Canadian boreal forest ecosystem structure and function in a changing climate: impact on fire regimes

M.G. Weber and M.D. Flannigan

Abstract: Boreal forest fire regime, which encompasses fire intensity, frequency, seasonality, size, type (crown versus surface), and severity (depth of burn), is an organizing factor of boreal forest landscapes and highly dependant on climate. This review combines what is known about boreal forest dynamics from paleological studies, with the information derived from state-of-the-art climate and vegetation modeling, to present possible scenarios of the impact of anticipated climate change on boreal forest ecosystem structure and function, particularly in relation to fire regimes. Anticipated climatic/atmospheric impact on plant physiological, communal, ecosystem, and finally landscape-level interactions with fire are reviewed. All indications from the modeling sector point towards unprecedented increased regional or seasonal temperatures, with projected changes most pronounced at high latitudes and there greatest in winter. Anticipated climate change scenarios are expected to alter dramatically the boreal forest ecosystems and fire regimes with which they are currently in equilibrium. Changed fire regimes could be represented by increased annual area burned because of an extended fire season, increased fire frequency, and severity. Simulation studies show the potential for greatly reduced boreal forest area and increased fragmentation due to climate change. Fire regime as an ecosystem process is highly sensitive to climate change because fire behaviour responds immediately to fuel moisture, which is affected by precipitation, relative humidity, air temperature, and wind speed. This interaction between climate change and fire regime has the potential to overshadow the importance of the direct effects of global warming on species distribution, migration, substitution, and extinction. Such a scenario suggests that rate and magnitude of fire-regime-induced changes to the boreal forest landscape could greatly exceed anything expected due to atmospheric warming alone. Socioeconomic implications of altered fire regimes in a changing climate are discussed in terms of adaptive fire management strategies, age class distribution, and such global stewardship issues as biodiversity, carbon cycling, and sequestration.

Key words: climate change, fire regime, boreal forests, ecosystem structure and function, ecosystem processes.

Résumé : Les régimes d’incendies en forêt boréale, incluant l’intensité des feux, la fréquence, la saisonnalité, la dimension, le type (couronne contre surface) et la sévérité (profondeur du brûlé), constituent un facteur organisateur des paysages de la forêt boréale et dépendent fortement du climat. Dans cette revue, les auteurs combinent ce qui est connu au sujet de la dynamique des forêts boréales à partir d’études paléologiques avec l’information dérivée du climat dans l’état de l’art ainsi que les modèles de végétation, afin de présenter des scénarios possibles d’impact des changements climatiques anticipés sur la structure et le fonctionnment des écosystèmes de la forêt boréale, surtout en relation avec les régimes d’incendies. Ils revoient les impacts climatiques/atmosphériques anticipés au niveau de l’interaction du feu avec la physiologie des plantes, les communautés, les écosystèmes et finalement les paysages. Toutes les indications provenant de la modélisation vont dans la direction d’une augmentation sans précédent des températures locales et régionales, avec les changements projetés les plus marqués aux hautes latitudes et au cours de l’hiver. Selon les scénarios, on s’attend à ce que les changements climatiques altèrent dramatiquement les écosystèmes des régions boréales et les régimes d’incendies avec lesquels ils sont habituellement en équilibre. Les régimes d’incendies modifiés peuvent être représentés par l’augmentation des surfaces annuellement brûlées parce qu’une saison prolongée d’incendies en augmente la fréquence et la sévérité. Les études de simulations révèlent la possiblité d’une réduction considérable de la surface de la forêt boréale et d’une fragmentation accrue due aux changements climatiques. Le régime d’incendies comme processus écologique est très sensible au changement climatique parce que le comportement du feu réagit immédiatement à l’humidité du combustible, lequel est affecté par les précipitations, l’humidité relative, la température de l’air et la vitesse du vent. Cette interaction entre le changement de climat et le régime d’incendies pourrait potentiellement masquer l’importance des effets directs du réchauffement global sur la distribution des espèces, leurs migrations, leurs substitution et leur extinction. Un tel scénario suggère que le taux et l’ordre de grandeur des changements induits par le régime d’incendies sur les paysages forestiers boréaux pourrait largement dépasser tout ce qui est attendu sur la seule base du réchauffement atmosphérique. Les auteurs discutent les implications socio-économiques d’une

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M.G. Weber[1] and M.D. Flannigan. Canadian Forest Service, Northern Forestry Centre, 5320 122nd Street, Edmonton, AB T6H 3S5, Canada.

[1] Author to whom all correspondence should be addressed (e-mail: mweber@nofc.forestry.ca).

altération des régimes d'incendies dans un contexte de changements climatiques, en termes de stratégies adaptées d'aménagement du feu, de la distribution des classes d'âge et de problématiques de régie globale telles que la biodiversité, le cycle du carbone et la séquestration.

Mots clés : changement climatique, régimes d'incendies, forêts boréales, structure et fonctionnement des écosystèmes, processus écosystémiques.
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Introduction

In the boreal forests of North America fire is the keystone ecosystem process that organizes the physical and biological attributes of the biome over most of its range. Windstorms, insect and disease outbreaks, timber harvesting, and flooding are examples of additional disturbances with significant impacts at the local or regional level (Fleming and Volney 1995; Werner 1986), but fire is by far the most ubiquitous spatiotemporal agent. The physiognomy of the boreal forest at any time, now, in the past, and in the future, is not so much a function of fire, the physicochemical phenomenon, as it is of fire regimes. The concept of fire regimes, in addition to considerations of fire as a singular event that may reset the successional clock of forest ecosystems, encompasses fire frequency, size, intensity, seasonality, type, and severity (cf. Flannigan 1993; Malanson 1987; Merrill and Alexander 1987). The ecological importance of some of these component parts of fire regime has been put into perspective by Malanson (1987) and Whelan (1995). Thus, fire frequency affects ecosystems through interrupting or terminating individuals' life cycles. If fires recur more or less regularly, selection pressure will favour those organisms that better take advantage of the recurrence at a given interval. Fire size determines landscape patchiness and influences dispersal of propagules from the edges of the disturbance. Fire intensity, often strongly correlated with fire interval through fuel loading, rapidly responds to local weather and regional climate. Intensity, within the confines of a single burn, can vary greatly depending on the fuel type and loading, topography, microclimatic influences, and characteristics of the previous disturbance, among others. The season of the year at which fire occurs is one of the determinants of the successional trajectories on which ecosystems embark after fire. The time of year may affect fire intensity through differences in surface and crown fuel moisture contents. The seasonal phenological state of the plants burned will determine the characteristics of the vegetative or seed reproductive response and have a pronounced effect on the structure of postfire ecosystems and landscapes. Fire type refers to crown versus surface fires, which are largely controlled by fire intensity. Fire type, like intensity, can vary across the area of the burn, giving rise to a mosaic of postfire plant communities that might be initiated by crowning, surface fires, intermittent crowning, or a combination thereof. Fire severity is a description of the depth of burn into the surface soil organic layers and therefore another important controlling factor of postfire ecosystem structure and function through direct impacts on underground plant root and reproductive tissues, soil seed bank, and forest floor microbial populations. These component parts of fire regime with their intricate linkage to boreal forest ecosystem structure and function are, in turn, highly dependent on climate (Kirschbaum and Fishlin 1996). Any critical examination of boreal forest ecosystem structure and function in a changing climate must, therefore, pay close attention to the potential impact on fire regime.

The underlying premise of this synthesis is an acknowledgment of the weight of available scientific lines of evidence in favour of a sustained increase in global mean surface temperature of 1–3.5°C by 2100 (Schneider 1992; Watson et al. 1996). Atmospheric temperature variations have routinely occurred in the Earth's recent and distant geological past (McDowell et al. 1991). One of the differences between climatic warming episodes prior to and after the industrial revolution (1750) is the unprecedented rate at which it has been occurring post-1750, with increasingly convincing evidence pointing to anthropogenic causes (Kaufmann and Stern 1997). Long-term preindustrial climatic change occurred at geological scales and has been ascribed to planetary events such as plate tectonics with a time frame of millions of years or to astronomical forcing (Milankovich cycle), linked to changes in the Earth's orbital parameters, with periodicities between 10 000 and 100 000 years (Boutron 1995; Harrington 1987; McDowell et al. 1991; Webb 1992). Rapid changes, however, have also punctuated the Earth's climatic history and been recorded on planetary, continental, or regional scales, owing to catastrophic events such as volcanism and meteor or asteroid impacts (Harrington 1987).

The other difference from preindustrial climate change is the major cause of the current global episode, namely, anthropogenically produced radiatively active gases in the atmosphere, principally carbon dioxide (CO_2), methane (CH_4), and nitrous oxide (N_2O). These gases are now at greater concentrations than at any time in the past 160 000 years, as determined from Greenland and Antarctic ice cores (Boutron 1995; Harrington 1987). More importantly, even if emissions were to be held at current levels, there would still be a constant increase in atmospheric concentrations of these "greenhouse" gases for at least two more centuries because of the inertia of the systems involved (Watson et al. 1996). Of the three greenhouse gases, CO_2 has contributed the most pronounced radiative effect over the last 100 years and the physical chemistry of these gases represents the conceptual foundation for the models on which the climate-change scenarios for the next century are based.

Simulation modeling

The most important suite of models currently used by climate-change modelers are the general circulation models (GCMs). Their usefulness, input requirements, and output reliability have recently been reviewed by Caya et al. (1995) and Johannesson et al. (1995) for Canada and other nordic countries, respectively. The caveat to be remembered when studying GCM-derived climate-change scenarios, at the global or regional level, is that a climate-change scenario is not a prediction of future climate. Instead, as pointed out by Johannesson et al. (1995), climate-change scenarios are first and foremost research tools used to assess plausible consequences of future climate changes in the absence of reliable predictions of future climate. In spite of various difficulties (Caya et al. 1995; Flannigan and Van Wagner 1991; Johannesson et al. 1995), GCMs currently represent the only reasonable method that can be used for tracking the complex interactions between changes in the radiative forcing of greenhouse gases and the circulation of the atmosphere and oceans that will determine future climate development (Gregory and Mitchell 1995; Lau et al. 1996; Mearns 1989).

