embodied in a forest gap model.

Key words: *central Europe; eastern North America; FORCLIM; forest composition and biomass; forest ecology; forest gap models; global temperate forests; Pacific Northwest (United States); validation.*

INTRODUCTION

Current scientific concerns regarding the terrestrial impacts of global change include the responses of forest composition and biomass to rapid changes in climate (Kirschbaum et al. 1996, Melillo et al. 1996, Solomon et al. 1996). Forest gap models (Botkin et al. 1972, Shugart 1984) have often been used to address these issues at local and regional scales (e.g., Solomon 1986, Pastor and Post 1988, Prentice et al. 1991, Bugmann 1997a). Models based on the concept of gap dynamics (Watt 1947) were first developed by Botkin et al. (1972) and have evolved by the efforts of many workers since then (e.g., Shugart and West 1977, Shugart 1984, Pastor

and Post 1985, Prentice and Leemans 1990). The ecological mechanism embodied by forest gap models is the control of forest composition and structure exerted by canopy gaps formed after the death of dominant trees, and it is implemented through competition among individual trees for light and other resources (Watt 1947). The ecological process emerging from this is succession from shade-intolerant, rapidly growing trees to shade-tolerant, long-lived species. Successional composition and rates are modified by climatic constraints, with attendant changes in size structure, stem density, and species biomass (Shugart 1984).

These features imply that gap models have a high potential for application in management questions because these models can be used to explore, for example, the stand-level implications of forest management regimes, air pollution, or climate change, which act at the level of the individual tree. However, such scaling capabilities require (1) that robust relationships between environmental factors and ecological processes

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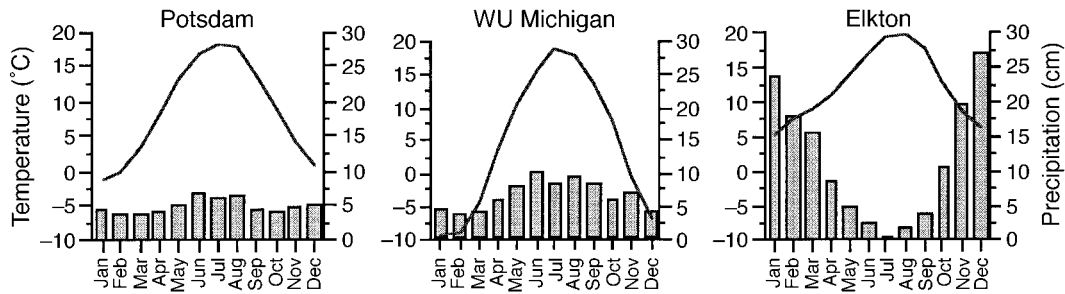


FIG. 1. Comparison of climates of central Europe (Potsdam, Germany, left), eastern North America (Western Upper Michigan Climate Division, center), and the Pacific Northwest of the United States (Elkton, Oregon, right). Lines are monthly mean temperatures (T); bars are monthly precipitation totals (P).

are used in the models, and (2) that these relationships are valid beyond the environmental conditions that are found in a given study region today. Although most gap models share the same basic structure, each retains a different set of assumptions regarding the selection of ecological factors to be modeled and their exact mathematical formulation. For example, some models incorporate nutrient cycling (Pastor and Post 1985), whereas others assume this to be negligible for long-term successional dynamics (Kienast 1987), and a variety of approaches are used to model, e.g., the dependence of tree growth on temperature (cf. Bugmann 1996a). Obviously, the selection of factors and formulations reflects the current climatic regime of the sites for which a specific model was developed.

Indeed, a number of recent studies demonstrated that some gap models cannot be transferred from one geographical area, corresponding to one climatic regime, to an adjacent geographical area, corresponding to another climatic regime, without extensive modifications of the model structure and its parameters (e.g., Leemans 1992, Lasch and Lindner 1995, Cumming and Burton 1996; cf. Bugmann et al. 1996a). Often, the modified model loses its applicability under the conditions for which it had originally been developed (e.g., Lasch and Lindner 1995). The fact that the structure of many models appears to be site- and climate-specific casts doubts on their applicability under novel climatic conditions. As a consequence, the currently available models can hardly be used as a set to simulate forest responses to common climate change scenarios worldwide (cf. Smith 1996). A solution to this problem is to attempt the development of one single model structure that is valid under a wide range of environmental conditions.

Over the past years, we have been working towards this goal by extending a single gap model to function simultaneously in different geographical areas with exactly the same model structure, while changing only the climatic data, soil properties, and the set of species included in the simulations. We began with FORCLIM V2.4, a model capable of reproducing the composition and aboveground biomass of near-natural forests at multiple locations and along climate gradients in the

European Alps (Fischlin et al. 1995, Bugmann 1996a). We applied this model without structural modifications to forests along a latitudinal gradient in eastern North America, with satisfactory results except towards the dry treeline in the southeastern United States (Bugmann and Solomon 1995). Its applicability was extended to central Europe in general by modifications to the simulated mechanism of soil moisture dynamics and drought response (Bugmann and Cramer 1998: FORCLIM V2.6). At the same time, its ability to reproduce forest composition and stand biomass in southeastern North America increased as well (Bugmann and Cramer 1998).

Both central Europe and eastern North America possess a strong temperature seasonality with cold winters, and low precipitation seasonality with adequate moisture for tree growth in midsummer. The Pacific Northwest (PNW) of the United States, however, is subject to a very different climate that is characterized by weak temperature seasonality with relatively warm winters, and extremely strong precipitation seasonality with a large winter peak and very little precipitation in midsummer (Fig. 1). Consequently, PNW forests are dominated by different tree genera (e.g., *Pseudotsuga*, *Chamaecyparis*, *Libocedrus*, *Arbutus*), and exhibit different carbon storage capacities than eastern North America and Europe (cf. Franklin 1988, Franklin and Dyrness 1988, Harmon et al. 1990). While PNW forests have been the focus of gap model development before (e.g., Dale and Hemstrom 1984, Urban et al. 1993, Burton and Cumming 1995, Cumming and Burton 1996), these studies focused only on the PNW, rather than on developing models that can function elsewhere without structural change.

The objectives of the present paper are threefold: first, to describe the extension of the applicability of the FORCLIM model to the climate of the PNW. The model modifications we introduce focus on the responses of forest physiognomy and species distribution to the overwhelming influence of moisture seasonality and growing season properties in the PNW (Waring and Franklin 1979, Waring and Schlesinger 1985). We also point out the relevance of these modifications in the face of recent criticisms of gap models (e.g., Bonan

and Sirois 1992, Pacala and Hurtt 1993, Loehle and LeBlanc 1996, Schenk 1996).

Second, to compare FORCLIM's capability to simulate forest composition and biomass in the PNW to measured characteristics of forests in the area that were not used for structuring the model or estimating its parameters.

Third, to re-examine the applicability of the new model version to eastern North America and central Europe, and to discuss the implications of these results for the potential to develop a unified, generic gap model that applies to all temperate forests.

Each of the above exercises is designed to simulate the behavior of steady-state forests under current climatic conditions, rather than to examine their successional dynamics, which will be the subject of another paper.

METHODS

The FORCLIM model

Gap models simulate the establishment, growth, and mortality of individual trees on small patches of land (often, 0.08 ha) as a function of species natural histories and the extrinsic and intrinsic conditions of the stand. To obtain forest development at larger spatial scales, the successional patterns of patches from many simulation runs are averaged. This concept is supported by many plant succession studies showing that a forest ecosystem may be described by the average growth dynamics of a multitude of patches with different successional ages. Shugart (1984) provided a comprehensive overview of the background and general formulation of forest gap models. The specific assumptions, equations, and parameter estimation procedures for the FORCLIM model were described in detail by Bugmann (1994, 1996a: FORCLIM-P and FORCLIM-S), Bugmann and Cramer (1998: FORCLIM-E), and Bugmann (1996b: modifications for the PNW as reported below).

Overview of FORCLIM V2.6.—The FORCLIM model V2.6 (Bugmann 1996a, Bugmann and Cramer 1998) was developed for central European and eastern North American conditions based on the model FORECE (Kienast 1987). FORCLIM consists of three modular submodels, each of which can be run independently or in combination: FORCLIM-E is a submodel for the abiotic environment, including a new soil water balance model developed by Bugmann and Cramer (1998). FORCLIM-S is a submodel for soil carbon and nitrogen turnover, modified from Pastor and Post (1985). FORCLIM-P is a submodel for tree population dynamics based on the well-established concept of gap dynamics (Watt 1947, Shugart 1984).

Actual growth of each tree is simulated by calculating a maximum diameter-specific growth rate that is decreased based on the occurrence of environmental factors at suboptimal levels. Environmental factors considered in FORCLIM are light availability, soil ni-

trogen availability, summer temperature, and drought. Light availability across the canopy is calculated for each tree using the Beer-Lambert law (Botkin et al. 1972). The influence of nitrogen availability on tree growth is simulated by differentiating three types of functional response to low nutrient availability based on the approach by Aber et al. (1979), and assigning each species to one response type. The effect of summer temperature on tree growth is calculated using a parabolic relationship between the annual sum of degree-days above a 5.5°C threshold and the growth rate of the trees ("degree-day index"; Botkin et al. 1972). Drought is expressed as the annual transpiration deficit, $1 - E/D$ ("drought index"), where E is the actual annual transpiration rate of the trees, D is the annual atmospheric demand of water from the soil, and soil evaporation is assumed to be negligible (Bugmann and Cramer 1998). The form of the maximum growth equation is similar to a logistic equation (Moore 1989); it is based on the assumption that annual biomass increment is proportional to the amount of sunlight the leaves receive (Botkin et al. 1972). The four growth-limiting factors are combined in a nonlinear manner to derive an estimate of the realized growth rate of the trees (Bugmann 1996b).

Tree establishment rates in FORCLIM are determined from light availability at the forest floor, browsing intensity, and absolute 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). These three factors are formulated in a species-specific manner: light availability and winter temperature are used as discrete thresholds that prevent regeneration when it is too dark or too cold for a species, whereas increasing browsing intensity acts to reduce the species-specific establishment probability in a continuous manner.

Tree mortality is modeled as a combination of an age-related and a stress-induced mortality rate (Botkin et al. 1972, Kienast 1987, Solomon and Bartlein 1992), giving rise to high mortality of small trees due to strong competition for light, and a high mortality of old trees due to low vigor (cf. Bugmann 1994). 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 link between tree growth and mortality.

A systematic sensitivity analysis performed with the model (Bugmann 1994) revealed that the simulated overall species composition and aboveground biomass are little sensitive to parameter variations within their range of uncertainty. However, the abundance of individual species may vary markedly depending on the parameter values used. Hence, while the projections obtained from the model are robust on a qualitative basis, their precision is limited due to uncertainty in the parameter data set.

Model modifications for the Pacific Northwest (FORCLIM V2.9).—The adaptations of FORCLIM for the PNW centered on tree responses to aspects of the PNW climate that are different from the European and eastern North American climate for which FORCLIM and its predecessors (e.g., JABOWA, Botkin et al. 1972; FORET, Shugart and West 1977; FORENA, Solomon 1986; FORECE, Kienast 1987) had been developed. Those differences include much greater annual rainfall, with little falling during the growing season and mild winter temperatures typically above freezing (Fig. 1). On the one hand, during the winter when the soil water potential of the unfrozen ground is high, winter deciduous trees have no leaves with which to photosynthesize, while evergreens can sequester carbon any time temperature permits. On the other hand, summer drought is so severe that few angiosperm tree species are able to survive, while the xylem anatomy of gymnosperms is less disadvantageous (Waring and Schlesinger 1985, Neilson et al. 1992). Coupled with these climatic properties is the remarkably low frequency of large-scale disturbances like fire and windthrow in the PNW (e.g., Agee 1993). Taken together, these features permit conifer trees to dominate PNW forests and to attain great size and longevity.

The strategy for adapting FORCLIM for the PNW was to add as little detail to the model as possible while still including the functional response of tree behavior to its unique climate. FORCLIM V2.6 and many other forest gap models are based on four implicit assumptions regarding climate and phenology that do not hold in the PNW and thus had to be relaxed:

1. *Winter temperature is so low that cold-season evapotranspiration is negligible.*—Consequently, drought in many models was expressed as an index of the annual ratio of actual to potential evapotranspiration (or similar measures), with the winter months contributing little to the annual index. Such a formulation is incapable of capturing the strong summer droughts in the PNW, and it was necessary to derive an index that adequately portrays the ecological effects of PNW drought periods.

