

SPATIALLY EXPLICIT AND STOCHASTIC SIMULATION OF FOREST- LANDSCAPE FIRE DISTURBANCE AND SUCCESSION

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Abstract. Understanding disturbance and recovery of forest landscapes is a challenge because of complex interactions over a range of temporal and spatial scales. Landscape simulation models offer an approach to studying such systems at broad scales. Fire can be simulated spatially using mechanistic or stochastic approaches. We describe the fire module in a spatially explicit, stochastic model of forest landscape dynamics (LANDIS) that incorporates fire, windthrow, and harvest disturbance with species-level succession. A stochastic approach is suited to forest landscape models that are designed to simulate patterns over large spatial and time domains and are not used deterministically to predict individual events.

We used the model to examine how disturbance regimes and species dynamics interact across a large (500 000 ha), heterogeneous landscape in northern Wisconsin, USA, with six land types having different species environments, and fire disturbance return intervals varying from 200 to 1000 yr. The model shows that there are feedbacks over time between species, disturbance, and environment, resulting in the re-emergence of patterns that characterized the landscape before extensive alteration. Landscape equilibrium of species composition and age-class structure develops at three scales from the initial, disturbed landscape. Over 100–150 yr, fine-grained successional processes cause gradual disaggregation of the initial pattern of relatively homogenous composition and age classes. Species such as eastern hemlock (*Tsuga canadensis*), largely removed from the landscape by past human activities, only slowly re-invade. Next, patterns on the various land types diverge, driven by different disturbance regimes and dominant species. Finally, aging of the landscape causes the probabilities of larger and more severe fires to increase, and a coarse-grained pattern develops from the disturbance patches. Influence of adjacent land types is shown as fires spread across land type boundaries, although modified in spread and severity. As found by others, altered landscapes are likely to retain their modified pattern for centuries, suggesting that nonequilibrium conditions between tree species and climate will persist under predicted rates of climate change.

The results suggest that this modeling approach can be useful in examining species-level, broad-scale responses of heterogeneous landscapes to changes in landscape disturbance, such as modified management or land-use scenarios, or effects of global change.

Key words: *fire distributions; fire disturbance; heterogeneity; ignition and spread; LANDIS; landscape ecology; landscape equilibrium; landscape model; spatially explicit and stochastic; species resilience; succession; verification and calibration.*

INTRODUCTION

Significant theoretical and empirical advances have been made in the past two decades in understanding the nonequilibrium nature of forest communities and ecosystems (Pickett et al. 1994), and the importance of periodic disturbance in driving recovery, compositional change, and feedbacks in ecosystem processes (e.g., Loucks 1970, Shugart 1984, Pastor and Post 1986). Applying these advances to large, heterogeneous landscapes, with varying environments and disturbance regimes, is particularly challenging because of the spatial

interactions involved and the corresponding long time domains (Turner et al. 1993, Baker 1995, Foster et al. 1997). This is particularly true where information on species-level successional change is required. In many cases, ecological questions involving large-scale processes such as wind and fire disturbance, or regional assessments of forest harvesting or global change, can best be answered with simulation models (Mladenoff and Baker 1999). Here we describe a modeling approach to examine how fire disturbance and spatially driven, species-level recovery interact on a large, disturbed, heterogeneous landscape (~500 000 ha). Landscape heterogeneity is caused by spatial variation in environmental conditions and disturbance rates along mesoclimatic gradients, and because of past human use.

Forest fire disturbances can be simulated spatially

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using either mechanistic or stochastic approaches. These two approaches often differ significantly in the time scales simulated as well as other aspects. Mechanistic approaches typically focus on a single fire event over the length of an individual fire, while stochastic approaches often focus on multiple fire events over long time periods. However, models based largely on one approach often have some features of the other. Mechanistic approaches are generally descendants of the pioneering work of Rothermel (1972) and simulate fire behaviors such as ignition and spread in great detail with short time resolution (e.g., Finney 1999). Fire ignition is affected by the physical and chemical features of fine fuels and their interactions with weather conditions and is a process that occurs on the order of minutes (Rothermel 1972). Fire spread is measured at hourly time scales and incorporates great variation, since fuel conditions, vegetation resilience, topography, and the weather factors including wind direction, may vary from site to site (Rothermel 1972). Mechanistic models use mathematical equations to link the physical environment to the resulting phenomena deterministically (Rothermel and Deeming 1980, Anderson 1982, Rothermel et al. 1986, Andrews 1986, Cohen 1986, Vasconcelos and Guertin 1992, Finney 1994). These mechanistic approaches have led to fundamental understanding of fire behavior and reasonable success in predicting local fire spread (Finney 1994, 1999, Coleman and Sullivan 1996). However, disparities in time scales currently limit their application over large spatial and temporal domains (Rothermel 1991, Finney 1999).

Stochastic simulation approaches use probability distributions in combination with random number generators to determine fire events, unlike the more deterministic and mechanistic approaches. These approaches have evolved from studies of fire frequency and fire probability, a theory summarized by Johnson (1992). The pioneering work of Heinselman (1973) in dating historical fires to derive fire boundaries by studying forest patch age distribution showed that as a landscape-scale phenomenon, fire can be successfully described through study at large temporal scales (tens to hundreds of years) with probability distributions of fire size and frequency. By investigating heterogeneous landscapes at large time domains, research has shown that disturbance is an important generator of heterogeneity at all scales (e.g., White 1979, Hubbard 1980, Romme 1982, Armesto and Pickett 1985, Clark 1989, Turner et al. 1989, Baker 1989, Johnson et al. 1990, Takle et al. 1994).

Landscape models have been developed that use stochastic approaches to examine the relationship between fire regimes and landscape heterogeneity, as well as fire-affected landscape changes through time (Green 1989, Baker et al. 1991, Urban et al. 1991, 1999, Turner et al. 1994, Keane et al. 1996, Gardner et al. 1996, 1999, Mladenoff et al. 1996, Roberts 1996, Mladenoff and He, 1999). Although designed to address a variety

of questions, these landscape models share several common features: longer temporal resolution or model time step (usually 1–10 yr) than mechanistic fire-spread models, ability to simulate large spatial extents with multiple fire events, and the use of stochastic algorithms. Since the temporal resolutions used by stochastic approaches are much coarser than those of mechanistic approaches, detailed fire processes such as lightning-caused ignition or individual tree growth cannot be precisely simulated over time. Therefore in landscape models, fine-scale processes are integrated across temporal scales not by simulating them directly but representing them as aggregated spatial and temporal phenomena.

The extent to which fine-scale mechanistic components are integrated into landscape models varies depending on the model purpose and design limitations. On the other hand, large-scale and longer term processes such as vegetation dynamics, and fuel accumulation and decomposition, which are not addressed in mechanistic models but can affect fire patterns (Romme and Despain 1989, Turner et al. 1993), need to be integrated into landscape modeling. The overwhelming information processing needs at landscape scales often require significant simplifications in many landscape models. This can limit model application to only a narrow set of conditions. For example, Green (1989) developed a landscape model to simulate fire, seed dispersal, and forest spatial pattern. Stochastic algorithms were used to simulate fire. The mechanism employed to simulate fire spread resulted in elliptical fire patterns that are theoretically valid but do not typically occur in heterogeneous, real landscapes. DISPATCH, developed by Baker et al. (1991), integrates weather data with a random algorithm to simulate fire ignition and size based on distributions. It simulates fire in greater detail at various time steps if the corresponding weather information is provided. DISPATCH assumes stand replacement by fire, in which stand ages are represented by the time since last fire. Therefore, variable fire severity and vegetation or species succession are not explicitly simulated. EMBYR, a probability-driven landscape model by Gardner et al. (1996), simulates fire under different climate regimes. Fire probability in each cell is a function of weather, fuel, and wind. A vegetation map is interpreted as fuel types and updated each iteration via a Markov recovery model. Spatial vegetation dynamics are not directly simulated. FIRE-BGC (Keane et al. 1996) represents a significant effort in scaling ecological processes simulated at the individual tree level up to the landscape level. This approach has a hierarchical design (landscape-site-stand-species-tree). FIRE-BGC uses FIRE-SUM, a gap model (Keane et al. 1989), to simulate all individual trees contained in simulated plots (Keane et al. 1996). FIRE-BGC uses FARSITE, a mechanistic fire behavior model (Finney 1994) to simulate fires at stochastic or fixed intervals. Methods used to scale up and

down are not spatially explicit. FIRE-BGC has over a thousand parameters that need to be quantified for a successful simulation and is computationally intensive. A 200-yr simulation of 100–120 stands containing two species takes >20 h on several workstations (Keane et al. 1996) and at least eight replications are needed (Keane et al. 1989).

LANDIS (Mladenoff et al. 1996) is an effort to design a landscape model that balances the integration of ecological processes across different spatial and temporal scales to be able to simulate large areas over long time spans, and within current computational capability. The purpose of the model is to simulate species-level forest dynamics in combination with fire, wind-throw, and harvesting, with adequate mechanistic realism for a range of spatial scales. LANDIS is a spatially explicit, stochastic, raster-based model (Mladenoff et al. 1996, Mladenoff and He 1999), based on an object-oriented modeling approach (Rumbaugh et al. 1991). Each cell is a spatial object tracking (1) the presence or absence of 10-yr age cohorts of individual species, (2) fuel regimes based on their accumulation and decomposition characteristics, (3) mean fire/wind return interval, and (4) the time since last fire/wind disturbance, and (5) species establishment ability in particular environments. LANDIS is similar to LANDSIM, a polygon-based landscape model by Roberts (1996), in that successional dynamics are based on life history characteristics of species. Similarly, the model is currently based on a 10-yr time step. LANDIS differs from LANDSIM in including greater mechanistic detail in spatial interactions, such as the realism of spatial seed dispersal and the possibility of patch disaggregation and formation due to the raster format. LANDIS simulates dynamics of up to 30 tree species and is currently being applied to an area of 1.5 million ha in northern Wisconsin (He et al. 1999; Mladenoff and He 1999, H. S. He et al., *unpublished manuscript*). A 500-yr simulation of a 500 × 800 cell map with 23 species takes ~1 h on an Intel Pentium 300-based computer (He et al. 1996). In this paper, we will discuss the design and stochastic behavior of the LANDIS fire module and the approach used for verification and model calibration. We then apply the model to a real landscape to address the question of how disturbance and successional dynamics interact in changing forest patterns on a large, heterogeneous landscape. Adequately describing these large-scale and long-term natural dynamics is a necessary precursor to understanding subsequent human-caused effects.

APPROACH AND METHODS

Fire module design

Basic distributions.—To simulate large-scale spatial dynamics, LANDIS does not mechanistically simulate all processes incorporated in the model, and several processes are represented categorically rather than as

continuous distributions. Fires are not purely stochastic in terms of ignition, location, size, and shape. It has long been noted that some areas are more fire-prone than others. The differences often are represented by using mean fire-return intervals, i.e., the mean number of years for fire to recur on a certain site (Pickett and Thompson 1978, Pickett and White 1985, Pickett et al. 1989, Johnson 1992, Johnson and Gutsell 1994). Depending on their extent, large landscapes can be stratified into ecoregions or land types, relatively homogeneous subareas that are characterized by different soil moisture/nutrient regimes and fire disturbance regimes. This landscape stratification can be done at various scales, depending on landscape structure, available data, and the question being addressed with the model. Similar to the approaches used in other studies (Baker et al. 1991, Johnson 1992, Turner et al. 1993), in LANDIS the mean fire-return interval is used to calculate fire probability using the following equation, modified from Johnson (1992):

$$P = B \times \text{If} \times \text{MI}^{-(e+2)} \quad (1)$$

where P is the fire probability of a cell, MI is the mean fire-return interval of a given land type on which the cell resides, B is the fire probability coefficient designed for model calibration ($B = \text{MI}$ by default), and If is the number of years since last fire on that cell. With the above distribution, P varies among land types with MIs, and it can be further altered linearly by If recorded for each single cell. For example, if fire burns a given cell in a given time step, If of the cell is reset to 0, and P for that cell is calculated as 0 during that time step. This eliminates the possibility of cells being burned twice in the same time step regardless of how short MI is.