GCMs, the great majority simulating a doubled atmospheric CO_2 ($2 \times CO_2$) content and its attendant temperature increase and precipitation changes, have been variously combined with vegetation-based models to predict the ecological responses of terrestrial ecosystems to a changed climate (e.g., Claussen and Esch 1994). Vegetation models, like their climatic counterparts, show great diversity because they are based on a variety of assumptions and reflect the scientific backgrounds and mathematical preferences of their creators. Critical reviews of extant models, their performance, robustness, and other performance criteria have been provided by Ågren et al. (1991) and Malanson (1993). Briefly, ecological models incorporating climate-change simulations can be grouped into three broad categories, namely, transfer, stand-level, and physiological models (Malanson 1993). Transfer models relate present day vegetation to present day climate and use this as a direct basis to project future distribution. They are conceptually based on the Holdridge life zone classification system (Holdridge 1947) and use the projected climate from a GCM to plot anticipated new geographical ranges of individual species, genera, or vegetation types. Examples of workers using this approach include Emanuel et al. (1985) and Monserud et al. (1993) for global projections, and Lenihan and Neilson (1995) and Rizzo and Wiken (1992) for the Canadian domain. Stand-level models deal with much smaller spatial scales and take into consideration interactions among species and individuals such as regeneration, competition, growth, and mortality in a changing climate (e.g., Kellomäki and Väisänen 1996; McGuire et al. 1993; Prentice et al. 1993; Solomon 1986). Physiological models have been developed for various scales from plant, through stand and region, to continent and global. They are characterized by a common use of the mechanistic response of individual species to climate change (Prentice et al. 1991*a*), including photosynthetic pathways, leaf area index, and net primary productivity (Ågren et al. 1991; Woodward 1987; Woodward and Lee 1995).

Reconstruction of past environments

Another effective means to gain insight into structure and function of likely future forest ecosystems in a changed climate is the examination of the historical record. The underlying principle of this approach is that paleoclimatic trends and the corresponding paleoecological development of vegetation types may be used as a guide to the future, recognizing that entirely new assemblages, with no historical analogue, must also be considered (Martin 1993). An added advantage of the paleotechnique is its application as a reliability check for existing GCMs and other vegetation-based models; i.e., a certain GCM or ecological model can be used to simulate known past conditions and the outputs compared with our knowledge of the actual historic events for verification (Hall and Valdes 1997; MacDonald et al. 1991; Webb 1992). Paleological events, climatic as well as ecological, have been reconstructed for different geographical areas, extending back into the historical and geological record for millions of years (Schneider 1992). Techniques used to reassemble and visualize environments of past geological epochs and historical eras often involve examination of sequentially deposited layers of sediment in lake or ocean bottoms (e.g., Clark 1988*a*; Overpeck et al. 1989; Pielou 1991). Annual snow and ice deposition represent similar archives of past biospheric conditions and have been used to extend the record back more than 200 000 years (Boutron 1995). Reconstruction of more recent events, encompassing the period from the start of the last deglaciation to the present (Holocene), has often employed palynological methods. Recent studies investigating North American Holocene trends in general and boreal forest developments in particular, include Campbell and Campbell (1994), Campbell and McAndrews (1993), Davis (1983, 1989), Gajewski and Garralla (1992), Garralla and Gajewski (1992), Pielou (1991), and Solomon and Bartlein (1992), among others. These and other investigations have successfully tracked climatic variations and vegetation development during those relatively rapid and recent Holocene events, known as the climatic optimum or hypsithermal interval (about 5000 to 9000 years ago) and the Younger Dryas. The latter event, started ca. 11 000 years ago, was characterized by cooling of near ice age intensity, especially in eastern North America and Europe, and lasted for approximately 1000 years until the present day interglacial finally established itself (Pielou 1991; Schneider 1992; Webb 1992).

Pollen analysis, especially when combined with charcoal deposition, is a powerful indicator of the interaction of past vegetation assemblages with two important components of fire regime, namely, intensity and frequency. Clark (1988*b*, 1988*c*, 1990*a*, 1990*b*) has provided detailed accounts of southern boreal vegetation development and its interrelation with fire during the last 750 years. The importance of fire regime during the recent Holocene in shaping the postglacial landscape locally and continent wide, and the pitfalls, limitations, and caveats associated with pollen and charcoal analysis and interpretation, have been thoroughly reviewed by Clark (1988*a*, 1990*b*) and Pielou (1991).

It may be instructive at this point to review briefly the role of aboriginal activities on the fire situation in Canada during recent pre-European times. Presumably, the annual fire load before European contact would have included lightning fires in addition to aboriginal fires, all burning without control (cf. Lewis 1982). Van Wagner (1988) feels that this scenario probably resulted in average annual areas burned, much in excess of what is experienced today and drastic local consequences to past forest landscapes.

Day (1953), Lewis (1977, 1982), and Myers and Peroni (1983) make a convincing case for early and very sophisticated approaches to and understanding of the dynamics of fire for the management of plant and animal resources in a boreal environment (Lewis 1977). Myers and Peroni (1983) argue that humans who occupied pyrogenic vegetation types, such as the boreal forest, can be expected to have had a hand in their ignition, maintenance, and expansion. Examples exist from the southern United States to Australia (Lewis 1982; but see

Russel and Forman 1984). One type of evidence for manipulation of vegetation types is derived from the pollen record where major shifts in overstory and understory vegetation has been linked to human invasion or abandonment of an area. Similarly, stratigraphic records of fire from charcoal analysis of lake sediments in southern Ontario has been used to argue for strong aboriginal control over forest composition spanning centuries (Clark and Royall 1995), although alternative hypotheses involving climate change during the "Little Ice Age" (ca. 1550–1850), domestic fires, and agricultural burning have also been proposed (Campbell and McAndrews 1995).

Another line of evidence was provided by Lewis (1977) through recording of oral histories of aboriginal boreal forest dwellers. Evaluation of responses indicated regular and sometimes large scale use of fire on an annual basis. The overall objective of the use of prescribed fire by aboriginals was the maintenance of a certain seral stage in vegetation development or to set back successional stages to some desired point. The reasons for vegetation management using fire were varied. One of the major reasons cited was the maintenance of open, meadow-like areas for browse production. Browse was initially for game animals and later included provision for horses. Open areas, created by prescribed burning, also facilitated ease of travel, hunting, visibility, and reduction of fire hazard. Boreal forest aboriginals of northern Alberta claim that fire-maintained open areas were subject to invasion by woody plants after their annual burning practices were curtailed by Europeans (Lewis 1977). Other reasons for using fire was to maintain landscape diversity, because it was recognized that for successful hunting, trapping, and foraging it "...is better to have all kinds of places not the same" (informant interviewed by Lewis 1977). Indications thus are that people had widespread impact throughout the boreal forest for thousands of years before European arrival (Lewis 1982; Sauer 1950). Current views of what constituted preindustrial North American forested landscapes and how they were maintained must therefore explicitly incorporate the dynamic presence of aboriginal peoples as active components of the landscape.

The highest resolution for past climatic and related environmental events has been obtained for the most recent northern hemisphere vegetation developments using dendrochronological techniques. Recent advances in tree ring analysis have allowed reconstruction of hemispheric (D'Arragio and Jacoby 1993) to local climatic conditions, including past fire frequencies from several 100 to 2000 years ago (Johnson 1992; Swetnam 1993). When dendrochronological investigations are combined with analyses of age class distribution (Bergeron 1991; Dansereau and Bergeron 1993; Johnson 1992; Johnson and Larsen 1991), stratigraphic charcoal analysis from thin sections of varved lake sediments (Clark 1988*b*), and pollen analysis (Clark 1990*a*; MacDonald et al. 1991) locally detailed pictures emerge of postglacial climatic fluctuations, species migration into deglaciated areas (Davis 1981), and past fire regime. Collectively, these studies suggest that even the most rapid rates of boreal forest tree species migration onto deglaciated surfaces could not match those required by the currently expected rates of climatic change over most of the boreal forest.

The balance of this review will combine what is already known about boreal forest dynamics during the Holocene with the information derived from state-of-the-art GCM and vegetation modeling to present possible scenarios of the impact of the anticipated climate change on boreal forest ecosystem structure and function, particularly in relation to fire regimes. We will examine anticipated climatic/atmospheric impacts on plant physiological, communal, ecosystem, and finally landscape-level interactions with fire in the boreal forests of Canada. All indications from the modeling sector point towards unprecedented increased regional or seasonal temperatures, with anticipated changes being most pronounced at high latitudes and, there, greatest in winter (Kirschbaum and Fishlin 1996). Considering the close coupling of the climate to fire regime, the importance of fire regime to boreal forest ecosystem structure and function, and the national and global stewardship issues associated with the maintenance of this resource, prudence demands that careful attention be paid to the scientific and social concerns related to climate change and fire regimes.

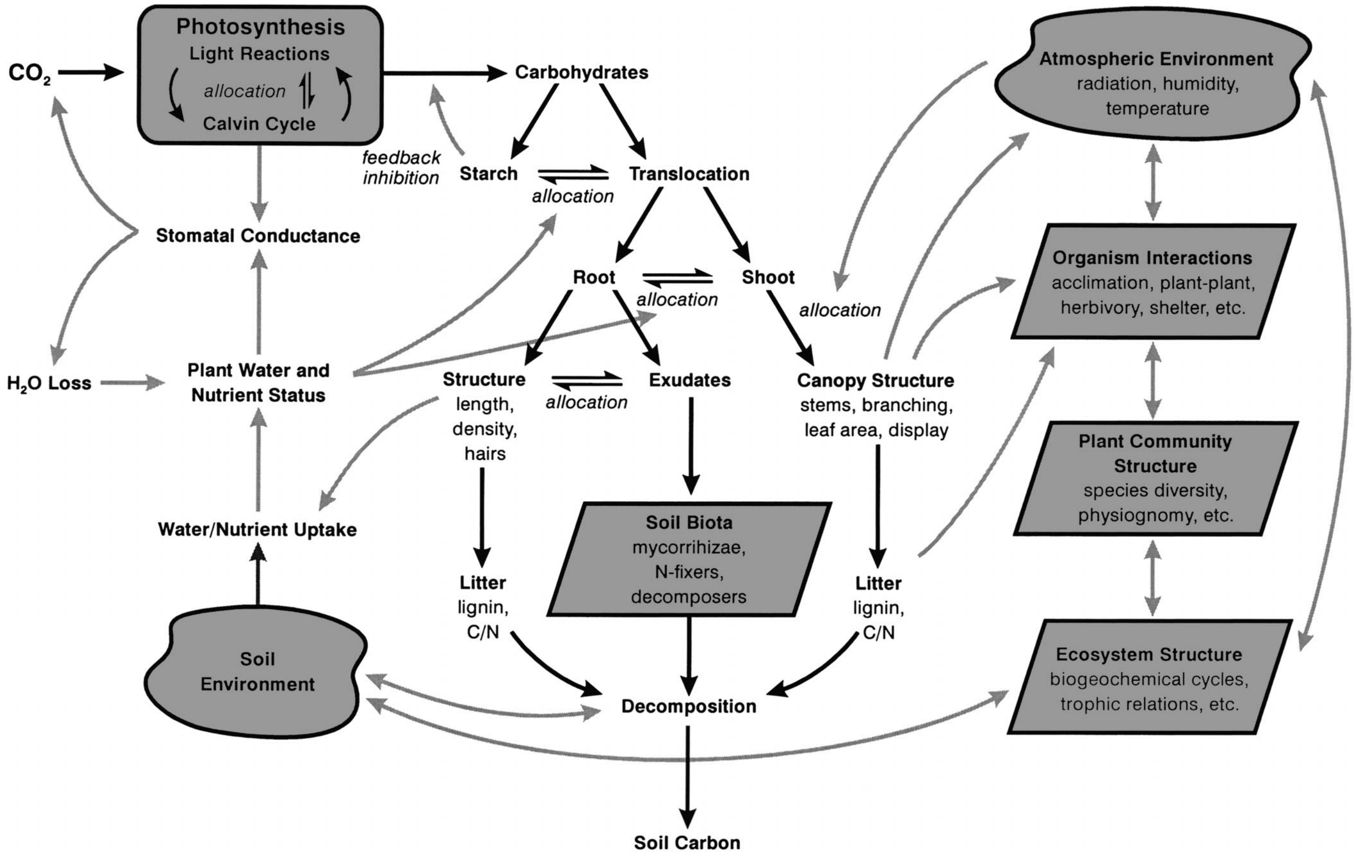
Physiological responses to atmospheric change and the cycling of nutrients and matter

