

COMPARING THE PERFORMANCE OF FOREST GAP MODELS IN NORTH AMERICA

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Abstract. Forest gap models have a long history in the study of forest dynamics, including predicting long-term succession patterns and assessing the potential impacts of climate change and air pollution on forest structure and composition. In most applications, existing models are adapted for the specific question at hand and little effort is devoted to evaluating alternative formulations for key processes, although this has the potential to significantly influence model behavior. In the present study, we explore the implications of alternative formulations for selected ecological processes via the comparison of several gap models. Baseline predictions of forest biomass, composition and size structure generated by several gap models are compared to each other and to measured data at boreal and temperate sites in North America. The models FORCLIM and LINKAGES v2.0 were compared based on simulations of a temperate forest site in Tennessee, whereas FORSKA-2V, BOREALIS and FORCLIM were compared at four boreal forest sites in central and eastern Canada. Results for present-day conditions were evaluated on their success in predicting forest cover, species composition, total biomass and stand density, and allocation of biomass among species. In addition, the sensitivity of each model to climatic changes was investigated using a suite of six climate change scenarios involving temperature and precipitation. In the temperate forest simulations, both FORCLIM and LINKAGES v2.0 predicted mixed mesophytic forests dominated by oak species, which is expected for this region of Tennessee. The models differed in their predictions of species composition as well as with respect to the simulated rates of succession. Simulated forest dynamics under the changed climates were qualitatively similar between the two models, although aboveground biomass and species composition in FORCLIM was more sensitive to drought than in LINKAGES v2.0. Under a warmer climate, the modeled effects of temperature on tree growth in LINKAGES v2.0 led to the unrealistic loss of several key species. In the boreal forest simulations, FORCLIM predicted significant forest growth at only the most mesic site, and failed to predict a realistic species composition. In contrast, FORSKA-2V and BOREALIS were successful in simulating forest cover, general species composition, and biomass at most sites. In the climate change scenarios, FORCLIM was highly sensitive, whereas the other two models exhibited sensitivity only at the drier central Canadian sites. Although the studied sites differ strongly with respect to both the climatic regime and the set of dominating species, a unifying feature emerged from these simulation exercises. The major differences in model behavior were brought about by differences in the internal representations of the seasonal water balance, and they point to an important limitation in some gap model formulations for assessing climate change impacts.



1. Introduction

The application of forest gap models to study long-term forest dynamics has a long tradition in North America, where these models originated (Botkin et al., 1972; cf., Bugmann, 2001a). Questions addressed in such studies include forest succession under current climatic conditions (e.g., Botkin et al., 1972; Shugart and West, 1977; Bormann and Likens, 1979), the impacts of possible future temperature and precipitation patterns on forest structure and composition (e.g., Solomon, 1986; Pastor and Post, 1988; Dale and Franklin, 1989; Urban et al., 1993), the direct effects of CO₂ (e.g., Botkin et al., 1973; Shugart and Emanuel, 1985), and pollution problems (e.g., Kercher and Axelrod, 1984; Shugart and McLaughlin, 1985). Typically, in these studies an existing model has been adapted for the specific question at hand. Little effort has been devoted to the quantitative evaluation of alternative formulations for different ecological processes, although such alternative formulations have the potential to significantly influence model behavior (cf., Bugmann et al., 1996).

A full structural sensitivity analysis of ecological models, i.e., fully quantifying the influence of alternative process formulations on model behavior, would require a systematic and factorial approach, where individual formulations are changed in one specific model, one at a time. Model behavior would need to be analyzed under all possible combinations of process formulations. In the case of forest gap models, which are rather complex and incorporate many different processes, such an approach is hardly feasible. A more pragmatic but still quite informative approach is to compare the predictions from different models that have been developed for different sites and/or different research questions under a standardized set of site conditions (climate, soils, etc.). Differences in model behavior can be tracked down to individual ecological processes, whose formulations can then be evaluated and assessed.

In the present study, the behavior of several gap models is examined at four sites in the Canadian boreal zone and at a temperate forest site in Tennessee. Simulated forest structure and species composition under current climate are compared to independent data from the test sites to assess the capability of the models to reproduce present-day vegetation. The factors responsible for differences in model behavior are analyzed, and the different model formulations employed are critically evaluated. Then, simulations of the responses of forest composition and structure to hypothetical long-term climate changes are performed to evaluate and compare model behavior and sensitivity to conditions different from those prevailing today. In our analysis, we did not consider the effects of fertilization by enhanced atmospheric CO₂ because little is known regarding these effects on adult trees, and because in most gap models it is difficult to incorporate CO₂ effects mechanistically (cf., Bugmann, 2001a; Norby et al., 2001).

Initially, our intention was to include many different models and test sites in the exercise, because an increased diversity of models and environmental conditions

increases the likelihood of divergent model behavior. Thus, we identified more than half a dozen models for comparisons at up to 10 test sites. However, several models were either too complex to be transferred to new sites without significant research efforts – this included SORTIE (Pacala et al., 1993, 1996) and FIRE-BGC (Keane et al., 1996) – or the researchers felt that the model structure was not suitable for application to test sites in climatic regions different from the ones for which the model was developed – this included LINKAGES v2.0 (Wullschleger et al., *unpublished*), FORSKA-2V (Price et al., 1999a), and BOREALIS (Clark, 2001). Hence, only a much reduced set of simulation exercises was possible in the present study. The models FORCLIM and LINKAGES v2.0 were used in the temperate forest simulations, whereas FORSKA-2V, BOREALIS and FORCLIM were compared at the four boreal sites. Baseline predictions of forest biomass, species composition and size structure generated by each model were compared to one another and, where possible, to measured data.

The objectives of this paper are:

1. to elucidate the model-specific causes of (i) divergences between model behavior and measured data under current climatic conditions, and (ii) divergences in the sensitivity of different models to altered temperature and precipitation regimes;
2. to use this understanding to identify priorities for further research on the processes that prove to be sensitive in gap models, thus contributing to better assessments of how forest structure and composition may respond to future climate change.

2. Material and Methods

2.1. FOREST MODELS

A comparison of the four forest gap models used in this study is given in Table I, and summary descriptions are presented below.

2.1.1. FORSKA-2V

FORSKA-2V is based on the FORSKA-2 model (Prentice et al., 1993), and was developed to investigate the effects of changing temperature and precipitation on boreal forests in central Canada (Price et al., 1999a). These forests extend across a broad ecoclimatic gradient where low temperatures are generally considered limiting to tree growth in the north, whereas low rainfall and high evapotranspiration (ET) cause soil moisture limitations in the south (e.g., Hogg, 1994; Hogg and Hurdle, 1995). Simulating forest dynamics along this gradient required (1) accounting for interannual variability of temperature and precipitation, a factor not considered in FORSKA-2, and (2) improving the water balance submodel. Earlier studies

Table I

A comparison of features of the four gap models used in the present study. For a detailed description and discussion of the features (see Bugmann, 2001a). Categories printed in *italics* in the leftmost column are those where the models differ. V = tree volume; LA = leaf area; H_{bole} = bole height

	LINKAGES v2.0	FORCLIM	FORSKA-2V	BOREALIS
a) Basic assumptions				
<i>Vertical structure</i>	Disk	Disk	Cylinder	Cylinder
Horizontal structure (within patch)	Homogeneous	Homogeneous	Homogeneous	Homogeneous
Neighborhood relationship (between patches)	None	None	None	None
<i>Entities being modeled</i>	Individual	Cohort	Individual	Individual
<i>Links structure and function</i>	Yes (H ₂ O only)	No	No	No
Multiple life forms?	No	No	No	No
<i>Time step</i> (<i>growth/bioclimate</i>)	Annual/daily water balance	Annual/monthly bioclimate	Annual/quasi- daily water bal	Bi-annual/quasi- daily water bal
b) Establishment				
Unlimited seed availability	Yes	Yes	Yes	Yes
Winter temperature	Yes	Yes	Yes	Yes
Spring/fall frosts	No	No	No	No
Soil moisture	Yes	Yes	Yes	Yes
Temperature sum	Yes	Yes	Yes	Yes
<i>Herbivory</i>	Yes	Ungulates	No	Spruce budworm
Min light	Yes	Yes	Yes	Yes
Max light	No	Yes	No	No
c) Growth: General approach				
<i>State variable(s)</i>	DBH	DBH	V, LA, H _{bole}	V, LA, H _{bole}
<i>Production</i>	Net growth (DBH)	Net growth (DBH)	Phenomenological	Phenomenological
Allocation	Allometric	Allometric	Allometric	Allometric
Competition	Light	Light	Light	Light
<i>Soil C/N turnover</i>	Yes	Yes	No	No
d) Growth: Environmental influences				
<i>Light</i>	JABOWA	JABOWA	Phenomenol.	Phenomenol.
<i>Nitrogen</i>	Aber	Aber	No	No
<i>Temperature</i> (<i>GDD = annual sum of</i> <i>growing degree-days</i>)	Parabolic GDD	Asymptotic GDD	GDD min only (threshold)	GDD min only (threshold)
<i>Soil moisture</i>	'Drought days' linked to stomatal behavior	AET/PET-type drought index	Energy balance driven water balance	Orig FORSKA (Cramer and Prentice)
<i>CO₂</i>	No	No	No	Yes
<i>Combination</i> (<i>Factors A,B,C,D</i>)	MIN(A,B,C,D) (Liebig)	$\sqrt[3]{(A \cdot B \cdot C \cdot D)}$	A · B · C · D	A · B · C · D
e) Mortality				
Constant with age	Yes (max tree age)	Yes (max tree age)	Yes (shade tol)	Yes (shade tol)
<i>Stress mortality</i>	Relative DBH	Relative DBH	Growth	Growth
<i>Stress mortality</i>	Increment	Increment	Efficiency	Efficiency
<i>Extrinsic disturbances</i>	Not treated	Generic	Generic	Fire, insects

with FORSKA-2 that were based on long-term monthly means of temperature and precipitation (e.g., Price and Apps, 1996) resulted in overestimated annual evapotranspiration (ET), causing unrealistic soil water deficits and reduced growth. In the water balance submodel developed for FORSKA-2V, ET is simulated using the Priestley and Taylor (1972) formulation, with the alpha coefficient being a linear function of the simulated soil water content. In this way, decreased soil water content implicitly reduces canopy conductance, which causes the simulated ecosystem to conserve soil water at sites with low annual rainfall. This modification results in more realistic annual trends in soil water content, and hence more realistic forest growth.

For the present study, FORSKA-2V was further modified to allow an increase in sapling recruitment following disturbance. Black spruce (*Picea mariana*) and jack pine (*Pinus banksiana*), two major species in the North American boreal zone, often regenerate prolifically because of cone serotiny following fire, while aspen typically resprouts from stumps of trees that have died back due to fire, drought or insect defoliation. To take this into account in the model, the regeneration rates of all species were increased by a factor of 50 in the first year after a disturbance. This modification was found to improve agreement between modeled and observed time-series of biomass and stem density in central Canada (Price et al., 1999a). The disturbance submodel in FORSKA-2V is generic (Prentice et al., 1993), but in the present context it mainly concerns fire.

2.1.2. BOREALIS

BOREALIS (Clark, 2001) is also based on FORSKA-2, but in contrast to FORSKA-2V, it retains the soil water balance submodel of the original FORSKA-2 and uses the long-term averages of temperature and precipitation as abiotic drivers. However, BOREALIS differs from FORSKA-2 and FORSKA-2V in two ways. First, it has specific growth chilling requirements as described by Sykes and Prentice (1995, 1996); second, it incorporates large-scale disturbance routines, such as pest infestations and wildfires, as sources of tree mortality. Most other derivatives of the original FORSKA-2 model (including FORSKA-2V) share a common method of simulating the disturbance regime. This method is based on a Weibull function to determine the probability that individual forest patches are re-initialized to bare ground, either in a random fashion or with an increasing age bias (i.e., older stands are more susceptible to disturbance). BOREALIS, however, was specifically adapted to better capture forest disturbance dynamics. The forest insect routines are based on empirical data for spruce budworm (Morin et al., 1993; Morin 1994; Bergeron et al., 1995; Bergeron and Leduc, 1997). Simulations in the present study were run without the spruce budworm effects, however, so that the results could be compared directly to those of the other models. The fire regime is modeled using the number of fires and fire size. The simulated number of fires per year is based on observed data, and follows a Poisson distribution with the mean equal to 1. The fire size follows a negative exponential distribution with the mean fire size equal to

1% of the entire landscape. Therefore, both the number of fires and their sizes are randomly selected from these two distributions. The default average fire return time is 100 years and was not modified in any of the simulation experiments described here.

