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MODEL OF TRANSIENT CHANGES IN ARCTIC AND BOREAL VEGETATION IN RESPONSE TO CLIMATE AND LAND USE CHANGE[1]

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Abstract. One of the greatest challenges in global-change research is to predict the future distribution of vegetation. Most models of vegetation change predict either the response of a patch of present vegetation to climatic change or the future *equilibrium* distribution of vegetation based on the present relationship between climate and vegetation. Here we present a model that is, to our knowledge, the first model of ecosystem change in response to *transient* changes in climate, disturbance regime, and recruitment over the next 50–500 yr. The frame-based model uses quantitative and qualitative variables to develop scenarios of vegetation change from arctic tundra to boreal forest in response to global changes in climate (as predicted by general circulation models [GCMs]), fire, and land use. Seed availability, tree growth rate, and probability of fire were the model parameters that most strongly influenced the balance between tundra and boreal forest in transitional climates. The *rate* of climatic warming strongly affected the time lag between the onset of climate change and the simulated ecosystem response but had relatively little effect on the rate or pattern of ecosystem change. The model calculated that, with a gradual ramped change of 3°C in the next century (corresponding to average rate of warming predicted by GCMs), any change from tundra to forest would take 150 yr, consistent with pollen records. The model suggested that tundra would first be invaded by conifer forests, but that the proportion of broad-leaved deciduous forest would increase, reflecting increased fire frequency, as climatic warming continued. The change in fire frequency was determined more strongly by climatically driven changes in vegetation than by direct climatic effects on fire probability. The *pattern* of climatic warming was more important than the rate of warming or change in precipitation in determining the rate of conversion from tundra to forest. Increased climatic variability promoted ecosystem change, particularly when oscillations were long relative to the time required for tree maturation. Management policies related to logging and moose-predator control affected vegetation as much or more than did changes in climate and must be included in future scenarios of global changes in ecosystem distribution. We suggest that frame-based models provide a critical link between patch and equilibrium models in predicting ecosystem change in response to transient changes in climate over the coming decades to centuries.

Key words: arctic; boreal forest; climatic change; fire; insects; model; transient dynamics; tree line.

INTRODUCTION

Predicting the time course of change in the structure and distribution of natural ecosystems is a major challenge in evaluating the role of the terrestrial biosphere in future climatic change (NRC 1994). Past climatic changes altered the distribution of species and biomes (Davis 1981, COHMAP 1988) at a scale large enough to cause potentially important changes in terrestrial carbon storage (Prentice and Fung 1990, Smith and Shugart 1993) and regional energy balance (Shukla et al. 1990, Bonan et al. 1992, Foley et al. 1994). Equally large changes in biome distribution are expected in response to future climatic change (Davis and Botkin 1985, Pastor and Post 1988). Equilibrium models based on correlation of vegetation with climate (Rosenzweig 1968, Cramer and Leemans 1993) or known environmental tolerances of plant functional groups (Box 1981, Woodward 1987, Prentice et al. 1992) successfully reconstruct past patterns of vegetation change and provide a strong basis for predicting the long-term patterns of future vegetation change. However, vegetation is seldom in equilibrium with climate (Davis 1981), and many of the factors regulating climate (e.g., the concentrations of radiatively active trace gases like CO_2, CH_4, and N_2O) are changing more rapidly than at any time in the last several million years (Houghton et al. 1990). Thus, it is critical that we develop additional models to predict the *rate* of vegetation change over the period spanning the next decades to centuries, the

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time period of most immediate concern to human populations.

Most knowledge of processes governing rate of vegetation change comes from studies of successional changes in vegetation following disturbance (Crocker and Major 1955). Gap dynamics models, incorporating this information, predict changes in community composition based on physiological responses of plants to successional changes in light and temperature (Shugart and West 1980, Bonan 1990) and associated changes in soils and nutrient cycling processes (Pastor and Post 1986, 1988). These models realistically simulate the dynamics of successional change following disturbance (Pastor and Post 1986, Bonan 1990) and past patterns of vegetation in response to climatic change (Solomon and Shugart 1984, Davis and Botkin 1985). However, disturbance and seed input are generally assumed to be random (Davis and Botkin 1985, Bonan 1990) or ignored in patch scale models of succession (Solomon 1986, Shugart et al. 1992), although both disturbance and seed input/migration rate have changed in the past (Davis 1981, Clark 1988) and will undoubtedly change in the future (Flannigan and Van Wagner 1991, Torn and Fried 1992).

Because of the importance of predicting the time course of vegetation response to changing climate, several models of transient vegetation change are currently being developed. Smith and Shugart (1993) estimated a transient carbon efflux to the atmosphere in response to global warming, based on globally averaged rates of disturbance, immigration, and succession from current vegetation to the equilibrium vegetation predicted with a doubling of the atmospheric CO_2 concentration. This model demonstrated the potential importance of transient vegetation change for global carbon balance but did not incorporate ecological information specific to any given vegetation transition. Other models use biome-specific effects of climate on vegetation to map the distribution of vegetation with climate (Neilson et al. 1992). These models are being modified to predict transient changes in vegetation in response to transient changes in precipitation and potential evapotranspiration (PET), as well as transient changes in diebacks and invasion of various lifeforms (Neilson et al. 1992). These models are particularly appropriate for modeling of ecotones between biomes, where major changes in vegetation structure and function are expected (Neilson 1993*a*, Noble 1993). By focusing on specific types of transitions, such as a forest–grassland ecotone (Noble 1993), it is possible to explore the interactions of climate, disturbance, and dispersal in influencing rates and patterns of vegetation change. However, there are currently no models that predict the transients in vegetation in response to realistic scenarios of altered climate, seed input, and disturbance frequency over the time period spanning the next decades to centuries (Shugart et al. 1992, Solomon 1992). To fill this gap, we present a model that calculates the transients of ecosystem change in response to changes in these variables.

The boundary between tundra and boreal forest has intrigued ecologists because its location is closely linked to climate (near the July mean temperature of 10°C; Bryson 1966) and its historical movements have responded sensitively to changes in climate (Griggs 1934, Hopkins 1972). Because boreal forest differs substantially from tundra in carbon storage and albedo, changes in the location of tree line should have large effects on regional energy budget and global climate (Prentice and Fung 1990, Bonan et al. 1992, Foley et al. 1994). Here we present a dynamic model that explores how upland tundra vegetation might respond to scenarios of change in climate and land use over the next 50–500 yr. Our modeling approach differs from most previous dynamic models of vegetation change because it operates at a coarser level of resolution over larger spatial scales with a longer time step and emphasizes factors that govern switches among ecosystem types rather than the steady-state or successional processes that occur in ecosystems under relatively constant climatic and disturbance regimes.

METHODS

Model overview

All model runs begin in upland tundra because it is the most widespread tundra type (Bliss and Matveyeva 1992) and is expected to change to forest in response to climatic warming over the time period spanning the next decades to centuries (Pastor and Post 1988). The vegetation types simulated (upland tundra, conifer forest, broad-leaved deciduous forest, and grassland) differ strongly in distribution with respect to climate, disturbance regime, and factors causing switches to new vegetation types (Van Cleve et al. 1991, Bliss and Matveyeva 1992). Although these are the major upland ecosystem types throughout the circumpolar arctic/boreal zone, the model was parameterized primarily with data from Alaska.

The model (described in detail in the Appendix) operates at a 10-yr time step and calculates vegetation change on a single 25-km^2 patch of upland tundra vegetation in response to constant or changing climate. The time step allows convenient replicated modeling of vegetation changes over time scales of decades to centuries (NRC 1994). The spatial scale is appropriate for eventual interface with mesoscale climate models. Vegetation change at this large scale is strongly tied to climate and disturbance regime (e.g., fire and insect outbreaks; Payette 1983, Holling 1992). Moreover, disturbance events that occur over large patches often trigger a shift to new stable states (Walker 1981, Holling 1986). The model currently ignores factors, such as topography, that govern vegetation distribution at smaller scales. Although the model at present simulates only one patch, the effects on that patch of neighboring

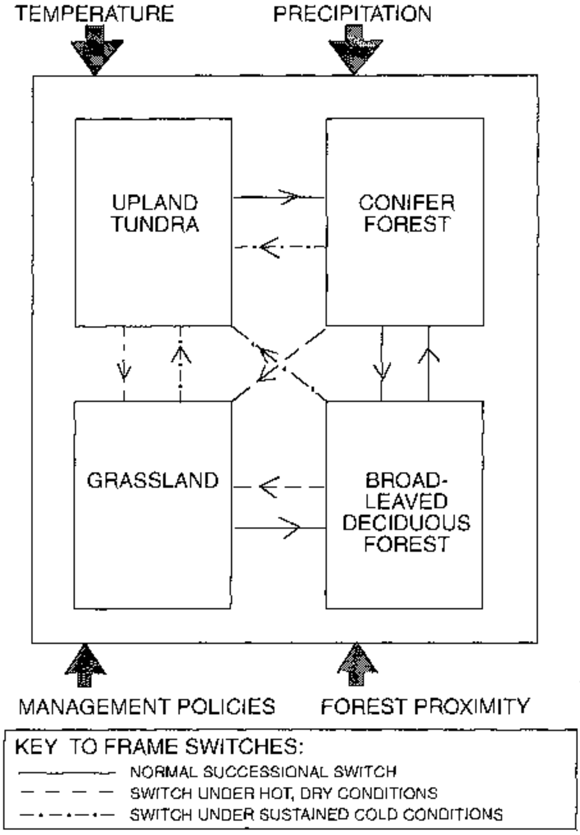

FIG. 1. General model structure showing major ecosystem types (frames) and the switches that occur among ecosystems under normal and abnormal climatic conditions.

patches are simulated through inputs such as seed rain (Noble 1993). The model simulates interactions among patches (e.g., seed rain and fire spread) through model inputs that specify the nature of neighboring patches.

The model exploits two innovative modeling constructs. First, the model consists of four independent submodels or "frames" representing moist upland tundra and three ecosystem types that might develop from upland tundra (Fig. 1; Starfield et al. 1993). Each submodel estimates changes through time in those variables that might cause a switch to a new ecosystem type (i.e., to another frame). At every time step, the submodel tests the rules that determine whether an ecosystem switch will occur (Neilson et al. 1992). When a switch occurs, the submodel appropriate to the new ecosystem type becomes operational and it, in turn, estimates changes in variables that might cause a switch to yet a different ecosystem type. Thus, only one submodel is operational at a time. This modeling approach emphasizes processes causing vegetation change, not variables controlling the productivity or species composition within a vegetation type, as developed in gap dynamics models (Shugart and West 1980, Pastor and Post 1986). The mechanistic simulation of key processes causing vegetation change distinguishes this modeling approach from Markov models (Getz and Haight 1989). We use a different simulation model in each frame because the factors governing vegetation change often differ among ecosystem types. The four frames, or 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). We ignore the substantial variation in species composition within these and other intermediate vegetation types (Payette 1992). Our approach incorporates features of the models of Noble and Slatyer (1980; use of vital attributes of potential colonizers to predict pathways of succession following fire) and Neilson et al. (1992; switch to new vegetation types under specified climatic conditions).

