

Spatial modeling of forest landscape change: approaches and applications

EDITED BY

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1

Development of forest and landscape modeling approaches

David J. Mladenoff and William L. Baker

Ecological basis of forest models

The forest landscape models encompassed by this book derive from several sources. Most largely descend from ecological models developed over approximately the past 30 years. They owe their conceptual basis to developments in concepts and theories of ecological succession, disturbance, and equilibrium and non-equilibrium ecological systems, including populations, communities, ecosystems, and landscapes. Clearly, these conceptual roots extend further back within ecology than the briefer, 30-year period of computer modeling. Most of the approaches presented here combine aspects of all of the above. Some of the models in this volume (most notably Sessions *et al.*, Chapter 9) also derive more broadly from the field of geographic information systems (GIS) and forest planning, management, and decision-making software.

The modeling approaches here also are generally both empirical and mechanistic, and many have practical application in analyzing change and management on real landscapes. Development and use of these forest landscape models liberally cross the lines of fundamental and applied research. The impetus for many of these modeling approaches clearly originates within the needs of resource management, and the growing interest in managing larger landscapes. Meeting these management needs often requires tools that can help assess the effects of different management scenarios. These scenarios often require decision-making horizons spanning broad temporal and spatial scales. Often, simulation models are the only way to assess alternatives that cannot be tested under such real-world conditions.

The models in this book also can be considered to lie within an area of ecology itself, namely landscape ecology. Landscape ecology, particularly in North America, derives its theoretical development most strongly from ecosystem and community ecology of the last four decades, and its applied aspects from environmental management (Golley, 1993). Spatial processes and interactions, large land areas, and heterogeneity are explicit added focuses of landscape ecology (Pickett and

Cadenasso, 1995; Turner, 1989). Both ecology and environmental or ecosystem management can trace their own growth to a common origin in the social and environmental climate of the 1960s, with the growth of publicly funded research and environmental concern and regulation (McIntosh, 1985).

Several concepts in ecology are, in particular, fundamental for the approaches described in this book. These are concepts of vegetation change based on disturbance and succession, and the non-equilibrium nature of vegetation and ecosystems, e.g., contributions and literature reviewed in Pickett and White (1985). Another important concept is that of scale, and especially the view of the importance of spatially explicit dynamics, operating at varied spatial and temporal scales, in vegetation change (Levin and Paine, 1974; Grubb, 1977; Loucks *et al.*, 1985). These concepts, along with advances in technical tools such as the computational capability and low cost of new computers, GIS software, and remote sensing, provide the foundation for the spatial modeling approaches presented here.

Theory and concepts of succession, disturbance, and equilibrium

There have been many excellent reviews of the development of successional theory and concepts and this development will not be described in detail again here (Connell and Slatyer, 1977; Drury and Nisbet, 1973; West *et al.*, 1981; McIntosh, 1985; Glenn-Lewin *et al.*, 1992). However, a synopsis of historical context and development of vegetation change concepts in ecology will be provided. These concepts are ultimately embedded in the modeling approaches described in this book. Also, a general genealogy of forest models that lead to the models presented later will be outlined.

Systematic study of succession developed in the 1890s and early 1900s, especially with the work of Cowles (1899, 1911) and Cooper (1926). Detailed theory and description of mechanisms were comprehensively developed by Clements (1916). Clements was instrumental in articulating concepts and mechanisms of succession as an orderly, deterministic progression from beginning points of vegetation composition to a climatically determined climax, that represented a stable equilibrium (Clements, 1916). Most importantly, the plant community was seen as responding as a single organism itself through time, and the inevitable climax, once reached, exhibited long-term stability. The intuitive appeal and heuristic usefulness of such a theory is in its order and predictability – features of great utility in developing a predictive science of ecology, and ultimately, useful predictive models. There is some risk in portraying a caricature, or in over-simplifying, the rich and detailed work of Clements. Nonetheless, it is this simplified view that became dogma with ecology (McIntosh, 1985).

Alternative models were developed early as well, by Gleason (1926) in the US, Ramensky in Russia (1924; cited in McIntosh, 1985), and Tansley in England (1935). Gleason especially criticized Clements and showed that succession had a much larger stochastic component, and that species respond individualistically to the environment. Species composition is due in part to chance events resulting in

an assemblage of species with similar environmental responses, but not due to deterministic change of the community as a whole (Gleason, 1927). Nevertheless, the intuitive appeal of the Clementsian approach largely prevailed in ecology until after the 1940s. In the 1950s more extensive, quantitative approaches validated Gleason's view, in locations of both steep environmental gradients (Great Smoky Mountains: Whittaker, 1956) and moderate gradients (Wisconsin: Curtis and McIntosh, 1951; Curtis, 1959).