2.1.3. *LINKAGES v2.0*

LINKAGES v2.0 (S. Wullschleger et al., *unpublished*) is derived from *LINKAGES* (Pastor and Post, 1985) to study the effects of climate change (i.e., temperature and precipitation) and inter- and intra-annual variations in climate on long-term forest dynamics. *LINKAGES v2.0* was modified to incorporate a more physiology-based representation of plant and soil controls on potential and actual evapotranspiration over that found in *LINKAGES*. Modifications include replacing the Thornthwaite and Mather (1957) monthly calculation of potential evapotranspiration with a daily two-layer scheme in which evaporation from the soil surface and canopy are treated separately (Shuttleworth and Wallace, 1985). A maximum leaf conductance to water vapor is specified for the stand and modified according to daily radiation, temperature, vapor pressure deficit and extractable soil water. Fractional drought days are calculated according to extractable soil water, in an approach similar to Prentice et al. (1993). *LINKAGES v2.0* retains all other components of the original *LINKAGES* model, which was based on the individual tree model *FORET* (Shugart and West, 1977). Particularly, *LINKAGES v2.0* incorporates litter production, decomposition and associated nitrogen dynamics similar to those in the *FORTNITE* model (Aber and Melillo, 1982). To date, *LINKAGES v2.0* has been tested only at the temperate forest site in Tennessee where it was developed.

2.1.4. *FORCLIM*

The version of *FORCLIM* used here is modified from *FORCLIM V2.9* (Bugmann and Solomon, 2000), which was also derived from *LINKAGES*. *FORCLIM* was originally developed to assess the impacts of climatic changes on tree species composition and biomass storage for forests in the Swiss Alps (Bugmann 1994, 1997a,b). However, the apparent structural similarity of many gap models led to the question whether *FORCLIM* might also be used in different regions. The first application was made along an extended climate gradient in eastern North America (cf., Solomon, 1986), where *FORCLIM* was found to replicate the dynamics, composition and biomass of a wide range of forests (Bugmann and Solomon, 1995). However, in other regions, the applicability of the model was found to be weak, particularly along drought gradients in central Europe and southeastern North America (Bugmann and Solomon, 1995; Bugmann, 1996). These weaknesses led to improvements in the soil moisture and drought response submodels (Bugmann and Cramer, 1998; Lindner et al., 1997). Further modifications regarding the effects of precipitation seasonality were introduced in *FORCLIM* based on a study of forests in the Pacific Northwest of the US (Bugmann and Solomon, 2000). The most recent

applications of the model include mountain forests in northeastern China (Shao et al., 2001) and in the Rocky Mountains (Bugmann, 2001b).

2.1.5. *Comparison of Model Structures*

A comparative analysis of the differences and similarities between the various models is given in Table I. Based on their ancestry, the four models segregate into two classes. The FORSKA-based models (BOREALIS, FORSKA-2V) use a cylindrical crown geometry, a phenomenological production model, and do not consider belowground processes, other than water availability; both include fire as a major large-scale disturbance, albeit based on different approaches. The LINKAGES-based models (LINKAGES v2.0, FORCLIM) use a disk crown geometry and a model for maximum diameter growth similar to the one in JABOWA (Botkin et al., 1972); both include belowground carbon and nitrogen dynamics, although this submodel was not used in the simulations conducted with FORCLIM; large-scale disturbances are not considered in the LINKAGES-based models.

The structural differences between the two model classes relate primarily to the growth-limiting processes (cf., Bugmann, 2001a). While temperature effects are modeled in the same manner in the two FORSKA descendants, LINKAGES v2.0 and FORCLIM differ significantly insofar as LINKAGES v2.0 retains the degree-day parabola introduced in JABOWA, whereas FORCLIM adopts an asymptotic approach that does not rely on maximum degree-day sums (cf., Bugmann and Solomon, 2000). Similarly, the combination of growth-limiting factors is handled the same in the FORSKA-based models, whereas different approaches are used in LINKAGES v2.0 and FORCLIM. With respect to the treatment of water availability, all four models differ in their approach. In BOREALIS, the original FORSKA submodel is adopted; in FORCLIM, an improved but still very simple bucket model with a monthly time step is used (Bugmann and Cramer, 1998). In LINKAGES v2.0, a parameterization for the stomatal control on transpiration and a daily time step is introduced, while retaining other elements of the original formulation (Pastor and Post, 1985). The approach in FORSKA-2V is similar to that of LINKAGES v2.0, in that stomatal feedbacks to evapotranspiration are represented. Based on these structural differences, one would expect that the models differ primarily in their projections with respect to the effects of temperature and drought on forest succession as mediated by tree growth and competition, and less so through establishment and mortality processes.

2.2. STUDY SITES

2.2.1. Temperate Forests

The behavior of LINKAGES v2.0 and FORCLIM was compared based on data from the Walker Branch Watershed (cf., Table II), a part of the U.S. Department of Energy's National Environmental Research Park near Oak Ridge, Tennessee (Johnson and Van Hook, 1989). According to Küchler (1975), the site's *steady-state* natural vegetation is mixed mesophytic forest, with dominance by white and red oak (*Quercus alba*, *Q. rubra*), yellow-poplar (*Liriodendron tulipifera*), sugar maple (*Acer saccharum*), American beech (*Fagus grandifolia*), basswood (*Tilia heterophylla*), and many co-dominant deciduous species (for a list of scientific and common names, cf., Table III). All land on what is today Walker Branch Watershed was abandoned in 1942 (Lafon et al., 2000). Thus, trees in the current forest vary in age from 40 to 70 years, and stands are largely dominated by chestnut oak (*Quercus prinus*), white oak, and red maple (*Acer rubrum*). Basal area ranges from 18.8 to 26.3 m² ha⁻¹ with a total stem density (>10 cm DBH) between 369 and 741 stem ha⁻¹ (Lafon et al., 2000).

A series of 306 permanent inventory plots was established on Walker Branch Watershed during the mid-1960s (Curlin and Nelson, 1968). Each plot consisted of four concentric circular areas, which permits sampling of the various tree diameter classes with approximately the same precision. Every four to seven years, these plots are re-inventoried and the diameter of each tree in the plot is recorded. The most recent inventory was in 1997 (M.A. Huston, *personal communication*). These permanent plot records, together with other published data from the Walker Branch Watershed (Johnson and Van Hook, 1989; Hanson et al., 1998; Lafon et al., 2000) were used to derive validation data sets with respect to species composition, aboveground biomass, total basal area, stem density, and other structural characteristics.

Data from other research plots in Walker Branch Watershed were used to calibrate the species-specific establishment rates in LINKAGES v2.0. Hence, a certain amount of 'tuning' was used to match observed forest properties. In contrast, FORCLIM was not calibrated for the present application. Its species-specific parameter values were derived from literature data (cf., Bugmann and Solomon, 1995), and its application to the Walker Branch site thus constitutes a test of the performance of this generic forest simulator in a site-specific study. Daily climate records for Walker Branch Watershed compiled for the period 1973 through 1998 were used as the baseline climate (Table II). Data included daily minimum and maximum temperature, solar radiation, wind speed and precipitation. From these data, estimates of daily mean temperature and vapor pressure deficit were derived and subsequently used as climatic input for LINKAGES v2.0. For FORCLIM, which requires inputs of monthly average temperature and monthly total precipitation, these variables were generated by aggregation from the daily data set.

Table II

Overview of the location, climatic data, basic soil properties and disturbance regimes of the study sites. Mean annual temperature, precipitation and estimated potential evapotranspiration (PET) at the four boreal sites were derived from Canadian Meteorological Service climate normals (from Environment Canada 1961–1990 and Price and Apps, 1995, 1996). Climatic data at Walker Branch watershed are unpublished on-site measurements for the period 1973–1998. Disturbance intervals, soil field capacity and wilting point values are estimates based on local field observations

Climate station	Temperate Forest		Boreal Forest Transect Case Study				Lac Duparquet	
	Walker Branch		Prince Albert	Thompson	Waskesiu	La Sarre		
Latitude	[°N]	36.0	53.22	55.80	53.92	48.70		
Longitude	[°W]	84.25	105.68	97.87	106.08	78.10		
Temperature	[°C]	14.4	0.1	-3.9	-0.2	0.1		
Precipitation	[mm]	1348	398	544	464	857		
Est. Annual PET	[mm]	N/A	444	295	385	385		
Field capacity	[mm]	250	150	300	250	170		
Wilting point	[mm]	100	50	100	100	100		
Disturbance interv.	[yr]	N/A	100	100	100	100		

Table III
Tree species used at the temperate study site

Latin name	Common name
<i>Acer rubrum</i>	Red maple
<i>Acer saccharum</i>	Sugar maple
<i>Carya glabra</i>	Pignut hickory
<i>Cornus florida</i>	Flowering dogwood
<i>Fagus grandifolia</i>	American beech
<i>Fraxinus americana</i>	American ash
<i>Juniperus virginiana</i>	Eastern redcedar
<i>Liriodendron tulipifera</i>	Yellow-poplar
<i>Nyssa sylvatica</i>	Black gum
<i>Pinus echinata</i>	Shortleaf pine
<i>Pinus virginiana</i>	Scrun pine
<i>Prunus serotina</i>	Black cherry
<i>Quercus alba</i>	White oak
<i>Quercus coccinea</i>	Scarlet oak
<i>Quercus falcata</i>	Southern red oak
<i>Quercus prinus</i>	Chestnut oak
<i>Quercus rubra</i>	Red oak
<i>Quercus stellata</i>	Post oak
<i>Quercus velutina</i>	Black oak
<i>Diospyros virginiana</i>	Common persimmon
<i>Oxydendron arboreum</i>	Sourwood
<i>Sassafras albidum</i>	Sassafras

2.2.2. Boreal Forests

Four boreal sites were investigated in this study (Table II). The first, Lac Duparquet, is located in the Missinaibi-Cabonga section of Northwestern Québec (Rowe, 1972). Climate data available for this site are from the La Sarre meteorological station, ca. 42 km north of Lac Duparquet (Table II). The research forest at Lac Duparquet is located at the southern limit of the boreal forest (Rowe, 1972), and the 10 tree species in Table IV characterize the area. In this region, the dominant species are typically balsam fir (*Abies balsamea*), black spruce (*Picea mariana*), white spruce (*P. glauca*), paper birch (*Betula papyrifera*), and trembling aspen (*Populus tremuloides*). Jack pine (*Pinus banksiana*) may be present at some sites, and where fire has not occurred for long periods, eastern white cedar (*Thuja occidentalis*) may be abundant (Bergeron and Dubuc, 1989). Early successional tree species can persist in low abundances in some stands until 200 years after fire. Mesic sites

Table IV

Tree species used at the four boreal study sites. 'Code' is the species code that is used in Table VII

Latin name	Code	Common name
<i>Abies balsamea</i> (L.) Mill.	ABBA	Balsam fir
<i>Betula papyrifera</i> Marsh	BEPA	White birch; paper birch
<i>Larix laricina</i> (Du Roi) K. Koch	LALA	Tamarack; larch
<i>Picea glauca</i> (Moench) Voss.	PIGL	White spruce
<i>Picea mariana</i> (Mill.) B.S.P.	PIMA	Black spruce
<i>Pinus banksiana</i> Lamb.	PIBA	Jack pine
<i>Pinus strobus</i> L.	PIST	Eastern white pine
<i>Populus balsamifera</i> L.	POBA	Balsam poplar; black poplar
<i>Populus tremuloides</i> Michx.	POTR	Trembling aspen; white poplar
<i>Thuja occidentalis</i> L.	THOC	Eastern white cedar

are most common in this study area, where aspen, paper birch or white spruce dominate in early successional stands. In older (>150 years) stands, balsam fir and cedar typically dominate (Bergeron and Dubuc, 1989).