2. *Winters are so cold that growth of all tree species is inhibited.*—Under this assumption, it was not necessary to introduce phenological constraints on the presence/absence of leaves in winter deciduous species. For the PNW, however, it was required to introduce a phenological switch to account for the fact that deciduous species cannot photosynthesize during winter, whereas evergreen species continue photosynthesis whenever air and soil temperatures are above freezing.

3. *Tree growth towards the warm boundary of each species' range is limited by temperature per se.*—This assumption has become heavily criticized over the past years (e.g., Bonan and Sirois 1992, Schenk 1996), and it is especially questionable in species that have narrow geographical ranges, such as in the PNW, so that in

these areas tree growth is limited strongly by temperature almost everywhere. Consequently, this formulation was replaced by an asymptotic function that produces maximum constraint of growth at cold extremes and no (temperature-related) constraint at the warm boundary of each species' range.

4. *Chilling requirements and their effects on phenology and tree regeneration do not need to be modeled explicitly.*—This assumption may be valid when winters are cold enough to meet the species' chilling requirements at all times. Since this is not the case in the PNW, a chilling requirement was added to FORCLIM that reduces regeneration rates when winter temperatures are too high to induce dormancy in species requiring dormancy, following the logic of Sykes et al. (1996).

These deficiencies and the four model modifications required to rectify them are described in detail below.

The drought index uDr calculated in FORCLIM V2.6 was

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

where m denotes the month, E_m is the amount of water transpired by the trees, and D_m is their evaporative demand for soil water (cf. Bugmann and Cramer 1998). Two important disadvantages of Eq. 1 are that (1) transpiration and demand are summed up over the whole year and not just over the growing season when moisture is effective, and (2) only the ratio of the two annual variables has been used; hence strongly seasonal drought regimes, which are characteristic of the PNW, generate no significant vegetative response. To rectify these deficiencies, the index was modified to

$$uDr = \begin{cases} 1 - \frac{\sum_{T_m \geq k} E_m}{\sum_{T_m \geq k} D_m} & \text{for evergreen species} \\ 1 - \frac{\sum_{\substack{(T_m \geq k) \wedge \\ m \in \{Apr...Oct\}}} E_m}{\sum_{\substack{(T_m \geq k) \wedge \\ m \in \{Apr...Oct\}}} D_m} & \text{for deciduous species} \end{cases} \quad (1')$$

where T_m is the mean temperature of month m , and k is a threshold temperature (5.5°C). The assumption behind Eq. 1' is that evergreen species can fix CO₂ whenever temperature is high enough, which is parameterized here by the threshold air temperature k , whereas winter deciduous species are constrained by the leafless period. For simplicity, leaves are assumed to be present from April through October (Eq. 1'). Although this assumption is adequate under the current climate in the temperate regions of concern here, application of this model at significantly different latitudes will require a combined photoperiodic/climatic definition of the leafless season. The new index (Eq. 1') reflects the proportion of the resulting growing season when water supply to the trees is insufficient for growth. Equation

I' modifies annual tree growth as required by the species-specific drought tolerance value (parameter $kDrT_s$) as described by Bugmann (1996a). Note that the subscript s denotes species-specific values; all other parameters and variables are not species specific.

In earlier versions of FORCLIM, the effects of summer temperature on tree growth were modeled using the following formula for calculating the annual sum of degree-days (degree-day index, uDD):

$$uDD = \sum_{m=Jan}^{Dec} \left[\text{MAX}(T_m - k, 0) \times kDays + gCorr(T_m) \right] \quad (2)$$

where T_m is monthly mean temperature, $kDays$ is the average number of days per month, and $gCorr$ is an empirical function (Bugmann 1994) that corrects the bias induced by estimating monthly growing degree-days from monthly mean temperature (Botkin et al. 1972) rather than from daily minimum and maximum temperature (Allen 1976). A serious disadvantage of Eq. 2 as applied to PNW forests is that it does not recognize that the length of the growing season is restricted by the leafless season for deciduous trees, whereas evergreen trees can fix CO_2 throughout the year as long as temperatures are high enough. To account for this, the equation was modified to:

$$uDD = \begin{cases} \sum_{T_m \geq k} \left[\text{MAX}(T_m - k, 0) \cdot kDays + gCorr(T_m) \right] & \text{for evergreen spp.} \\ \sum_{\substack{T_m \geq k \\ m \in \{Apr \dots Oct\}}} \left[\text{MAX}(T_m - k, 0) \cdot kDays + gCorr(T_m) \right] & \text{for deciduous spp.} \end{cases} \quad (2')$$

The temperature response function ($gDDGF_s$) of tree growth in FORCLIM V2.6 and earlier versions was

$$gDDGF_s = \text{MAX} \left[\frac{4(uDD - kDDMin_s)(kDDMax_s - uDD)}{(kDDMax_s - kDDMin_s)^2}, 0 \right] \quad (3)$$

This parabolic function (Eq. 3) was replaced by an asymptotic version that does not require the specification of the maximum temperature tolerance parameter, $kDDMax_s$:

$$gDDGF_s = \text{MAX}(1 - e^{(kDDMin_s - uDD) \times a}, 0) \quad (3')$$

where a is a parameter describing the slope of the curve. The parameter a was determined so that the growth rate is reduced by 25% relative to its optimum when $uDD = kDDMin_s + 1000$ for any species. Examples of Eq. 3 and 3' are depicted in Fig. 2.

The parabola (Eq. 3) used in earlier versions of FORCLIM and in many other gap models has long been

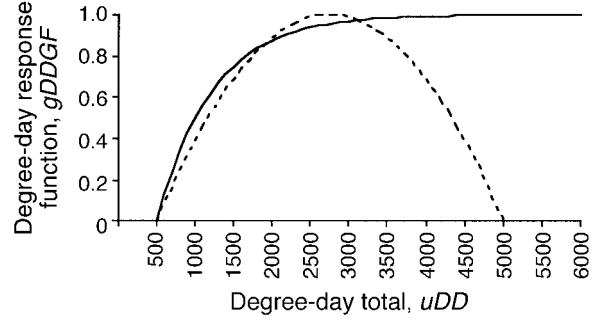


FIG. 2. Comparison of the degree-day response function ($gDDGF_s$) used in FORCLIM V2.9 (solid line, Eq. 3') vs. the parabolic response used in many earlier models (dashed line, Eq. 3).

criticized as weak or invalid (e.g., Bonan and Sirois 1992, Schenk 1996; but see, for example, Carter 1996). The original use of the parabolic degree-day response (Botkin et al. 1972, Shugart and West 1977, Shugart 1984) implied that the cold portion of the response function (Fig. 2) was a proxy for response to temperature itself, and the warm portion represents a proxy for growth declines due to temperatures above the photosynthetic optimum and due to increasing drought. However, temperatures high enough to inhibit growth do not occur even in the warmest parts of boreal and temperate tree ranges (cf. Larcher 1995: Table 2.11). Also, the simulation of declining tree growth within species ranges using degree-days as a proxy for drought (Eq. 3) became redundant when drought was introduced as a separate response variable (Solomon et al. 1984, Pastor and Post 1985).

Note that the new formulation (Eq. 3') predicts that the highest growth rates occur in the warmest (not moisture-limited) areas in which a species is found. This is consistent with the conclusions of Korzhukin et al. (1989) and Schenk (1996) that the largest trees of a species occur near its warmest boundary if moisture is not limiting, and with the expectations of largest growth increments there derived from model studies (Bonan and Sirois 1992).

In FORCLIM V2.6 and earlier versions, tree establishment was prevented when winter minimum temperature ($uWiT$) was lower than a species-specific threshold temperature ($kWiT_s$), thus killing leaf and flower buds (Solomon et al. 1984):

$$gWFlag_s = \begin{cases} 1 & kWiT_s \leq uWiT \\ 0 & \text{else.} \end{cases} \quad (4)$$

This cold-temperature limit to seedling establishment represents a likely means by which trees are excluded from areas north of their current ranges (e.g., Becwar and Burke 1982, Dexter et al. 1987). However, the loss of chilling that could be induced by global warming long has been of concern for PNW species (e.g., Levenson and Lev 1987, Cumming and Burton 1996). Therefore, we followed the logic of Sykes et al. (1996)

TABLE 1. Pacific Northwest tree species included in the current version of the FORCLIM model.

Latin name	Common name
<i>Abies amabilis</i>	Pacific silver fir
<i>Abies grandis</i>	Grand fir
<i>Abies lasiocarpa</i>	Subalpine fir
<i>Abies procera</i>	Noble fir
<i>Acer macrophyllum</i>	Big-leaf maple
<i>Alnus rubra</i>	Red alder
<i>Arbutus menziesii</i>	Madrone
<i>Chamaecyparis nootkatensis</i>	Alaska cedar
<i>Picea engelmannii</i>	Engelmann spruce
<i>Picea sitchensis</i>	Sitka spruce
<i>Pinus contorta contorta</i>	Shore pine
<i>Pinus contorta latifolia</i>	Lodgepole pine
<i>Pinus monticola</i>	Western white pine
<i>Pinus ponderosa</i>	Western yellow pine
<i>Pseudotsuga menziesii menziesii</i>	Pacific Coast Douglas-fir
<i>Pseudotsuga menziesii glauca</i>	Rocky Mountain Douglas-fir
<i>Quercus garryana</i>	Oregon white oak
<i>Thuja plicata</i>	Western red cedar
<i>Tsuga heterophylla</i>	Western hemlock
<i>Tsuga mertensiana</i>	Mountain hemlock

to add a complementary winter chilling requirement to initiate spring bud break, and thus, to induce seed production and regeneration (Eq. 4'):

$$gWFlag_s = \begin{cases} 1 & kWITN_s \leq uWiT \leq kWITX_s \\ 0 & \text{else} \end{cases} \quad (4')$$

where $kWiTN_s \equiv kWIT_s$, and $kWiTX_s$ is a new parameter denoting the maximum winter temperature tolerated by species s for regeneration.

Although nitrogen response was not used in the simulations described below, we note for completeness that an additional change was implemented in FORCLIM V2.9 to increase model applicability in central Europe: Previously, species had been classified into three response types (tolerance classes) with respect to the effects of nitrogen availability on tree growth. To enhance the resolution of site-specific differences particularly for regional model applications (cf. Bugmann 1996b, Bugmann et al. 1996b, Lindner et al. 1997), the number of response types was increased from three to five.

Parameter estimation

Species-specific parameters for the Pacific Northwest.—Each tree species in FORCLIM is characterized by 14 species-specific parameters. Application of FORCLIM V2.9 in the PNW required us to derive estimates of all species-specific parameters for the PNW species of interest. Twenty dominant species (Table 1) growing between the Pacific Ocean and the Great Basin Desert in Oregon (Fig. 3) were included in FORCLIM V2.9, and three approaches were used for estimating their species-specific parameters (notational conventions follow those by Bugmann 1996a):

First, for some parameters, the values were adopted

from earlier gap model studies for the PNW (Dale and Hemstrom 1984, Urban et al. 1993). Either the parameters were unchanged (shade tolerance of adult trees kLa); or, the parameters were recalculated to fit the definition used in FORCLIM (species type $sType$, intrinsic growth rate kG , shade tolerance of saplings kLy); or, due to limited data availability one single value was assigned across all species (tolerance of low nitrogen availability $kNTol$); or the values were differentiated for deciduous vs. evergreen species only (susceptibility to browsing $kBrow$, C:N ratio of leaf litter kLQ).

Second, for other parameters, the values used in other gap models were compared with those in natural histories (Franklin and Dyrness 1988) or silvics manuals (Harlow et al. 1979, Burns and Honkala 1990) and were modified where these sources indicated it was necessary (maximum age, height, and diameter, kAm , kHm , kDm , respectively).

Finally, for the parameters denoting extreme climatic tolerances (minimum degree-day requirement $kDDMin$, minimum and maximum winter temperature tolerance $kWiTN$, $kWiTX$, respectively, and drought tolerance $kDrT$), new values were recorded by overlaying transparency maps of the relevant bioclimatic variables (evergreen and deciduous degree-day totals, uDD , and minimum winter temperature $uWiT$, all three based on Dodson and Marks [1997], and evergreen/deciduous drought index $uDrT$ based on Daly et al. [1994] and Dodson and Marks [1997]) directly onto species distribution maps recording presence/absence (Little 1971). The *most extreme* value of each bioclimatic variable found within the species' geographic ranges was then recorded and used to assign the species-specific parameters $kDDMin$, $kWiTN$, $kWiTX$, and $kDrT$ (Bugmann 1996b). This approach assumes that species grow at their physiological limit with respect to the above bioclimatic variables in at least one point within their geographic range. At this point, a species' realized niche will be identical to its fundamental niche (sensu Grinnell 1924, James et al. 1984; cf. Sykes et al. 1996) with respect to the bioclimatic variable in question. Note that this procedure differs significantly from that used in other gap model studies where a value for a bioclimatic variable is selected that correlates best with, e.g., the *total* northern range limit of a species ("realized niche" only; Shugart 1998).