When considering the potential impact of climate change on the terrestrial ecosystem structure and function in general and boreal forest fire regimes in particular, attention must be given to all aspects of the global change issue, not just the temperature aspect of the expected environmental changes (Bazzaz and Fajer 1992; Woodward et al. 1991). Therefore, anticipated temperature increases and their effects at the various levels of organization from cellular to ecosystem must not be evaluated in isolation from the atmospheric impacts, especially elevated CO_2 concentrations (Koch and Mooney 1996). The reason for this cautionary approach is the realization that atmospheric change can have immediate and direct effects on the fuel-loading component of fire regime. Fuel loading is a forest ecosystem attribute reflecting local or regional conditions of biomass and hence litter production, soil thermal, moisture and nutrient regimes, forest floor thickness, microbial activity, and decomposition rates. Any or all of these factors may be impacted by atmospheric change and therefore affect fire regime.

Effects of changed physiology and processes

The global atmospheric concentration of CO_2 has risen from preindustrial levels of about 280 ppmv in the late 18th century to 360 ppmv in 1994 (Amthor 1995*a*; McGuire and Joyce 1995). Based on common leaf-level physiological observations of C_3 plants, which include all boreal forest tree and understory species, increased atmospheric CO_2 can be expected to enhance overall forest photosynthesis, which, in turn, would lead to accelerated plant growth and yield (Eamus and Jarvis 1989). This simplistic extension of basic principles of photosynthesis does not take into account some complex interactions between CO_2 concentration, stomatal conductance, photorespiration including the role of Rubisco (ribulose biphosphate carboxylase/oxygenase), and acclimation (e.g., Amthor 1995*a*, 1995*b*; Eamus and Jarvis 1989; McGuire and Joyce 1995; Mooney et al. 1991; Reynolds et al.1996). The controversy regarding the importance of CO_2 fertilization has been thoroughly reviewed by Idso and Idso (1994) who evaluated several hundred responses of plant carbon-exchange rates and dry weight to atmospheric CO_2 enrichment. Their review indicated that, on balance, the data showed that relative

Fig. 1. Conceptual model of plant carbon dynamics (black arrows) and important feedbacks and interactions (grey arrows) with other ecosystem compartments and trophic levels (after Reynolds et al. 1996).



growth-enhancing effects of atmospheric CO_2 enrichment was most pronounced when resource limitation and environmental stresses were most severe (but see Körner et al. 1996). Later Plöchl and Cramer (1995) and more recently Sellers et al. (1996) corroborated many of the previous findings by linking various types of models into a single-coupled biosphere–atmosphere model. Their simulation runs compared radiative and physiological effects of a $2 \times CO_2$ atmosphere by incorporating a coupled photosynthesis–conductance submodel into a vegetation canopy model and linking that to a GCM. This improved simple biosphere model showed that the physiological response of terrestrial vegetation to increased CO_2 concentration could be one of increased assimilation rates and hence biomass production, decreased canopy conductance, and warming over the continents, in addition to that due to the conventional "greenhouse effect" (Sellers et al. 1996).

The major problem encountered in this field of climate-change research, including modeling, is related to upscaling (Coleman et al. 1992). While the response of photosynthesis to CO_2 enrichment is readily observed at the single-leaf or isolated plant level, upscaling to the stand or even ecosystem level has proved elusive in light of the complexities of various plant–soil–atmosphere feedbacks (Fig. 1). Some of the feedbacks examined experimentally include nutrient relations (Jackson and Reynolds 1996; Johnson 1996; Nijs et al. 1995; Tingey et al. 1995; Werkman et al. 1996); soils, decomposition, and microbial processes (Anderson 1991, 1992; Coleman et al. 1992; Curtis et al. 1996; Esser 1992; Jenkinson et al. 1991; Pan et al. 1996; Robinson et al. 1995; Zak et al. 1996); plant respiration and carbon allocation (Ryan 1991); water relations and temperature (Constable et al. 1996; Eamus 1996; Johnsen 1993; Kellomäki and Väisänen 1996; Landhäusser et al. 1996; Major and Johnsen 1996; Werkman et al. 1996); and genetics and acclimation (Epron et al. 1996; Johnsen et al. 1996; Johnsen and Seiler 1996; Kerstiens et al. 1995). Although these studies have not resolved the CO_2 fertilization controversy at the ecosystem level, they have provided valuable information along the way to building the simulation models required to construct future scenarios in a changed climate. What would be required to resolve the issue experimentally for forest ecosystems is an open-air experiment with a design similar to the Jasper Ridge CO_2 experiment (Field et al. 1996). This multidisciplinary study investigates grassland ecosystem structure and function combining field plot, outdoor microcosms, growth chamber, and modeling approaches. Clearly, cost and technological barriers to duplicating such an experiment in a forest ecosystem are formidable.

One of the ways to overcome some of the currently intractable constraints to direct, integrated field experimentation is the incorporation of existing knowledge, gleaned from various other field studies, into contemporary ecosystem or vegetation models. Successful examples of this approach have been provided by Pastor and Post (1988) and more recently by Running and Nemani (1991), Bonan (1992*a*, 1992*b*), Shugart and Prentice (1992), and Sellers et al. (1996), with important implications for boreal forest fire regimes in a changing climate.

Thus, Pastor and Post (1988) linked a forest productivity/soil process model with a $2 \times CO_2$ GCM to explore the response of boreal forests to a warmer and drier climate. These authors examined ecosystem responses at a scale where the effect of fast-response, single-leaf physiology is minimized in favour of integration of competition, climatic fluctuations, and plant–soil interactions into biomass production. Their modeling results, applicable to the southeastern North American boreal forest, showed increased productivity and biomass on soils with adequate water retention. Where water retention was inadequate for tree growth, simulations suggested a decline in biomass production. Overall, the responses of the forests were a function of positive feedback between carbon and nitrogen cycles, secondarily modified by negative constraints of soil moisture availability and temperature. They concluded that the heterogeneity of the landscape, particularly the distribution of various soils, becomes the determinant of climate-change responses within and among biomes (Pastor and Post 1988).

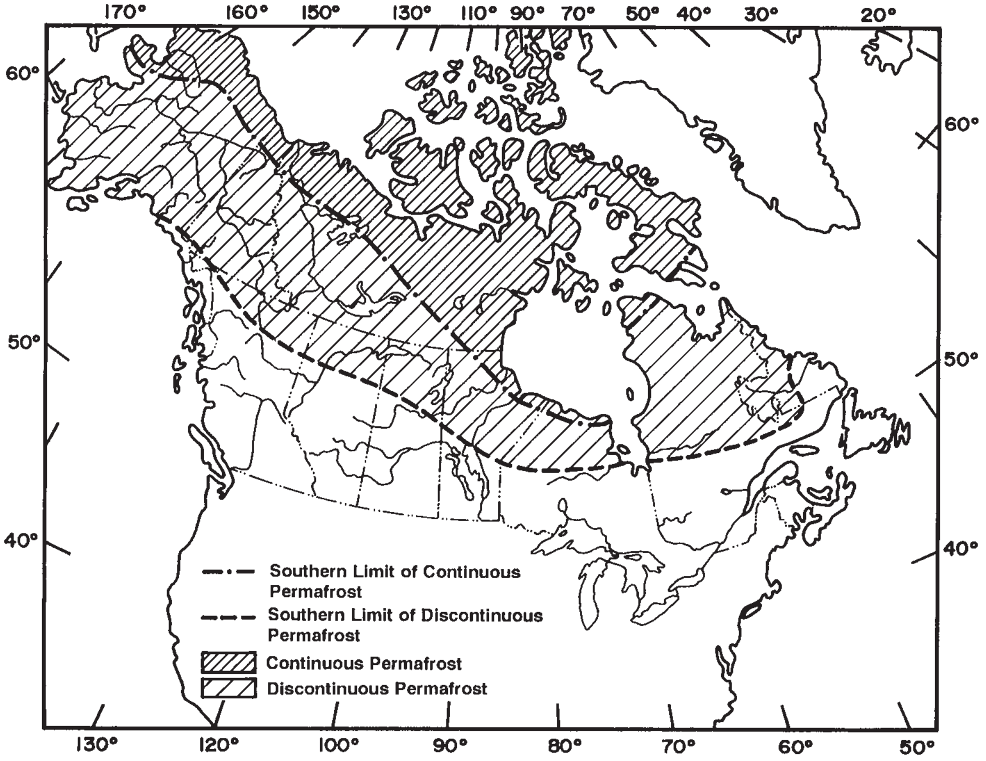
The importance of temperature control over boreal forest ecosystem processes has been repeatedly emphasized (Anderson 1991, 1992; Bonan 1992*a*; Van Cleve et al. 1983, 1991) and experimentally demonstrated by Van Cleve et al. (1986) for Alaskan Taiga ecosystems. The Alaska group produced substantial short-term changes to the physical and chemical nature of the substrate by artificial soil heating. Forest floor weight declined by 20% over the 3-year duration of the experiment. Microbial respiration in the forest floor increased significantly, as did soil solution NH_4, available P, and total N. The general trend of reduced forest floor mass, increased microbial activity, and greater concentration of available soil nutrients reflect accelerated decomposition, nutrient, and organic matter turnover rates in a warmer soil (see Robinson et al. 1995 for contrasting results). These ameliorated substrate conditions of normally cold soils resulted in higher tree foliage nutrient contents of N, P, and K and significantly elevated rates of black spruce needle photosynthesis (Van Cleve et al. 1986). One of the important findings of this study was the immediacy of the response of basic ecosystem functions to increased soil temperature. Impacts on fire regime can be expected to be equally swift because of modified surface and arboreal fuel production and configuration through altered biomass and litter production rates that affect forest floor depth and hence fire severity (Bonan et al. 1990).