The other three sites are located in central Canada. The most northerly is Thompson in Manitoba (Table II), where organic soils are common and the dominant species is black spruce. Occasional outcrops of mineral material carry aspen and/or jack pine (*Pinus banksiana*), depending on texture. The two southerly sites are located in Saskatchewan, one at Waskesiu Lake where there are some very productive stands, and the other at Prince Albert, about 70 km further south, at the edge of the prairie-forest transition. At Waskesiu Lake, most North American boreal species are present; black spruce and aspen dominate, and jack pine and white spruce are common. In the Prince Albert region, soils are predominantly freely-draining and seasonal water deficits are common. Hence, tree species adapted to drier conditions predominate, notably jack pine and aspen, although even here, low-elevation peatland sites favor black spruce and tamarack larch (*Larix laricina*).

From the data shown in Table II, the boreal sites can be broadly classified as 'cold-wet' (Thompson), 'warm-wet' (Waskesiu Lake), 'warm-very wet' (Lac Duparquet) and 'warm-dry' (Prince Albert). While mean annual precipitation is similar across the three western sites, dissimilar potential evapotranspiration results in divergent annual moisture deficits (Table II). The Prince Albert climate station is located on the northern edge of the prairie-forest transition rather than in the forested region where field data were collected. Accordingly, the observed climate is subject to strong advective influences from the drier prairie region, and thus greater annual moisture deficits. Annual precipitation at La Sarre is considerably

Table V

Changes of long-term average climatic parameters (annual mean temperature and annual precipitation sum) that were used to define six hypothetical climate scenarios in the present study

Scenario	Temperature (°C)	Precipitation change (%)	Code
0 (baseline)	0	0	0.0 + 0.0
1 (+1.5°, 0%)	+1.5	0	1.5 + 0.0
2 (+1.5°, -20%)	+1.5	-20	1.5 - 0.2
3 (+1.5°, +20%)	+1.5	+20	1.5 + 0.2
4 (+3.0°, 0%)	+3.0	0	3.0 + 0.0
5 (+3.0°, -20%)	+3.0	-20	3.0 - 0.2
6 (+3.0°, +20%)	+3.0	+20	3.0 + 0.2

higher than at any of the western sites due to its proximity to the Great Lakes, and water deficits are comparatively rare.

BOREALIS was calibrated for the Lac Duparquet site, and had not been previously applied elsewhere. FORSKA-2V was calibrated for central Canadian sites, and had not previously been applied at Lac Duparquet. Prior to this study, FORCLIM had not been applied at any of the four boreal sites described here, although it had previously been used to simulate other boreal forests in eastern Canada (Bugmann and Solomon, 1995).

2.3. SIMULATION EXPERIMENTS

A review of the methodology used in simulation studies with gap models can be found in Bugmann (2001a). The simulations for the present study were set up as follows:

First, we wanted to examine the simulated successional dynamics under the current climate for a period long enough to allow a climate-forest equilibrium to establish. To this end, the simulations were started from bare ground (cf., Bugmann, 2001a), and a simulation period of 600 years (cf., Solomon, 1986) was chosen. For this part of the simulation experiment, a hypothetical 'current climate' was generated by repeatedly looping through the time series of weather data described above, with the long-term averages given in Table II.

Next, the transition from the current climate to a hypothetical new climate was simulated between the simulation years 601 and 700. During this period, a linear change of temperature and precipitation means was employed to reach a new, constant average climate in the simulation year 700, as defined in Table V. Six climate change scenarios were used (Table V), which are identical to those in the

studies by Badeck et al. (2001) and Shao et al. (2001). These scenarios must not be considered as realistic predictions of anthropogenic changes of regional climates during the 21st century. Moreover, the purpose of these scenarios is not to make inferences about the potential responses of forests at the study sites to future anthropogenic climate change. Rather, they span a range of plausible climatic shifts for the sole purpose of assessing the sensitivity of the models to changes in climatic parameters.

Finally, the relaxation time of forest dynamics and the development of a new climate-forest equilibrium were studied under the changed climate. This was achieved by simulating forest dynamics under the new climate (Table V) from the simulation years 701 to 1200. Under this new climate, the monthly averages of temperature and precipitation were shifted by the degrees and percentages given in Table V, but the interannual variability was not altered relative to the current climate.

At the Tennessee site, where only FORCLIM and LINKAGES v2.0 were tested, the species pool under both the current and future climate scenarios was restricted to the 22 tree species present in the permanent inventory plots (Table III). Forest structure and composition as simulated for the year 50 of the succession were compared quantitatively with the measured data from the permanent plots on Walker Branch Watershed. The simulated equilibrium species composition under the current climate was compared qualitatively with the forest description of Küchler (1975).

At the boreal sites, FORSKA-2V, BOREALIS, and FORCLIM were run with the set of 10 species given in Table IV. In FORSKA-2V and BOREALIS, a disturbance regime as specified in Table II was used. As a consequence, the simulation results presented below for individual sites actually represent a landscape-scale average of forest properties (cf., Prentice et al., 1993), and not the simulated average development at the stand scale. The average stand age for the BOREALIS simulation results is approximately 70 years, assuming a negative exponential age-class distribution with a 100-year mean disturbance interval (Table II). For the FORSKA-2V results, the average stand age is approximately 83 years because a Weibull function was used to generate the disturbance events, using a shape parameter of 2 as well as a 100-year return interval. In FORCLIM, however, large-scale disturbances are not considered (Table I), and the FORCLIM simulation results thus reflect the average development across time at the stand scale. For Lac Duparquet, simulation results were compared to forest inventory data. These data were obtained from an archive compiled over the past 3 decades from extensive research on the vegetation dynamics in the 8045 ha 'Forêt d'enseignement et de recherche du Lac Duparquet' (cf., De Grandpré et al., 1993; Bergeron and Charron, 1994; Gauthier et al., 1996a,b; Kneeshaw and Bergeron, 1996, 1998; Kneeshaw et al., 1998; Bergeron, 2000). These data were summarized and used for comparison with model output.

For the three western boreal sites, simulation results were compared to data from the reports of Halliwell and Apps (1997a,b). These data were obtained at 53

temporary sample plots installed as part of the BOREAS experiment (Sellers et al., 1995). From these data, biomass and stem density were summarized for groups of plots that are located in close proximity to the three climate stations. Simulations of biomass and stem density were compared quantitatively to these data, while simulated species compositions were compared qualitatively to summaries of the dominant species reported in each group of sample plots.

All simulations with all models were repeated 200 times at each site. Results presented below are the averages of these 200 runs, corresponding to the 'shifting mosaic steady-state' of the forest (cf., Bormann and Likens, 1979; Shugart, 1984; Bugmann, 2001a).

3. Results

3.1. TEMPERATE FORESTS

3.1.1. *Vegetation under the Current Climate*

The early successional dynamics (first 300 simulation years) as projected by the two models differed in a couple of key attributes. Total biomass was simulated to reach a peak of 235 t ha^{-1} at ≈ 175 years in LINKAGES v2.0, whereas FORCLIM predicted no early successional peak (Figure 1). Also, the major early successional species that subsequently disappeared (from the simulated stand) were yellow-poplar, shortleaf pine (*Pinus echinata*) and red maple in LINKAGES v2.0, whereas they were shortleaf pine, yellow-poplar and black cherry (*Prunus serotina*) in FORCLIM (Figure 1).

LINKAGES v2.0 simulated realistic species composition during early succession, with 50-year-old stands dominated by yellow-poplar (28.1%), chestnut oak (17.8%), white oak (12.4%), and red maple (9.2%), totaling 67.5% of simulated basal area. The same species were most abundant in the field data, accounting for 75% of total basal area. In FORCLIM, where the stand is much more open at age 50, 12 of the 22 species were present with more than 5% of aboveground biomass. The two most abundant species were black cherry (12.2%) and yellow-poplar (10.5%); white oak and chestnut oak attained 7.2% and 5.9% of aboveground biomass. These simulated patterns are broadly representative of the species composition at Walker Branch Watershed (Lafon et al., 2000), but measured stem density ($1466 \text{ stem ha}^{-1}$; M.A. Huston, *personal communication*, 1999) was different from that simulated by LINKAGES v2.0 ($2123 \text{ stem ha}^{-1}$) and FORCLIM ($1121 \text{ stems ha}^{-1}$). Nonetheless, the frequency distribution of size classes in the permanent plots was similar to that projected by LINKAGES v2.0 (Figure 2). There was a tendency in LINKAGES v2.0 to underestimate the proportion of stems less than 5 cm in diameter, and to overestimate the relative contribution of stems 15 to 20 cm in diameter. FORCLIM clearly overestimated the proportion of stems in the smallest diameter class (Figure 2).

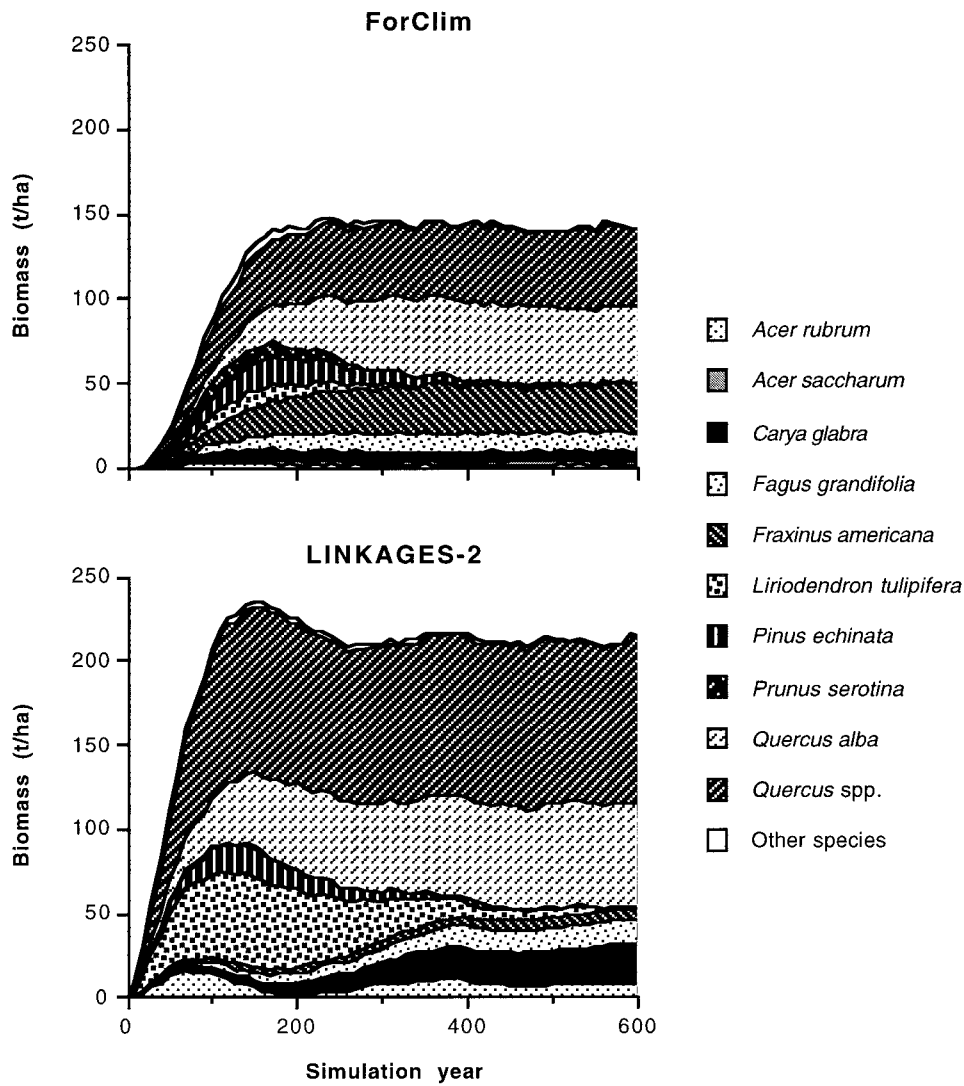


Figure 1. Simulated succession at Walker Branch Watershed under current climate, based on the 22 tree species that occur in the area.