These estimation procedures yielded plausible values for $kWiTN$ and $kWiTX$. However, estimates of the minimum degree-day requirement ($kDDMin$) and the drought tolerance parameters ($kDrT$) were unsatisfactory. The complex topography of the PNW produces precipitation and temperature gradients that are quite steep, and neither the maps of bioclimatic variables nor of species geography provided a resolution fine enough to adequately determine the extreme values of the former that are found in the range of the latter:

1) The initial estimates of the $kDDMin$ parameter obtained from overlaying maps of the degree-day sums

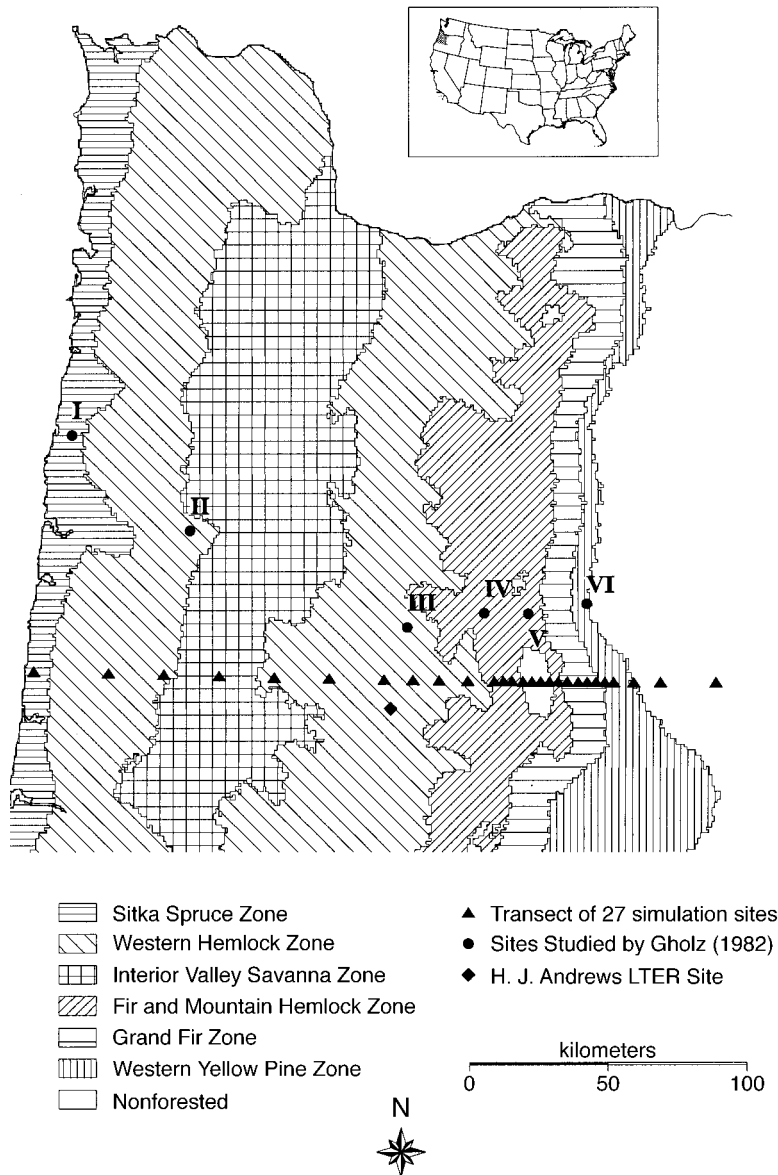


FIG. 3. Map of northwestern Oregon showing the various forest measurement sites and the transect at 44.13° N that was used for model verification.

on tree distribution maps yielded estimates that had a unit resolution of no more than $200^{\circ}\text{C} \times \text{days}$, and which could have been mismeasured on a species range map by \pm one unit. This uncertainty does not permit sums to be distinguished that characterize species differing only moderately in their degree-day requirements. Producing repeatable, objective, and valid values under these circumstances is quite difficult. Our procedure was to subdivide these coarse estimates using an objective numeric scaling of those tree species' climatic requirements illustrated by Franklin and Dyrness (1988: 161). For details, see Bugmann (1996b).

2) The estimates of the $kDrT$ parameter (species-specific maximum drought tolerance) obtained from

overlays of distribution maps with maps of the simulated drought index values, $uDrE$ and $uDrD$, matched the ranking of the species by Franklin and Dyrness (1988: 130). However, the coarse mapping of climate variables and species geography mentioned above meant that a few species had been assigned only slightly different drought indices, although Franklin and Dyrness (1988) indicate that their drought tolerances should differ considerably. Therefore, we modified the $kDrT$ parameters of *Alnus rubra*, *Acer macrophyllum*, *Pinus ponderosa*, and *Abies grandis* derived from mapping to coincide with their properties as described by Franklin and Dyrness (1988).

The methods of derivation and the complete set of

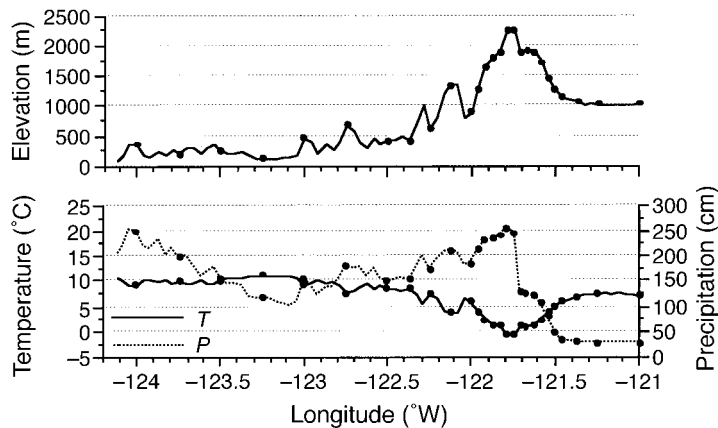


FIG. 4. Profiles of elevation, annual mean temperature (T), and annual precipitation sum (P) at 4-km resolution (Daly et al. 1994, Dodson and Marks 1997) along a longitudinal transect in the Pacific Northwest (cf. Fig. 3). Dots denote grid points chosen for the simulation studies.

all species-specific parameter values were described in detail by Bugmann (1996b).

Re-estimation of parameters for Europe/eastern North America.—Due to the reformulation of the model equations as described above, the definition of three species-specific parameters, i.e., $kDrT$, $kDDMin$, and $kNTol$, had changed in FORCLIM V2.9, and an additional parameter, $kWiTX$, had been introduced. Hence new estimates of these parameters had to be derived for the European and eastern North American species that had already been included in FORCLIM (Bugmann and Cramer 1998).

We recalculated the bioclimatic parameters for all the species according to an objective set of statistical rules: Lacking the specific climate data sets required, we regressed the simulated drought index, degree-day index, and winter temperature of model version 2.9, against the values of the respective output variables as simulated by model version 2.6 along a climate gradient in each of the two areas (Bugmann and Solomon 1995, Bugmann and Cramer 1998). The resulting regression equations were used to recalculate the corresponding species parameters. The methods of derivation and the complete set of all modified species-specific parameter values were described in detail by Bugmann (1996b).

Simulation experiments

Model verification for PNW forests.—Points along a transect at 44.13° north latitude (Figs. 3 and 4) were chosen for deriving and testing the effects of modified formulations of model equations (Eqs. 1'–4'). Hence the results obtained from these simulations do not constitute a model validation, but a model verification (sensu Swartzman and Kaluzny 1987). The transect extends from evergreen rain forests at the Pacific coast near the town of Reedsport, across the southernmost Willamette Valley near the town of Eugene, through the Cascade Mountains near the town of Sisters, and into the desert shrubland of the Great Basin interior near Bend, Oregon (cf. Franklin and Dyrness 1988). These and the

other PNW simulations included all 20 species given in Table 1.

The temperature data to run the model along the transect were obtained from the VEMAP database (Kittel et al. 1995) interpolated to 4 km resolution by the methods of Dodson and Marks (1997). Precipitation data were obtained from Daly et al. (1994). At all sample points, a deep, mesic soil with an available water capacity ("bucket size") of 20 cm water was assumed. The model setup FORCLIM-E/P was used. That is, we did not calculate belowground carbon and nitrogen dynamics for two reasons: first, we are currently lacking the respective species-specific parameters for the PNW (see estimation procedure for parameters $kNTol$ and kLQ above), and second, FORCLIM proved to be little sensitive to the inclusion of nitrogen cycling at regional scales (Bugmann 1994). We thus excluded nutrient competition in the model by assuming nutrient-rich soils with a nitrogen content of 100 kg/ha across the transect. No large-scale disturbances like fires or windthrow were simulated (Agee 1993). The steady-state species composition was calculated at each point along the transect following the simulation protocol developed by Bugmann (1997b).

Model tests with independent data in the PNW.—Three old-growth forests in the H. J. Andrews Long-Term Ecological Research (LTER) Site were selected for testing model behavior with independent forest data (e.g., Grier and Logan 1977, Garman and Hansen 1991). Requisite site history, long-term climate and soil data, as well as the species composition and size structure of the forests, were obtained from Garman and Hansen (1991). The forest data represent averages from six, four, and three stands, measured at elevations of 500, 1000, and 1400 m above sea level, respectively. These LTER data had also been used by Garman and Hansen (1991) to test a PNW version of the gap model ZELIG (Urban et al. 1993). Unfortunately, the areal extent of the measured stands is not known, which made it impossible to set up a simulation experiment

TABLE 2. Eastern North American test sites (Canada) and climatic divisions (United States) 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 according to Rowe (1972) and Küchler (1975).

Site/division	Latitude (°N)	Longitude (°W)	T (°C)	P (mm)	No.	Potential natural vegetation
Churchill	58	93	-7.3	396	...	Tundra
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</i> <i>mariana</i> , <i>Betula papyrifera</i>
Western Upper Michigan	47	89	4.9	817	106/107	<i>Pinus strobus</i> , <i>P. resinosa</i> , <i>Thuja occidenta-</i> <i>lis</i> , <i>Acer saccharum</i> , <i>Tsuga canadensis</i> , <i>Fagus grandifolia</i> , <i>Tilia americana</i>
Central Lower Michigan	44	85	8.3	760	100	<i>Acer</i> spp., <i>Fagus grandifolia</i> , <i>Fraxinus</i> spp., <i>Tilia</i> spp., <i>Carya</i> spp., <i>Quercus</i> spp.
West Central Ohio	40	84	10.9	930	100	<i>Carya</i> spp., <i>Quercus</i> spp., <i>Acer</i> spp., <i>Fraxi-</i> <i>nus</i> spp., <i>Fagus grandifolia</i>
Cumberland Plateau, Tennessee	36	85	14.2	1378	103	<i>Quercus</i> spp., <i>Fagus grandifolia</i> , <i>Lirioden-</i> <i>dron tulipifera</i> , <i>Acer</i> spp., <i>Castanea</i> <i>dentata</i> †
Southwest Georgia	31	85	19.6	1290	111/112	<i>Carya</i> spp., <i>Quercus</i> spp., <i>Liquidambar</i> <i>styraciflua</i> , <i>Pinus</i> spp.
Western Missouri	37	91	13.8	1095	111	<i>Carya</i> spp., <i>Quercus</i> spp., <i>Pinus</i> spp.
South Central Arkansas	34	93	17.9	1312	111	<i>Carya</i> spp., <i>Quercus</i> spp., <i>Pinus</i> spp.

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

† Extinct today due to the chestnut blight (cf. Shugart and West 1977).

that exactly matched the spatial scale of the measurements.

To match the LTER data, the FORCLIM-E/P model was run for 470 simulation years, corresponding to the estimated average age of the stands. Weather data had to be supplied using the weather generator of FORCLIM-E, since there is no reconstruction of monthly weather data available for the last 470 yr at H. J. Andrews. Simulations started from bare ground and included 200 forest patches (replicates) of 0.083 ha each; this implies that we simulated the average properties of a shifting mosaic steady state at a spatial scale of 200·0.083 ha = 16.7 ha, whereas the measurements certainly refer to a smaller spatial extent. Stand structure at the end of the simulations was compared with measured stand structure at the three elevations both qualitatively and, as far as feasible, quantitatively (Power 1993).