Even after the 1950s, the Clementsian view persisted, particularly within the developing field of systems ecology (Odum, 1969, 1971; Margalef, 1963). For several decades a notable rift existed in ecology exemplified on the one hand by the Clementsian-derived approach of systems ecology and, on the other hand, by the Gleasonian-based community and population – evolutionary approach (McIntosh, 1980; Peet and Christensen, 1980). More recent approaches have recognized a more integrated view of succession, and include plant demographics (Huston and Smith, 1987; Glenn-Lewin *et al.*, 1992).

Somewhat more slowly to develop than succession theory itself was the other half of the vegetation change equation – the importance of disturbance. This development required evolution in the concepts of succession and climax, and the implied stable equilibrium state of the climax, that had left little role for the perceived, rare disturbance events. Non-equilibrium notions of vegetation actually were articulated relatively early, and recognized the importance of observational scale, but were even more slowly accepted than were challenges to the Clementsian succession paradigm (Watt, 1947; Whittaker, 1953). More recent concepts of disturbance explicitly recognize the importance of stochasticity and variability in disturbance severity, spatial and temporal scale, and the integration of changing ecosystem processes, such as resource availability, with individual species responses to disturbance (Pickett and White, 1985). The recognition that these processes operate at varied spatial and temporal scales, that succession and disturbances can recur in ecological systems, and that these interactions have consequences for varied trajectories of vegetation change, set the stage for modeling forest landscapes in realistic ways.

Conceptual models of forest change

Several approaches developed to apply these changing successional concepts to predictive models, albeit non-spatial, during the 1970s. Those most developed were two related approaches, Markov transition models and vital-attribute models. These approaches exemplify more formal mathematical and rule-based formulations of succession theory, are useful heuristically, and began application of succession theory to studies of ecological change and management.

Stationary Markov models (Feller, 1968) have been used to characterize successional changes over time based on observed transitions in forests (Stephens and Waggoner, 1970; Waggoner and Stephens, 1970). Markov models are a mathematical approach utilizing a matrix of empirically determined transition probabilities to predict tree-species replacement and, therefore, composition over time. Short-

comings of this approach have been described many times, and include the problems that (i) successional change may not be stationary, i.e., the probabilities may not be constant over time; (ii) they are typically first-order models, meaning that only the current state is considered in determining the transition; and (iii) they are non-spatial, in that adjacency relationships are not considered in the transition probabilities (van Hulst, 1979; Binkley, 1980). Modifications of this approach exist, described as semi-Markov models, that address some of the above problems (Ginsberg, 1971).

Computer models of forest change

During the 1970s several approaches to converting succession theory and knowledge of forest stand dynamics appeared that we see as antecedents to many of the modeling methods in this book. These models were formulated at individual-tree, forest gap, and stand scales.

Relatively simple rule-based transition models, related to Markov models, were developed in Australia (Noble and Slatyer, 1980) and in the western US (Cattelino *et al.*, 1979). These transition models have greater flexibility than the simple Markov models, and began to incorporate various pathways due to disturbance and site characteristics, rather than converging to a single steady state. State changes were based on combinations of species life history characteristics or 'vital attributes' (Cattelino *et al.*, 1979) which respond to disturbances. The models proved to be ecologically useful, and were applied within the FORPLAN forest planning system of the US Forest Service (Potter *et al.*, 1979). These were some of the first models to be implemented on computers and used extensively in forest management for large areas, such as a National Forest, although, again, they were not explicitly spatial.

One of the most interesting and detailed of the early forest models was the FOREST model of Ek and Monserud (1974), developed for northern Wisconsin, USA. The model simulated reproduction, growth, and mortality of all trees in a forest stand. Each tree was spatially located, and adjacent effects of crown shading and seed dispersal were included. The model challenged the computational capabilities of computers at the time, included great detail, and also had extensive input parameter requirements. In many ways the FOREST model was a conceptually and mechanistically superior approach, especially for the 1970s. But the computational requirements and input needs limited its use.