Long-term monitoring of this type of ecosystem manipulation to assess the impact of altered ecosystem process rates on the forest ecosystem structure and hence fire regime is difficult technically and financially. An alternative is computer simulation; this was provided by Bonan et al. (1990) who extended the field experimentation of Van Cleve et al. (1986) in time and space. Details of the model used to produce the simulations can be found in Bonan et al. (1990). Their simulations assumed climate-change scenarios of 1, 3, and 5°C warming in the interior of Alaska, factorially coupled with 120, 140, and 160% increases in monthly precipitation from current values. To emphasize the importance of local site conditions in their response to expected climate change, the simulations were done for two contrasting forest types: a black spruce (*Picea mariana* (Mill.) B.S.P.) forest growing on a permafrost-dominated, poorly drained north-facing slope and a white spruce (*Picea glauca* (Moench) Voss), paper birch (*Betula papyrifera* Marsh.), and aspen (*Populus tremuloides* Michx.) forest located on a well-drained permafrost-free, south-facing slope (Viereck et al. 1983). According to these simulations, the effects of climatic warming on ecosystem structure and function in the northern boreal forest may not be so much a direct response to increased air temperature as to increased potential evapotranspiration demands. The analysis also revealed the importance of the forest floor organic layers in controlling ecosystem response to climatic warming. For example, a thick forest floor (20–30 cm) typical of many black spruce forests in interior Alaska and elsewhere is the major factor responsible for the cold, wet soil conditions that restrict nutrient availability and tree growth (Weber and Van Cleve 1981, 1984). In the absence of fire, the short-term response of these permafrost-dominated sites to climate warming was a decrease in the active layer depth (that layer of soil above permafrost which thaws out annually because of summer warming) owing to drying of the forest floor, which impeded thermal conductivity into deeper soil layers. In the long term, however, with recurrent forest fires, the drier organic layers were conducive to increased fire severity, removing greater amounts of forest floor material and thereby increasing active layer depth and further improving soil drainage (Bonan 1989; Bonan et al. 1990). Entire elimination of shallow or discontinuous permafrost would be a possible scenario under these conditions. The final outcome of this simulation run was the fire-driven conversion of the low productivity black spruce forests to mixed spruce hardwood forests growing on warmer soils. In contrast, on the well-drained, south-facing spruce hardwood forest sites, increased potential water loss in a warmer climate reduced soil moisture, resulting in site conversion of these stands to dry aspen forests. Greatest simulated reduction in soil moisture resulted in steppe-like vegetation with elimination of the tree overstory on these sites. Increases in precipitation in a warmer climate offset the effects of increased potential evapotranspiration demands and mitigated forest-cover changes (Bonan et al. 1990). This study highlighted the sensitivity of divergent forest ecosystems to water balance and its interaction with fire regime under climate change. A paleoecological study from the central boreal forest of Canada (Ritchie 1983) corroborates this simulation study by also suggesting a shift of forest to prairie under drier and warmer conditions. Kellomäki and Väisänen's (1996) climate-change simulations for the Finnish boreal forest produced similar reduced soil moisture scenarios due to enhanced overstory evapotranspiration. These and other studies (Van Cleve et al. 1986) also emphasized soil temperature as a controlling factor over ecosystem processes, especially on cold soils. Given the widespread distribution of permafrost throughout the North American boreal forest (Fig. 2) and the control it exerts over above and below ground processes, dramatic changes to forest dynamics and fire regime seem inevitable. Climate-change-induced site conversion alone, accelerated by recurrent fires as described above, would alter fire regime. New species complexes as they develop in response to atmospheric change and finally persist in equilibrium with the prevailing climate will be characterized, each step of the way, by fire regime distinctly different from the previous one.

Carbon and nitrogen cycling

The very close coupling of the nitrogen and carbon cycles within the plant and the ecosystem as a whole makes them

Fig. 2. Permafrost distribution in North America.

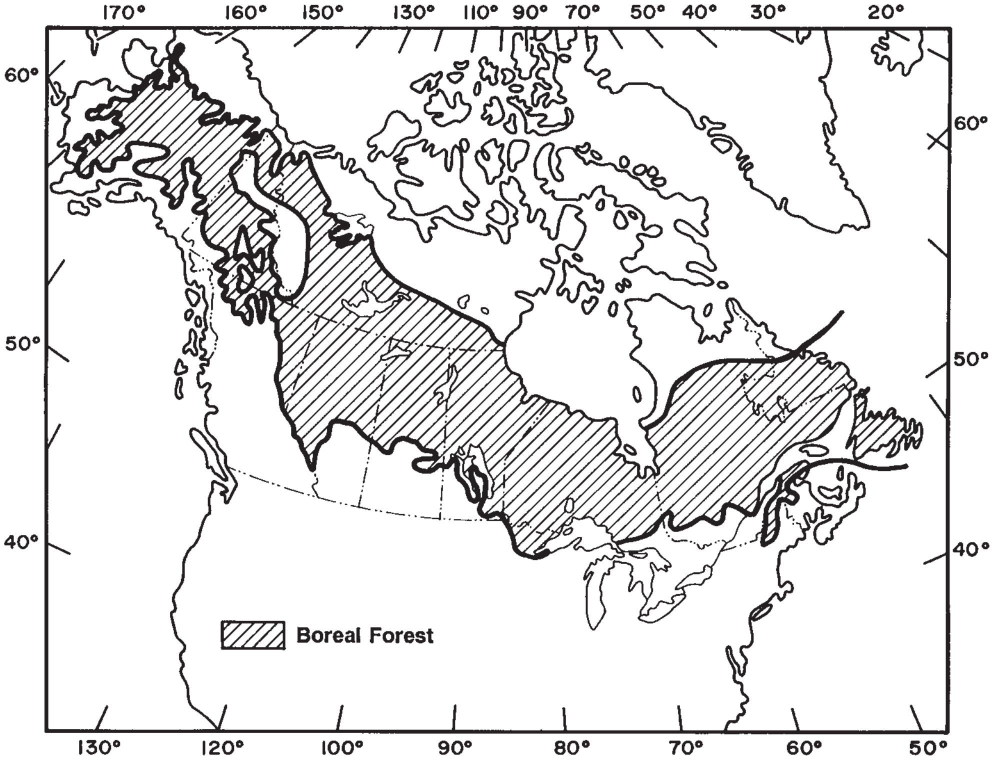


particularly susceptible to modifications under global change, as one or the other cycle may be altered by elevated CO_2 and climate change. Alteration in one of these two cycles can be expected to have immediate repercussions on the other because of the interaction and feedback between the two (Pastor and Post 1986; Reynolds et al. 1996). For example, the ability for increased carbon acquisition by plants in a higher CO_2 atmosphere could be limited by available soil N, which is in turn controlled by decomposition rates. The main avenue for interaction between C and N cycles may actually be via decomposition and litter quality. The reciprocal linkage between ecosystem cycles (N and C) and attributes (decomposition rates and litter quality) assumes added importance in the boreal forest biome for several reasons: (*i*) greater temperature impacts predicted for northern latitudes under climate change, affecting all temperature-sensitive processes, including decomposition and nutrient cycling (Anderson 1992); (*ii*) boreal forest ecosystems being uniformly nitrogen limited and expected to respond to ameliorated nutrient conditions (Van Cleve et al. 1986); *(iii*) the boreal forest's historical role in the global carbon cycle as a carbon sink and likely reduction in sink strength under climate change (Kurz et al. 1995; Kurz and Apps 1993); and (*iv*) effects of altered decomposition rates on fire regime via fire severity and changed organic layer thickness.

The principal pathway whereby elevated CO_2 interacts with decomposition is through effects on litter quality (O'Neill 1994). Litter characteristics, such as lignin and nutrient content, and most importantly C/N ratios strongly influence decay patterns and N availability, which, in turn, controls the rate of biomass accumulation (Pastor and Post 1986; Reynolds et al. 1996). Therefore, elevated CO_2 can alter ecosystem litter quality directly by affecting the C/N ratios of the plant material periodically deposited on the forest floor or indirectly by changes in species composition of plant communities and their associated litter characteristics (O'Neill 1994). Evidence for direct effects of CO_2 enrichment on C/N ratios in plant tissue is inconclusive, especially because C/N ratios of living tissue may not be the same as senescent tissue shed as litter (Reynolds et al. 1996). In the case of a CO_2-caused shift in plant community species composition, changes in litter quality are expected because the type of carbon compounds in litter, and hence C/N ratios are species specific (Pastor and Post 1986). C/N ratios control N availability; i.e., the narrower the litter C/N ratios, the more rapid the microbial decomposition rates, which, in turn, increase nitrogen availability for plant uptake and biomass production (Reynolds et al. 1996; Ryan 1991). As pointed out above, any time forest floor decomposition rates are altered owing to soil warming, increased depth of active layer over permafrost, improved soil drainage, or accelerated substrate microbial activity, direct impacts on fire regime are probable via fire severity (depth of burn). Improved soil drainage as a result of soil warming at northern latitudes is an important consideration for any climate-change scenario (e.g., Anderson 1992; Bonan 1989; Dang and Lieffers 1989; Lashof 1989) because of the implications for organic-layer drying and hence fire severity.

Combining increased fire severity in a changing climate with increased fire frequency could accelerate carbon mineralization rates in the arctic and subarctic soils that underly most of the boreal forests of North America (Anderson 1991). These faster carbon mineralization rates under warmer and drier conditions are due to low stabilization of soil organic matter and enhanced microbial responses to small changes in soil moisture and temperature (Anderson 1991). Accelerated

Fig. 3. Distribution of the boreal forest biome in North America.



C mineralization eventually feeds back to atmospheric CO_2 loading, possible biomass production impacts, litterfall quality and quantity, and decomposition rates. As a point of departure for further information on the implications of such a scenario for global carbon cycling, mobilization of carbon stores from boreal forests, the carbon source/sink controversy, and feedback to global climate change, the reader is referred to Anderson (1992), Apps et al. (1995), Kasischke et al. (1995), Kurz et al. (1995), Oechel et al. (1993), and Thomas and Rowntree (1992).

Most of the atmospheric change-generated impacts are actually environmental stresses and may therefore predispose individuals and ecosystems to secondary stressors like insect and disease attack and susceptibility to drought (cf. Jones et al. 1993). Should this dynamic result in increased aboveground mortality and stand breakup, fire regime may be affected immediately and in the short term owing to increased surface fuel loading and hence increased fire intensity. The implications of these changes as a whole to boreal forest fire regimes, distribution, and ecotonal shifts form the subject of the next section.