At 50 simulation years, predicted aboveground biomass (cf., Figure 1) did not agree with measured data at Walker Branch Watershed. Model results averaged 110 t ha^{-1} in LINKAGES v2.0 and only 37 t ha^{-1} in FORCLIM, while measured biomass amounts to 164 t ha^{-1} (Johnson and Van Hook, 1989). Thus, both models underestimated the rate of colonization in mixed mesophytic secondary forest succession, but to varying degrees (cf., Figures 1 and 2). This led to differences in basal area at 50 simulation years, with $25 \text{ m}^2 \text{ ha}^{-1}$ in LINKAGES v2.0, compared to a mere $5.2 \text{ m}^2 \text{ ha}^{-1}$ in FORCLIM. Still, the LINKAGES v2.0 projections are

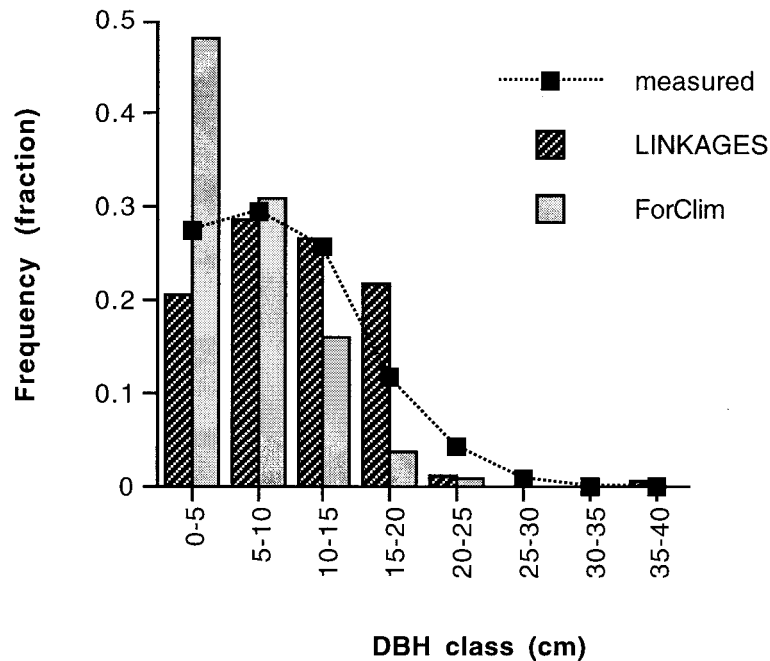


Figure 2. Frequency distribution of diameter size classes for a 50-year-old stand as measured on 64 inventory plots on Walker Branch Watershed, and as simulated by LINKAGES v2.0 and FORCLIM.

within the 18.8 to 26.3 $\text{m}^2 \text{ha}^{-1}$ range reported for 50-year-old stands at the study site (Lafon et al., 2000), whereas the FORCLIM projections are clearly too low.

Conversely, the simulation results from the two models were similar in their late successional trends (Figure 1). LINKAGES v2.0 produced stands dominated by oaks (white > red > chestnut > black > scarlet), and lower amounts of hickory and beech. The equilibrium species composition simulated by FORCLIM after 600 years was also dominated by oaks (white > black > chestnut > scarlet), and lower amounts of beech, hickory, and American ash. The various oak species accounted for 75% and 65% of the total equilibrium biomass in LINKAGES v2.0 and FORCLIM, respectively. The prevalence of these species in the two models is consistent with descriptions of the composition of mixed mesophytic forests (Küchler, 1975), although the large amount of American ash projected by FORCLIM is not supported by Küchler (1975).

Estimates of total aboveground biomass simulated by the models after 600 years of succession under current climate differed considerably, with LINKAGES v2.0 projecting 210 t ha^{-1} and FORCLIM projecting 145 t ha^{-1} . These biomass differences are paralleled by differences in the estimates of total basal area at the end of the 600-year simulation, which was 32 $\text{m}^2 \text{ha}^{-1}$ in LINKAGES v2.0 compared to 23 $\text{m}^2 \text{ha}^{-1}$ in FORCLIM. Unfortunately, measured biomass and basal area

Table VI

Estimates of biomass, basal area and stem density under various temperature and precipitation regimes as simulated by LINKAGES v2.0 for the Walker Branch Watershed study site. Data are the average of 200 replicate plots and values are representative for the end of the 1200 year simulation. Values in parentheses are the percent changes in biomass and stem density relative to the baseline scenario

Scenario	LINKAGES v2.0		FORCLIM	
	Biomass (t ha ⁻¹)	Stem density (ha ⁻¹)	Biomass (t ha ⁻¹)	Stem density (ha ⁻¹)
0 (baseline)	213	1318	142	1160
1 (+1.5°, 0%)	202 (-5.2%)	1424 (+8.0%)	97 (-31.7%)	975 (-15.9%)
2 (+1.5°, -20%)	130 (-39.0%)	1613 (+22.4%)	45 (-68.3%)	777 (-33.0%)
3 (+1.5°, +20%)	211 (-0.9%)	1423 (+8.0%)	153 (+7.7%)	1190 (+2.6%)
4 (+3.0°, 0%)	136 (-36.2%)	1618 (+22.8%)	69 (-51.4%)	925 (-20.3%)
5 (+3.0°, -20%)	74 (-65.3%)	1698 (+28.8%)	24 (-83.1%)	466 (-59.8%)
6 (+3.0°, +20%)	208 (-2.3%)	1443 (+9.5%)	127 (-10.6%)	1040 (-10.3%)

data for comparable old-growth forests are not available to evaluate these model projections.

3.1.2. *Vegetation under the Changed Climates*

Changes in total aboveground biomass at the temperate forest site under altered temperature and precipitation regimes were similar between LINKAGES v2.0 and FORCLIM (Figure 3). Increases in temperature, either alone or in combination with decreases in precipitation, led to reduced biomass except for one case (Table VI). Compared to the baseline scenario, LINKAGES v2.0 simulated a modest decrease in biomass under a 1.5 °C increase in temperature (scenario 1), a stronger decrease under +3.0 °C (scenario 4), and even stronger decreases under the warm-dry scenarios 2 and 5. FORCLIM was more sensitive to all scenarios, with a very strong decrease in biomass under scenario 5 (Table VI). In both models, a 20% increase in precipitation compensated for much of the decrease in forest biomass associated with a 1.5 or 3.0 °C increase in temperature (Table VI). These negative effects of elevated temperature and reduced precipitation on forest biomass in both models were paralleled by decreases in basal area (data not shown).

In contrast to the biomass response, the sensitivity of stem density differed between the models (Table VI). In LINKAGES v2.0, stem density increased in all scenarios compared to the baseline simulation. The increases under the warm-dry scenarios 2 and 5 were mainly for stems less than 5 cm in diameter (data not shown). This implies that the model 'sees' a forest with greater numbers of smaller trees under these conditions. In FORCLIM, however, stem density decreased in

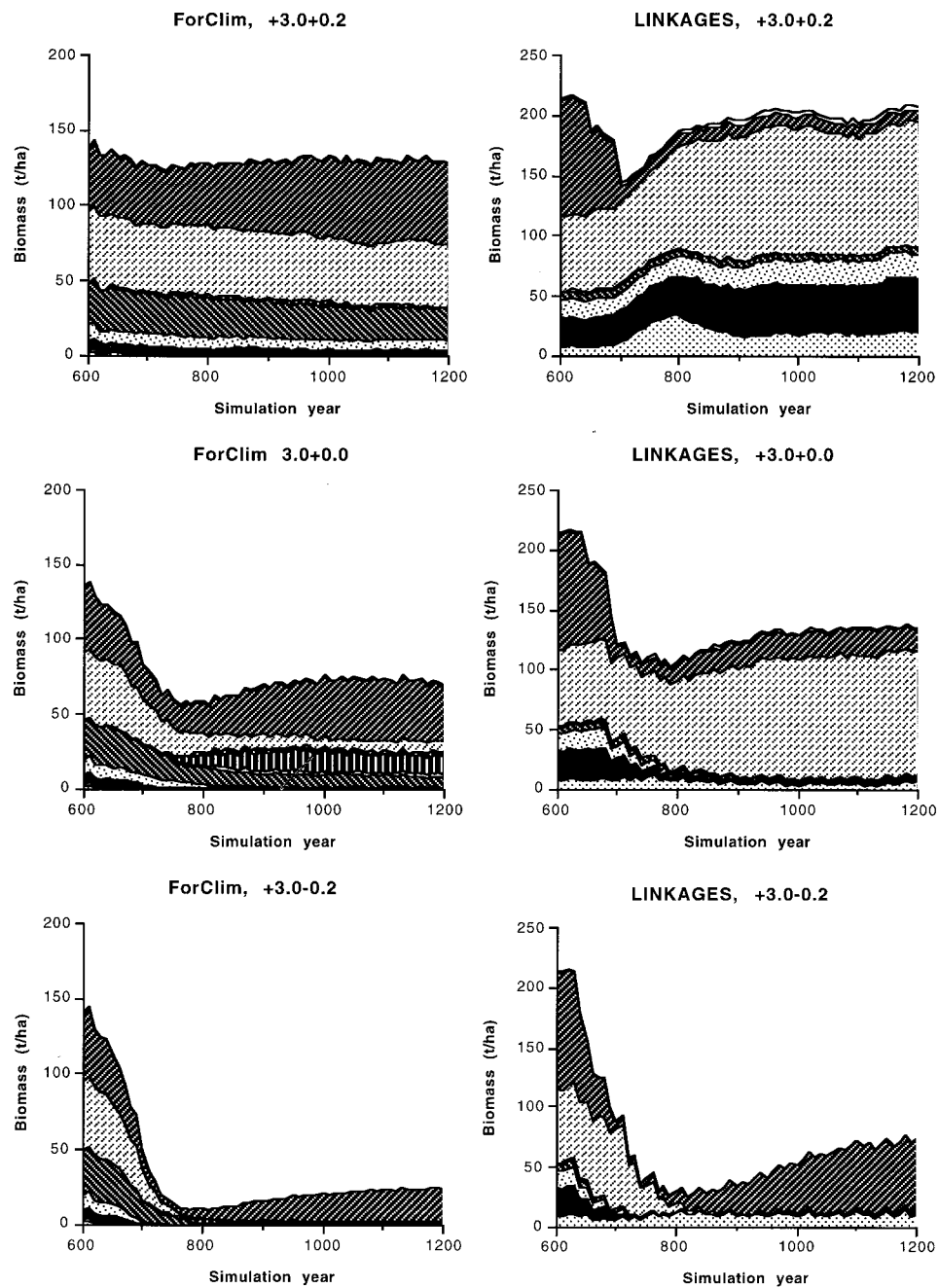


Figure 3. A comparison of responses of LINKAGES v2.0 and FORCLIM to three climatic change scenarios. Patterns are the same as in Figure 1.

Table VIIa

Summary of observed stand biomass and stem density for the eastern boreal forest site a Lac Duparquet, Quebec. Data are summarized from Kneeshaw and Bergeron (1998) and Paré and Bergeron (1995)

Stand age (yr)	Main species (decreasing order of importance)	Average above- ground biomass (t ha ⁻¹)	Average density (stems > 10 cm DBH) (stem ha ⁻¹)
77	POTR, BEPA, ABBA, PIGL	173	1991
124	ABBA, POTR, BEPA, PIGL, THOC	144	1803
171	ABBA, POTR, BEPA, PIGL, THOC	126	1932
234	ABBA, THOC, BEPA	105	1907

most scenarios, but particularly under the driest conditions. In this model, the relative share of large trees increased (data not shown), indicating that establishment events were simulated to occur less frequently, but established trees were able to grow, which is more characteristic of savanna-like forests (cf., Bugmann, 2001b).

Simulated species composition for the Walker Branch Watershed site was sensitive to increases in temperature and changes in precipitation in both models (typical examples of model behavior are given in Figure 3). However, the models differed with respect to the responses of individual species. Under a 3 °C temperature increase and increased precipitation, LINKAGES v2.0 projected the decline of red oak and chestnut about 50 years after the onset of climatic change. This was associated with reduced total biomass followed by a gradual recovery that lasted several centuries, primarily due to increasing white oak biomass. Under the same scenario, FORCLIM projected no stand-level dieback events, but a small reduction of overall biomass and an increased abundance of the more drought-adapted southern red oak at the expense of black and white oak. Under scenarios 1, 2, 4 and 5 (cf., Table V), FORCLIM always projected a higher abundance of drought-adapted species (southern red oak and, as drought increased, shortleaf pine, and eventually post oak) than LINKAGES v2.0. This behavioral difference paralleled the different extent of the biomass reduction under these scenarios, as discussed above. However, both models agreed that temperature increases and especially decreased precipitation would lead to a strong reduction in biomass of hickory, beech, ash, chestnut oak, white oak, and northern red oak.