Fire size is also defined from the following equation integrating random factors and the mean fire size:

$$S = A(10.0)^r \text{MS} \quad (2)$$

where S is the fire size, MS is the mean fire size, A is the fire disturbance size coefficient designed for model calibration ($A = 0.34$ by default), and r is a normalized random number generated from Eq. 3 (modified from Ross 1988):

$$r = \sqrt{-0.75 \log a_1 \sin(\pi^2 a_2)} + C \quad (3)$$

where a_1 and a_2 are two floating point random numbers from a uniform random number generator ($0.0 < a_1 < 1.0$, $0.0 < a_2 < 1.0$), and C is a constant that ensures the statistical mean of r is 0.0 (by default $C = 0.1340$).

Since $r \sim N(0, \sigma^2)$, S has the following lognormal distribution (Fig. 1):

$$F(S \leq x) = \frac{1}{\sqrt{2\pi}\sigma} \times \int_{-\infty}^z e^{-x^2/2\sigma^2} dx \quad (4)$$

where $z = \ln(x)/\ln(10a - \text{MS})$.

By such a design, disturbance sizes are stochastic and follow the above distribution (Eq. 4) with small

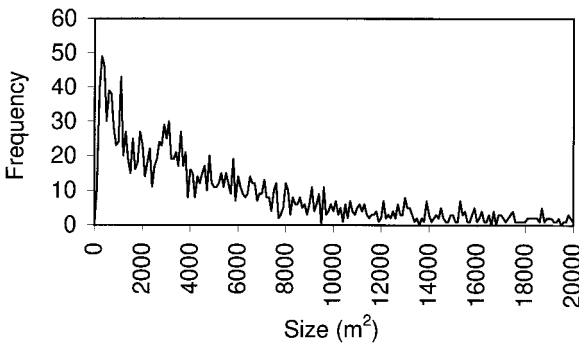


FIG. 1. Frequency distribution of 2000 fire disturbance sizes from Eq. 2; MS (mean fire size) = 10 000 m².

disturbance sizes more likely to occur than large disturbances (Fig. 1), as is typically observed (Johnson 1992). On real landscapes, disturbance size and frequency distributions may be characterized by high variances. This design incorporates the ability to generate rare, large fire sizes (Baker 1989, Romme and Despain 1989). However, the statistical maximum fire size possible within a given time span is often not known, and variance in size of these large fires is poorly understood. The most appropriate fire size probability density function is not known. In this fire module, maximum fire size, derived from limited historical data or empirically, is used to estimate a reasonable S (Eq. 2, $S < \text{maximum size}$).

Distributions of MI and MS can be derived empirically or estimated from the literature (e.g., for our region, Heinselman 1973, 1981, Canham and Loucks 1984, Frelich and Lorimer 1991). These distributions are then sampled during the simulation and implemented stochastically on the landscape over time. To place a given stochastic fire with size S on the landscape, several other relationships need to be defined.

Fuel and fire severity.—Substantial studies on forest fuels have been done by others developing mechanistic fire models (e.g., Rothermel 1972, Deeming et al. 1974, Anderson 1983, Andrews 1986, Brown and Simmerman 1986). However, fuel accumulation through time, a process occurring on the order of decades, is not well understood across large, heterogeneous landscapes. The amount of fuel on a site is a major factor affecting fire intensity (Rothermel 1983). In LANDIS, a simple framework is designed to reflect the relationship between fuel quantity and years of accumulation on different land types. This relationship assumes that fuel accumulation is a function of the number of years of forest production since last fire or cutting, and the rate of decomposition, which varies by land type (Mladenoff et al. 1996). Fine-scale differences due to species differences are not simulated.

On xeric land types with slow decomposition rates, fuel accumulation eventually exceeds that on mesic land types (Fig. 2a). Although a more realistic curve is not currently available, this relationship can be gen-

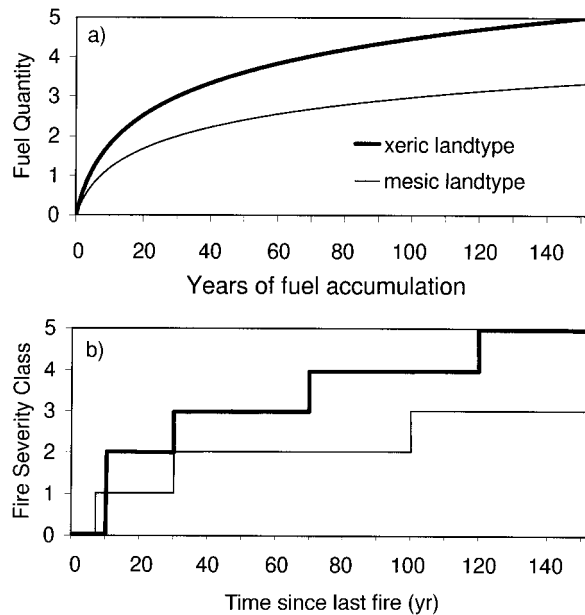


FIG. 2. (a) Conceptual representation of forest fuel quantity (unitless) as a function of accumulation time, which varies by land type. (b) Categorical representation of fire severity classes as a function of time since last fire, derived from (a).

eralized categorically as fire severity classes reflecting the relationship of fuel accumulation and time since last fire, assuming that fire removes all fuel if it occurs (Fig. 2b). A longer accumulation time results in greater fire severity when a fire eventually occurs. This design preserves the feasibility of incorporating more realistic data for various land types and/or including specific vegetation fuels if they are available in the future. Currently, severity classes are 1–5 with a class 5 fire the most severe.

Species fire resilience.—Fire is a bottom-up disturbance, and fires of increasing severity affect younger age classes first. Also, fire tolerance varies among species. To implement these two characteristics, species fire tolerance classes, containing five categories from 1 to 5, are designed to reflect the differences of fire tolerance among species. Species fire-susceptibility classes are designed to reflect differences related to age. Species life-span proportions are calculated as species age divided by longevity. Five life-span proportions (0–20, 21–50, 51–70, 71–85, and 85–100%) correspond to fire-susceptibility classes 1–5, respectively. Susceptibility class 1 is the youngest and most susceptible to fire-caused mortality, and class 5 is the oldest and the least susceptible. Species-specific fire-tolerance class combined with age-specific fire-susceptibility class determines whether a species cohort of a certain age can survive a fire event of a given severity class (Fig. 3a–e).

For example, when a severity class 1 fire occurs, it kills all but the oldest age class (life-span >85% of species longevity) of a species in fire tolerance class

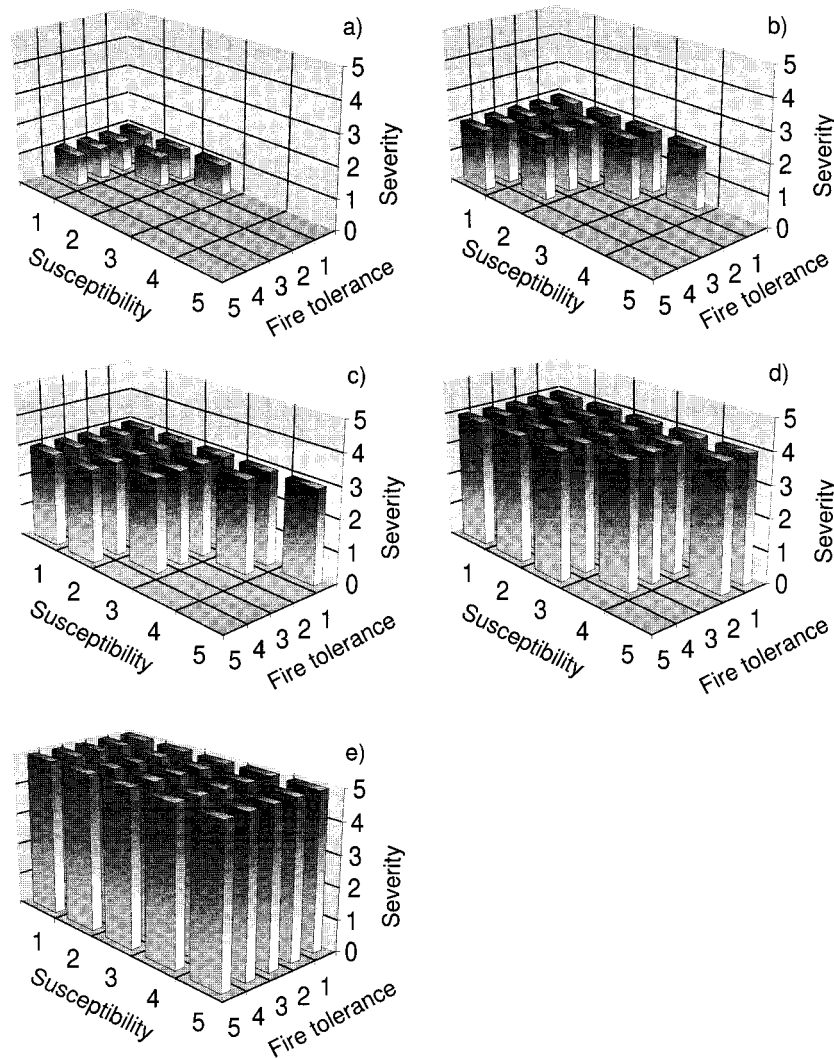


FIG. 3. Fire severity classes vs. fire tolerance (species) classes and susceptibility (age) classes; (a)–(e) refer to fire severity classes 1–5, respectively. Each individual bar represents the removal range of species of a given age class.

1, the two youngest cohorts (life-span <50%) of species in fire tolerance class 2, and the youngest cohort of species in fire-tolerance class 3 (Fig. 3a). When a severity 5 fire occurs, it removes all cohorts (Fig. 3e).

Fire ignition.—Fire ignition in LANDIS involves selection of random locations and ignition checking. The number of cells for ignition checking (IgN) is initially determined from the ignition coefficient (IgN = ignition coefficient × total cell number), a required parameter that sets the proportion of cells to be checked; this parameter can be adjusted to reflect the ignition frequency characteristics of the study area. For each iteration, the ignition algorithm randomly locates a cell for ignition-checking, if not ignited, IgN decreases by one, and checking continues until IgN = 0. If IgN decreases to 0 and no single, successful ignition is found, there will be no fire disturbance for the particular iteration. Once an ignition is successful, instead

of decreasing by one, IgN is reduced exponentially and stochastically with the following equation:

$$IgN = IgN / e^{(a_1 + a_2)} \quad (5)$$

where a_1 and a_2 are two uniform random numbers, $0.0 < a_1 < 1.0$, $0.0 < a_2 < 1.0$. With such a design, the number of fires that occur at each 10-yr time step is not proportional to the initial IgN. The module is able to initiate multiple fires, but the chance of initiating second or additional fires within the same iteration is stochastically decreased.

Once a cell is randomly located for ignition, P is computed for that cell (Eq. 1). Pr, a random number ($0.0 < Pr < 1.0$) is generated using the uniform random number generator. Ignition is successful only if $P > Pr$. Therefore, ignition in LANDIS is a function of P affected by only MI and lf (Eq. 1). Ignitions more likely occur in the cells with shorter MI and/or lf. For ex-

ample, land types at high elevation and on south-facing slopes with high lightning-strike probabilities, may have shorter MIs, larger P values, and therefore greater chance of ignition.