Landscape-level changes and fire regimes

Boreal forests and fire regime

The boreal forest represents the largest forest region in Canada. It forms an uninterrupted, transcontinental band from Newfoundland in the east to the Yukon Territory in the west and continues into the state of Alaska (Fig. 3). In Canada this biome covers about 315×10^6 ha and occupies 75% of all wooded land and 67% of exploitable forest (Canadian Council of Forest Ministers 1997; Kuusela 1992). Within this forest region, fire is a ubiquitous agent and appears to be occurring more often annually and burning over increasingly larger areas since fire records have been kept (Fig. 4). Careful analysis of the Canadian forest fire statistics has been provided by Weber and Stocks (1998) who ascribe the observed increase in fire occurrence to a growing population coupled with more intensive forest use and an expanded and more sophisticated fire detection capability across the country. The increase in the annual area burned over the last 3 decades, with the most dramatic increase observed in the 1980s and early 1990s (Fig. 4), is primarily due to periods of short-term extreme fire weather in western and central Canada (Stocks 1991). Lightning is the cause of 35% of Canada's fires but is disproportionately responsible for 85% of the total area burned. Another oddity is reflected in the fact that 2–3% of the fires that do grow larger than 200 ha will eventually contribute about 98% of the total area burned in Canada (Fig. 5) (Weber and Stocks 1998).

These continental North American boreal forest ecosystems and their fire regimes are expected to be dramatically altered by projected climate-change scenarios. Keeping in mind the caveat that anticipated future ecosystem responses are consequences of assumptions and scenarios, not precise forecasts, the most pertinent climatic GCM projections are as follows: (*i*) temperature increases over the period 1900–2050 in the order of 1–2°C in summer and 1–3°C in winter; (*ii*) regional changes in precipitation in summer and winter, mostly in the ±20% range; and (*iii*) drier soils in summer with an average of about 2–8 mm less water (Kirschbaum and Fishlin 1996). The regionality of the climate-change scenarios has been emphasized by Bergeron and Flannigan (1995) who pointed out the large regional variability across the boreal forest that precludes broad generalizations. Their study explored the relationship between climate change and fire frequency using the Canadian Atmospheric Environment Service's GCM to simulate

Fig. 4. Annual area burned by forest fires in Canada from 1930 to 1996.

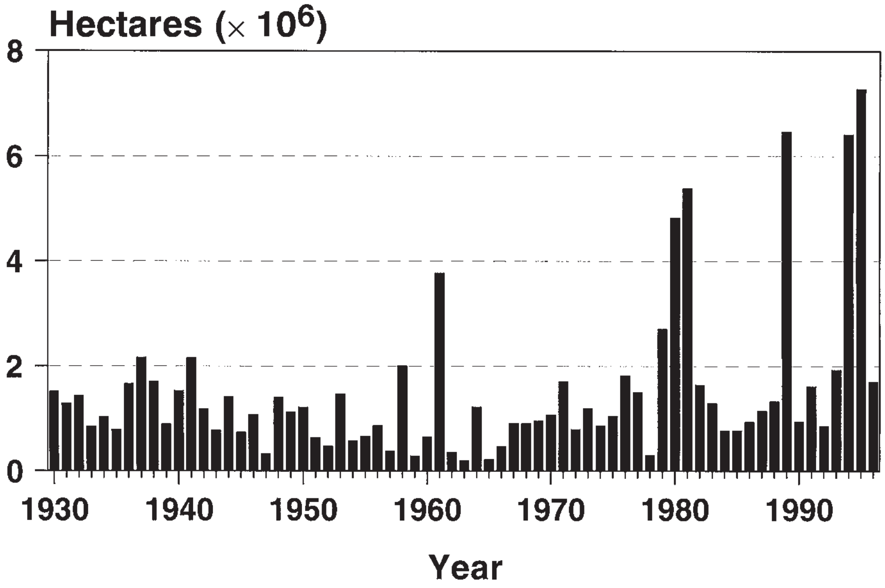
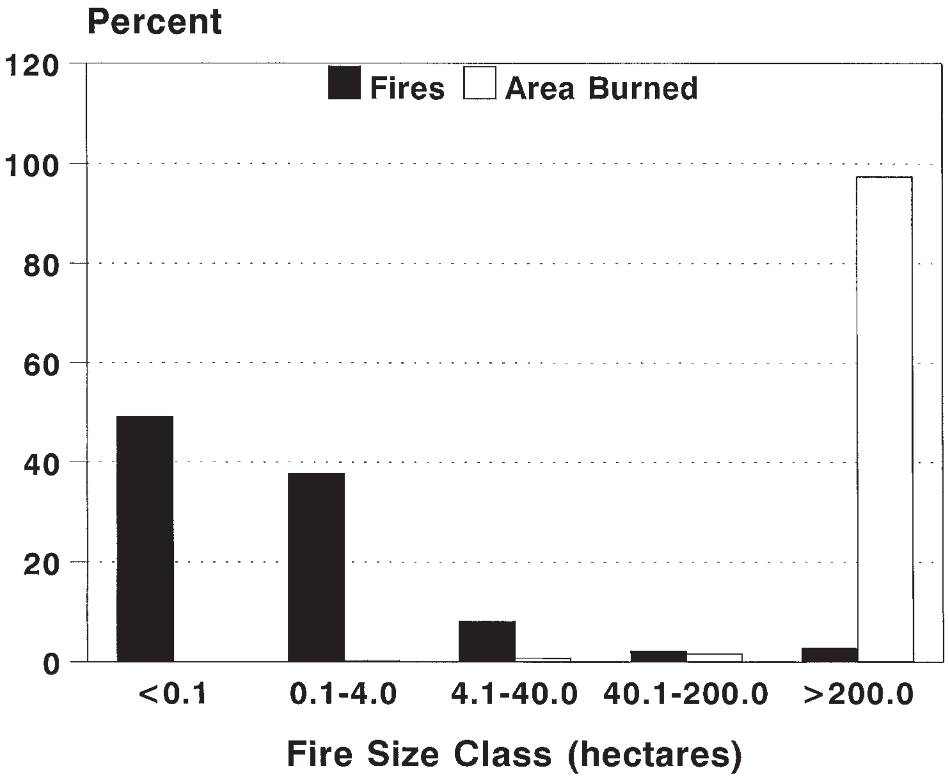


Fig. 5. Forest fire size class distribution in Canada from 1970 to 1985 (after Stocks 1991).



components of the Canadian Forest Fire Danger Rating System (Stocks et al. 1989) in a 2 × CO_2 world. Results from their simulation runs indicated that average fire weather index (FWI), which is a measure of the fire intensity of a spreading fire, increased dramatically over central Canada and sections of western Canada but actually decreased over much of eastern Canada. According to these results, fire frequency in the southeastern boreal forest would decrease. This finding was consistent with tree-ring-derived fire history trends in the general area since the end of the Little Ice Age (Bergeron and Flannigan 1995; Bergeron and Archambault 1993) and appeared to be due to a reduced frequency of drought periods since the Little Ice Age (Bergeron and Archambault 1993). Frequency and duration of drought periods have been shown previously to be strongly related to area burned, especially in western Canada (Flannigan and Harrington 1988). Such bifurcation of projected trends in fire regime, into eastern and western scenarios, emphasizes the caution with which some of the climate-change generalizations have to be treated, especially when reduced to regional scales. Recent advances in simulation modeling are attempting to achieve these regional high-resolution climate projections (Caya et al. 1995), which would be required for the realistic assessments of the impacts of climate change on local fire regime.

According to the scenario projected by Bergeron and Flannigan (1995), changes in fire regime can be expected to occur to the west of central Canada. These projections imply longer and warmer growing seasons, appreciably milder winters with the possibility of less extreme temperature minima, and permafrost reduction, which is related to annual mean temperatures (Kirschbaum and Fishlin 1996). In terms of fire regime, the changes in temperature, soil water, and vapour pressure deficit may translate into increased area burned, extended fire season where climatic conditions are conducive to burning earlier in the spring through later in the autumn (Wotton and Flannigan 1993), and increased fire frequency (Flannigan and Van Wagner 1991; Stocks 1993). Flannigan and Van Wagner (1991) explored the relationship between seasonal fire severity rating and annual area burned across Canada using various GCMs, simulating a $2 \times CO_2$ climate. The fire severity rating is a measure of the work needed to suppress a wildfire and used by fire management agencies to average fire danger in time and space. Their model outputs suggested a 50% increase in seasonal severity rating, with a possible similar increase in burned area. Retrospective studies using stand-origin maps, fire scars, tree-ring analysis, and fire-frequency models (Johnson and Gutsell 1994; Swetnam 1993), as well as paleotechniques (Clark 1988*b*, 1989, 1990*b*; MacDonald et al. 1991; Overpeck et al. 1990) concur with modeling exercises of future scenarios by showing that fire frequency and intensity have increased in past warmer and drier climates.

The changing face of the boreal forest

The crucial difference between past climatic changes and the present event is the speed at which the current episode is expected to proceed. Changes in climatic forcing are projected to be one or two orders of magnitude faster than rates of climatic change experienced by boreal forests during most of the past 100 000 – 200 000 years (Kirschbaum and Fishlin 1996). There are only two known recent episodes of rapid climatic change, both characterized by abrupt cooling, however, rather than warming. One was the Younger Dryas Event, which endured for about 1000 years, the other the Little Ice Age with a duration of about 300 years. The projected, anthropogenically induced, climate-change scenarios are expected to occur within the next 50–100 years, a rate of change for which there is no reference in the past. It would, however, be unwise to dismiss what is known about vegetation and climate changes in North America since the last glaciation, for instance, as irrelevant to late 20th century climate-change events because of differences in past and expected rates of climate change. Of particular relevance to the current debate is the body of paleowork related to the migratory rates of forest species in response to past climatic changes (e.g., Davis 1981, 1983, 1989; Huntley 1991; Overpeck et al. 1991; Prentice et al. 1991*b*; Webb and Bartlein 1992). Findings derived from these studies generally agree that migration rates of forest tree species in response to postglacial warming was very close to the maximum possible for the species investigated (Huntley 1991). The implications of these results to vegetation dynamics of boreal forest landscapes in the near future appear serious because of the lag in vegetation response to the anticipated rapid climate change. Known tree species migration rates during past warming episodes have been shown to be slower than would be required of present populations to remain within similar climatic conditions over the next 50–100 years. Poleward migration rates of 1.5–5.5 km/year would be required given current climate-change projections, which appear to be in excess of boreal tree species capabilities (Esser 1992; Gear and Huntley 1991). This disequilibrium between vegetation and climate will persist until the rate of climate change is slowed (Overpeck et al. 1991; Webb and Bartlein 1992), and until such time could be aggravated by altered fire regimes. Also, soils, which are one of the determinants of ecosystem development, are relatively inert to climatic fluctuations and would take much longer to change in physical or chemical composition. This fact will severely restrict the development and migration of ecosystems, even if the climate is favourable. An exception to this rule are the cryosols of permafrost terrain. As permafrost retreats in response to climate warming, soil forming processes can again resume and may significantly shorten the transition time to other vegetation types, especially when coupled with increased fire frequency (Rizzo and Wiken 1992; Suffling 1995; Waelbroek 1993).

