



A frame-based spatially explicit model of subarctic vegetation response to climatic change: comparison with a point model

T. Scott Rupp^{1*}, Anthony M. Starfield¹ & F. Stuart Chapin, III²

¹Department of Ecology, Evolution, and Behavior, University of Minnesota, St. Paul, MN 55108, USA

²Institute of Arctic Biology, University of Alaska, Fairbanks, AK 99775, USA

*Current address: Forest Soils Laboratory, University of Alaska, Fairbanks, AK 99775, USA; e-mail: psulions@alaska.net

Received 13 November 1998; Revised 27 April 1999; Accepted 23 July 1999

Key words: boreal forest, climatic change, explicit, fire, insects, landscape dynamics, model, spatially subarctic, transient dynamics, treeline

Abstract

An important challenge in global-change research is to simulate short-term transient changes in climate, disturbance regime, and recruitment that drive long-term vegetation distributions. Spatial features (e.g., topographic barriers) and processes, including disturbance propagation and seed dispersal, largely control these short-term transient changes. Here we present a frame-based spatially explicit model (ALFRESCO) that simulates landscape-level response of vegetation to transient changes in climate and explicitly represents the spatial processes of disturbance propagation and seed dispersal. The spatial model and the point model from which it was developed showed similar results in some cases, but diverged in situations where interactions among neighboring cells (fire spread and seed dispersal) were crucial. Topographic barriers had little influence on fire size in low-flammability vegetation types, but reduced the average fire size and increased the number of fires in highly flammable vegetation (dry grassland). Large fires were more common in landscapes with large contiguous patches of two vegetation types while a more heterogeneous vegetation distribution increased fires in the less flammable vegetation type. When climate was held constant for thousands of years on a hypothetical landscape with the same initial vegetation, the spatial and point models produced identical results for some climates (cold, warm, and hot mesic), but produced markedly different results at current climate and when much drier conditions were imposed under a hot climate. Spruce migration into upland tundra was slowed or prevented by topographic barriers, depending on the size of the corridor. We suggest that frame-based, spatially explicit models of vegetation response to climate change are a useful tool to investigate both short- and long-term transients in vegetation at the regional scale. We also suggest that it is difficult to anticipate when non-spatial models will be reliable and when spatially explicit models are essential. ALFRESCO provides an important link between models of landscape-level vegetation dynamics and larger spatio-temporal models of global climate change.

Introduction

A major challenge in predicting ecosystem response to global change is the adequate representation of the transient dynamics of vegetation change (Loehle and LeBlanc 1996; Chapin and Starfield 1997). Equilibrium models of vegetation based on correlation with climate (Prentice et al. 1992; Cramer and Leemans 1993; Lenihan and Neilson 1995) indicate the direc-

tion and magnitude of change, but reveal little about the rate and pattern of change (Neilson 1993). Vegetation is seldom in equilibrium with climate (Davis 1981, 1986; Prentice et al. 1991), and the factors that regulate climate are changing at an unprecedented rate (Houghton et al. 1990; Cattle and Crossley 1995; Robinson et al. 1998). In addition, even the long-term direction of vegetation change is sensitive to the patterns and processes that occur during transient

vegetation change (Turner et al. 1994a, 1997; Fastie 1995). Because vegetation strongly affects the rate and nature of climatic change (Bonan et al. 1992, 1995; Foley et al. 1994), an equilibrium approach may also result in inaccurate predictions of the drivers of future vegetation distribution.

Models that simulate community composition in response to plant physiological (Bonan 1990; Kellomaki and Kolstrom 1992; Keane et al. 1996) and biogeochemical processes (Pastor and Post 1986, 1988; Running and Coughlan 1988; Running and Gower 1991) realistically simulate successional change following disturbance (Pastor and Post 1986; Bonan 1990) and long-term vegetation responses to climatic change (Solomon and Shugart 1984; Davis and Botkin 1985). However, these models assume disturbance and seed availability are either random (Bonan 1990; Kellomaki and Kolstrom 1992), or they are not modeled spatially (Solomon 1986; Shugart et al. 1992), although both disturbance and seed availability will likely change in the future (Flannigan and Van Wagner 1991; Torn and Fried 1992; Starfield and Chapin 1996) as in the past (Davis 1981; Clark 1988).

Recent developments in disturbance modeling provide a framework for integrating the influence of landscape-level disturbance on vegetation distribution into models of larger spatial and temporal scales (Turner et al. 1989, 1993, 1994b; Turner and Romme 1994; Ratz 1995). Gardner et al. (1996) developed a landscape-scale model of fire spread that simulates the effect of temporal variability in weather conditions on the spatial heterogeneity and extent of the area burned. Their results showed that climate-induced changes in fire regime significantly altered age structure and spatial arrangement of forest stands.

Mechanistic models of seed dispersal provide information on local or long-distance dispersal patterns (Greene and Johnson 1995, 1996), identifying species-specific dispersal limitations and the effect of seed-source proximity and configuration on patterns of seed rain. Turner et al. (1997) found post-disturbance species distribution and densities were strongly tied to proximity of a seed source, suggesting the dispersal process influences community dynamics and vegetation trajectory in response to disturbance (Clark 1991, 1996; Clark et al. 1996). Current dispersal theory identifies the need to represent both local and long-distance dispersal dynamics in models of landscape-level vegetation change (Clark et al. 1998a, b).

The demonstrated importance of spatial processes in determining landscape-scale vegetation pattern sug-

gests that simulation of the spatial processes of disturbance propagation and seed dispersal will also be important in modeling transient responses of vegetation to climatic change (Dale 1997). Several models of transient vegetation change have been developed (Neilson et al. 1992; Noble 1993; Smith and Shugart 1993; Nikolov 1995), but none of these simulate the interaction between disturbance and vegetation dynamics at a landscape-level with realistic scenarios of climate change. Starfield and Chapin (1996) developed a non-spatial model that calculates the transients of vegetation change from upland tundra to boreal forest in response to scenarios of altered climate, seed availability, and disturbance frequency. The major weakness of their model is the inability to accurately simulate seed availability and propagation of disturbance, which requires the development of a geographically explicit model (Noble 1993).

Here we present a frame-based, spatially explicit model ALFRESCO (Alaskan Frame-based Ecosystem Code) of subarctic vegetation response to transient climatic change in Alaska, based on the earlier point model (Starfield and Chapin 1996). A frame-based model partitions the temporal changes in vegetation into a set of states or frames (Noble and Slatyer 1980; Noble 1987). Each frame runs as an independent sub-model, simulating processes important to a particular frame and which may cause a switch to a different frame (Starfield et al. 1993). This model combines disturbance events, seed dispersal, and succession on a landscape at a spatio-temporal scale appropriate for investigating both transient and long-term effects of climatic change. We describe how the point model is developed into a spatially explicit model. We then address the calibration of the spatial model. Finally, we perform a series of controlled model experiments on hypothetical landscapes to investigate the differences between the two models. The emphasis in this paper is on the strengths and weaknesses of the point and spatial models. In a follow-up paper we explore the implications for vegetation change in northwest Alaska (Rupp et al. Submitted-*b*).

Methods

Model overview

We simulate vegetation distribution using frames that represent alternative states of upland vegetation (upland tundra, white spruce forest, broad-leaved deciduous forest, and dry grassland) found in subarctic Alaska (Figure 1). The model consists of a suite of individual frame submodels. Within each submodel frame, those factors (biotic and abiotic) that may be responsible for a switch to another ecosystem type (frame) are simulated. When a switch in ecosystem type occurs, the new frame model is activated. The ecosystem types were chosen as the simplest possible representation of the complex vegetation mosaic occupying uplands in the circumpolar arctic and boreal zones (Solomon 1992), and ignore the substantial variation in species composition within these and other intermediate vegetation types (Payette 1992; Starfield and Chapin 1996). The model operates on a 10-yr time step and a spatial scale of 2×2 km grid cells; each cell has eight immediate neighbors (the 'queen' option for cellular automata). The time step is the average frequency of severe fire years in the North American boreal forest (Flannigan and Harrington 1988) and allows replicated modeling of vegetation change over time scales of decades to centuries (NRC 1994; Starfield and Chapin 1996). The spatial scale is appropriate for interfacing with mesoscale climate models (Starfield and Chapin 1996). We deliberately chose temporal and spatial scales that are larger than those used to simulate the behavior of individual fires, because our primary objective was to simulate the long-term average changes in regional vegetation rather than responses to specific fires. Our model is calibrated to provide realistic values of fire number and area burned for particular combinations of vegetation and climate at the temporal and spatial scales used in ALFRESCO. The model is a step forward toward including disturbance in dynamic global and regional vegetation models that operate at a coarse scale (0.5°). These coarse-scale models cannot include realistic topographic effects on fire probability and spread (Kittel et al. in press).

Maps of climate, initial vegetation type, and topography (elevation) can be hypothesized or input into the model from data sets in a geographic information system (GIS) database. In our model, elevation data are used to identify barriers to migration (seed dispersal) and disturbance (fire spread) (Hadley 1994).

Topography exerts a strong influence on vegetation distribution and successional trajectory at northern latitudes, through its effects on microclimate (Van Cleve et al. 1991, 1996). The probability of high moose browse pressure is a model input that influences rate of succession (Pastor and Naiman 1992; Kielland 1997) and hence fuel loads. In this study, we assume that moose browse probability is identical for each grid cell in the landscape.

All model simulations were conducted on virtual landscapes (240×240 km or 42×20 km) that represent a typical Alaskan subarctic forest-tundra ecotone. The driving variables in ALFRESCO are climate (growing-season temperature and precipitation), disturbance, and seed dispersal (Figure 1). These variables, each discussed below, then determine tree establishment, succession, and other processes controlling landscape-level vegetation change.