Table VIIIb
 Summary comparison of observed stand biomass and stem density with spatial averages from simulations using BOREALIS and FORSKA-2V for the western boreal forest sites. Observed data are for trees of age reported to be 70 or older, extracted from Halliwell and Apps (1997a,b)

Climate station and numbers of stands in data set	Main species (decreasing order of importance)	Stand age (yr)	Aboveground biomass (t ha ⁻¹)			Stand density (stem ha ⁻¹)		
			Obs. (Min..Max)	BOREALIS	FORSKA-2V	Obs. (Min..Max)	BOREALIS	FORSKA-2V
WASKESIU LAKE (Saskatchewan) 21 stands	PIMA, PIBA,	Min: 70	20-52	75	70	6325-17959	632	1234
	POTR, PIGL,	Mean: 97	73-111			1356-4627		
	Mixed	Max: 151	185-268			340-1039		
PRINCE ALBERT (Saskatchewan) 8 stands	PIBA, PIMA,	Min: 70	31-69	46	43	4694-12661	193	988
	POTR	Mean: 114	52-97			2271-6180		
		Max: 130	161-182			319-728		
THOMPSON (Manitoba) 24 stands	PIMA, POTR,	Min: 76	9-32	-	60	9486-20257	-	1055
	PIBA, Mixed	Mean: 108	86-151			1438-4258		
		Max: 194	103-182			162-346		

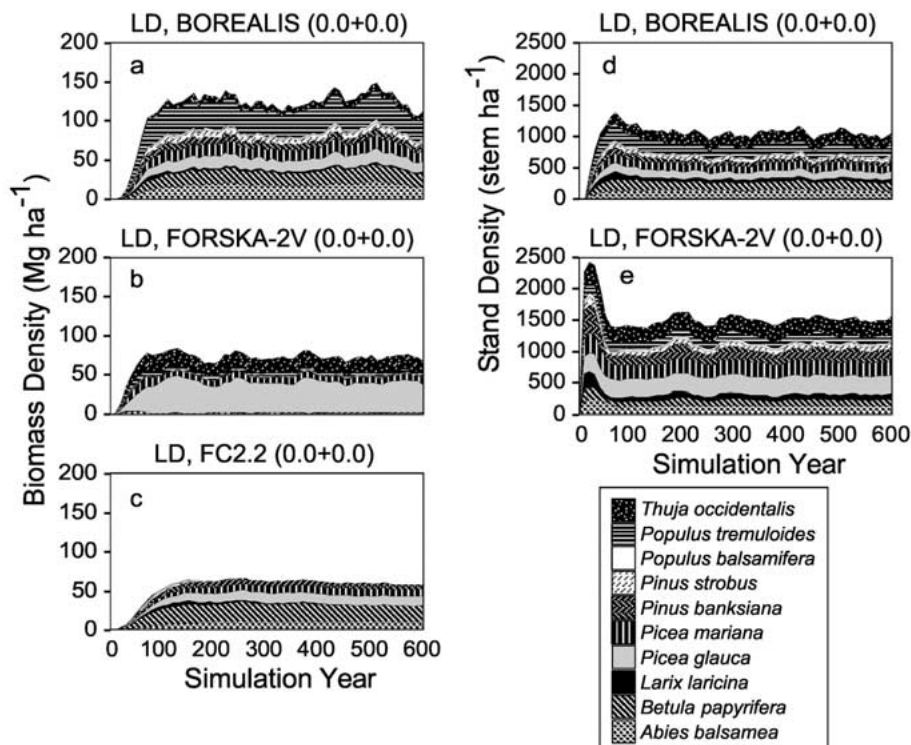


Figure 4. Comparison of boreal forest indicators simulated by the three gap models at Lac Duparquet under present-day climate. (a) BOREALIS biomass; (b) FORSKA-2V biomass; (c) FORCLIM biomass; (d) BOREALIS stem density; (e) FORSKA-2V stem density.

3.2. BOREAL FORESTS

3.2.1. Vegetation under the Current Climate at Lac Duparquet

BOREALIS and FORSKA-2V generated biomass estimates of around 80 t ha^{-1} at 80 years, and 125 t ha^{-1} at 100 years, whereas FORCLIM's prediction of 43 t ha^{-1} at 80 years and 53 t ha^{-1} at 100 years was appreciably lower (Figure 4). In contrast, Paré and Bergeron (1995) have shown that total aboveground biomass in the early successional forests of this region can reach 200 t ha^{-1} at 75 years, but decreases thereafter (Table VIIa). This region has some of the highest recorded biomass for aspen-dominated forests, reaching nearly 300 t ha^{-1} at 80 years in some areas (Paré and Bergeron, 1995; see also Table VIIa). Hence, the results obtained with all three models are markedly lower than the observations.

FORSKA-2V stem numbers were generally higher than those of BOREALIS across time, but both models typically reported spatial averages in the range 1200 to $1500 \text{ stem ha}^{-1}$, suggesting stands rich in small stems with relatively few large ones. In reality, the stem densities for canopy trees in forests near Lac Duparquet are approximately $2000 \text{ stem ha}^{-1}$ at 77 years, and only slightly lower in older

stands (Table VIIa). Hence, the underestimation of biomass is paralleled by an underestimation of stem densities in both FORSKA-2V and BOREALIS (simulated stem numbers were not available from FORCLIM).

Both BOREALIS and FORSKA-2V projected the presence of the correct species at Lac Duparquet (cf., Bergeron and Charron, 1994; Bergeron and Dubuc, 1989; Table VIIa, Figure 4). However, the models were less successful in estimating accurate proportions of each species, either in biomass or stem density terms. In particular, FORSKA-2V predicted stand biomass dominated by white spruce and white cedar, with smaller proportions of aspen and black spruce. The simulated predominance of white cedar was unrealistic for 70–80 year old stands (Table VIIa). Also, FORSKA-2V did not project the presence of balsam fir at the levels that would typically occur in these forests. However, both jack pine and larch contributed little to overall simulated stand biomass in the equilibrium state (Figure 4b), which is consistent with reality. Compared to the species composition projected by FORSKA-2V, the composition simulated by BOREALIS was considerably more diverse, with most species being about equally represented (Figure 4d vs. 4e). In biomass terms, the simulated stands were dominated by aspen, which is quite realistic if we take their average age into account (≈ 70 yr, cf., Section 2.3).

FORCLIM had little success in predicting the development of undisturbed stands at Lac Duparquet (Figure 4c). This model projected dominance of early successional stands by paper birch, which is realistic (Table VIIa), and jack pine, which is not characteristic of undisturbed forests in this region. In addition, the simulation results lacked dominance by aspen in this stage. Even in the late successional stage (i.e., at the end of the 600-yr simulation period under the current climate, Figure 4c), the stands simulated by FORCLIM continued to be dominated by paper birch. In this stage, the characteristic balsam fir contributed little to stand biomass, and cedar was entirely absent (cf., Table VIIa).

3.2.2. *Vegetation under the Current Climate at Central Canadian Sites*

Notably, FORCLIM produced almost no stems or biomass under any of the three site conditions described here, and thus will not be included in this section. Reasons for this model failure will be discussed in Section 4.

In the closed forest at Waskesiu Lake, FORSKA-2V generated a stand with most of the 10 species represented (Figure 5d). In biomass terms, however, the simulated stand was dominated by white spruce, with approximately equal smaller proportions of black spruce and aspen (Figure 5b). In reality, most species are present, but the plot data indicate higher proportions of black spruce and relatively few white spruce (Table VIIb). Simulated stand density peaked at 1800 stem ha^{-1} early in the succession, but reached an equilibrium at about 1200 stem ha^{-1} (Figure 5d). Considering that the simulated stand age is about 83 years (cf., Section 2.3), simulated density was quite low compared to observations (Table VIIb). However, it is important to note that small diameter trees (<1 cm DBH) are not considered in most gap models (cf., Bugmann, 2001a). They are included in the field data,

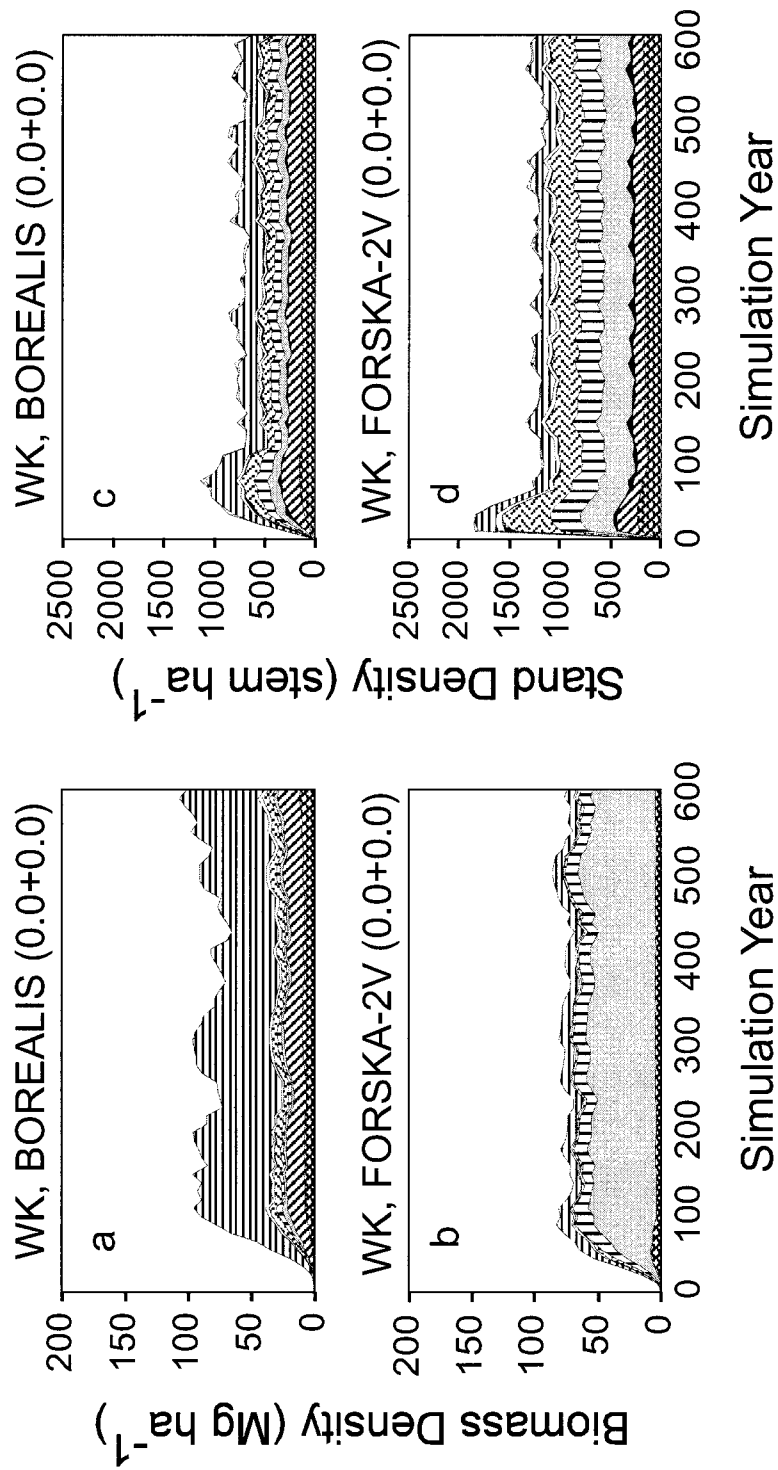


Figure 5. Forest biomass and stem density at Waskesiu Lake simulated for present-day climate by BOREALIS and FORSKA-2V. (a) BOREALIS biomass; (b) FORSKA-2V biomass; (c) BOREALIS stem density; (d) FORSKA-2V stem density. Legend as for Figure 4.

however, and actually constitute a significant fraction of overall observed stem density (Table VIIb). Simulated steady-state biomass at Waskesiu Lake was 70–80 t ha⁻¹, which was high compared to measured data for 70 year-old stands, but at the lower end of the range reported for stands of about 100 years (Table VIIb). Hence, the estimates of biomass are reasonable and the simulated stem densities may be typical for stems >1 cm DBH.

