Virginia Journal of Science
Volume 41, Number 4A
Winter 1990

Forest Vegetation Structure on the Eastern Shore of Virginia *circa* 18,000 Years B.P.

Gordon B. Bonan[1] and **Bruce P. Hayden**
Department of Environmental Sciences
University of Virginia, Charlottesville, Virginia 22903

ABSTRACT

Pollen records from 18,000 years B.P. indicate that the forests of southeastern United States were composed primarily of pine and spruce species, with lesser amounts of fir and birch. We used a simulation model of extant boreal forest dynamics to reconstruct the composition and structure of these forests on the Eastern Shore of Virginia, where full-glacial pollen was available to test the model and climate and soils data were available to drive the model. The species dominating the simulated forests were not consistent with the pollen record. In particular, the dominant pine species was white pine, yet white pine pollen has not been found in the pollen record. Although the discrepancies between simulated forests and paleoecological data indicated that our climate parameters may have been too warm, our air temperatures were consistent with appropriate reconstructions from modern analogues and atmospheric general circulation models, when corrected for possible errors. Deficiencies in the simulated effects of air temperature sums on tree growth may have caused the lack of correspondence between simulated and observed data.

Key words: forest simulation model, Delmarva peninsula, full- glacial forests

INTRODUCTION

During the last glacial maximum 22,000-13,500 years B.P., pollen assemblages throughout southeastern United States were dominated by pine (*Pinus*) and spruce (*Picea*), with some fir (*Abies*), birch (*Betula*), and minor oak (*Quercus*) pollen (Delmarva Peninsula [Sirkin *et al.*, 1977; Denny *et al.*, 1979]; Chesapeake Bay Opening [Harrison *et al.*, 1965]; Rockyhock Bay, N.C. [Whitehead, 1973, 1981]; Singletary Lake, N.C. [Frey, 1951, 1953; Whitehead, 1964]; White Pond, S.C. [Watts, 1980a,b]; Hack Pond, Va. [Craig, 1969]; Northwest Georgia [Watts, 1970]). This pine- spruce pollen zone has been interpreted as reflecting widespread jack pine (*Pinus banksiana*) and/or red pine (*Pinus resinosa*) and black spruce (*Picea mariana*) and/or red spruce (*Picea rubens*) forest vegetation throughout southeastern United States (Whitehead, 1973, 1981; Watts, 1980a,b; Delcourt and Delcourt, 1987). However, the exact structure and composition of these forests is largely unknown.

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[1] Current address: National Center for Atmospheric Research, P. O. Box 3000, Boulder, Colorado 80307.

Limitations in the floristic resolution of pollen records and difficulties in translating pollen abundance into stand structure have precluded detailed forest reconstructions. In this paper, we use a "gap" model of environmental processes and stand dynamics for boreal forests (Bonan, 1988a,b) to simulate the structure and composition of full-glacial forest vegetation in southeastern United States. We focus on the Eastern Shore of Virginia, where paleoecological data are available to test the model and climate and soils data are available to drive the model.

METHODS

Gap models of forest dynamics provide a useful means to synthesize forest ecological hypotheses (Shugart, 1984) and can be used to examine the processes controlling paleoecological forest vegetation patterns (Solomon *et al.*, 1980, 1981; Solomon and Shugart, 1984; Solomon and Webb, 1985). The boreal forest gap model (Bonan, 1988a,b) simulates the annual birth, growth, and death of individual trees on a small forest plot. Optimal tree growth is a function of a species-specific growth rate, tree diameter, and tree height and is decreased multiplicatively to the extent that site conditions (growing season temperature sums, available light, soil moisture, nutrient availability, depth of seasonal soil thawing) are less than optimal for a particular species or individual. Regeneration is constrained for these same site conditions and for other effects such as a thick forest floor organic layer, seed availability following forest fires, and vegetative reproduction. Mortality is a function of potential longevity, stress, and forest fires. Simulated fire intensity is a function of fuel buildup; fire severity is a function of forest floor moisture content.