Spatial model driving variables

Climate

Climate input to the model is provided as a series of alternative maps of temperature and precipitation. In this paper each map is uniform across the landscape. When the model is applied to real landscapes, we will use geographic patterns of climate that are consistent with topography and latitude (e.g., colder in mountains and to the north) and with observed synoptic climatology (e.g., more precipitation near coastal moisture sources). The model generates growing season climate (May–September) based on four climatic regimes representing (1) colder than current climate, (2) current climate, (3) warmer than current climate or (4) significantly hotter than current climate. Each climatic regime has an associated probability distribution of choosing a particular map of temperature and precipitation, which are assumed to be independent of one another and independent of the climate from the previous time step (Starfield and Chapin 1996). The temperature and precipitation in each grid cell is then converted to a temperature and precipitation class ($1 = < 6.5^\circ$, $2 = 6.5 - 9.5^\circ$, $3 = 9.5 - 12.5^\circ$, or $4 = > 12.5^\circ$) that have defined effects on vegetation (Starfield and Chapin 1996). For example, the colder than current climate regime generates temperature class 1 with probability 0.8 and temperature class 2 with probability 0.2.

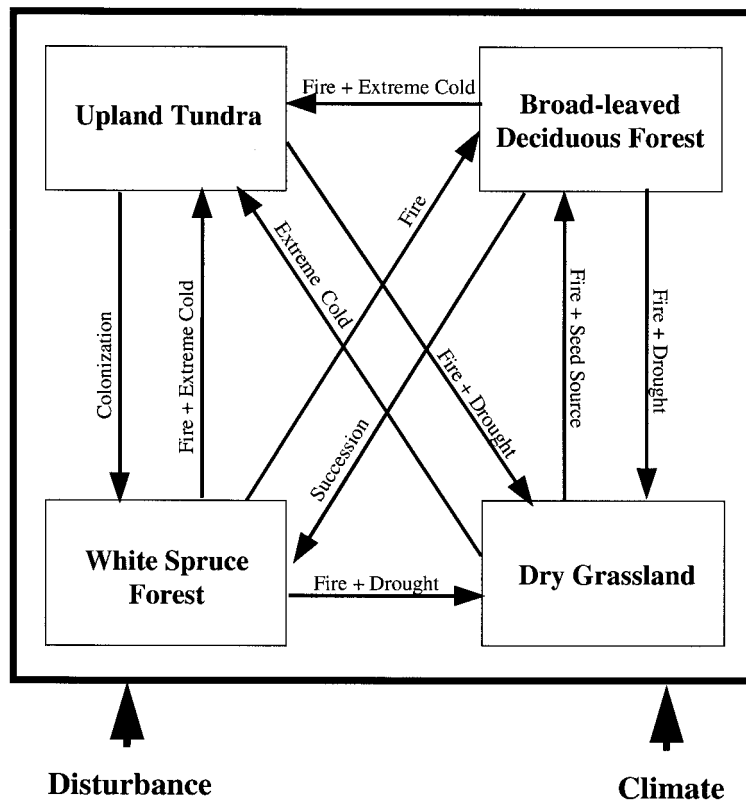


Figure 1. Model structure showing ecosystem types (boxes) and the potential switches (arrows) that occur among ecosystems (adapted from Starfield and Chapin 1996). Disturbance and climate are the driving external variables in the model.

Disturbance

Climate, vegetation type, canopy cover, and time since last disturbance drive disturbance events. Fire spread across the landscape is simulated using a cellular automaton approach, where an ignited grid cell may spread to any of its eight neighboring cells. Fire ignition within a cell is determined stochastically with a random number generator as a function of the flammability of the cell. The flammability of the receptor cell and the effects of topographic barriers (elevation > 600 m) control fire spread from one cell to another. In all ecosystem types, fire probability (the probability of a fire that kills the majority of trees in a cell) is assumed to be an inverse function of an 'effective wetness' index (Trigg 1971; Clark 1988), which increases with decreasing temperature and increasing precipitation (Thorntwaite and Mather 1957; Starfield and Chapin 1996). The shape of the relationship between fire probability and effective wetness is assumed to be the same among ecosystems (based on data from boreal forests), but actual probabilities differ among

vegetation types, due to factors that are specific to each ecosystem, as described below.

Upland tundra flammability is affected by conifer canopy cover (a measure of available fuels) and time since last fire, with fire probability being low during the first 40 yr following fire, reflecting low fuel loads (Clark 1988; Bonan 1990). The probability of fire in broad-leaved deciduous forest is low, similar to that of upland tundra (Sylvester and Wein 1981) without trees and only 20% of the probability of fire in white spruce forest (Johnson 1992). Fire probability in white spruce forest is high due to the high surface area and high flammability of conifer needles and fine branches (Susott 1982; Chrosciewicz 1986) on the forest floor. During the first 20 yr following a switch from broad-leaved deciduous forest to white spruce forest, fire probability is the same as that of the broad-leaved deciduous forest, due to the less flammable nature of broad-leaved deciduous forest fuels (Johnson 1992). Mountain cells (elevation > 600 m) are assumed to contain little or no fuels and function as barriers to fire spread.

We currently assume insect outbreaks do not spread to neighboring cells and function as described by Starfield and Chapin (1996).

Seed dispersal

Seed dispersal is limited to a distance of 4 km (well beyond any observed dispersal distance for boreal conifer tree species). Mountains (elevation > 600 m) act as physical barriers to dispersal. For example, an upland tundra cell will first look around to its eight immediate neighbors for barriers and seed sources. If no seed source is found, then the neighbors of that cell's neighbors are checked for seed sources. However, if a barrier is encountered, the barrier cell's neighbors are not searched. At this point, if no forest seed sources have been found, the seed source parameter is set to 0. The number of neighboring forested cells determines the availability of seed to a given cell, which along with climate controls canopy cover growth. If no forested neighbors exist and tree canopy cover is < 1%, then no increase in canopy cover occurs in that cell for that time step.

Ecosystem Types

Overview

The submodels (frames) used in ALFRESCO are identical to those described by Starfield and Chapin (1996). We provide a general overview of each frame and refer the reader to Starfield and Chapin (1996) for detailed justification of model structure, parameters, and rules for switching among frames (a detailed description can be found at – <http://www.lter.alaska.edu/pubs/ALFRESCO.html>).

Upland tundra

Moist upland tundra (tussock and shrub tundra) is the predominant vegetation type on gently rolling hills in the North American Arctic (Bliss and Matveyeva 1992; Starfield and Chapin 1996). Other major arctic tundra types are wet meadow tundra, which we ignore because it is uncommon in the Alaskan treeline region, and heath, which occupies higher elevations. The most plausible change from upland tundra in response to climatic warming is to conifer forest due to invasion of white spruce forest (Figure 1), because this is the forest type that most commonly occurs south of the Alaskan arctic tree line (Bliss and Matveyeva 1992; Starfield and Chapin 1996). A switch to dry grassland, which occurred during the Pleistocene (Hopkins et al. 1982), may also occur under extremely dry conditions.

White spruce forest

In western North America white spruce is the primary forest type to develop on upland tundra in response to climatic warming (Brubaker et al. 1983). White spruce is the dominant tree species found at both elevational and latitudinal treeline in Alaska (Viereck 1979) and is the successional climax species in the uplands (Van Cleve et al. 1991). Following fire, early successional broad-leaved deciduous shrubs and trees (Larsen 1965; Viereck 1973; Payette and Gagnon 1985) replace white spruce forests (Figure 1). Under unfavorable climate conditions for white spruce seedling establishment, upland tundra (cold conditions) or dry grassland (hot, dry conditions) may invade the site (Viereck and Van Cleve 1984).

Broad-leaved deciduous forest

Willow, birch, and aspen, with an understory of white spruce seedlings dominate early successional boreal forest. As stand age increases, spruce becomes co-dominant with the hardwoods whose density begins to decline due to age-related tree mortality. Eventually white spruce becomes the dominant species on the site (Figure 1). The less flammable broad-leaved vegetation will burn only in extremely dry conditions, being replaced by a new cohort of hardwoods from both vegetative regrowth and seedlings. During the initial establishment period, under unfavorable climate for recolonization, a switch to either upland tundra (cold conditions) or dry grassland (hot, dry conditions) may occur. Both heavy moose browsing pressure and extremely cold climate can accelerate the successional switch to white spruce forest (Kielland et al. 1997).

Dry grassland

Dry grassland is not a current vegetation type in the upland tundra zone, but was the dominant type during the Pleistocene (Hopkins et al. 1982). Grasslands do occur under dry conditions in the boreal forest zone (Edwards and Armbruster 1989). Under cold climatic conditions dry grassland may switch to upland tundra (Starfield and Chapin 1996; Chapin and Starfield 1997; Figure 1). Once established, grassland persists on the landscape due to its short fire return interval (i.e., burns every 10 yr). However, dry grassland will switch to a broad-leaved deciduous forest type under climate conditions that are favorable for deciduous seedling establishment (not too dry), if a seed source exists.

Model calibration

Most parameter values are identical to those in the point model and have been justified previously (Starfield and Chapin 1996) based upon comparison with field observations. Two major phases of model calibration were necessary. The first was extrapolation from the point model to the spatial model, and secondly scaling from one spatial scale (5×5 km point model) to another (2×2 km spatial model). The calibration of the spatial model is, in effect, one of our experiments and is described below.

Model analysis and experiments

We addressed the following questions:

1. How does one compare the results from a point model with those from a spatially explicit model?
2. How does one calibrate one model against the other and against available data?
3. Once calibrated, how do the two models differ with respect to fire patterns under different circumstances?
4. How do the two models differ in their vegetation predictions for long term equilibrium climates?
5. Finally, how do the models compare in their predictions of shorter term transient dynamics of vegetation?