The second innovative modeling construct is the use of qualitative variables (Starfield 1991). Many variables that contribute strongly to vegetation change (e.g., seed availability) are poorly documented or highly variable. However, there is often a good qualitative understanding of how these factors respond to climate and affect vegetation (Heinselman 1981, Zasada et al. 1992). Therefore, where the data are available and the relationships well known, the model uses quantitative variables, but, where data are scarce and general ecological relationships are well understood, the model uses qualitative variables to incorporate additional understanding. For example, most variables in the model take values in a continuous range from 1 to 4, with each integer corresponding to a biologically interpretable value for the parameter. Each conifer canopy class corresponds to a range of conifer canopy cover on a logarithmic scale where class 1 corresponds to 0–7% cover while class 4 corresponds to >50% cover; each potential seed rain corresponds to seed input expected with differing densities of mature trees. This convention of giving variables values ranging from 1 to 4 allows us to simulate an actual value (e.g., 2.3 for canopy cover) where appropriate to avoid abrupt discontinuities in equations, while using the qualitative canopy class (such as class 2) to sketch in the influence of canopy on other variables (such as seed rain). Similarly, Neilson et al. (1992) predict vegetation distribution based on seasonality of precipitation, subsuming the complicated effects of precipitation seasonality on seedling establishment, growth, and fire. The structure of the submodels and relationships among variables are defined by matrices (Appendix) that provide a level of resolution consistent with the scale at which we are modeling.

In general, our philosophy is to keep the model as simple as possible with respect to possible vegetation types and processes within ecosystems, enabling us to trace readily the logical consequences of the assumptions and relationships in the model. We explored possible inclusion of many other parameters, relationships, and vegetation types not reported here but excluded them after finding that they did not strongly alter the

TABLE 1. Probability of occurrence of average summer temperature and total summer precipitation (June–August) for the four climatic regimes used in the model. See *Methods: Driving variables* for references and explanation.

Climatic parameter	Climatic regime			
	Tundra	Tree line	Boreal	Hot-boreal
Temperature (°C)				
<10	0.80	0.10	0.00	0.00
10–13	0.20	0.80	0.15	0.00
13–16	0.00	0.10	0.80	0.20
>16	0.00	0.00	0.05	0.80
Precipitation (mm)				
<80	0.75	0.20	0.07	0.00
80–140	0.20	0.40	0.36	0.25
140–200	0.05	0.30	0.36	0.35
>200	0.00	0.10	0.21	0.40

nature and timing of switches among ecosystems. These variables included soil fertility, soil moisture, permafrost depth, and shrub biomass. In some cases these variables may be more important in explaining the internal dynamics of a particular ecosystem type than in causing a switch from one ecosystem type to another. In other cases, the effects of these variables may be strongly correlated with effects of other variables already included in the model so that they add little additional explanatory power. After developing and parameterizing the model, we used it in a series of model experiments to test model stability under constant climate, its sensitivity to change in model parameters and structure, and the time course of vegetation response to various scenarios of change in climate and land use.

Driving variables

The external driving variables for the model are climate (temperature and precipitation), number of neighboring forest patches, and policies governing logging, fire control, and moose density (Fig. 1). These driving variables then determine probability of fire, insect attack, tree establishment, succession, and other processes governing ecosystem change.

The model generates climate based on four climatic regimes representing summer temperature and precipitation of (1) the northern limit of upland moist tundra; (2) tree line; (3) present boreal forest; and (4) hot-boreal forest. Associated with each climatic regime is a probability distribution of temperature and precipitation classes (Table 1). For example, the climate regime of upland tundra generates temperature class 1 (<10°) with probability 0.8 and temperature class 2 (10°–13°) with probability 0.2. The tundra climate is based on the probability distribution of 3° classes of average summer (June through August) temperature and 60-mm classes of total summer precipitation at Barrow, Alaska (71° N, 157° W), a coastal tundra site, based on the record from 1922 through 1992 (Eisheid 1994). Because Barrow is colder than any upland tundra site, we shifted the summer temperature distribution from a mean of 2.7° (the Barrow mean) to a mean value of 8.5°, the mean value measured over a 10-yr period at Sagwon and Franklin Bluffs (both 69° N, 148° W), the two northernmost moist-upland tundra sites in Alaska with temperature data. The tree-line climate assumed by the model is intermediate between the tundra and boreal-forest climates and is similar to the climate observed north and south of the Alaskan tree line (68° N, 149° W), based on a <10-yr temperature record (Haugen 1982). The boreal forest climate is based on the probability distribution of 3° classes of average summer (June–August) temperature and 60-mm classes of total summer precipitation at Fairbanks, Alaska (65° N, 148° W), based on the record from 1922 through 1992 (Eisheid 1994). The hot-boreal climate is warmer than the current average boreal-forest climate and is similar to that observed at Fort Yukon (67° N, 145° W), the warmest, most continental part of interior Alaska (Trigg 1971, Yarie 1981). Thus, both temperature and precipitation cover the likely range of values that may have occurred in the past or may occur in the future in areas that are currently upland tundra (Maxwell 1992). The difference in mean temperature between each climatic regime (3°) coincidentally equals the average change in arctic summer air temperature predicted over the next 100 yr by three general circulation models (GCMs; Maxwell 1992). As validation and to avoid complications of interpreting the climatic basis of tree line in the east–west-oriented Brooks Range, we calculated average summer (June through August) temperature during the period of record for all weather stations ($n = 37$) in central, northern, and western Alaska and estimated from vegetation maps the average proportion of tundra and forest in upland sites in a 1000-km^2 area around each weather station (Selkregg 1974*a*, *b*). All sites with <10° summer temperature were 100% tundra; those with >13° were ≥85% forest, and sites with 10°–13° (corresponding to our tree-line climate) had mixtures of forest and tundra, indicating that the vegetation–climate relationship in the model is broadly representative of Alaska.

The timing and pattern of climatic change are defined for each model run by specifying when the switch occurs from one climatic regime to the next. Within a given climatic regime, temperature and precipitation at each time step are determined by a random number generator according to the probability distribution appropriate to that climate (Table 1). There was only a weak negative relationship ($R^2 = 0.16$) between average summer temperature and total summer precipitation in the boreal forest site, so the model assumes that temperature and precipitation are independent of one another for all four regimes. Climates that are intermediate between the four regimes are simulated by choosing one or the other regime with a specified probability. For example, a gradual ramped progression from tundra to tree-line climate can be simulated by randomly choosing between the two regimes with the odds favoring tundra climate at the start and then steadily shifting toward tree-line climate.

Seed rain is an input parameter that increases with increasing number of adjacent forest patches, according to relationships shown in the Appendix.

Management policies are incorporated in the model by altering probabilities of logging, fire, and moose browsing (*Methods: Model experiments*). In the absence of explicit management, we assume that moose densities and fire probabilities are determined by ecological and climatic factors and that no logging occurs, i.e., the model is parameterized for unmanaged ecosystems.

Ecosystem types

Upland tundra.—The model begins in upland tundra with a climate typical of the northern limit of this vegetation type. Moist upland tundra is the predominant vegetation type on gently rolling hills. It includes tussock tundra in western North America or eastern Russia, shrub tundra in other regions of the Arctic (Bliss and Matveyeva 1992), and forest tundra with <50% tree cover. We assume that the most likely change from upland tundra is to conifer forest reflecting gradual tree invasion, because this is the most common forest type south of the arctic tree line (Bliss and Matveyeva 1992) and because this is the forest type that most commonly invaded tundra following past episodes of climatic warming (Davis 1981, COHMAP 1988, Payette 1992, Brubaker et al. 1995) except in extremely exposed sites, where no forest advance occurred (Payette et al. 1989) and during the climatic optimum 9000 yr before the present, when poplar invaded tundra (Brubaker et al. 1995). We also allow the possibility of a switch to dry grassland, as occurred during the Pleistocene (Hopkins et al. 1982). We ignore wet meadow tundra and mountain heath, the two other common arctic tundra types, because they occur in poorly drained lowlands and on steep mountain slopes, respectively, and are unlikely to form from upland tundra on rolling hills in response to climatic change. We also ignore polar desert of extremely high latitudes, which is also unlikely to form from upland tundra.

The rate of conifer expansion into tundra in the model depends on the rate of increase in percentage cover of conifer canopy (a function of seed source and temperature, but not precipitation; Black and Bliss 1980, Payette et al. 1985) and tree mortality as a result of insect outbreaks or fire (Payette and Gagnon 1985, Holling 1992). Conifer seed input to tundra is assumed to increase with increasing conifer canopy cover and with number of neighboring forest patches, although some seed input by long-distance transport (Payette and Filion 1985, Cooper 1986) is assumed even in the absence of neighboring forest patches (Appendix). When canopy cover by conifers exceeds 21%, the model assumes that establishment is limited by growth conditions rather than by seed input. We assume no tree establishment at the lowest summer temperatures (<10°; Brubaker et al. 1995; F. S. Chapin, III, *personal observation*). Values for potential seed input and the temperature response of canopy increment were selected to give (1) observed rate of conversion from tundra to forest under conditions of high seed input (70 yr) and no nearby seed input (100 yr) at Glacier Bay, Alaska at boreal summer temperatures (Table 2) and (2) a slow rate of conifer expansion with the tree-line climate and abundant seed, 20–30 km/100 yr (Solomon 1992). The temperature response of canopy increment is assumed to reflect direct temperature effects on winter bud mortality (Payette et al. 1985), conifer seed production (Black and Bliss 1980, Zasada et al. 1992), seedling establishment (Black and Bliss 1980), and seedling growth and layering (Lawrence and Oechel 1983, Payette et al. 1985) and the indirect temperature effects on melting of permafrost, soil aeration, and nutrient supply (Chapin 1983). An independent check on the validity of values of growth rate of canopy area is provided by rates at which forest canopy doubles during tree-line advance (*Methods: Model calibration*; Solomon 1992). Sensitivity analyses explored the effect of the rate of canopy increment on model results.

TABLE 2. Time required to convert tundra to forest in absence of fire and insect attacks (forest invasion time [yr]). (Here, we define forest as >50% conifer cover regardless of the size or age of trees.) Simulated values are shown in parentheses.

	Climatic regime		
	Tree line[1]	Boreal[2]	Hot-boreal[3]
No forest within 10 km	>400 (620)	100 (105)	80 (90)
Abundant seed rain	250 (235)	70 (70)	60 (60)

Notes: Superscript numbers denote sources: (1) J. Yarie, *personal communication*; (2) Fastie 1995; (3) values were inferred, based on the observation that tree growth occurs most rapidly in warm microclimates within the boreal zone (Van Cleve et al. 1991).

Conifer canopy can decrease in tundra as a result of fire or insect outbreaks (Payette and Gagnon 1985, Holling 1992). In all of our ecosystem types, fire probability (i.e., the probability of fire sufficiently intense to kill most trees) is assumed to be a function of an "effective rainfall" index (Trigg 1971, Clark 1988), which increases with decreasing temperature and increasing precipitation (Thornthwaite and Mather 1957; Appendix). We assume that the shape of the relationship between fire probability and effective rainfall does not differ among ecosystems (and base this relationship on data from boreal forests), but that the actual fire probabilities differ among ecosystems (see Appendix). Fire probability can also be affected by additional factors in each ecosystem type. For example, in tundra, fire has a lower probability of occurring than in other frames and is also a function of conifer cover and the time since the last fire (Appendix). We assume low fire

TABLE 3. Fire return time (yr) in different vegetation types and climates. Forest tundra is tundra with 7–50% conifer cover. Return times in conifer forests include time spent in early successional deciduous stages. Simulated values are shown in parentheses for each ecosystem in its equilibrium climate.

	Climatic regime			
Ecosystem type	Tundra	Tree line	Boreal	Hot-boreal
Tussock tundra	>400^{1} (408)	250^{1}	200^{2}	120
Forest tundra	1450^{3}†	180^{3} (136)	130^{4}	100
White spruce forest	>400	300^{5}†	120 (121)	110^{6} (103)
Black spruce forest	>400	80^{3,5}	70^{7}	40^{6}
Birch–aspen forest	>400	80	60^{2}	30^{6}
Grassland	>400	60	40	20

Notes: Superscript numbers denote sources: (1) Wein 1976; (2)Viereck and Schandelmeier 1980; (3) Payette 1992; (4) Heinselman 1981; (5) Rowe et al. 1974; (6) Yarie 1981; (7) Van Cleve et al. 1991. Values without references were interpolated from other data in the table.

