Landscape Ecology **14:** 121–135, 1999.

Soil saturation effects on forest dynamics: scaling across a southern boreal/northern hardwood landscape

John F. Weishampel[1,*], Robert G. Knox[2] and Elissa R. Levine[2]
[1]*Department of Biology, University of Central Florida, Orlando, FL 32816-2368, USA;*
[2]*Code 923 Biospheric Sciences Branch, NASA Goddard Space Flight Center, Greenbelt, MD 20771, USA*

Received 17 May 1997; Revised 20 October 1997; Accepted 2 May 1998

Key words: aggregation, biomass, drainage class, GIS, soil maps, succession model, waterlogging

Abstract

Patch modeling can be used to scale-up processes to portray landscape-level dynamics. Via direct extrapolation, a heterogeneous landscape is divided into its constituent patches; dynamics are simulated on each representative patch and are weighted and aggregated to formulate the higher level response. Further extrapolation may be attained by coarsening the resolution of or lumping environmental data (e.g., climatic, edaphic, hydrologic, topographic) used to delimit a patch.

Forest patterns at the southern boreal/northern hardwood transition zone are often defined by soil heterogeneity, determined primarily by the extent and duration of soil saturation. To determine how landscape-level dynamics predicted from direct extrapolation compare when coarsening soil parameters, we simulated forest dynamics for soil series representing a range of drainage classes from east-central Maine. Responses were aggregated according to the distribution of soil associations comprising a 600 ha area based on local- (1:12,000), county- (1:120,000) and state- (1:250,000) scale soil maps. At the patch level, simulated aboveground biomass accumulated more slowly in poorer draining soils. Different soil series yielded different communities comprised of species with various tolerances for soil saturation. When aggregated, removal of waterlogging caused a 20–60% increase in biomass accumulation during the first 50 years of simulation. However, this early successional increase and the maximum level of biomass accumulation over a 200 year period varied by as much as 40% depending on the geospatial data. This marked discrepancy suggests caution when extrapolating with forest patch models by coarsening parameters and demonstrates how rules used to rescale environmental data need to be evaluated for consistency.

Introduction

The realization that some local ecological processes do not readily ‘scale-up’ has bolstered interest in applying individual-based forest models to explore landscape to global scale phenomena (Shugart and Smith 1996). These patch or gap models address broad-scale questions by using stratified sampling to simulate patches representing different environmental conditions and aggregating the area-weighted results to represent a landscape mosaic (Shugart et al. 1992). This form of direct extrapolation (King 1991, Johnson 1996) assumes homogeneous conditions within a patch and typically ignores patch to patch interactions which may be related to the spatial configuration of the landscape (Shugart 1996). Although individual-based forest models have depicted trajectories of patches that comprise contiguous, environmentally heterogeneous landscapes (e.g., Pearlstine et al. 1985; Shao et al. 1994), aggregated, landscape-level responses (Rastetter et al. 1992) have not been reported. Hence, details of applying this scaling approach, e.g., determining coherent levels (O’Neill 1988) or what spatiotemporal resolutions of environmental (i.e., climatic, edaphic, hydrologic) data provide the most appropriate context in which to run these forest models, have not been resolved.

The complex patterning of communities located near the transition zone between the southern boreal and northern hardwood forests is often determined by edaphic influences (Kimmins 1996), expressed largely by soil moisture regimes which may favor the development of forested and unforested bogs (Glebov and Korzukhin 1992; Pastor and Mladenoff 1992). Though the regional formation of wetlands is primarily dependent on climatic variables, e.g., insolation, temperature, and precipitation, finer scale mosaic patterning of forested wetlands is a function of water table levels which are dependent on topography and local soil properties (Solomon 1992). Recognizing the importance of soil/hydrological properties, vegetation patches located near this ecotone are often coarsely classified into wet, mesic, and dry categories (Bonan and Shugart 1989). Though simulations efforts (e.g., Solomon 1986; Pastor and Post 1986; Pastor and Post 1988; Martin 1992; Bugmann and Solomon 1995) have largely concentrated on drier, upland forests, hydrological controls have been included for one series of succession models (e.g., Botkin and Levitan 1977; Botkin et al. 1989; Botkin and Nisbet 1992a, 1992b; Botkin 1993) for this region.

However, relationships between wetland and groundwater are intricate (van der Heijde 1988); thus, determining soil moisture regimes to parameterize a patch model for this heterogeneous landscape is problematic. Because the number of observation wells needed to adequately describe the saturation level varies with the complexity of the soil profile (USDA SCS 1971) and horizontal and vertical properties of soils which were subject to glacial activity are highly variable over relatively short distances (Levine et al. 1994; Levine and Knox 1997), many wells would need to be installed at a variety of depths for each soil series. Moreover, temperature fluxes of northern soils yield freeze/thaw periods and spring snow melt and subsequent drawdown produced by vegetative growth create significant seasonal variation of depths to water table. These temporal patterns require wells to be frequently monitored over many years to account for interannual changes in precipitation and temperature.

Here, we interfaced a forest patch model with a soil physics model to explore the aggregative affects of waterlogging on forest biomass for an edaphically heterogeneous landscape. The soil physics model was used to estimate saturation conditions and parameterize a gap model for a range of soil properties (from somewhat excessively to very poorly drained) found in east-central Maine. To determine whether there were consistent extrapolation trends associated with coarsening resolution or lumping of spatial data, we compared the combined model results scaled to soil distributions from local (1:12,000), county (1:120,000), and state (1:250,000) maps.

Methods

Study area

International Paper's Northern Experimental Forest (NEF) in east-central Maine (45 °15′ N, 68 °45′ W) has served as the site of an intensive field and multisensor aircraft campaign that emphasized the use of remote sensing to study forested landscapes (Goward et al. 1994). The NEF comprises ≈7000 ha consisting of hemlock-spruce-fir (primarily *Tsuga canadensis, Picea rubens, P. mariana*, and *Abies balsamea*), aspen-birch (primarily *Populus tremuloides*, *P. grandidentata*, *Betula papyrifera*, and *B. alleghaniensis*) and hemlock-hardwood mixtures.

The soils at the NEF are generally classified within the suborder ‘orthods’ which is representative of the forested soils found at the transition zone between boreal and northern hardwood forests (Rourke et al. 1978). The slope of the NEF is relatively flat, possessing a maximum elevation change of 135 m over 10 km. This shallow relief decreases the rate of lateral drainage and promotes ponding during spring melting. The snow pack is typically continuous from December to March. Due to the region's glacial history and more recent alluvial events, soil drainage classes vary from somewhat excessively drained eskers to very poorly drained topographic depressions that possess a compacted, impermeable horizon. Trees in excessively drained soils may suffer from drought effects, whereas trees in poorly drained soils are subject to anoxic conditions in the rooting zone. Because of differential sensitivity of tree species to soil saturation regimes, the NEF consists of a mosaic of stands of different species composition, biomass levels, and stem densities. These forest variables have been correlated with spectral reflectance, i.e., NDVI (Levine et al. 1994), and radar backscatter (Ranson and Sun 1994a, 1994b) patterns exhibited across the NEF landscape.

Soil moisture relationships in a forest model

The Forest Ecosystem Dynamics modeling environment (Levine et al. 1993; Knox et al. 1997), a network of individual biotic and abiotic models that simulate remotely sensed patterns associated with forest succession, included the gap model, ZELIG (Urban 1990; Urban et al. 1991). Employing the same general

Table 1. Tree species parameters used in implementation of ZELIG for the NEF.