The first question is addressed in the analysis section below; the remaining questions are then addressed, directly or indirectly, in a series of simulation experiments that are described following the analysis section.

Analysis

The point model is identical to the spatial model, except that explicit contagion processes (seed dispersal and fire spread) represented implicitly in the point model rather than explicitly simulated. Consequently, the point model is not sensitive to neighboring cells. It follows that the implicit representation of seed dispersal and fire spread is static and crude. We compared the models by running identical versions of the point model independently in each grid cell (2×2 km) on the same landscapes as the spatial model.

The point model (Starfield and Chapin 1996) was originally parameterized to represent processes at a large (arbitrary 5×5 km) scale on a homogenous terrain. However, interactions among landscape units that involve fire spread and seed dispersal typically occur at smaller scales (2×2 km or less) so we developed

the spatial model to operate at a 2×2 km scale. We therefore had to ask how the parameters should change in a landscape divided into 2×2 km instead of 5×5 km cells. Most of the point model parameters remain the same. For example, imagine a 20×20 km landscape where p represents the probability of an insect outbreak that reduces canopy cover by 50% in an upland tundra cell. If it is divided into 16 cells (5×5 km grid cells) then, on average, insects will affect $16p \times 25 \text{ km}^2 = 400p$. If it is divided into 100 cells (2×2 km grid cells) and we keep p constant, insects will affect $100p \times 4 \text{ km}^2 = 400p$. It follows that p is scale-independent. We therefore focused our study of scale effects on fire, which is clearly a scale-dependent process as we have modeled it.

Fire ignition and spread experiments

The probability of a fire in the point model concatenates two probabilities: (a) the probability that a fire will be initiated and spread through the cell, and (b) the probability that a fire will be initiated in an imaginary neighboring cell and will spread into the cell of the point model. Since the point model cannot know anything about the flammability of the neighboring cells, it assumes (in its calibration) some average effect. In contrast, ALFRESCO models fire ignition and spread within a cell and fire spread between neighboring cells as two separate processes. Consequently, the flammability parameters in ALFRESCO have a different meaning to those in the point model and therefore have different values. In order to compare the point model with ALFRESCO, it is essential that the flammability parameters should in some way be equivalent. It is unlikely that one could find a set of equivalent parameters that would produce identical results in all situations, but one can strive to match certain gross characteristics (such as percentage of the landscape that burns) in certain simple situations (such as homogeneous landscapes). We investigated this in our first three sets of experiments.

Set A – Fire ignition and spread parameters in the point model had previously been calibrated against field data (Starfield and Chapin 1996). In this set of experiments we calibrated the spatially explicit fire spread routine so that ALFRESCO yielded similar average total area burned (Figure 2), to that predicted by the point model on homogenous landscapes. There was a strong linear relationship between the calibrated spatial flammability values and predicted average total area burned (Figure 3). Linear regression was therefore used to develop a calibration equation (Figure 3)

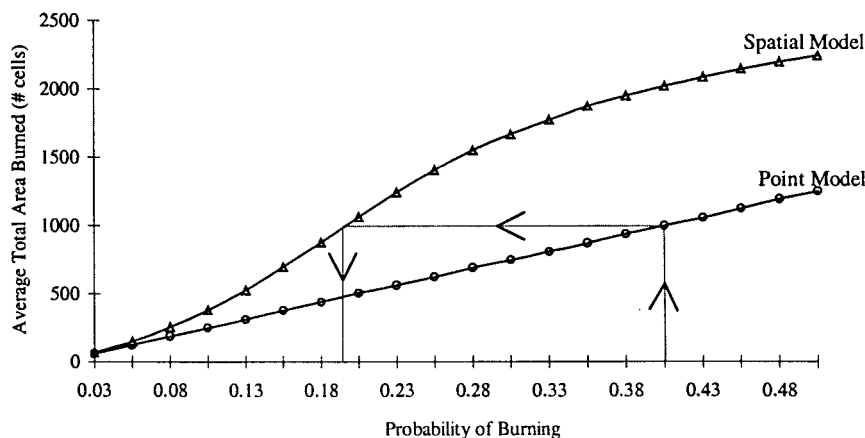


Figure 2. Comparison of average area burned for the point (circles) and spatial (triangles) model fire-spread routines. Each simulation assumed identical flammability values for all grid cells and was replicated 100 times (for each flammability level) on a hypothetical landscape 200×200 km using 2×2 km grid cells. The dashed lines and arrows show how the equivalent flammabilities of the point and spatial models were determined.

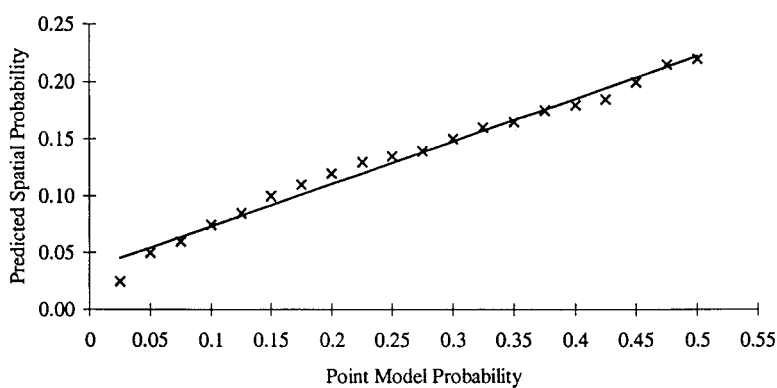


Figure 3. Regression of predicted spatial fire probabilities and point model probabilities that yield the same average area burned (Figure 2). The spatial model calibration equation was: $Y = 0.036 + 0.373(X)$. $R^2 = 0.99$ and $p < 0.001$.

for conversion of point model flammability parameters (Starfield and Chapin 1996) to equivalent spatial model flammabilities. The point model cannot simulate fires of different sizes; the spatial model can. Having calibrated to preserve the average total area burned we then used the spatial model to generate the distribution of individual fire sizes for different flammability levels (0.10–0.40).

Set B – We next explored how the two models might differ with respect to fire spread on a heterogeneous landscape. In this set of experiments, the influence of vegetation patch size was investigated by creating different vegetation patterns on the landscape. We measured the average number of grid cells burned (by vegetation type) and the average number of large fires (> 30 grid cells or 120 km^2) on a landscape (120×120 grid cells) with two vegetation types (broad-

leaved deciduous – low flammability; dry grassland – high flammability) distributed in a chessboard manner for vegetation patch sizes of 1×1 , 2×2 , 3×3 , 4×4 , 5×5 , 6×6 , 10×10 , 15×15 , 20×20 , and 30×30 cells.

Set C – The objective of the final set of fire experiments was to identify the influence of barriers on fire spread. Average number of fires and average individual fire size were measured for 100 replicate simulations on a homogeneous landscape with no barrier, a continuous barrier running the width of the landscape, and barriers extending $1/2$ and $2/3$ the width of the landscape (Figure 4).

Seed dispersal experiments

Since the point model does not recognize neighboring cells, it assumes a constant (user-specified) seed rain. This is a restrictive assumption and limits the scenar-

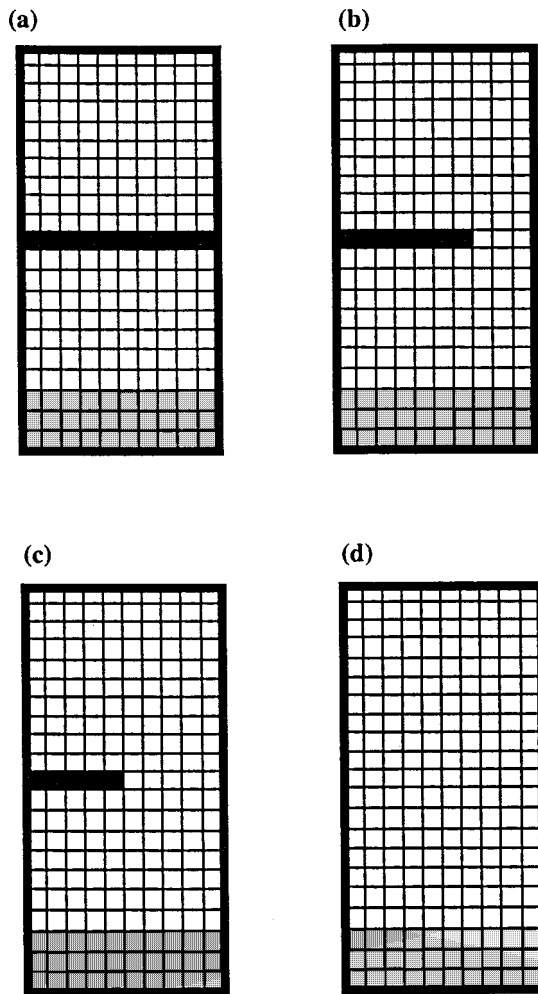


Figure 4. Hypothetical landscape used in barrier experiments showing landscape with (a) complete barrier, (b) 2/3 barrier, (c) 1/2 barrier, and (d) no barrier. The barriers are shaded in black. The gray (white spruce forest) and white (upland tundra) cells indicate the initial vegetation distribution. Landscape was 840 km^2 (2×10 cells).

ios one can simulate with the point model. In the next two sets of experiments we investigated how the spatial model could be used in two such scenarios. Fire was excluded in both sets of experiments to isolate the influence of seed dispersal.

Set D – We measured white spruce forest migration rate on a north-south transect on a landscape 21×10 cells for both the point and spatial models (Figure 5a). The 3 southern-most rows were initially set to white spruce forest with the remainder of the landscape set to upland tundra. Climate for the entire landscape was kept at a constant warm climate (conditions conducive to forest migration). The time required for conver-

sion of upland tundra cells to white spruce forest was calculated with respect to distance from the initial forest-tundra ecotone.