This model simulates local and regional patterns of solar radiation, soil moisture, and soil freezing and thawing throughout northern North America, Scandinavia, and the Soviet Union (Bonan, 1988a) and forest structure and vegetation patterns in several bioclimatic regions of the North American boreal forest (Bonan, 1988a,b). Bonan (1988a,b) provides a more detailed descripton of model formulation. In contrast to these previous analyses, here we assumed that trees were stressed when their realized growth was less than 10% of their optimal growth.

The available species pool was limited to the major northern hardwood and boreal species of the genera (pine, spruce, fir, birch, oak) found in the pollen record (Tables 1, 2). Required parameters for these species were taken from known silvics (Fowells, 1965) or other gap model analyses (Solomon *et al.*, 1984; Bonan, 1988a,b).

Paleoecological forest reconstructions require climate data contemporary with the pollen data. Full-glacial climate conditions in southeastern United States have been estimated from the modern analogues of the pollen data (Watts, 1970, 1980a,b; Whitehead, 1981) and from atmospheric general circulation models (Manabe and Broccoli, 1985; Kuzbach and Wright, 1985; Kutzbach and Guetter, 1986; Kutzbach, 1987). As an alternative, we used data from Moran (1972) to estimate required full-glacial climate parameters (Table 3). We reconstructed mean monthly air temperatures by fitting a sine wave to Moran's (1972) mean monthly January and July air temperatures. Monthly precipitation and mean monthly cloudiness were estimated from modern values corrected for full-glacial changes in tropical storm frequency and zonal wind flow (Moran, 1972). Required long-term monthly standard deviations were obtained from climatic records from eastern Canada (Bradley *et al.*, 1985). We recognize the limitations of this approach. However, all climatic

TABLE 1. Description of required species parameters.

AGEMAX	-	maximum age of species (yrs)
DBHMAX	-	maximum diameter at breast height (cm)
HTMAX	-	maximum height (m)
G	-	growth parameter
LITE	-	shade tolerance classification (1: tolerant, 2: intermediate, 3: intolerant)
SMOIST	-	maximum percentage of growing season that the species can tolerate soil moisture below the wilting point
N	-	average stump sprouts per tree
DMN	-	minimum diameter at breast height for sprouting (cm)
DMX	-	maximum diameter at breast height for sprouting (cm)
KTOL	-	fire tolerance (1: tolerant, 2: intermediate, 3: intolerant)
NUTR	-	nutrientstresstoleranceclass(1:tolerant, 2: intermediate, 3: intolerant)
IPFR	-	ability to grow on permafrost (1: good, 2: poor)
IMO	-	ability to reproduce on moss-organic layer (1: tolerant, 2: intermediate, 3: intolerant)
IBW	-	vulnerability to spruce budworm outbreaks (1: high, 2: low)
ALC	-	fraction of full sunlight when reproduction is inhibited
GDDMIN	-	minimum growing degree-days in the species' range
GDDMAX	-	maximum growing degree-days in the species' range
SWTCH	-	reproduction switches [SWTCH(1) is true if the species has serotinous cones. SWTCH(2) is true if the species has copious, light, wind dispersed seeds. SWTCH(3) is true if the species can reproduce by layering].

reconstructions incorporate errors to various degrees. Comparisons of our climate estimates with previous estimates provides an additional test of the validity of our forest reconstruction independent of the comparisons of simulated and observed vegetation data.

Pollen data typically record vegetation at the scale of 100- 1,000 km^2 (Delcourt and Delcourt, 1987). By averaging forest dynamics over many plots, gap models simulate forest vegetation over a similar spatial area (Solomon and Webb, 1985). However, this area is assumed to be homogenous in terms of climate and soil parameters. Although separate simulations can characterize forest dynamics for different site conditions, interfacing gap models with pollen data requires reconstruction of forests over the composite of habitats that the palynological data record.

Full-glacial forest habitats on the Delmarva peninsula are thought to range from freshwater bogs and swamps to extensive sand barrens (Emery *et al.*, 1967; Denny and Owens, 1979; Denny *et al.*, 1979). In these analyses, we used three different site conditions: mesic, nutrient rich; mesic, nutrient poor; and dry sites (Table 4). In addition, fire is an important component of modern boreal forests (Bonan, 1988a). Each site condition was replicated under short and long fire cycles.

Table 2. Species parameters. Dashes indicate extraneous parameters.