Slightly earlier, Botkin *et al.* (1972) developed JABOWA, the first of the forest gap simulators, for forests of the Northeastern US. This model and its many descendants incorporated the ecological realism of simulating detailed succession at the forest gap level. The JABOWA model of Botkin *et al.* spawned numerous modifications and model versions, particularly by Shugart and colleagues (Shugart, 1984, 1998). Gap models have been adapted worldwide, and have made important contributions to understanding forest-stand dynamics in nearly every type of forest ecosystem. Useful reviews of these implementations and the gap model evolution are also numerous (Shugart, 1984, Urban and Shugart, 1992).

Applications of gap models are often assumed to portray change at the single-tree gap scale, and results interpreted accordingly. However, this was not typically the scale at which most versions operated. The original JABOWA model simulated a 0.01 ha (10 m × 10 m), tree-size plot. The FOREST model and its descendants simulate a plot size significantly larger than this, typically 0.08–0.1 ha (Shugart, 1984). The computational problems inherent in the FOREST model were somewhat avoided in this conceptualization. An entire forest stand simulation could be approximated, assuming homogeneity, by averaging multiple single plot runs. Later versions of the gap model added detail by a return to the single-tree scale, and with spatial implementations, simulating a network of plots in a stand-sized grid of 4–9 ha (Smith and Urban, 1988; Sarkar *et al.*, 1996). Since the original gap models were single-plot, and non-spatial, they typically did not include disturbances such as fire (but see Kercher and Axelrod, 1984). Gap models have been usefully applied to many problems since early in their development, including management (Aber *et al.*, 1982) and climate change (Solomon, 1986; Pastor and Post, 1988; Shugart, 1998).

Most models at this time were addressing within-stand change. A few approaches attempted to directly address larger-scale, landscape or regional forest change, and stand out for the early period of their development, as the FOREST model does at the stand level. Models were developed for regions of the US under the US IBP Program (Loucks *et al.*, 1981). A differential equation model that simulated regional forest change across the North central US Lake States was developed by Shugart *et al.* (1973). The model was non-spatial, and did not include disturbance. Change was similar to the Markov tree models described above, but in this case transitions were between major forest cover classes. The third model, for the Georgia Piedmont, is particularly interesting in that it included land-use cover-classes as well as natural forest changes (Johnson and Sharpe, 1976). This model was not only a deterministic successional model, but included possible alterations on the landscape by logging, fire, and grazing. The model output described percentage changes in the cover classes for the region under different change rates for the disturbance parameters (Johnson and Sharpe, 1976).

Recently, Pacala *et al.* (1993) have developed a spatially explicit, stand-level model (SORTIE) based on new and more detailed field data and calibrations of seed dispersal, recruitment, growth, and mortality. In this approach, individual trees are each located in a stand. In this respect and in its greater data requirements, it owes much to the approach in the FOREST model developed by Ek and Monserud (1974). In its mechanisms and array of submodels, SORTIE derives its structure from the JABOWA-FORET gap models (Pacala *et al.*, 1993). The advantages of SORTIE are that it incorporates stronger field data-derived relationships in its submodels than did the previous gap models. Its disadvantages are that, like FOREST in the past, simulating large areas with a spatially explicit, single-tree model has great computational cost. Typically, stands of <10 ha can be simulated with reasonable processing time (Pacala *et al.*, 1993). The model also has its power built on the need for extensive new data collection for input parameter calibration,

data not yet available for most locations outside of its original development locale of southern New England.

Forestry growth and yield models

Forestry models under this group differ in their purposes and derivation from the more ecological models described above. The development of this field has been reviewed several times (Munro, 1974; Loucks *et al.*, 1981; Dale *et al.*, 1985; Parks and Alig, 1988). These models derived from forest growth and yield data and predictive equations at first concerned with predicting aggregate stand growth increment for potential harvest, such as STEMS (Belcher *et al.*, 1982). Later individual-tree simulation models bridged this field with the ecological models. The FOREST model is within this overlapping group and is appropriately described above as well.

Forest management and planning models

Models under this general area actually begin to separate from the more biologically based succession and forest growth models, and overlap with more general management planning, land-use planning, and decision-support software systems. There has often been a close link between the growth and yield models and these planning models (Iverson and Alston, 1986). Some distinction of scale can be made, differentiating larger scale, strategic planning or regional timber-supply models, and smaller scale, growth and yield and tactical decision models. One of the best known models is the FORPLAN model of the US Forest Service (Iverson and Alston, 1986). Models of this type are often complex, and have been criticized for past versions that lacked ecological dynamics and variability, or spatial considerations, which were then not included in resulting projections and plans (Johnson, 1992). This is a complex and growing area, and despite shortcomings, has been important in extending the development and use of computers models for large-scale planning, and assessing management consequences on large forest ownerships.

