

THE EFFECTS OF CLIMATE CHANGE ON LANDSCAPE DIVERSITY: AN EXAMPLE IN ONTARIO FORESTS

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Abstract. The predicted increase in climate warming will have profound impacts on forest ecosystems and landscapes in Canada because of increased temperature, and altered disturbance regimes. Climate change is predicted to be variable within Canada, and to cause considerable weather variability among years. Under a $2 \times \text{CO}_2$ scenario, fire weather index (FWI) is predicted to rise over much of Ontario by 1.5 to 2 times. FWI may actually fall slightly, compared to current values, in central eastern Ontario (Abitibi), but for central-south Ontario it is expected to rise sharply by as much as 5 times current values. We predict that the combination of temperature rise and greater than average fire occurrence will result in a shrinkage of area covered by boreal forest towards the north and east; that some form of Great Lakes forest type will occupy most of central Ontario following the 5 C isotherm north; that pyrophilic species will become most common, especially jack pine and aspen; that patch sizes will initially decrease then expand resulting in considerable homogenization of forest landscapes; that there will be little 'old-growth' forest; and that landscape disequilibrium will be enhanced. If climate change occurs as rapidly as is predicted, then some species particularly those with heavy seeds may not be able to respond to the rapid changes and local extinctions are expected. Anthropogenically-altered species compositions in current forests, coupled with fire suppression over the past 50 years, may lead to forest landscapes that are different than were seen in the Holocene period, as described by paleoecological reconstructions. In particular, forests dominated by white pine in the south and black spruce in the middle north may not be common. Wildlife species that respond at the landscape level, i.e., those with body sizes >1 kg, will be most affected by changes in landscape structure. In particular we expect moose and caribou populations to decline significantly, while white-tailed deer will likely become abundant across Ontario and Quebec.

1. Introduction

In Canada, a significant warming trend has occurred (with variation) since the end of the Little Ice Age (~1850) and there is evidence that the rate of warming has accelerated in recent years (Environment Canada, 1992). In this paper, we take as a given that global warming will occur and base most of our arguments on a $2 \times \text{CO}_2$ scenario; the potential extent, timing, and rate of global warming are left for others to debate. Landscape in forests is the matrix in which forest ecosystems exist in time and space, and they are scaled in hundreds of square kilometres. We refer to forest ecosystems synonymously as forest patches (or stands) in the sense of various forest ecosystem classifications that define forest types using ordinations on gradients of soil moisture and richness (e.g., Sims *et al.*, 1989; Meades and Moores, 1989). Landscapes are comprised of many forest ecosystems.

In Ontario, there are three major forest types: boreal, Great Lakes-St. Lawrence, and Carolinian (Rowe, 1972); here we discuss possible changes in the first two types as a result of climate change. Boreal and Great Lakes forests are defined by climate regimes and the resultant mix of dominant tree species that can tolerate certain combinations of temperature, precipitation, soil type, and disturbance regime. The transition zone between the two forest types loosely corresponds to the 5°C mean annual isotherm in eastern Ontario and Quebec, and to the 4°C isotherm in western Ontario. Great Lakes forests are characterized by a longer growing season and more precipitation than the drier, colder boreal forests. Fire is the major natural disturbance of both forest types, but the pattern of fires differs considerably for each. Fires in boreal forests are often large stand-destructive crown fires that may burn 1000's of hectares. Small fires that burn under 100 ha are common but the largest fires primarily are responsible for landscape structure, with less than 5% of the fires responsible for more than 95% of the area burned (Van Wagner, 1978). Fires in Great Lakes forests are most often surface fires that do not generate sufficient heat to destroy large trees, and rarely do they flare up into the canopy. These latter fires generate small openings in the forest, and kill young shade-tolerant trees and shrubs, thereby altering succession, beneath the mature forest canopy. The rolling topography of much of the Great Lakes forest areas affects fire size by restricting fire trajectories. In both types of fire (surface and crown), the intensity is affected by the amount of fuel available and by rate of spread. These two factors are controlled by time since last fire (i.e., accumulation of fuels), weather, logging operations, disease and insect infestations, age of the forest, forest type (i.e., species mix), and ultimately by climate.

Our purpose here is to examine factors that control landscape diversity and to apply our understanding of forest processes to possible changes that will occur at the landscape level as a result of climate change. The paper represents a summary of work by many authors including our own modelling efforts.

2. Categorization of Forest Landscapes

Some theory has been developed to characterize 'patch dynamics' (Levin and Payne, 1974; Baker, 1992) as an analogue to population dynamics. Meaningful measures of landscape variables include: patch size, age, shape, type, diversity, and number of patches. Patch shape is often measured as fractal dimension, and by a ratio of edge to interior. Amount of edge is also an often-used criterion for describing a landscape, particularly when discussing the role of patterns in structuring animal communities. Landscapes have two scales, one in space and the other in time. Measurement of these variables and their spatio-temporal dynamics has been greatly simplified by GIS.

2.1. THEORIES OF LANDSCAPE DIVERSITY

Landscapes must be defined in terms of spatial and temporal scales (Allen and Hoekstra, 1992). At smaller scales, human and natural disturbances control pattern, while at larger (and longer time) scales, topography and climate are the driving forces. Climate change can thus affect both scales through local natural disturbances and their accumulation in time and space. Predictability of landscape pattern becomes very much a question of the scale of the landscape considered. Most of the prediction (e.g., for forest management units of 5000 km²) that we would like to do involves middle-number systems that are inherently non-linear, with non-constant constraints. As a result, prediction is impossible (Allen and Hoekstra, 1992; Holling, 1992a) (although we will offer some best guesses in this paper). However, at a broader scale, where topography and climate ultimately control the systems (10's of thousands of square kilometres), prediction becomes more plausible.

Many authors have suggested that landscapes exist in some form of equilibrium and that forest ecosystems are predictable and their re-assembly is possible following disturbance. In fact, these ideals form the basis for 'sustainable development'. There are three main theories of landscape equilibrium.

- 1) The "steady-state shifting mosaic" concept (Bormann and Likens, 1979) suggests that on a large enough area, all ecosystems always exist in their various successional forms, even though various places on the landscape change with disturbances. This concept is highly unlikely to apply to landscapes driven by large-scale disturbances like Ontario forests, with their non-homogeneous nature, and several attempts to validate this hypothesis have failed (Romme, 1982; Baker, 1989).
- 2) "Stationary landscape equilibrium with stochastic perturbation" (Loucks, 1970) suggests that stability exists on landscapes as a result of predictable disturbance frequency in time. Data from most forest types suggest however that history and serendipity have as much or more to do with ecosystem development than predictable disturbance regimes.
- 3) Suffling (1991, 1995), using data from Ontario, has advanced the argument that landscapes are in constant disequilibrium; a view shared by Baker (1995) based on considerable modelling of northern Minnesota forests.