Scientific name	(Common name)	Age	DBH	H	GR	GDD-	GDD+	DTmin	L	M	N
Abies balsamea	(Balsam fir)	200	50	1500	69	250	2404	0.211	1	1	3
Acer pensylvanicum	(Striped maple)	75	15	500	150	889	5500	0.567	2	3	3
Acer rubrum	(Red maple)	150	100	3000	176	1260	6601	0.322	2	3	3
Acer saccharum	(Sugar maple)	300	150	3000	89	1204	3200	0.567	1	2	2
Betula alleghaniensis	(Yellow birch)	250	75	3000	106	1420	3084	0.600	3	2	2
Betula papyrifera	(Paper birch)	140	100	2500	160	700	2500	0.544	4	3	3
Betula populifolia	(Gray birch)	250	25	1000	37	1007	2880	1.000	5	2	3
Fagus grandifolia	(American beech)	366	100	3000	72	1327	5556	0.489	1	3	2
Larix laricina	(Tamarack)	335	75	2500	66	280	2660	0.156	5	3	3
Picea mariana	(Black spruce)	250	40	2000	70	265	1929	0.156	2	3	3
Picea rubens	(Red spruce)	300	100	3000	89	500	2580	0.489	2	2	3
Pinus strobus	(Eastern white pine)	450	150	3500	68	1500	3183	1.000	3	3	3
Populus grandidentata	(Bigtooth aspen)	70	75	2500	316	1100	3169	0.400	5	3	2
Populus tremuloides	(Quaking aspen)	125	75	2200	158	889	5556	0.700	5	3	2
Thuja occidentalis	(Northern white cedar)	400	100	2400	55	1000	2188	0.100	2	3	3
Tsuga canadensis	(Eastern hemlock)	650	150	3500	47	1324	3100	0.489	1	2	3

Variables are as follows: Age = maxium age (yr); DBH (cm); H = height (cm); GR = Growth rate (dimensionless); GDD− and GDD+ = minimum and maximum growing degree-days (5.56 °C base); DTmin = minimum depth to watertable (m); L = shade tolerance (rank 1 = very tolerant); M = drought tolerance (1 = least tolerant); N = nutrient stress tolerance (1 = least tolerant). Species variables were obtained from Pastor and Post (1985), except for DTmin values which were obtained from Botkin (1993).

methodology from models developed over 25 years ago, this class of individual-based models is thought to offer a reasonable approach to predict long-term responses of forest vegetation to environmental change (Malanson 1993a; Shugart and Smith 1996).

ZELIG represents a generic form of gap model designed to serve as a readily adaptable framework for cross-site comparisons of forested systems. In its original published form (Urban 1990), the only hydrological effect was that decreasing soil moisture would induce drought stress. Following Pastor and Post (1986), it uses a Thornthwaite bucket model to calculate monthly actual (AET) and potential evapotranspiration (PET) for given edaphic, i.e., field capacity (FC) and permanent wilting point (PWP), and climatic conditions, i.e., temperature and precipitation. To predict the effects of drought stress, a drought-day index, i.e., the proportion of days during the growing season in which soil moisture is below the PWP, is calculated annually. This index is incorporated into a growth multiplier which relates basal area growth to a given species-specific tolerance class. If PET $<$ precipitation, excess water is added to the soil-water column. If water depth exceeds the FC, it is treated as run-off. However, the terrain of the NEF is relatively flat and drainage tends to be slow. As a result, some soils remain saturated for periods exceeding the monthly time step. Such saturation may lead to anaerobic conditions which can affect root respiration, pH, decomposition of organic matter, and for less tolerant tree species, inhibit establishment and growth and increase mortality rates. Hence, ZELIG would have been incapable of reproducing the heterogeneity in forest composition and structure caused by soil saturation common to the NEF.

Like the maligned temperature relationship (Loehle and LeBlanc 1996), species responses to waterlogging stress has been to use crude parabolic (Phipps 1979; Pearlstine et al. 1985) or sigmoidal (Botkin and Levitan 1977) functions that relate to the optimal depth to water table for a species. However, as with all growth multipliers, each species probably possesses its own uniquely shaped soil saturation response curve (Malanson 1993b) which changes with growth. Furthermore, field measurements of forested wetlands in Minnesota showed aboveground net primary productivity and biomass to be more sensitive to fluctuations in groundwater than to average depth to water table (DT) (Grigal and Homann 1994). Thus, using an annual time increment and an average DT may be less appropriate than a seasonally or monthly changing water table.

Focusing on scaling effects, we modified and incorporated the simple waterlogging growth multiplier described in Botkin (1993) to the gap model. The original equation depicts a site wetness factor for a species (WeF_i) as:

$$WeF_i = \max[0, 1 - (DT\min_i/DT)], \qquad (1)$$

where $DT\min_i$ = minimum distance to the water table tolerable for species i and DT is the average growing season depth to water table. Because we believed that waterlogging-sensitive species were excessively penalized at depths to the water table well below the rooting zone, the growth multiplier was slightly modified to:

$$WeF_i = \begin{cases} 0 & \text{if } DT\min_i > DT, \\ (DT - DT\min_i)^2/[DT\min_i^2 + (DT - DT\min_i)^2] & \\ & \text{if } DT\min_i \le DT. \end{cases} \qquad (2)$$

This change maintains the general form of the growth multiplier, but reduces the differences among tolerance classes at high DTs (Figure 1) while approximating sigmoidal vegetation height patterns observed with increasing DT (Verry 1997). With this multiplier, there is a range of responses for the species pool available at the NEF (Table 1). Species can be grouped into waterlogging tolerance classes based on their DTmin's. Tolerant species with low DTmin's at the NEF include larch (*Larix laricina*) and northern white cedar (*Thuja occidentalis*). Intolerant species with high DTmin's include eastern white pine (*Pinus strobus*) and quaking aspen (*Betula populifolia*).

Derivation of soil moisture parameters

To obtain soil hydrology parameters necessary for the forest succession simulations, we used a soil process model FroST (Frozen Soil Temperatures). The FroST model (Levine and Knox 1997) was developed as a modification of the 'Residue' model described by Bristow et al. (1986) and Bidlake et al. (1992). FroST (Figure 2) simulates the dynamic aspects of mass and energy transfer in a soil-vegetation-atmosphere system using numerical methods to describe fundamental physical processes.

Although microtopographic effects play a significant role in soil saturation at the NEF, these are not modeled explicitly by the one-dimensional FroST. Soil mapping units, however, include topography as part of their distinguishing criteria and thus related effects are inherent to model parameterization. For this study, data for soil series (Table 2a) and relevant information for nodes at specific depths within horizons were obtained. Nodes were chosen either as midpoints within a soil horizon as described in the soil profile description or to represent a specific depth. Data for each soil node included: node depth (m), distance to next upper node (m), thickness of the soil layer (m), air-entry matric potential (J/kg), bulk density (Mg/m^3), slope of the log-transformed moisture characteristic, saturated hydraulic conductivity (kg s/m^3), particle density (Mg/m^3), clay mass fraction (%), initial soil temperature (°C), and initial volumetric water content (%). A saturated zone, the lower boundary soil node, was designated at a specific depth for each soil based on the hydrologic group classification given in the soil survey (USDA SCS 1990). The groups are defined by the Soil Survey Division Staff (1993) according to the saturated hydraulic conductivity and the depth to free water surface (water table). Group A has the highest conductivity and deepest occurrence of internal free water, and group D has the lowest conductivity and the shallowest occurrence of internal free water. For purposes of setting up the starting conditions for FroST, soils classified as group A were given an initial saturated horizon of 12 m, group B at 2.5 m, group C at 1.0 m, and group D at the soil surface (Table 2b).