Fire spread.—Fire spread is a process that integrates the components discussed above to place an actual fire on the heterogeneous landscape, where potentially each cell has a different fire probability P . Fire spread is a function of wind direction, fire size, fire probability, the susceptibility of species, the fire-tolerance class of species, and spatial configuration. Once an ignition location is determined, the coordinates of the four adjacent cells are entered into a priority queue (Carrano 1995) in a random order. The first cell in the queue has a higher priority of fire spread, and, therefore, the direction from the ignition cell to the priority cell mimics wind direction. Once a fire spreads to a given cell, the cell may or may not be disturbed depending on whether $P \geq Pr$ (Eq. 1). If $P < Pr$, fire cannot spread onto that cell, another surrounding cell is chosen, and the process repeats. Otherwise, if on the cell is checked and used to determine fire severity on the cell (Fig. 2b). The species or age cohorts killed are based on the existing species and their age and the interactions of fire tolerance, species susceptibility, and fire severity (Fig. 3a–e). Fire spreads until either S is reached, or the surrounding cells cannot burn ($P < Pr$), or non-forest surrounds the cell. Fires are more likely to spread to cells with high P and can spread across land-type boundaries where P changes. As a result, fire shape is not deterministic or fixed but rather is the result of interactions among species, fuel, S , P , and spatial patterns.

Successional dynamics.—Succession involves spatial dispersal of seeds among cells on the landscape and the differential capability for species establishment and growth on different land types. Succession is a competitive process among species and is driven by species replacement according to differential shade tolerance, disturbance susceptibility, vegetative reproduction, sexual maturity and longevity of species, and other life history characteristics of species (Mladenoff et al. 1996). Species' parameters are derived from various literature sources (e.g., Loehle 1988, Burns and Honkala 1990). Successional processes in the model are described in fuller detail and tested elsewhere (He et al. 1996, Mladenoff et al. 1996, Mladenoff and He 1999).

Module design verification

Across temporal scales, fire-return intervals have direct impacts on landscape composition and structure. A successful simulation of MIs on various land types across the landscape is necessary to adequately portray these complex spatial dynamics. MS, another feature of fire disturbance, also varies among regions. To what extent MI and MS, key fire characteristics of a landscape, can be adequately simulated is closely tied to

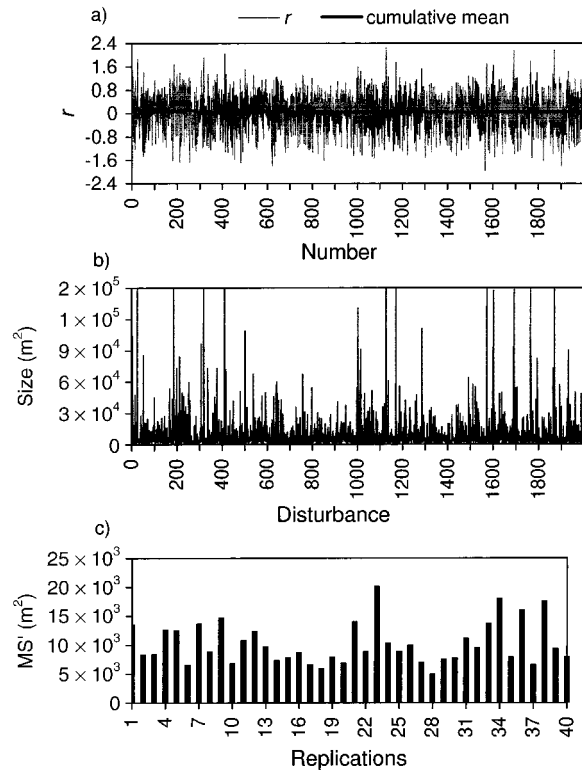


FIG. 4. Distribution of (a) 2000 normalized random numbers r , from Eq. 3, (b) the corresponding 2000 disturbance sizes from Eq. 2, and (c) the 40 approximated LANDIS simulated mean disturbance sizes from (b). The results are based on the assumption that fire occurs every iteration, and total iterations are 50 (500 yr).

the module design and the mechanism of the random number generators used. The LANDIS fire module interacts with millions of random numbers when a 500-yr simulation of a landscape with 10^4 cells is conducted. Thus an essential step is to verify the random number series in relation to means and variances of the disturbance process. This is essential to understanding model variance and limits and in model calibration for a particular region. Detailed model sensitivity analyses appear elsewhere (Mladenoff and He 1999).

Variation of a single LANDIS run.—Individual disturbance size is a function of r (Eq. 2). It is apparent that r exhibits high variability, with mean = 0.0002 and $SD = 0.59$ from 2000 trials. The cumulative mean stabilizes at 0 after ~ 100 random numbers (Fig. 4a). Since LANDIS uses a 10-yr time step, assuming a fire occurs every iteration suggests that for a single model run, a stable MS (Eq. 2) can be achieved with a 1000-yr run. However, since many simulations are fewer than 1000 yr, or over a limited landscape extent, higher variation in simulated MS is expected and in fact does occur in real systems (Heinselman 1981). Assuming that the model iterates 50 times (500 yr) and fire occurs once with each iteration, 2000 disturbance size events (Fig. 4b) correspond to 40 replications of a 500-yr run.

The mean of every 50 disturbances represents the simulated MS of each LANDIS run (Fig. 4c). As indicated, the simulated MS has high variance. In this example, with designed MS = 10 000 m² at an 85% confidence level, simulated MS of a single LANDIS run can vary from -50% (4715 m²) to +50% (15 284 m²).

For many nonspatial simulation models or spatial models that contain one dynamic element (e.g., fire probability), model replications can be used to ensure that correct means and variances are simulated (e.g., Botkin and Nisbet 1992). Methods exist to validate spatial simulation results by aggregating attributes summarized from mapped results (Turner et al. 1989). However, for spatially explicit and stochastic landscape models such as LANDIS, there is no valid algorithm available to integrate spatial maps from replicate runs into one that averages all factors. Of course, map summaries from replicate simulations, such as means and variability of species area, can be calculated to verify model performance. But to examine spatial dynamics, verification of single model runs is necessary.

Verification of a single model run.—For a simulated mean disturbance size MS' (MS prime), the degree to which it approximates the known MS of the study area can be described as a proportion (Guertin and Ramm 1996):

$$\varepsilon = (MS'/MS - 1)100\% \quad (6)$$

where, ε is the difference in percentage, or percentage error. From Eq. 2, MS' can be expressed as

$$MS' = A \times MS \times \left[\sum_{j=1}^n (10.0)^{r_j} \right] / n \quad (7)$$

where n is the total number of iterations. If MS' is correctly simulated, or $MS' \approx MS$, then $A = n / [\sum_{j=1}^n (10.0)^{r_j}]$. It is obvious that A , the fire size coefficient, affected only by r , can be increased or decreased to minimize ε .

MI is similar to the fire cycle (Johnson 1992), the time required to burn an area equal in size to the land type. For example, on a land type with a 500-yr mean fire-return interval, over a 500-yr LANDIS simulation, the total burned area should equal the land type area. However, some cells may never burn and some burn more than once. Thus, the theoretical disturbance area for land type i can be calculated with

$$TDA_i = LA_i \times N/MI_i \quad (8)$$

where TDA_i is the total theoretical disturbance area on land type i , LA_i is the area of land type i , N is the number of years simulated ($N = n \times 10$), and MI_i is the mean interval defined on land type i .

The difference of simulated MS' and MI can be measured by the method used for MI':

$$\varepsilon = (1 - TDA_i/SDA_i)100\% \quad (9)$$

where SDA_i is the simulated disturbance area on land

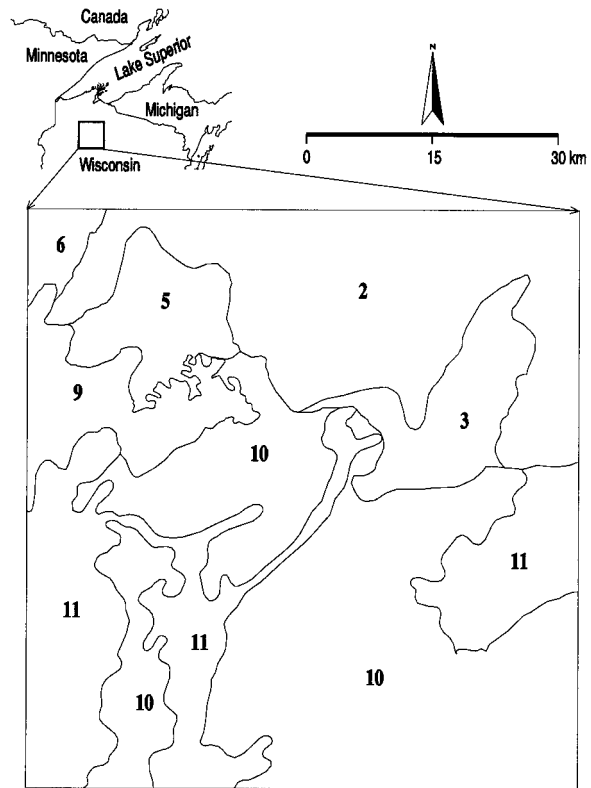


FIG. 5. Study region, location, and land types within the study area in northern Wisconsin.

type i . The fire probability coefficient B affects P and therefore indirectly SDA_i and can be adjusted to increase or decrease MI' accordingly. It is more difficult to calibrate MI due to the nonlinear features of fire probability P vs. MI . Sensitivity analysis indicated that changes of MI do not result in an equal change in P (Mladenoff and He 1999). Therefore decreasing B has greater impact on short MI s than on long MI s due to the linear relationship of P vs. B (Eq. 1). This can be improved with more interactive calibration runs, or using other distributions, such as the Weibull, that incorporate a shape coefficient that can be altered to change the fire probability curve (Johnson 1992).

Study area

To examine disturbance and successional dynamics on a heterogeneous landscape, we apply the model to a landscape with six land types and 23 species in northern Wisconsin, USA (44° N, 91° W; Fig. 5). The area comprises nearly 500 000 ha and is located in the transitional zone between boreal forest to the north and temperate forests to the south (Curtis 1959, Pastor and Mladenoff 1992). Land-type boundaries are derived from an existing quantitative ecosystem classification (Host et al. 1996). This is a largely forested, glacial region, with little topographic relief. Quaternary geology and mesoclimatic gradients are the greatest de-

terminants of environmental variation in the region, with dominant substrates of very well-drained sandy soils in land types 5 and 9, moderate- to well-drained silt loams in land types 2 and 6, and loam to silty-loam soils in land types 10 and 11 (Host et al. 1996). Summers in the region are short and mild (July mean 18°C), and winters are cold (January mean -10°C) with snow cover from November to April. Annual precipitation is ~80 cm. The region underwent extensive forest clearing during the past 100 yr and is composed of young, second-, and third-growth forests (Mladenoff and Pastor 1993). Dominant species in the area include sugar maple (*Acer saccharum*), northern red oak (*Quercus rubra*), eastern hemlock (*Tsuga canadensis*), yellow birch (*Betula alleghaniensis*), paper birch (*B. papyrifera*), quaking aspen (*Populus tremuloides*), white pine (*Pinus strobus*), red pine (*P. resinosa*), and jack pine (*P. banksiana*).