† Outliers from the general pattern.

probabilities in the first 40 yr after a fire reflecting low fuel load (Clark 1988, Bonan 1990). Fire probabilities and the multiplier used to reduce fire probability in tundra relative to conifer forest were adjusted to match observed fire return times (Table 3). The effect of fire is to remove the existing tree canopy, i.e., reduce canopy to <7% (Payette and Gagnon 1985). Because the dominant conifer species at the arctic tree line (white spruce in western North America, Norway spruce in Scandinavia, and larch in Siberia) do not have a buried seed pool or serotinous cones (Zasada et al. 1992), we assumed that seed availability following fire is determined by surviving canopy (canopy <7%) and proximity of neighboring forest. Black spruce, the dominant tree-line species in eastern Canada, and lodgepole pine in central Canada do have semi-serotinous cones and could recover more rapidly following fire than we have simulated. Forest dieback resulting directly from climatic cooling, as during the little ice age, occurs only in rare stands that escape fire (Payette et al. 1989) and is ignored in our model.

Tree canopy can also decline in tundra as a result of insect attack (Kallio and Lehtonen 1973, Holling 1992). We assume that insect outbreaks severe enough to kill entire stands are determined primarily by canopy cover and drought, i.e., low effective rainfall (Appendix; *Methods: Model calibration*; Mattson and Haack 1987, Holling 1992). As a separate experiment we also include the possibility of insect attack under conditions of extreme cold (Kallio and Lehtonen 1973). Insect outbreaks in the model reduce tree canopy by 25%.

Tundra can switch to dry grassland after fire if precipitation remains very low during two consecutive time steps (20 yr) after the fire. Under other circumstances, tundra is assumed to regenerate after fire (Wein and Bliss 1973, Auclair 1983). The model switches from tundra to conifer forest when conifer canopy cover exceeds 50% (canopy class 4). In accordance with the literature, we assume that at <50% canopy, tundra regenerates after fire, regardless of prevailing climate (Wein and Bliss 1973, Auclair 1983).

Conifer forest.—The conifer forests that have developed from tundra in response to past climatic warming events are primarily white spruce in North America (Brubaker et al. 1983), black spruce and pine in eastern North America (Payette 1992), Scots pine in Scandinavia (Tukhanen 1980, Sirois 1992), and larch in Siberia (Tikhomirov 1970, Sirois 1992). Conifer forests are the successional climax through most of the boreal forest (Van Cleve et al. 1991). The model assumes that fire and logging are the major factors causing a switch out of conifer forest. Logging is a management option that is defined for each model run. The probability of fire depends on climate, being greatest at low effective rainfall according to the basic relationship between fire probability and effective rainfall (*Methods: Ecosystems: tundra*). This relationship was determined by matching fire return times under each climatic regime against observed fire return times in boreal forest (Table 3). The model assumes that insects do not cause a switch out of conifer forest under most circumstances because dead trees in a closed conifer forest are replaced by other conifers from the understory. The effect of insects on fire probability is included in normal fire return times observed in boreal forest. Consequently, insects are not modeled explicitly in the conifer frame.

Following fire or logging, the nature of the replacement vegetation depends on climate for the first 20 yr of vegetation recovery. Normally, conifer forests are replaced by early successional trees and shrubs after fire or logging, leading to a shift to the broad-leaved, deciduous-forest frame (Larsen 1965, Viereck 1973, Payette and Gagnon 1985). However, if temperatures are typical of cold tundra for the first 20 yr after disturbance, the conifer forest is replaced by tundra (Sirois 1992). If climate is extremely hot and dry (effective rainfall = 1) for 20 yr, the site regenerates as dry grassland. This pattern of grassland preventing forest regeneration has been observed in interior Alaska following logging, when conditions are unfavorable for tree establishment (Viereck and Van Cleve 1984).

Broad-leaved deciduous forest.—Early successional boreal forests are usually dominated by willow, birch, and aspen and undergo succession to conifer forest. The model assumes that, in the absence of fire or logging, the switch from deciduous to conifer forest occurs with 20% probability after 80 yr, with 60% probability after 90 yr, and with 100% probability after 100 yr (Viereck 1970, Bonan 1990, Van Cleve et al. 1991). Succession is assumed to occur more quickly in cold climates, where low temperature inhibits the growth of deciduous trees more than of understory conifers (Lawrence and Oechel 1983), perhaps because of low nutrient availability (Pastor and Post 1986). This and reduced fire frequency explain the decreased proportion of broad-leaved forests in cooler regions of the boreal forest in the model. Fire or logging can prevent succession to conifers and return the site to the post-disturbance regime described for the conifer frame (Van Cleve et al. 1991), generally followed by development of deciduous forest. The probability of fire in the broad-leaved forests has the standard trend with effective rainfall (Appendix) but is only 20% of the fire probability observed in conifer forests because of the lower flammability of deciduous vegetation (*Methods: Model calibration*; Viereck 1973). After fire, the ecosystem normally reverts to early successional broad-leaved forest, but can move to tundra after 20 yr of extremely cold conditions or to grassland after 20 yr of hot dry conditions, as described in the conifer frame.

Grassland.—Dry grassland is uncommon in the tundra zone today but was the dominant vegetation type during the Pleistocene (Hopkins et al. 1982). Dry grasslands also occur in a boreal forest zone under dry conditions (Edwards and Armbruster 1989). The model assumes that the grassland switches to tundra after 20 yr of very cold weather. Fire probability in grassland is assumed to respond to effective rainfall, as described in the conifer frame (Appendix), but the probabilities are all multiplied by 2.5 to simulate a generally higher fire frequency in grassland relative to other ecosystem types in the same climatic zone (D'Antonio and Vitousek 1992). If temperature and precipitation are appropriate for forest growth after a fire, and seed availability is high (reflecting presence of neighboring forest), we assume a high probability of reverting to deciduous forest (Appendix). At moderate seed availability, the model assumes that probability of reversion to forest is 60% of the maximal reversion rate.

Model calibration

The matrices in the Appendix contain the model parameters. These are our best estimates for many of the parameters, but in some cases, although we are confident of the trends in the matrices, we are unsure of the magnitudes of the actual numbers. After some initial computer experiments and sensitivity analyses, we identified five key parameters to which the model was particularly sensitive and needed calibration: conifer canopy growth, fire frequency and probability of insect outbreak in the upland tundra frame, and fire frequency in both the conifer and deciduous forest frames. For each of these, we introduced a calibration factor: the growth factor multiplied all the entries in the matrix for conifer canopy growth (as a function of temperature and seed input) by the same amount; the insect factor similarly multiplied all the probabilities of a severe outbreak by the same amount, while the three fire factors each multiplied the basic probabilities of a fire (as a function of effective rainfall) by the same amount (Appendix). We were able to find appropriate values for these factors through a series of computer experiments.

Starting in the upland tundra frame with no conifer canopy cover, we found the mean time (n = 500 replicate simulations) to switch to the conifer-forest frame under conditions of no insects and suppressed fires. The results are shown in Fig. 2a for different climatic regimes and seed availability scenarios. Comparing these graphs with the data in Table 2 suggests that a growth factor of 1.0 is appropriate (i.e., the growth rates in the Appendix are reasonable). With this growth factor, we then repeated the experiment for different insect and tundra fire factors in the tree-line climate. The results, presented in Fig. 2b, suggest that a tundra fire factor of 0.4 combined with an insect factor of 2.5 gave reasonable rates of forest invasion. Thus, the fire frequency in conifer forest (Appendix) was multiplied by 0.4 to give fire frequency in tundra at each rainfall regime. We deliberately chose a relatively high factor for insects, because below this value, insects had little effect on model behavior (Fig. 2), whereas they have substantial effects on tree dynamics at tree line in the real world (Holling 1992). Tundra fire factors <0.4 produced model results similar to those that we report here.

To calibrate the fire factors in the conifer and deciduous forest frames, we started in the deciduous frame, under a boreal climate regime, and ran the model for 5000 yr (n = 500 simulations). This gave an equilibrium value for the number of replicates ending in the deciduous frame divided by the number ending in the conifer frame (the equilibrium deciduous to conifer ratio). We also kept track in the model of the ages of all stands. We fitted a negative exponential to the cumulative frequency of stands of different ages (Van Wagner 1978, Yarie 1981) to compute an average fire interval for each of the frames. The results (Fig. 3) led to estimates for factors of 0.7 and 0.15 for the conifer and deciduous forest frames, respectively. These numbers were chosen both to match reported fire return times (Table 3) and to give a reasonable deciduous-to-conifer ratio, which was more sensitive to fire frequency.

Model experiments

After calibrating the model, we performed a series of model experiments. In the first set of experiments we ran the model to equilibrium (5000 yr) under the four different climate regimes (tundra, tree-line, boreal, and hot-boreal climates) represented by the probability distributions in Table 1. For each of the four climatic

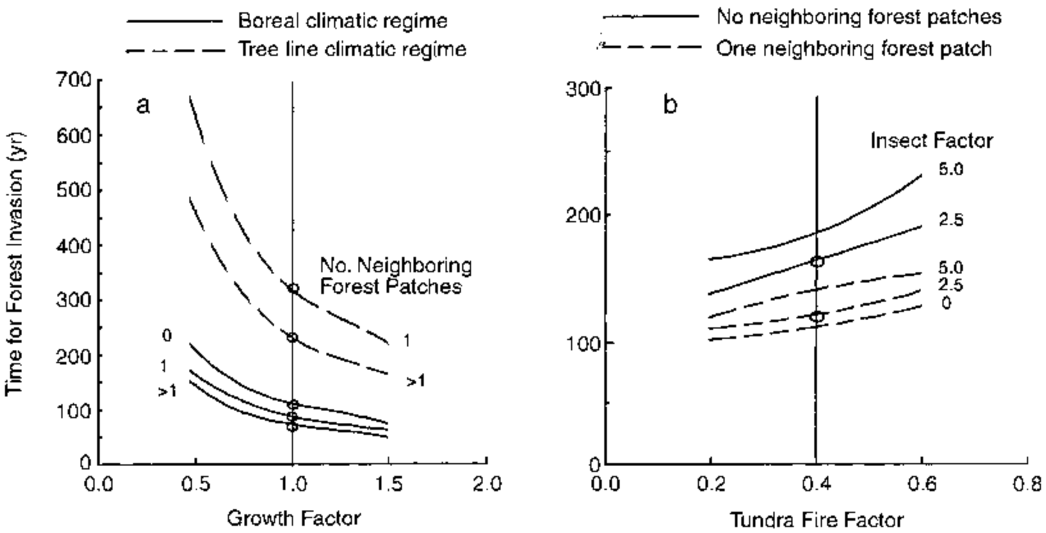

FIG. 2. Model calibration to determine relationship between time required for forest invasion into tundra as a function of (a) canopy growth rate, number of neighboring forest patches, and climate and (b) tundra fire probability (relative to conifer forests), probability of insect attack, and number of neighboring forest patches in a tree line climate. Circled values are those used in the model.

regimes and two initial ecosystem types (tundra and conifer forest), we calculated the proportion of the simulations in which each ecosystem was present after 5000 yr ($n = 500$ replicate simulations). We then determined equilibrium ecosystem types at 20 climates that were intermediate in temperature and precipitation between the tundra and boreal climates. As validation, we estimated the proportion of tundra and forest in upland sites from 1:1 000 000 vegetation maps in a 1000-km^2 area around 37 weather stations (Selkregg 1974*a, b*) that differed from those used in developing the climate–vegetation relationship. For the 29 sites with both climatic and remote sensing data, we also estimated the relative abundance of conifer and deciduous forest cover (Anonymous 1994).