Input data required for the canopy nodes were reflectivity, zero plane displacement height (m), and momentum roughness length (m), which were obtained from structural characteristics of vegetation at the NEF. Climate data for the years 1988-1992 collected at the NEF were used to drive the model using inputs: day of year, time of day, total incoming solar radiation (W/m^2), atmospheric air temperature (°C), atmospheric relative humidity (%), wind speed (m/s), and daily precipitation (cm).

Simulations and scaling procedures

Site characteristics (e.g., monthly average and standard deviation values of temperature and precipitation) and autecological parameters (e.g., tree age, height and diameter maxima; growth and sapling establishment rates; light, water, fertility, and temperature tolerances) were derived from empirical data and published sources (e.g., Pastor and Post 1985, Botkin 1993, Weishampel et al. 1997) for conditions and species at the NEF. Because the model contained stochastic elements (e.g., weather, mortality, and re-

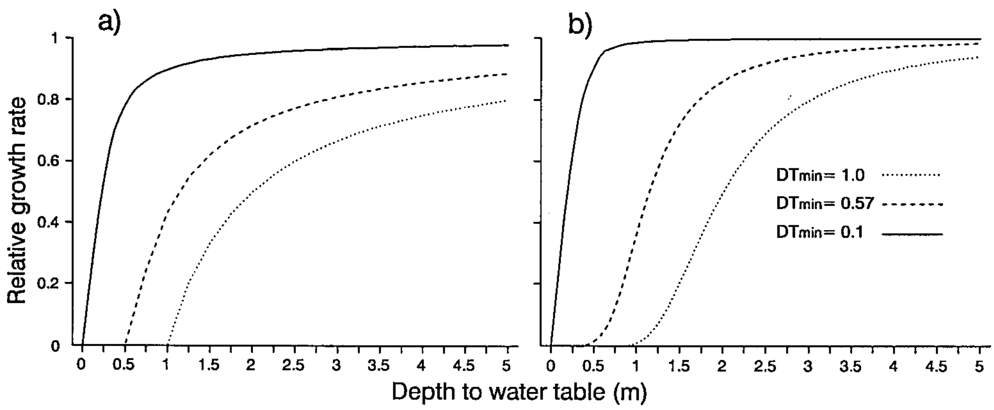

Figure 1. Comparison of species growth responses for (a) Botkin (1993) and (b) modified waterlogging growth multipliers.

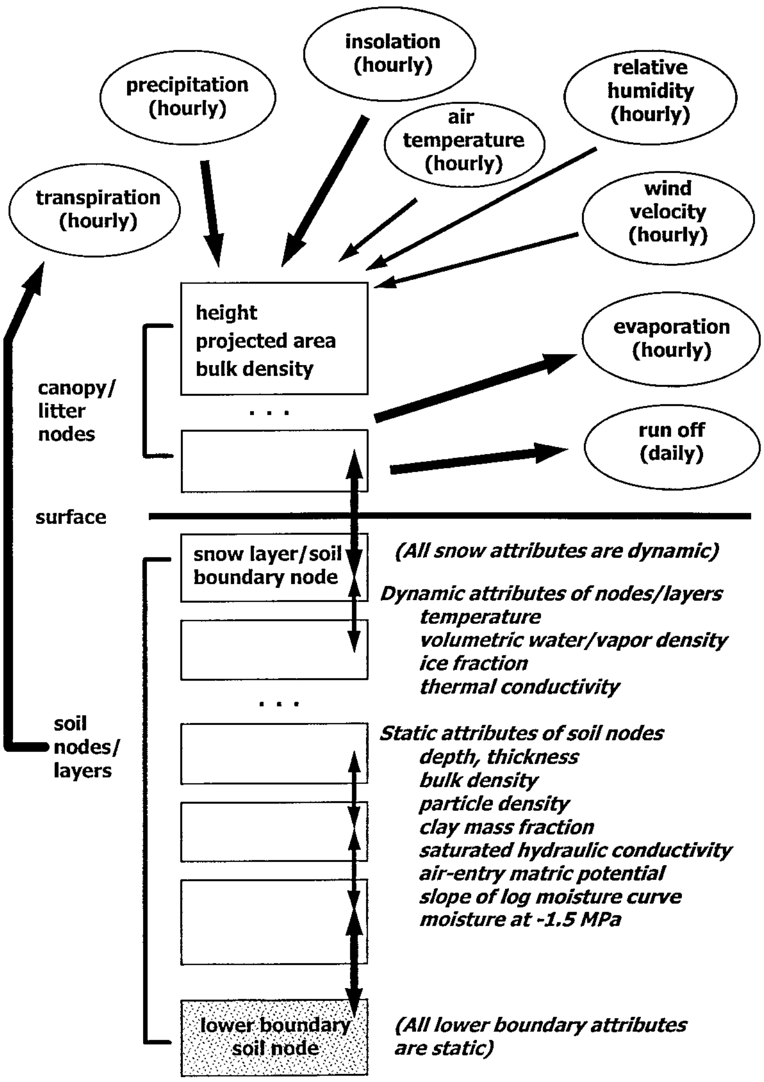

Figure 2. Schematic of fluxes in the soil physics model FroST version 1.1.

Table 2a. Dominant soil series found at the NEF at local, county and state scales.

Series	Drainage class	Parent material
Adams[1] (Typic Haplorthod)	Somewhat excessively	Outwash
Biddeford[2] (Histic Humaquept)	Very poorly	Marine sediments
Boothbay[1] (Aquic Eutrochrept)	Somewhat poorly	Lacustrine and marine sediments
Brayton[3,4] (Aeric Haplaquod)	Poorly	Till
Burnham[2,3] (Typic Haplaquept)	Somewhat poorly	Till
Buxton[3,4] (Dystric Eutrochrept)	Somewhat poorly	Lacustrine and marine sediments
Colonel[1] (Aquic Haplorthod)	Somewhat poorly	Till
Croghan[1] (Aquic Haplorthod)	Somewhat poorly	Outwash
Dixfield[1] (Typic Haplorthod)	Moderately well	Till
Hermon[3,4] (Typic Haplorthod)	Somewhat excessively	Outwash
Howland[2,3](Aquic Haplorthod)	Somewhat poorly	Till
Kinsman[1] (Aquic Haplorthod)	Very poorly	Outwash
Lyman[4] (Lithic Haplorthod)	Somewhat excessively	Bedrock
Marlow[1] (Typic Haplorthod)	Well	Till
Masardis[3,4] (Typic Haplorthod)	Somewhat excessively	Outwash
Medomak[5] (unknown)	Very poorly	Alluvium
Monarda[2] (Aeric Haplaquod)	Poorly	Till
Monson[4] (Lithic Dystrochrept)	Somewhat excessively	Bedrock
Peacham[1] (Histic Humaquept)	Very poorly	Till
Plaisted[2] (Typic Haplorthod)	Well	Till
Roundabout[5] (unknown)	Poorly drained	Alluvium
Scantic[1] (Typic Haplaquept)	Poorly	Lacustrine and marine sediments
Tunbridge[3,4](Entic Haplorthod)	Moderately well	Till
Westbury[1] (Aeric Haplaquod)	Poorly	Till
Wonsqueak[5] (unknown)	Very poorly	Organic Materials

[1]Data derived from Soil Survey of NEF (USDA SCS 1990).
[2]Data dervied from Penobscot County Soil Survey Report (Goodman et al. 1963).
[3]Used input file from similar soil (see Tables 3b and 3c).
[4]Data derived from STATSGO data base (USDA SCS 1993).
[5]Not included in this study.

cruitment), replicates with different random number seeds were averaged to estimate the system's behavior. Thirty runs, each consisting of nine, spatially independent 10 $\times$ 10 m plots, were simulated starting from bare ground conditions for each of the 14 soils series which comprise approximately 95% of the NEF (Table 2). To isolate soil moisture effects, differences in nutrient status of the soil series were not included even though nutrient availability is a function of decomposition which is reduced by waterlogged conditions. For comparison, half of the simulations did not include waterlogging effects and used laboratory estimates of FC, the other half included waterlogging effects and used estimates of DT and effective FC predicted with FroST. Laboratory estimates of FC and PWP were derived from measurements of soil moisture at -0.03 MPa and -1.5 MPa, respectively. These were obtained by pressure-plate extraction techniques (USDA NRCS 1996) for soil samples of the predominant soil series found at the NEF (USDA SCS 1990).