Under the latter theory, landscapes are constantly 'catching up' to disturbance regimes that change at two temporal scales, one of long-term on the order of several hundred years (e.g., a warming trend since 1850), and a shorter decadal variation, such as the current general warming trend, or the significant cooling period from 1940 to 1970 (Layser, 1980). The spatial organization of forest ecosystems may be dynamic in response to long and short-term climate fluctuation.

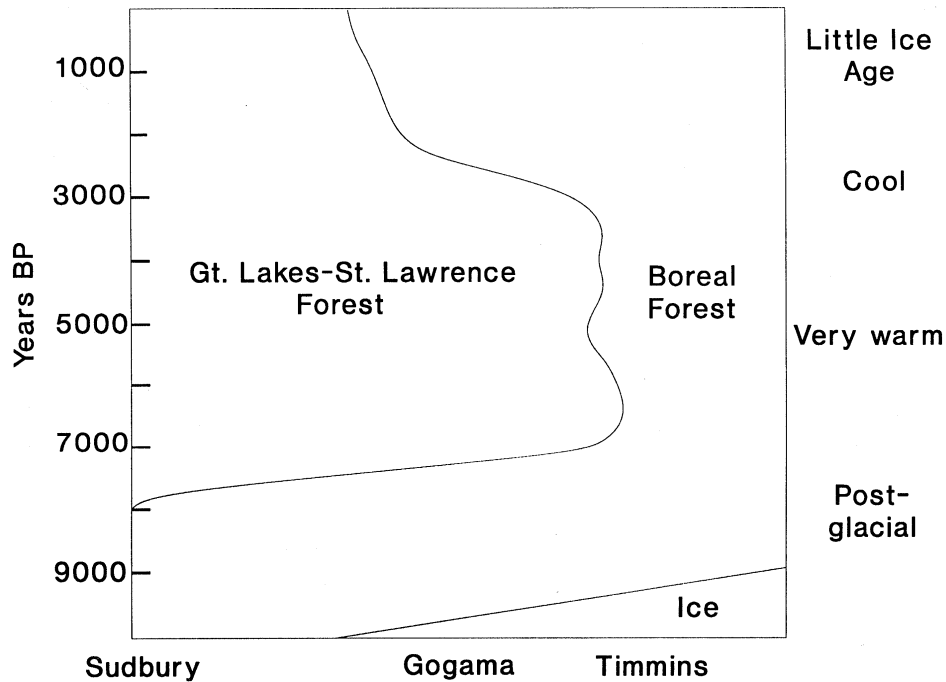


Figure 1. Paleocological forest record for central Ontario showing change in forest types in time north to south. (From: Liu, 1990).

2.2. WHAT CAN WE LEARN ABOUT FOREST LANDSCAPES BASED ON EVIDENCE FROM THE PAST?

There are several excellent paleoecological studies of forests in Ontario and Quebec and northern Minnesota showing that forest types and landscape structure have changed dramatically with the gradual warming since the last Holocene glaciation (Liu, 1990; Payette, 1993; Graumlich and Davis, 1993). The data most relevant to this paper are from Liu (1990) who showed that the transition zone between Great Lakes and boreal forest types migrated steadily north from 10,000 BP until about 7000 BP (Figure 1). An extremely warm period (hypsithermal) from 7000 to 3000 years BP resulted in Great Lakes forest types prevailing as far north as Timmins before falling back to the current line south of Gogama about 2500 years ago. Jacobson and Dieffenbacher-Krall (1995) showed a marked contraction in the distribution of white pine (*Pinus strobus*), a major tree species of the Great Lakes forest, with the 0.5 C cooling trend and associated reduced incidence of fire, over the past 1000 to 1500 years. Charcoal and pollen records correlate fire maxima with warmer, drier periods, and fire minima with cooler, wetter periods (Clark, 1988), and Bergeron and Archambault (1993) found cooler but drier periods also resulted

in increased fires, implicating the long-term role of climate, particularly moisture levels, in forest change.

Several important distinctions exist between paleoecologically-inferred forest change and current climate-induced forest change. First, past changes in climate occurred slowly over centuries, and because forests responded in 1 to 2 generations (Baker, 1995), slow migration of forest systems (tree species) at the rate of 30–40 km per century was possible. Current projections of global warming indicate that climate change will occur much more rapidly than in the past, suggesting that forest response, as reconstructed from pollen records, may not be applicable to future forests, except in the broadest sense of forest change (Solomon, 1992). In other words, rate of climate change may outstrip the rate at which many forest trees can respond, resulting in highly altered forest ecosystems and landscape patch dynamics. These altered ecosystems will likely represent new assemblages that do not have past analogues. Other authors have also commented on the possibility of lags in vegetation response to climate change (Davis, 1989; Delcourt and Delcourt, 1987).

Second, fire suppression throughout the latter half of the past century has resulted in fuel loads in many forests that are three times normal (Clark, 1990), suggesting that future fires may be much larger and hotter than they otherwise would be. Such systems are ‘over-connected’ (Holling, 1992a) and are ultimately moved to another more stable state by disturbance. Recent larger than normal fires in Yellowstone Park (1988) and in much of boreal Canada (1995) may be taken as a clear indication of these artificially-altered fuel regimes.

Third, widespread forest harvesting has altered age-class structure, patch size, and vegetation composition of forests at the landscape level. Most modelling of climate change assumes that particular forest types and age classes are dominant, and generally they are not. For example, the models of Pastor and Post (1988) and Overpeck *et al.* (1990) assume the prevalence of spruce (*Picea* spp.) and balsam fir (*Abies balsamea*) in boreal forest systems, when in fact mixed forest of poplar (*Populus* spp.)-white birch (*Betula papyrifera*)-balsam fir is the dominant type over large areas as a result of logging. Altered competitive dynamics among plants may exist as a result of logging and fire suppression, and because of recent invasions by non-endemic diseases and pests such as white pine blister rust (*Cronartium ribicola*), gypsy moth (*Lymantria dispar*), and poplar leaf rust (*Malampsora larici-populina*).

Therefore, the past teaches us that forests respond to climate, and that the role of climate is of ultimate importance in determining landscape and ecosystem structure. However, the rate of global warming limits the specific applicability of past information to current predictive capability, and changes such as the existence of serious forest pests, that did not occur even 1000 years ago, may affect future tree populations.