	AGE MAX	DBH MAX	HT MAX	G	LITE	SMOIST	N	DMN	DMX	KTOL	NUTR	IPFR	IMO	IBW	ALC	GDD MIN	GDD MAX	SWITCH
Abies balsamea Balsam fir	200	86	23	103.1	1	0.20	-	-	-	3	1	2	1	1	-	560	2386	FFT
Betula alleghaniensis Yellow birch	300	100	31	90.8	2	0.20	3	12	50	3	2	-	2	-	0.6	1100	2700	FTF
Betula papyrifera White birch	140	76	30	187.2	3	0.30	1	10	32	3	1	2	2	-	0.6	484	2036	FTF
Picea glauca White spruce	200	76	34	147.3	1	0.30	-	-	-	3	1	2	2	2	-	280	1911	FFF
Picea mariana Black spruce	250	46	27	93.5	1	0.30	-	-	-	3	1	1	1	2	-	247	1911	TFT
Picea rubens Red spruce	400	60	23	50.9	1	0.30	-	-	-	3	1	-	2	2	-	1247	2462	FFF
Pinus banksiana Jack pine	150	64	30	173.8	3	0.50	-	-	-	1	1	2	3	-	0.3	830	2216	TFF
Pinus resinosa Red pine	300	91	30	87.8	3	0.40	-	-	-	1	1	-	3	-	0.3	1100	2035	FFF
Pinus strobus Eastern white pine	450	102	46	87.6	2	0.30	-	-	-	2	1	-	2	-	0.2	1100	3165	FFF
Quercus rubra Northern red oak	400	100	30	66.0	2	0.30	2	12	40	3	2	-	3	-	-	1100	4571	FFF

TABLE 3. Modern and full-glacial climatic parameters.

Month	Temperature[a]			Precipitation[a]			Cloudiness[b]	
	18,000 B.P.	Modern	Std. Dev.	18,000 B.P.	Modern	Std. Dev.	18,000 B.P.	Modern
J	2.6 °C	3.8 °C	2.1	8.0 cm	8.4 cm	2.9	0.4	0.6
F	4.0	4.5	2.3	8.0	8.3	3.1	0.4	0.6
M	6.6	8.1	1.9	10.0	10.2	3.9	0.5	0.5
A	10.0	13.4	1.3	7.0	7.5	2.9	0.5	0.7
M	14.2	18.5	1.2	8.0	8.2	3.6	0.5	0.5
J	16.2	22.9	1.2	8.5	9.1	3.9	0.6	0.6
J	17.0	25.2	1.3	9.5	11.4	4.4	0.6	0.5
A	16.2	24.3	1.3	8.5	11.4	4.3	0.6	0.6
S	14.2	21.2	1.3	8.0	8.8	4.1	0.5	0.6
O	10.0	15.8	1.2	7.5	8.6	3.4	0.5	0.3
N	6.6	10.3	1.6	7.0	7.8	2.8	0.5	0.5
D	4.0	4.8	1.9	7.5	8.3	3.0	0.4	0.6

July average minimum temperature: 8°C (18,000 B.P.), 20°C (modern)
July average maximum temperature: 25°C (18,000 B.P.), 30°C (modern)
Latitude: 37.6°
Longitude: 75.8°
Elevation: 5 m
Slope: 0 %

[a] modern value from Painter, Va (Crockett, 1972)
[b] modern value from Norfolk, Va (NOAA, 1987)

TABLE 4. Full-glacial site parameters used in the simulation model.

SITE	MOISTURE CONTENT[a]			Relative Nutrient Availability	FIRE REGIME	
	SAT	FC	PWP		Cycle[b]	Intensity[c]
mesic,	35	25	10	1.00	100	10
nutrient rich				200	10	
mesic,	35	25	10	0.33	100	10
nutrient poor				200	10	
dry	18	12	5	1.00	0	10
					100	10

[a] soil moisture contents at saturation SAT, field capacity FC, and permanent wilting point PWP (cm)
[b] inverse of the annual probability of a stand burining (yrs)
[c] stand biomass at which fires are catastrophic (kg/m^2)

The fire intensity parameter was set to ensure the majority of fires were catastrophic. These parameters mimiced the fire regime of modern northern forests (Bonan, 1988a).