Aboveground productivity from the simulations for the different soil types were aggregated for a 600 ha area extracted from local (1:12,000), county (1:120,000), and state (1:250,000) soil maps. These simulations represent direct extrapolation using different scales of parameter lumping. The local map was created as a soil survey of part of the NEF in 1990 by the USDA Soil Conservation Service in Orono, ME (USDA SCS 1990). Soil series distributions at the county scale were obtained by digitizing the soil maps associated with the study area from a 1963 USDA county soil survey of Penobscot County, Maine (Goodman et al. 1963). Additional information regarding the local and county soil maps is available at the Forest Ecosystem Dynamics WWW site (Fifer

Table 2b. Hydrologic soil grouping, measured PWP and predicted DT for selected soil series used as inputs to FroST.

Series	Hydrologic group	Summed laboratory PWP (cm)	Modeled DT (m)
Adams	A	4.8	4.00
Biddeford	D	22.1	0.00
Boothbay	C	12.8	0.35
Colonel	C	9.6	1.23
Croghan	B	10.3	1.05
Dixfield	C	8.1	3.4
Kinsman	C	10.8	0.84
Marlow	C	8.7	3.3
Monarda	C	6.3	0.34
Peacham	D	15.0	0.62
Plaisted	A	3.8	3.0
Scantic	C	18.2	0.25
Westbury	C	5.7	0.71
Lithic*	A	2.9	10.00

*Category included to account for Lyman and Monson series identified at the state level in the STATSGO database without an analog at local or county levels.

1998). At the state level, soil polygon data were obtained from the State Soil Geographic data base (STATSGO) map for Maine (USDA SCS 1993).

Because land area represented by a given map increases as scale decreases, less detail is depicted on smaller scale maps, i.e., maps with coarser resolution. Thus, generalized maps of counties or states rarely consist of mapping units comprised of a single soil series. More often, these mapping units represent associations of more than one soil series or other taxonomic unit (e.g., soil family, subgroup, or great group). The 600 ha map at the local scale consisted of eight soil associations consisting of twelve soil series; at the county scale, five soil series comprised four associations; and at the state scale, thirteen soil series comprised a single association (Figure 3). The contribution of each association to the overall productivity of the landscape was weighted according to its areal extent. Within each association, the contribution of each series was weighted based on its percent composition. Table 2a gives the taxonomic classification, drainage class, and parent material of all the soil series used at each scale in this study. Because soil series not present in the local map existed in the smaller scale maps, analogs from the local map (Table 3) were substituted where appropriate. Three associations that

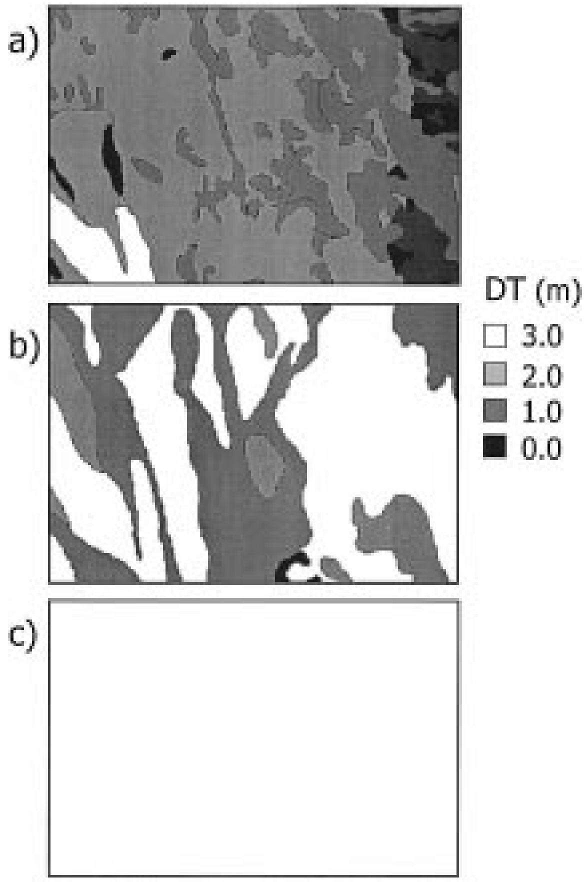

Figure 3. Spatial distribution of NEF soil associations for a 600 ha area from the (a) local (1:12,000), (b) county (1:120,000), and (c) state (1:250,000) maps. Gray shades correspond area-weighted average depths to water table for associations listed in Table 3.

comprised a small fraction (<1.25%) of the local and county scale data (and for which there was insufficient information to parameterize FroST) were excluded in the weighted aggregation. In the case of the STATSGO data, two lithic (shallow to bedrock) soil series, Lyman and Monson, which together comprise 15% of the association, did not have an appropriate analog at the local scale. To include these soil series in the scaling exercise, new soil hydrology parameters were estimated with FroST based on their description. Differences in biomass levels for simulations with and without waterlogging and for the three scales of aggregation were evaluated using ANOVA and Duncan's multiple comparison tests at 50 year intervals.

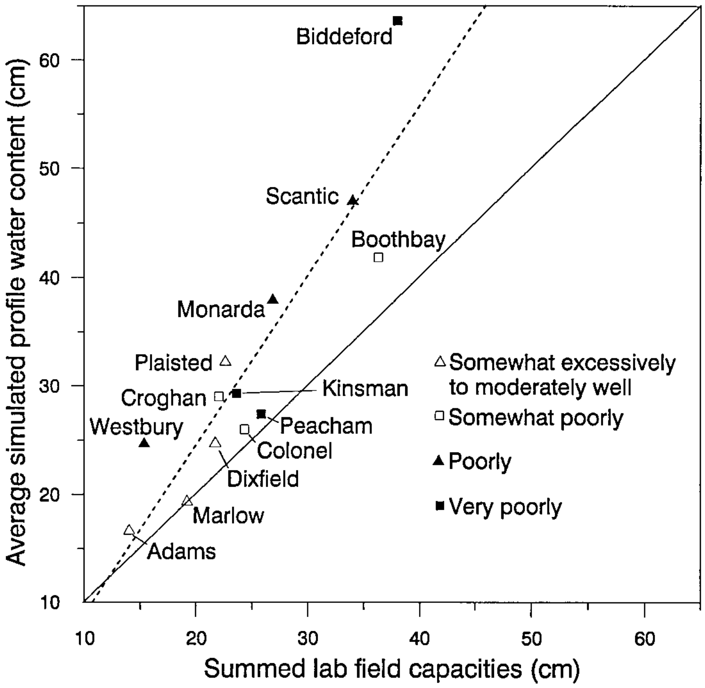

Figure 4. Comparison between measured and modeled field capacities for the predominant soil series (excluding lithic soils) at the NEF. The solid line is a 1:1 correspondence between the measured and modeled field capacities; the dashed line is a regression line of the relationship.