Model tests in eastern North America and central Europe.—To test model behavior in eastern North America, the set of sites was used that had been described by Bugmann and Solomon (1995). The location, climatic data, and species composition of near-natural forests for the sites are given in Table 2. At every site, the steady-state species composition was calculated according to the method by Bugmann (1997b). The 72 tree species from eastern North America included in the FORENA model (Solomon 1986) were used for this set of simulations.

To test model behavior in central Europe, a set of sites along a climatic gradient from cold-wet to warm-dry conditions was chosen (Bugmann and Cramer

1998). This gradient is quite typical of the climatic conditions prevailing in central Europe (Bugmann 1996c). The conditions for these simulation experiments were described in detail by Bugmann and Cramer (1998). The location, climatic data, and expected species composition for the sites are given in Table 3. Thirty species of central Europe as listed in Bugmann (1994) were used for these simulations.

RESULTS

Model verification for Pacific Northwest forests

The FORCLIM model projects an almost continuous decrease of aboveground biomass from west to east along the Oregon transect (Fig. 5), ranging from 700–800 Mg/ha in *Picea sitchensis* zone forests (terminology of Franklin and Dyrness 1988; cf. Fig. 3) to 250 Mg/ha in closed-canopy *Pinus ponderosa* forests, and declines steeply towards the steppe in eastern Oregon (Franklin and Dyrness 1988). Note that the amount of simulated biomass is not constrained through a site-specific maximum biomass parameter, as is done in many other models (e.g., Shugart and West 1977, Kienast 1987, Leemans and Prentice 1989, Urban et al. 1993), but rather is predicted solely from the climate data and the tree species characteristics (cf. Bugmann 1996a).

Stand biomass was measured by Gholz (1982) from west to east at seven forested sites arranged essentially along this transect (Fig. 3). Gholz (1982: 475; excluding live branch biomass, which is not simulated by FORCLIM) also recorded a declining trend, with 983–

TABLE 3. 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	Latitude (°N)	Longitude (°E)	Elevation (m)	<i>T</i> (°C)	<i>P</i> (mm)	BS (cm)	PNV
Bever S	46.6	9.9	1712	1.5	841	10	<i>Pinus cembra</i> , <i>Pinus montana</i> , <i>Larix decidua</i>
Cleuson	46.1	7.4	2100	1.3	1020	10	<i>Pinus cembra</i> , <i>Picea excelsa</i> , <i>Larix decidua</i>
Bever N	46.6	9.9	1712	1.5	841	10	<i>Picea excelsa</i> , <i>Larix decidua</i>
Davos	46.8	9.8	1590	3	1007	10	<i>Picea excelsa</i> , <i>Larix decidua</i>
Adelboden	46.5	7.6	1325	5.5	1351	15	<i>Picea excelsa</i> , <i>Fagus sylvatica</i> , <i>Abies alba</i>
Huttwil	47.1	7.8	638	8.1	1290	20	<i>Picea excelsa</i> , <i>Fagus sylvatica</i> , (<i>Abies alba</i>)
Bern	46.9	7.4	570	8.4	1006	20	<i>Fagus sylvatica</i> , (<i>Picea excelsa</i>)
Schaffhausen	47.7	8.6	400	8.6	882	15	<i>Fagus sylvatica</i> , (<i>Quercus</i> spp.)
Basel	47.5	7.6	317	9.2	784	15	<i>Fagus sylvatica</i> , (<i>Quercus</i> spp.)
Schwerin	53.6	11.4	45	8.2	625	24	<i>Fagus 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>Pinus silvestris</i> , <i>Quercus</i> spp.

Notes: Tree nomenclature is according to Hess et al. (1980). Other symbols: N = steep north-facing slope; S = steep south-facing slope (cf. Bugmann 1994).

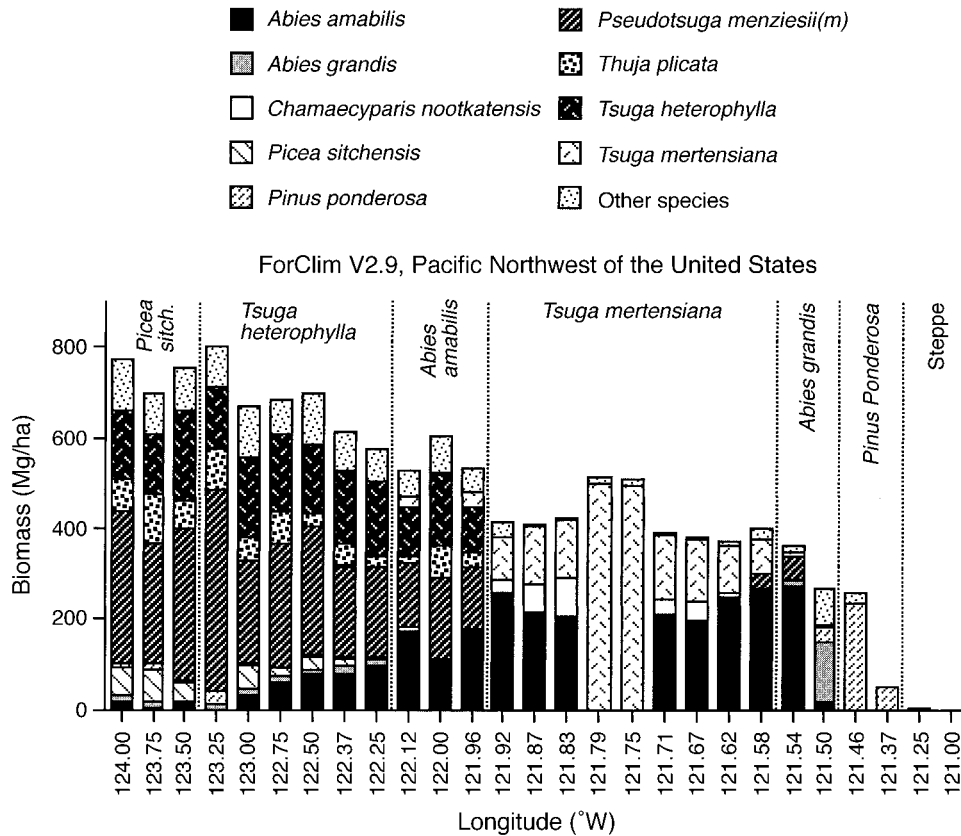


FIG. 5. Equilibrium species composition as simulated by FORCLIM V2.9 along an environmental gradient at latitude 44.13° N from the Pacific coast (left) to the steppe (right) in Oregon. The dotted lines denote boundaries between vegetation zones (cf. Fig. 3), and the names on top of the bars indicate the vegetation zone according to Franklin and Dyrness (1988).

1348 Mg/ha in the *Picea sitchensis* zone, 805 Mg/ha in the *Tsuga heterophylla* zone of the Coast Range, and 419 Mg/ha in the same forest type on the lower slopes of the Cascades. The midelevation *Abies amabilis* zone had 485 Mg/ha, with 243 Mg/ha in high-elevation *Tsuga mertensiana* zone stands and 106 Mg/ha in open *Pinus ponderosa* stands. Thus, the simulated and measured stand biomass values are quite similar for each zone relative to the differences among zones along the transect, except in high-elevation *Tsuga mertensiana* stands. FORCLIM projects the following characteristics of compositional differences among the Franklin and Dyrness (1988) forest types from west to east (Fig. 5):

1) From longitudes 124.0° to 123.5° W, *Picea sitchensis* forests dominated (in order of importance) by *Pseudotsuga menziesii*, *Tsuga heterophylla*, *Thuja plicata*, and *Picea sitchensis* were simulated. This composition corresponds well to the descriptions of the *Picea sitchensis* zone (Franklin and Dyrness 1988). Old-growth forests of the *Picea sitchensis* zone are dominated by hemlock because Douglas-fir does not regenerate under a dense canopy (Franklin and Dyrness 1988). These descriptions clearly refer to individual old-growth stands. The model output shown in Fig. 5, however, is based on a simulated landscape-scale equilibrium characterized by a mixture of old-growth as well as young stands, where gaps are opened regularly, thus allowing the moderately shade-tolerant Douglas-fir to regenerate. Therefore, the simulated abundance of Douglas-fir in this zone appears plausible (Fig. 5).

2) Forests dominated by *Pseudotsuga menziesii*, *Tsuga heterophylla*, and *Thuja plicata* were simulated from longitudes 123.25° to 122.25° W, covering the Coast Range and the lower slopes of the Cascades. The abundance of *Abies amabilis* increases as temperature decreases and the midelevations of the Cascade Mountains are approached (Fig. 4). The *Tsuga heterophylla* zone forests typical of this area (Fig. 3) are dominated by *Pseudotsuga menziesii*, *Tsuga heterophylla*, and *Thuja plicata* (Franklin and Dyrness 1988). The simulated dominance by Douglas-fir early, then by western hemlock later (timing not shown) also matches the succession in the *Tsuga heterophylla* zone (Franklin and Dyrness 1988). However, the Douglas-fir–Oregon oak (*Quercus garryana*) forests believed to be typical of the Willamette Valley (Franklin and Dyrness 1988) at longitude 123.25°W (Fig. 3) are not simulated by the model. The open vegetation found in the Willamette Valley today reflects the disturbance regime, most notably natural and anthropogenic fires (Franklin and Dyrness 1988). With less frequent fires, Douglas-fir–Oregon oak forests are expected to thrive (Franklin and Dyrness 1988). In the absence of fire, as assumed in the simulations, the simulated forest typical of the *Tsuga heterophylla* zone is plausible (Fig. 5). In both the *P. sitchensis* and the *T. heterophylla* zone, FORCLIM simulates the presence of 5–10% biomass of *Abies procera*, a species that should not be present in these zones.

3) From longitudes 122.12° to 121.96° W, forests dominated by *Abies amabilis*, *Pseudotsuga menziesii*, and *Tsuga heterophylla* are simulated. This composition compares well with descriptions of *Abies amabilis* zone forests, which cover middle elevations in the eastern Cascades (Franklin and Dyrness 1988). Simulations of the successional pattern for 1200 yr, starting from bare ground (not shown) yield a dominance of *Abies procera* and *Pseudotsuga menziesii* in the early stage. *Abies procera* disappears almost completely by the simulation year 700, whereas the abundance of *P. menziesii* drops to about half of its maximum recorded in the early phase (Fig. 5). These dynamics appear realistic as compared to the descriptions by Franklin and Dyrness (1988).

4) Forests dominated by *Abies amabilis*, *Chamaecyparis nootkatensis* and *Tsuga mertensiana* are simulated from longitudes 121.92° to 121.83° W and from 121.71° to 121.58° W. These results correspond to descriptions of the location and composition of the closed-canopy variant of the *Tsuga mertensiana* zone (*ibid.*). The simulated abundance of *Abies amabilis* at these elevations appears to be too high, perhaps due to the coarse estimates of the parameters describing the climatic distribution limits of the species (see *Methods* section). On the other hand, *T. mertensiana*, *A. amabilis*, and *C. nootkatensis* are the major late-successional species (Franklin and Dyrness 1988), and these three are also the most abundant species in the simulations (Fig. 5). Simulations of the transient model behavior over 1200 yr with FORCLIM (not shown) indicate that *Abies lasiocarpa* is an early successional species, which is realistic (Franklin and Dyrness 1988), but this species attains too little biomass in the landscape-average equilibrium values shown in Fig. 5 (cf. the longitudes 121.71° and 121.62° W).

5) At longitudes 121.79° and 121.75° W, i.e., at the highest elevations along the transect, *Tsuga mertensiana*–*Abies lasiocarpa* forests were simulated. These elevations (Fig. 3) should be occupied by the open woodland variant of the *Tsuga mertensiana* zone near treeline, and *Picea engelmannii* is a characteristic species of these woodlands and krummholz (Franklin and Dyrness 1988). Instead, we simulated a dense *Tsuga mertensiana* forest averaging 510 Mg/ha (cf. the 243 Mg/ha of Gholz 1982 for closed-canopy forests) and a complete absence of *P. engelmannii*, indicating a clear failure. Yet simulations at other high-altitude treelines (see *Model tests in central Europe*, below, and Bugmann 1997a) produce credible biomass and species composition. Hence, these errors suggest that *Tsuga mertensiana* and *Picea engelmannii* natural histories are not adequately portrayed in the present model version.

6) *Abies grandis* zone forests provide the transition from high-elevation *Tsuga mertensiana* forests to the open pine woodlands of the lower eastern Cascades (Franklin and Dyrness 1988). The model simulated a

narrow strip of forest dominated by *Abies grandis*, *Pseudotsuga menziesii*, and *Acer macrophyllum* from 121.54° to 121.5° W, corresponding fairly well to the *Abies grandis* zone. The species composition in this zone varies widely with locale, but *A. grandis* and *P. menziesii* are the most typical late-successional species. FORCLIM also projects the presence of *A. macrophyllum* at the landscape scale; this early successional species should not be present in this zone.