These models that developed within the forest management field also tended to diverge from other forest models after the 1970s, similar to the split between the forestry and ecological models. Within this management and planning field, GIS applications developed that were more decision-making software than models in a strict sense, and they were not ecological. These applications did not typically consider, for example, natural disturbance rates or variability, or spatial interactions in their planning algorithms (Johnson and Scheurman, 1977; Hoganson and Burke, 1997).

Disturbance models

The final group of models that form part of the basis for the models in this book are disturbance models. Much of the information and initial modeling efforts

within this group were empirically based fire spread models, developed to understand fire behavior for suppression purposes (Van Wagner, 1969; Rothermel, 1972; Gardner *et al.*, Chapter 7). This information was later extended to forest management models (Kessell, 1976). Subsequent ecological research on forest disturbance, including fire (Heinselman, 1973, 1981; Van Wagner, 1978; Johnson, 1992) and later windthrow (Canham and Loucks, 1984; Runkle, 1982; Frelich and Lorimer, 1991), also laid important groundwork for later integration into ecological models.

Development of landscape modeling approaches

The spatial landscape models in this book have some of their roots in the forest ecology and modeling discussed in the last two sections, but technological developments in the 1980s shifted both these areas of research toward spatial phenomena and large land areas. Landscape ecology, the study of ecological phenomena on large land areas (the scale of kilometers), has roots much earlier in the twentieth century, but bloomed in the 1980s. While satellite imagery and geographical information systems (GIS) were available earlier, Landsat Thematic Mapper (TM) data at 30-m resolution and small workstations with GIS software made spatial analyses of large land areas more feasible in the 1980s.

When models of landscape change were reviewed in the late-1980s (Baker, 1989), there were relatively few examples of spatial models, in part because the impacts of this technological revolution were just unfolding. In the middle of the 1980s, common models of landscape change were dominated by distributional approaches. Distributional landscape models focus on “. . . the distribution of land area among classes of landscape phenomena . . .” (Baker, 1989 p.113); an example is Shugart *et al.*'s (1973) model of succession among 15 forest types in the western Great Lakes, based on forest cover data. While the Shugart *et al.* model used differential equations, also popular were difference-equation (matrix) models using Markov, semi-Markov, and projection approaches; an example is the Rejmanek *et al.* (1987) model of vegetation dynamics in the Mississippi delta region.

However, in the middle 1980s, there were several threads of development leading to spatially explicit landscape models. In spatially explicit models, the behavior of an individual cell or pixel cannot be predicted without knowing its location relative to other cells. The earliest spatially explicit landscape model may be the gradient fire model of Kessell (e.g., 1979), which uses spatially estimated vegetation and fuels data to simulate spatial fire patterns and post-fire succession. The Kessell model was deeply rooted in forest ecology and management traditions, building on gradient analysis and incorporating existing disturbance models discussed in the last section.

In addition to the Kessell model, in the last half of the 1980s spatially explicit models of shifting cultivation and secondary forest succession (Wilkie and Finn, 1988), and coastal marshland changes (Browder *et al.*, 1985; Sklar *et al.*, 1985) appeared. These models were less rooted in the forest ecology and modeling literat-

ure, but instead began to apply emerging landscape ecology ideas in a spatial modeling framework.

Another thread of development was from mathematical and physical theory about properties of arrays of cells. One aspect of this thread is cellular automata models, whose roots are in information theory of the 1960s. A cellular automaton in its simplest form is a grid-cell model where complex dynamics arise from simple neighborhood interaction rules (Wolfram, 1984). A neighborhood-based transition model of landscape changes in Georgia appeared in the late 1980s (Turner, 1988). A second aspect of this thread is percolation modeling, derived from fractal theory and spatial properties of arrays. In the late 1980s percolation models were used to analyze the spread of disturbances across a landscape (Turner *et al.*, 1989).