Results

Predictions of soil water conditions

For the 13 predominant soil series at the NEF (excluding the lithic soils), sums of laboratory field capacities were correlated with average moisture levels in FroST simulations (R^2 = 0.82, $P < 0.001$), but many soils retained more moisture in the multilayer simulations than would be expected from simple pressure plate measurements on isolated soil samples (Figure 4). The somewhat excessively drained soil, Adams, and the very poorly drained soil, Biddeford, possessed the lowest and the highest moisture levels, respectively, in both the summed laboratory FC and the average simulated profile water content estimates. In general, the better drained soils exhibited lower field capacities than the more poorly drained soils. Poorly drained soils had the larger excesses over those expected from laboratory FC with free drainage.

FroST yielded a range of depths to water table for the soil series (Table 2b). To a certain extent, these predictions corresponded to drainage class, i.e., well drained soils had deeper DTs than more poorly drained soils. The somewhat excessively to moderately well drained soils were on average 2.8 m deeper than the more poorly drained soils. Though average DT for the somewhat poorly drained class was greater than the averages for the poorly and the very poorly drained classes as expected, the average for the poorly drained class was less deep than the average for the very poorly drained class. Laboratory data for the Kinsman series were from a somewhat poorly drained profile rather than the very poorly drained ‘taxadjunct’ Kinsman soils mapped at the NEF. Peacham soils found in depressions with better drained series were possibly more difficult to simulate correctly without lateral water movement.

Waterlogging effects on species composition

Using ZELIG without the waterlogging multiplier, edaphic responses were a result of drought effects determined by FC and PWP estimates. However, given the cold, humid (80–100 cm precipitation/year), continental climate of the NEF, typically AET = PET, thus species responses were very similar for the different soil drainage classes (Figure 5a). Intermediately waterlogging tolerant species, primarily red spruce (*Picea rubens*) and paper birch (*Betula papyrifera*), dominated the stand throughout the 200 year simulation. Waterlogging intolerant species outcompeted

Table 3a. Composition of 600 ha NEF area using information from the 1:12,000 local soil map (USDA SCS 1990).

Soil association	Percent composition of landscape	Series comprising soil association	Percent composition of association*
Colonel-Westbury	50.61	Colonel	50
		Westbury	50
Colonel-Dixfield	21.59	Colonel	50
		Dixfield	50
Peacham-Westbury	8.08	Peacham	70.6
		Westbury	29.4
Boothbay-Scantic	6.05	Boothbay	50
		Scantic	50
Croghan-Kinsman	5.22	Croghan	56.3
		Kinsman	43.7
Colonel-Dixfield-Marlow	4.83	Colonel	17.6
		Dixfield	47.1
		Marlow	35.3
Biddeford	2.45	Biddeford	100
Bucksport-Wonsqueak**	0.93	Bucksport	60
		Wonsqueak	40
Roundabout-Medomak**	0.24	Roundabout	35
		Medomak	65

*Does not account for inclusions.
**Not included in aggregation.

tolerant species during the early stages of succession, but were supplanted by waterlogging tolerant species after ≈ 75 years. Overall basal area on the somewhat excessively drained soil was reduced due to drought effects.

When including the waterlogging multiplier, species trajectories varied based on the drainage class of the soil (Figure 5b) as found with earlier simulations (Botkin et al. 1989; Botkin and Nisbet 1992a, 1992b, Botkin 1993) based on the Botkin and Levitan (1977) multiplier. Well drained soils revealed little difference from those without waterlogging. As DT decreased, species trajectories changed so that the importance of more waterlogging tolerant species increased. For the somewhat poorly drained soil, tolerant species accounted for roughly a third of the entire basal area after 100 years. In the scenario with very poorly drained soil, tolerant species, primarily northern white cedar (*Thuja occidentalis*), were the only ones which persisted, consistent with NEF field data (Levine et al. 1994).

Waterlogging effects on aboveground biomass

Without waterlogging, simulations using the soil series at the NEF all exhibited a similar sigmoidal pattern of aboveground biomass accumulation (depicted by the better drained soils in Figure 6) leveling off at ≈100 years. However, the amount of biomass at 200 years ranged between 100 and 200 mg/ha. These differences are primarily related to drought effects. The correlation coefficient between the average biomass levels between 50 and 200 yr and the difference between FC and PWP, i.e., the available moisture content, was 0.86 ($P < 0.001$). Available moisture content, however, does not necessarily correspond to drainage class; e.g., available moisture content for the Plaisted series, although it is well drained due to its gravelly loam texture, is comparable to a poorly drained soil series such as Monarda which is classified as a silt loam.

With waterlogging and simulated field capacity, biomass trajectories segregated according to drainage classes. More poorly drained soils were less productive than better drained soils during the first 100 years of succession (Figure 6). However, by 150 years, biomass levels from some of the poorly drained

Table 3b. Composition of 600 ha NEF area using information from the 1:120,000 county soil map (Goodman et al. 1963). Analogs for series are in parentheses.

Soil association	Percent composition of landscape	Series comprising soil association	Percent composition of association*
PrC	58.41	Plaisted	100
MrB	32.46	Monarda	50
		Burnham (Colonel)	50
HvB	8.60	Howland (Croghan)	100
Mu**	0.54	Muck	100

*Does not account for inclusions.
**Not included in aggregation.

Table 3c. Composition of 600 ha NEF area using information from the 1:250,000 state soil map (USDA SCS 1993). Analogs for series are in parentheses.

Soil association	Percent composition of landscape	Series comprising soil association	Percent composition of association*
ME008	100	Brayton (Westbury)	20
		Dixfield	12
		Hermon (Adams)	11
		Lyman (Lithic)	11
		Peacham	11
		Biddeford	8
		Colonel	7
		Marlow	6
		Monson (Lithic)	4
		Buxton (Boothbay)	3
		Scantic	3
		Masardis (Adams)	2
		Tunbridge (Dixfield)	2

*Does not account for inclusions.

soils exceeded those without waterlogging which may reflect the absence of saturation-related nutrient differences. In general, these trajectories resembled the growth patterns of tolerant species in very poorly drained soils (Figure 5). One very poorly drained soil series, Biddeford, which corresponds to open bogs in the NEF landscape, possessed a DT estimated at 0 m and yielded no tree growth as expected with the waterlogging function.

Scaling effects

The aggregative effect from waterlogging across the 600 ha landscape was similar to effects on soil series with slower drainage rates, i.e., aboveground biomass levels were significantly lower during the first 100 years (Figure 7). Waterlogging amounted up to a 40% reduction for the local-scale and state-scale projections and up to a 20% reduction for the county level projections in biomass. After 125 years, aboveground biomass from the simulations with waterlogging converged with the simulations without waterlogging. This waterlogging effect was fairly consistent among various scales. However, absolute levels of biomass varied substantially, maintaining up to a 40% difference between the projections based on state and county data. Soil composition data from the county map (1:120,000 scale) yielded the highest biomass levels, nearly 200 mg/ha after 200 years.