RESULTS

Reconstructed air temperatures showed decreased seasonality in which summers were colder than prevailing conditions, but winters were not much different from modern conditions (Table 3). Simulated full-glacial solar radiation was not much different from modern values (Fig. 1). Orbital parameters at both times are similar (Berger, 1978) and the only simulated differences were due to slight changes in estimated full-glacial cloud cover. Air temperature and solar radiation were used to estimate potential evapotranspiration (Bonan, 1988a,b). Simulated potential evapotranspiration was reduced under the colder climate 18,000 years B.P. (Fig. 2), offsetting the lower summer precipitation (Table 3) so that the monthly water deficit decreased from modern values.

For each of the six different site and fire cycle combinations, forest composition was determined based on relative species biomass after 500 years of simulation, when forest composition and structure approximated equilibrium conditions (Shugart, 1984). On all sites, pine was the dominant taxon (Table 5). White pine was the dominant species; jack pine was of secondary importance. Balsam fir, red spruce, and yellow birch were also important. White spruce, black spruce, and white birch did not grow on any of the six site conditons. Red pine and red oak were minor components of the simulated forest.

DISCUSSION

Gap models simulate tree biomass whereas palynological data record relative pollen abundance. Taxon calibrations have been developed to translate the observed pollen spectrum into the composition of surrounding forest vegetation (*e.g.*, Webb *et al.*, 1981; Delcourt *et al.*, 1984). At the generic level the simulated forest structure and composition closely matched Delcourt and Delcourt's (1987) forest reconstruction for the Delmarva Peninsula (Table 6). However, using taxon calibrations to estimate forest structure is fraught with difficulties and interpretations of pollen-based forest structure must be made with caution (Webb *et al.*, 1981; Solomon, 1986b; Prentice and Webb, 1986; Prentice, 1988).

Regardless of this problem, the species-level composition of the simulated forests was not consistent with fossil pollen analyses. All simulated forests were dominated by white pine (Table 5). However, the pollen of white pine, a *Haploxylon* pine species which from pollen morphology can be distinguished from *Diploxylon* pine species (Whitehead, 1964; Craig, 1969; Watts, 1979), has not been found during full-glacial conditions on the coastal plain of northeastern North Carolina (Whitehead, 1981). Indeed, the full-glacial, southeastern United States pine-spruce zone is thought to indicate jack pine (*Pinus banksiana*) and/or red pine (*Pinus resinosa*) and black spruce (*Picea mariana*) and/or red spruce (*Picea rubens*) forest vegetation (Whitehead, 1973, 1981; Watts, 1980a,b; Delcourt and Delcourt, 1987). Moreover, fossilized full-glacial white spruce cones have been identified in the costal plain of Georgia (Watts, 1980a), yet white spruce could not grow under our reconstructed climate for the Eastern Shore.