Set E – On the same hypothetical landscape we measured the influence of topographic barriers to seed dispersal. The probability and time to conversion of upland tundra to white spruce forest were measured for 3 different cells on the landscape (Figure 5b) without a barrier, a continuous barrier, and with barriers 1/2 and 2/3 the width of the landscape.

Equilibrium climate experiments on a hypothetical landscape

The next objective was to compare the pattern of vegetation change for the two model versions on a simple hypothetical landscape under equilibrium conditions (constant climate for 10,000 yr). The initial landscape (21×10 cells) was composed of white spruce forest in the 3 southernmost rows and upland tundra in the remainder of the landscape.

Set F – We measured equilibrium vegetation distribution on the hypothetical landscape under four constant climate regimes (cold, current, warm, and hot). Each scenario was replicated 500 times. Herbivore browsing pressure was kept low (0.1).

Set G – High moose browse pressure directly affects the rate of succession by increasing the rate of change from early successional broad-leaved deciduous forest to white spruce forest. The indirect effects of herbivory influence the disturbance regime through changes in vegetation distribution that directly influence the flammability of the landscape (herbivory increases the proportion of highly flammable spruce forest on the landscape). We set the probability of high moose browse pressure first to 0.1 and then 1.0, and measured the distribution of white spruce and broad-leaved deciduous forest as well as the average number of grid cells burned each decade.

Results

Fire Ignition and Spread

Set A – The point model makes the decision to burn each grid cell independently, one cell at a time; one can count how many cells are burned on a landscape but there is no basis for assessing fire size. In contrast, fire spread is explicitly simulated in the spatial model, allowing an estimate of the number of separate fire events and the extent (number of grid cells burned)

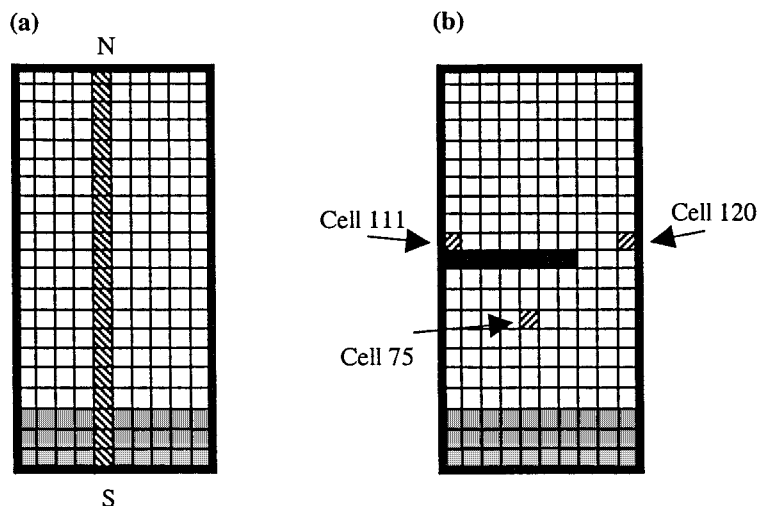


Figure 5. Location of (a) north-south transect (hatched cells) and (b) individual cells (hatched) monitored in the white spruce forest migration experiments; including initial distribution of upland tundra (white cells), white spruce forest (gray cells), and topographic barrier (black cells). Landscape was 840 km^2 ($2 \times 2 \text{ km}$ cells).

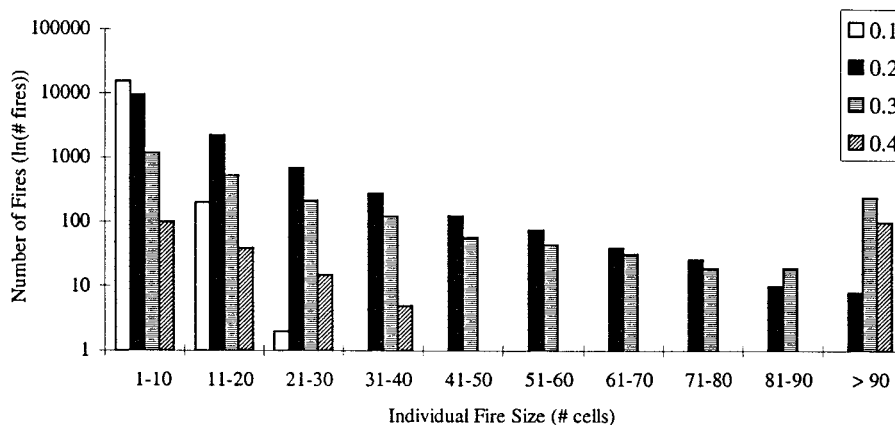


Figure 6. Frequency distribution of the size of fires (number of grid cells burned) in the spatial model for a homogenous landscape of 14,400 cells with flammabilities of 0.1, 0.2, 0.3, and 0.4 (bars). Each simulation was replicated 100 times. Number of fires is on a logarithmic scale.

of each event. In the spatial model the frequency distribution for fire sizes in a homogeneous landscape depended on the flammability value (Figure 6). Low flammability resulted in many small fires (never exceeding 30 grid cells in size), while high flammability resulted in fewer small fires with several large fires. The calibration of ALFRESCO yielded flammability values that were generally < 0.10 for upland tundra and broad-leaved deciduous forest, suggesting that these vegetation types could generally support only small fires (Figure 6). In contrast, white spruce forest and dry grassland with flammabilities of 0.19 and 0.26, respectively, under extremely dry conditions, also produced mostly small fires, but large fires (> 30 grid cells or 120 km^2) occurred regularly, accounting

for as much as 80 percent of the total area burned. This is consistent with observations in Canada (Van Wagner 1983; Stocks 1991) and Alaska (Alaska Fire Service 1992; Kasischke and French 1995).

Set B – The point model is sensitive to the proportion of cells with different flammabilities, but insensitive to how they are clustered on the landscape and therefore to vegetation pattern. In contrast (Figure 7) the spatial model suggests that different scales of heterogeneity of broad-leaved deciduous forest and dry grassland distribution lead to major differences in the spatial extent of fires as well as the relative proportion of vegetation types that burn. When patch sizes are large, the number of broad-leaved deciduous cells that burn is similar to predictions of the point model but,

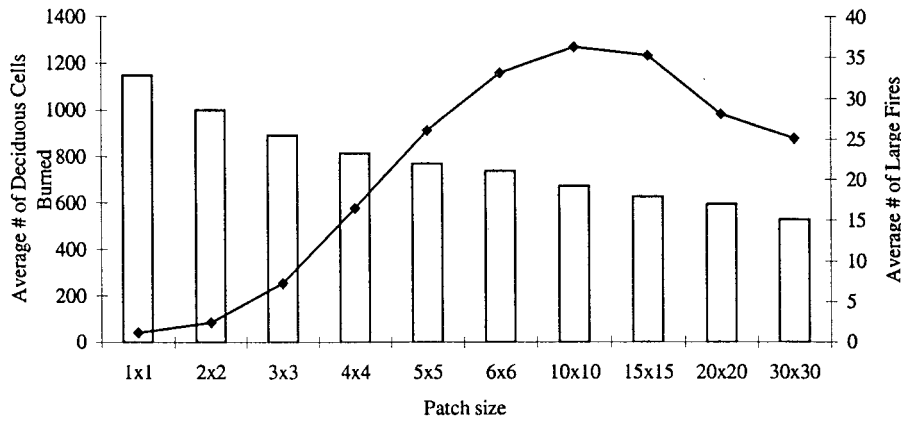


Figure 7. Average number of broad-leaved deciduous forest cells burned (bars) and the average number of large fires (solid line) for different patch sizes of dry grassland ($p = 0.26$) and broad-leaved deciduous forest ($p = 0.07$) in the spatial model. Large fires are defined as fire size $> 120 \text{ km}^2$. Replicated 100 times on a hypothetical landscape $240 \times 240 \text{ km}$ ($2 \times 2 \text{ km}$ cells) with 50% grassland and 50% deciduous forest cells arranged in a chessboard pattern.

as patch size decreases, more deciduous cells are adjacent to flammable grassland cells so that the number of deciduous cells that actually burn increases by a factor of 2. As patch size decreases, so too does the proportion of large fires on the landscape. These results are consistent with other model experiments on the interaction of disturbance and vegetation pattern (Green 1989; Turner et al. 1989; Ratz 1995). Similar results were obtained when the experiment was repeated, substituting white spruce forest for dry grassland (results not shown).

Set C – The point model has no mechanism to detect barriers, so we used the explicitly spatial model to investigate the role of topography in fire dynamics. We tested the influence of barriers (restricting fire spread) in the spatial model by setting the landscape to a single vegetation type and running simulations with no barrier, a complete barrier, and a barrier 1/2 and 2/3 the width of the landscape (Figure 4). As expected, fire spread showed little response to barriers in the spatial model except at high flammability values. Only the most flammable vegetation type (dry grassland) was sensitive to barriers on the landscape (Table 1). As the degree of vegetation connectivity decreased (going from no barrier to a complete barrier) in this highly flammable vegetation type, the average number of fires increased, and average fire size decreased. This suggests that landscapes without topographic barriers to fire spread, under warmer climates (and associated increased fire frequency), will produce more homogeneous landscapes when burned, whereas landscapes with barriers will produce patterns of vegetation that are more heterogeneous and sensitive to landscape bar-

riers and patterns of flammability (Turner et al. 1993; Hadley 1994).