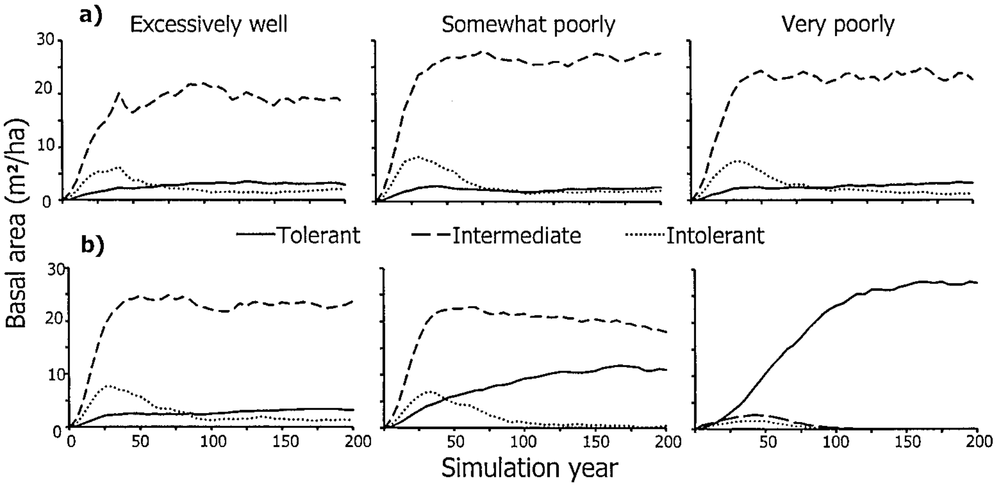

Figure 5. Average species trajectories for three drainage classes for simulations (a) without and (b) with the waterlogging growth multiplier. The tolerant class includes all NEF tree species with DTmin $\leq$ 0.3 m; for intermediate, 0.3 m $<$ DTmin $<$ 0.6 m; for intolerant, DTmin $\geq$ 0.6 m.

Soil composition data from the state map (1:250,000 scale) yielded the lowest biomass levels, approximately 120 mg/ha at 200 years. The biomass levels derived with information from the local map approached 160 mg/ha at 200 years. Though these levels were inconsistent with water table depths based on area-weighted averages (Figure 3) of the landscape, they were closely aligned with the average annual drought-day indices based on area-weighted soil responses. This is related to the available soil moisture (i.e., FC - PWP) which was highest for the county and lowest for the state soil maps.

Discussion

Successional pathways of southern boreal-northern hardwood forests are highly dependent on edaphic conditions which tend to be fairly heterogeneous (Pastor and Mladenoff 1992; Levine et al. 1994). Most global warming scenarios predict increased temperatures and higher evaporative demand for this transition zone that should lead to warmer substrates and lowered water tables (Price and Apps 1993). Hence, the inclusion of water table dynamics may be critical to how forests occupying poorer draining soils respond.

However, predicting landscape-level responses of these diverse systems is not as straightforward as running patch scale models using coarse-scale soil hydrological parameters. In terms of the forest model, this approach treated soil moisture properties (i.e., DT, FC, PWP) as a static. To more realistically simulate soil hydrology, a direct coupling of hydrological and ecological dynamics would be needed to adjust for shifts in AET associated with successional changes in the forest composition. When an evapotranspirative feedback was included from a gap model to a biophysical atmospheric model (Martin 1992), it was found that soil drying increased dramatically causing a shift from forests to grasslands. This implies that water table drawdown by AET could promote a change from waterlogging tolerant to less tolerant species as found on the better drained soils. Thus, there is a need to create physiologically tractable growth relationships (Bonan 1993; Bugmann and Martin 1995) which relate to soil saturation for these models.

Although changes in DT were not included as part of climate change scenarios using a similar growth multiplier approach (Botkin 1993), a sensitivity analysis of a gap model by Botkin and Nisbet (1992b) showed slight DT changes ($\pm$10%) produced minor change in forest structure for a given soil. Parameters derived from the soil physics model for the variety of soils found at the NEF were substantially different and yielded dramatic differences in species composition and aboveground biomass levels. Differences in DT from somewhat excessively drained to very poorly drained soil series were much larger than the 2–6 cm differences tested by Botkin and Nisbet (1992b). If DTs were to increase to levels found in drier soil series, the NEF could exhibit a change in species composition that corresponds to an increase in aboveground productivity during early stages of

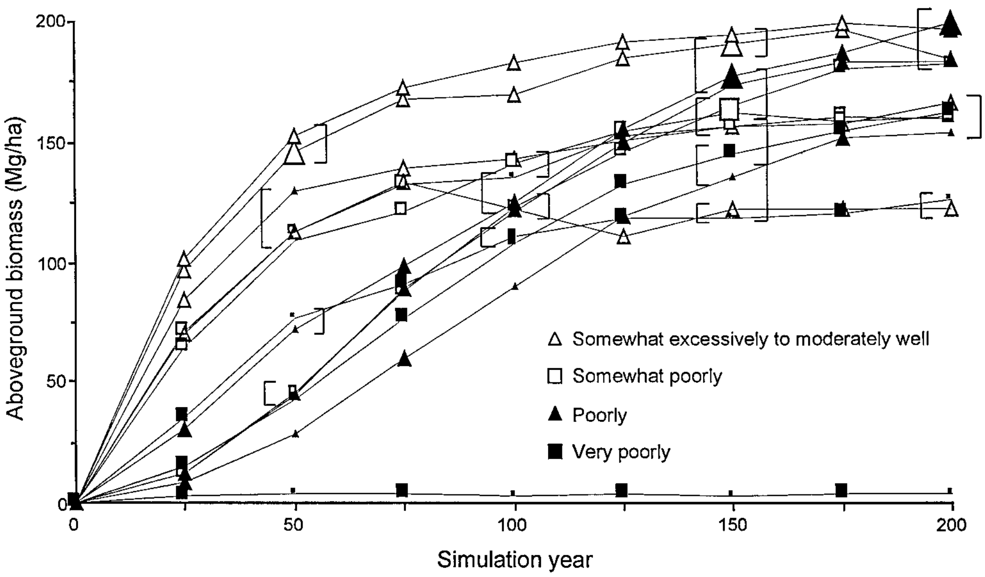

Figure 6. Average aboveground biomass trajectories for the 13 predominant soil series with the waterlogging growth multiplier. At 50, 100, 150, and 200 years, enlarged and reduced markers respectively represent significantly ($P < .05$) higher and lower biomass levels than simulations without the waterlogging growth multiplier. Brackets at these time steps indicate biomass levels that are not significantly different.

succession. Thus, more poorly drained regions may accumulate biomass more rapidly and better function as aboveground carbon sinks with increasing temperatures and drier conditions. This is somewhat analogous to drainage practices that are commonly used to reclaim northern wetlands for forestry (Vompersky and Sirin 1997).

Based on the aggregated landscape, regardless of scale, effects of waterlogging (in the absence of fertility-related effects) on aboveground biomass were most apparent during early periods of succession. After 125 years, aboveground biomass trajectories from the aggregate landscape that included waterlogging effects converged with null model runs. This similarity was surprising as the edaphic information regarding the areal extent of drainage classes from the three different soil maps varied considerably (Figure 3). At the local scale, poorly and very poorly drained soils comprised <50% of the 600 ha NEF area. Compared to the local soil map, the state map overestimated somewhat excessively drained soils for the 600 ha landscape. Compared to the local soil map, the county map underestimated and overestimated the extent of poorly and well-drained soils, respectively.

It was not expected that scaled-up predictions based on lumped soil properties would agree with those based on more edaphic heterogeneity. Certain local areas may be wetter or drier on average than others and such fine-scale patterns may not be captured with coarser mapping units. This was the situation with area-weighted average DT (Figure 3) which increased from 1.3 to 2.1 to 3.0 m as scale increased. However, area-weighted FC and PWP depths did not follow a similar, regular change with coarsening map resolution. When aggregated across the NEF landscape, differences in these scaled variables turned out to be more critical than DT-related effects associated with using coarser soil information to simulate forest dynamics. Differences in drought-related stress resulting from differences in available soil moisture reduced aboveground biomass more than soil saturation effects. Nevertheless, the relative effects of waterlogging to drought were consistent as scales changed.