BOREALIS also generated a diverse mix of species at Waskesiu Lake (Figure 5c), but stand biomass was dominated strongly by aspen and birch (Figure 5a). Aspen biomass fluctuated considerably with time, indicating greater sensitivity of this species to interannual climatic variability than in FORSKA-2V (Figures 5a vs. 5b). Both peak (~1200 stem ha⁻¹) and equilibrium (~750 stem ha⁻¹) stem densities were lower in the simulations (Figure 5c) than observed (Table VIIb). Simulated aboveground biomass (Figure 5a) was rather high for 70-year old stands, but still reasonable given the range of values reported in Table VIIb.

At the driest site near Prince Albert, FORSKA-2V projected an unproductive forest consisting of roughly equal proportions of aspen, jack pine and white spruce (Figure 6b). The dominance by aspen and jack pine is plausible, but white spruce should be less common because climatic conditions are usually too dry to permit natural regeneration of this species. Again, stand densities projected by FORSKA-2V (Figure 6d) were markedly lower than observed (Table VIIb), which is partly due to the lack of the very small trees in gap models, as mentioned above. Simulated biomass varied widely (Figure 6b), but at levels that are somewhat lower than the measurements (Table VIIb). This model behavior can be explained by the fact that the climate at the Prince Albert station is influenced by advection from the warmer and drier prairie regions immediately to the south, whereas the forest sites are located further to the north (Halliwell and Apps, 1997a). Since we had to use climatic data from the Prince Albert station, we anticipated that FORSKA-2V, which is sensitive to seasonal moisture deficits, would project lower productivity and higher mortality than observed at the measurement sites.

A similar caveat should be applied to the BOREALIS results for the Prince Albert site. Simulated species composition was unrealistic, with stand biomass being dominated by white spruce and small amounts of aspen (Figure 6a, Table VIIb). Biomass varied between 40 and 60 t ha⁻¹, a range that agrees quite well with observations (Table VIIa). However, stem numbers simulated by BOREALIS were even lower than in FORSKA-2V (Figure 6c, Table VIIb), perhaps indicating higher mortality in response to severe drought, which may be due to the lack of stomatal control on evapotranspiration (cf., Table I).

At Thompson, FORSKA-2V simulated equilibrium biomass typically in the range of 50–70 t ha⁻¹, which is somewhat higher than the highest biomass measurements for 70-yr old stands in this region, and somewhat lower than the observations from stands with an average age of 108 years. Thus, the simulated values, which correspond to 85-yr old stands, agree with these data quite well (Table VIIb). Also at this site, simulated stand densities were much lower than

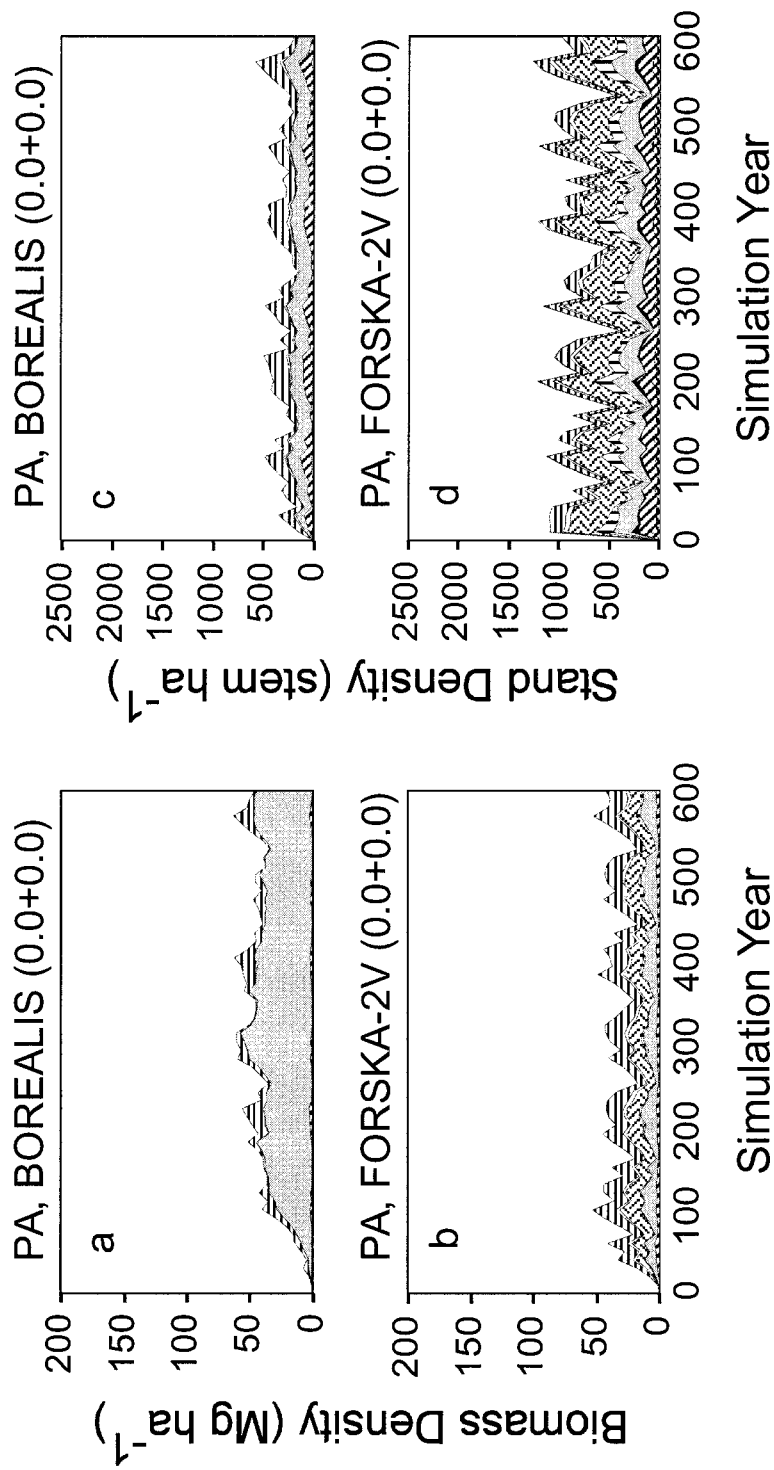


Figure 6. Forest biomass and stem density at Prince Albert simulated for present-day climate by BOREALIS and FORSKA-2V. (a) BOREALIS biomass; (b) FORSKA-2V biomass; (c) BOREALIS stem density; (d) FORSKA-2V stem density. Legend as for Figure 4.

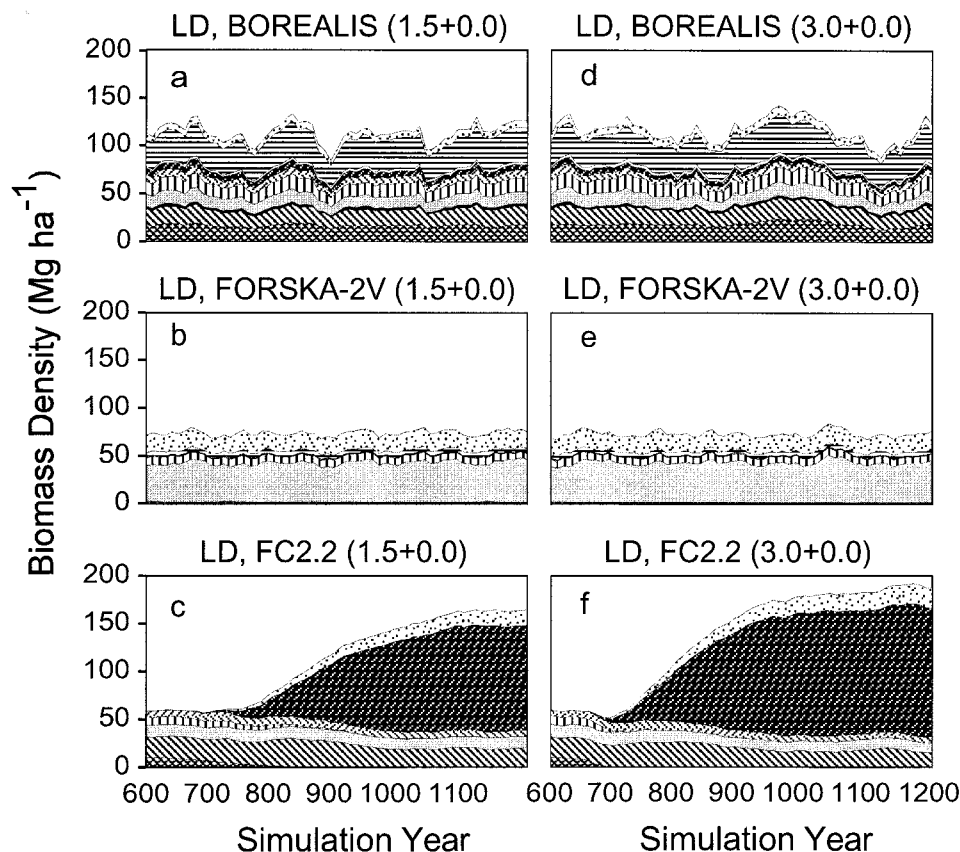


Figure 7. Forest biomass at Lac Duparquet simulated for the 1.5 + 0.0 (left) and 3.0 + 0.0 (right) climate scenarios by BOREALIS (a, d), FORSKA-2V (b, e) and FORCLIM (c, f). Legend as for Figure 4.

observed densities (Table VIIIb), which can exceed 50,000 stem ha⁻¹ in young and slow-growing pine stands. In such cases, the trees are often only 1–2 m tall and therefore would not be explicitly represented in a gap model simulation (cf., Bugmann, 2001a; Price et al., 2001). Neither FORCLIM nor BOREALIS were able to simulate forest growth at Thompson under the current climate or under any of the climate scenarios. The reasons for this will be discussed in Section 4, but further results for the Thompson site will not be presented here.

3.2.3. Vegetation under the Changed Climates at Lac Duparquet

BOREALIS and especially FORSKA-2V were remarkably insensitive to changes in temperature and precipitation (Figure 7, Table VIII). Only FORCLIM predicted a notable change in forest structure (Figures 7c,f), where warming, in the absence of precipitation decreases, triggered a significantly more productive forest dominated by eastern white pine. These changes were paralleled by a reduction in the

Table VIII
 Estimates of biomass and stem density under the seven climate scenarios as simulated by FORCLIM, BOREALIS and FORSKA-2V at three boreal forest sites. Data are averages of 200 replicate plots averaged for the last 100 years (ten 10-year intervals) of each 600-year simulation. Site codes are: LD: Lac Duparquet, Québec, PA: Prince Albert, Saskatchewan, WK: Waskesiu Lake, Saskatchewan. Values in parentheses are the percent changes in biomass and density relative to the baseline (0.0+0.0) scenario

Site	Scenario	FORCLIM		BOREALIS		FORSKA-2V	
		Biomass t ha ⁻¹	Density stem ha ⁻¹	Biomass t ha ⁻¹	Density stem ha ⁻¹	Biomass t ha ⁻¹	Density stem ha ⁻¹
LD	0.0 + 0.0	58.0	682	125.8	1034	72.5	1511
	1.5 + 0.0	163.6 (+182%)	724 (+6.2%)	121.4 (-3.5%)	1129 (+9.2%)	75.1 (+3.6%)	1517 (+0.4%)
	1.5 - 0.2	38.1 (-34%)	155 (-77%)	121.9 (-3.1%)	1068 (+3.3%)	74.6 (+2.9%)	1535 (+1.6%)
	1.5 + 0.2	122.1 (+111%)	860 (+26%)	112.4 (-11%)	1107 (+7.1%)	74.1 (+2.2%)	1527 (+1.1%)
	3.0 + 0.0	188.5 (+225%)	699 (+2.5%)	106.8 (-15%)	1139 (+10%)	72.7 (+0.3%)	1542 (+2.1%)
	3.0 - 0.2	0.0 (-100%)	0 (-100%)	108.2 (-14%)	1058 (+2.3%)	74.4 (+2.6%)	1532 (+1.4%)
	3.0 + 0.2	139.2 (+140%)	861 (+26%)	127.3 (+1.2%)	1075 (+4.0%)	70.9 (-2.2%)	1579 (+4.5%)
PA	0.0 + 0.0			46.9	326	36.7	912
	1.5 + 0.0			5.4 (-89%)	642 (+97%)	16.4 (-55%)	927 (+1.6%)
	1.5 - 0.2			5.4 (-89%)	156 (-52%)	8.9 (-76%)	654 (-28%)
	1.5 + 0.2			36.8 (-22%)	509 (+56%)	43.2 (+18%)	979 (+7.3%)