Successful migration of tree species is a function of several distinct but interconnected steps, each of which has to be brought to completion during the life cycle of the individual. Seedlings have to be established, survive to reproductive maturity, and in turn, produce new propagules. Long-distance poleward migration requires many repetitions of this sequence of steps until a dynamic equilibrium between climate and vegetation is reestablished. Current climate-change scenarios suggest that this orderly northward progression of plant communities is precluded by the speed of anticipated warming (Webb 1995). Barriers to migration are the climatically induced limits to tree physiological adaptations on the one hand (Arris and Eagleson 1989) and out-of-phase fire regime on the other. For example, if a given species' migratory ability is asynchronous with the change in one of the fire-regime components, such as frequency, the species may become locally extinct or greatly reduced in abundance, and probably rather quickly.

Tree mortality due to adaptational limitations may be immediate and locally contained or widespread. Factors contributing to population decline or mortality include strong competitors favoured in a warmer and possible drier climate, reduction in symbiont populations such as mycorrhizae (Perry et al. 1987) or insect pollinators, disruptions in dormancy induction or release (Hänninen 1991; Murray et al. 1989), changes in control over cone serotiny (Gauthier et al. 1996*a*), and changes in seed production, ripening, and dissemination. The resultant local extinctions of some species would open up spatial and functional niches for the invasion of others, thereby fundamentally altering the shape of the boreal landscape from what it is today. New species assemblages could thus be constituted from various mixtures of recent arrivals and previous residents, some of which may find the changed climate conducive to greater productivity. This scenario was actually simulated for black spruce at the southeastern limit of its range, which indicated that this tree species grows best there, assuming soil moisture is not limiting (Bonan and Sirois 1992). Kirschbaum and Fishlin (1996) point out that such a development may also result in transiently enhanced species diversity because of forest fragmentation and formation of a richer mosaic of patches consisting of some remaining old communities and a variety of invaders taking advantage of the locally more favourable conditions.

Altered fire regimes

The close coupling of fire regime to climate makes it reasonable to assume that the changes in boreal forest landscape physiognomy will be accelerated by changes in fire regime that can be expected to proceed apace with climate change. There are three main agents that drive the change towards the altered face of the boreal forest landscape, namely, the changed vegetation or fuels complex, the changed potential for fire occurrence (lightning or human caused), and the change in fire severity due to changes in fire weather (Fosberg et al. 1996).

Of these three agents, the fuel complexes are expected to change through a climatically induced shift in species distribution, local mortality, and replacement of whole ecosystems. For example, at the southern edge of the boreal forest with a maritime influence, northern deciduous trees species and balsam fir (*Abies balsamea* (L.) Mill.) may displace the current mix of spruces, pines, larch, poplar, and birch. In midcontinental areas vegetation assemblages may shift to grasslands or xerophytic steppe vegetation (Emanuel et al. 1985; Kauppi and Posch 1985; Ritchie 1983; Rizzo and Wiken 1992). The altered vegetation types create a feedback loop to fire regime through altered surface fuel production, stand and canopy architecture, and changed decomposition and nutrient-cycling patterns, which affect organic matter depth and accumulation (Martin 1993). During the transition period, added fuel loading may be experienced for varying lengths of time owing to overstory mortality and stand breakup, increasing the fire severity component of fire regime and thereby contributing to accelerated ecosystem conversion or replacement. Fosberg et al. (1993), using the correlation model of fire intensity and fire spread in conjunction with the Köppen climate analog, suggested that fire intensity would double in the southern portion of the current boreal forest zone because of the changed forest fuel type. In the central and northern boreal zone modeled fire intensity remained largely unchanged because of little alteration to the fuel types; i.e., simulations suggest that the greatest and most immediate impacts can be expected to become apparent at the boreal forest borders.

The second agent of change to impact on fire regime in the boreal forest is changed ignition probability from both natural and human causes. Fosberg et al. (1996) and Price and Rind (1994) propose a lightning frequency increase of 30– 40% between latitudes 50°N and 70°N. Lorimer and Gough (1988) determined from historical records that lightning fire frequency is highest during drought years, apparently because of higher ignition probability during dry periods, a condition that can be expected to be exacerbated in a changed climate. These authors did not attempt to model people-caused changes in ignition probability, but speculated that increased human population pressure in and around the boreal forest fringe might act as an added ignition source. Increased natural ignition frequencies alone, especially within the context of an expanded fire season in a 2 × CO_2 world (Wotton and Flannigan 1993), represents an important aspect of fire regime affecting future boreal forest ecosystem structure and function.

Increased fire frequency is the supporting rationale for the anticipated change in age class distribution of fire-adapted boreal forest ecosystems. Greater fire frequency would favour the preponderance of younger age classes in the landscape vegetation mosaic and facilitate continued occupation of sites by early successional species assemblages (Brubaker 1986).

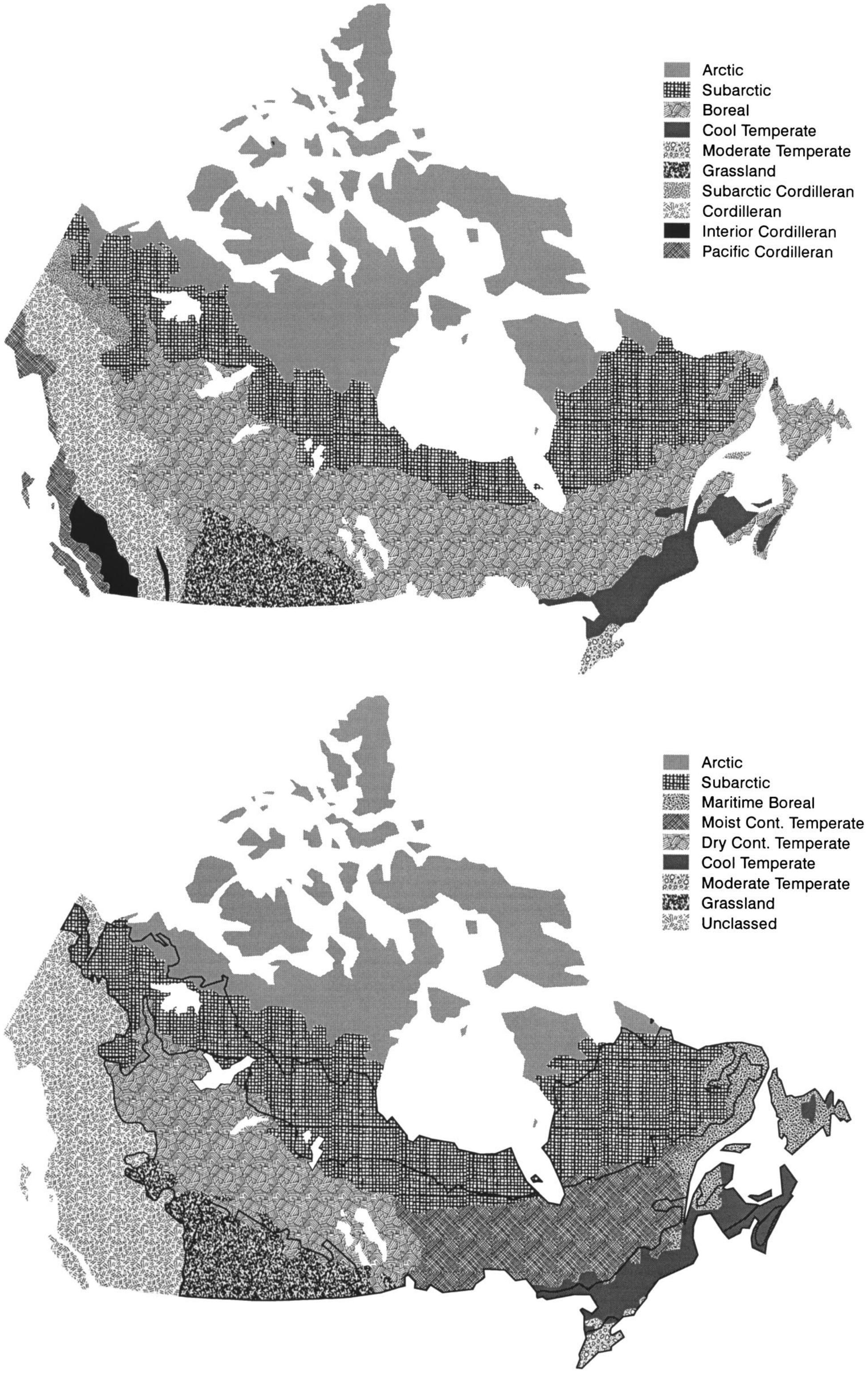
The third agent of climate change to affect fire regime is fire severity as affected by fire weather. Fire severity has been defined above and fire weather is a collective term describing those weather parameters that influence fire occurrence and subsequent behaviour (Merrill and Alexander 1987). In the boreal forest, extreme fire weather refers to those conditions that are conducive to high-intensity, fast-spreading forest fires that replace forest stands over large areas. Fire weather changes of the boreal forests of Canada and Alaska have been simulated for a 2 × CO_2 world by Fosberg et al. (1996) using output from the Canadian Climate Centre atmospheric GCM (McFarlane et al. 1992). The Canadian Climate Centre GCM contains 10 layers vertically, is based on a nominal 3.75° latitude/longitude grid, and incorporates interactive cloud parameterization. The level of sophistication of this model is further demonstrated when considering that it is constructed using improved solar- and terrestrial-heating calculations, a complex treatment of land surface processes that includes vegetation and soil type, and a simple ocean layer mixed with a sea ice component. Using base climatology from 191 stations in Canada, this model projects warming of 6–8°C in the continental regions of Canada and 2–4°C for Alaska (Fosberg et al. 1996; Stocks and Lynham 1996). According to this model, winter precipitation shows little deviation from the current climate, but spring temperatures are projected to be uniformly warmer by 2–6°C throughout the boreal zone. Temperatures during the rest of the fire season remained unchanged according to this model. Spring precipitation projections show 8–30% increases over present conditions, while middle to late (July–September) fire season precipitation patterns were projected to decrease. Taken together with the simulations provided by Wotton and Flannigan (1993), the picture that emerges is one of an extended fire season, especially into the autumn, during which fire severity and ignition potential increase over large continental areas of the Canadian and Alaskan boreal forest (Fosberg et al. 1996).

Boreal forest boundaries and ecotones

Two fundamental questions that remain to be answered are related to the temporal and spatial aspects of climate change; i.e., what is the impact on boreal forest boundaries, ecosystem distribution, and ultimately overall size, and what is the speed with which the changes can be expected to occur?