Over the last decade these threads of development from forest ecology, disturbance ecology, landscape ecology, and the mathematics of cellular automata and percolation arrays have interacted to lead us to the present state of spatial modeling, demonstrated in this book. Models emphasizing forest ecology and modeling of small land areas, such as gap models, are now reaching development in a spatially explicit form on large land areas, represented by the ZELIG version FACET (Urban *et al.*, Chapter 4). Models that have roots in the cellular automata framework, such as METAFOR (Urban *et al.*, Chapter 4) and DISPATCH (Baker, Chapter 11) continue to be useful for modeling contagious processes such as disturbance spread, but have been broadened to include more complex neighborhood dynamics (e.g., FORMOSAIC: Liu *et al.*, Chapter 3). Indeed, grid-cell models such as DISPATCH (Baker, Chapter 11) and HARVEST (Gustafson and Crow, Chapter 12) may have roots in cellular automata, but include processes operating at scales other than the immediate neighborhood.

This trend toward multi-scale models is paralleled by a trend toward multi-process spatial models, exemplified in LANDIS (Mladenoff and He, Chapter 6), LANDSIM (Roberts and Betz, Chapter 5), FORMOSAIC (Liu *et al.*, Chapter 3) and DELTA (Dale and Pearson, Chapter 10), but present in many of the other models, even those with narrower purposes. For example, the fire spread model, *FARSITE* (Finney, Chapter 8), uses grid-cell input data, but a vector-format to model the spreading fire front and has exogenous climate drivers that control fire spread, as well as a spotting routine that leapfrogs local dynamics of fire spread. The Sessions *et al.* (Chapter 9) SAFE FORESTS model focuses on fire dynamics and timber harvesting, but with other constraints. These multi-scale, multi-process models take cellular or vector neighborhood models, that recall the automata approach, and marry them with successional models, dispersal models, movement models, and disturbance models that interact in a spatially explicit format that is not simply neighborhood-based. Bottom-up models, such as cellular automata, demonstrated that complex dynamics can arise from simple neighborhood interactions, but these new models include important non-neighborhood processes that modify and control local neighborhood dynamics. Underlying this shift toward multi-scale, multi-process models is a changing world view away from a simple choice between top-down or bottom-up approaches (Baker and Mladenoff, Chapter 13).

Current challenges in forest landscape modeling

The forest landscape models presented in the rest of this book share a common, but varied, lineage with the historical work described in this chapter. To some degree, most are based on either ecological disturbance and succession principles from ecology and forestry, or earlier landscape transition models that were non-spatial.

How much multi-scale, multi-process detail is needed to model a forest landscape in a spatially explicit way? In the last chapter of this book an attempt will be made to synthesize how the models in this book answer this question. However, here at the beginning, only some of the relevant parts of this query will be posed. How much of the detail of individual-tree and population processes inside forest stands is necessary, and what are the essential processes? Are within-stand processes alone, if replicated across the landscape, sufficient to capture the essential dynamics of the landscape? How should stand-level processes vary in different environments? What processes inside a stand lead to natural (e.g., fire) and human (e.g., logging) disturbances, and how should these be modeled? Forest fragmentation is an increasing global phenomenon. Do our models include the essential changes that accompany fragmentation? Some landscape models include spatial dispersal and disturbance spread, but are other spatial processes needed? Regional and global processes are of increasing importance, as are local and global socioeconomic forces, and it may be asked how well our models represent these processes. Do people play a role in the dynamics of our models? Modelers to some extent answer these questions by including richness of detail in processes they feel are important, and by de-emphasizing or excluding processes that they feel are less important. However, what is included in each model is also a function of the purpose of the model.

In reading about the models in the following chapters, consider their genealogy, their purpose, and how these questions are answered. Viewed from two decades ago, the achievements represented here were almost inconceivable; a decade ago there was only a hint of the emerging directions. It is hoped you will see that these models are headed somewhere that will be important to us, even though it clearly will not be a single, grand, final model. Perhaps a diversity of spatial models of landscapes can extend our vision in different ways, for various purposes and scales. It has always been found hardest to call up the long-term vision and sweeping gaze needed to see the landscape for the trees.

References

- Aber, J. D., Melillo, J. M. and Federer, D. A. (1982). Predicting the effects of rotation length, harvest intensity, and fertilization on fiber yield from northern hardwood forests in New England. *Forest Science*, **28**, 31–45.
- Baker, W. L. (1989). A review of models of landscape change. *Landscape Ecology*, **2**, 111–33.
- Belcher, D. M., Holdaway, M. R. and Brand, G. A. (1982). *A description of STEMS* –