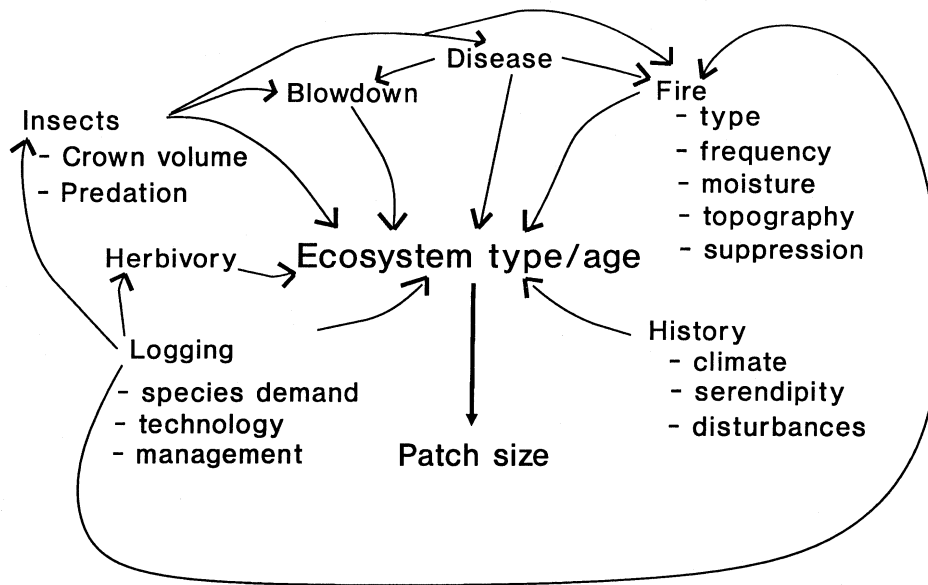


Figure 2. Disturbance model for forest ecosystems, showing interrelationships among disturbance factors.

2.3. FACTORS THAT GOVERN LANDSCAPE PATTERN

A broad scale pattern is imposed on landscapes by topography and climate (Allen and Hoekstra, 1992). Superimposed are four main factors proximately affecting landscape pattern: frequency of disturbance, size of the disturbance, rate of recovery from the disturbance, and size of the landscape (Turner *et al.*, 1995). These factors are, in turn, influenced at mesoscales by human intervention and site-level processes. The importance of history at the site (i.e., the current [or past] species mix in the system) and stochasticity of the disturbance regime (e.g., insect infestation then fire, or several small fires because of high moisture in a given year, or a conflagration during an extremely dry summer without any prior insect outbreak) are also important in determining ultimate direction of an ecosystem and a landscape. We have tried to illustrate the complexity of disturbance in forest systems by showing the connectedness among the processes and by listing several key factors that relate to intensity of each form of disturbance (Figure 2). To further illustrate, consider the single disturbance component called 'insects'. The complexity associated with tree mortality from insect infestation comes from a variety of sources: the species of insect, the amount of genetic variation and adaptability to current weather in the insect population, predation levels by birds on the insects (that is in turn influenced by deforestation in the tropics), the leaf volume (influenced by species mix and age of the stand [Holling 1992b]), whether or not insecticides are or have been applied, and weather effects on the survivorship of insect cohorts.

The resultant effect of an infestation on the landscape then is affected by all of these factors. Assuming that a species, such as spruce budworm (*Choristoneura fumiferana*), 'escapes' and causes a large die-off of conifers, the forest trajectory will then be determined again by stochasticity. Should the dead trees not be burned during a relatively short period of time, the accumulated moisture in fallen dead wood will likely prevent fire from occurring and both the ecosystem trajectory and landscape will be different than if a fire had occurred (Stocks 1987).

How tree species respond to disturbance is dictated by their autecology. Certain tree species are adapted to fire as a means of propagation; these include all of the pines, black spruce (*Picea mariana*), the poplars, and to a lesser extent white birch. Other species tend to seed under an established forest canopy and develop in the shaded conditions, including most of the Great Lakes forest hardwoods (maples [*Acer* spp.], yellow birch [*Betula lutea*], beech [*Fagus grandifolia*], and oaks [*Quercus* spp.]), balsam fir, and white spruce (*Picea glauca*). Species with large-seeds such as beech, hickories (*Carya* spp.), hornbeams, and oaks do not 'migrate' as quickly as species with lighter seeds or those whose seeds may be dispersed by animals. Finally, many species cannot tolerate exceptional cold and so are confined to more southern areas. These are all factors that need to be considered when attempting to predict what the effects of global warming may be, with associated increased insects infestation and fire occurrence.

The complex inter-relationships between nature and human intervention have altered many ecosystems in North America. An interesting example is provided by the role that ungulates now play in altering successional pathways and climax forest types. In Newfoundland, moose (*Alces alces*) were introduced in the early 1900's. Elevated populations of these animals, coupled with fire suppression has resulted in several new forest ecosystems in areas where logging has occurred (Thompson and Mallik, 1989; Thompson and Curran, 1993). In Ontario and the upper eastern United States, white-tailed deer (*Odocoileus virginianus*) populations are at historic highs as a result of increased habitat availability, increased food from agriculture, the elimination of natural predators, strict hunting regulations, and winter feeding programmes. In all areas where deer herbivory has been studied, the elimination of plant species (such as hemlock [*Tsuga canadensis*]) and altered forest succession has occurred (Hough, 1965; Frelich and Lorimer, 1985; Alverson *et al.*, 1988). These are examples of site-level effects that have influenced landscape patterns, and illustrate the complex nature of forest ecosystems in settled areas.

A final factor that affects landscape pattern is altered availability of seed source as a result of past logging practices over extensive areas. Three species that had dominated large forest areas in the past have been particularly affected by logging: black spruce, white pine, and red pine (*Pinus resinosa*). Data from Aird (1985) and Ont. Min. Nat. Res. (1995) clearly show a 75% decline in red and white pine harvest, corresponding to a similar reduction in available forests dominated by these two species. Similarly, Baker *et al.* (1996) modelled a decline in the amount of black spruce in Ontario of about 80% over the next 50 years from an already