There seems to be consensus, between both field and simulation studies, that climate change will result in a greatly reduced boreal forest area and increased fragmentation (Emanuel et al. 1985; Monserud et al. 1993; Neilson 1993; Rizzo and Wiken 1992) and that the process will likely be accelerated by the altered disturbance regime (Turner and Romme 1994). Figure 6 shows the outputs of a 2 × CO_2

Fig. 6. Current (upper) and projected (lower) ecoclimatic provinces of Canada for a 2 × CO_2 climatic scenario using the GISS general circulation model (modified from Rizzo and Wiken 1992). Cont., continental.



simulation run using the Goddard Institute of Space Studies (GISS) model. According to this model, boreal forest area will be halved as a result of the discontinuity of the boreal and cool temperate provinces; the reduction of the subarctic and boreal ecoclimatic provinces; the increase in the size of the cool temperate, moderate temperate, and grassland ecoclimatic provinces; and the formation of transitional grasslands and semidesert ecoclimatic provinces (Rizzo and Wiken 1992).

Lenihan and Neilson (1995) expanded on this work by using the rule-based Canadian climate–vegetation model (CCVM) and inclusion of the Geophysical Fluid Dynamics Laboratory (GFDL) GCM. They examined five forest types (*Picea*; *Picea–Pinus*; *Picea–opulus–Pinus*; *Picea–Abies*; and *Pice–Pinus–Acer–Abies*) distinguished under current climatic conditions and found them to persist in the doubled-CO_2 simulations. However, there were significant changes in their distribution, areal extent, and dominance as landscape components, depending on the model used (Lenihan and Neilson 1995).

Tree-line dynamics at the southern and northern limits of the boreal forest are expected to be most sensitive to climate change (see Noble 1993 for a dissenting view) and alteration in disturbance regime and have received a great amount of attention within the framework of past and future global change (e.g., Black and Bliss 1980; Hogg and Hurdle 1995; Landhäusser and Wein 1993; Payette and Lavoie 1994; Payette and Filion 1985; Sirois et al. 1994). Indications are that, at least in the eastern boreal forest, the northern tree line has advanced into areas previously occupied by tundra ecosystems when climatically opportune (Payette and Filion 1985).

The plasticity of the tree line in relation to prevailing climate suggests that tree-line dynamics, during the Holocene and at present, has been marked by both equilibrium and disequilibrium conditions in time and space (Campbell and McAndrews 1993; Payette and Lavoie 1994; Szeicz and MacDonald 1995). Northern tree-line dynamics in a changing climate would be secondarily modified by altered fire regimes in the northern part of the boreal forest. For example, fires spreading across the forest tundra ecotone could locally displace the tree line to positions in disequilibrium with the climate (Sirois and Payette 1991). Timoney and Wein (1991) surveyed the western arctic tree line between the Mackenzie Delta in the west and northern Manitoba in the east and determined that fire return intervals showed a trend of increasing fire activity from 1950 through the 1970s. Postfire invasion of tundra by forest species has been observed by Landhäusser and Wein (1993) in the western arctic. They observed a postfire decrease of *Picea mariana* and *Picea glauca* in previously treed areas and a replacement by *Populus balsamifera* and *Betula papyrifera* with extension of the deciduous species into tundra areas. This represents a fire-generated fuel-type change across the tree line with all the accompanying changes in ecosystem structure and function.

The southern boreal forest ecotone, characterized by aspen parkland in the west and various deciduous admixtures in the east, is expected to respond to climate change in different ways regionally as pointed out by Bergeron and Dansereau (1993) and Bergeron and Flannigan (1995). In the east (east of Lake Superior), shade-tolerant tree species such as balsam fir, favoured by a decrease in fire frequency and increased precipitation, may persist and thrive or even expand if they are able to continue to occupy sites in the presence of competitors and insect pests (Fleming and Volney 1995), both of which could be newly arrived and (or) more aggressive than previously experienced (Williams and Liebhold 1995). In the west (west of Lake Superior), retraction of the southern boreal forest boundary in response to expansion of grassland seems to be indicated and fire weather indices along this part of the southern boreal forest are expected to increase in a $2 \times CO_2$ climate (Bergeron and Flannigan 1995; Flannigan and Van Wagner 1991). Pressure on the southern boreal forest ecotone due to increased fire activity in the west may be aggravated by a drastic impact on moisture regimes across the aspen parkland (Hogg and Hurdle 1995). Environmental stress along ecotonal boundaries can become intense in areas where the forest has become fragmented into small patches owing to natural or anthropogenic disturbance (Hogg and Hurdle 1995), thus increasing the speed of retreat of the southern boreal forest boundary.

Fragmentation of forest ecosystems or species' ranges may also occur within current or future boundaries of the boreal forest, not just at its borders. Thus, Flannigan (1993), studying the abundance of red pine (*Pinus resinosa* Ait.) in relation to fire regime, determined that the abundance of this species is negatively correlated with fire intensity, implying that fire regime with increased fire intensity might well reduce the abundance of this pine as a component of the southern boreal landscape. As well, those species dependent on fire for opening of serotinous cones will be adversely affected by any change in fire regime that might prolong the fire residence time in the crowns or the depth of the flaming front. Despain et al. (1996) found that maximum germination of lodgepole pine (*Pinus contorta*) seed occurred after surface fires, followed by crown fires with a 10- to 20-s exposure time of serotinous cones to the crown fire flame front. Increasing exposure time to flames had a drastic effect on germination rates, which were reduced to 0.3–14% after 60 s. As pointed out by Turner and Romme (1994), crown fires always contain areas of both low- and high-intensity fires and create a complex mosaic of burn severity across the landscape. Anticipated climate change may modify not only the frequency of crown fires, but also their severity, with important implications for ecosystem structure and function as well as landscape dynamics (cf. Gauthier et al. 1996*b*). Fire regimes may be more sensitive to climate change than any other ecosystem process (Clark 1990*a*) because fire behaviour responds immediately to fuel moisture, which is affected by precipitation and relative humidity. Fire regime can also be expected to respond rapidly to changes in fuel loading and arrangement as a result of overstory mortality. A synergistic agent in this regard may be insect attack (Fleming and Volney 1995) and blowdown (Flannigan et al. 1989), two other common boreal forest disturbances. Both disturbances have been implicated in increased fire hazard and insect attack especially has become a concern for fire management agencies (Stocks 1987). In the case of insect infestation, the mechanism is one whereby forest canopy removal and tree mortality by defoliation results in faster rates of surface fuel drying from increased solar radiation and easier wind penetration into the stand (Bonan and Shugart 1989). The drier conditions, combined with greater fuel loads from tree components such as bark, branches, and toppled trees themselves, may temporarily increase fire hazard and fire intensity after ignition. Although there is only limited historical evidence for this concurrence (Furyaev et al. 1983), increased lightning activity, as proposed by Fosberg et al. (1996), could make this scenario a reality in a changed climate. The interaction between climate change and fire regime could therefore potentially overshadow the importance of the direct effects of global warming on species distribution, migration, substitution, and extinction. If this scenario comes to pass, the rate of change of the boreal forest landscape could greatly exceed anything expected owing to atmospheric warming alone.

Socioeconomic and policy implications

Fire and forest management

Fire protection expenditures for Canada, for 1993–1995, the last years for which official statistics are available, ranged between a low of $142 million and a high of $275 million in 1993 and 1995 dollars, respectively (Canadian Council of Forest Ministers 1997). Most of that money was spent fighting boreal forest fires, by virtue of the geographical extent of this forest region, and represents 25% of the total cost of forest management in Canada. The cost of forest protection from fire is directly proportional to the area burned annually and has been increasing steadily, in step with the increase in area burned over the last two decades or so (Fig. 4) (Canadian Council of Forest Ministers 1997).

Strategic planning for fire management and fire as a competitor for timber supply in the boreal forests of Canada (Boychuk and Martell 1996; Martell 1994;Van Wagner 1983; Van Wagner 1991) will have to take the new fire regime into account. Anticipated increases in fire severity must take into consideration financial requirements necessary to maintain existing or possibly expanded levels of resource protection. Should the prediction of a prolonged fire season come to pass, serious attention will have to be given to the size of the seasonal suppression staff, and the tools and equipment needed to carry out the job during a longer and conceivably more severe fire season. Wotton and Flannigan (1993) cautioned that according to their analysis, the period in which fire control organizations would need to be prepared to fight forest fires would increase by 22%. Under this scenario, personnel and equipment resource requirements for fire suppression must include provisions for deployment to small fires to limit damage and containment of large fires that traditionally cause the majority of social and environmental damage (Weber and Stocks 1998). Martell (1994) examined historical fire data as part of a timber supply analysis for some regions of northwestern Ontario. Within the context of this study he concluded that the effectiveness of Ontario’s forest-fire management system had prevented significant reductions in timber supply in most districts studied. We contend that the new fire regime would dictate greatly increased fire management expenditures if current levels of timber supply are to be safeguarded.

Increased levels of protection would also be required if massive reforestation and afforestation strategies would be adopted as a means of carbon sequestration (Botkin et al. 1993). Neither the economic nor ecological implications of such an approach to global warming are entirely clear (Englin and Callaway 1995; Harmon et al.1990; Schroeder and Ladd 1991; Vitousek 1991), but if enshrined in policy these implications would obviously have to be followed up with appropriate protection of lands so designated.

One of the simulation studies dealing with the impact of global warming on wildland fire showed that, in a 2 × CO_2 climate, area burned and frequency of escaped fires were consistently higher than what is observed under present conditions (Torn and Fried 1992). Policy makers can be expected to be increasingly called upon to prioritize values at risk and allocate public expenditures accordingly. A reasonable set of fire management guidelines could include increased protection of high-value areas, while expanding areas currently only under limited protection (Stocks 1993). Therefore, the economics of a projected increase in wood availability in the boreal zone due to climate change must be weighed against the increased cost of intensified forest management and protection (Solomon 1996). As well, the potential skewing of the age class distribution towards a younger age class structure because of increased fire frequency must be considered when assessing economic impacts on the boreal forest as a whole. The long-term economic and social repercussions of the replacement of large areas of coniferous growth by hardwood species (Aerts 1995), some of which may be economically inferior or result in displacement of wildlife species, similarly await detailed examination.

Nontimber resources

The economic analysis issue is further complicated by the fact that boreal forests, in Canada and elsewhere, are no longer viewed simply as a provider of raw materials for industry or the general economic dynamo of a country. At the end of the millennium, nonmarket values of the boreal resource have captured global awareness to a degree that at least rivals, if not surpasses, traditional economic concerns (Xu et al. 1995). Forest nations like Canada, therefore, have stewardship responsibilities toward the boreal forest region that extend far beyond its national boundaries.