7) *Pinus ponderosa* zone forests and woodlands grade into *Juniperus* zone woodlands of eastern Oregon (Franklin and Dyrness 1988). FORCLIM simulated open forests composed of *Pinus ponderosa* and some *Quercus garryana* from 121.46° to 121.37° W, comparing well to descriptions of the *Pinus ponderosa* zone (Franklin and Dyrness 1988). These authors note that in the absence of disturbance, *A. grandis* and *P. menziesii* typically outcompete *P. ponderosa* and *Q. garryana* on moister sites. Since the sites that were simulated here are located close to the steppe (Fig. 3), the dominance of *P. ponderosa* and *Q. garryana* appears realistic. Where steppe vegetation dominates (Franklin and Dyrness 1988), i.e., east of longitude 121.25° W, the model produces no forest vegetation.

We conclude from the foregoing that FORCLIM realistically depicts the broad-scale features of forest community density and composition along this strong environmental gradient of both temperature and precipitation (Fig. 4). Erroneous behavior of the model is clearly present but is restricted mainly to places where nondominant species are either measured or simulated to be of minor abundance (e.g., *Abies procera* in the western part of the transect; Fig. 5), or where steep environmental gradients preclude obtaining accurate species natural history parameters (e.g., *Tsuga mertensiana* and *Picea engelmannii*).

Model tests with independent data in the PNW

The basal area composition measured in forests at 500, 1000, and 1400 m elevation at the Andrews LTER site is shown in Fig. 6 (Garman and Hansen 1991). Qualitatively speaking, the simulated species composition exhibits features similar to the measured composition. Both the LTER and FORCLIM data sets are characterized by the dominance at all three sites by *Pseudotsuga menziesii*, at the lower two sites by *Tsuga heterophylla* and *Thuja plicata*, at the upper two sites by *Abies amabilis*, and at the uppermost site by *Tsuga mertensiana*. Total LTER and FORCLIM basal area is similar at the 500-m and 1400-m sites, and would be similar at the midelevation site if not for the large *P. menziesii* LTER values that FORCLIM was unable to reproduce.

Because FORCLIM generally yields too little basal area across the gradient and simulated species diversity is too high, most quantitative comparisons (cf. Power 1993) indicate a poor fit. For example, the percentage similarity coefficients (Bugmann 1997b) between pre-

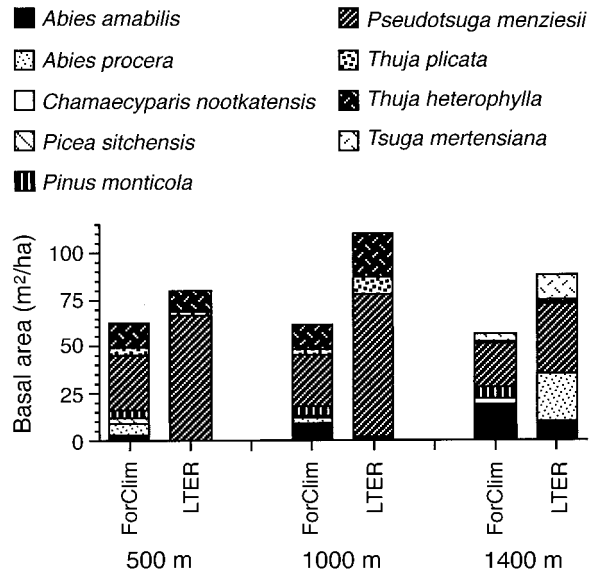


FIG. 6. Validation of FORCLIM V2.9 against independent basal area data at three elevations (500, 1000, 1400 m) in H. J. Andrews LTER forest (measured data obtained from Garman and Hansen [1991]).

dicted and measured data were between 52 and 70% only, which is unsatisfactory. However, regressions of predicted vs. measured relative basal area yielded no significant difference from a zero intercept (F test, $\alpha = 5\%$) at 1000 and 1400 m, and no significant difference from a slope of 1 (t test, $\alpha = 5\%$) at 1400 m. We conclude that the match between predicted and measured data is adequate, especially since we are comparing a simulated average shifting-mosaic steady state on 16.7 ha against measured samples from considerably smaller areas, which are subject to an unknown variability. Note also that the total aboveground biomass simulated for the year 470 at the lowest elevation amounts to 795 Mg/ha (data not shown), which is only 3.1% higher than a measured 771 Mg/ha (DeAngelis et al. 1981). In the same watershed, Grier and Logan (1977) later measured (without branch biomass) from 459 to 911 (mean = 645) Mg/ha in five adjacent community types. Measured biomass data for the other elevations were not available.

FORCLIM stem size distributions are very similar to LTER data at all three elevations (Fig. 7): regressions of predicted vs. measured data yielded no significant differences from a zero intercept (F test, $\alpha = 5\%$) and a slope of 1 (t test, $\alpha = 5\%$) at any elevation except for the regression slope at 1400 m. This match is particularly impressive considering that unrecorded disturbances (e.g., ground fires, insect infestations) during the past 470 yr could have induced significant deviations from the simulated "undisturbed" stem size distributions (Waring and Schlesinger 1985). Early gap model experiments were notably deficient in reproduc-

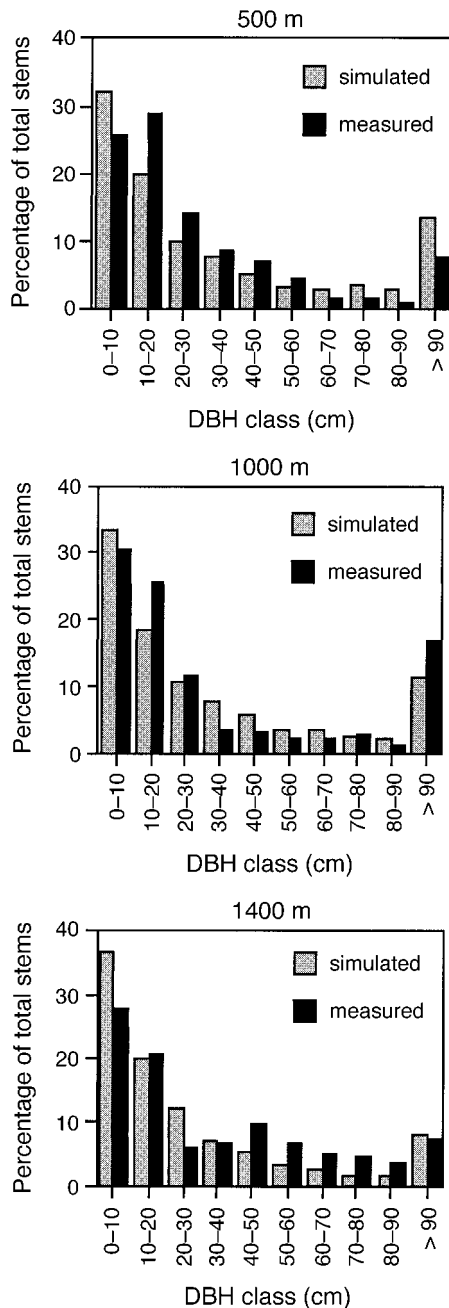


FIG. 7. Validation of FORCLIM V2.9 against independent stand structure data at three elevations (500, 1000, 1400 m) in H. J. Andrews LTER forest (measured data obtained from Garman and Hansen [1991]).

ing these stem size distributions, especially in the largest size class (Garman and Hansen 1991).

We conclude from the transect comparisons and from these independent simulations of stand data at the H. J. Andrews LTER that FORCLIM adequately mimics aboveground biomass, forest stand composition, and size structure in this region of the PNW.

Model tests in eastern North America

The simulation results of model version 2.6 for eastern North American conditions were discussed in detail by Bugmann and Cramer (1998). Here, we focus on simulation results that have changed between model versions 2.6 and 2.9 along the environmental gradient in eastern North America (Fig. 8), and compare them with the corresponding features of near-natural forests (cf. Table 2).

The pattern of aboveground biomass is similar between model versions 2.6 and 2.9 (Fig. 8). The maximum biomass attained by FORCLIM is 200–250 Mg/ha, which compares well with measured data (DeAngelis et al. 1981). Model version 2.9 appears to be more realistic than model versions 2.6 (Bugmann and Cramer 1998) and 2.4 (Bugmann and Solomon 1995) by projecting a steeper decrease of aboveground biomass towards both the cold (cf. Botkin and Simpson 1990, Price and Apps 1996) and the dry (Monk et al. 1970) treelines. This biomass gradient in eastern North America is also consistent with the new model behavior in central Europe (cf. Fig. 9).

At Armstrong, Ontario, *Betula papyrifera* (Rowe 1972; Fig. 8) produced an anomalously high biomass in model version 2.6 (Bugmann and Cramer 1998). The disconcerting absence of normally dominant and relatively fire and drought-tolerant pine species (*Pinus banksiana*, *P. resinosa*, *P. strobus*) in versions 2.4 and 2.6 continued with version 2.9 throughout the cold region. Although we simulate forest composition in the absence of fire, the result still suggests errors in the estimation of the drought tolerance parameters rather than in the drought treatment itself, which differs considerably among the three model versions.

In the Western Upper Michigan Climatic Division of northern hardwoods, *Quercus macrocarpa* was too abundant, as it was in model version 2.6 (Bugmann and Cramer 1998). This species characteristically dominates only open woodlands farther west and is otherwise a minor component in these mesic, closed forests. *Acer saccharum* and *Fagus grandifolia* are still simulated as dominant species, but another important species, *Tsuga canadensis*, is reduced to small amounts (cf. Kuchler 1975). The decreased abundance of white cedar (*Thuja occidentalis*) in the new model version, and the appearance of *Betula alleghaniensis* in northern Michigan are both more plausible. *Betula alleghaniensis*, one of the few late-successional birch species, previously could not be simulated with gap models in this region (cf. Solomon 1986, Solomon and Bartlein 1992).

Southern pines, mainly *Pinus echinata*, appear in the simulations as the prairie-forest border is approached in western Missouri and south-central Arkansas. The entry of southern pine species into the simulated forest represents a significant improvement in model capability, after unsuccessful attempts to model them in the past (e.g., Solomon 1986, Bugmann and Solomon

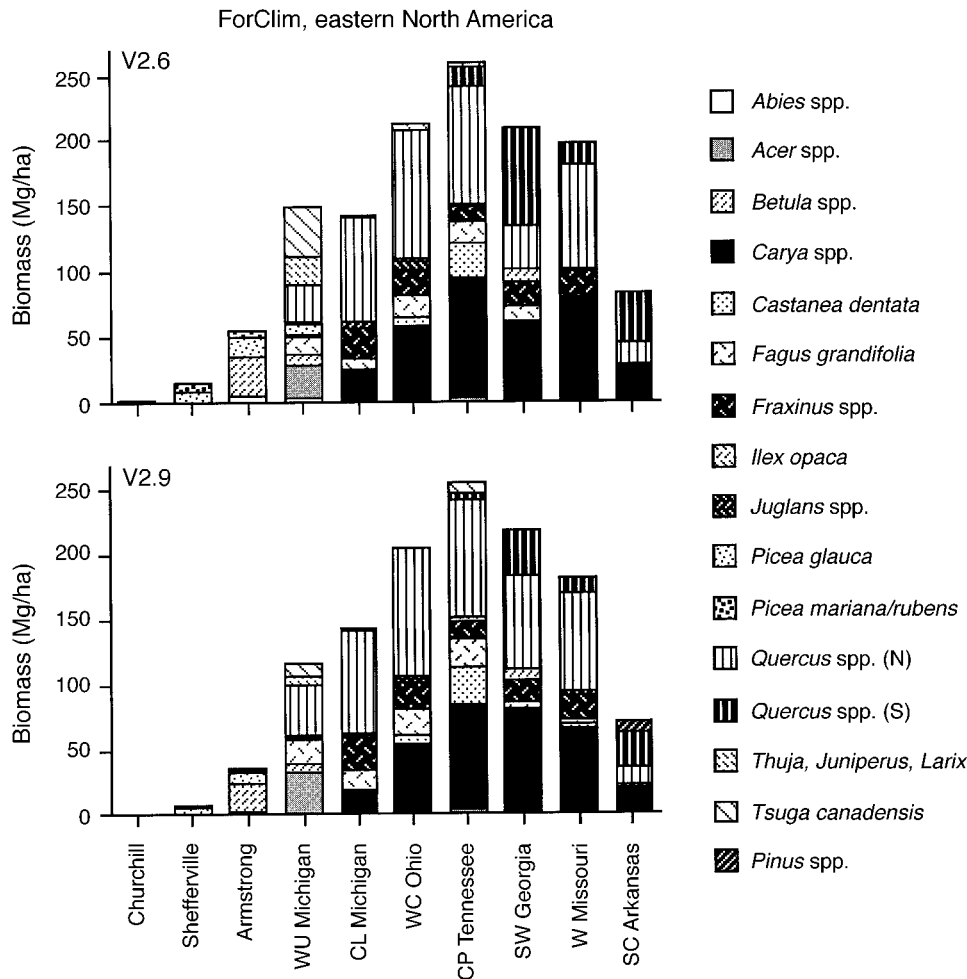


FIG. 8. Equilibrium species composition as simulated by FORCLIM V2.6 (top) and FORCLIM V2.9 (bottom) along an environmental gradient in eastern North America (left = cold-moist, right = warm-dry). All 72 species simulated are tabulated by Solomon et al. (1984).