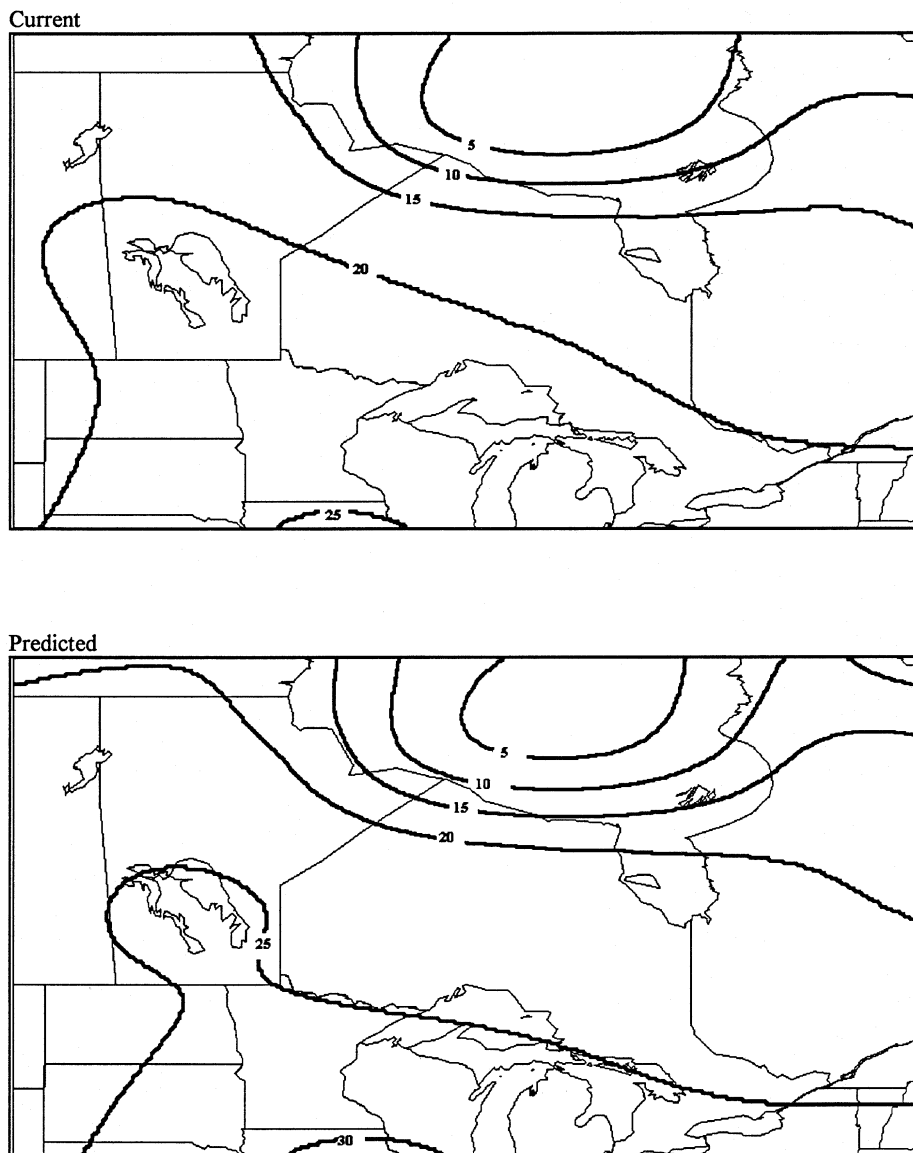


Figure 3. Mean July temperature ($^{\circ}\text{C}$).

substantially depleted forest (Hearnden *et al.*, 1992). The lack of seed source, especially coupled with altered disturbance regimes under global warming may further reduce the prominence of these species, thereby altering the complexity of forest patches and producing a more homogenous landscape than might otherwise occur.

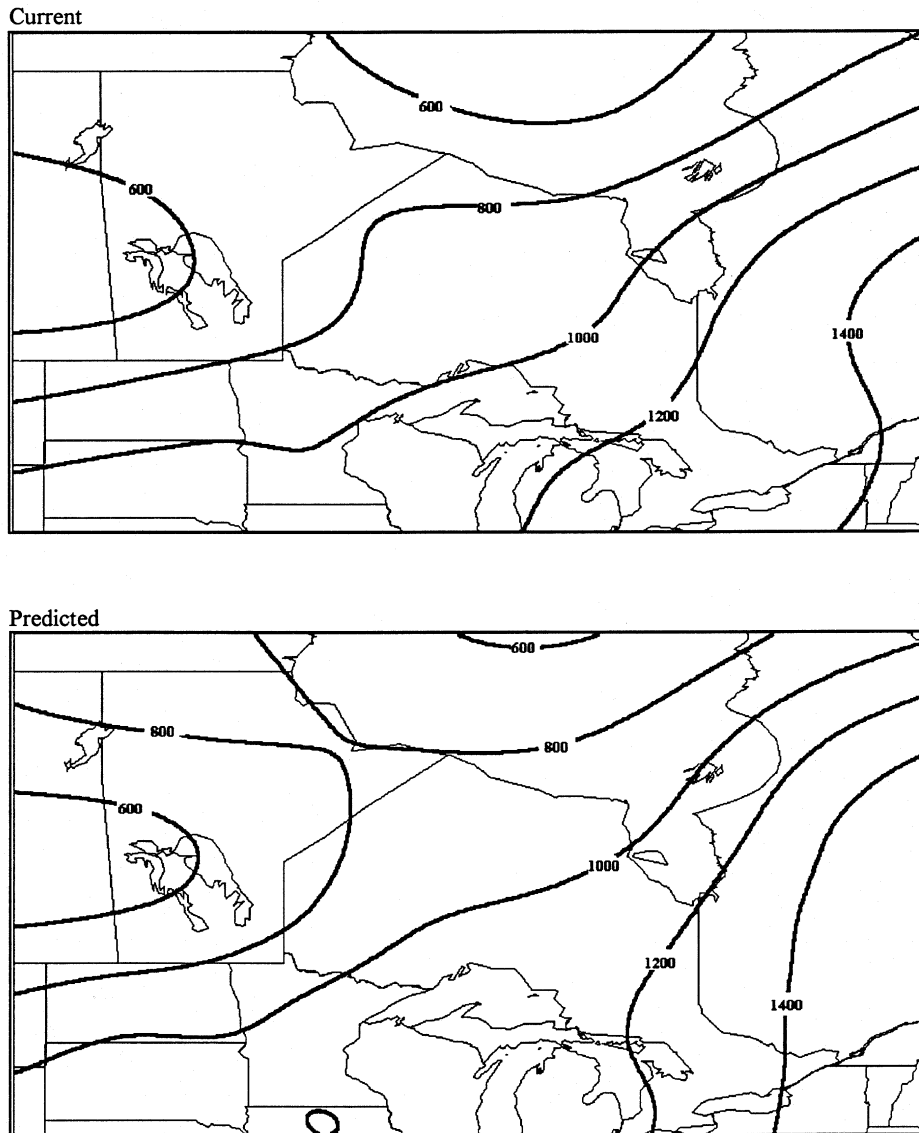


Figure 4. Mean annual precipitation (mm).

2.4. WHAT FACTORS THAT DRIVE LANDSCAPE PATTERN WILL BE AFFECTED BY CLIMATE CHANGE?

Using a $2 \times \text{CO}_2$ climate change scenario* (Figures 3 and 4), there will be two broad effects on forest landscapes: first, warming will affect species distributions as

* This study used the Canadian Global Circulation Model that has a transform grid spacing of 3.75 by 3.75° with full diurnal and annual cycles (Boer *et al.*, 1992; McFarlane *et al.*, 1992).