Table VIII
(continued)

Site	Scenario	FORCLIM		BOREALIS		FORSKA-2V	
		Biomass t ha ⁻¹	Density stem ha ⁻¹	Biomass t ha ⁻¹	Density stem ha ⁻¹	Biomass t ha ⁻¹	Density stem ha ⁻¹
PA	3.0 + 0.0			14.0 (-70%)	290 (-11%)	34.5 (-6.0%)	977 (+7.1%)
	3.0 - 0.2			1.7 (-96%)	125 (-63%)	8.9 (-76%)	670 (-27%)
	3.0 + 0.2			28.3 (-40%)	533 (+64%)	44.4 (+21%)	1000 (+9.6%)
WK	0.0 + 0.0			94.4	741	76.0	1242
	1.5 + 0.0			104.2 (+10%)	707 (-4.6%)	77.2 (+1.6%)	1314 (+5.8%)
	1.5 - 0.2			95.0 (+0.6%)	759 (+2.4%)	77.1 (+1.4%)	1217 (-2.0%)
	1.5 + 0.2			107.3 (+14%)	737 (-0.5%)	75.6 (-0.5%)	1385 (+12%)
	3.0 + 0.0			110.6 (+17%)	715 (-3.5%)	77.5 (+2.0%)	1382 (+11%)
	3.0 - 0.2			88.4 (-6.4%)	801 (+8.1%)	78.3 (+3.0%)	1201 (-3.3%)
	3.0 + 0.2			89.0 (-5.7%)	845 (+14%)	73.1 (-3.8%)	1474 (+19%)

abundance of the other species. This pattern was virtually identical for temperature increases of both 1.5 and 3.0 °C, which suggests that a threshold for the dominance of eastern white pine was exceeded already with a temperature increase of 1.5 °C at Lac Duparquet. Although we cannot evaluate the validity of this prediction, a shift to a forest composed of a more drought-tolerant species, such as eastern white pine, seems plausible if warming occurred without any change in precipitation regime.

Also, unlike FORSKA-2V and BOREALIS, FORCLIM was highly sensitive to changes in the precipitation regime (Table VIII). With a 20% decrease in rainfall, biomass and stem density were reduced by 34% and 77%, respectively, when temperature was elevated by 1.5 °C, and the forest was completely eliminated under a 3 °C temperature increase. Although these results are extreme, they are not necessarily anomalous. Of greater concern is that a 20% increase in precipitation resulted in reduced biomass and density relative to the 1.5+0.0 and 3.0+0.0 scenarios (Table VIII). This suggests that there is a very narrow range of temperature and precipitation combinations that permit forest growth at Lac Duparquet according to the FORCLIM model.

3.2.4. *Vegetation under the Changed Climates at Waskesiu Lake and Prince Albert*

At the Waskesiu Lake and Prince Albert sites, BOREALIS and FORSKA-2V exhibited similar responses of stand biomass and density to elevated temperature (Figures 8 and 9). At Waskesiu Lake, no strong changes in species composition were predicted by either model under a warmer climate (Figure 8). BOREALIS exhibited a greater biomass response to a 3 °C warming than FORSKA-2V (17% vs. 2% increase), but a smaller and opposite stand density response (−3.5% vs. +11%) (Table VIII, Figure 8). Both models generally predicted changes in biomass and density that were positively correlated with changes in precipitation, as expected.

At Prince Albert, both models responded more strongly to simulated changes in climate (Table VIII). With FORSKA-2V, both biomass and stem density increased with the +20% precipitation scenarios and decreased markedly with the −20% scenarios. Higher temperatures generally led to reduced biomass and density relative to the present-day baseline scenario. Additionally, the 1.5 °C temperature increase had a slightly more negative effect than the 3 °C increase, particularly for biomass under an unaltered precipitation regime (Table VIII, cf., Figure 9). Most likely, this result is anomalous and shows that even a model that is considered reliable and robust under many conditions can still produce implausible results under a specific set of simulated environmental conditions. BOREALIS was 2–3 times more sensitive than FORSKA-2V, with reduced biomass being predicted for all climate change scenarios (cf., Figure 9), although not surprisingly, the largest decreases were induced by reduced precipitation. Species composition, however, was simulated to be relatively insensitive to these climatic changes by both FORSKA-2V and BOREALIS (Figure 9). White spruce retained its unrealistic dominance

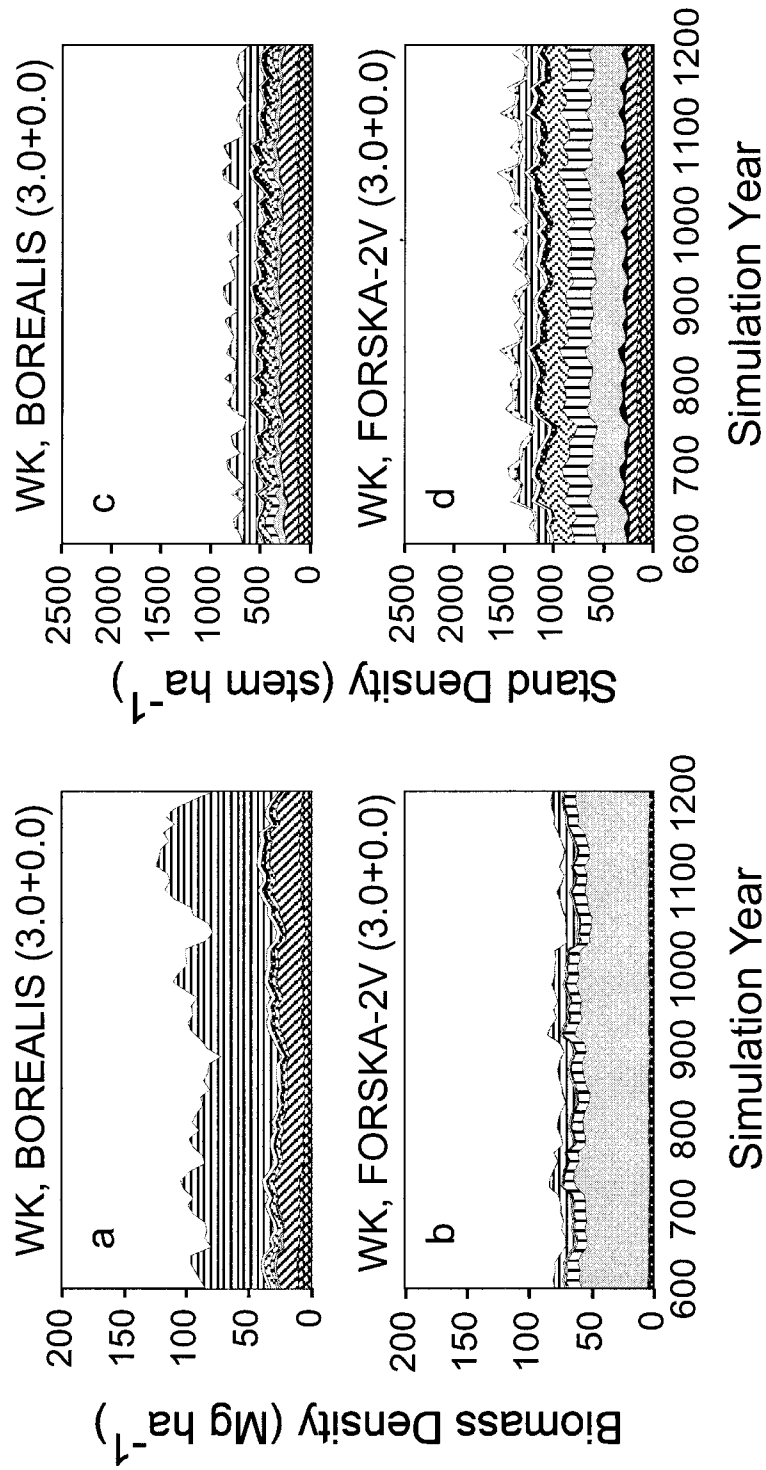


Figure 8. Forest biomass (a, b) and stem density (c, d) at Waskesiu Lake simulated for the 3.0+0.0 climate scenario by BOREALIS (top) and FORSKA-2V (bottom). Legend as for Figure 4.

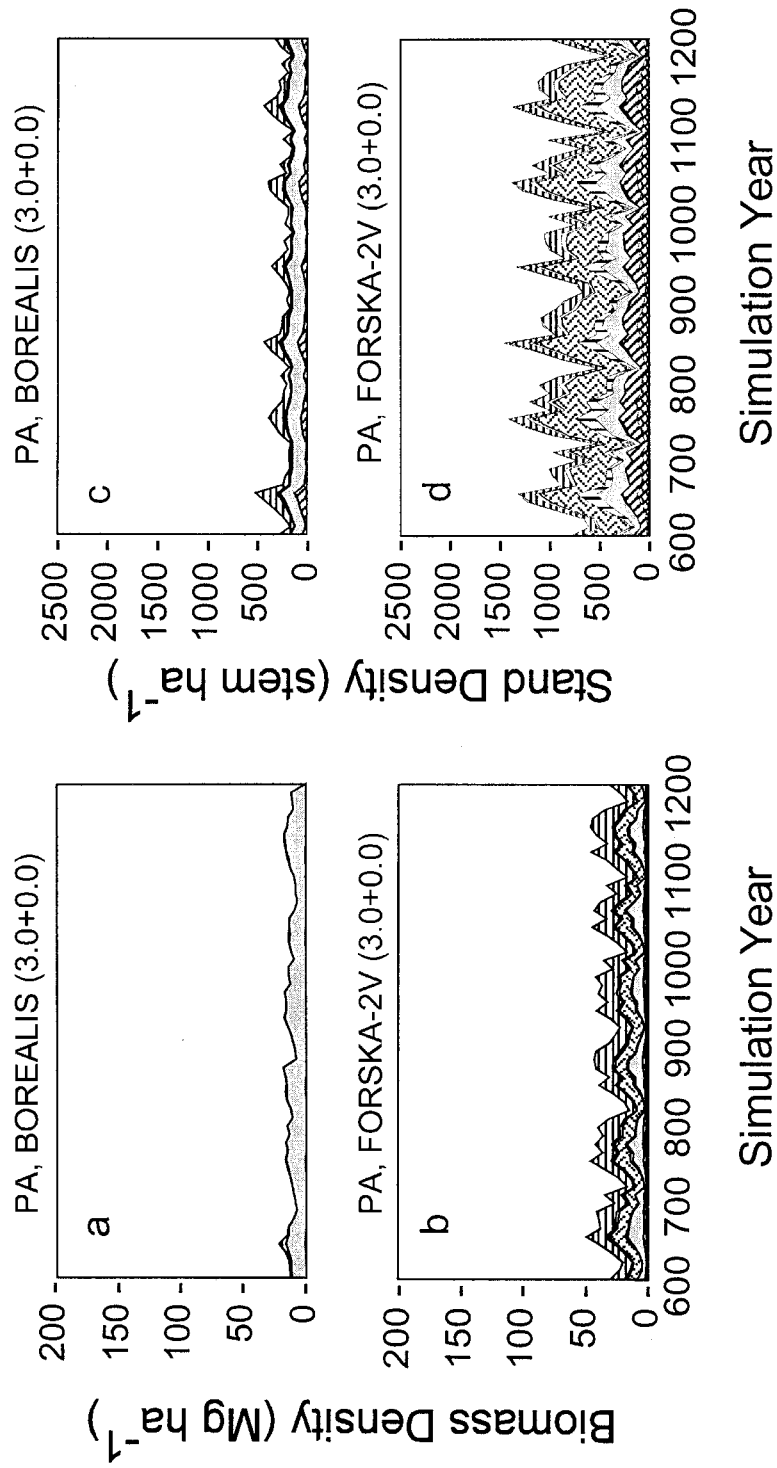


Figure 9. Forest biomass (a, b) and stem density (c, d) at Prince Albert simulated for the 3.0+0.0 climate scenario by BOREALIS (top) and FORSKA-2V (bottom). Legend as for Figure 4.

in the BOREALIS simulation, whereas a more plausible mixture of jack pine and aspen was predicted by FORSKA-2V.