In this exercise, the choice of which geospatial information was used was more critical than whether or not soil saturation effects were included. As a result of how soil properties for an arbitrarily chosen 600 ha area from the NEF were lumped, model predictions based on data from county soil map overestimated and those based on the state soil map underestimated productivity levels when compared to those based on the more detailed local soil map. This 40% range in productivity predictions demonstrates how aggregation error from decreasing map scale could be propagated by simulations that rely on map data. Furthermore, the

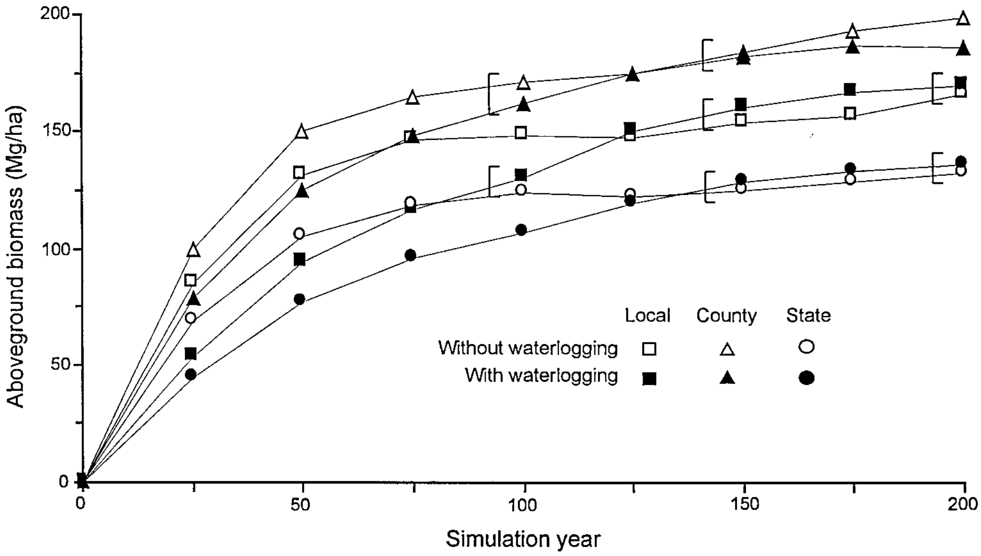

Figure 7. Aboveground biomass trajectories aggregated to a 600 ha area based on soil information from maps of the local (1:12,000), county (1,120,000), and state (1:250,000) scales for simulations with and without waterlogging. Brackets at 50, 100, 150, and 200 years indicate biomass levels that are not significantly different.

fact that biomass levels increased as map resolution decreased from 1:12,000 to 1:120,000 then decreased as map resolution decreased from to 1:120,000 to 1:250,000 suggests that there are no simple scaling rules for soil heterogeneity which could be applied for this area. Hence, this study reinforces the idea (Kirkby et al. 1996) that the process of scaling-up may not be easily achieved by running multiple patch scale models for heterogeneous areas and summing their results. Moreover, renormalization (Johnson 1996) of geospatial data may be needed to minimize aggregation error associated with parameter lumping.

Acknowledgements

Research was supported in part by an National Research Council (NRC) Research Associateship and by funding for the Forest Ecosystem Dynamics (FED) project through NASA's Terrestrial Ecosystem and Modeling Program (NAG 5-3262). The authors would like to thank Steve Fifer for assisting with the geographical analysis, Dean Urban with help in estimating tree species parameters and providing the ZELIG source code, and three anonymous reviewers for their insightful comments.

References

Bidlake, W. R., Campbell, G. S., Papendick, R. I. and Cullum, R. F. 1992. Seed zone temperature and moisture conditions under conventional and no-tillage in Alaska. Soil Sci Am J 56: 1904–1910.

Bonan, G. B. 1993. Do biophysics and physiology matter in ecosystem models? Climatic Change 24: 281–285.

Bonan, G. B. and Shugart, H. H. 1989. Environmental factors and ecological processes in boreal forests. Ann Rev Eco Syst 20: 1–28.

Botkin, D. B. 1993. Forest Dynamics: An Ecological Model. Oxford Univ. Press, New York.

Botkin, D. B. and Levitan, R. E. 1977. Wolves, moose and trees: an age specific trophic-level model of Isle Royale National Park. IBM Research Report in Life Sciences RC 6834.

Botkin, D. B. and Nisbet, R. A. 1992a. Projecting the effects of climate change on biological diversity in forests. *In* Consequences of the Greenhouse Effect for Biological Diversity. pp. 277–293. Edited by R. Peters. Yale Univ. Press, New Haven, Connecticut.

Botkin, D. B. and Nisbet, R. A. 1992b. Forest response to climatic change: effects of parameter estimation and choice of weather patterns on the reliability of projections. Climatic Change 20: 87–111.

Botkin, D. B., Nisbet, R. A. and Reynales, T. E. 1989. Effects of climate change on forests of the Great Lake States. *In* The Potential Effects of Global Climate Change on the U. S., Appendix D – Forests. Edited by J. B. Smith and D. A. Tirpak. U. S. EPA, Washington DC.

Bristow, K. L., Campbell, G. S., Papendick, R. I. and Elliot, L. F. 1986. Simulation of heat and moisture transfer through a surface residue-soil system. Agric For Meterol 36: 193–214.

Bugmann, H. and Martin, P. 1995. How physics and biology matter in forest gap models. Climatic Change 29: 251–257.

Bugmann, H. K. M. and Solomon, A. M. 1995. The use of a European forest model in North America: a study of ecosystem response to climate gradients. J Biogeogr 22: 477–484.

Fifer, S. 1998. Forest Ecosystem Dynamics (FED) welcome page: Available as: http://fedwww.gsfc.nasa.gov.

Glebov, F. Z. and Korzukhin, M. D. 1992. Transitions between boreal forest and wetland. *In* A Systems Analysis of the Global Boreal Forest. pp. 241–266. Edited by H. H. Shugart, R. Leemans and G. B. Bonan. Cambridge Univ. Press, New York.

Goodman, V., Riley, R. M., Whitney, B. A., Arno, J. R., La Flamme, K. J., Von Day, S., Hardesty, J. S., Lovejoy, D. B. and Worcester, B. 1963. Soil Survey of Penobscot County, Maine. U.S. Govt. Printing Office, Washington, D.C.

Goward, S. N., Williams, D. L. and Peterson, D. L. 1994. NASA multisensor aircraft campaigns for the study of forest ecosystems. Remote Sens Environ 47: 107–108.

Grigal, D. F. and Homann, P. S. 1994. Nitrogen mineralization, groundwater dynamics, and forest growth on a Minnesota outwash landscape. Biogeochemistry 27: 171–185.

Johnson, A. R. Spatiotemporal hierarchies in ecological theory and modeling. 1996. *In*: GIS and Environmental Monitoring: Progress and Research Issues. pp. 451–456. Edited by M. F. Goodchild, L. T. Steyaert, B. O. Parks, C. Johnston, D. Maidment, M. Crane, and S. Glendinning. GIS World Books, Fort Collins, CO.

Kimmins, J. P. 1996. Importance of soil and role of ecosystem disturbance for sustained productivity of cool temperate and boreal forests. Soil Soc Am J 60: 1643–1654.

King, A. W. 1991. Translating models across scales in the landscape. *In* Quantitative Methods in Landscape Ecology. pp. 479–517. Edited by M. G. Turner and R. H. Gardner. Springer-Verlag, New York.