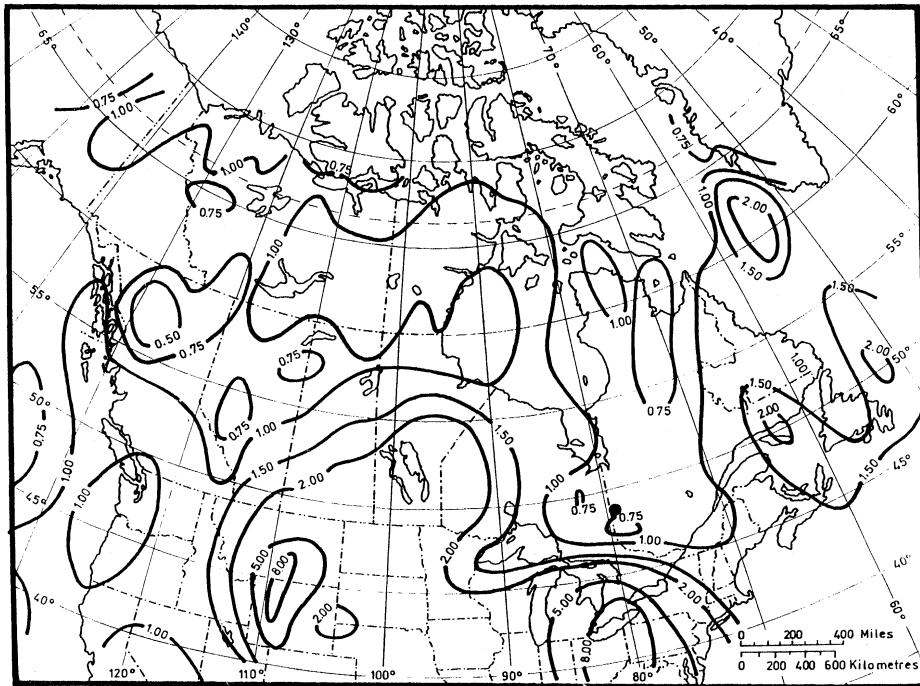


Figure 5. FWI ratio ($2 \times \text{CO}_2/1 \times \text{CO}_2$). (From: Bergeron and Flannigan, 1995.)

a result of change in growing season for plants, and habitat change and altered snow depth for animals; and second, changes to disturbance regimes will alter ecosystem distribution, and possibly ecosystem type, across landscapes. In particular, climate change will have an effect on the fire regime, and in turn on the type and extent of forests in Ontario, and in Canada.

Considerable modelling of fire regimes and forest change under global warming has been done in Minnesota (Clark, 1988, 1990; Baker, 1995), in boreal systems (Pastor and Post, 1988; Overpeck *et al.*, 1990; Suffling, 1991, 1995), in eastern Canada (Flannigan and Woodward, 1994), and generally for Canada (Flannigan and Van Wagner, 1991; Wotton and Flannigan, 1993). The general conclusion of all of these models is that where the fire weather index (FWI) (Van Wagner, 1987) rises, fire interval will be reduced and fire size will increase. Flannigan and Van Wagner (1991) predicted an approximate increase of 40–46% more forest will burn annually at $2 \times \text{CO}_2$ than under current climate, in an average fire season that will be 22% longer than at present (Wotton and Flannigan, 1993). Bergeron and Flannigan (1995) have predicted that changes in the FWI will not be equal across Canada or even within Ontario (Figure 5). Fire severity will change, but will actually decline in some areas of western Quebec and eastern Ontario, but it may double in western areas of the province. As examples, FWI in the Ottawa Valley

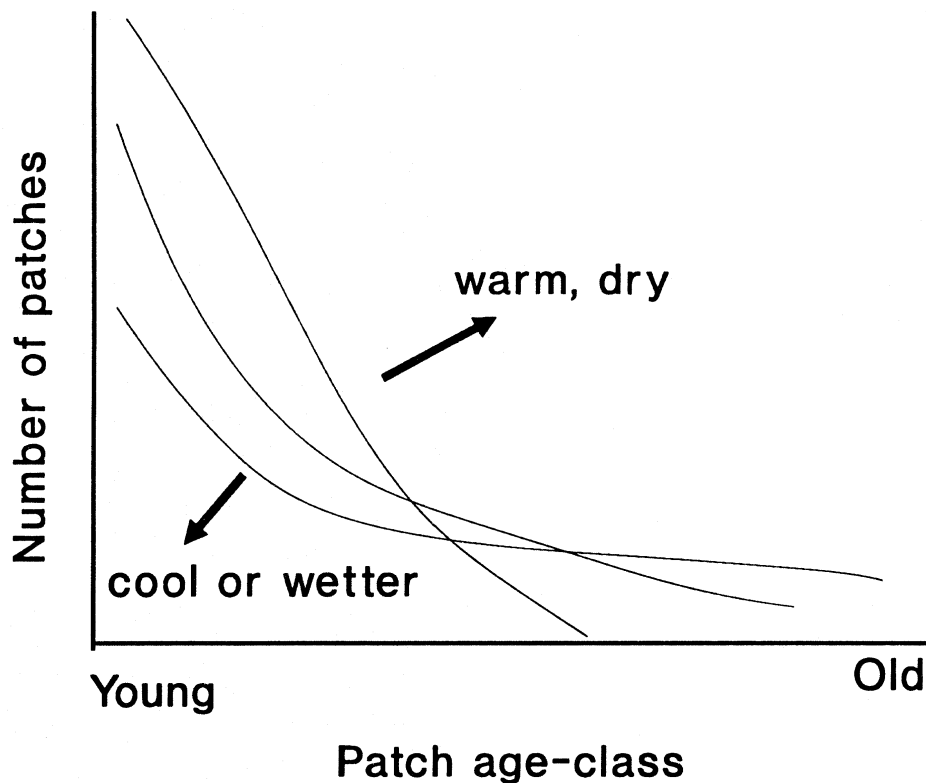


Figure 6. Patch age-class distribution (Van Wagner, 1978) and the predicted effects of climate change.

and Algonquin Park is predicted to rise from 8.0 to 12.0, while at Atikokan the rise will be considerable, from 11.4 to 22.8. Change in fire regime of much of the eastern boreal forest is predicted to be minimal. Although FWI is predicted to fall or remain the same in much of central-eastern Ontario, mean annual temperature in this area (and across Ontario) is predicted to rise by as much as 5 C (Figure 3). New temperature regimes will enable changes in forest species composition, and considerable change to forest distributions must be expected over most of the province.