- the stand and tree evaluation and modeling system*. USDA Forest Service, General Technical Report NC-79. St. Paul, MN.
- Binkley, C. S. (1980). Is succession in hardwood forests a stationary Markov process? *Forest Science*, **26**, 566–70.
- Botkin, D. B., Janak, J. F. and Wallis, J. R. (1972). Some ecological consequences of a computer model of forest growth. *Journal of Ecology*, **60**, 849–73.
- Browder, J. A., Bartley, H. A. and Davis, K. S. (1985). A probabilistic model of the relationship between marshland–water interface and marsh disintegration. *Ecological Modelling*, **29**, 245–60.
- Canham, C. D. and Loucks, O. L. (1984). Catastrophic windthrow in the presettlement forests of Wisconsin. *Ecology*, **65**, 803–9.
- Cattellino, P. J., Noble, I. R., Slatyer, R. O. and Kessell, S. R. (1979). Predicting the multiple pathways of plant succession. *Environmental Management*, **3**, 41–50.
- Clements, F. E. (1916). *Plant succession: an analysis of the development of vegetation*. Carnegie Institute Publication 242. Washington, DC.
- Connell, J. H. and Slatyer, R. O. (1977). Mechanisms of succession in natural communities and their role in community stability and organization. *American Naturalist*, **111**, 1119–44.
- Cooper, W. S. (1926). The fundamentals of vegetation change. *Ecology*, **7**, 391–413.
- Cowles, H. C. (1899). The ecological relations of the vegetation on the sand dunes of Lake Michigan. *Botanical Gazette*, **27**, 95–117, 167–202, 281–308, 361–9.
- Cowles, H. C. (1911). The causes of vegetation cycles. *Botanical Gazette*, **51**, 161–83.
- Curtis, J. T. and McIntosh, R. P. (1951). An upland continuum in the prairie–forest border region of Wisconsin. *Ecology*, **32**, 476–96.
- Curtis, J. T. (1959). *The vegetation of Wisconsin*. Madison, WI: University of Wisconsin Press.
- Dale, V. H., Doyle, T. W. and Shugart, H. H. (1985). A comparison of tree growth models. *Ecological Modelling*, **29**, 145–69.
- Drury, W. H. and Nisbet, I. C. T. (1973). Succession. *Journal of the Arnold Arboretum*, **54**, 331–68.
- Ek, A. R. and Monserud, R. A. (1974). *FOREST: A computer model for the growth and reproduction of mixed species forest stands*. Research Report A2635. College of Agricultural and Life Sciences. University of Wisconsin–Madison. Madison, WI.
- Feller, W. (1968). *An introduction to probability theory and its applications*. Vol. 1 3rd. edn. New York, NY: Wiley.
- Frellich, L. E. and Lorimer, C. G. (1991). Natural disturbance regimes in hemlock–hardwood forests of the upper Great Lakes region. *Ecological Monographs*, **61**, 159–62.
- Ginsberg, R. B. (1971). Semi-Markov processes and mobility. *Journal of the Mathematical Society*, **1**, 233–62.
- Gleason, H. A. (1926). The individualistic concept of the plant association. *Bulletin of the Torrey Botanical Club*, **53**, 1–20.
- Gleason, H. A. (1927). Further views of the succession concept. *Ecology*, **8**, 299–326.
- Glenn-Lewin, D. C., Peet, R. K. and Veblen, T. T. (eds.). (1992). *Plant succession: Theory and prediction*. London, UK: Chapman and Hall.
- Golley, F. B. (1993). Development of landscape ecology and its relation to environmental management. In *Eastside forest ecosystem health assessment*. Volume II.