We conducted sensitivity analyses on critical parameters, alone and in combination, to determine their effect on equilibrium vegetation after 5000 yr ($n = 500$ simulations). In the tree-line climate, most relevant parameters (seed availability, probability of tundra fire, probability of boreal fire, probability of tundra and boreal fire, tree growth rate, and probability of insect attack) were tested in separate simulations with values ranging from 0 to twice the value used in the standard simulation. In addition, we varied probability of high moose from 0 (the standard value) to 1. We then ran simulations under different combinations of parameters to test interactions between the probability of tundra fire and other parameters to which the model was particularly sensitive (tree growth rate, probability of insect attack, and seed availability). In the boreal and hot-boreal climates we examined the effect of increasing or decreasing fire probability by 50% from the standard value. Under each of these sets of conditions we determined the proportion of simulations ($n = 500$) in which each ecosystem was present after 5000 yr.

To explore alternative climate change scenarios, we followed the time course of changes in ecosystem type, number of fires in each ecosystem, number of insect outbreaks in tundra, tree canopy in tundra, and the number of switches among each pair of ecosystem types in response to different patterns and rates of change from the tundra to the boreal climate regime (Table 1). All simulations began with the tundra ecosystem at equilibrium with tundra climate and with seed input typical of the tree-line situation (<7% tree canopy in the simulated ecosystem; one neighboring forest patch). We then explored different scenarios of climate change from year 0 to 400. During the final 100 yr of each simulation (year 400–500), we assumed a constant boreal climate (Table 1). Results are presented as the proportion of simulations ($n = 1000$) in which each ecosystem type was present at each 10-yr time step.

In scenario 1, climate was changed instantaneously from the tundra to the boreal climate (Table 1). In a second set of scenarios (2–4), climate was ramped continuously from tundra to boreal climate over 100, 200, or 400 yr, respectively. This was done by gradually reducing the probability of a tundra temperature and precipitation regime, and increasing the probability of a boreal climatic regime over the specified period of climate change. In all other simulations (5–10), conditions were adjusted so that the cumulative heat sum (i.e., the sum of summer temperatures) over the first 400 yr (the period during which climate was changed) was equal to that in a constant tree-line climate (Table 1). In scenario 5, climate changed abruptly from tundra to tree-line climate at year 100 and to boreal climate

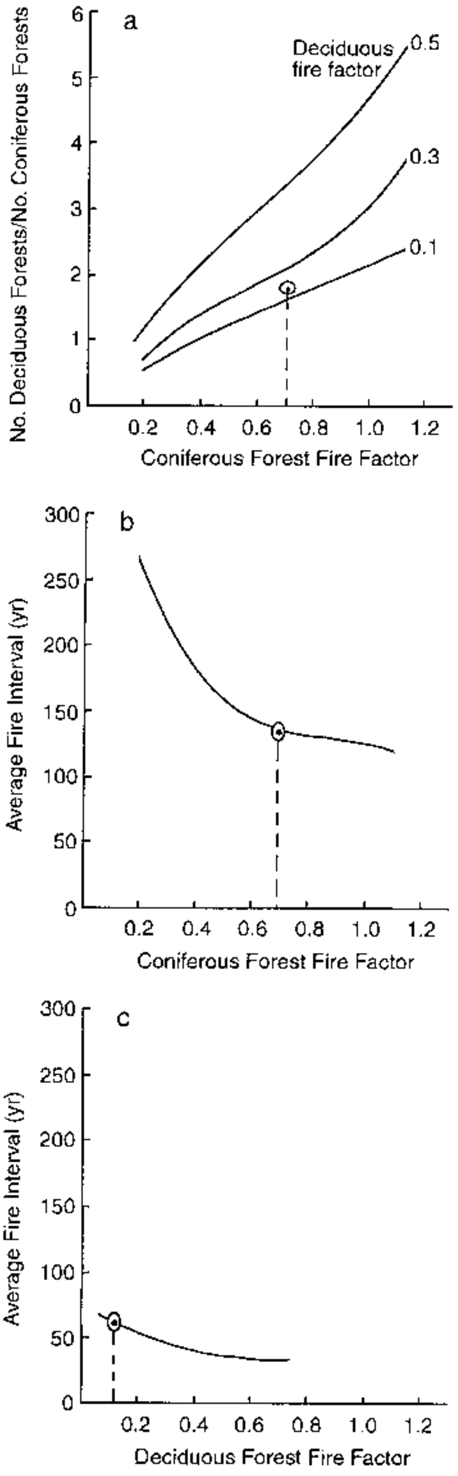

FIG. 3. Model calibration to determine (a) the relationship between the ratio of the number of simulations (n = 500) ending in deciduous forest divided by the number of simulations ending in conifer forest at equilibrium (5000 yr) in the boreal climate as a function of fire probability in conifer and deciduous forests. Also shown is the average fire interval as a function of (b) fire probability in conifer forests and (c) fire probability in deciduous forests. Circled values are those used in the model.

at year 300. In scenario 6, climate was determined randomly (tundra, tree line, or boreal) at each time step during the first 400 yr, then was held at the boreal climate. In scenario 7, climate oscillated with the following step changes: tree-line climate at year 0, boreal climate at year 100, tree-line climate at year 200, tundra climate at year 300, boreal climate at year 400. In scenario 8, climate oscillated in the same pattern as in scenario 7, but the changes occurred at 50-yr intervals.

In another set of climate change scenarios, temperature increased from the tundra to the tree-line temperature regime at year 100 and to the boreal temperature regime at year 300 (i.e., as in scenario 5), but rainfall was either increased to boreal rainfall at year 100 and to hot-boreal rainfall at year 300 (scenario 9) or kept low (tundra rainfall) throughout the simulation (scenario 10).

To simulate the effects of different land use policies, we first examined the impact of various fire suppression and logging policies on equilibrium vegetation (i.e., after 5000 yr; n = 500 simulations). These simulations were run with fire probability determined by climate (our standard condition) and where fire probability was reduced to 10% of the standard value to represent fire control. Within both fire regimes we examined three logging regimes: (1) logging all deciduous forests after 70 yr and logging all conifer forests 30 yr after they switched from some previous ecosystem type (i.e., from deciduous forest or tundra); (2) logging conifer forests only, 30 yr after they switched from some previous ecosystem type; and (3) 50% probability of logging a conifer forest 30 yr after it switched from some previous ecosystem type. In each case, conifer trees are ≈120 yr old when logged.

We also examined the effect of high moose densities resulting from intensive predator control (an input variable) on forest regeneration and equilibrium vegetation. If moose are abundant in the first 20 yr after fire, they speed succession to evergreen forests by selectively browsing deciduous shrubs and tree seedlings and reducing competition for the less palatable coniferous trees (Bryant et al. 1983, deToit et al. 1991). The model assumes that this causes a switch to evergreen dominance after 20 yr, as observed at Isle Royal (Pastor et al. 1993). However, even at high moose densities, deciduous trees can escape browsing by moose and form a deciduous forest under favorable climatic conditions (Appendix). Under ecologically regulated moose densities, the model assumes no effect of moose on succession (i.e., the moose effect is included in naturally observed patterns and rates of succession).

RESULTS

Equilibrium distribution of vegetation

Climatic gradients.—At equilibrium, the ecosystem type calculated by the model under constant climate depended only on climate and was independent of the

TABLE 4. Probability of each ecosystem type being present in the simulated patch under constant climate (percentage of 500 replicate simulations in which the specified ecosystem is present after 5000 yr). Values shown in parentheses are means ± 1 SE of the percentage cover of the specified ecosystem type present in a 1000-km² area surrounding each climate station found in the specified climate zone (calculated from Fig. 4).

	Climatic regime			
Ecosystem type	Tundra	Tree line	Boreal	Hot-boreal
Tundra	100 (100 ± 0)	30 (38 ± 7)	0 (3 ± 1)	0
Conifer	0 (0 ± 0)	44 (62 ± 5)	31 (45 ± 6)	29
Deciduous	0 (0 ± 0)	26 (0 ± 0)	69 (52 ± 8)	69
Grassland	0 (0 ± 0)	0 (0 ± 0)	0 (0 ± 0)	2
Number of sites†	8	13	14	0

Note: Climates are defined in Table 1. Results were identical, regardless of whether simulations began in tundra or conifer forest.

† Number of climate stations where these ecosystem distributions were determined in each climatic zone.

ecosystem type in which the simulation began. Only tundra occurred in the tundra climate, and only conifer and broad-leaved deciduous forests occurred in the boreal and hot-boreal climates (Table 4). The tree-line climate produced a forest ecosystem twice as often as tundra, regardless of whether the simulation began in tundra or in forest. Among forested ecosystems, broad-leaved deciduous forest occurred least often at tree line and most often in the boreal and hot-boreal climates. These predicted patterns of ecosystem distribution correspond closely with those observed in Alaska (Fig. 4, Table 4; Selkregg 1974*a, b,* Anonymous 1994) and with patterns predicted by gap dynamics models (Pastor and Post 1988), suggesting that our simple frame models adequately capture the within-stand dynamics of our major ecosystem types.

Along a gradual gradient from the tundra to the boreal climate, the equilibrium distribution of ecosystem types was most sensitive to climate at the intermediate tree-line climate (Fig. 4). The gradient in climate had little influence on the relative abundance of ecosystem types we modeled at either warm or cold climatic extremes. Conifer forests were the most common ecosystem type only in climates close to and slightly warmer than the tree-line climate. At warmer boreal climates, early successional broad-leaved deciduous forests dominated because of increased fire frequency.

Tree-line sensitivity analysis.—Canopy growth rate, seed availability, and probability of fire were the model parameters that most strongly influenced the equilibrium balance between tundra and forest in the tree-line climate (Fig. 5). As seed availability and canopy growth rate increased, the equilibrium shifted toward forest. By contrast, tundra fires and insect attacks reduced the cover of colonizing trees in tundra, causing an increase in the proportion of tundra at equilibrium. Fires in boreal forest also increased the proportion of tundra by increasing the number of occasions when

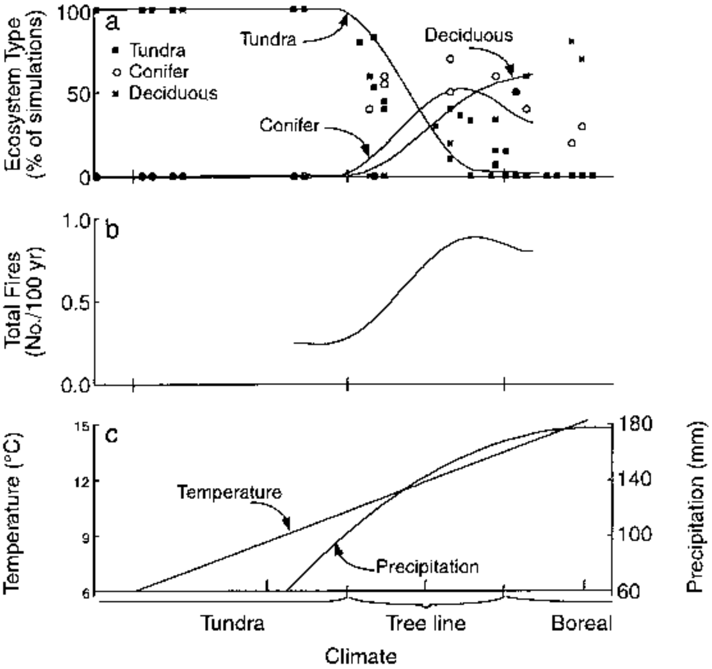

FIG. 4. (a) The probability (% of 500 replicate simulations) of each ecosystem type being present in the simulated vegetation patch after a 5000-yr simulation under constant climate. Climate was varied among simulations by altering the probability of tundra, tree-line, and boreal climates (Table 1). Data points indicate the observed relationship between vegetation and climate (data from Selkregg 1974*a, b,* Anonymous 1994). Also shown are (b) the total number of fires simulated in each climatic regime and (c) the temperature and precipitation regimes for each climatic regime.