1995; L. K. Mann, *personal communication* 1987). This realistic behavior (Küchler 1975) follows from the extended growing-season length and reduced drought effects on evergreen species as compared to deciduous ones simulated under these warm-dry conditions. In the real landscape, pines are still more dominant, but in the absence of fire and in view of the soil water capacity parameter employed, they probably would be outcompeted by hickory (*Carya* spp.) and oak (*Quercus* spp.) both here and in southwest Georgia. Hence the simulation results, which do not reflect the effects of disturbance and sandy coastal plain soils, appear plausible.

Model tests in central Europe

The simulation results of model version 2.6 for European conditions were discussed in detail by Bugmann and Cramer (1998). Here, we focus entirely on those aspects of the simulation results that have changed between model versions 2.6 and 2.9 along the environ-

mental gradient in Europe (Fig. 9), and compare them to the expected composition of near-natural forests (cf. Table 3).

The new model version (V2.9) predicts a maximum aboveground biomass of ~ 400 Mg/ha in the center of the gradient, which agrees well with descriptions of European virgin forests (Leibundgut 1993). In addition, the model yields a smoother gradient of aboveground biomass, which at the same time is considerably steeper towards the cold (left) and the dry treeline (right). This pattern is more realistic than the behavior of the old model version (cf. Duvigneaud and Denaeyer 1983, Ellenberg 1986). Note that the difference between minimum and maximum simulated biomass at both ends of the gradient was only ~ 80 Mg/ha in FORCLIM V2.6 (Cleuson vs. Huttwil and Cottbus vs. Sion, respectively), whereas in model version 2.9 this difference has increased to a more realistic ~ 200 Mg/ha.

No major changes in simulated species composition occur with the new model version except for the fol-

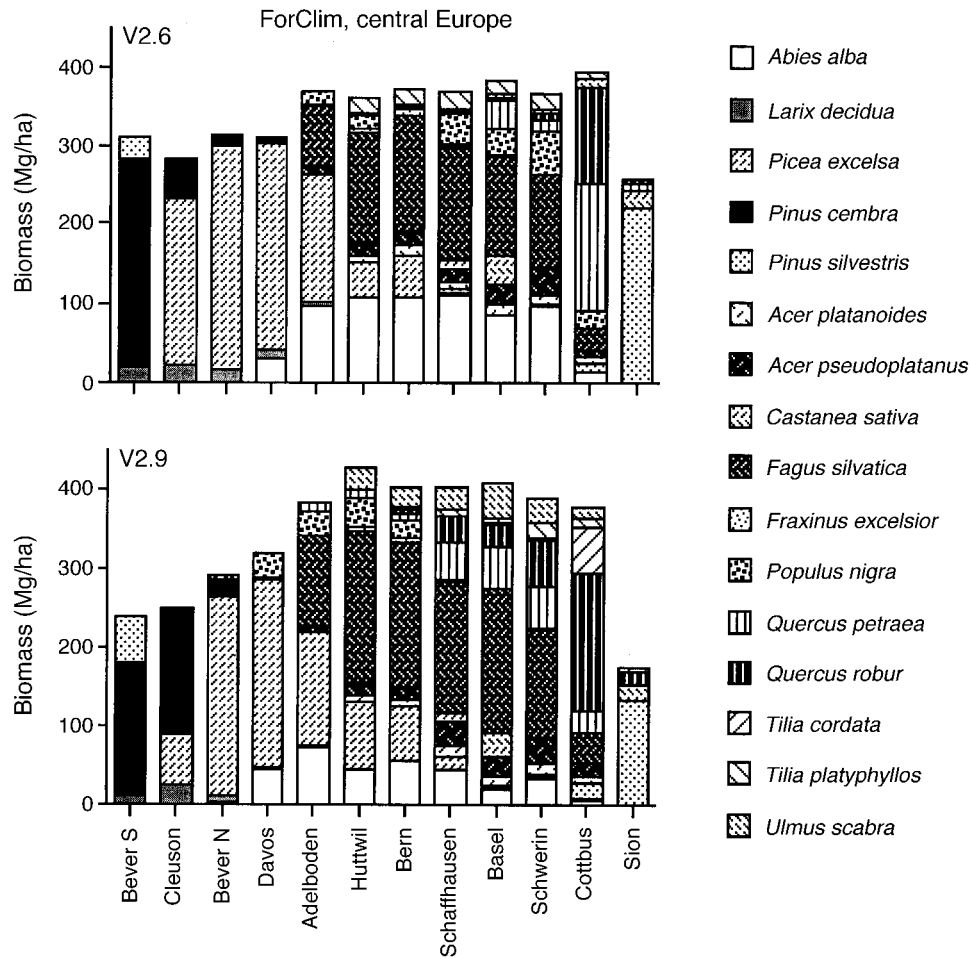


FIG. 9. Equilibrium species composition as simulated by FORCLIM V2.6 (top) and FORCLIM V2.9 (bottom) along an environmental gradient in Europe (left = cold-moist, right = warm-dry). All 30 species simulated are tabulated by Bugmann (1994).

lowing: (1) the anomalous abundance of *Populus nigra* at Davos, Adelboden, Huttwil, and Bern (Ellenberg and Klötzli 1972) has increased in the new model version, although *P. nigra* still is a minor species only; (2) at Cleuson, FORCLIM V2.9 projects a significantly higher abundance of *Pinus cembra*, a feature that is more typical of these high-elevation central alpine locations than the dominance of *P. excelsa* simulated by model version 2.6 (Ellenberg and Klötzli 1972); (3) the new model version yields a decreased abundance of *Abies alba* at the sites in the center of the gradient (Huttwil through Schwerin) while maintaining them at higher elevations. In reality, *A. alba* is abundant at montane sites (e.g., Adelboden) and does not commonly occur in the European lowlands (i.e., from Schaffhausen towards warmer conditions; Ellenberg 1986). The new model version captures the distribution of this species more realistically.

We conclude that the behavior of FORCLIM V2.9 in central Europe has generally improved as compared to model version 2.6. Note that this was achieved although

none of the modifications of the model structure was designed for this purpose. Instead, the improved behavior is a by-product of the new ability of the model to simulate responses to seasonality of moisture in PNW forests (Fig. 5); this seasonality probably also plays a role in the competition between evergreen and deciduous species in Europe.

DISCUSSION

The foregoing results document our progress in developing a single forest stand model which is valid over a wide range of environmental conditions. We based this work on FORCLIM, a gap model that had been designed to simulate forest dynamics under temperate climates featuring cold winters and an absence of pronounced precipitation seasonality (Bugmann 1996a). The model was successfully applied to this purpose in both central Europe and eastern North America (Bugmann and Solomon 1995, Bugmann and Cramer 1998). In the present study we modified FORCLIM to mimic individual species responses to the strong seasonality

in moisture availability and the higher winter temperature prevailing in the Pacific Northwest of North America.

We established that the modified model generates realistic estimates of variations in forest composition and biomass along a temperature and moisture gradient in Oregon, ranging from the temperate rain forests at the Pacific coast across the Cascades to the steppe in eastern Oregon. Most values of stand biomass and species composition were simulated within published measurements, and the accuracy of the simulated stand size structure at three elevations of H. J. Andrews LTER was found to be at least as high as that of other studies using gap models (e.g., Hemstrom and Adams 1982, Dale and Hemstrom 1984, Garman and Hansen 1991, Urban et al. 1993). Then we tested FORCLIM's utility along extended environmental gradients in the regions of its origin, i.e., in eastern North America and central Europe. In both regions, simulated species composition improved at least in parts of the gradients. Total above-ground stand biomass, an emergent property of the FORCLIM model, was correctly simulated along the transects in all three regions, yielding maximum values of 800, 400, and 250 Mg/ha for the Pacific Northwest, central Europe, and eastern North America, respectively, matching the strong differences in measured values within and between transects.

These improvements in model performance and the extension of the model to new and different conditions were not without flaws, and we believe that the treatment of ecological processes leaves room for improvement. For example, substantial realism could be added with mechanistic disturbance submodels, based on the results of disturbance-free simulations in fire and pest epidemic-prone forests. Simulated forests in eastern North America are missing fire-adapted *Pinus banksiana* at Shefferville, and *P. banksiana* as well as fire-prone *P. resinosa* and *P. strobus* at Armstrong and western Upper Michigan (Maissurow 1935, Rowe 1972, Heinselmann 1973). The simulated abundance of *Pinus echinata* and other fire-prone southern pines is still low compared to that actually found in south central Arkansas, western Missouri (Steyermark 1940), and southwest Georgia (Christiansen 1988). In the PNW, simulated *Tsuga heterophylla* forests in the Willamette Valley (123.25° W) and the *Pinus ponderosa* sites in the eastern Cascades (121.37° and 121.46° W) are obvious candidates for significant improvement with addition of a fire simulator to the model. Previous gap model routines to simulate fire effects (e.g., Shugart and Noble 1981, Kercher and Axelrod 1984) may be incorporated into FORCLIM directly, while other forms of disturbance (e.g., insect and disease epidemics; wind; flood; snow and landslide; timber harvest) and their interactions may present larger but not insurmountable difficulties.

The FORCLIM results also documented imperfections in our ability to characterize species natural histories.

The simulations revealed that we have not yet solved the fundamental problem of extracting ecophysiologically relevant environmental thresholds for species growth and regeneration from range limits in mountainous areas. This is particularly evident in the simulated absence of *Abies procera* from areas in its current PNW range, and in its presence in adjacent, warmer areas (Fig. 5). The abundance of full-sized *Tsuga mertensiana* in currently treeless alpine areas suggests a similar problem. Many areas of western North America, as well as other temperate regions, possess topographic variation strong enough to telescope the entire temperature and moisture range of a species into a few horizontal kilometers. A spatial approach such as overlaying species' range maps onto 4-km climatic data provides only coarse estimates of the species' climatic limits, even where the climate data are accurate. We are currently attempting to use fine-resolution digital elevation models to disaggregate the range of values represented in each spatial unit of the climate data base, but without assurance of success.

While we expect to solve these problems eventually, some basic assumptions underlying the estimation of species-specific parameters from distribution data have given rise to several critical reviews (e.g., Loehle and LeBlanc 1996, Schenk 1996) and warrant discussion here. The criticisms can be summarized as two related questions. First, do calculations of photosynthetic potential, and of the ability of individuals to survive beyond their geographic range limits, invalidate the assumption that tree growth declines towards a species' cold range limit (Bonan and Sirois 1992)? Second, does the difference between potential geographic range (fundamental niche of Grinnell 1924) and occupied range (realized niche, Grinnell [1924]) invalidate the selection of a single extreme climate tolerance from within a species' occupied range (e.g., Loehle and LeBlanc 1996, Schenk 1996)?

Bonan and Sirois (1992) used a photosynthesis model to conclude that lack of warmth at high-latitude range boundaries does not limit growth, contradicting both Eqs. 3 and 3'. They pointed to the presence of individual trees well beyond the boundary of continuous distributions as confirmation. In contrast to these model predictions, tree ring data (e.g., Fritts 1991, Schweingruber et al. 1991, Briffa et al. 1995) and other evidence (e.g., Körner 1998) demonstrate the overriding importance of growing season temperature to tree growth at the cold treeline. It may be augmented by winter low temperatures that kill needles and thus reduce photosynthetic capacity, but the direct effect on growth of growing season temperature is well established. Clearly, individuals may survive beyond the broad-scale limits of closed forest due to microclimatic influences that cannot be captured by the coarse geographic scale of climatic extremes extracted by our approach.