Seed dispersal and migration rate

Set D – The point model cannot test neighbors for seed sources. Instead, the number of forested neighbors is an input to the model, and it is assumed that this number does not change throughout the simulation. Furthermore, even if the number of forested neighbors is set to zero, all upland tundra cells are assumed to have at least a minimal white spruce forest canopy cover (1–7%). This assumption allows further canopy development under a favorable climate for tree establishment and results in eventual conversion of upland tundra to white spruce forest. This may be appropriate if the point model is restricted to the forest-tundra ecotone (the original purpose of the model) but can be misleading if the model is used to predict the rate of forest migration beyond the ecotone (Figure 8).

In contrast, ALFRESCO allows seed input to upland tundra cells only within 4 km (2 cells) of spruce cells. Upland tundra cells farther than 4 km from the nearest spruce cell are assumed to have no canopy development (0%). Consequently, the time for conversion of upland tundra to white spruce forest increased with distance from the initial forest-tundra ecotone (Figure 8). The spatial model yielded an average spruce forest migration rate of approximately 4 km per 100 yr, under a warm climate regime. The model underestimated the rate of forest migration compared to past (10–45 km per 100 yr; Davis 1983) and predicted future (20–30 km per 100 yr; Solomon 1992)

Table 1. (a) Average number of fires and (b) average fire size (# of 2×2 km cells) for the spatial model with homogenous vegetation types (broad-leaved deciduous forest, white spruce forest, or dry grassland) in a landscape with a continuous barrier the width of the landscape, a barrier two-thirds the width of the landscape, a barrier half the width of the landscape and, no barrier (see Figure 4). The landscape was 240×240 km (14400 cells). Each scenario was replicated 100 times.

Vegetation	Full Barrier	2/3 Barrier	1/2 Barrier	No Barrier
(a) # Fires				
Deciduous	728	730	733	733
Spruce	392	388	382	375
Grassland	24	20	19	18
(b) Fire Size (# cells)				
Deciduous	1.8	1.8	1.8	1.8
Spruce	20.6	20.9	21.3	21.9
Grassland	441.3	535.6	571.4	624.5

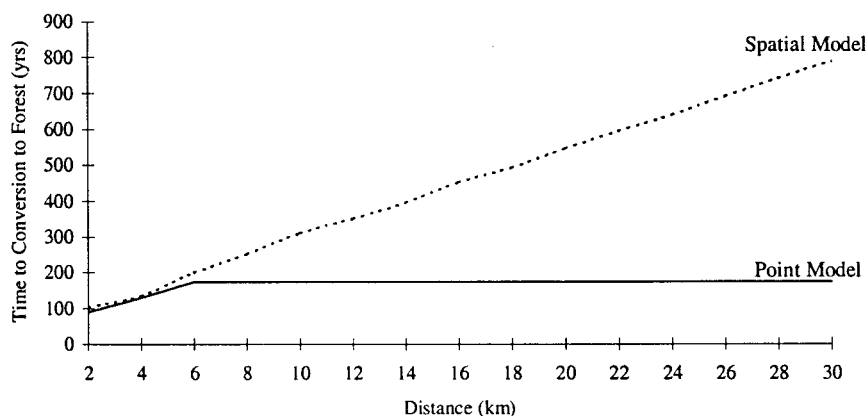


Figure 8. Comparison of time to conversion of upland tundra to white spruce forest for the point (solid line) and spatial (dashed line) models. Landscape was 840 km^2 with a north-south transect (see Figure 4) 2×42 km (2×2 km cells).

forest migration rates. In simulations with the point model, tundra was converted to forest within 200 yr, regardless of the distance from treeline (Figure 8). The spatial model can be used to estimate forest migration rates; the point model cannot, except close to tree-line (the situation for which it was originally intended (Starfield and Chapin 1996)).

Set E – The spatial model views cells with an elevation of > 600 m as a barrier to dispersal and ceases to search for seed sources beyond barrier cells. In contrast, the point model does not recognize barriers and allows for the conversion of upland tundra cells to spruce forest even beyond a continuous high-elevation mountain range. We measured the effect of barriers on seed dispersal and subsequent forest establishment at

3 different cells on the hypothetical landscape (Figure 5) for the spatial model. A continuous barrier (the width of the landscape) completely eliminated the migration of spruce forest north of the barrier (Figure 9), whereas partial barriers slowed conversion of upland tundra to white spruce forest by 300–400 yr (comparison of cells 120 and 111). For the partial barriers, as landscape connectivity increased (number of barrier cells decreased) the time for conversion to spruce forest decreased.

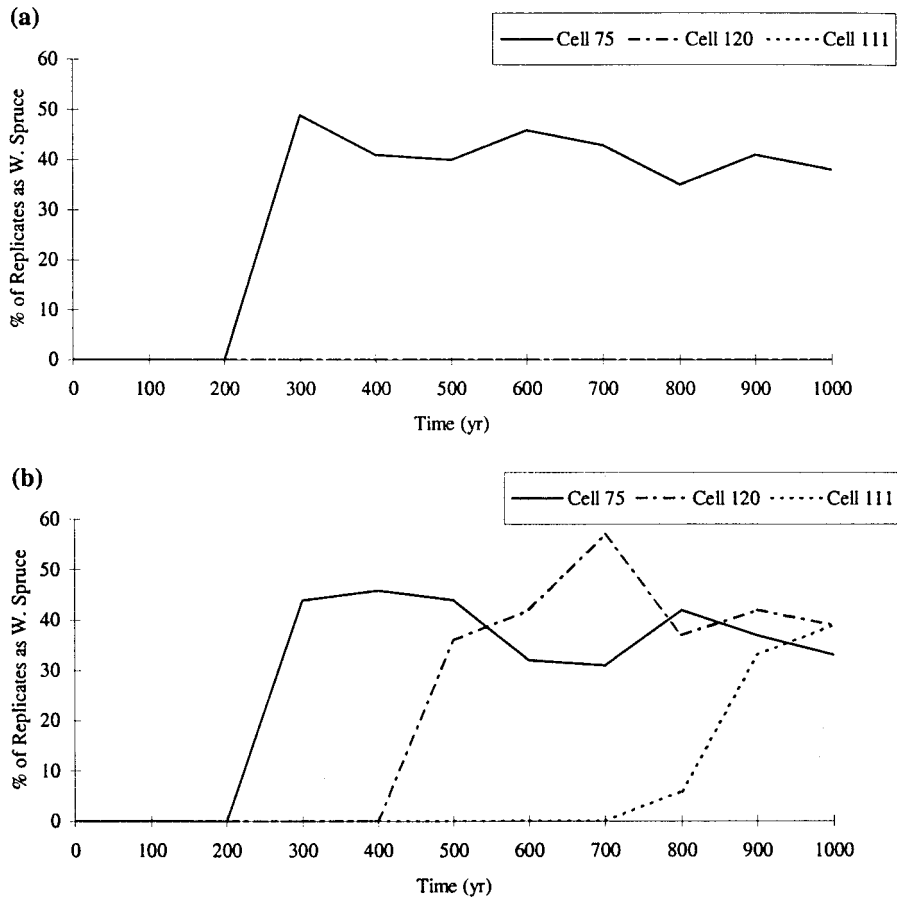


Figure 9. Probability of individual upland tundra cells switching to white spruce forest, for (a) complete barrier (cells north of barrier never switch) and (b) 2/3 barrier, over time. Cell 75 is south of the barrier-corridor, cell 120 is north of the barrier-corridor, and cell 111 is northwest of the barrier-corridor. Average for 100 replicate model runs. See Figure 5 for experimental layout of landscape and location of individual cells.

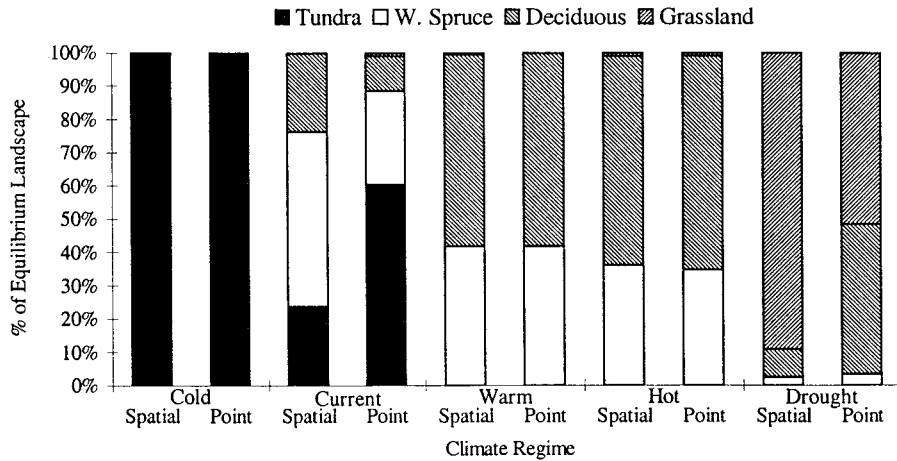


Figure 10. Equilibrium results (10,000 yr, replicated 500 times) for the hypothetical landscape, showing percent distribution of vegetation types under cold, current, warm, hot, and drought (hot temperature class regime with a 0.75 probability of precipitation class 1 and 0.25 for class 2) climates for both the spatial and point models. Landscape was 40 × 20 km.