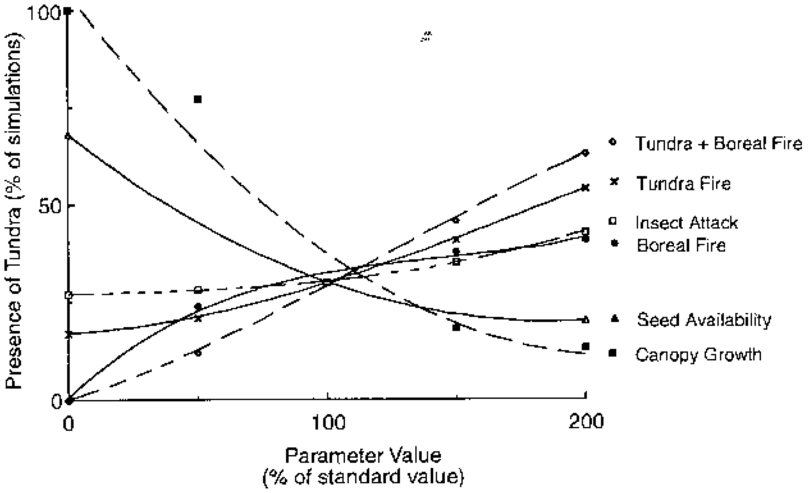

FIG. 5. Analysis of sensitivity to model parameters of the equilibrium distribution of ecosystems in the tree-line climate. Each point represents the mean of 500 replicate simulations.

succession could revert to tundra rather than boreal forest. Doubling the probability of insect attacks in extremely cold decades (temperature = 1; Table 1), as observed in Scandinavia (Kallio and Lehtonen 1973), had negligible effect on the proportion of tundra (*results not shown*). Simulation results were most sensitive to seed availability, canopy growth, and boreal fire at values less than our standard value, and to tundra fire at values greater than our standard value. In general these are the situations where comparisons with field data constrained the calibration of our model.

The importance of canopy growth rate and seed availability depended strongly on the probability of fire. For example, with a low probability of tundra fire, as might occur with fire suppression, a patch of tundra had a high probability of becoming forest, regardless of seed availability, canopy growth rate, and probability of insect attack (Fig. 6). However, at high fire

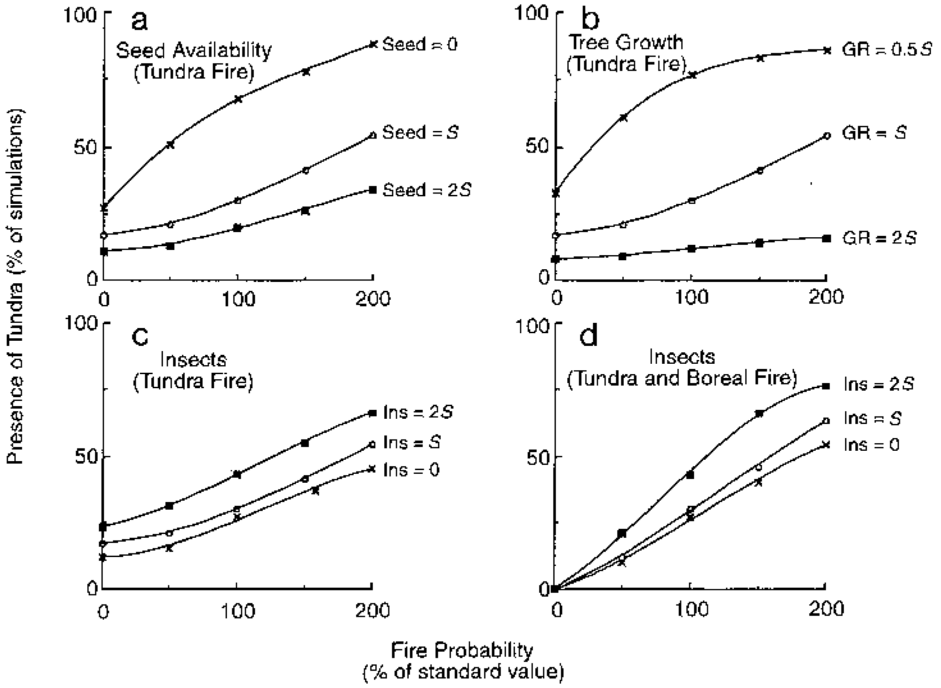

FIG. 6. Probability of tundra being present in the simulated vegetation patch after a 5000-yr simulation under tree-line climate and varying probability of tundra fire and (a) seed availability (Seed), (b) canopy growth rate (GR), and (c) probability of severe insect attack (Ins). (d) Also shown is the probability of tundra being present with varying probability of severe insect attack and probability of boreal and tundra fire. Values used in these simulations range from zero to twice the standard (*S*) value. Each point represents the mean of 500 replicate simulations.

TABLE 5. Probability of conifer forest being present in the simulated vegetation patch (percentage of 500 replicate simulations in which the specified ecosystem is present after 5000 yr) and average time between fires, under either boreal or hot-boreal climate.

Simulation condition	Probability of conifer forest (%)		Fire return time (yr)	
	Boreal	Hot-boreal	Boreal	Hot-boreal
Standard	37	30	121	103
Low-fire probability	54	47	181	143
High-fire probability	26	23	98	87
Tundra rainfall	28	22	96	57
Boreal rainfall	37	24	121	81
Hot-boreal rainfall	41	30	146	103

Note: The alternative ecosystem type under these climates is deciduous forest. Simulations represent a sensitivity analysis of the factors having greatest effect on ecosystem type in the boreal and hot-boreal climates. Fire probability was altered in all ecosystem types (±50%). Rainfall was altered according to regimes characteristic of tree-line, boreal, and hot-boreal climates (Table 1).

TABLE 6. Summary of simulation conditions in which climate was changed from tundra climate to boreal-forest climate over a 400-yr period.

Climate scenario†	Time period for 6°C change (yr)	Nature of change	Cumulative heat sum over 400 yr (% of standard)
1	0	One step	200
2	100	Continuous ramp	175
3	200	Continuous ramp	150
4	400	Continuous ramp	100
5	200	Two step changes	100
6	400	Random fluctuations	100
7	200	Oscillating	100
8	100	Oscillating	100
9	200	Scenario 3, high rain	100
10	200	Scenario 3, low rain	100

† Except in scenarios 1–3, the cumulative heat sum over the 400-yr period of climate change was kept the same.

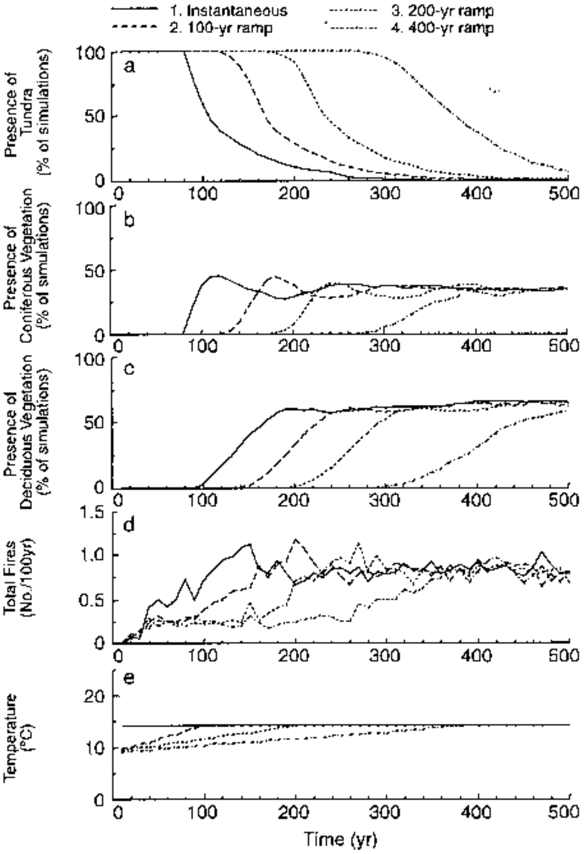

FIG. 7. Vegetation response to differing rates of climate change, shown as the probability of (a) tundra, (b) conifer forest, and (c) deciduous forest being present in the simulated vegetation patch during the first 500 yr of climate change ($n = 1000$ simulations for each climate scenario). Also shown are the time courses of (d) the total number of fires, and (e) average summer temperature. Scenarios shown are an instantaneous change from the tundra to the boreal climate at yr 0 (scenario 1), and gradual ramped changes over 100 yr (scenario 2), over 200 yr (scenario 3), and over 400 yr (scenario 4).

frequency, as might occur with more human-induced fires, a patch was more likely to remain tundra in the tree-line climate unless tree canopy expanded much more rapidly or seed availability was higher than we assumed in the standard simulation. By contrast, fire probability had relatively little influence on the impact of insect attacks on ecosystem composition, even under conditions of fire suppression. In summary, the equilibrium composition of vegetation in the tree-line climate was highly sensitive to rate of canopy growth, seed availability, and fire probability, particularly when these factors were altered in combination.

Boreal-forest sensitivity analysis.—In both the boreal and hot-boreal climates, the relative abundance of conifer and broad-leaved deciduous forests at equilibrium was quite sensitive to fire probability (Table 5). A higher fire probability increased the proportion of simulations giving deciduous forests, whereas fire suppression increased the proportion of simulations giving conifer forest. At any given fire probability, deciduous forests occurred more frequently in the hotter climate. Increased rainfall (from tundra to boreal to hot-boreal climate) caused a comparable increase in conifer forest by reducing fire frequency, especially in the boreal climate.

Response to climatic change

An instantaneous 6°C temperature rise from tundra to boreal climate (scenario 1; Table 6) gives a limit to the fastest rate at which tundra ecosystems might respond to climatic warming in the model. In response to this large step change in climate, tundra first switched to forest after an 80-yr lag (Fig. 7), reflecting the time required for tree establishment and growth. The proportion of tundra then declined exponentially, dropping 50% by year 110 and 90% by year 220. This conversion of tundra to forest occurred despite a linear

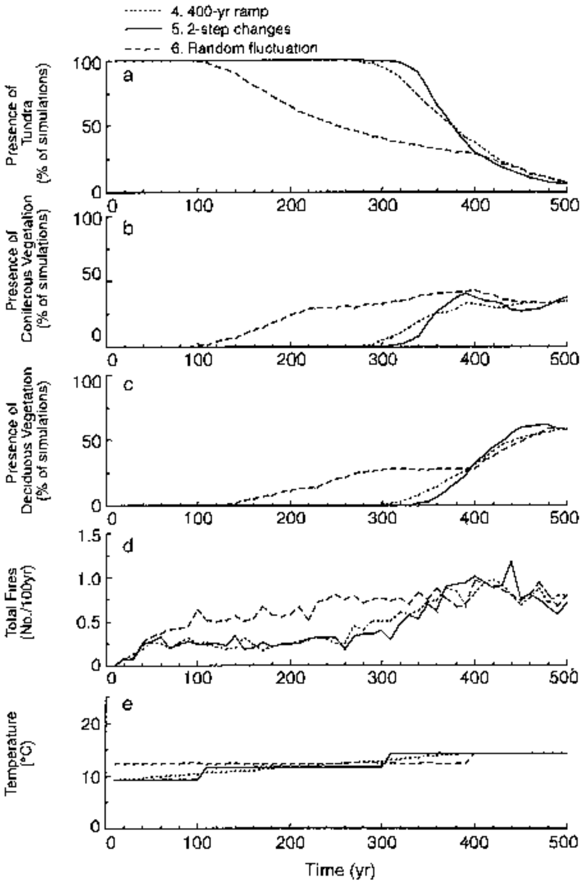

FIG. 8. Vegetation response to different patterns of climate change, shown as the probability of (a) tundra, (b) conifer forest, and (c) deciduous forest being present in the simulated vegetation patch during the first 500 yr of climate change (n = 1000 simulations for each climate scenario). Also shown are the time courses of (d) total number of fires and (e) average summer temperature. Cumulative heat sum of all simulations is the same for years 0–400 as in a constant tree-line climate. Scenarios shown are a change from the tundra to the tree-line climate at 100 yr followed by a change to the boreal climate at 300 yr (scenario 5) and a random selection of tundra, tree-line, or boreal climate from year 0–400, followed by a constant boreal climate (scenario 6).

increase in fire frequency during the first 150 yr, reflecting the impact of increasing fuel load on fire frequency. Conifers colonized initially, but deciduous forest became progressively more important from year 100 to 200. Fire frequency declined when deciduous forests became more common than conifer forests. Thus, fire frequency did not change instantly as a simple function of climate but responded primarily to changes in species composition, both within an ecosystem type (the first 80 yr) and with conversion to new ecosystem types (year 80–200).