3. Predicted Changes in Forest Landscapes as a Result of Climate Change

Fire is the major disturbance factor that influences landscape structure at the mesoscale in Ontario forests. The predicted rise in FWI resulting in shorter fire interval, coupled with temperature change, will produce the following effects on landscape structure (Suffling, 1991; Flannigan and Van Wagner, 1991; Baker, 1995): larger mean patch size, less old growth forest (younger mean forest age), reduced

diversity of patches over much of Ontario (greater forest homogeneity) (except see below), and lower mean shape (defined as area/perimeter). Current patch age distribution in unlogged forests takes a generally negative binomial form (Van Wagner, 1978). A warm dry climate will have the effect of truncating the patch age-class distribution and initially of increasing the number of patches (Figure 6). In the west and central regions of the province where fire frequency is expected to be high, ultimately as more area burns and patches meld together, the number of patches will decline and forests will become younger and more homogeneous. Towards the north and northeast of the province where fire interval may rise slightly, remain the same, or even decline, landscape diversity should increase (Suffling *et al.*, 1988). In this area, the occupation of sites by boreal as well as Great Lakes species will result in a diverse mosaic.

The distribution of certain tree species is controlled directly by fire. For example, the northern extent of the distribution of red pine, juniper (*Juniperus communis*), and to a lesser extent white pine are dictated by the fire regime (Diotte and Bergeron, 1988; Flannigan and Woodward, 1994). Here, these species are found only in isolated pockets or on islands and lake shores because they cannot tolerate the more severe fires of interior boreal forests. Increasing fire frequency will influence the species that can succeed following fire, and with sufficiently frequent fires, forests can become shrublands followed by prairie (Clark, 1990). In boreal areas, we expect jack pine (*Pinus banksiana*) to become a dominant forest type (Flannigan and Wotton, 1994) together with trembling aspen (*Populus tremuloides*), co-occurring in mixed and or in pure stands. Some areas, such as central Ontario, normally have a long rotation time that has been exacerbated by fire suppression (e.g., Temagami where fire free interval has increased 10 fold [Day and Carter, 1990]). These areas may be in continual disequilibrium because climate change will superimpose a new disturbance regime, when the landscape has not yet adjusted to the fire suppression regime coupled with logging (Baker, 1995). Similarly in boreal landscapes, Suffling (1995) argues that a temporal disequilibrium will continue to occur because the rotation time exceeds the development of a new climate regime.

Temperature change alone will result in new forest landscapes. In order to predict landscape structure we must look a level below landscape to predict consequences on species that dominate ecosystems, and then scale up to landscape. Plant species adapted to warmer climates are expected to move north with disturbances and the transition zone between boreal and Great Lakes forest types will shift markedly north (Figure 3). Plant communities are largely structured by competitive processes, and an invasion northwards of more southern species, better adapted to warm climate, will displace boreal species, as has been seen in the past (Liu, 1990). However, these simple processes will be altered (as noted above) by several factors: fire suppression, altered seed sources due to logging, the probability of increased mortality from disease (Overpeck *et al.*, 1990), feedback through increased soil productivity (ie., greater N availability) (Pastor and Post, 1988), and the predicted rapidity of global warming. Predicting outcomes as a result of these influences on

forests is highly speculative, and few modelling efforts have attempted to deal with vegetation types, and human-related changes in vegetation types under climate change scenarios. It is likely that stands of Great Lakes forest existing currently in isolated extralimital pockets, in regions where fire frequency is not expected to rise, will become important as a source of seeds, particularly if warming occurs more rapidly than the rate at which forests can respond.

Climatic variability could result in additional stresses for both plants and animals. Indications are that the future climate may be highly variable, resulting in more extremes of weather including temperature and moisture. Prolonged periods of drought, extreme heat or extreme cold, deep snows, and winter rains could result in reduced vigour and increased mortality of species. This will be particularly important at the northern edges of species' distributions where populations may exist tenuously.

Certainly generalist species, those that tolerate a wide range of conditions and have several means of reproduction, will prevail over those species that have narrow ecological tolerances. For example, poplar species (trembling aspen, large-tooth aspen [*Populus grandidentata*], and balsam poplar [*P. balsamifera*]), species that thrive in disturbed areas and reproduce by suckering after fire will clearly become more prevalent, particularly in central Ontario, where pine has been largely removed. Poplar species have already benefited as a result of forest harvesting (Hearnden *et al.*, 1992; Carleton and MacLellan, 1994), particularly at the expense of white and red pine in Great Lakes forest and of black spruce in boreal regions. The fact that these species are already widespread augers well for continued success in the face of global warming. More frequent large fires in central and western Ontario will reduce the average forest age and favour species that can rapidly invade or reproduce following fire over those that require a canopy under which to develop.

Suffling (1995) proposed a model that assesses forest change under global warming (decreased fire-free interval) in terms of probability of individual tree species propagation. The model predicts that short fire intervals favour jack pine and aspen while longer intervals favour black spruce and shade tolerant species, particularly balsam fir. Under a reduced fire-free interval, spruce/fir-dominated forests were predicted to decline with a northward expansion impeded by highly paludified soils of the Hudson Bay lowlands. Suffling (1995) also predicted that the jack pine- poplar forest type will expand throughout the remaining boreal zone.

Predicting future forest condition is difficult even in systems suspected of being stable. Current forest landscapes have been altered substantially by forest harvesting, application of pesticides, and fire suppression; and if indeed landscapes are in disequilibrium, then prediction except at the broadest level becomes impossible. We believe, based on the current evidence and modelling efforts, that considerable homogenization of the forest landscape will occur under global warming because of the decrease in fire interval and an early increase in fire severity. Pyrophilic species such as jack pine and aspen will increase markedly throughout the boreal forest, reducing forest complexity and structure because of large patch size and

reduced species composition. Great Lakes forests will generally move northwards as a function of temperature, and their characteristics will be largely similar to those of today in areas where fire regimes are expected to be the same or less than today. Areas occupied by extralimital Great Lakes forest communities will become highly important as seed sources from which these forests will expand. In areas where fires have been suppressed, and white and red pine removed by selective logging, aspen forest will become dominant over tolerant hardwoods, simplifying forest systems over much of central Ontario. In western Ontario, continual fires and warming will lead to an aspen parkland condition along the border with Manitoba and western Minnesota, also contributing to the simplified landscapes that we predict for most of Ontario forests. Although we generally expect forest landscape diversity in Ontario to become more homogeneous than currently, there will likely be exceptions in the north and east. In northeast and east-central Ontario, we expect local landscape diversity to increase with a slow invasion of the area by Great Lakes species.