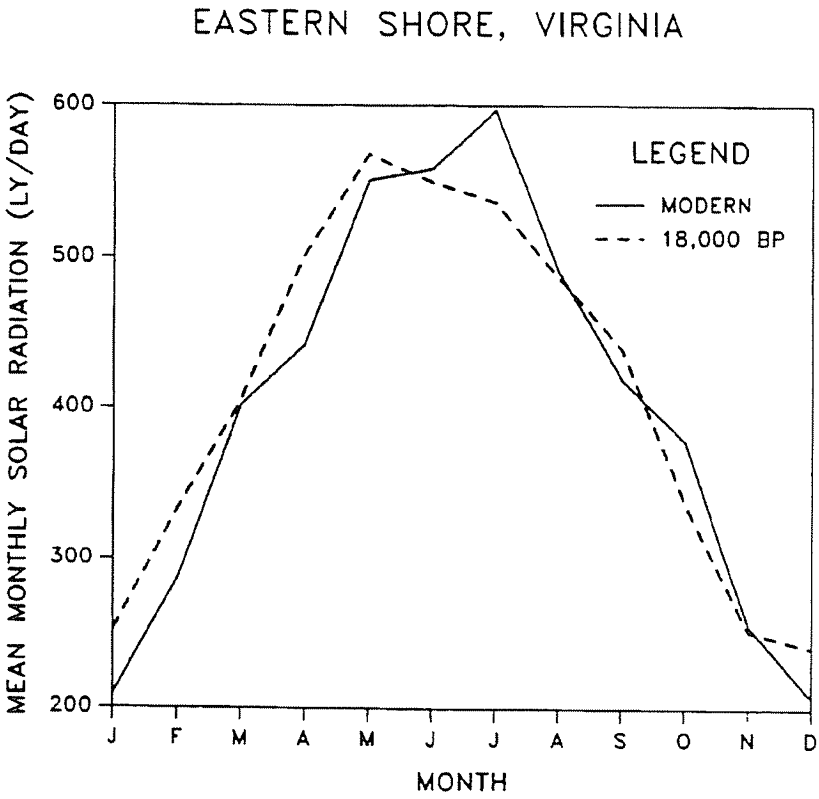

FIGURE 1. Simulated mean monthly solar radiation: modern and 18,00 years B. P.

Some researchers have speculated that white pine found full- glacial refugia in the west (Craig, 1969; Watts, 1970). Forest dynamics were simulated again, but this time without white pine in the species pool (*i.e*, assuming that white pine had refugia further west). Again simulated species composition was inconsistent with paleoecological data. In particular, on the dry site, which is thought to have been extensive throughout the Delmarva Peninsula during full-glacial conditions (Denny and Owens, 1979; Denny *et al.*, 1979), jack pine contained up to 50% of stand biomass, and spruce, birch, and fir were of less importance (Table 7). However, red oak comprised 9% of stand biomass. There is some controversy whether the oak pollen found in this region is significantly above background levels (Delcourt and Delcourt, 1987; Webb, 1987, 1988). Oak is a prolific producer of pollen and the low relative pollen abundance (0-5% arboreal pollen [Harrison *et al.*, 1965; Sirkin *et al.*, 1977]) does not indicate the amount of oak simulated in these analyses.

The discrepancies between simulated forests and paleoecological data could have reflected climatic parameters that were warmer than the actual climate 18,000 years B.P. Available growing degree-days (5.6°C base) for our reconstructed climate averaged 1865 degree-days and with stochastic variation ranged from 1567-2336. This range exceeded the maximum growing degree-days for white birch, white spruce, black spruce, jack pine, and red pine. Only balsam fir, yellow birch,

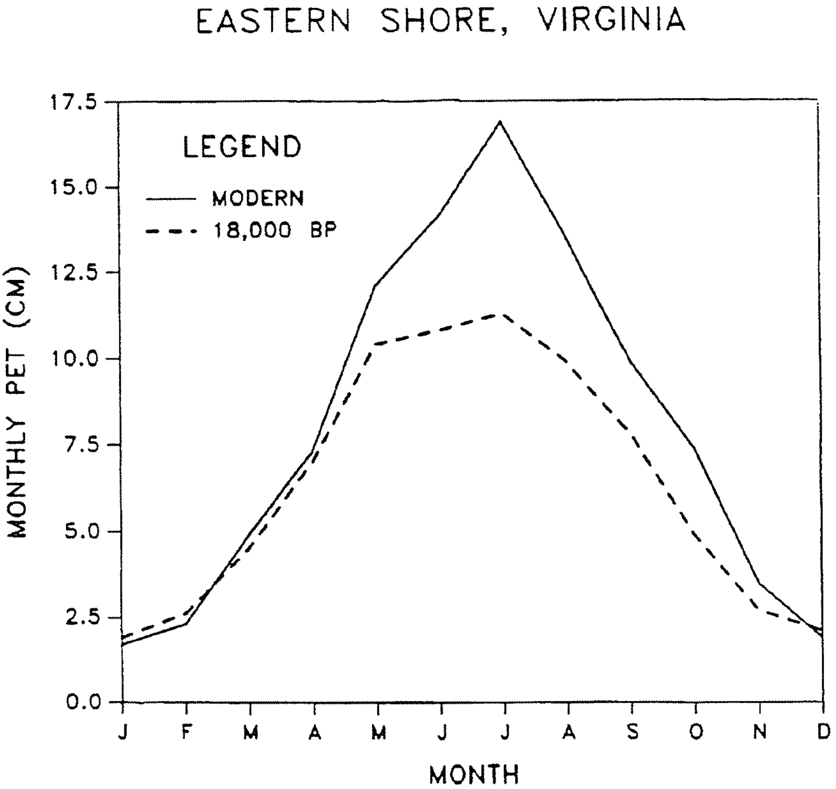

FIGURE 2. Simulated monthly potential evapotranspiration (PET): modern and 18,00 years B. P.

white pine, and northern red oak had growing degree-day parameters within the simulated range (Table 2).