Equilibrium vegetation distribution on a hypothetical landscape

Set F – The previous experiments highlight both differences and similarities between the spatial and point models with respect to fire spread and seed dispersal as separate processes. In this set of experiments, we investigated how the similarities and differences (when fire spread and seed dispersal interact) influenced long-term (equilibrium) vegetation under different climate regimes on a hypothetical landscape without barriers. Under cold conditions (an upland tundra climate) the entire landscape switched to upland tundra in both the point and spatial models (Figure 10), due to climatic (temperature) constraints (Hobbie and Chapin 1998). There was also agreement between the two models under warm (typical northern boreal forest) and hot (similar to southern boreal forest) climates; in both cases the equilibrium landscape resulted in a mix of deciduous (approximately 65%) and white spruce (approximately 35%) forests. However, the two models differed substantially (Figure 10) at current climate (forest-tundra ecotone) and if one postulates a much drier hot climate (frequent drought). In the latter case, the spatial model predicted a higher proportion of dry grassland cells (approximately 90% of the landscape compared to 50% in the point model). In the point model, cells switched from forest to dry grassland when forest fires coincided with drought; grassland fires maintained grassland cells if they occurred during drought conditions, but switched cells back to forest under more mesic conditions. In the spatial model, grassland fires during drought spread into neighboring forest cells, converting them to grassland and thereby increasing distance to surviving seed sources. This led to the establishment of extensive grasslands maintained by fire, that did not switch back to forest. Grassland in the spatial model perpetuated itself while in the point model it appeared and disappeared stochastically as precipitation levels changed. We suspect a similar interplay between disturbance and climatic events underlies differences between the two models at current climate, as discussed below.

Set G – In both the point and spatial models, white spruce forest extent doubled (Table 2) when the probability of moose browse increased. We expected both models to respond with increased area burned, since the effect of moose browsing is to increase the rate of successional change from low flammability broad-leaved deciduous forest to highly flammable white spruce forest. In fact, the point model predicted

a slight increase in total area burned each decade, whereas the spatial model predicted a 40% decrease in total area burned (Table 2). This resulted in more cells succeeding to spruce, which increased the fire size in the spatial model.

Discussion

Comparison of point and spatial models

The equilibrium distribution of vegetation predicted by ALFRESCO on a hypothetical landscape (with a uniform climate) for different climatic regimes was similar to observed subarctic and boreal vegetation patterns (Selkregg 1974a, b; Anonymous 1994; Starfield and Chapin 1996). However, ALFRESCO predicted a greater abundance of white spruce forest cells and less upland tundra cells than the point model, under current climate. This reflects differences between the point and spatial models in the representation of spatially dependent processes such as fire spread and seed dispersal (Baker et al. 1991).

An important limitation to point models of transient vegetation dynamics (Starfield and Chapin 1996) is that they assume constant seed availability or disregard entirely the process of seed dispersal, germination, and survival. Spatially explicit models of seed dispersal identify neighboring seed sources and employ a maximum dispersal distance threshold (McCaughey et al. 1986; Green 1989; Keane et al. 1996). ALFRESCO identifies seed sources up to 4 km away (2 grid cells) and views elevation (> 600 m) as a physical barrier to seed dispersal and germination (Zasada et al. 1978; Viereck 1979). Therefore, we assume seed does not disperse across high mountain barriers on upslope winds (Greene and Johnson 1995) or along the snowpack (Greene and Johnson 1997).

A common technique for spatial modeling of fire ignition and spread is the ‘cellular automaton’ (Wolfram 1984). Green (1989) ignited fires at random locations and chose an elliptical shape of fixed size and frequency as determined by a negative exponential and Poisson distribution, respectively. Flammability was determined by successional stage (time since last disturbance). Ratz (1995) modeled both the ignition and spread of fire through a landscape of grid cells, using random numbers and the flammability of each cell that was a function of successional stage. Similar algorithms of fire spread can be found in other models dealing with fire (Antonovski et al. 1992; Baker 1992,

Table 2. Comparison of vegetation distribution, total area burned and the proportion of deciduous and white spruce cells burned each decade for (a) the spatial model and (b) point model. High moose browse probability set to 0.1 and 1.0 were compared for 5000 yr (replicated 100 times) on a hypothetical landscape (210 grid cells) under a warm climate regime.

Probability high moose browse	# Deciduous forest cells	# White spruce forest cells	Percent of deciduous cells burned	Percent of white spruce cells burned	Percent total forested cells burned
(a) Spatial Model					
0.10	125.2	84.5	7.2	14.4	10.1
1.00	60.1	149.2	6.5	6.3	6.3
Probability high moose browse	Ave. # deciduous forest cells	Ave. # # White spruce forest cells	Percent of deciduous cells burned	Percent of white spruce cells burned	Percent total forested cells burned
(b) Point Model					
0.10	129.5	80.5	4.3	13.7	7.9
1.00	62.3	147.7	4.5	10.2	8.5

1993). More complicated models of fire ignition and spread incorporate the additional effects of wind speed and direction, moisture, and spatial distribution of fuels (Rothermal 1972; Albini 1976; Keane et al. 1996; Finney 1998).

ALFRESCO follows the automaton approach, where flammability of an individual cell is a function of a wetness index (proxy for drought severity), time since last disturbance, ecosystem type, fuel load (as determined by insect outbreak and herbivore browsing), and topographic relief (elevational barriers). The model realistically simulated patterns of fire frequency and proportion of landscape burned typical of interior Alaskan ecosystems. These disturbance patterns, in turn, influence (in the model and reality) vegetation type and pattern. Post-fire establishment patterns are strongly affected by both the severity and extent of the disturbance and the proximity to potential seed sources, (Turner et al. 1997). The degree of vegetation heterogeneity across the landscape then again influences the shape and extent of future fires in both the model and reality (Turner et al. 1997). ALFRESCO produced fewer but larger fires as heterogeneity increased, suggesting large fires may act as a negative feedback to landscape-level vegetation heterogeneity.

These are the kinds of interactions that can only be simulated in a model that is explicitly spatial and contribute to differences in predictions of vegetation distribution between ALFRESCO and the point model. The experiment with high moose densities illustrates the complexity that can arise from such interactions.

The development and testing of point models is a useful first step towards embedding them in a spatially explicit landscape because the lack of spatial effects in point models make them easier to understand. However, point and spatial models can only be partially calibrated against one another (for homogeneous but not heterogeneous landscapes).

It follows that point models can only be partially calibrated against landscape data. For example, in the original point model (Starfield and Chapin 1996), the relative abundance of forest types on a landscape were compared with the frequency of those same forest types in replicate runs of the point model. However, when the point model is used in ALFRESCO, even after fire parameters have been calibrated, a different abundance of forest types is produced at equilibrium in some climates (Figure 10). Therefore, it can be risky to convert from frequency in the landscape to frequency of point simulations because the landscape frequency

might have been produced by spatial interactions the point model cannot simulate.

Future model uses and development

The results obtained with ALFRESCO on hypothetical landscapes suggest that its spatially explicit attributes are critical to modeling real landscapes. The Brooks Range, positioned in the same region as current latitudinal treeline (Viereck 1979), may restrict forest establishment under a warming climate. The pollen record supports importance of this geographic barrier; during the last climatic optimum white spruce forest did not migrate north of the Brooks Range (Brubaker et al. 1983; Anderson 1988; Hu et al. 1993). In a follow-up paper we will look closely at both short- (50–150 yr) and long-term (500 yr) implications of climatic warming in northwest Alaska with special reference to the potential overriding control of topography on vegetation distribution.

Other exercises on real landscapes will require some modifications of the model. Currently the model only simulates insect outbreaks at the forest-tundra ecotone, where they are likely to be relatively isolated. However, the spatial dynamics of insects (dispersion from one cell to another) could play a major role in ecosystem structure and function in boreal forests. Future modeling efforts will seek to simulate the spatial dynamics of insect outbreaks in boreal forests and possibly also of herbivores and their movements. Black spruce ecosystems are also an important component of interior Alaskan boreal forest, influencing disturbance regimes and vegetation trajectory (Van Cleve and Viereck 1981; Van Cleve et al. 1991, 1996). We will therefore develop a black spruce frame to simulate boreal forest response to climatic change. The model will then allow us to investigate the response of subarctic and boreal forest to changes in disturbance regime, species range, herbivore pressure, insect outbreak, and land use. Our objective is to provide a 'virtual' laboratory for investigating the response of vegetation to management strategies and land use policies dealing with issues of global change.

Conclusions

ALFRESCO accurately predicted the general response of vegetation to climatic change and identified disturbance regime and seed dispersal as major controls over the pattern and rate of vegetation change.

Comparisons between ALFRESCO and the point model on which it is based show that both models,

under some circumstances (e.g., when climatic influences are overriding) give similar results. However, there are many situations where the two models differ and where explicit modeling of spatial processes (fire spread and seed dispersal) is essential for understanding and predicting both transient and equilibrium vegetation distribution in response to a warming climate. It is possible to argue, with hindsight, when a point model is adequate and when it is essential to use an explicitly spatial model. Unfortunately it is not always possible to make this determination ahead of time, and, as in the example of high moose probabilities (Table 2), relying on intuition and a point model that agrees with intuition can be misleading. We conclude that accurate models of landscape-level vegetation response to climatic change must be spatially explicit because only spatial models can reliably simulate fire spread and seed dispersal, two of the driving processes of vegetation change.

Acknowledgements

This research was supported by NSF grants as components of Arctic System Science (OPP-9630913 and OPP-9318532) and the Bonanza Creek LTER program (DEB-9211769). A detailed description of the spatial model is also available on the Bonanza Creek LTER World Wide Web server; access the information at <http://www.lter.alaska.edu/pubs/ALFRESCO.html>.

References

- Alaska Fire Service. 1992. 1992 fire statistics and season summary. Bureau of Land Management, U.S. Dept. of Interior, Fairbanks, AK.
- Albini, F.A. 1976. Computer-based models of wildland fire behavior: a user's manual. U.S. Forest Service, Intermountain Forestry and Range Experiment Station, Ogden, Utah.
- Anderson, P.M. 1988. Late Quaternary pollen records from the Noatak and Kobuk River drainages, northwestern Alaska. *Quat. Res.* 29: 263–276.
- Anonymous. 1994. Alaska land characteristics data set – interim land cover classification. Eros Data Center and Eros Alaska Field Office, National Mapping Division, U.S. Geological Survey, Anchorage, Alaska, USA.
- Antonovski, M.Ya., Ter-mikaelian, M.T. and Furyaev, V.V. 1992. A spatial model of long-term forest fire dynamics and its applications to forests in western Siberia. pp. 373–403. *In* A systems analysis of the global boreal forest. Edited by H.H. Shugart, R. Leemans and G.B. Bonan. Cambridge University Press, Cambridge, UK.
- Baker, W.L. 1992. Effects of settlement and fire suppression on landscape structure. *Ecology* 73: 1879–1887.