Input data and major parameters

The model input map of current forest landscape pattern represents spatial distributions of dominant canopy species from a classification of multitemporal Landsat TM/MSS (thematic mapper/multi-spectral scanner) satellite imagery. Final classes were at species and genus levels for most forest types (Wolter et al. 1995). Secondary associated species and age class information were derived by integrating the TM classification with forest inventory plot data (Hansen 1992), stratified by land types (He et al., *unpublished manuscript*). A total of 23 species and 134 unique site combinations resulted on the input map. Individual species establishment coefficients (0–1) were derived to reflect the relative growth capability of each tree species under the environmental conditions of different land types (He et al. 1998). All life history attributes of species were derived from the literature as reported elsewhere (Mladenoff et al. 1996, Mladenoff and He, *in press*). Historical fire data (MS and MI) were interpreted from empirical studies in the region (Heinselman 1973, 1981, Canham and Loucks 1984, Frelich and Lorimer 1991). MS is set to 3200 ha, ~3% of the total area. Maximum fire size is 16 000 ha, ~15% of the landscape. MIs vary among land types from 200 yr (land types 5 and 9), to 500 yr (land types 3 and 11), to 800 yr (land type 10), and 1000 yr (land types 2 and 6). The final landscape input map contained 121 362 cells (358 × 339) with a 200 × 200 m cell size, or 4854 km².

A 500-yr simulation was conducted without including windthrow or forest cutting to focus on fire effects. Model output maps are produced at each iteration for disturbances, individual species, and age classes. Individual species maps can be aggregated to a higher level of forest classes with user-defined reclassification methods (Mladenoff et al. 1996). This information can apply to either a specific land type or to the overall landscape. The reclassification algorithm calculates the

dominant forest type to represent each cell when multiple species occur on a given cell. Since cohort data are presence/absence and not quantitative abundance in a cell, species age in relation to longevity is weighted in classifying dominants or forest types (He et al. 1996).

RESULTS

Model calibration and verification

Model calibration and reproduction of land-type disturbance regimes were done interactively through each individual run. Desired results may not be achieved with a single adjustment since the coefficients are used in combination with random-number-related algorithms. After calibration, MS' is 2800 ha, $\epsilon = -13.6\%$ (Fig. 6a). The simulated MIs on land types with MI = 1000, 800, 500, and 200 yr after calibration (Fig. 6b–e), were 3172 ($\epsilon = 217\%$), 719 ($\epsilon = -10\%$), 529 ($\epsilon = 6\%$), and 180 yr ($\epsilon = -10\%$), respectively. While MIs on most land types are closely simulated, MI' on land types with MI = 1000 yr has significantly higher error. The short simulation period (500 yr) in relation to the simulated MI (1000 yr), and the relatively small extent of this landscape and the particular land type both contribute to this high error. Functionally, however, this has little effect on simulation results of vegetation dynamics compared to a longer, equilibrated simulation of this MI. The difference in vegetation response is minimal when MI is much longer than species longevity and the successional cycle (H. S. He and D. J. Mladenoff, *unpublished data*). In this simulation MI or MI' exceeds the life-span of all tree species by at least two times.

With the stochastic approach, the precise location or form of an individual fire is not replicable except using a fixed random-number seed (He et al. 1996). On land types where MS' and MI' are accurately simulated, we can assert that the realistic or desirable fire regimes are correctly reproduced over the entire period of simulation. Although an individual fire event may vary with different random number seeds, the actual set of simulated fire sizes approximates the empirical distribution (Fig. 1) with small fires occurring more frequently than large fires. The spatial pattern of a fire is not deterministic. Rather, it is controlled by the fire characteristics such as MIs and lfs involved in the event, in combination with the stochastic algorithms. For example, if a given set of sites on the landscape was burned during the last iteration, the new fire is unlikely to spread on these sites. This produces the expected fire patterns. Thus patterns observed on maps of an individual simulation are discussed in the results not as a mechanistic prediction, but as an example of a calibrated run with verified general behavior.

Examination of fire events within a time-step.—The effects of simulating individual fire events can be analyzed spatially by examining the response of individ-

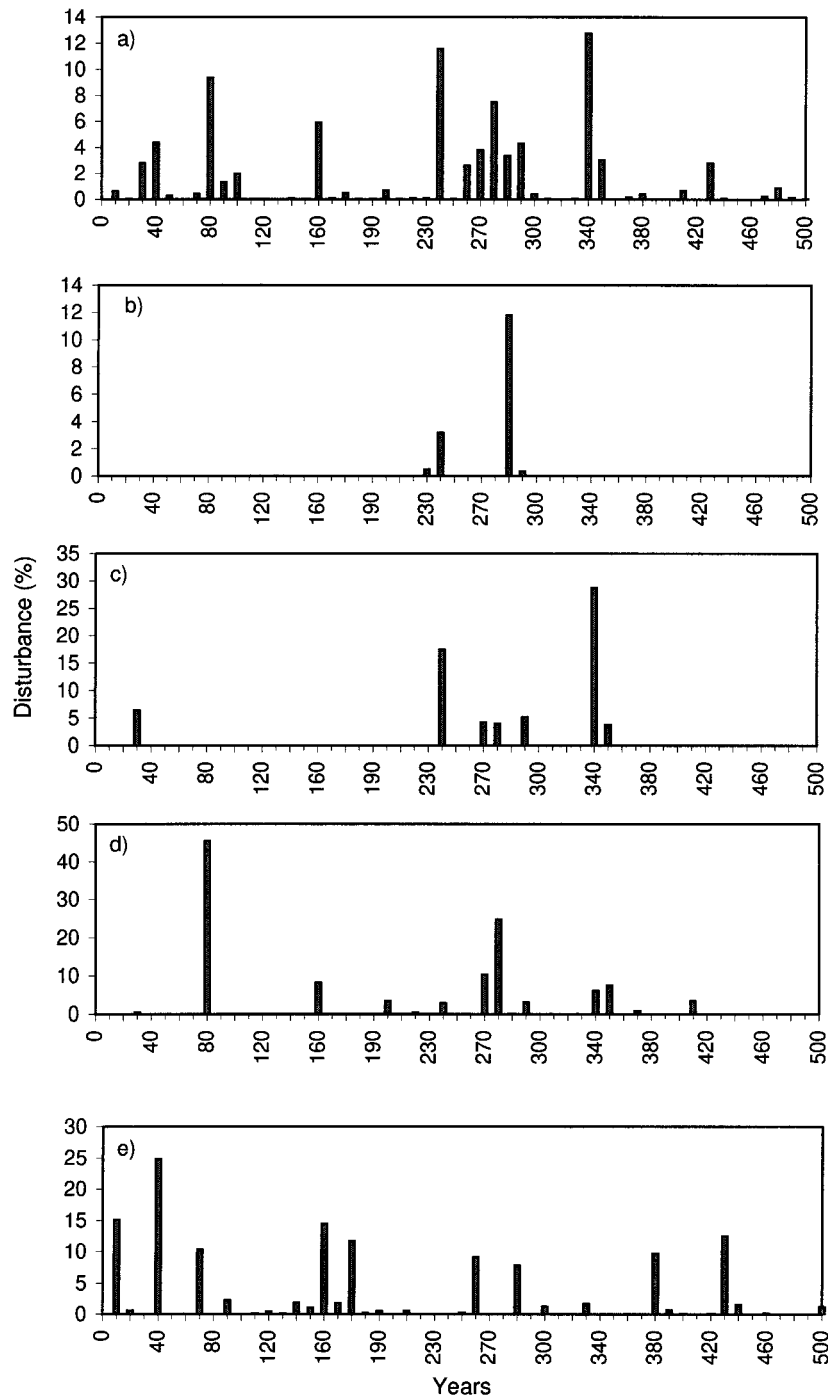


FIG. 6. Simulated fires after calibration for (a) the entire landscape, and for (b) land type 2 (MI [mean fire return interval] = 1000), (c) land type 10 (MI = 800), (d) land type 11 (MI = 500), and (e) land type 5 (MI = 200).

ual species and their age cohorts (Fig. 6a–e). This is a useful process for evaluating model performance and interpreting disturbance and species dynamics, but is not a deterministic prediction of actual single events. For example, multiple fires occurring at year 290 have variable fire severity classes due to the different fuel conditions in each cell, resulting in irregular fire shapes

and heterogeneity within single fire patches (Fig. 7a). As discussed, fires can occur within one land type (upper left fire, Fig. 7a, hereafter called fire A), or cross land-type boundaries (middle right fire, Fig. 7a, hereafter called fire B). Before year 290 fires, at year 280, most of land type 2 is dominated by sugar maple, a late successional species, with age classes averaging

170 years (Fig. 7b). Fire is typically uncommon on this mesic land type ($MI' = 3172$ yr, $MI = 1000$ yr). The age of sugar maple indicates that fuel has accumulated in that area for at least 170 yr, assuming the characteristic decomposition that would occur on this mesic land type. Therefore, a relatively high severity fire is expected once one occurs in that area. As observed, fire A, primarily a fire of severity class five, removed the 170-yr-old sugar maple, a very fire intolerant species (Fig. 7d).

The major portion of fire B was populated with 40-yr-old northern red oak at year 280 (Fig. 7c) indicating that a fire likely occurred in this area 40 yr ago (Fig. 6a). A low-severity fire was expected here due to the short time of fuel accumulation. Fire B, primarily a severity 2 fire, removed only the young oak cohorts (Fig. 7e). Northern red oak regeneration on land types 3, 10, and 11, where fire B occurred, is noticeable with 0–10 yr old red oak saplings occurring sparsely after the fire (Fig. 7e). Quaking aspen, an early-successional species, established following fires A and B (Fig. 8f).

Fire impacts and individual species response by land type.—Fire impacts during the 500-yr simulation can be further analyzed by examining species trajectories by land type. The trajectories of the most abundant species on four land types, representing four different MIs, are shown with abundance calculated as the percentage of cells in a land type containing each species (Fig. 8a–d). Fluctuations in the species trajectories result from interactions among life history characteristics, dispersal, competition, succession, fire disturbance, and the establishment abilities of species on the land types. Dominant roles of each of these components can be found in these trajectories at different temporal stages. For example, the decline of sugar maple on land type 10 from year 110 is due to the majority of them approaching their natural longevity (Fig. 8b). The high abundance of sugar maple and low abundance of hemlock at year 0 result from historical human impacts (Mladenoff and Pastor 1993, Mladenoff and Stearns 1994). The increases of hemlock from year 0 to 240 and balsam fir from year 0 to 130 on land type 10 (Fig. 8b), and both of them from year 0 to 70 on land type 11 (Fig. 8c), are gradual recoveries from current conditions, and approaching pre-European abundances of these species (Finley 1976).

Large fires cause the most abrupt changes in species trajectories. The year-80 fire (Fig. 6a), primarily on land type 11 (Fig. 6d), caused the significant decrease of sugar maple as well as abrupt declines of white pine, hemlock, and balsam fir (Fig. 8c). The year-340 fire (Fig. 6a, c) removed substantial amounts of hemlock and balsam fir on land type 10 (Fig. 8b). In most cases, early-successional species benefit from the open space created by fire, such as in the response of aspen to the year-80 and year-340 fires (Fig. 8b, c). Other large fires such as the one at year 240 occurred on the other land types not included in our examples.

Environmental conditions that affect the ability of species to establish also play important roles in determining species abundance on different land types (He et al. 1998). For example, hemlock, starting at very low abundance, increased much more rapidly on land type 11 (Fig. 8c) than land type 2 (Fig. 8a). Due to poor species establishment on sandy soil and short MI' , overall species abundance is low on land type 5 (Fig. 8d). However, red pine, jack pine, and red oak, the drought-tolerant species, are successful in the dry conditions on land type 5. In general, both long MI and short MI result in lower species diversity, as observed on land type 2 with $MI' = 3172$ yr (Fig. 8a) and land type 5 with $MI' = 180$ yr (Fig. 8d). With less frequent fires, highly shade-tolerant species such as sugar maple, hemlock, and balsam fir outcompete more intolerant species to become dominant (Fig. 8a–c).