The climate parameters used in these analyses were not much different than those reconstructed from pollen analyses. Our mean July temperature (17.0°C) was similar to pollen-derived estimates for southeastern United States (16 to 20°C [Watts, 1970, 1980a,b; Whitehead, 1981]). We used a warmer mean January temperature (2.6°C) than pollen-derived reconstructions (-10 to -22°C [Watts, 1970, 1980a,b; Whitehead, 1981]). However, these modern analogue estimates did not incorporate important full-glacial changes in seasonality. Our reconstucted air temperatures were consistent with Bryson and Wendland's (1967) and Solomon and Shugart's (1984) hypothesis of decreased seasonality during full-glacial conditions in which summers were colder than present but winters were not much different than present. Full-glacial climates simulated by atmospheric general circulation models indicated similar conditions (Manabe and Broccoli, 1985; Kutzbach and Wright, 1985; Kutzbach and Guetter, 1986; Kutzbach, 1987).

Results from the National Center for Atmospheric Research Community Climate Model (NCAR CCM) atmospheric general circulation model indicated full-glacial mean January and July temperatures were decreased by 0-5°C from modern values throughout southeastern United States (Kutzbach and Wright,

TABLE 5. Simulated forest structure for the six different forest sites.

	NUTRIENT RICH Fire Cycle		NUTRIENT POOR Fire Cycle		DRY SITE Fire Cycle	
	100 yrs	200 yrs	100 yrs	200 yrs	50 yrs	100 yrs
Balsam fir	11.6 %	10.8 %	19.7 %	17.9 %	10.5 %	12.3 %
Birch spp.	19.8	14.1	10.7	5.4	23.7	20.6
Yellow birch	19.8	14.1	10.6	5.4	23.0	20.4
White birch	0.0	0.0	0.1	0.0	0.7	0.2
Red spruce	11.3	20.3	10.2	19.5	5.2	8.2
Red oak	0.9	0.3	0.7	0.5	3.1	0.9
Pine spp.	56.5	54.4	58.6	56.5	57.5	57.9
Jack pine	20.4	8.5	17.6	7.9	35.3	20.5
Red pine	0.2	0.1	0.4	0.2	1.4	0.6
White pine	35.9	45.8	40.6	48.4	20.8	36.8

1985; Kutzbach and Guetter, 1986; Kutzbach, 1987). Applying this range of temperature reductions to modern temperatures on the Eastern Shore results in a January temperature (-1 to 4°C) similar to ours but a warmer July temperature (20 to 25°C). Manabe and Broccoli (1985) used a different atmospheric general circulation model coupled with an oceanic model to simulate full-glacial climate conditions. They also found that winter and summer surface temperatures in southeastern United States were only 0- 4°C colder than modern values.

However, summer air temperatures simulated by general circulation models may be too warm. Webb *et al.* (1987) coupled modern pollen/climate response surfaces and climate data generated by the NCAR CCM to reconstruct pollen spectra for the past 18,000 years. During full-glacial conditions, these simulations underestimated spruce and northern pine pollen and overestimated oak pollen in southeastern United States. These errors may indicate the simulated climate was too warm by 2-4°C (Webb *et al.*, 1987). Applying this reduction to the NCAR CCM July temperature estimate results in temperatures ranging from 16 to 23°C, which is more consistent with our value.

Our annual precipitation (98 cm) was also consistent with the range of estimated values. Modern analogue estimates of annual precipitation in southeastern United States range from drier than normal (70-75 cm [Watts, 1970; Whitehead, 1981]) to slightly drier than normal (105 cm [Watts, 1980a,b]). NCAR CCM simulations indicate winter precipitation was unchanged and summer precipitation was decreased by 25-30% of modern values (Kutzbach and Wright, 1985; Kutzbach and Guetter, 1986; Kutzbach, 1987). Applying a 30% reduction to modern growing season (May to September) precipitation on the Eastern Shore results in an annual precipitation of 93 cm. Manabe and Broccoli (1985) found that annual precipitation in the region of the Eastern Shore was reduced by 0.0-0.05 cm/day from modern

TABLE 6. Observed and simulated full-glacial forest structure.