This speculation clearly indicates the need for improved modelling of forest vegetation processes at the landscape level. Such models must explicitly include feedback loops to model insect and disease responses to species and temperature changes, and soil modifications from new moisture and nutrient regimes, altered fire regimes and feedbacks reflecting altered fuel loads with reduced fire intervals, and a reasonable approach to initial landscape and forest age and species mix structure.

4. Consequences on Wildlife of Forest Landscape Change under Global Warming

One of the responses to the 'so what?' question of altered forest landscapes under global warming is how wildlife species will respond. Wildlife species respond to habitats at scales that relate to their body size (Harestad and Bunnell, 1979). Some species by virtue of their large body size will be more affected by change at the landscape scale than other, smaller species (Holling, 1992b). So, changes in patch size and distribution would be expected to have effects on animals that adapted to former patch size and distribution.

Unlike plants that have a restricted dispersal capability, animals can respond numerically very rapidly to changes in habitat and climate. Or, to state the obvious, animal decisions are taken over a time scale of days and months while changes in forest ecosystems take decades. Dispersal capability is log-linearly related to body size (G. Sutherland, UBC, unpubl. data) and most animals with a body size greater than 500 g are capable of moving many kilometres in a short period of time. As climate changes and vegetation ultimately responds, animal distributions across landscapes also change. There are indications that, during the warming trend from 1900–1940 followed by the cooling trend from 1940–1970 (Thomas, 1952; Layser,

1980), animals that respond to landscape pattern changed their ranges during this 70-year period. Fisher (*Martes pennanti*), porcupine *Erethizon dorsatum*), white-tailed deer, caribou (*Rangifer tarandus*), lynx (*Felis lynx*), bobcat (*F. rufus*), gray fox (*Urocyon cinereoargenteus*), and marten (*Martes americana*) were all known to have altered their distributions in Ontario (and elsewhere), probably in response to climate changes (de Vos, 1952; Peterson, 1957, Outram, 1967; Van Zyll de Jong, 1971). Marten disappeared from the Algonquin region of Ontario during the 1940's and where fisher were once common near Chapleau and Wawa, they are now rare. Gray fox were absent from Ontario at the time of confederation but were commonly observed in the 1930's (Outram, 1967). Caribou have vanished from much of their southern range although this is mostly attributed to habitat loss (Bergerud, 1974); climate has never been seriously considered as a factor. These rapid changes may not have been a simple cause and effect between population expansion and climate, because of habitat change through logging, and uncontrolled trapping (and poisoning) of furbearers during the 1930's and 40's. However, there is no reason to expect porcupine to respond to trapping pressure, gray foxes expanded into Ontario during the 1930's, and white-tailed deer distribution in Ontario has changed rapidly through short periods of particularly warm years with minimal snowfall, such as during the period from 1987–1994 (D. Voigt, OMNR pers. comm.). During the early 1900's, white-tailed deer existed as single pan-provincial population from Kenora to Quebec, whereas today they do not occur north of Lake Superior and there are two separated populations (Outram, 1967; Voigt, 1990).

Consequences of global warming for wildlife will be the same as for trees: temperature effects, altered competitive regimes, modified subtle interactions relating to diseases, and habitat change. We suggest that altered forest landscapes, reduced patch diversity, reduced amount of old forest, and the possible reduction in tree species distributions will have considerable consequences for animals that operate at the level of ecosystem and above. Moose and white-tailed deer provide instructive examples. These two species require a mixture of young forest for food (shrubs and forbs) as well as some older forest, particularly dense mature conifers for shelter from snow depth that impedes movements, and in the case of moose, escape from summer heat. Further, deer carry a parasite (*Paralaphostrongylus tenuis*) (a nematode) that is fatal in moose (Anderson and Lancaster, 1974). Currently the zone of overlap between the two species is limited (Figure 7) and they tend to separate spatially in common areas, but under global warming there might be considerable overlap between the two species along a broad band in central Ontario (Figure 7). The northern limit for deer parallels a zone of moderate winter severity (Voigt, 1990) and roughly parallels the 6 C mean annual isotherm in eastern Ontario where snow accumulation is deep, and the 4 C isotherm in western Ontario where snow is not as deep. Under global warming it appears that Ontario will generally receive less snow throughout the province, the 6 C isotherm will move considerably north, and the 'spring green-up', a time important to animals in negative energy coming out of winter, will occur much earlier (Figure 8). Under this scenario, most