The rate of climatic warming affected the *time lag* between the onset of climate change and the ecosystem response more strongly than the *rate* of vegetation change, once the change was initiated. A gradually ramped temperature increase of 6° over 100–400 yr (spanning the range of rates of summer warming predicted by GCMs for tundra; Maxwell 1992) resulted in time lags of 110–280 yr before tundra changed to forest, reflecting the strong dependence of seed availability and tree establishment on periods of warm weather. These warm decades occurred only in the later years of the climate change. Maximal rates of conversion from tundra to forest were similar for simulations ranging from instantaneous to a 200-yr ramped change (≈12% per decade) but were about half as fast for the 400-yr ramped change in climate (Fig. 7). Regardless of the rate of climatic warming, conifers first invaded tundra followed by a gradual increase in abundance of broad-leaved deciduous forest. With the 400-yr ramp, vegetation had not yet reached equilibrium after 500 yr. The increase in fire frequency with climatic warming was dependent on vegetation. In the most rapid warming scenario (100-yr ramp) the increased fire frequency with climatic warming resembled that described for the instantaneous climate change (but delayed by 50 yr). However, with slower warming (1.5 or 3°/100 yr), fire frequency increased for 40 yr, then reached a plateau for at least 100 yr that was independent of rate of climatic change until conifer forests became an important component of the landscape. Thus, with both rapid and gradual climatic change, changes in the fire disturbance regime were closely linked to vegetation response to climate.

The *pattern* of climatic warming had large effects on rates of conversion from tundra to forest (Table 6, Figs. 8–10). In a series of simulations with a 6° warming over 400 yr, we kept the cumulative heat sum (i.e., the area beneath the climate curve) the same for all scenarios (Table 6). A continuously ramped climate change over 400 yr (scenario 4) resulted in a 280-yr lag (Fig. 8). In scenario 5, in which there were two step changes in climate (after 100 and 300 yr), the ecosystem response was similar to that of scenario 4 but was delayed by 50 yr and occurred more precipitously than in scenario 4. By contrast, when climate was allowed to fluctuate randomly between the tundra, tree-line, and boreal climates (scenario 6), the conversion from tundra to forest began almost as soon as with the immediate step change to the boreal climate (Figs. 7 and 8) because the occasional warm decades that occurred early in this climate scenario allowed tree establishment and growth. This rapid conversion of tundra to forest in scenario 6 occurred despite the high number of tundra fires (a consequence of gradual tree invasion). These results suggest that an increase in climate variability can be at least as important as the magnitude or rate of climate change in causing changes in fire frequency and ecosystem distribution.

Climatic oscillation caused a different pattern of vegetation change than did monotonic climatic warming. In scenario 7, climate was allowed to warm with two step changes over 200 yr (similar to scenario 5, but

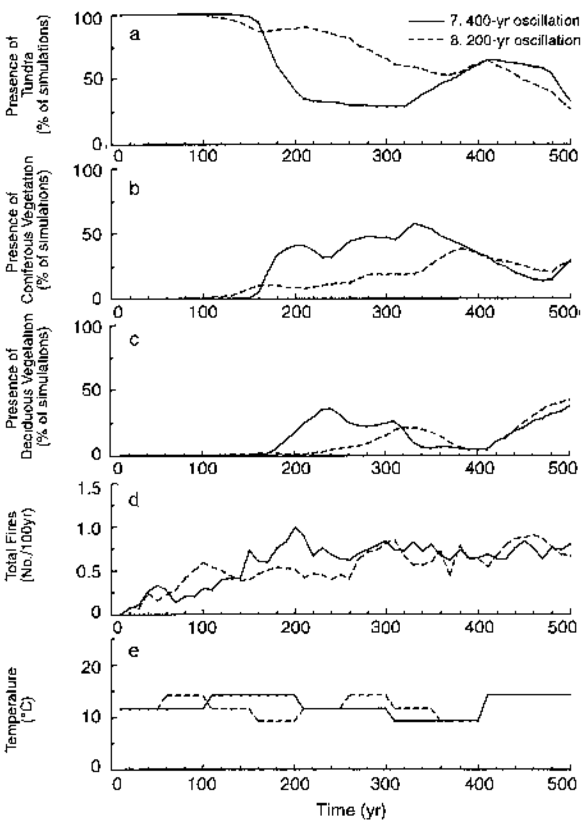

FIG. 9. Vegetation response to different patterns of climatic oscillation, shown as the probability of (a) tundra, (b) conifer forest, and (c) deciduous forest being present in the simulated vegetation patch during the first 500 yr of climate change (n = 1000 simulations for each climate scenario). Also shown are the time courses of (d) total number of fires and (e) average summer temperature. Cumulative heat sum of all simulations is the same as in a constant tree-line climate. In scenario 7, climate oscillated with the following step changes: tree-line climate at yr 0, boreal climate at yr 100, tree-line climate at yr 200, tundra climate at yr 300, boreal climate at yr 400. In scenario 8, climate oscillated in the same pattern as in scenario 7, but the changes occurred at 50-yr intervals.

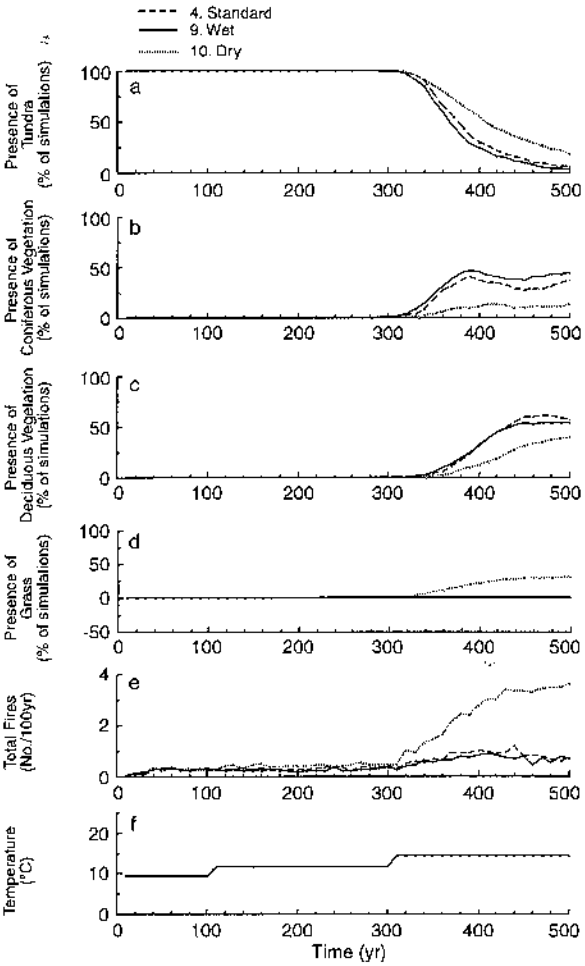

FIG. 10. Vegetation response to different patterns of precipitation change, shown as the probability of (a) tundra, (b) conifer forest, and (c) deciduous forest, and (d) grass being present in the simulated vegetation patch during the first 500 yr of climate change (n = 1000 simulations for each climate scenario). Also shown are the time courses of (e) total number of fires and (f) average summer temperature. Cumulative heat sum of all simulations is the same as in a constant tree-line climate. Temperature increased from the tundra to the tree-line temperature regime at year 100 and to the boreal temperature regime at year 300 (i.e., the same as in scenario 5), but rainfall was either increased to a greater extent than in the standard run (i.e., increased to boreal rainfall at year 100 and to hot-boreal rainfall at year 300; scenario 9) or kept low (equivalent to tundra rainfall) throughout the simulation (scenario 10).

beginning at a warmer temperature to keep heat sum the same), then to cool at the same rate. The initial rate of decline in abundance of tundra was identical to that of scenario 5 because the climate change was identical (Figs. 7 and 9). However, the recovery of tundra with climatic cooling began with shorter time lag (120 yr) than the warming response (170 yr), but occurred twice as slowly (8% increase in tundra per decade) as with climatic warming (16% decrease per decade). The shorter time lag for recovery of tundra occurred partly because the model allows reversion to tundra if there are two consecutive decades of very cold weather immediately after a fire, whereas conversion of tundra to forest requires tree invasion, a process that requires at least 70 yr under optimal temperature and absence of fire. The rate of tundra recovery is slower than the rate of tundra loss in the model because the probability of having two consecutive decades of extremely cold weather after a fire is less than the probability of continued tree canopy increase from open forest tundra to closed canopy forest.

The periodicity of climatic oscillation markedly influenced the rate of ecosystem change predicted by the model (Fig. 9). Climate that warmed and cooled with a 400-yr oscillation (like the little ice age) showed more rapid establishment of both conifer and broad-leaved deciduous forests in tundra than did climate with a 200-yr oscillation because the more rapidly oscillating cli-

TABLE 7. Impact of fire control and various logging and moose-predator control policies on the probability of each ecosystem type being present in the simulated vegetation patch under either boreal or hot-boreal climate (percentage of 500 replicate simulations in which the specified ecosystem is present after 5000 yr).

		Boreal climate		Hot-boreal climate	
Vegetation type	Management policy	Fire	Low fire	Fire	Low fire
Conifer forest	No management	37	86	30	80
	Log all forests	1	0	0	0
	Log conifer forests	18	25	20	23
	Log 50% conifer forests	28	75	24	67
	Moose predator control	52	91	39	83
Deciduous forest	No management	63	13	69	17
	Log all forests	99	97	99	90
	Log conifer forests	82	73	79	69
	Log 50% conifer forests	71	24	75	29
	Moose predator control	47	8	60	13
Grassland	No management	0	1	1	3
	Log all forests	0	3	1	10
	Log conifer forests	0	2	1	8
	Log 50% conifer forests	1	1	1	4
	Moose predator control	1	1	1	4

mate provided insufficient time for tree establishment and growth during warm periods before climatic cooling halted or reversed this trend.

These scenarios assume that climatic warming is accompanied by increased summer precipitation, as predicted on average by climate change scenarios (Maxwell 1992). However, changes in precipitation are uncertain. In scenario 9, where temperature increased as in scenario 5 but precipitation increased more rapidly, tundra was invaded slightly more rapidly by conifer forest and subsequently by deciduous forest (Fig. 10). In scenario 10, in which average precipitation did not change with climatic warming, tundra was converted more slowly to forest and to dry grassland, reflecting frequent fires. These precipitation scenarios, which bracket GCM predictions of altered summer precipitation, had less effect on rate of forest advance than did different patterns of climatic warming (scenarios 4–8). The formation of substantial amounts of dry grassland under the dry scenario (scenario 10) suggests that qualitatively different ecosystems than those that occur currently could become important with climatic warming, if climate becomes warmer and drier.