- Ecosystem management: principles and applications*, ed. M. E. Jensen and P. S. Bourgeron, pp. 37–44. USDA Forest Service, Missoula, MT, USA.
- Grubb, P. J. (1977). The maintenance of species richness in plant communities: The importance of the regeneration niche. *Biological Reviews of the Cambridge Philosophical Society*, **52**, 107–45.
- Heinselman, M. L. (1973). Fire in the virgin forests of the Boundary Waters Canoe Area, Minnesota. *Quaternary Research*, **3**, 329–82.
- Heinselman, M. L. (1981). Fire and succession in the conifer forests of northern North America. In *Forest succession: concepts and application*. ed. D. C. West, H. H. Shugart, and D. B. Botkin. New York, NY: Springer-Verlag.
- Hoganson, H. M. and Burk, T. E. (1997). Models as tools for forest management planning. *Commonwealth Forestry Review*, **76**, 11–17.
- Huston, M. A. and Smith, T. M. (1987). Plant succession: Life history and competition. *American Naturalist*, **130**, 168–98.
- Iverson, D. C. and Alston, R. M. (1986). *The genesis of FORPLAN: A historical and analytical review of Forest Service planning models*. USDA Forest Service, General Technical Report INT-214.
- Johnson, E. A. (1992). *Fire and vegetation dynamics: Studies from the North American boreal forest*. Cambridge, UK: Cambridge University Press.
- Johnson, K. N. and Scheurman, H. L. (1977). Techniques prescribing optimal timber harvest and investment under different objectives – discussion and synthesis. *Forest Science Monograph* 18. Washington, DC: Society of American Foresters.
- Johnson, K. N. (1992). Consideration of watersheds in long-term forest planning models: The case of FORPLAN and its use on the national forests. In *Watershed management: Balancing sustainability and environmental change*, ed. R. J. Naiman, pp. 347–60. New York, NY: Springer-Verlag.
- Johnson, W. C. and Sharpe, D. M. (1976). Forest dynamics in the northern Georgia piedmont. *Forest Science*, **22**, 307–22.
- Kercher, J. A. and Axelrod, M. C. (1984). A process model of fire ecology and succession in a mixed-conifer forest. *Ecology*, **65**, 1725–42.
- Kessell, S. R. (1976). Gradient modeling: A new approach to fire modeling and wilderness resource management. *Environmental Management*, **1**, 39–48.
- Kessell, S. R. (1979). *Gradient modeling: resource and fire management*. Springer-Verlag, New York.
- Levin, S. A. and Paine, R. T. (1974). Disturbance, patch formation, and community structure. *Proceedings of the National Academy of Sciences, USA*, **71**, 2744–7.
- Loucks, O. L., Ek, A. R., Johnson, W. C. and Monserud, R. A. (1981). Growth, aging, and succession. In *Dynamic properties of forest ecosystems*, ed. D. E. Reichle, pp. 37–86. Cambridge, UK: Cambridge University Press.
- Loucks, O. L., Plumb-Mentjes, M. L. and Rogers, D. (1985). Gap processes and large-scale disturbances in sand prairies. In *The ecology of natural disturbance and patch dynamics*, ed. S. T. A. Pickett and P. S. White, pp. 71–83. Orlando, FL: Academic Press.
- Margalef, R. (1963). On certain unifying principles in ecology. *American Naturalist*, **97**, 357–74.
- McIntosh, R. P. (1980). The background and some current problems of theoretical ecology. *Synthese*, **43**, 195–255.

- McIntosh, R. P. (1985). *The background of ecology: Concept and theory*. Cambridge, UK: Cambridge University Press.
- Munro, D. D. (1974). Forest growth models. A prognosis. In *Growth models for tree and stand simulation*, ed. J. Fries, pp. 7–21. Department of Forest Yield Research, Royal College of Forestry, Stockholm, Sweden.
- Noble, I. R. and Slatyer, R. O. (1980). The use of vital attributes to predict successional changes in plant communities subject to recurrent disturbances. *Vegetatio*, **43**, 5–21.
- Odum, E. P. (1969). The strategy of ecosystem development. *Science*, **164**, 1289–93.
- Odum, E. P. (1971). *Fundamentals of ecology*. 3rd edn. Philadelphia, PA: Saunders.
- Pacala, S. W., Canham, C. D. and Silander, J. A. Jr. (1993). Forest models defined by field measurements: I. The design of a northeastern forest simulator. *Canadian Journal of Forest Research*, **23**, 1980–8.
- Parks, P. J. and Alig, R. J. (1988). Land base models for forest resource supply analysis: A critical review. *Canadian Journal of Forest Research*, **18**, 965–73.
- Pastor, J. and Post, W. M. (1988). Response of northern forests to CO₂-induced climate change. *Nature*, **334**, 55–8.
- Peet, R. K. and Christensen, N. L. (1980). Succession: A population process. *Vegetatio*, **43**, 131–40.
- Pickett, S. T. A. and White, P. S. (eds.). (1985). *The ecology of natural disturbance and patch dynamics*. Orlando, FL: Academic Press.
- Pickett, S. T. A. and Cadenasso, M. L. (1995). Landscape ecology: Spatial heterogeneity in ecological systems. *Science*, **269**, 331–4.
- Potter, M. W., Kessell, S. R. and Cattelino, P. J. (1979). FORPLAN: A forest planning language and simulator. *Environmental Management*, **3**, 59–72.
- Ramensky, L. G. (1924). Basic regularities of vegetation covers and their study. (In Russian). *Vestnik Optynogo dela Stedne-Chernoz. Ob., Voronezh*, 37–73.
- Rejmanek, M., Sasser, C. E. and Gosselink, J. G. (1987). Modeling of vegetation dynamics in the Mississippi River deltaic plain. *Vegetatio*, **69**, 133–40.
- Rothermel, R. C. (1972). *A mathematical model for predicting fire spread in wild land fuels*. USDA Forest Service, Intermountain Forest and Range Experiment Station, Research Paper INT-115. Ogden, UT.
- Runkle, J. R. (1982). Patterns of disturbance in some old-growth mesic forests of eastern North America, *Ecology*, **63**, 1533–46.
- Sarkar, S., Cohen, Y. and Pastor, J. (1996). Mathematical formulation and parallel implementation of a spatially explicit ecosystem control model. In *Conference proceedings, Grand challenges in computer simulations*, Society for computer simulations, New Orleans: LA.
- Shugart, H. H., Jr., Crow, T. R. and Hett, J. M. (1973). Forest succession models: A rationale and methodology for modeling forest succession over large regions. *Forest Science*, **19**, 203–12.
- Shugart, H. H. (1984). *A theory of forest dynamics: The ecological implications of forest succession models*. New York, NY: Springer-Verlag.
- Shugart, H. H. (1998). *Terrestrial ecosystems in changing environments*. Cambridge, UK: Cambridge University Press.
- Sklar, F. H., Costanza, R. and Day, J. W. Jr. (1985). Dynamic spatial simulation modeling of coastal wetland habitat succession. *Ecological Modelling*, **29**, 261–81.
- Smith, T. M. and Urban, D. L. (1988). Scale and the resolution of forest structural pattern. *Vegetatio*, **74**, 143–50.