Species abundance over the 500-yr model run can be described quantitatively in terms of means and variation by land type when the MIs have been simulated within known and realistic ranges. While mean abundance suggests a species equilibrium level, the coefficient of variation ($CV = SD/mean$) describes variability in species abundance over the 500 yr. Where the coefficient of variation increases, species abundance becomes less stable over time. In general, the most common and shade-tolerant species have lower coefficients of variation compared to less common and shade-intolerant species (Table 1). Sugar maple on land type 2 illustrates a species that is temporally more stable than less abundant species such as jack pine on land type 2 (Table 1). However, the equilibrium state is also strongly affected by interaction of site characteristics and the initial abundance level, due largely to past human activities. For example, hemlock and sugar maple on land type 10 are both less stable than sugar maple on land types 2 and 11 (Table 1).

Frequent fire is necessary to maintain the less common, shade-intolerant species on the landscape. The coefficients of variation for these species typically decrease when mean fire return intervals increase, such as with jack pine on land type 5 ($MI = 200$) vs. other land types, and big-toothed aspen on land type 10 ($MI = 800$) and 11 ($MI = 500$) vs. land type 2 ($MI = 1000$) (Table 1). Some mid-level shade-tolerant species on land types with MI in the middle range for the landscape, such as red oak on land type 11 and yellow birch on land type 10, have low coefficients of variation (Table 1).

Major forest types on the overall landscape.—Eight aggregate forest types were calculated based on species dominants in cells, with forest-type classes of aspen, birch, maple, oak, hemlock, pine, mixed-deciduous forests, and mixed conifers (Fig. 9). Mixed-deciduous forests are forests dominated by deciduous species other than those above, including basswood, white ash, hickory, and cherry. Mixed-conifer forests include species not listed above, such as balsam fir and white spruce.

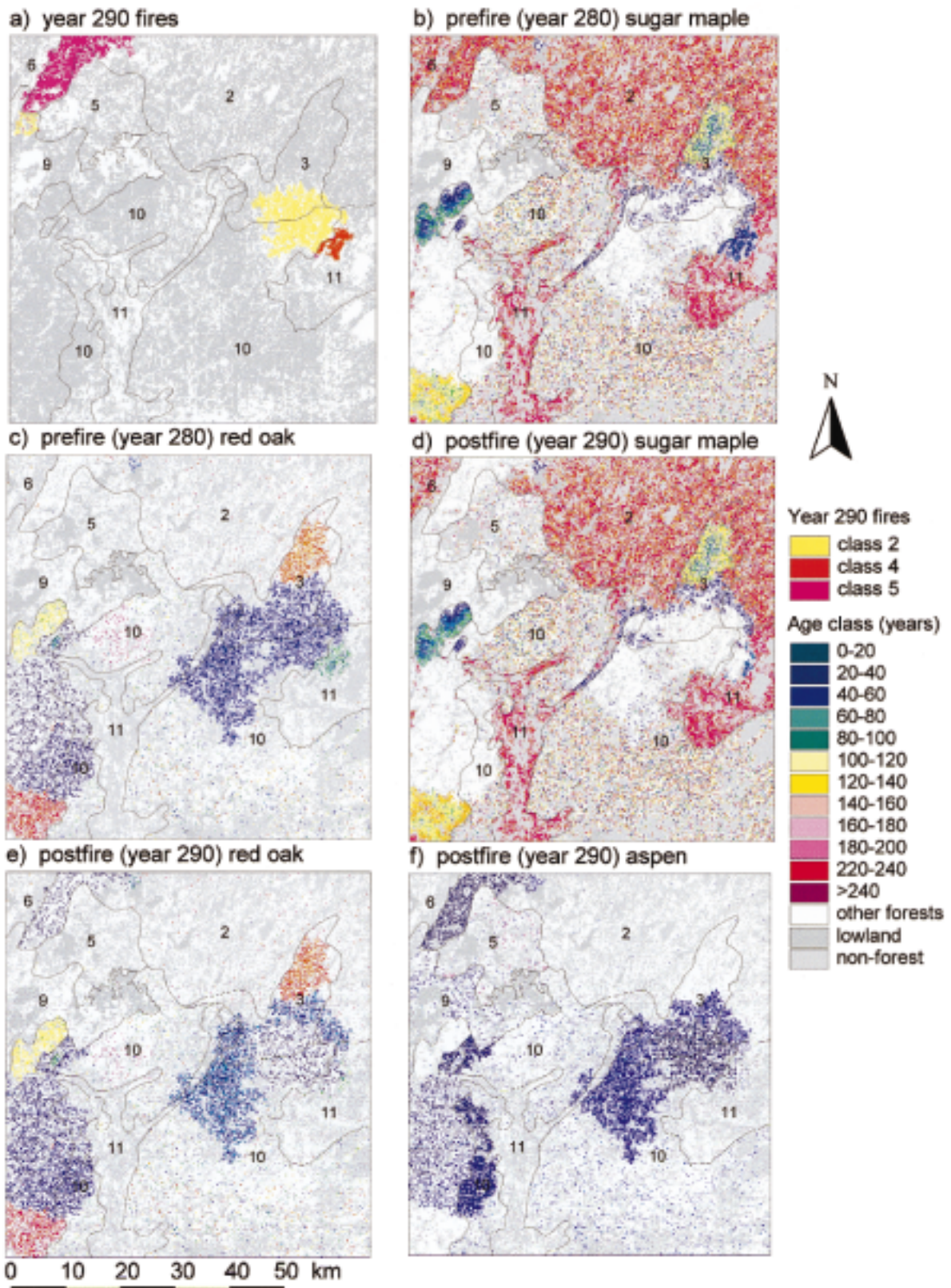


FIG. 7. Maps of (a) fires at year 290, (b) sugar maple, and (c) red oak preceding the fire time step (year 280); and (d) sugar maple, (e) red oak, and (f) quaking aspen following the fire occurrence (year 290).

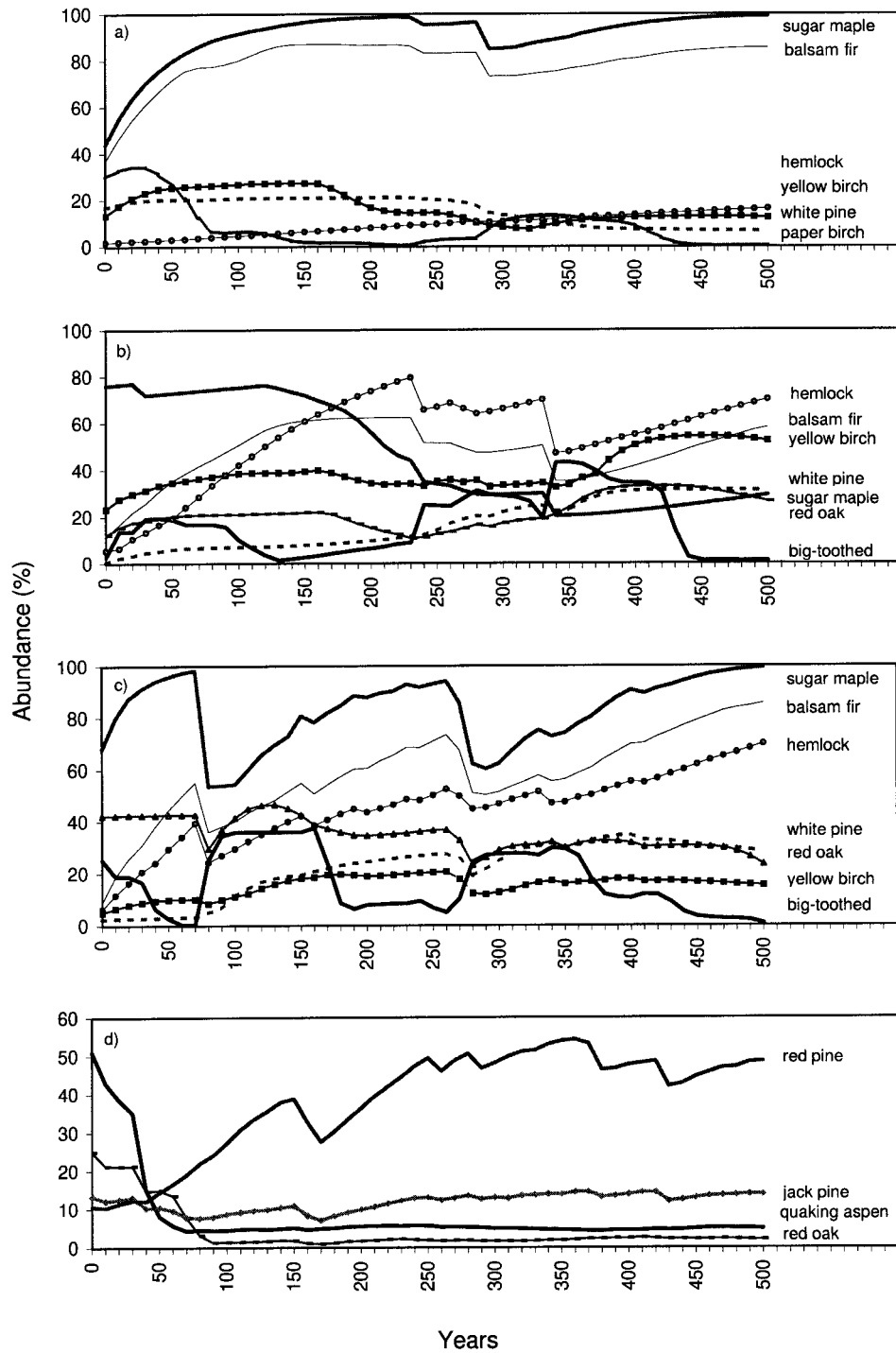


FIG. 8. Major species abundances on land types (a) 2, (b) 10, (c) 11, and (d) 5, respectively. Big-toothed = big-toothed aspen.

The results indicate that maple forest (primarily sugar maple) is the dominant type on this landscape over the 500-yr simulation. Maple covers nearly one-third of the landscape over the 500-yr run (mean = 30.2%, Fig. 9). Oak (mean = 11.0%) and birch (mean = 8.8%) forests make up ~20% of the landscape, and aspen

5.7% of the landscape. Hemlock (mean = 12.0%), mixed-deciduous (mean = 13.4%), and conifer forests (5.1%) account for the remaining portion of the landscape.

The proportions of the landscape dominated by different forest types vary over time (Fig. 9). High co-

TABLE 1. Species means and coefficients of variation (cv) by land types.