Taken together, we do not perceive adequate evi-

dence on which to base elimination of Eq. 3', which is a proxy for the several extrinsic temperature forces operating on tree growth at low temperatures. However, we quite agree with the conclusion by Bonan and Sirois (1992) and others, that temperatures at low latitude (warm) range limits should support optimal tree growth, and we have embodied this concept in FORCLIM V2.9 by the elimination of simulated growth reductions because of a high value of the growing degree-day sum (Eq. 3').

Loehle and LeBlanc (1996) and Schenk (1996) stated that the realized niche reflected by current range limits is so much smaller than the fundamental niche in which climate actually permits growth and reproduction that the former should not be used at all. Competition, disturbance, and even predation may result in large differences between the autecological (fundamental) and the synecological (realized) range limit of the species. Consequently, it likely is inappropriate to determine the best fit between, e.g., the sum of growing degree-days and the *total* northern range limit of a species, as done in many previous studies. Note that the method used in our study extracts a *single extreme* value found at any range limit, whereas most limits of that geographic range coincide with milder conditions. In the "unoccupied" areas between these milder conditions and the singular extreme condition, species may well be absent because of "competition with other tree species, soil characteristics, barriers to dispersal, and distribution of pests and pathogens" (Loehle and LeBlanc 1996). A gap model like FORCLIM, implementing the parameter estimation procedure described here, is capable of simulating the absence of tree species in the "unoccupied" areas caused by soil characteristics or competition with other tree species. While we are still using the realized niches for parameter estimation, our method tries to approach the species' fundamental niches. Hence, we do not perceive adequate evidence to abandon our approach to defining the climatic extremes that a species can withstand.

A theoretical construct that excludes any use of parts of the species' realized geographic range (e.g., Pacala and Hurtt 1993, Pacala et al. 1993) could provide an alternative to the assumption that at least some of current species' boundaries coincide with their maximum climatically determined range. To date, such attempts have been notoriously inaccurate in all but the most carefully site-calibrated situations (e.g., Pacala et al. 1993). Where they have been successful, they were used to simulate single-species stands (Friend et al. 1993), or they were based on a few general plant types (Friend et al. 1997). Note that FORCLIM currently operates with 122 tree species (30 European, 72 eastern North American, and 20 PNW species). Putting such a theoretical construct into practice throughout the temperate forests of the world would require a huge amount of field data and ecosystem experimentation, which may never be available.

Instead of trying to implement such a theoretical construct across many biogeographical regions, we used a twofold approach to increase the robustness of the model structure and the simulation results obtained from FORCLIM: First, we replaced a number of formulations that had been heavily criticized (such as the parabolic growth response to degree-days) by improved parameterizations, and we tested the robustness of other formulations (like the drought response) by comparative simulation studies along extended transects in climatically different regions. Second, we adopted a parameter estimation procedure in which we tried to approach the species' fundamental rather than realized niches, and we used strict rules for estimating species parameters and documented the few cases where we perceived ecological evidence to deviate from our own rules.

This increased rigor in the modeling approach did not result in a deterioration of model projections, but in improved model behavior and a wide range of applicability of the FORCLIM model V2.9. Thus we conclude that the uncertainties concerning the form of the growth reduction function at species' range limits and the issue of fundamental vs. realized niches do not bar the development of a model that can project the composition and biomass of the major forest communities as a function of climate, soils, and time, at least for the temperate regions of the world.

Indeed, the results of this study present the strongest evidence to date that the composition and aboveground biomass of a broad variety of forests can be predicted successfully within the framework of a single, generic forest stand simulator. In this simulator, the control of forest succession is determined by canopy gaps formed after the death of dominant trees, as constrained by competition for sunlight and other resources. Much of the variance in forest composition and biomass that we can measure from one place to another in central Europe, in eastern North America, and in the Pacific Northwest of the United States is consistent with this hypothesis as incorporated into FORCLIM V2.9. We find it especially encouraging that model modifications introduced for one region (e.g., the PNW) have led to improved model behavior in the other two regions, which suggests that these modifications indeed are generic and not region-specific (cf. Bugmann et al. 1996a).

Temperate forests outside the three study regions of this paper occur in east Asia (Japan, Korea, China, and the far east of Russia) and, with comparably small areal extent, in Chile, Australia, western Tasmania, New Zealand, and South Africa (Walter and Breckle 1991, 1994). Examination of the climates of these areas (Walter and Breckle 1991, 1994) reveals that all their characteristic features can also be found in parts of either central Europe, eastern North America, or the Pacific Northwest of the United States that were covered by the present simulation studies. Therefore we conclude

that incorporating a few physical and ecological processes of broad biotic significance into gap models can result in simulations of ecological gradients that are representative of temperate forests in general. The most important prerequisite for achieving a unified gap model of the global temperate forests would be to include submodels that deal with the major disturbances occurring in many of those forests, most prominently fire, insect infestations, and windthrow. We are convinced that the outlook for developing such a unified model is quite optimistic.

Finally, the results of this study have implications for our ability to simulate the response of temperate forests to climate change. While we can never prove that a model will be capable of simulating the ecological impacts of novel climatic conditions, we have shown that FORCLIM realistically depicts forest biomass and species composition along complex gradients of temperature and moisture extending from the cold to the dry treeline in three biogeographic areas that are characterized by different seasonality and interannual variability of temperature and precipitation. These simulation exercises and model tests significantly increase the robustness of simulation results obtained under scenarios of anthropogenic climatic change, as compared to the results from models that have been demonstrated to function within a considerably smaller area or at a few sites only. Our study thus is a step towards providing land managers and policymakers with robust tools for assessing the impacts of anthropogenic climate changes on forest resources.

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LITERATURE CITED

- Aber, J. D., D. B. Botkin, and J. M. Melillo. 1979. Predicting the effects of different harvesting regimes on productivity and yield in northern hardwoods. *Canadian Journal of Forest Research* **9**:10–14.
- Agee, J. K. 1993. *Fire ecology of Pacific Northwest Forests*. Island Press, Washington, D.C., USA.
- Allen, J. C. 1976. A modified sine wave method for calculating degree days. *Environmental Entomology* **5**:388–396.
- Becwar, M. R., and M. J. Burke. 1982. Winter hardiness limitations and physiography of woody timberline flora. Pages 307–323 in P. H. Li and A. Sakai, editors. *Plant cold hardiness and freezing stress: mechanisms and crop implications*, Volume 2. Academic Press, New York, New York, USA.
- Bonan, G. B., and L. Sirois. 1992. Air temperature, tree growth, and the northern and southern range limits to *Picea mariana*. *Journal of Vegetation Science* **3**:495–506.
- Botkin, D. B., J. F. Janak, and J. R. Wallis. 1972. Some ecological consequences of a computer model of forest growth. *Journal of Ecology* **60**:849–872.
- Botkin, D. B., and L. G. Simpson. 1990. Biomass of the North American boreal forest. *Biogeochemistry* **9**:161–174.
- Briffa, K. R., P. D. Jones, F. H. Schweingruber, S. G. Shiyatov, and E. R. Cook. 1995. Unusual twentieth-century summer warmth in a 1,000-year temperature record from Siberia. *Nature* **376**:156–159.
- Bugmann, H. 1994. On the ecology of mountainous forests in a changing climate: a simulation study. Dissertation Number 10638, Swiss Federal Institute of Technology, Zurich, Switzerland.
- Bugmann, H. 1996a. A simplified forest model to study species composition along climate gradients. *Ecology* **77**:2055–2074.
- Bugmann, H. 1996b. A forest stand model in the mountains of Oregon: development and computer code. Report to the U.S. Environmental Protection Agency, Corvallis, Oregon, USA.
- Bugmann, H. 1996c. Functional types of trees in temperate and boreal forests: classification and testing. *Journal of Vegetation Science* **7**:359–370.
- Bugmann, H. 1997a. Sensitivity of forests in the European Alps to future climatic change. *Climate Research* **8**:35–44.
- Bugmann, H. 1997b. An efficient method for estimating the steady state species composition of forest gap models. *Canadian Journal of Forest Research* **27**:551–556.
- Bugmann, H., and W. Cramer. 1998. Improving the behaviour of forest gap models along drought gradients. *Forest Ecology and Management* **103**:247–263.
- Bugmann, H., R. Grote, P. Lasch, M. Lindner, and F. Suckow. 1996b. Auswirkungen von Klimaänderungen auf die Wälder in Brandenburg. Pages 56–79 in M. Stock and F. Tóth, editors. *Mögliche Auswirkungen von Klimaänderungen auf das Land Brandenburg—Pilot studie*. Report, Potsdam-Institut für Klimafolgenforschung, Potsdam, Germany.
- Bugmann, H. K. M., and A. M. Solomon. 1995. The use of a European forest model in North America: a study of ecosystem response to climate gradients. *Journal of Biogeography* **22**:477–484.
- Bugmann, H. K. M., Yan Xiaodong, M. T. Sykes, Ph. Martin, M. Lindner, P. V. Desanker, and S. G. Cumming. 1996a. A comparison of forest gap models: model structure and behaviour. *Climatic Change* **34**:289–313.
- Burns, R. M., and B. H. Honkala. 1990. *Silvics of North America*. Volume I: Conifers; Volume II: Hardwoods. Agriculture Handbook Number 654, United States Department of Agriculture, Forest Service, Washington, D.C., USA.
- Burton, P. J., and S. G. Cumming. 1995. Potential effects of climatic change on some western Canadian forests, based on phenological enhancements to a patch model of forest succession. *Water, Air and Soil Pollution* **82**:401–414.
- Carter, K. K. 1996. Provenance tests as indicators of growth response to climate change in 10 north temperate tree species. *Canadian Journal of Forest Research* **26**:1089–1095.
- Christiansen, N. L. 1988. Vegetation of the southeastern Coastal Plain. Pages 317–363 in M. G. Barbour, and W. D. Billings, editors. *North American terrestrial vegetation*. Cambridge University Press, New York, New York, USA.
- Cumming, S. G. and P. J. Burton. 1996. Phenology-mediated effects of climatic change on some British Columbia forests. *Climatic Change* **34**:213–222.
- Dale, V. H., and M. Hemstrom. 1984. CLIMACS: a computer model of forest stand development for western Oregon and Washington. U.S. Forest Service Pacific Forest and Range Experiment Station Research Paper PNW-327.