Genera	Observed[a]	Simulated
Pine	50 %	54-59 %
Spruce	15-35	5-20
Fir	10	10-20
Birch	12	5-24
Oak	minor	0-3

[a] from Delcourt and Delcourt (1987)

TABLE 7. Simulated forest structure:without white pine.

	NUTRIENT RICH Fire Cycle		NUTRIENT POOR Fire Cycle		DRY SITE Fire Cycle	
	100 yrs	200 yrs	100 yrs	200 yrs	50 yrs	100 yrs
Balsam fir	20.9 %	23.3 %	36.4 %	0.7 %	8.7 %	24.5 %
Birch spp.	42.5	36.2	20.7	20.9	17.9	24.1
Yellow birch	42.3	36.0	20.6	20.9	17.8	23.9
White birch	0.2	0.2	0.1	0.0	0.1	0.2
Red spruce	13.1	24.0	21.9	35.0	12.9	12.3
Red oak	1.1	0.9	1.5	1.7	9.4	5.5
Pine spp.	22.4	15.5	19.6	11.7	51.1	33.6
Jack pine	21.9	15.2	19.1	11.5	50.5	32.8
Red pine	0.5	0.3	0.5	0.2	0.6	0.8

values. Applying this reduction to modern values results in annual precipitation of 90 to 108 cm.

In short, the full-glacial climate parameters we used in our analyses were consistent with the range of appropriate previous estimates. The discrepancies between observed paleoecological data and simulated forests may, therefore, have reflected inadequacies in the forest simulation model. Of particular importance in the context of paleoecological forest reconstructions is the growing degree-days growth multiplier, which is used to scale tree growth and regeneration for sub-optimal air temperatures. The effect of air temperature sums on individual tree performance is assumed to be parabolic, scaled to zero at the minimum and maximum growing degree-days in a species' range and scaled to one halfway between these values (Shugart, 1984). This formulation causes tree growth and reproduction to decline to zero as climatic conditions approach the northern and southern range limits of a species.

In these analyses, we used Solomon *et al.*'s (1984) growing degree-day parameters (Table 2). In geographic testing of a gap model, this parameterization of climate/vegetation interactions resulted in simulated regional forest vegetation patterns that were consistent with observed patterns (Solomon *et al.*, 1984; Solomon, 1986a). However, our analyses indicate that these parameters may be wrong. Moreover, the formulation of the growing degree-day growth multiplier may have accentuated differences between observed and simulated forest composition. The parabolic form of the growth multiplier causes the model to be quite sensitive to slight differences in annual growing degree-days when at the edges of a species' range and insensitive when in the center of it's range. Solomon *et al.*'s (1984) parameters put our reconstructed climate at or near the southern range limit of many of the simulated tree species. Clearly, the validity of the parabolic growth multiplier must be resolved before gap models can provide robust projections of the ecological consequences of climate changes.

This study has highlighted the importance of interfacing forest stand models with paleoecological data. An accurate understanding of paleoclimates and paleoecological forest composition can only occur through independent forest and climate reconstructions. Forest stand models provide one means of doing so. In addition, paleoecological data provide a controlled test of these models and can help to identify inaccuracies in model formulation (*e.g.*, air temperature effects). Such testing is necessary given the widespread use of gap models to project the ecological consequences of future climate change scenarios (*e.g.*, Solomon *et al.*, 1984; Solomon, 1986a; Pastor and Post, 1988).

ACKNOWLEDGEMENTS

This work was initiated while G.B. Bonan was a graduate student at the Department of Environmental Sciences, University of Virginia and was supported in part by a NASA grant NASA-NAG-5- 1018 and a National Science Foundation grant BSR-8702333-02. This manuscript was prepared for publication while G.B. Bonan was a National Research Council research associate at the NASA/Goddard Space Flight Center, Greenbelt, MD.

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