Kirkby, M. J., Imeson, A. C., Bergkamp, G., and Cammeraat, L. H. 1996. Scaling up processes and models from the field plot to the watershed and regional areas. J Soil Water Cons 51: 391–396.

Knox, R. G., Kalb, V. L., Levine, E. R. and Kendig, D. J. 1997. A problem-solving workbench for interactive simulation of ecosystems. IEEE Comp Sci Eng 4: 52–60.

Levine, E. R., Ranson, K. J., Smith, J. A., Williams, D. L., Knox, R. G., Shugart, H. H., Urban, D. L. and Lawrence, W. T. 1993. Forest ecosystem dynamics: linking forest succession, soil process and radiation models. Ecol Model 65: 199–219.

Levine, E. R., Knox, R. G. and Lawrence, W. T. 1994. Relationships between soil properties and vegetation at the Northern Experimental Forest, Howland, Maine. Remote Sens Env 47: 231–241.

Levine, E. R. and Knox, R. G. 1997. Modeling soil temperature and snow dynamics in northern forests. J Geophys Res Atmos 102: 29407–29416.

Loehle, C. and LeBlanc, D. 1996. Model-based assessments of climate change effects on forests: a critical review. Ecol Model 90: 1–31.

Malanson, G. P. 1993a. Comment on modeling ecological response to climatic change. Climatic Change 23: 95–109.

Malanson, G. P. 1993b. Riparian Landscapes. Cambridge University Press, New York.

Martin, P. 1992. EXE: a climatically sensitive model to study climate change and CO_2 enhancement effects on forest. Aust J Bot 40: 717–735.

O'Neill, R. V. 1988. Hierarchy theory and global change. *In* Scales and Global Change. pp. 29–45. Edited by T. Rosswall, R. G. Woodmansee and P. G. Risser. John Wiley & Sons Ltd., New York.

Pastor, J. and Mladenoff, D. J. 1992. The southern boreal-northern hardwood forest border. *In* A Systems Analysis of the Global Boreal Forest. pp. 216–240. Edited by H. H. Shugart, R. Leemans and G. B. Bonan. Cambridge University Press, New York.

Pastor, J. and Post, W. M. 1985. Development of a linked forest productivity-soil process model. ORNL/TM-9519. Oak Ridge National Lab, Oak Ridge, TN.

Pastor, J. and Post, W. M. 1986. Influence of climate, soil moisture, and succession on forest carbon and nitrogen cycles. Biogeochemistry 2: 3–27.

Pastor, J. and Post, W. M. 1988. Response of northern forest to CO_2-induced climate change. Nature 334: 55–58.

Pearlstine, L., McKellar, H. and Kitchens, W. 1985. Modelling the impacts of a river diversion on bottomland forest communities in the Santee River floodplain, South Carolina. Ecol Model 29: 283–302.

Phipps, R. L. 1979. Simulation of wetlands forest vegetation dynamics. Ecol. Model. 7: 257-288.

Price, D. T. and Apps, M. J. 1993. Integration of boreal ecosystem-process models within a prognostic carbon budget model for Canada. World Res Rev 5: 15–31.

Ranson, K. J. and Sun, G. 1994a. Mapping biomass of a northern forest using multifrequency SAR data. IEEE Trans Geosci Rem Sens 32: 388–396.

Ranson, K. J. and Sun, G. 1994b. Northern forest classification using temporal multifrequency and multipolarimentric SAR images. Rem Sens Environ 47: 142–153.

Rastetter, E. B., King, A. W., Cosby, B. J., Hornberger, G. M., O'Neill, R. V., and Hobbie, J. E. 1992. Aggregating fine-scale ecological knowledge to model coarser-scale attributes of ecosystems. Ecol Appl 2: 55–70.

Rourke, R. V., Ferwerda, J. A. and LaFlamme, K. J. 1978. The soils of Maine. Misc. Rep. No. 203. Life Sciences and Agric Exp Station and USDA SCS, University of Maine, Orono, ME.

Shao, G., Schall, P. and Weishampel, J. F. 1994. Dynamic simulations of mixed broadleaved-Manage *Pinus koraiensis* forests in the Changbaishan Biosphere Reserve of China. For Ecol 70: 169–181.

Shugart, H. H. 1996. Importance of structure in understanding global change. *In* Global Change and Terrrestrial Ecosystems. p. 117–126. Edited by B. Walker and W. Steffen. Cambridge University Press, New York.

Shugart, H. H. and Smith, T. M. 1996. A review of forest patch models and their application to global change research. Climatic Change 34: 131–153.

Shugart, H. H., Smith, T. M. and Post, W. M. 1992. The potential for application of individual-based simulation models for assessing the effects of global change. Ann Rev Ecol Syst 23: 15–38.

Soil Survey Division Staff. 1993. Soil survey manual. USDA Handbook No. 18. U.S. Govt Printing Office, Washington, D.C.

Solomon, A. M. 1986. Transient response of forests to CO_2-induced climate change: simulation modeling experiments in eastern North America. Oecologia 68: 567–579.

Solomon, A. M. 1992. The nature and distribution of past, present and future boreal forests: lessons for a research and modeling agenda. *In* A Systems Analysis of the Global Boreal Forest. Pp. 291–307. Edited by H. H. Shugart, R. Leemans and G. B. Bonan. Cambridge University Press, New York.

Urban, D. L. 1990. A versatile model to simulate forest pattern: a user's guide to ZELIG version 1.0. University of Virginia, Charlottesville, VA.

Urban, D. L., Bonan, G. B., Smith T. M. and Shugart. H. H. 1991. Spatial applications of gap models. For Ecol Manage 42: 95–110.

USDA NRCS. 1996. Soil survey laboratory methods manual. Soil Survey Investigations Report No. 42., Ver. 3.0. USDA, Natural Resources Conservation Service, National Soil Survey Center, Lincoln, NE.

USDA SCS. 1971. Handbook of soil survey investigations field procedures. U. S. Govt Printing Office, Washington, DC.

USDA SCS. 1990. Soil survey and interpretations of selected land in Maine. International Paper Company Experimental Forest, Howland, Maine. USDA, SCS, Orono, ME.

USDA SCS. 1993. State soil geographic data base (STATSGO): Data users guide. Misc. Pub. No. 1492. USDA, Natural Resources Conservation Service, Lincoln, NE.

van der Heijde, P. K. M. 1988. Spatial and temporal scales in groundwater modelling. *In* Scales and Global Change. pp. 195–223. Edited by T. Rosswall, R. G. Woodmansee and P. G. Risser. John Wiley & Sons Ltd., New York.

Verry, E. S. 1997. Hydrological processes of natural northern forested wetlands. *In* Northern Forested Wetlands: Ecology and management. pp. 163–188. Edited by C. C. Trettin, M. F. Jurgensen, D. F. Grigal, M. R. Gale and J. K. Jeglum. Lewis Pub., New York.

Vompersky, S. E. and Sirin, A. A. 1997. Hydrology of drained forested wetlands. *In* Northern Forested Wetlands: Ecology and Management. pp 189–211. Edited by C. C. Trettin, M. F. Jurgensen, D. F. Grigal, M. R. Gale and J. K. Jeglum. Lewis Pub., New York.

Weishampel, J. F., Knox, R. G., Ranson, K. J., Williams, D. L. and Smith, J. A. 1997. Integrating remotely sensed spatial heterogeneity with a 3-D forest succession model. *In* The Use of Remote Sensing in the Modeling of Forest Productivity at Scales from the Stand to the Globe. pp. 109–133. Edited by H. L. Gholz, K. Nakane and H. Shimoda. Kluwer Academic Publishers, Dordrecht, the Netherlands.