- Daly, C., R. P. Neilson, and D. L. Phillips. 1994. A statistical-topographic model for mapping climatological precipitation over mountainous terrain. *Journal of Applied Meteorology* **33**:140–158.
- DeAngelis, D. L., R. H. Gardner, and H. H. Shugart. 1981. Productivity of forest ecosystems studied during IBP: the woodlands data set. Pages 567–672 in D. E. Reichle, editor. *Dynamic properties of forest ecosystems*. International Biological Programme Publication Number 23, Cambridge University Press, Cambridge, UK.
- Dexter, F., H. T. Banks, and T. Webb III. 1987. Modeling Holocene changes in the location and abundance of beech populations in eastern North America. *Review of Palaeobotany and Palynology* **50**:273–292.
- Dodson, R., and D. Marks. 1997. Daily air temperature interpolated at high spatial resolution over a large mountainous region. *Climate Research* **8**:1–20.
- Duvigneaud, P., and S. Denaeyer. 1984. Net primary productivity and mineral cycling in the main forest types and tree plantations in Belgium. Pages 357–375 in G. I. Agren, editor. *State and change of forest ecosystems*. Report Number 13, Swedish University of Agricultural Sciences, Uppsala, Sweden.
- Ellenberg, H. 1986. *Vegetation Mitteleuropas mit den Alpen in ökologischer Sicht*. Fourth edition. Verlag Eugen Ulmer, Stuttgart, Germany.
- Ellenberg, H., and F. Klötzli. 1972. Waldgesellschaften und Waldstandorte der Schweiz. *Mitteilungen der Eidgenössischen Anstalt für das forstliche Versuchswesen* **48**:587–930.
- Fischlin, A., H. Bugmann, and D. Gyalistras. 1995. Sensitivity of a forest ecosystem model to climate parametrization schemes. *Environmental Pollution* **87**:267–282.
- Franklin, J. F. 1988. Pacific Northwest forests. Pages 103–130 in M. G. Barbour, and W. D. Billings, editors. *North American terrestrial vegetation*. Cambridge University Press, New York, New York, USA.
- Franklin, J. F., and C. T. Dyrness. 1988. *Natural vegetation of Oregon and Washington*. Oregon State University Press, Corvallis, Oregon, USA.
- Friend, A. D., H. H. Shugart, and S. W. Running. 1993. A physiology-based gap model of forest dynamics. *Ecology* **74**:792–797.
- Friend, A. D., A. K. Stevens, R. G. Knox, and M. G. R. Cannell. 1997. A process-based, terrestrial biosphere model of ecosystem dynamics (HYBRID v3.0). *Ecological Modelling* **95**:249–287.
- Fritts, H. C. 1991. *Reconstructing large-scale climatic patterns from tree-ring data*. University of Arizona Press, Tucson, Arizona, USA.
- Garman, S. L., and A. J. Hansen. 1991. A preliminary analysis of the performance of ZELIG at three elevations in the Oregon Cascades. Report to the U.S. Environmental Protection Agency, Environmental Research Laboratory, Corvallis, Oregon, USA.
- Gholz, H. L. 1982. Environmental limits on aboveground net primary production, leaf area, and biomass in vegetation zones of the Pacific Northwest. *Ecology* **63**:469–481.
- Grier, C. C., and R. S. Logan. 1977. Old growth *Pseudotsuga menziesii* communities of a western Oregon watershed: biomass distribution and production budgets. *Ecological Monographs* **47**:373–400.
- Grinnell, J. 1924. Geography and evolution. *Ecology* **5**:225–229.
- Harlow, W. M., E. S. Harrar, and F. M. White. 1979. *Textbook of dendrology*. Sixth edition. McGraw-Hill, New York, New York, USA.
- Harmon, M. E., W. K. Ferrell, and J. F. Franklin. 1990. Effects on carbon storage of conversion of old-growth forests to young forests. *Science* **247**:699–702.
- Heinselman, M. L. 1973. Fire in the virgin forests of the Boundary Waters Canoe Area, Minnesota. *Quaternary Research* **3**:329–382.
- Hemstrom, M., and V. D. Adams. 1982. Modeling long-term forest succession in the Pacific Northwest. Pages 14–23 in J. E. Means, editor. *Forest succession and stand development research in the Northwest*. Forest Research Laboratory, Oregon State University, Corvallis, Oregon, USA.
- Hess, H. E., E. Landolt, and R. Hirzel. 1980. *Flora der Schweiz*. Second edition. Volumes 1–4. Birkhäuser, Basel, Switzerland.
- James, F. C., R. F. Johnston, N. O. Warmer, G. J. Niemi, and W. J. Broecklin. 1984. The Grinnellian niche of the wood thrush. *American Naturalist* **124**:17–47.
- Kercher, J. R., and M. C. Axelrod. 1984. A process model of fire ecology and succession in a mixed-conifer forest. *Ecology* **65**:1725–1742.
- Kienast, F. 1987. FORECE—A forest succession model for southern central Europe. ORNL/TM-10575, Oak Ridge National Laboratory, Oak Ridge, Tennessee, USA.
- Kirschbaum, M. U. F., A. Fischlin, M. G. R. Cannell, R. V. O. Cruz, W. Galinski, and W. Cramer. 1996. Climate change impacts on forests. Pages 95–129 in R. T. Watson et al., editors. *Climate change 1995—Impacts, adaptations and mitigation of climate change: scientific-technical analyses*. Contribution of Working Group II to the Second Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK.
- Kittel, T. G. F., N. A. Rosenbloom, T. H. Painter, D. S. Schmel, and VEMAP Modeling Participants. 1995. The VEMAP integrated database for modeling United States ecosystem/vegetation sensitivity to climate change. *Journal of Biogeography* **22**:857–862.
- Körner, C. 1988. A re-assessment of high elevation treeline positions and their explanation. *Oecologia* **115**:445–459.
- Korzukhin, M. D., A. E. Rubina, G. B. Bonan, A. M. Solomon, and M. Y. Antonovsky. 1989. The silvics of some east European and Siberian boreal forest tree species. WP-89-56, International Institute for Applied Systems Analysis, Laxenburg, Austria.
- Kramer, K., 1995. Phenology and growth of European trees in relation to climate change. Dissertation. Landbouw Universiteit, Wageningen, The Netherlands.
- Krausch, H.-D. 1992. Potentielle natürliche Vegetation. In *Ökologische Ressourcenplanung Berlin und Umland-Planungsgrundlagen*. Planning Group, Berlin, Germany.
- Küchler, A. W. 1975. Potential natural vegetation of the conterminous United States 1:3'168'000. *American Geographical Society Special Publication Number 36*.
- Larcher, W. 1995. *Physiological plant ecology*. Springer, Berlin, Germany.
- Lasch, P., and Lindner, M. 1995. Application of two forest succession models at sites in north east Germany. *Journal of Biogeography* **22**:485–492.
- Leemans, R. 1992. The biological component of the simulation model for boreal forest dynamics. Pages 428–445 in H. H. Shugart, R. Leemans, and G. B. Bonan, editors. *A systems analysis of the global boreal forest*. Cambridge University Press, Cambridge, UK.
- Leemans, R., and I. C. Prentice. 1989. FORSKA, a general forest succession model. Institute of Ecological Botany, Uppsala, Sweden.
- Leibundgut, H. 1993. *Europäische Urwälder—Wegweiser zur naturnahen Waldwirtschaft*. Haupt, Bern, Switzerland.
- Leverenz, L. W., and D. J. Lev. 1987. Effects of carbon dioxide-induced climate changes on the natural ranges of six major commercial tree species in the western United States. Pages 123–155 in W. E. Shands and J. S. Hoffmann, editors. *The greenhouse effect, climate change, and U.S.*

- Forests. The Conservation Foundation, Washington, D.C., USA.
- Lindner, M., H. Bugmann, P. Lasch, M. Flechsig, and W. Cramer. 1997. Regional impacts of climatic change on forests in the state of Brandenburg, Germany. *Agricultural and Forest Meteorology* **84**:123–135.
- Little, E. L., Jr. 1971. Atlas of United States trees. Volume 1. Conifers and important hardwoods. U.S. Forest Service Miscellaneous Publication Number 1146.
- Loehle, C., and D. LeBlanc. 1996. Model-based assessments of climate change effects on forests: a critical review. *Ecological Modelling* **90**:1–31.
- Maissurow, D. K. 1935. Fire as a necessary factor in the perpetuation of white pine. *Journal of Forestry* **33**:373–378.
- Melillo, J. M., I. C. Prentice, G. D. Farquhar, E.-D. Schulze, and O. E. Sala. 1996. Terrestrial biotic responses to environmental change and feedbacks to climate. Pages 445–481 in J. T. Houghton, L. G. Meira Filho, B. A. Callander, N. Harris, A. Kattenberg, and K. Maskell, editors. *Climate Change 1995—The science of climate change*. Contribution of Working Group I to the Second Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK.
- Monk, C. D., G. I. Child, and S. A. Nicholson. 1970. Biomass, litter and leaf surface area estimates of an oak–hickory forest. *Oikos* **21**:138–141.
- Moore, A. D. 1989. On the maximum growth equation used in forest gap simulation models. *Ecological Modelling* **45**:63–67.
- Neilson, R. P., G. A. King, and G. Koerper. 1992. Toward a rule-based biome model. *Landscape Ecology* **7**:27–43.
- Pacala, S. W., C. D. Canham, and J. A. Silander, Jr. 1993. Forest models defined by field measurements: I. The design of a northeastern forest simulator. *Canadian Journal of Forest Research* **23**:1980–1988.
- Pacala, S. W., and G. C. Hurtt. 1993. Terrestrial vegetation and climate change: integrating models and experiments. Pages 57–74 in P. M. Kareiva, J. G. Kingsolver, and R. B. Huey, editors. *Biotic interactions and global change*. Sinauer Associates, Sunderland, Massachusetts, USA.
- Pastor, J., and W. M. Post. 1985. Development of a linked forest productivity–soil process model. ORNL/TM-9519, United States Dept. of Energy, Washington, D.C., USA.
- Pastor, J., and W. M. Post. 1988. Response of northern forests to CO₂-induced climate change. *Nature* **334**:55–58.
- Power, M. 1993. The predictive validation of ecological and environmental models. *Ecological Modelling* **68**:33–50.
- Prentice, I. C., W. Cramer, S. P. Harrison, R. Leemans, R. A. Monserud, and A. M. Solomon. 1992. A global biome model based on plant physiology and dominance, soil properties and climate. *Journal of Biogeography* **19**:117–134.
- Prentice, I. C., and R. Leemans. 1990. Pattern and process and the dynamics of forest structure: a simulation approach. *Journal of Ecology* **78**:340–355.
- Prentice, I. C., M. T. Sykes, and W. Cramer. 1991. The possible dynamic response of northern forests to global warming. *Global Ecology and Biogeography Letters* **1**:129–135.
- Price, D. T., and M. J. Apps. 1996. Boreal forest responses to climate-change scenarios along an ecoclimatic transect in central Canada. *Climatic Change* **34**:179–190.
- Rowe, J. S. 1972. Forest regions of Canada. Department of the Environment, Canadian Forestry Service Publication Number 1300.
- Schenk, H. J. 1996. Modeling the effects of temperature on growth and persistence of tree species: a critical review of tree population models. *Ecological Modelling* **92**:1–32.
- Schweingruber, F. H., K. R. Briffa, and P. D. Jones. 1991. Yearly maps of summer temperatures in western Europe from A.D. 1750 to 1975 and western North America from 1600 to 1982. *Vegetatio* **92**:5–71.
- Shugart, H. H. 1984. A theory of forest dynamics. The ecological implications of forest succession models. Springer-Verlag, New York, New York, USA.
- Shugart, H. H. 1998. Terrestrial ecosystems in changing environments. Cambridge University Press, Cambridge, UK.
- Shugart, H. H., and I. R. Noble. 1981. A computer model of succession and fire response of the high-altitude *Eucalyptus* forest of the Brindabella Range, Australian Capital Territory. *Australian Journal of Ecology* **6**:149–164.
- Shugart, H. H., and D. C. West. 1977. Development of an Appalachian deciduous forest succession model and its application to assessment of the impact of the chestnut blight. *Journal of Environmental Management* **5**:161–179.
- Smith, T. M., editor. 1996. The application of patch models of vegetation dynamics to global change issues. *Climatic Change* **34**:131–313.
- Solomon, A. M. 1986. Transient response of forests to CO₂-induced climate change: simulation modeling experiments in eastern North America. *Oecologia* **68**:567–579.
- Solomon, A. M., and P. J. Bartlein. 1992. Past and future climate change: response by mixed deciduous–coniferous forest ecosystems in northern Michigan. *Canadian Journal of Forest Research* **22**:1727–1738.
- Solomon, A. M., N. H. Ravindranath, R. B. Stewart, M. Weber, and S. Nilsson. 1996. Wood production under changing climate and land use. Pages 487–510 in R. T. Watson, M. C. Zinyowera, and R. H. Moss, editors. *Climate Change 1995—Impacts, adaptations and mitigation of climate change: Scientific-technical analyses*. Contribution of Working Group II to the Second Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK.
- Solomon, A. M., M. L. Tharp, D. C. West, G. E. Taylor, J. W. Webb, and J. L. Trimble. 1984. Response of unmanaged forests to CO₂-induced climate change: available information, initial tests and data requirements. DOE/NBB-0053, National Technical Information Service, U.S. Department of Commerce, Springfield, Virginia, USA.
- Steyermark, J. A. 1940. Studies of the vegetation of Missouri, I: natural plant associations and succession in the Ozarks of Missouri. *Field Museum of Natural History Botanical Series* **9**:349–475.
- Swartzman, G. L., and S. P. Kaluzny. 1987. *Ecological simulation primer*. Macmillan, New York, New York, USA.
- Sykes, M. T., I. C. Prentice, and W. Cramer. 1996. A bioclimatic model for the potential distribution of north European tree species under present and future climates. *Journal of Biogeography* **23**:203–233.
- Urban, D. L., M. E. Harmon, and Ch. B. Halpern. 1993. Potential response of Pacific northwestern forests to climatic change, effects of stand age and initial composition. *Climatic Change* **23**:247–266.
- Walter, H., and S.-W. Breckle. 1991. *Ökologie der Erde, Volume 4. Spezielle Ökologie der Gemässigten und Arktischen Zonen ausserhalb Euro-Nordasiens*. UTB, Gustav Fischer Verlag, Stuttgart, Germany.
- Walter, H., and S.-W. Breckle. 1994. *Ökologie der Erde, Volume 3. Spezielle Ökologie der Gemässigten und Arktischen Zonen Euro-Nordasiens*. UTB, Gustav Fischer Verlag, Stuttgart, Germany.
- Waring, R. H., and J. F. Franklin. 1979. Evergreen coniferous forests of the Pacific Northwest. *Science* **204**:1380–1386.
- Waring, R. H., and W. H. Schlesinger. 1985. *Forest ecosystems: concepts and management*. Academic Press, London, UK.
- Watt, A. S. 1947. Pattern and process in the plant community. *Journal of Ecology* **35**:1–22.