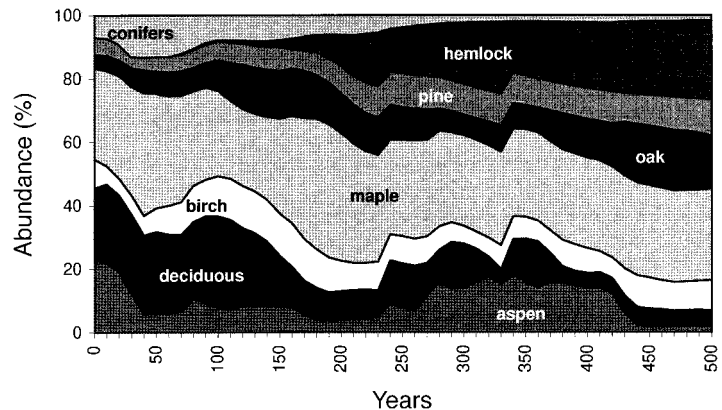
Species	Land type											
	2		3		5		9		10		11	
	%	CV	%	CV	%	CV	%	CV	%	CV	%	CV
Hemlock	9.2	0.5	37.9	0.2	0.1	0.9	2.8	0.6	53.7	0.4	44.5	0.3
White pine	15.2	0.4	1.3	0.2	2.3	0.9	1.2	0.8	17.0	0.6	21.9	0.5
Red pine	4.6	0.9	80.1	0.2	38.2	0.4	21.7	0.2	0.3	1.5	0.7	0.4
Jack pine	0.3	4.0	6.5	0.4	11.8	0.2	0.7	1.3	0.0	3.7	0.0	4.1
Balsam fir	78.8	0.1	23.4	0.3	3.2	2.2	2.7	0.7	47.4	0.3	57.5	0.3
Sugar maple	90.7	0.1	12.0	1.3	2.4	2.2	1.7	1.8	46.5	0.5	82.4	0.2
Red maple	4.0	1.8	15.3	0.8	2.0	1.4	1.5	2.3	9.7	1.2	6.6	0.6
Red oak	8.6	0.4	11.6	0.6	3.6	1.5	1.5	1.2	21.8	0.3	35.0	0.2
Quaking aspen	5.6	1.9	0.1	4.0	8.1	1.3	0.2	2.5	15.3	0.8	8.4	0.8
Big-toothed aspen	3.2	1.2	45.9	0.3	3.2	2.0	2.1	0.5	16.7	0.8	16.8	0.7
Yellow birch	16.8	0.4	14.0	0.9	0.1	1.3	0.9	1.5	39.3	0.2	15.1	0.3
Paper birch	8.5	1.1	72.6	0.2	4.3	1.4	18.0	0.2	9.5	0.6	17.1	0.4

efficients of variation for the early-successional forest types such as aspen (cv = 0.60) reflect the high variation of these shade-intolerant forest types. Dominant shade-tolerant types such as maple have corresponding low variation (cv = 0.13). At the landscape scale, a large, gradual increase in hemlock-dominated forest from its original low level follows the decrease in abundance of the mixed-deciduous forest (Fig. 9). Hemlock is the most shade tolerant of the species on this landscape and approaches a stable proportion. However, because it recovered from very low levels, hemlock forest has an overall high coefficient of variation over time (cv = 0.70, the highest among all types). Resulting high coefficients of variation are also expected for the mixed-conifer and deciduous forests since these less common classes incorporate a variety of species without clear dominants (Fig. 9).

Long-term spatial trends in overall landscape changes can be examined in sequential composition and age output maps from the simulation (Fig. 10). Spatial output of a given year is highly stochastic, while sequential output reveals the landscape trend over a longer time-span. This output provides insight not apparent from the aggregated data in graphs (Figs. 6, 8, 9) or from examining short-term, detailed changes

(Fig. 7). The initial (current) landscape is fragmented with a fine-grained patch structure (Fig. 10a), and largely contains young forests, typically in 30–90 yr age classes (Fig. 10b). Young maple, aspen, and mixed-deciduous forest are most common in the landscape, with pine being fairly abundant. Red pine and jack pine are primarily located on land types 5 and 9, and hemlock is very uncommon (Fig. 10a). At year 100, as the landscape ages (largely 90–150 yr age classes), successional changes begin to develop a coarser patch structure, in both composition and age classes. A few new fire patches are evident, showing aspen and young age classes (Fig. 10c, d). By year 200, the pattern of large-scale maple dominance appears on land type 2 (Fig. 10e) and much of the maple forest is ~180–240 yr (Fig. 10f). Hemlock-dominated forests begin to appear more commonly on land types 10 and 11, but still in a dispersed, fine-grained pattern (Fig. 10e). As some aspen and other intolerant, mixed-deciduous forests age, they are succeeded in dominance by an increase in yellow birch (Fig. 10e). By year 300, sugar maple continues to replace pine and other less tolerant species as dominant on land type 2. A few more aspen forests are created by fires (Fig. 10g). Larger patches of hemlock forest coalesce especially on land type 10 (Fig.

FIG. 9. Dominant general forest types on the entire landscape.



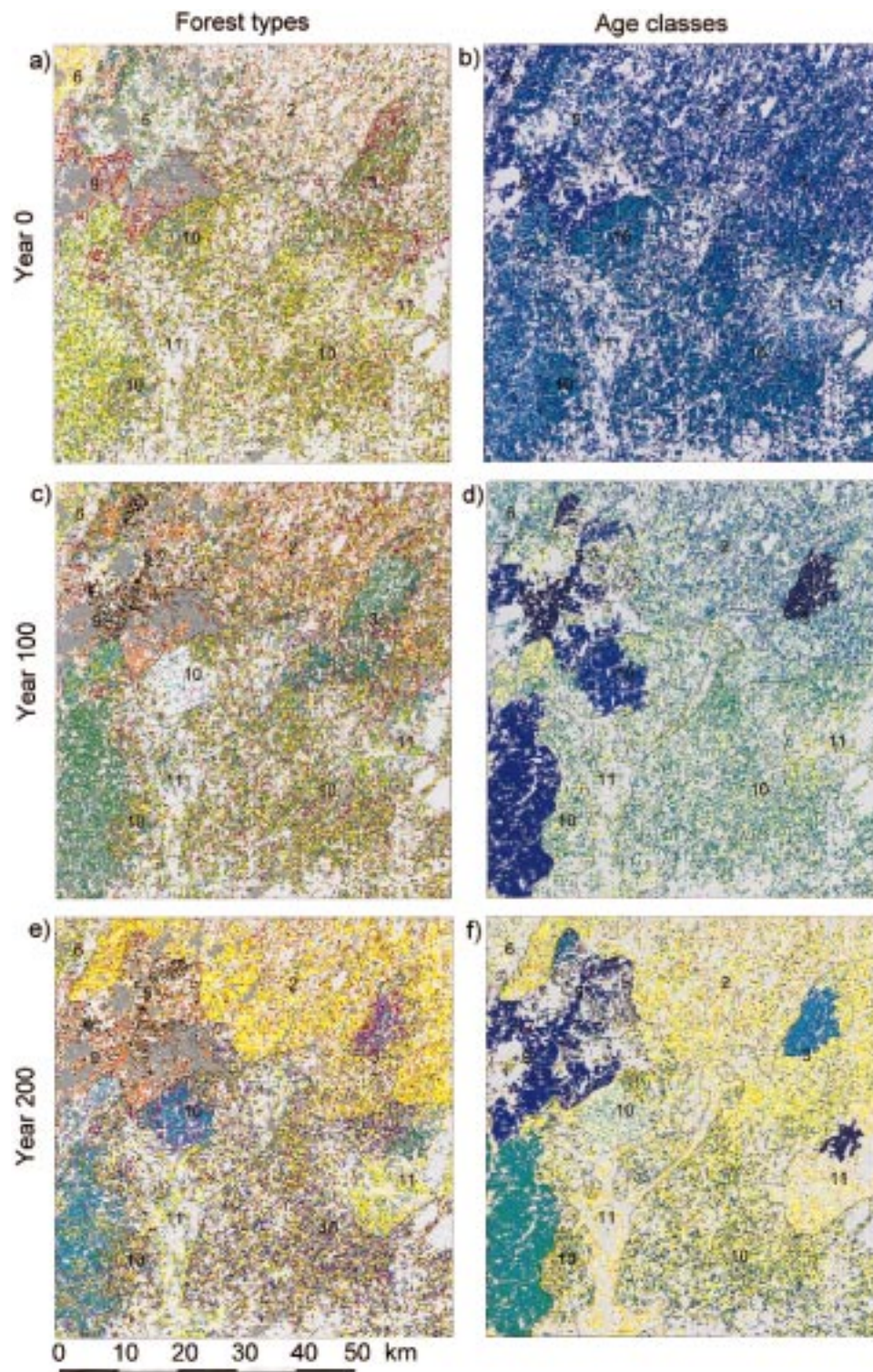


FIG. 10. Dominant forest types (a, c, e, g, i, k) and age class distributions (b, d, f, h, j, l) for years 0, 100, 200, 300, 400, and 500, respectively. Numbers on figures indicate land types.

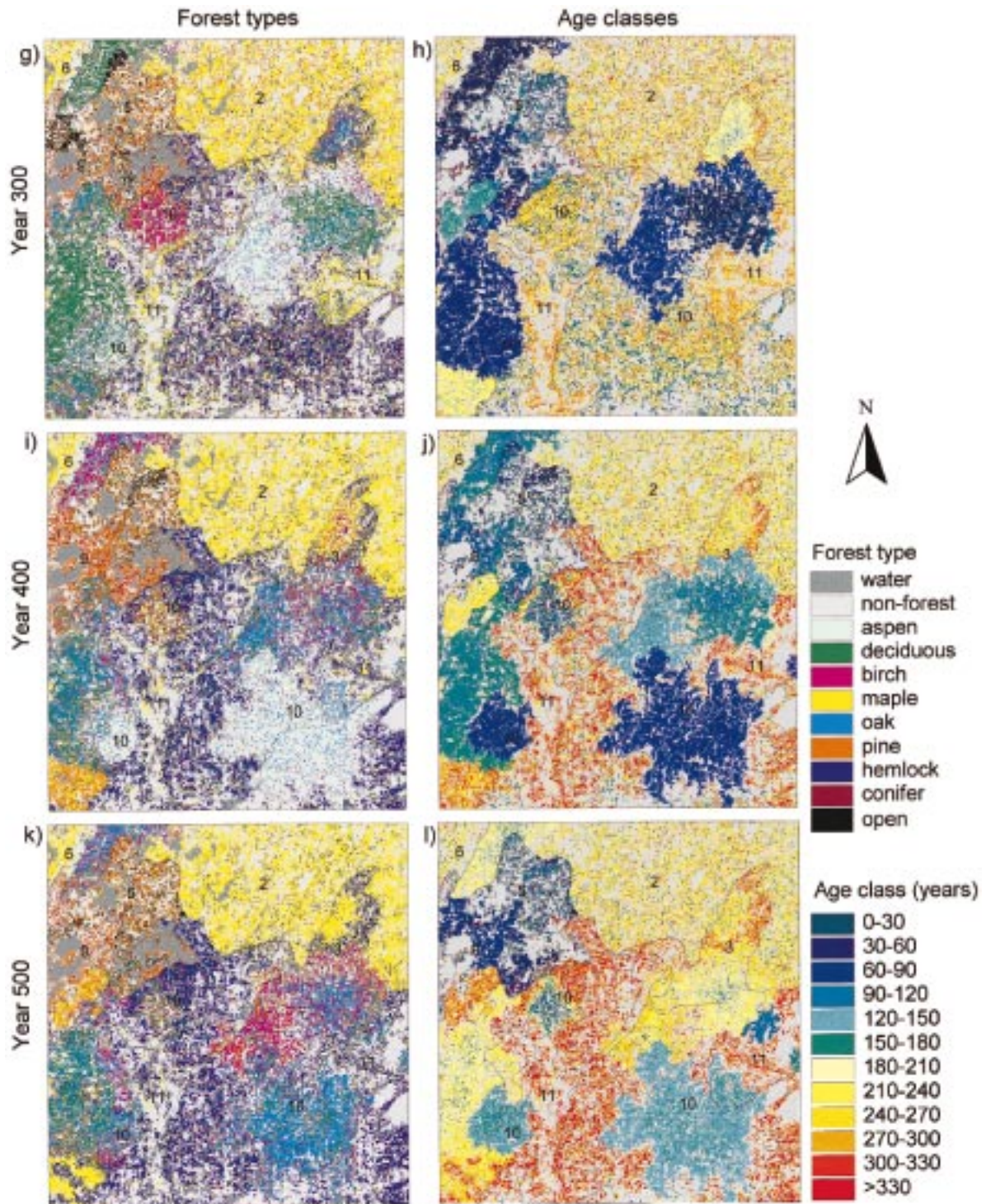


FIG. 10. Continued.