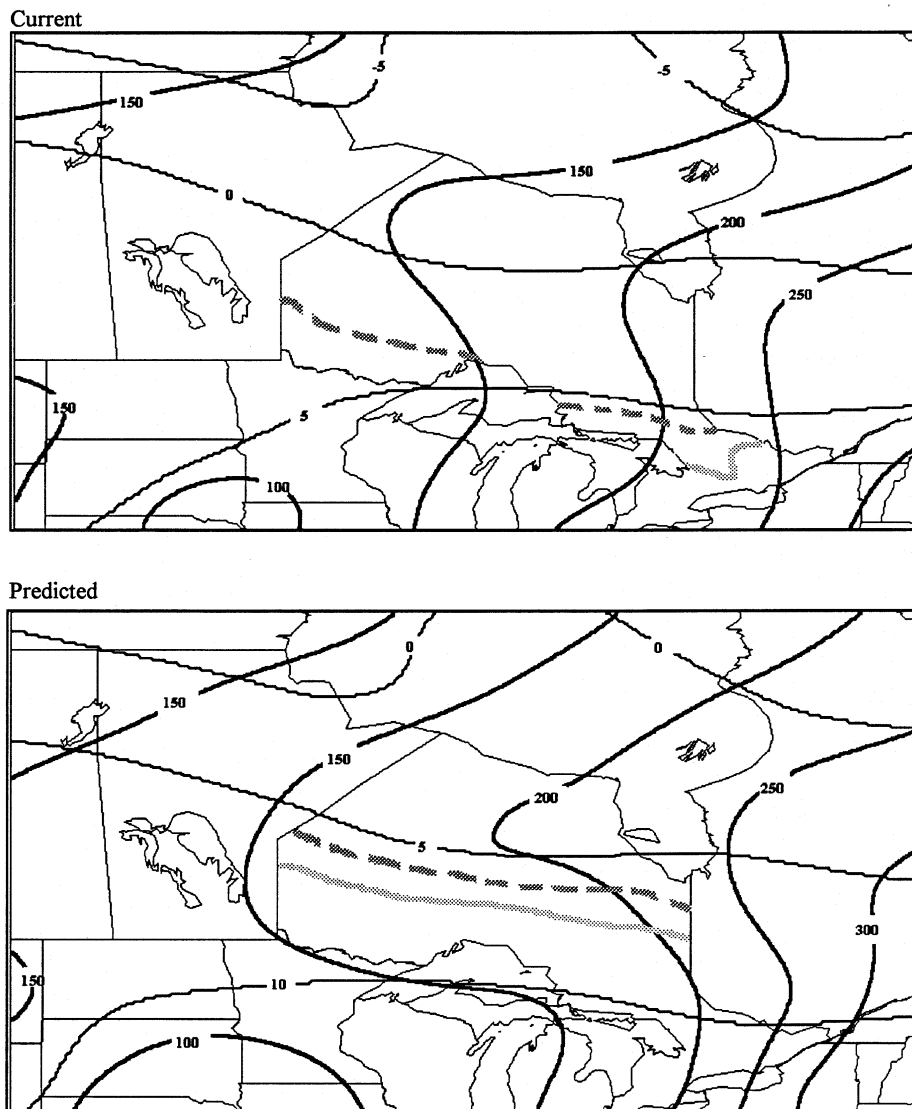


Figure 7. Accumulated snowfall – thick black contours (cm); mean annual temperature – thin black contours ($^{\circ}\text{C}$); southern limit of moose range – solid grey line; and, northern limit of whitetail deer range – broken black line.

of the current moose range will become available to deer. The combination of higher summer temperatures that moose cannot tolerate, mortality from parasites carried by deer, less preferred habitat, and possibly elevated predation by wolves as a result of higher available biomass from the combination of moose and deer, suggests to us that moose will withdraw to a limited area in the extreme north of the province in true boreal forest. On the other hand, a lack of good conifer cover,

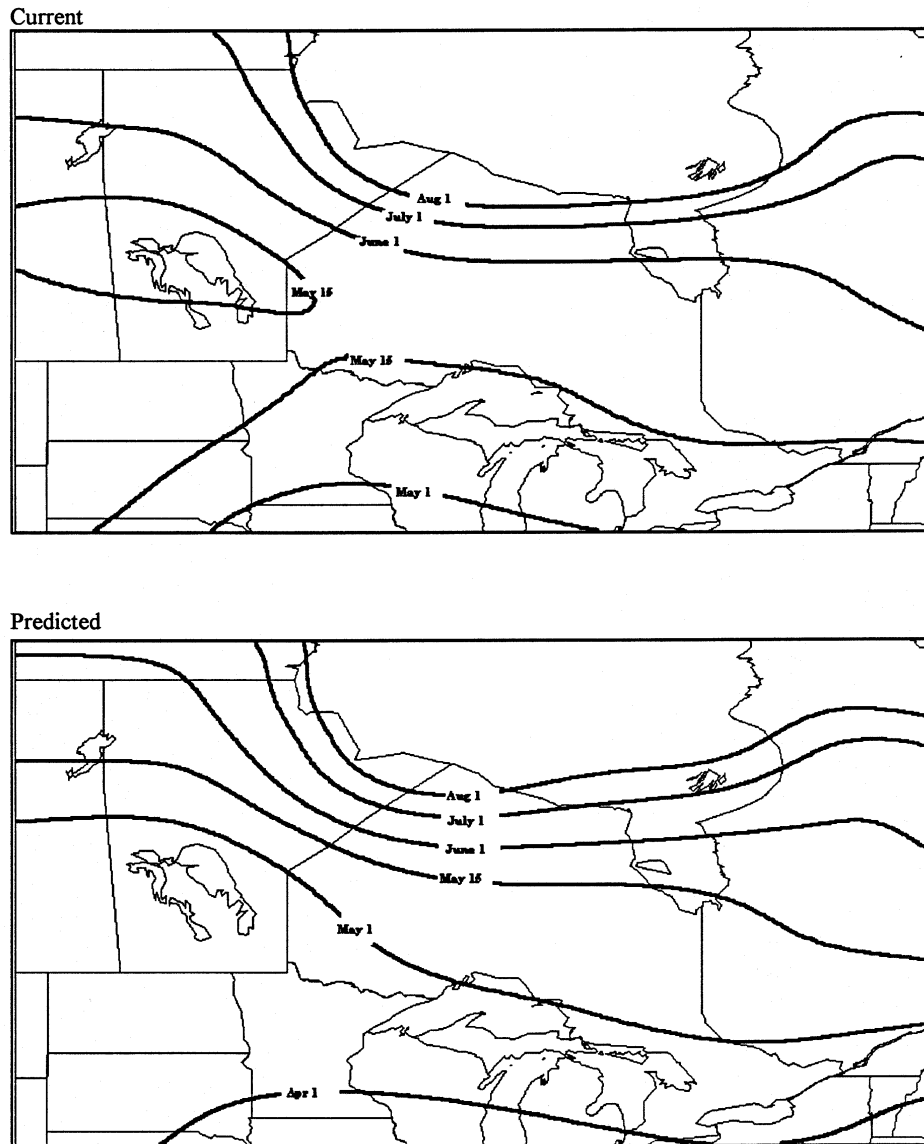


Figure 8. Date of leaf flush = 42 growing degree days.

as a result of increased fire incidence over several decades, will lead to lower population densities of both species in northern areas than might otherwise be expected. Although the central-Ontario forests may be dominated by aspen and other deciduous species, cooler sites will maintain conifers, as is seen today in Algonquin Park, and these sites will become important wintering areas for deer. As noted above, boreal climate warming will probably increase fire incidence and, in turn, the mix

of available habitats. In the past, caribou have responded to changes in the boreal fire regime (Fritz *et al.*, 1993). A sharp increase in forest fire incidence in the early 19th century resulted in decline in woodland caribou because of the decline in old growth forests. These changes were also intimately meshed with human predation pressure. Therefore, we conclude that species responding to patch structure and patch age at a landscape scale will be considerably affected under global warming.

5. Conclusions

Climate change has occurred previously in Canada. History shows that modern plant communities have existed for only a few thousand years, and that forest landscape structure has changed considerably since as little as 3000 years ago. Predictions are complicated by the linkages among forest disturbances, anthropogenic factors (including current logging practices and fire suppression), and the uncertainty over the rate of climate change. If the predictions of an unprecedented rapidity in the rate of change are correct, then clearly there will be considerable alterations in forest ecosystems and their arrangement on the landscape. Such changes will result primarily because of a higher incidence of wildfire, but also because of altered competition regimes among forest species. Enhancement of landscape disequilibrium will occur and new forest ecosystems will emerge primarily dominated by broad-leaved species in the south and central portions of Ontario, and by a mixture of jack pine and aspen in north-central (boreal) areas of the province. These changes will have consequences for individual plant species, ecosystem structures, and the associated wildlife communities across landscapes. Broad changes in forest types will lead to range shifts in the principal ungulates in Ontario with increases in population of white-tailed deer, and decreases in range and numbers of moose and woodland caribou after several decades of increased fires.

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