4. Discussion

4.1. TEMPERATE FORESTS

LINKAGES v2.0 projected reasonably accurate forest composition and structure at Walker Branch Watershed. To a certain extent, this was a consequence of the fact that some 'tuning' of the species-specific establishment rates had been performed, whereas the FORCLIM results were obtained without any site-specific model modifications. The behavior of FORCLIM was almost as accurate as that of LINKAGES v2.0, even though the model had been developed with the aim of operating in most of the globe's temperate and some boreal forests (cf., Bugmann and Solomon, 2000). The addition of physiological mechanisms for predicting the water balance and the associated daily time step in LINKAGES v2.0 increased our confidence in its utility for projecting forest responses to changes in climate. The fact that the responses of LINKAGES v2.0 and FORCLIM under the six scenarios of climatic change were qualitatively identical and quantitatively similar suggests that the much simpler parameterization of the water balance and drought effects in FORCLIM is appropriate, at least under the set of environmental conditions investigated here.

Although the behavior of the two models was similar with respect to above-ground biomass under the scenarios of climatic change, there were two important differences with respect to their transient behavior and the resulting species composition.

First, under all climate scenarios that were characterized by a temperature increase of 3 °C, LINKAGES v2.0 projected a rapid disappearance of some species, specifically red and chestnut oak (*Q. rubra* and *Q. prinus*), regardless of the precipitation regime. An analysis of the 26-year climate record showed that much of this forest decline could be explained based on the parabolic growth response of both red and chestnut oak to growing-season temperature. For example, growing degree-days for Walker Branch Watershed during 1976 to 1998 (the climate record used in this study) ranged from a low of 2916 to a high of 4177 (data not shown). A 3 °C increase in temperature would raise these growing degree-day estimates to 4011 and 5272, respectively, and thus exceed the species-specific maximum tolerated degree-day values. As a result, the temperature-induced growth reduction was 100% (i.e., permitting zero growth) in 15 of 26 years and for chestnut oak in 25 of 26 years. Therefore, within the constraints of LINKAGES v2.0, a 3 °C increase in temperature was simulated to be a strong autecological limitation to the growth of these species.

This parabolic temperature-growth relationship incorporated in LINKAGES v2.0 and other gap models leads to the rapid dieback of various species under

warmer temperatures, which is problematic (cf., Bugmann, 2001a). We believe that this model response may be an artifact of the unrealistic assumption that tree growth declines towards the warm range limit of a species even in the absence of drought. FORCLIM, on the other hand, which has eliminated the parabolic dependency of growth on growing degree-days, produced much fewer dieback events, and those that occurred were the result of increased drought, rather than temperature *per se*. Hence we suggest that the parabolic degree-day response function used in LINKAGES v2.0 and many other gap models should be abandoned. However, it is not clear what function should be used in its place. Bugmann and Solomon (2000) used an asymptotic function that mimicked the 'cold' half of the original parabola function, but did not impose a growth reduction under higher temperatures. Talkkari et al. (1999), on the other hand, compared three growing degree-day formulations (original, 'physiological' and 'truncated physiological'), and concluded that their gap model was not sensitive to the growing degree-day response curve when applied to the cool climates of northern Finland. They cautioned, however, that the situation might be different if the model were applied under conditions prevailing near the southern edge of a species' geographic distribution, which would be the case at Walker Branch Watershed under some climate scenarios.

Second, although the response of the two models to drought was fairly similar at the stand level, a more detailed analysis of the results revealed that the environment was perceived to be drier by FORCLIM. For example, under a temperature increase of 3 °C that is accompanied by a precipitation decrease of 20%, biomass was simulated to be much lower in FORCLIM ($\approx 25 \text{ t ha}^{-1}$) than in LINKAGES v2.0 ($\approx 80 \text{ t ha}^{-1}$; cf., Figure 4). Under these conditions, post oak (*Q. stellata*) was the only species that contributed significant biomass in FORCLIM, whereas LINKAGES v2.0 featured $\approx 15\%$ of red maple (*Acer rubrum*) under the same conditions. Thus, the different degree of temporal detail (monthly versus daily) and physiology that is included in the two soil moisture submodels led to somewhat different projections at the species level that may be important if these models are to be used for informing the policy-making process, or for land managers. Based on the present simulation experiments, we cannot state with certainty which of the two models is more accurate under the changed climate, but one would surmise that the more detailed model should be 'better' (cf., Bugmann and Martin, 1995). Quantitative tests with the two models under a wider range of conditions (e.g., along climate gradients) would be required to resolve this issue.

4.2. BOREAL FORESTS

The responses of FORSKA-2V along the moisture gradient encapsulated in the central Canadian study sites are fairly similar to observations in this region, and can be explained even in the special case of the Prince Albert site, which is located on the prairie-forest border. The presence and absence of specific tree species, the

shift in species composition along the moisture gradient, and the change in forest structure found in the region today, were captured to a large extent by FORSKA-2V. Undoubtedly, this is partly due to the fact that the model had been developed for application in this region. FORSKA-2V was also able to portray forest composition reasonably well for the less extreme conditions in central Quebec, where the model BOREALIS functions well, which again is due to the fact that the latter model had been developed for this particular study site.

The main reason why FORSKA-2V performed better than the other models at the central Canadian sites is its improved representation of evapotranspiration (Table I). This appears to be crucial in a region where low precipitation causes both BOREALIS and FORCLIM to run out of water too rapidly, resulting in excessive reductions in growth and increases in mortality. BOREALIS, and particularly FORCLIM, performed less successfully in the southern boreal region, presumably because they did not capture stomatal feedbacks on evapotranspiration with decreasing soil water content.

The FORCLIM model, which had been developed and tested for a wide range of temperate forests, failed to simulate forest growth at any of the boreal test sites other than in the relatively maritime climate of Lac Duparquet. It appears that there is a problem with FORCLIM's water balance calculation, such that it is overly sensitive to drought conditions at high latitudes. This is in contrast to its aforementioned success at the temperate study site, Walker Branch. It seems that the model overestimates potential evapotranspiration (based on the formula by Thornthwaite and Mather, 1957) at latitudes above $\approx 50^\circ\text{N}$ and, as a consequence, actual evapotranspiration is also overestimated. This leads to unrealistically low soil moisture during the growing season and a drought-induced absence of woody vegetation in interior Canada. Our reasoning is corroborated by the behavior of the model at high latitudes in Europe (cf., Badeck et al., 2001). At a cool-wet boreal test site in Sweden (Fagelmyrkölen), FORCLIM erroneously projected very dry conditions associated with a complete drop-out of the characteristic spruce and birch species, which were replaced by a low-biomass pine forest. These simulated anomalies in both Europe and central Canada are evidence for the limited applicability of simple parameterizations beyond the conditions for which they were developed and tested.

4.3. GENERAL ISSUES

The simulation exercises presented in this paper, their evaluation against independent data sets, and the analysis of some mathematical relationships used in the different models suggest several general conclusions and research priorities.

First, differences among the model results ranged from minor to rather dramatic. The direct comparison of the results from each of the test sites reveals certain characteristics, strengths and weaknesses of the different models, but it is equally important to consider the role of site and species parameters. In the case of the four models used here, site parameters are relatively easy to estimate, although some

(such as soil water holding capacity) tend to be inaccurate. The issue of species parameters, however, is more complex. It is often difficult to obtain the detailed ecological and silvicultural data that are required to estimate all of the species-specific parameters of a model. Consequently, different procedures may be used in different models to estimate the same or very similar parameters, resulting in different numerical values. Defining a 'unified' set of species parameters that could be used in several models at a given test site would be desirable, but it is a laborious task. As a consequence, the fact that the models differ not only in their structure, but also in their parameter sets complicates the comparison of model behavior. We think that there is considerable potential in harmonizing the species-specific parameter values across different models, especially for those parameters that are defined identically or very similarly in the various models. Such parameters include maximum tree dimensions, minimum temperature thresholds, and others.

Second, a major problem occurs in the comparison of simulated data with measured data in the context of forest gap models (cf., Bugmann, 2001a). Stand growth (often chronosequence) data typically do not give an appropriate representation of spatially averaged stand characteristics, whereas gap models are performing an implicit spatial averaging when large-scale disturbances are included in the simulations, as was done in FORSKA-2V and BOREALIS. Price et al. (1999b) showed that for ecosystems where natural disturbances are an important factor, the effect of disturbances on the age class structure of the forest must be considered in assessing the results of gap model simulations. Average values of stand indicators (e.g., biomass, stem density and basal area), which are generated by the models, are often lacking from observed data sets, because these tend to be samples from a range of ages and are often biased toward older stands.

There are two possible solutions to this problem: (1) Use the model to construct stand growth curves by ignoring disturbances and then compare the simulation results directly with observed chronosequences. We recommend that future model comparison exercises should perform at least one simulation experiment like this for all models at all sites; (2) Obtain more detailed inventory data so that estimates of regional averages can be correctly area-weighted, or use remotely sensed data (e.g., aerial photography, satellite data) to analyze vegetation patterns over large areas (cf., Weishampel et al., 1992). Although the latter is more difficult to achieve, it provides crucial information. Note that in the case of Walker Branch Watershed, a large number of permanent sample plots have been established and could be used to provide unbiased estimates of mean biomass, stem density and basal area. We are convinced that other sites are equally well suited for such inventory analysis, and these should be identified as a much-needed resource for gap model evaluation.

Third, while real forests are driven by many interacting biotic and abiotic processes, none of the models considered here captures all these processes for a given forest in a unified manner. For example, BOREALIS was developed explicitly to represent the disturbance processes of fire and insect outbreaks. On the other hand, FORSKA-2V was developed to better represent water balance processes.

Hence, each model excels in areas specific to its research goals. This might help to explain the differences reported here, but – more importantly – it suggests that there is potential for developing a ‘community gap model’ that would build on a library of process descriptions. This library would be implemented in a modular way, with clearly defined interfaces between modules. This in turn would allow for a ‘plug-and-play’ approach to building families of new gap models that could largely be based on existing components (cf., Reynolds and Acock, 1997). This would also facilitate more rigorous model comparisons.

Fourth, some divergent behavior among the models in this study was due to parameterizations of the same processes at different levels of resolution (e.g., water balance submodels). These divergences should be reduced by comparing the different parameterizations against physiologically or biophysically based formulations, so as to identify the most appropriate approach. In this context, it is important to separate biophysical parts of gap models (e.g., calculation of water balance, or microclimate within the forest stand) from the ecological parts (e.g., modeling of the intrinsic growth rate, or competition). Future model comparisons should focus on individual (biophysical or physiological) processes instead of addressing the overall behavior of gap models.

In some cases, this may lead to the conclusion that a full, biophysically or physiologically based description must be incorporated in gap models, whereas in other cases it may highlight the appropriateness of a simplified parameterization. Notably, it will be important to incorporate the effects of CO₂ fertilization in forest gap models if they are to be used in a predictive mode for an assessment of the ecological effects of future environmental conditions (cf., Bugmann, 2001a; Norby et al., 2001).

Finally, although the geographic coverage of our simulation studies was limited, a unifying feature emerged from the simulated responses to climatic change at the widely different temperate and boreal test sites studied here. Notwithstanding the issue of species composition and the role that temperature itself may play in determining species decline, our simulations suggest that drought was the dominant environmental factor. For example, the different parameterizations of temperature effects on tree growth in FORCLIM and LINKAGES v2.0 led to some differences in the simulated behavior, but the overriding feature exhibited by both models was their strong and qualitatively similar response to the changing availability of soil moisture. Based on the assumption that the scenarios of climatic change used in the present study are of similar magnitude as the changes that we may expect to occur in the coming century (cf., Kattenberg et al., 1996), we tentatively infer that the combined changes of temperature and precipitation that result in shifts of the drought regime may be more important drivers of future forest productivity and species composition than temperature *per se*. In a model comparison context, this suggests that future work with gap models should focus on testing and developing improved representations of the water balance modules if they are to be used for making predictions about how forests might respond to climate change.

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