10g). While most forest reaches ages of 180–270 yr, the contrast of young forest patches from fire becomes more apparent (Fig. 10h). By year 400, the landscape pattern continues to develop a coarser grain in both age class and composition (Fig. 10i, j). Hemlock dominates on land types 10 and 11, maple dominates on land types 2 and 3, and primarily red pine and jack pine dominate on land types 5 and 9 (Fig. 10i, j). Early and mid-successional forest types occur in large fire patches embedded within the more general trend to dominance by more shade-tolerant species. At the 500-yr point, the rate of overall landscape change is decreasing as some species approach an equilibrium abundance, also reflected in little change in age class abundance (Figs. 8, 9, and 10k, 1).

DISCUSSION

Simulation results and implications

The results suggest several implications for understanding ecological dynamics on forest landscapes that would not be entirely intuitive if studied as aggregate phenomena or examined on simpler, homogeneous landscapes, or on artificial landscapes. Simulating a real landscape from current conditions illustrates the prolonged effect of human impacts of the past 100 yr and their constraints on forest landscape recovery. Simulation studies have looked at changes in patch-mosaic patterns from timber harvesting in the Pacific Northwest (Wallin et al. 1996) and patch-age patterns from fire and fire suppression in northern Minnesota (Baker 1989, 1992). This work has shown that direct and indirect human impact may produce long-term alterations to forest landscape patch structure that persist for decades to centuries. Our results illustrate a similar pattern and add the detail of species-level successional dynamics in response to landscape disturbance. Our simulation suggests that even by restoring pre-European disturbance regimes, formerly dominant species in our region, such as hemlock, yellow birch, oak, and pine, require 100–500 yr to recover their former proportions. Human alteration of these landscapes to a degree that limits seed sources, along with altered disturbance regimes, contributes to slow species recovery. Although patch age-class equilibrium may be restored somewhat sooner, a landscape with largely young age classes initially has lower probabilities of large and severe fires. This further implies that, as others have suggested on real landscapes (Davis 1986), long-term nonequilibrium between tree species and climate will continue to prevail, given projected rates of climate change over the next 1–2 centuries.

Simulating disturbance and fine-scale species response on a heterogeneous, disturbed landscape illustrates effects of past human alteration on the rate of landscape recovery, and the development of patterns at three scales in both tree-species composition and age-class structure. Initially, this landscape is domi-

nated by a relatively homogeneous age-class structure and mixed, early-successional forests that are fairly similar across land types. At the finest scale, this initial relatively homogeneous, young age-class structure gradually disaggregates, occurring slowly at first while the forests age. After 100–150 yr, the effects of fine-grained successional processes begin to become apparent. Formerly dominant, tolerant species that were largely removed during the last century and have low dispersal capability, such as hemlock, only gradually recover across the landscape. Secondly, landscape recovery manifests itself at larger scales as land types differentiate compositionally, based on characteristic successional trajectories. Finally, changes are observable at a middle scale. As the landscape ages and the probability of large, severe fires increases, coarser grained heterogeneity develops as fire patches colonized with young, early-successional species punctuate the larger and smaller scale patterns.

The results also illustrate, specifically, the interaction of fire and species response across land types with differing environments and disturbance regimes. Mesic land types with long fire-return intervals can have severe disturbances, although infrequent, that produce greater alterations to the landscape than the more frequent fires on xeric land types. Fires on mesic landscapes, when they occur, will eliminate dominant shade-tolerant species such as sugar maple. This will result in invasion by early-successional species such as aspen, producing long-term alterations in landscape composition. But these are infrequent events, and variation in landscape composition over time tends toward equilibrium dominated by the shade-tolerant species. On xeric land types, an equilibrium condition also develops but at a different scale from that on mesic land types. Frequent fires tend to keep the landscape in pine- and oak-dominated forests, but with a more patchy and variable landscape composition over time. Mid-tolerant species are maintained most consistently, with lowest variability, on land types with intermediate disturbance regimes. These land types also tend to have highest species diversity (Fig. 8b, c), consistent with patterns found for intermediate disturbance frequencies at smaller scales in forests (Auclair and Goff 1971, Grubb 1977, Denslow 1980). Landscape equilibrium (Baker 1989, Turner et al. 1993) is dependent on landscape heterogeneity, landscape extent, and time scales. In this heterogeneous system, equilibrium in landscape structure and composition is approached on the larger land types dominated by shade-tolerant species, but not on land types with shorter fire-return intervals, at the scales simulated.

These large-scale, spatial simulations also show how disturbances flow and are modified across real landscapes. Xeric land types have frequent fires, and there are boundary effects where fires can move onto more mesic land types. The more frequent, lower intensity fires on the xeric land types are generally met with

lower fire probabilities and reduced likelihood of spread on the mesic land type, depending on the contrast of environments between the two adjacent land types. But occasionally, if susceptibility is high on the adjacent cells of the mesic land type, the fire can change to a greater severity class than originated on the xeric land type. The effect of these dynamics across land-type borders is to soften land-type differences in species composition at their boundaries. The effect is also partly dependent on boundary contrast between adjacent land types, in terms of species environment and disturbance regime. These landscape boundaries can be areas where species diversity may be highest. For conservation purposes, these results provide further emphasis for the need to manage landscape complexes, where discrete management boundaries are minimized, so that natural dynamics can operate across environmental gradients.

Modeling approach implications

Application of the spatial and stochastic approach described here to model a forest landscape illustrates use of the LANDIS model and provides insight into the dynamics of disturbances and species responses on a large, heterogeneous landscape. LANDIS uses a stochastic fire simulation approach and is not designed to predict individual events that may occur in the future at particular locations. Rather the modeling approach serves as an useful tool for examining long-term spatial dynamics and the consequences of various disturbance changes and management effects.

The model uses either empirical or assumed mean fire-return intervals and size-frequency distributions. Model calibration and verification are important to ensure that model assumptions are correctly simulated. However, some verification and validation for a stochastic, spatial model cannot be done using methods such as Monte Carlo techniques. Conducting multiple, replicate simulations is often not feasible, and there are no acceptable algorithms for averaging a series of spatial maps with multiple attributes. Model validation in the traditional sense may not be meaningful or feasible for large-scale, stochastic models (Rykiel 1996). Thus verification and calibration of a single run are important for stochastic models such as LANDIS. The model calibration techniques we used allow verification and calibration through an iterative process, by comparing single-model runs with an adjusted set of parameters. Selected output from single-model runs can then be evaluated against assumptions, with model errors evaluated as percentage deviation from designed values. Results indicate that high variance can be expected when representing long fire-return intervals with relatively short simulations, or on relatively small landscapes, even though the run is carefully calibrated. Depending on modeling needs, the range of variation in disturbance parameters can be expanded or constrained using this approach.

The categorical nature of several model parameters in LANDIS and the semiquantitative model output (tree species presence/absence in a cell) has several advantages. The model produces generally robust results and reduces any false precision that could result from producing more detailed, tree-density or biomass outputs from simple inputs. This model structure also allows relatively easy incorporation of more detailed parameter information as it becomes available or adaptation of the model in different regions. While improved parameter information and empirical data are always desirable, they often do not exist at large scales, and conservation and management decisions continue to be made on a far less reliable, ad hoc basis.

CONCLUSION

We have described a stochastic modeling approach and applied the model to examine spatial dynamics of fire disturbance and species-level recovery on a large, heterogeneous landscape that has experienced extensive alteration by human land use. The model illustrates the feasibility of simulating individual species through time at a resolution that provides adequate mechanistic detail, but is computationally efficient enough to simulate large, heterogeneous landscapes over centuries. The results illustrate the complex dynamics that occur between disturbances and species-level change at large scales, both spatially and over a long time period. Studying such dynamics on landscapes that incorporate spatial heterogeneity in environments appears to be important in understanding what patterns these dynamics will produce and how long it will take. In our results, even in those land types that recover from past human activities to approach a landscape compositional equilibrium, the time required is several centuries. Feedbacks in the model among species, disturbance, and land types produce emergent patterns on the landscape at several scales over time.

Our approach may be useful in examining the effects of disturbance regimes that are modified by global change, or the impacts of various land use and management practices over time, and their interaction with landscape structure in influencing the pattern and rate of forest landscape change. Ultimately, stochastic models should be used as tools with defined purposes and limitations, and results interpreted accordingly. In our applications, emphasis is placed on the general nature of patterns and dynamics produced at large scales, rather than predictive ability for specific local events.