Response to land use

We examined the potential impact of several land use scenarios on the equilibrium distribution of boreal ecosystems (i.e., probability of each ecosystem type after a 5000-yr simulation) in both the boreal and hot-boreal climate. Intensive logging of all deciduous forests after 70 yr and conifer forests 30 yr after they switched to conifer from some other ecosystem type (i.e., when conifer trees were typically ≈120 yr old) led to elimination of conifer forests, regardless of fire control policy (Table 7). In the hot-boreal climate, there was substantial conversion from forest to grassland when this intense forest harvest was combined with fire suppression. Logging of only conifer forests reduced the abundance of conifer forests relative to their abundance in unmanaged forests, particularly in the boreal climate. If the probability of logging of conifer forests was only 50%, the abundance of conifer forests was nearly as high as that in unmanaged forests. This effect of logging intensity on forest composition was most pronounced under conditions of fire suppression. High moose populations, as might result from predator control, substantially increased the proportion of conifer forests at equilibrium by removing deciduous species at the sapling stage and allowing more rapid succession to conifer forest. Moose had less effect in the hot-boreal climate, where the high fire probability and reversion to deciduous forest counteracted the effect of moose.

DISCUSSION

Equilibrium distribution of ecosystems

The equilibrium distribution of ecosystems simulated by the model closely matched the observed patterns (Selkregg 1974*a*, *b*). For example, the boreal forest of Alaska, from which the model was parameterized, is dominated by conifers at tree line, and deciduous forests increase in abundance to the south (Anonymous 1994), just as shown by the model. The prediction by the model of tundra vegetation in tundra climate is not surprising, because the model does not allow tree growth at extremely cold temperatures. However, the relative abundance of ecosystem types in other climatic zones is a consequence of the simulated interaction of tree invasion, fire, insect attack, and succession. The simulation of a realistic relationship between climate, tree line, and boreal vegetation composition under appropriate conditions of constant climate suggests that the model captures the basic dynamics governing vegetation distribution and change. Although the validation data were collected from the same geographic region for which the model was developed and thus, in a sense, are pseudoreplicated, the specific sites for validation were distinct and involved quite different transects from boreal to arctic conditions. For example, the model was developed along a climatic transect crossing the Brooks Range, but most validation sites were from nonmountainous arctic–boreal gradients elsewhere in Alaska.

The vegetation predicted by the model at tree line was highly sensitive to fire frequency, seed availability, tree growth rate, and insect attack (Fig. 5). Although there is a limited historical record from which to estimate fire return times in northern ecosystems (Wein 1976, Heinselman 1981, Yarie 1981, Auclair 1983, Dyrness et al. 1986), the sensitivity of fire probability to climate is reasonably well understood (Trigg 1971, Heinselman 1981) because of its importance in developing fire control programs. Our simulated fire return times, based on this climate–fire relationship, closely matched current estimates of field values (Table 3). We did not use observed fire return times to construct the model; the data we used were drawn from the same region (boreal North America) as the fire return times and thus are not entirely independent. Our results suggest that fires in both tundra and boreal forest will strongly influence tree-line dynamics, and that climatic and, especially, vegetation effects on fire frequency must be incorporated into models estimating transients of vegetation change in response to changing climate.

The sensitivity of tree establishment and growth to climate is not well known and represents an important research need. Forest succession models use the climatic distribution limits of a species to estimate the growth response and assume a smooth parabolic response of growth to temperature between the cold and warm distribution limits of a species (Shugart and West 1980). However, at tree line, viable seed is produced only in exceptionally warm years (Zasada et al. 1992), and the advance of tree line is quite sensitive to temperature (Griggs 1934, Sirois 1992). Both natural patterns and the results of our model suggest that a better understanding of these low-temperature thresholds and other non-linearities of temperature responses is crucial to predictions of future rate of forest advance (Payette et al. 1985).

The relative insensitivity of our model to probability of insect attack is partially a consequence of the similarity of response of both fire probability and insect attack to drought conditions. We suggest that insects will strongly affect the nature of tree-line dynamics only if they occur more frequently, have greater ecological impact, or respond to different climatic or ecological factors than we have considered in our model. For example, in Scandinavia, insect attacks have a strong influence on tree-line dynamics, perhaps reflecting either (1) the rarity of fire in Scandinavia or (2) the tendency of outbreaks to occur in extremely cold years (Kallio and Lehtonen 1973), which is not included in our standard set of model conditions. Addition of a low-temperature trigger for insect outbreaks in our model had little effect on equilibrium distribution of ecosystems, so we suggest that in Scandinavia the absence of fire and development of old stands that become stressed by nutrient limitation, physiological aging, and fungal attack (Sveinbjornsson 1992) is a major factor explaining the prominence of insect effects on tree line in this region. Based on our model, we expect insect outbreaks to become increasingly important in causing ecosystem change if climatic warming is associated with more active fire suppression or if islands of trees occur in regions of naturally low fire frequency.

The increase in proportion of deciduous forest with increasing fire frequency and decreasing rainfall in our model reflects the importance of fire in resetting the successional clock in Alaska's boreal forest (Van Cleve et al. 1991). In interior Alaska, white-spruce forests are best developed on floodplains where they are protected from fire (Viereck et al. 1983). In southeastern Alaska, where summer temperatures are similar to those in interior Alaska but high rainfall precludes fire, spruce forests dominate forested sites (Cooper 1923). The driest parts of interior Alaska are characterized by high fire frequency and a high proportion of deciduous forests (Yarie 1981). These observations are consistent with our model simulations.

Climate change scenarios

The time lag between the onset of climate change and the ecosystem response ranged from 80 to 280 yr, depending on the climate scenario. The rule for switching from tundra to the conifer-forest frame is deterministic (switch when forest canopy exceeds 50%). Blurring this transition (replacing this rule with a suite of probabilistic rules) had an insignificant impact on the time lag of 80–280 yr. This range is consistent with the 150-yr lag between climate change and forest establishment observed in pollen cores (MacDonald et al. 1993). Similar time lags are predicted by patch models of vegetation change (Davis and Botkin 1985, Solomon 1986, Pastor and Post 1988) and indicate that models that predict vegetation change over the next century based on the equilibrium relationship between climate and vegetation (Rosenzweig 1968, Prentice et al. 1992) will seriously overestimate the extent of movement of forest vegetation. Because of the long time lag in vegetation movement, studies of the response of *current ecosystems* to climate change should be a useful basis for predicting terrestrial feedbacks to atmospheric processes over the coming decades.

To predict the transients of vegetation change over long time periods (>50 yr), we must understand controls over disturbance regime and invasions of new growth forms (e.g., trees or grasses). Rare events such as fire and insect outbreaks, along with climatic controls over establishment, frequently trigger these ecosystem shifts. In sites that escape such disturbances, vegetation can remain largely unchanged through major climatic changes (Payette et al. 1989). Fire models that include CO_2-induced climatic warming predict a 46% increase in fire severity rating and a 40% increase in area burned (Flannigan and Van Wagner 1991). Recent warming trends are correlated with a more than doubled annual area burned in the Canadian boreal forest (Van Wagner 1988). Thus, there is good reason to expect dramatic changes in disturbance regime in northern regions. Ecosystem shifts between tundra, forest, and grassland that are caused by altered disturbance regime should cause qualitatively different interactions between terrestrial ecosystems and the atmosphere (Shukla et al. 1990, Bonan 1992). For example, a shift from tundra to boreal forest should reduce winter albedo and provide a positive feedback to regional warming (Bonan 1992), and a shift from boreal forest to grassland might reduce evapotranspiration sufficiently to cause a regional decline in precipitation (Shukla et al. 1990).

Our results suggest that the *pattern* of climatic change has at least as much effect on the rate of forest advance into tundra as does the *rate* of change, because extremely warm periods are required for tree establishment and once trees are established they can survive and grow slowly by vegetative reproduction during cold episodes. This pattern of episodic growth is typical of tree-line individuals and has been useful in reconstructing climate chronologies from tree rings (Payette et al. 1989). The frequency of extremely warm years most strongly governs tree-line advance in both our model and the paleorecord. Thus, thresholds and nonlinearities in temperature response to climatic change should be expected (Pastor and Post 1993), making equilibrium modeling unsuitable for predicting transients in vegetation change.

The switch from tundra to boreal forest in the model was surprisingly insensitive to changes in precipitation (scenarios 9 and 10), given the sensitivity of fire probability to precipitation. In other scenarios climate was altered to maintain the currently observed relationship between temperature and precipitation. The relatively small impact of altered precipitation in causing a vegetation shift from tundra to forest reflects the temperature thresholds for seed production and seedling establishment (Zasada et al. 1992) and the feedbacks of tree establishment and growth on fuel load and fire probability (Wein 1976). Thus, an improvement in ability of GCMs to predict future temperature variability may be more important than predicting precipitation in estimating future rates of ecosystem change at tree line.

The time constant of climatic oscillation strongly influenced model output. When rapid climatic oscillations prevented trees from maturing, time lags were longer and there was less vegetation change than with slower oscillations. Thus, knowing the probability of extremely warm years within a short (< 90 yr) climatic cycle is more important than accounting for 10-yr cycles in fire frequency (Fox 1978, Sinclair et al. 1993) in modeling ecosystem shifts.

Land use scenarios

Our results suggest that fire suppression programs affect the rate of forest advance into tundra just as much as climatic warming and must be included in any scenario that estimates the impact of changing boreal/tundra vegetation on global energy balance (Bonan et al. 1992) or carbon storage (Prentice and Fung 1990). Our modeling results and those of Marsden (1983) are consistent with the pollen record in indicating that recent fire suppression has major effects on forest dynamics (Clark 1988). Our results also suggest critical interactions and thresholds among management scenarios. Logging has much greater effect on forest composition when probability of logging a conifer stand exceeds 50%. However, the same vegetation composition can be achieved with higher logging probability combined with fire suppression or with control of moose predators in the absence of fire suppression. If logging or high moose populations cause long-term degradation of soil nutrients (Pastor et al. 1993), these management practices may not be as sustainable as our model suggests. If regeneration and internal stand dynamics are strongly modified by management, as with forest planting, patch dynamics models (Pastor and Post 1986) could be used to develop new rules for switching among frames. Thus, a combination of patch dynamics models and our model of ecosystem change might provide greatest insight into long-term sustainability of management practices.

The modeling paradigm and future model development

The present model provides an overview of the major types of vegetation changes that might occur in boreal ecosystems in the coming decades to centuries in response to various scenarios of climatic change. The modeling paradigm (frame-based modeling and the use of both qualitative and quantitative variables) helps to focus on this objective and facilitates modeling at a level of resolution appropriate to predictions of regional patterns of vegetation change. We suggest that this modeling approach also facilitates the description of the model and communication of its major assumptions. More detailed ecological considerations contributed to the model, not as an explicit part of the model structure, but rather as an explanation for modeling relationships at a grosser level of resolution (Neilson et al. 1992). For example, the temperature effect on the increment in conifer canopy area in tundra incorporated direct temperature effects on seed production, seedling establishment, and growth as well as indirect effects such as the melting of permafrost, soil aeration, and nutrient supply. The temperature responses of each of these separate variables and their effects on rate of conifer canopy expansion are so poorly known that inclusion of each process separately would not have increased our predictive power and might have complicated the interpretation of results. Where patterns of vegetation change are driven primarily by internal dynamics, these internal controls must be incorporated explicitly into the models (Pastor and Post 1986, 1993). By contrast, our model used very simple internal dynamics that abstracted the broad ecosystem response to climatic driving variables (Pastor and Post 1986, Reynolds et al. 1993), allowing us to explore other factors such as climatic effects on disturbance that have not been evaluated previously.