- Baker, W.L. 1993. Spatially heterogeneous multi-scale response of landscapes to fire suppression. *Oikos* 66: 66–71.
- Baker, W.L., Egbert, S.L. and Frazier, G.F. 1991. A spatial model for studying the effects of climatic change on the structure of landscapes subject to large disturbances. *Ecol. Modelling* 56: 109–125.
- Bliss, L.C. and Matveyeva, N.V. 1992. Circumpolar arctic vegetation. *In* Arctic ecosystems in a changing climate: an ecophysiological perspective. pp. 58–89. Edited by F.S. Chapin, III, R.L. Jefferies, J.F. Reynolds, G.R. Shaver and J. Svoboda. Academic Press, San Diego, California, USA.
- Bonan, G.B. 1990. Carbon and nitrogen cycling in North American boreal forests. II. Biogeographic patterns. *Can. J. Forest Res.* 20: 1077–1088.
- Bonan, G. B., Pollard, D. and Thompson, S.L. 1992. Effects of boreal forest vegetation on global climate. *Nature* 359: 716–718.
- Bonan, G.B., Chapin, F.S. III and Thompson, S.L. 1995. Boreal forest and tundra ecosystems as components of the climate system. *Climatic Change* 29: 145–167.
- Brubaker, L.B., Garfinkel, H.L. and Edwards, M.E. 1983. A Late-Wisconsin and Holocene vegetation history from the central Brooks Range: implications for Alaskan paleoecology. *Quat. Res.* 20: 194–214.
- Cattle, H. and Crossley, J. 1995. Modelling arctic climate change. *Phil. Trans. Roy. Soc. London A352*: 201–213.
- Chapin, F.S., III and Starfield, A.M. 1997. Time lags and novel ecosystems in response to transient climatic change in arctic Alaska. *Climatic Change* 35: 449–461.
- Chrosiewicz, Z. 1986. Foliar heat content variations in four coniferous tree species of central Alberta. *Can. J. Forest Res.* 16: 152–157.
- Clark, J.S. 1988. Effect of climate change on fire regimes in northwestern Minnesota. *Nature* 334: 233–235.
- Clark, J.S. 1991. Disturbance and tree life history on the shifting mosaic landscape. *Ecology* 72: 1102–1118.
- Clark, J.S. 1996. Testing disturbance theory with long-term data: alternative life-history solutions to the distribution of events. *Am. Nat.* 148: 976–996.
- Clark, J.S., Royall, P.D. and Chumbley, C. 1996. The role of fire during climate change in an eastern deciduous forest at Devil's Bathtub, New York. *Ecology* 77: 2148–2166.
- Clark, J.S., Macklin, E. and Wood, L. 1998a. Stages and spatial scales of recruitment limitation in southern Appalachian forests. *Ecol. Monog.* 68: 213–235.
- Clark, J.S., Silman, M., Kern, R., Macklin, E. and HilleRisLambers, J. 1998b. Seed dispersal near and far: patterns across temperate and tropical forests. *Ecology* (in press).
- Cramer, W.P. and Leemans, R. 1993. Assessing impacts of climate change on vegetation using climate classification systems. *In* Vegetation dynamics and global change. pp. 190–217 Edited by A.M. Solomon and H.H. Shugart. Chapman and Hall, New York, NY.
- Dale, V.H. 1997. The relationship between land-use change and climate change. *Ecol. Appl.* 7: 753–769.
- Davis, M.B. 1981. Quaternary history and the stability of forest communities. *In* Forest succession: concepts and applications. pp. 132–153. Edited by D.C. West, H.H. Shugart and D.B. Botkin. Springer-Verlag, New York, NY.
- Davis, M.B. 1983. Quaternary history of deciduous forests of eastern North America and Europe. *Ann. Missouri Bot. Gardens* 70: 550–563.
- Davis, M.B. 1986. Climatic instability, time lags, and community disequilibrium. *In* Community Ecology. pp. 269–284. Edited by J. Diamond and T.J. Case. Harper and Row, New York, NY.
- Davis, M.B. and Botkin, D.B. 1985. Sensitivity of cool-temperate forests and their fossil pollen record to rapid temperature change. *Quat. Res.* 23: 327–340.
- Edwards, M.E. and Armbruster, W.S. 1989. A tundra-steppe transition on Kathul Mountain, Alaska, USA. *Arctic Alpine Res.* 21: 296–304.
- Fastie, C.L. 1995. Causes and ecosystem consequences of multiple pathways of primary succession at Glacier Bay, Alaska. *Ecology* 76: 1899–1916.
- Finney, M.A. 1998. FARSITE: Fire area simulator – model development and evaluation. U.S. Dept. of Agriculture, Forest Service, Rocky Mountain Research Station. Research Paper RMRS-RP-4.
- Flannigan, M.D. and Harrington, J.B. 1988. A study of the relation of meteorological variables to monthly provincial area burned by wildfire in Canada (1935–80). *J. Appl Meteor.* 27: 441–452.
- Flannigan, M.D.F. and Van Wagner, C.E. 1991. Climate change and wildfire in Canada. *Can? J. Forest Res.* 21: 66–72.
- Foley, J.A., Kutzbach, J.E., Coe, M.T. and Levis, S. 1994. Feedbacks between climate and boreal forests during the Holocene epoch. *Nature* 371: 52–54.
- Gardner, R.H., Hargrove, W.W., Turner, M.G. and Romme, W.H. 1996. Global change, disturbances and landscape dynamics. *In* Global change and terrestrial ecosystems. pp. 149–172. Edited by B. Walker and W. Steffen. Cambridge University Press, Cambridge.
- Green, D.G. 1989. Simulated effects of fire, dispersal and spatial pattern on competition within forest mosaics. *Vegetatio* 82: 139–153.
- Greene, D.F. and Johnson, E.A. 1995. Long-distance wind dispersal of tree seeds. *Can. J. Bot.* 73: 1036–1045.
- Greene, D.F. and Johnson, E.A. 1996. Wind dispersal of seeds from a forest into a clearing. *Ecology* 77: 595–609.
- Greene, D.F., and E.A. Johnson. 1997. Secondary dispersal of tree seeds on snow. *Journal of Ecology*. 85: 329–340.
- Hadley, K. S. 1994. The role of disturbance, topography, and forest structure in the development of a montane forest landscape. *Bull. Torrey Bot. Club* 121: 47–61.
- Hobbie, S.E. and Chapin, F.S. III. 1998. The response of tundra plant biomass, aboveground production, nitrogen, and CO₂ flux to experimental warming. *Ecology* 79: 1526–1544.
- Holling, C. S. 1992. The role of forest insects in structuring the boreal landscape. *In* A systems analysis of the global boreal forest. pp. 170–191. Edited by H.H. Shugart, R. Leemans and G.B. Bonan. Cambridge University Press, Cambridge.
- Hopkins, D.M., Matthews, J.V., Schweger, C.E. and Young, S.B. (eds). 1982. *Paleoecology of Beringia*. Academic Press, New York, NY.
- Houghton, J.T., Jenkins, G.J. and Ephraums, J.J. (eds). 1990. *Climate change: the IPCC scientific assessment*. Cambridge University Press, Cambridge.
- Hu, F.S., Brubaker, L.B. and Anderson, P.M. 1993. A 12 000 year record of vegetation change and soil development from Wien Lake, central Alaska. *Can. J. Bot.* 71: 1133–1142.
- Johnson, E.A. 1992. *Fire and vegetation dynamics: studies from the North American boreal forest*. Cambridge University Press, Cambridge.
- Kallio, P. and Lehtonen, J. 1973. Birch forest damage caused by *Oporinia automnata* (Bkh.) in 1965–66 in Utsjoki, N. Finland. *Rep. Kevo Subarctic Res. Station* 10: 55–69.
- Kasischke, E.S. and French, N.H.F. 1995. Locating and estimating the areal extent of wildfires in Alaskan boreal forests using multiple-season AVHRR NDVI composite data. *Remote Sensing Env.* 51: 263–275.