Topics at the forefront of public and scientific debate include sustainability of such nonfibre forest assets as plant and animal biodiversity (Bergeron and Harvey 1997; Davis and Zabinski 1992; Graham 1992; Heywood 1995; Peters and Lovejoy 1992) and water supply (Aber et al. 1995), and the role of the boreal forest in the global carbon cycle (Apps et al. 1995, 1993; Kurz and Apps 1993). Many of the issues related to biodiversity, carbon cycling, and altered boreal forest fire regime in a changing climate have yet to be resolved experimentally or through computer simulation. Studies from other biomes, however, may offer a glimpse of what could be in store for the boreal forest. A ground-breaking study by Naeem et al. (1994) showed that declining biodiversity reduced ecosystem performance, especially CO_2 absorption, and productivity in environmentally controlled, laboratory-based, terrestrial microcosms. These findings were extended by Tilman et al. (1996) to field-based grassland ecosystems and demonstrated that the loss of species threatened ecosystem productivity, sustainabilty of nutrient cycling, and overall ecosystem stability. The grassland lessons may be extended, in the most general sense, to boreal forest ecosystem structure and function in a changing climate, where altered fire regimes might reduce species diversity in time and space. Decreased CO_2 absorption capability of diversity-impoverished vegetation, especially in combination with ongoing harvesting activity, would also reduce the carbon sink strength of the boreal forest with direct effects on the global carbon cycle and positive feedback to global warming (Apps et al. 1993; Bonan et al. 1992; Kohlmaier et al. 1995; Kurz and Apps 1993). The interaction of forest harvesting with climate change and fire regime in the boreal forest has received very little research attention and must be addressed aggressively to complete the picture of global change impacts on boreal forest ecosystems.

Biodiversity, which is more than simply a measure of the number of species, describes the variety of life over a wide spectrum of levels, from genetics through the taxonomic and ecological hierarchies to communities, habitats, and ecosys-

Table 1. North American boreal forest biome carbon pools and fluxes (modified from Apps et al. 1993).

Parameter	Canadian boreal forest	Alaskan boreal forest
Area (Mha)		
Forest	304	52
Peatland	89	11
Pools (Pg C)[a]		
Plant biomass[b]	8	2
Plant detritus	—[c]	1
Forest soil	65	10
Peat	113	17
Forest products	0.2[d]	<0.1
Fluxes (Tg C/year) [e,f]		
Forest[g]	62	6
Peatland	25	3
Forest products	8	<1

[a] 1 petagram (Pg) = 10^{15} g.
[b] Above- and below-ground live biomass.
[c] Plant detritus estimates included in soil C pool.
[d] Residual C content of products harvested 1940–1980.
[e] 1 teragram (Tg) = 10^{12} g.
[f] All flux values are net transfers from the atmosphere.
[g] All biomass and soil C pool dynamics.

Table 2. Biomass and combustion produced emissions from forest fires (modified from Cofer et al. 1996).

Combustion product	Emission (Tg/year)	Atmospheric impact
CO_2	$9.0\times10^3 – 15\times10^3$	Greenhouse gas
CO	$4.0\times10^2 – 9.0\times10^2$	Photochemistry
CH_4	$1.7\times10 – 3.8\times10$	Greenhouse gas
Nonmethane hydrocarbons	$1.5\times10 – 3.8\times10$	Photochemistry
Total particulates	$4.0\times10 – 17\times10$	Radiation
Organic C	$3.0\times10 – 9.0\times10$	
Elemental C	$0.5\times10 – 2.0\times10$	
NO_x	$0.5\times10 – 3.8\times10$	Photochemistry
H_2	3.0 – 9.0	Photochemistry
N_2O	0.4 – 2.0	Stratosphere
NH_3	0.5 – 6.0	Greenhouse gas
SO_x	1.0 – 7.0	Tropospheric chemistry
CH_3Cl	0.2 – 0.9	Photochemistry

tems (Haslett 1996). Degradations of boreal forest ecosystems due to changed fire regime will involve complex and poorly understood changes in soil–plant relations unlikely to be reversed by quick fixes. Interaction between the factors responsible for maintenance of high animal biodiversity are equally complex and information on their control is equally limited, but agreement seems to exist that animal biodiversity as an ecosystem attribute can only be managed by habitat and ecosystem management (Markham and Malcolm 1996; Myers 1995; Walsh 1992). If altered fire regimes will indeed lead to rapid forest cover changes at the landscape level, indications are that wildlife species that respond at that level (body size >1 kg) will be most affected by changes in landscape structure (Thompson et al. 1997). Studies dealing with the complexities of plant–fauna interactions at the close of the Pleistocene in relation to climate warming and the extent to which they may be used as a guide to future climate-change scenarios include those by Campbell et al. (1994), Graham (1992), and Zimov et al. (1995). A common thread that runs through these papers is the understanding that it would be preferable if habitat degradation could be prevented rather than be permitted to occur because reversals of ecosystem degradation and reduction in biodiversity are very costly and extremely time consuming (Perry and Borchers 1990). Potential impact of biodiversity loss or shifts in species distributions in time and space could have grave consequences for those aboriginal boreal forest dwellers who are still pursuing traditional life styles. Although accustomed to striking, short-term fluctuations in wildlife populations (Winterhalder 1983), their coping strategies may be inadequate to account for the long-term and rapid changes anticipated under a climate-driven change in fire regime.

The nontimber values that are impacted by climate change represent the most difficult issues facing policy makers today because their resolution requires consideration of technological feasibility, economic viability, political desirability, administrative manageability, social acceptability, and ecological soundness (Schneider 1989; Zinck and Farshad 1995).

Carbon cycling

The other compelling topic of international concern at the policy level is the role of Canada's boreal forests in the global carbon cycle (Kasischke et al. 1995). The theme has been thoroughly explored in a volume edited by Wisniewski and Sampson (1993). Apps et al. (1993) and Kurz and Apps (1993; 1995) provide a coherent picture of the contributions of the boreal forests to the global carbon cycle (Table 1) and how it might be impacted by altered fire regime. These authors recognize that one of the most significant factors influencing the transient response of the boreal zone to global change is the potential for dramatic changes in the disturbance regime, particularly fire intensity and frequency. They determined that a threefold difference in area burned, as observed between 1986 and 1989 (Fig. 4), was reflected in an 86% reduction in the net ecosystem C sink. These authors cautioned that C transfers associated with fire must be balanced against the uptake from regenerating forests and their enhanced productivity. However, computer simulations for the boreal forest and field research from tundra areas to the north indicate that these ecosystems may already have changed from CO_2 sink to source, which may increase in strength as atmospheric warming proceeds (Oechel et al. 1993; Solomon and Leemans 1997).

Increased fire frequency and intensity of boreal forest fire regimes under climate change have a further positive feedback to global warming because of the composition of fire emissions. Cofer et al. (1996) list 15 biomass combustion products that can be expected from boreal forest fires (Table 2), several of which are radiatively active gases and hence contributors to the greenhouse effect. High-intensity, stand-replacing forest fires, common in the boreal zone, typically loft emissions to near stratospheric altitudes and have the potential to reinforce the self-feeding loop between global warming and increasing fire occurrence in the boreal forest (Cofer et al. 1996).

Conclusions

Fire is a pivotal ecosystem process in the North American boreal forest. The importance of fire to ecosystem structure and function of fire-dependent systems is demonstrated by removing it as a process and observing the effects of its absence. An example of this landscape-level experiment has been provided by excluding fire from those national parks where it had played a historical role for millenia before the implementation of a fire exclusion policy (Woodley 1995). The vegetation characteristics and landscape mosaics that had served as the rationale for designating these areas as parks in the first place were rapidly disappearing in the absence of fire. Fire exclusion in certain National Parks was therefore recognized as ill advised and has been replaced by a vigorous program of ecosystem restoration through careful reintroduction of fire (Alexander and Dubé 1983; Van Wagner and Methven 1980; Weber and Taylor 1992; Weber and Stocks 1998).

In light of the available evidence from paleoinvestigations, field experiments, and simulation studies, climate change with its accompanying alteration in fire regime (intensity, frequency, seasonality, size, type, and severity) will have similar far-reaching impacts on boreal forest ecosystem structure and function. Indications are that the physiognomy of the boreal forest, as we know it today, would be radically altered, mostly because of the unprecedented speed at which the changes are proceeding. Fire regime as an ecosystem process is highly sensitive to climate change because fire behaviour responds immediately to fuel moisture, which is affected by precipitation, relative humidity, air temperature, and wind speed. Recognition of this relationship leads us to conclude that the rate and magnitude of fire-regime-induced changes to the boreal forest landscape could greatly exceed anything expected owing to atmospheric warming alone.

The new fire regime would affect such aspects of boreal forest structure as age class distribution, species mix and landscape mosaics, ecotones, and forest boundaries. Functional parameters subject to change include biomass production, litterfall, decomposition, organic matter, and nutrient turnover rates, as well as carbon sequestration and susceptibility to pathogens and insect attack, all of which have feedback loops to climate change and fire regime through altered fuel moisture, quantity, and configuration.

These projected changes pose formidable challenges to policy makers concerned with socioeconomic aspects of boreal forest management and stewardship. At issue are tangible and economically tractable commodities like timber supply and fire management costs and intractable human costs to boreal forest dwellers and the global community as a whole. The latter include habitat loss, the attendant reduction in long-term plant and animal biodiversity, and impacts on planetary atmospheric conditions.

Research strategies to help us cope with anticipated changes have been proposed by Kirschbaum and Fishlin (1996) to improve the predictive power of current modeling approaches, Solomon (1996) for new research products needed to conduct an accurate assessment of the socioeconomic impacts of forest responses to climate change, and Brown (1996) to improve our ability to estimate the mitigation potential of forestry practices. We urge research policy makers to consider the following areas of research for priority allocation of resources: (*i*) the interaction of boreal forest harvesting with fire regime in a changing climate; (*ii*) the linkage of insect and disease outbreaks to the new fire regime; and (*iii*) establishment and continued support of a system of research sites, along the lines of the U.S. Long Term Ecological Reserve program, but with a latitudinal focus, to formalize long-term monitoring of ecosystem structure and function in a changing climate. Policy makers must also strive to create a research environment that encourages, facilitates, and maintains collaborative efforts between the natural and social sciences. This is not an original request, but reflects our concern for the lack of attention and analysis devoted to the social processes that aid or impede transformation of scientific knowledge into popular acceptance by society (von Storch and Stehr 1997).

These calls for increased research and monitoring activities have to be balanced by an immediate application of what is already known because, as pointed out by Thomas (1979) and quoted in Hunter (1990) “ to say we don’t know enough is to take refuge behind a half-truth and ignore the fact that decisions will be made regardless of the amount of information available.” The inherent conservatism of scientists when making predictions and recommendations for policy makers would probably benefit from occasional application of Ockham’s razor. One of the many vernacular versions of Ockham’s razor states we should favour the simplest hypothesis that is consistent with the data (Jefferys and Berger 1992). Scientific advice for considerations by policy makers must be based on the best available data, but should convey the sense of increased urgency felt by the scientific community that boreal forest ecosystem structure and function are about to undergo fundamental change.

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