- Solomon, A. M. (1986). Transient response of forests to CO₂-induced climate change: Simulation experiments in eastern North America. *Oecologia*, **68**, 567–79.
- Stephens, G. R. and Waggoner, P. E. (1970). The forests anticipated from 40 years of natural transition in mixed hardwoods. *Bulletin of the Connecticut Agricultural Experiment Station*. New Haven, CT.
- Tansley, A. G. (1935). The use and abuse of vegetational concepts and terms. *Ecology*, **16**, 284–307.
- Turner, M. G. (1988). A spatial simulation model of land use changes in a Piedmont county in Georgia. *Applied Mathematics and Computation*, **27**, 39–51.
- Turner, M. G. (1989). Landscape ecology: the effect of pattern on process. *Annual Review of Ecology and Systematics*, **20**, 171–97.
- Turner, M. G., Gardner, R. H., Dale, V. H. and O'Neill, R. V. (1989). Predicting the spread of disturbance across heterogeneous landscapes. *Oikos*, **55**, 121–9.
- Urban, D. L. and Shugart, H. H. (1992). Individual-based models of forest succession. In *Plant succession: Theory and prediction*, ed. D. C. Glenn-Lewin, R. K. Peet, and T. T. Veblen, pp. 249–93. London, UK: Chapman and Hall.
- Van Hulst, R. (1979). On the dynamics of vegetation: Markov chains as models of succession. *Vegetatio*, **40**, 3–14.
- Van Wagner, C. E. (1969). A simple fire growth model. *Forestry Chronicle*, **45**, 103–4.
- Van Wagner, C. E. (1978). Age class distribution and the forest fire cycle. *Canadian Journal of Forest Research*, **8**, 220–7.
- Waggoner, P. E. and Stephens, G. R. (1970). Transition probabilities for a forest. *Nature*, **225**, 1160–1.
- Watt, A. S. (1947). Pattern and process in the plant community. *Journal of Ecology*, **35**, 1–22.
- West, D. C., Shugart, H. H., and Botkin, D. B. (eds.). (1981). *Forest succession: Concepts and application*. New York, NY: Springer-Verlag.
- Whittaker, R. H. (1953). A consideration of climax theory: The climax as a population and pattern. *Ecological Monographs*, **23**, 41–78.
- Whittaker, R. H. (1956). The vegetation of the Great Smoky Mountains. *Ecological Monographs*, **26**, 1–80.
- Wilkie, D. S. and Finn, J. T. (1988). A spatial model of land use and forest regeneration in the Ituri forest of northeastern Zaire. *Ecological Modelling*, **41**, 307–23.
- Wolfram, S. (1984). Cellular automata as models of complexity. *Nature*, **311**, 419–24.