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LITERATURE CITED

- Anderson, H. E. 1982. Aids to determining fuel models for estimating fire behavior. USDA Forest Service, General Technical Report **INT-122**.
- . 1983. Predicting wind-driven wild land fire size and shape. USDA Forest Service, Research Paper **INT-305**.
- Andrews, P. L. 1986. BEHAVE: Fire behavior prediction and fuel modeling system - BURN subsystem, Part I. USDA Forest Service, General Technical Report **INT-194**.
- Armesto, J. J., and S. T. A. Pickett. 1985. Experiments on disturbance in old-field plant communities: impact on species richness and abundance. *Ecology* **66**:230–240.
- Auclair, A. N., and F. G. Goff. 1971. Diversity relations of upland forests in the western Great Lakes area. *American Naturalist* **105**:499–528.
- Baker, W. L. 1989. Landscape ecology and nature reserve design in the boundary waters canoe area, Minnesota. *Ecology* **70**:23–35.
- . 1992. The landscape ecology of large disturbances in the design and management of nature reserves. *Landscape Ecology* **7**:181–194.
- . 1995. Landscape analysis of the forest-tundra ecotone in Rocky Mountain National Park, Colorado. *Professional Geographer* **47**:361–375.
- Baker, W. L., S. L. Egbert, and G. F. Frazier. 1991. A spatial model for studying the effects of climatic change on the structure of landscapes subject to large disturbances. *Ecological Modeling* **56**:109–125.
- Botkin, D. B., and R. A. Nisbet. 1992. Forest response to climatic change—effects of parameter estimation and choice of weather patterns on the reliability of projections. *Climatic Change* **20**:87–111.
- Brown, J. K., and D. G. Simmerman. 1986. Appraising fuels and flammability in western aspen: a prescribed fire guide. USDA Forest Service, General Technical Report **INT-205**.
- Burns, R. M., and B. H. Honkala, coordinators. 1990. *Silvics of North America*. USDA Forest Service, Washington, D. C., USA.
- Canham, C. D., and O. L. Loucks. 1984. Catastrophic windthrow in the presettlement forests of Wisconsin. *Ecology* **65**:803–809.
- Carrano, F. M. 1995. Data abstraction and problem solving with C++—walls and mirrors. Benjamin/Cummings, Redwood City, California, USA.
- Clark, J. S. 1989. Ecological disturbance as a renewal process: theory and application to fire history. *Oikos* **56**:17–30.
- Cohen, J. D. 1986. Estimating fire behavior with FIRECAST: User's manual. USDA Forest Service, General Technical Report **PSW-90**.
- Coleman, J. R., and A. L. Sullivan. 1996. A real-time computer application for the prediction of fire spread across the Australian landscape. *Simulation* **67**:230–240.
- Curtis, J. T. 1959. *The vegetation of Wisconsin: an ordination of plant communities*. University of Wisconsin Press, Madison, Wisconsin, USA.
- Davis, M. B. 1986. Climatic instability, time lags, and community disequilibrium. Pages 269–284 in J. Diamond and T. J. Case, editors. *Community ecology*. Harper & Row, New York, New York, USA.
- Deeming, J. E., J. W. Lancaster, M. A. Fosberg, R. W. Furman, and M. J. Schroeder. 1974. The national fire-danger rating system. USDA Forest Service, General Technical Report **RM-84**.
- Denslow, J. S. 1980. Patterns of plant species diversity during succession under different disturbance regimes. *Oecologia* **46**:18–21.
- Finney, M. A. 1994. Modeling the spread and behavior of prescribed natural fires. Pages 138–143 in *Proceeding of 12th Conference of Fire and Forest Meteorology*. Society of American Foresters, Jekyll Island, Georgia, USA.
- . 1999. Mechanistic modeling of landscape fire patterns. In D. J. Mladenoff and W. L. Baker, editors. *Spatial modeling of forest landscape change: approaches and applications*. Cambridge University Press, Cambridge, UK.
- Foster, D. R., J. D. Aber, J. M. Melillo, R. D. Bowden, and F. A. Bazzaz. 1997. Forest response to disturbance and anthropogenic stress. *BioScience* **47**:437–445.
- Frelich, L. E., and C. G. Lorimer. 1991. Natural disturbance regimes in hemlock-hardwood forests of the upper Great Lakes region. *Ecological Monographs* **61**:145–164.
- Gardner, R. H., W. W. Hargrove, M. G. Turner, and W. H. Romme. 1996. Climate change, disturbances and landscape dynamics. Pages 149–172 in B. H. Walker and W. L. Steffen, editors. *International Geosphere-Biosphere Programme, Book Series Number 2*. Cambridge University Press, Cambridge, UK.
- Gardner, R. H., W. H. Romme, and M. G. Turner. 1999. Scale-dependent processes on predicting patterns of forest fires. In D. J. Mladenoff and W. L. Baker, editors. *Spatial modeling of forest landscape change: approaches and applications*. Cambridge University Press, Cambridge, UK.
- Green, D. G. 1989. Simulated effects of fire, dispersal and spatial pattern on competition within forest mosaics. *Vegetatio* **82**:139–153.
- Grubb, P. J. 1977. The maintenance of species-richness in plant communities: the importance of the regeneration niche. *Biological Review* **52**:107–145.
- Guertin, P. J., and C. W. Ramm. 1996. Testing Lake States TWIGS: five-year growth projections for upland hardwoods in northern lower Michigan. *Northern Journal of Applied Forestry* **13**:182–188.
- Hansen, M. H. 1992. *The eastwide forest inventory data base: user's manual*. USDA Forest Service, General Technical Report **NC 151**.
- He, H. S., D. J. Mladenoff, and J. Boeder. 1996. LANDIS, a spatially explicit model of forest landscape disturbance, management, and succession—LANDIS 2.0 users' guide. Department of Forest Ecology and Management, University of Wisconsin-Madison, Madison, Wisconsin, USA.
- He, H. S., D. J. Mladenoff, V. C. Radeloff, and T. R. Crow. 1998. Integration of GIS data and classified satellite imagery for regional forest assessment. *Ecological Applications* **8**:1072–1083.
- Heinselman, M. L. 1973. Fire in the virgin forests of the boundary waters canoe area, Minnesota. *Quaternary Research* **3**:329–382.
- . 1981. Fire intensity and frequency as factors in the distribution and structure of northern ecosystems. Pages 7–57 in H. A. Mooney, T. M. Bonnicksen, and N. C. Christensen, editors. *Fire regimes and ecosystem properties*. USDA Forest Service, General Technical Report **WO-26**.
- Host, G. E., Polzer, P. L., Mladenoff, D. J., and Crow, T. R., 1996. A quantitative approach to developing regional ecosystem classifications. *Ecological Applications* **6**:608–618.
- Hubbard, K. G. 1980. Relating fire occurrence to weather conditions on the Great Basin rangelands. *Journal of Range Management* **33**:360–362.
- Johnson, E. A. 1992. *Fire and vegetation dynamics: studies from the north American boreal forest*. Cambridge University Press, Cambridge, UK.
- Johnson, E. A., G. I. Fryer, and M. J. Heathcote. 1990. The influence of man and climate on frequency of fire in the interior wet belt forest, British Columbia. *Journal of Ecology* **78**:403–412.
- Johnson, E. A., and S. L. Gutsell. 1994. Fire frequency models, methods and interpretations. *Advances in Ecological Research* **25**:239–286.

- Keane, R. E., S. F. Arno, and K. J. Brown. 1989. FIRE-SUM—an ecological process model for fire succession in western conifer forests. USDA Forest Service, General Technical Report **INT-266**.
- Keane, R. E., P. Morgan, and S. W. Running. 1996. Fire-BGC—a mechanistic ecological process model for simulating fire succession on coniferous forest landscapes of the northern Rocky Mountains. USDA Forest Service, Research Paper **INT-484**.
- Loehle, C. 1988. Forest decline: endogenous dynamics, tree defenses, and the elimination of spurious correlation. *Vegetatio* **77**:65–78.
- Loucks, O. L. 1970. Evolution of diversity, efficiency, and community stability. *American Zoologist* **10**:17–25.
- Mladenoff, D. J., and W. L. Baker. 1999. Development of forest modeling approaches. In D. J. Mladenoff and W. L. Baker, editors. *Spatial modeling of forest landscape change: approaches and applications*. Cambridge University Press, Cambridge, UK.
- Mladenoff, D. J., and H. S. He. 1999. Design and behavior of LANDIS, an object-oriented model of forest landscape disturbance and succession. In D. J. Mladenoff and W. L. Baker, editors. *Spatial modeling of forest landscape change: approaches and applications*. Cambridge University Press, Cambridge, UK.
- Mladenoff, D. J., G. E. Host, J. Boeder, and T. R. Crow. 1996. LANDIS: a spatial model of forest landscape disturbance, succession, and management. Pages 175–180 in M. F. Goodchild, L. T. Steyaert, and B. O. Parks, editors. *GIS and environmental modeling: progress and research issues*. GIS World Books, Fort Collins, Colorado, USA.
- Mladenoff, D. J., and J. Pastor. 1993. Sustainable forest ecosystems in the northern hardwood and conifer forest region: concepts and management. Pages 145–180 in G. H. Aplet, N. Johnson, J. T. Olson, and V. A. Sample, editors. *Defining sustainable forestry*. Island Press, Washington, D.C., USA.
- Mladenoff, D. J., and F. Stearns. 1993. Eastern hemlock regeneration and deer browsing in the northern great lakes region—a re-examination and model simulation. *Conservation Biology* **7**:889–900.
- Pastor, J., and D. J. Mladenoff. 1992. The southern boreal-northern hardwood forest border. Pages 216–240 in R. L. Shugart and G. B. Bonan, editors. *A systems analysis of the global boreal forest*. Cambridge University Press, Cambridge, UK.
- Pastor, J., and W. M. Post. 1986. Influence of climate, soil moisture, and succession on forest carbon and nitrogen cycles. *Biogeochemistry* **2**:3–27.
- Pickett, S. T. A., J. J. Amesto, and S. L. Collins. 1989. The ecological concept of disturbance and its expression at various hierarchical levels. *Oikos* **54**:129–136.
- Pickett, S. T. A., J. Kolasa, and C. G. Jones. 1994. Ecological understanding: the nature of theory and the theory of nature. Academic Press, San Diego, California, USA.
- Pickett, S. T. A., and J. N. Thompson. 1978. Patch dynamics and the design of nature reserves. *Biological Conservation* **13**:27–47.
- Pickett, S. T. A., and P. S. White. 1985. *The ecology of natural disturbance and patch dynamics*. Academic Press, New York, New York, USA.
- Roberts, D. W. 1996. Modeling forest dynamics with vital attributes and fuzzy systems theory. *Ecological Modeling* **90**:161–173.
- Romme, W. H. 1982. Fire and landscape diversity in sub-alpine forests of Yellowstone National Park. *Ecological Monographs* **52**:199–221.
- Romme, W. H., and D. G. Despain. 1989. The Yellowstone fires. *Scientific American* **261**:37–46.
- Ross, S. 1988. *A first course in probability*. Macmillan, New York, New York, USA.
- Rothermel, R. C. 1972. A mathematical model for predicting fire spread in wild land fuels. USDA Forest Service, Research Paper **INT-115**.
- . 1983. How to predict the spread and intensity of forest and range fires. USDA Forest Service, General Technical Report **INT-143**.
- . 1991. Predicting behavior and size of crown fires in the northern Rocky Mountains. USDA Forest Service, Research Paper **INT-483**.
- Rothermel, R. C., and J. E. Deeming. 1980. Measuring and interpreting fire behavior for correlation with fire effects. USDA Forest Service, General Technical Report **INT-93**.
- Rothermel, R. C., R. A. Wilson, G. A. Morris, and S. S. Sackett. 1986. Modeling moisture content of fine dead wildland fuels input to the BEHAVE fire prediction system. USDA Forest Service, Research Paper **INT-359**.
- Rumbaugh, J., M. Blaha, W. Premerlani, F. Eddy, and W. Lorensen. 1991. *Object-orientated modeling and design*. Prentice-Hall, New York, New York, USA.
- Rykiel, E. J., Jr. 1996. Testing ecological models: the meaning of validation. *Ecological Modeling* **90**:229–244.
- Shugart, H. H. 1984. A theory of forest dynamics: the ecological implications of forest succession models. Springer-Verlag, New York, New York, USA.
- Takle, E. S., D. J. Bramer, W. E. Heilman, and M. R. Thompson. 1994. A synoptic climatology for forest fires in the NE US and future implications from GCM simulations. *Journal of Wildland Fire* **4**:217–224.
- Turner, M. G., V. H. Dale, and R. H. Gardner. 1989. Predicting across scales: theory development and testing. *Landscape Ecology* **3**:245–252.
- Turner, M. G., W. H. Romme, and R. H. Gardner. 1994. Landscape disturbance models and the long-term dynamics of natural areas. *Natural Areas Journal* **14**:3–11.
- Turner, M. G., W. H. Romme, R. H. Gardner, R. V. O'Neill, and T. K. Kratz. 1993. A revised concept of landscape equilibrium: disturbance and stability on scaled landscapes. *Landscape Ecology* **8**:213–227.
- Urban, D. L., M. F. Acevedo, and S. L. Garman. 1999. Scaling fine-scale processes to large scale patterns using models derived from models: meta-models. In D. J. Mladenoff and W. L. Baker, editors. *Spatial modeling of forest landscape change: approaches and applications*. Cambridge University Press, Cambridge, UK.
- Urban, D. L., G. B. Bonan, T. M. Smith, and H. H. Shugart. 1991. Spatial applications of gap models. *Forest Ecology and Management* **42**:95–110.
- Vasconcelos, M. J., and D. P. Guertin. 1992. FIREMAP—Simulation of fire growth with a geographic information system. *International Journal of Wildland Fire* **2**:87–96.
- Wallin, D. O., F. J. Swanson, B. Marks, and J. H. Cissel, and J. Kertis. 1996. Comparison of managed and pre-settlement landscape dynamics in forest of the Pacific Northwest, USA. *Forest Ecology and Management* **85**:291–309.
- White, P. S. 1979. Pattern, process, and natural disturbance in vegetation. *Botanical Review* **45**:229–299.
- Wolter, P. T., D. J. Mladenoff, G. E. Host, and T. R. Crow. 1995. Improved forest classification in the Northern Lake States using multi-temporal Landsat imagery. *Photogrammetric Engineering and Remote Sensing* **61**:1129–1143.