Although ecosystem models are difficult or impossible to validate, the patterns generated by our model are consistent with naturally observed patterns. These include the equilibrium relationship of vegetation to climate and the similarity of predicted pattern and time lag of vegetation change with patterns observed in the pollen record.

Some of the major weaknesses in our model—inability to predict seed input and propagation of disturbances such as fire and insect outbreaks—can be remedied by making the model geographically explicit (Noble 1993). Processes that might be relatively unimportant in the present model could well assume importance when we make it geographically explicit. For example, the dry grassland ecosystem does not play a significant role in this model: frequent fires quickly switch the system back to deciduous forest. However, in a geographically explicit model these fires are likely to spread into neighboring forests, possibly leading (under warm, dry conditions) to more extensive grasslands (Marsden 1983, Antonovski et al. 1992). A geographically explicit model will also enable us to incorporate vegetation effects on climate through changes in albedo (a function of tree cover and forest type), evapotranspiration, and carbon storage (Neilson 1993*b*, Smith and Shugart 1993).

The use of a simple frame-based model with qualitative variables has enabled us to incorporate a broad body of information and experience from essentially static "pictures" along gradients (such as climate gradients) into a plausible dynamic model. We suggest that this modeling approach will be particularly valuable in coupling terrestrial models with atmospheric models of climatic change because (1) the dynamics of vegetation change on time scales of decades to centuries are critical to biosphere–atmosphere interactions and (2) the coarse level at which we have represented vegetation is appropriate for our current level of understanding of the processes that couple land and atmosphere. By modeling at a relatively coarse level of resolution, we can take a more comprehensive view of processes affecting vegetation change and can explore the interaction of direct climatic effects on regeneration and ecosystem processes, indirect climatic effects on disturbance regime, and plausible changes in land management. Frame-based models also provide a skeleton that can be fleshed out to address questions relating to the dynamics within ecosystems. Questions of changes in species composition or changes in carbon storage within an ecosystem type require a more detailed modeling approach, incorporating individual species and their effects on ecosystem processes (Pastor and Post 1988). We suggest that simple frame-based models provide a structure that can easily incorporate more detail when needed and that a combination of frame-based and patch dynamic modeling will become increasingly necessary as our knowledge base improves.

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APPENDIX

MODEL DESCRIPTION

The model time step is 10 yr. The inputs to the model are initial ecosystem type (frame), climate (temperature and precipitation, which are allowed to change over the simulation according to a defined climate change scenario), number of neighboring forest patches (a constant), and management scenario: probability of logging deciduous and evergreen forest, fire suppression policy (expressed as probability that a climatically determined fire will be suppressed), and predator control (probability of high moose herbivory). Unless otherwise stated, a model always starts in the tundra frame with a tundra climate and a tree canopy class of 1 (<7% tree canopy). Each time step, regardless of frame, begins by determining summer temperature and rainfall from the designated climate, using a random-number generator and the probability distribution of temperature and precipitation classes characteristic of that climate (Table 1). For simulations of gradual climatic change, we gradually change the probability of encountering a given climate, then determine the actual climate according to the probabilities in Table 1, thus giving a smooth transition in climate. Effective rainfall index is computed from rainfall and temperature as in Table A1.

At the beginning of each time step, only one frame is active. The model makes the calculations and decisions for that frame. If a frame switch occurs, the model activates a new frame at the next time step. Each subsection, following, is a description for each frame of the calculations and decisions made during a time step when that frame is operational.

Tundra frame

1) Increase the time since the last fire by 10 yr.

2) If there was a fire in the previous decade and if the effective rainfall index was 1 in both the previous and current decade, there is a 0.75 chance of switching to the grassland frame. If the switch to grassland occurs, the rest of these calculations are aborted.

3) Generate a seed input index from the number of forested neighbor patches and the current tree canopy class as in Table A2. (If there was a severe insect outbreak the previous decade, use the previous seed index.)

4) Increment tree canopy as a function of temperature and the seed index as in Table A3.

5) The probability of a severe insect outbreak depends on the tree canopy class and the effective rainfall index and is obtained by multiplying the value in Table A4 by 2.5 (see *Methods: Model calibration*); determine whether an outbreak occurs.

6) If a severe insect outbreak occurs, 0.5 is deducted from the tree canopy class.

7) The probability of a fire is determined from the fire probability in boreal forest as a function of the effective rainfall index (see *Methods: Ecosystem types: conifer forest*). This boreal fire probability is then multiplied by a factor that depends on the time since last fire and the tree canopy class as in Table A5. Finally, fire probability is multiplied by 0.4 (see *Methods: Model calibration*). Determine whether a fire occurs.

8) If there is a fire, reduce the tree canopy to canopy class 1.0 and set the time since last fire to 0.

9) If the tree canopy class is >3, switch to the conifer-forest frame; otherwise stay in the tundra frame.

Conifer-forest frame

1) The "limbo indicator" is normally =0, but under certain circumstances (conditions too cold or dry for trees to establish; see step 4 below) it can be 1 or 2. If it is 1, and the summer temperature class is <3, switch to the tundra frame; otherwise switch to the deciduous-forest frame. If the limbo indicator is 2 and the effective rainfall index is 1, then switch to the grassland frame; otherwise switch to the deciduous-forest frame.

2) If the limbo indicator is 0, the probability of a fire is a function of the effective rainfall index; this fire probability is multiplied by 0.7 (see *Methods: Model calibration*), unless this is the first decade since a switch from the deciduous-forest frame, in which case the multiplier is 0.15. Determine whether a fire occurs.

3) If no fire occurs, ask whether the forest has been logged (clearcut). The probability of logging is a specified model input.

4) After a fire or logging, there is an immediate switch to the deciduous-forest frame if the temperature class is >1, and the effective rainfall index is >1. If the temperature class is 1, set the limbo indicator to 1; otherwise limbo is 0. If the temperature class is >1, and the effective rainfall index is 1, set the limbo indicator to 2 (with probability 0.75); otherwise switch directly to the deciduous-forest frame.

5) In the absence of fire or logging, stay in the conifer frame.

Deciduous-forest frame

1) If the temperature class is 1, add 2 to the variable "stunt" (which is set at 0 whenever one first enters this frame

TABLE A1. Effective rainfall index.

Summer temperature class†	Summer rainfall class‡ 1	2	3	4
1	3	4	4	4
2	2	3	4	4
3	1	2	3	4
4	1	1	2	3

† Class 1, <10°; Class 2, 10°–13°; Class 3, 13°–16°; Class 4, >16°.

‡ Class 1, <80 mm rainfall; Class 2, 80–140 mm rainfall; Class 3, 140–200 mm rainfall; Class 4, >200 mm rainfall.

TABLE A2. Index of potential seed input.

	Neighboring forest patches (No.)		
Canopy class†	0	1	>1
1	1	2	3
2	2	3	4
3	4	4	4

† Class 1, 0–7% cover; Class 2, 7–21% cover; Class 3, 21–50% cover.

TABLE A3. Growth of conifer canopy percentage cover (proportional increase/10 yr).

Summer temperature class†	Index of potential seed input 1	2	3	4
1	0	0	0	0
2	0	0.04	0.08	0.12
3	0.25	0.35	0.45	0.55
4	0.25	0.35	0.45	0.55

† Class 1, <10°; Class 2, 10°–13°; Class 3, 13°–16°; Class 4, >16°.

TABLE A4. Probability of severe insect outbreak in tundra.

	Effective rainfall index			
Canopy class	1	2	3	4
1	0	0	0	0
2 or 3	0.20	0.04	0.02	0.02

TABLE A5. Fire probability multipliers for tundra.

Time since last fire (yr)	Canopy class 1	2	3
<40	0.1	0.4	0.6
>40	0.3	0.5	0.8

TABLE A6. Boreal forest fire probability trend.

	Effective rainfall index 1	2	3	4
Fire probability	0.6	0.4	0.2	0.1

TABLE A7. Probability that broad-leafed trees will escape from heavy moose herbivory.

Summer temperature class†	Summer rainfall class‡ 1	2	3	4
1	0	0	0	0
2	0	0	0	0
3	0	0.3	0.7	0.9
4	0	0.5	0.8	1.0

† Class 1, <10°; Class 2, 10°–13°; Class 3, 13°–16°; Class 4, >16°.

‡ Class 1, <80 mm rainfall; Class 2, 80–140 mm rainfall; Class 3, 140–200 mm rainfall; Class 4, >200 mm rainfall.

TABLE A8. Probability of switching to broad-leaved forest from grassland after fire (when there are more than one neighboring forest patches).

Summer temperature class†	Summer rainfall class ‡ 1	2	3	4
1	0	0	0	0
2	0	0.4	0.7	0.7
3	0	0.6	1.0	1.0
4	0	0.3	0.9	1.0

† Class 1, <10°; Class 2, 10°–13°; Class 3, 13°–16°; Class 4, >16°.

‡ Class 1, <80 mm rainfall; Class 2, 80–140 mm rainfall; Class 3, 140–200 mm rainfall; Class 4, >200 mm rainfall.

or reenters it with a new cohort of broad-leaved saplings). If the temperature class is 2, add 1 to stunt.

2) As in the previous frame, the limbo indicator is normally 0. However, if it is 1, and the current temperature class is <3, switch to the tundra frame. If the temperature class is 3 or 4, begin a new cohort of broad-leaved saplings. If the limbo indicator is 2, and the effective rainfall index is 1, switch to the grassland frame; otherwise begin a new cohort of broad-leaved saplings. If a frame switch occurs at this step, ignore the remaining steps.

3) If there was a fire two decades before, and if the moose population was high in the last decade (a model input), then the probability of staying in the deciduous forest frame (i.e., the probability that broad-leaved saplings will escape from heavy moose herbivory) is a function of summer temperature and rainfall as in Table A7. If the broad-leaved saplings do not escape, switch to the conifer-forest frame, and the following steps are aborted.

4) The boreal fire probability (see *Methods: Ecosystem types: conifer forest*) is multiplied by 0.15 (see *Methods: Model calibration*). Determine whether a fire occurs.

5) If no fire occurs, ask whether the forest has been logged (clearcut), as specified in model input.

6) After either fire or logging, if the temperature is 1, set the limbo indicator to 1. If the temperature is >1 but the effective rainfall index is =1, set the limbo indicator to 2. If both temperature and effective rainfall index are >1, start a new cohort of broad-leaved saplings.

7) If there is no fire or logging, add 10 yr to the age of the broad-leaved trees. A switch to the conifer-forest frame will then occur (1) with probability 0.2 if the broad-leaved trees are >80 yr old; (2) with probability 0.6 if they are >90 yr old; (3) definitely if they are >100 yr old; (4) with probability 0.5 if the stunt factor is between 3 and 4; and (5) definitely if the stunt factor is >4. If no switch occurs, stay in the deciduous frame for the next time step.

Grassland frame

1) If rainfall was >1 and the temperature was =1 in the previous decade as well as this decade, switch to the tundra frame and abort the following steps.

2) Otherwise, determine the probability of a fire by multiplying the probability of a boreal fire (*Appendix: Conifer-forest frame*) by 2.5 if the herbivore population is low (i.e., high fuel load), or by 0.8 if the herbivore population is high. Decide whether or not a fire occurs.

3) If there is a fire, the probability of switching to the deciduous forest frame is a function of summer temperature and rainfall as in Table A8. This probability is multiplied by 0.6 if there are no neighboring forest patches. If no switch to the deciduous frame occurs, stay in the grassland frame.