- Keane, R.E., Morgan, P. and Running, S.W. 1996. FIRE-BGC – A mechanistic ecological process model for simulating fire succession on coniferous forest landscapes of the northern Rocky Mountains. Res. Pap. INT-RP-484. Ogden, Utah: U.S. Dept. of Agriculture, Forest Service, Intermountain Research Station.
- Kellomaki, S. and Kolstrom, M. 1992. Simulation of tree species composition and organic matter accumulation in Finnish boreal forests under changing climatic conditions. *Vegetatio* 102: 47–68.
- Kielland, K., Bryant, J.P. and Ruess, R.W. 1997. Moose herbivory and carbon turnover of early successional stands in interior Alaska. *Oikos* 80: 25–30.
- Kittel, T.G.F., Steffen, W.L. and Chapin, F.S. III. In press. Global and regional modeling of arctic-boreal vegetation distribution and its sensitivity to altered forcing. *Global Change Biology*.
- Larsen, J.A. 1965. The vegetation of Ennadai Lake area, N.W.T.: studies in subarctic and arctic bioclimatology. *Ecol. Monog.* 35: 37–59.
- Lenihan, J.M. and Neilson, R.P. 1995. Canadian vegetation sensitivity to projected climatic change at three organizational levels. *Climatic Change* 30: 27–56.
- Loehle, C. and LeBlanc, D. 1996. Model-based assessments of climate change effects on forests: A critical review. *Ecol. Model.* 90: 1–31.
- Mattson, W.J. and Haack, R.A. 1987. The role of drought in outbreaks of plant-eating insects. *BioScience* 37: 110–118.
- McCaughy, W.W., Schmidt, W.C. and Shearer, R.C. 1986. Seed-dispersal characteristics of conifers in the Inland Mountain West. *In Proc. symp. conifer tree seed in the Inland Mountain West.* pp. 50–62. Edited by R.C. Shearer. U.S. Dept. of Agriculture, Forest Service. General Technical Report. INT-203.
- Neilson, R.P. 1993. Transient ecotone response to climatic change: some conceptual and modelling approaches. *Ecol. Appl.* 3: 385–395.
- Neilson, R.P., King, G.A. and Koerper, G. 1992. Towards a rule-based biome model. *Landscape Ecol.* 7: 27–43.
- Nikolov, N.T. 1995. Modeling transient response of forest ecosystems to climatic change. *In Interior west global change workshop.* pp. 78–83. Edited by R.W. Tinus. U.S. Dept. of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station. RM-GTR-262.
- Noble, I.R. 1987. The role of expert systems in vegetation science. *Vegetatio* 69: 115–121.
- Noble, I.R. 1993. A model of the response of ecotones to climate change. *Ecol. Appl.* 3: 396–403.
- 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.
- NRC (National Research Council). 1994. The role of terrestrial ecosystems in global change: a plan for action. National Academy Press, Washington, D.C., USA.
- Pastor, J. and Post, W.M. 1986. Influence of climate, soil moisture, and succession of forest carbon and nitrogen cycles. *Biogeochemistry* 2: 3–27.
- Pastor, J. and Post, W.M. 1988. Responses of northern forests to CO₂-induced climate change. *Nature* 334: 55–58.
- Pastor, J. and Naiman, R.J. 1992. Selective foraging and ecosystem processes in boreal forests. *Am. Nat.* 139: 690–705.
- Payette, S. 1992. Fire as a controlling process in the North American boreal forest. *In A systems analysis of the global boreal forest.* pp. 170–191. Edited by H.H. Shugart, R. Leemans and G.B. Bonan. Cambridge University Press, Cambridge.
- Payette, S. and Gagnon, R. 1985. Late Holocene deforestation and tree regeneration in the forest-tundra of Quebec. *Nature* 313: 570–572.
- Prentice, I.C., Sykes, M.T. and Cramer, W. 1991. The possible dynamic response of northern forests to global warming. *Global Ecol. Biogeog. Lett.* 1: 129–135.
- Prentice, I.C., Cramer, W., Harrison, S.P., Leemans, R., Monserud, R.A. and Solomon, A.M. 1992. A global biome model based on plant physiology and dominance, soil properties and climate. *J. Biogeog.* 19: 117–134.
- Ratz, A. 1995. Long-term spatial patterns created by fire: A model oriented towards boreal forests. *Int. J. Wildland Fire* 5: 25–34.
- Robinson, C.H., Wookey, P.A., Lee, J.A., Callaghan, T.V. and Press, M.C. 1998. Plant community responses to simulated environmental change at a high arctic polar semi-desert. *Ecology* 79: 856–866.
- Rothermel, R.C. 1972. A mathematical model for predicting fire spread in wildland fuels. U.S. Forest Service. Research Paper INT-115.
- Running, S.W. and Coughlan, J.C. 1988. A general model of forest ecosystem processes for regional applications, I, Hydrologic balance, canopy gas exchange and primary production processes. *Ecol. Model.* 42: 125–154.
- Running, S.W. and Gower, S.T. 1991. FOREST-BGC, a general model of forest ecosystem processes for regional applications, II, Dynamic carbon allocation and nitrogen budgets. *Tree Physiol.* 9: 147–160.
- Selkregg, L.L. 1974a. Alaska regional profiles. Volume 5. Northwest region. University of Alaska Arctic Information and Data Center, Anchorage, Alaska, USA.
- Selkregg, L.L. 1974b. Alaska regional profiles. Volume 6. Northwest region. University of Alaska Arctic Information and Data Center, Anchorage, Alaska, USA.
- Shugart, H.H., Smith, T.M. and Post, W.M. 1992. The potential application of individual-based simulation models for assessing the effects of global change. *Annu. Rev. Ecol. Syst.* 23: 15–38.
- Smith, T.M. and Shugart, H.H. 1993. The transient response of terrestrial carbon storage to a perturbed climate. *Nature* 361: 523–526.
- Solomon, A.M. 1986. Transient response of forest to CO₂-induced climate change: simulation modeling experiments in eastern North America. *Oecologia* 68: 567–579.
- Solomon, A.M. 1992. The nature and distribution of past, present and future boreal forests: lessons for a research and modeling agenda. *In A systems analysis of the global boreal forest.* pp. 170–191. Edited by H.H. Shugart, R. Leemans and G.B. Bonan. Cambridge University Press, Cambridge.
- Solomon, A.M. and Shugart, H.H. Jr. 1984. Integrating forest-stand simulations with paleoecological records to examine long-term forest dynamics. *In State and change of forest ecosystems-indicators in current research.* pp. 333–356. Edited by G.I. Agren. Swedish University of Agricultural Science, Uppsala, Sweden.
- Starfield, A.M., Cummings, D.H.M., Taylor, R.D. and Quadling, M.S. 1993. A frame-based paradigm for dynamic ecosystem models. *AI Appl.* 7: 1–13.
- Starfield, A.M. and Chapin, F.S. III. 1996. Model of transient changes in arctic and boreal vegetation in response to climate and land use change. *Ecol. Appl.* 6: 842–864.
- Stocks, B.J. 1991. The extent and impact of forest fires in northern circumpolar countries. *In Global biomass burning: atmospheric, climatic and biospheric implications.* pp. 197–202. Edited by J.L. Levine. MIT Press, Cambridge, Massachusetts, USA.

- Susott, R.A. 1982. Characterization of the thermal properties of forest fuels by combustible gas analysis. *Forest Sci.* 28: 404–420.
- Sylvester, T.W. and Wein, R.W. 1981. Fuel characteristics of arctic plant species and simulated plant community flammability by Rothermel's model. *Can. J. Bot.* 59: 898–907.
- Thornwaite, C.W. and Mather, J.R. 1957. Instructions and tables for computing potential evaporation and the water balance. *Publ. Climat.* 10: 183–311.
- Torn, M.S. and Fried, J.S. 1992. Predicting the impacts of global warming on wildland fire. *Climatic Change* 21: 257–274.
- Trigg, W.M. 1971. Fire season climatic zones of mainland Alaska. U.S. Department of Agriculture, Portland, Oregon, USA.
- 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: 121–129.
- Turner, M.G., Romme, W.H., Gardner, R.H., O'Neill, R.V. and Kratz, T.K. 1993. A revised concept of landscape equilibrium: Disturbance and stability on scaled landscapes. *Landscape Ecol.* 8: 213–227.
- Turner, M.G. and Romme, W.H. 1994. Landscape dynamics in crown fire ecosystems. *Landscape Ecol.* 9: 59–77.
- Turner, M.G., Hargrove, W.H., Gardner, R.H. and Romme, W.H. 1994a. Effects of fire on landscape heterogeneity in Yellowstone National Park, Wyoming. *J. Veg. Sci.* 5: 731–742.
- Turner, M.G., Romme, W.H. and Gardner, R.H. 1994b. Landscape disturbance models and long-term dynamics of natural areas. *Natural Areas J.* 14: 3–11.
- Turner, M.G., Romme, W.H., Gardner, R.H. and Hargrove, W.W. 1997. Effects of fire size and pattern on early succession in Yellowstone National Park. *Ecol. Monog.* 67: 411–433.
- Van Cleve, K., and L. A. Viereck. 1981. Forest succession in relation to nutrient cycling in the boreal forest of Alaska. *In* Forest succession concept and application. pp. 185–211. Edited by D.C. West, H.H. Shugart and D. Botkin. Springer-Verlag, New York, NY.
- Van Cleve, K., Chapin, F.S. III, Dyrness, C.T. and Viereck, L.A. 1991. Element cycling in taiga forests: State-factor control. *BioScience* 41: 78–88.
- Van Cleve, K., Viereck, L.A. and Dyrness, C.T. 1996. State factor control of soils and forest succession along the Tanana River in interior Alaska, USA. *Arctic Alpine Res.* 28: 388–400.
- Van Wagner, C.E. 1983. Fire behaviour in northern coniferous forests and shrublands. *In* The role of fire in northern circumpolar ecosystems. pp. 65–80. Edited by R.W. Wein and D.A. MacLean. Wiley, New York, NY.
- Viereck, L.A. 1973. Wildfire in the taiga of Alaska. *Quat. Res.* 3: 465–495.
- Viereck, L.A. 1979. Characteristics of treeline plant communities in Alaska. *Holarctic Ecol.* 2: 228–238.
- Viereck, L.A. and Van Cleve, K. 1984. Some aspects of vegetation and temperature relationships in the Alaskan taiga. *In* The potential effects of carbon dioxide-induced climatic changes in Alaska. pp. 129–142. Edited by J.H. McBeath. School of Agriculture and Land Resources Management, University of Alaska, Fairbanks, Alaska, USA.
- Wolfram, S. 1984. Cellular automata as models of complexity. *Nature* 311: 419–424.
- Zasada, J.C., Foote, M.J., Deneke, F.J. and Parkerson, R.H. 1978. Case history of an excellent white spruce cone and seed crop in interior Alaska: cone and seed production, germination, and seedling survival. U.S. Dept. of Agriculture, Forest Service, Pacific Northwest Forest Experiment Station. General Technical Report. PNW-65.