FIRE ECOLOGY AND USE IN RELATION TO BOREAL FOREST ECOSYSTEM STRUCTURE AND FUNCTION

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ABSTRACT

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. Boreal forest ecosystem structure and function are described in terms of the adaptations evolved in response to the periodic occurrence of fire. Recognition of the role of fire as an ecosystem process in boreal regions has resulted in its use in contemporary Canadian forestry practice and ecosystem maintenance and restoration. Examples are provided showing how wildfire and prescribed fire affect the substrate (e.g., soil temperature) and ecosystem processes (e.g., decomposition, soil respiration, and nutrient use efficiency of tree seedlings). Application of a natural disturbance paradigm to boreal forest ecosystem management in Canada is presented, pointing out the challenges and opportunities to research and operational practice.

keywords: boreal forest, cone serotiny, ecosystem management, fire adaptations, soil nutrients, soil temperature, vegetation mosaics.

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INTRODUCTION

In North America the boreal forest represents the most extensive forest cover type, forming an uninterrupted, broad transcontinental crescent from Newfoundland to Alaska (Figure 1). There are minor excursions southward into the Appalachian Mountains of New England and into Minnesota and major ones into the western mountain systems of Canada and the United States (LaRoi 1967). In Canada and Alaska fully 75% of all wooded land and 67% of exploitable closed forest are located in the boreal forest (Kuusela 1992). Fire is the keystone ecosystem process in the boreal forest of North America 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 (Werner 1986, Fleming and Volney 1995), but fire is by far the most ubiquitous agent spatiotemporally.

Fire as an ecosystem process has been interacting with boreal vegetation at least since the Miocene (30 million years B.P.) or early Pliocene (12 million years B.P.), when the members of modern forest assemblages evolved (Weber and Taylor 1992). Therefore, by the end of the last glaciation (15,000 years B.P.), species' adaptations, including successional pathways after disturbance and forest ecosystems' interaction with fire, were well developed. When boreal forest ecosystems started developing on recently exposed surfaces from propagules originating south of the ice sheet or from unglaciated refugia, fire had already been incorporated as an ecosystem process into the development of the post-glacial landscape.

Recognition of fire as a natural disturbance agent has resulted in its widespread use as a forest management tool to accomplish various land and ecosystem management objectives in boreal and other forest regions. Impacts of wildfire and prescribed fire on substrate are myriad because of local and regional variations in the fire regime, which is an amalgam of fire frequency, intensity, severity, size, and time and season of occurrence. Each of these components, in turn, is affected by local climatic, fuel, terrain, and other conditions (Weber and Flannigan 1997).

Keeping in mind that variability will superimpose its imprint on fire impacts locally, this paper provides some overriding principles of fire impacts applicable to boreal forests and boreal forest substrates in general. The purpose of the presentation is to put the use of fire in context with the natural disturbance paradigm currently used to develop forest ecosystem management guidelines in the boreal forest, whereby forest harvesting is designed to approximate natural disturbance patterns.

EFFECT OF FIRE ON BOREAL FOREST SUBSTRATES

One of the major state factors controlling ecosystem processes over much of the boreal forest landscape is soil temperature (Van Cleve et al. 1986), especially on cold soils. Given the widespread distribution of permafrost, continuous and discontinuous, throughout the North American boreal forest (Figure 2), fire effects on cold soils can be expected to be significant on most sites. When a forest fire burns over permafrost-dominated terrain, the active layer (that which thaws out in

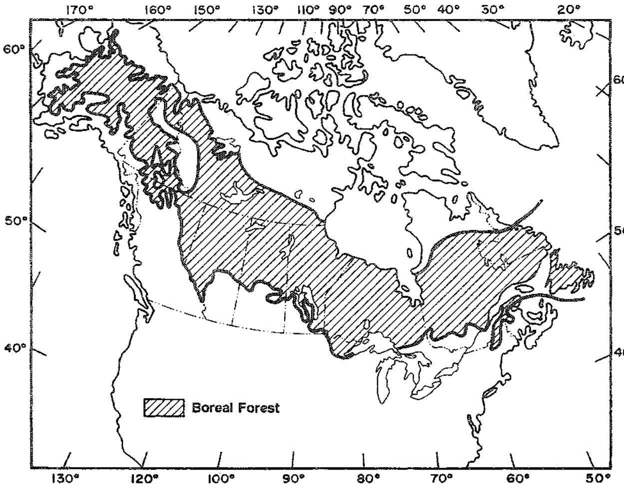

Fig. 1. The extent of the North American boreal forest (from Weber and Flannigan 1997).

Fig. 3. Black spruce forest at northern treeline near Inuvik, Northwest Territories. Note small clump of cotton grass, near bottom center of the photograph. (Photograph taken by M.G. Weber.)

the summer) tends to deepen for a few years in response to the increase in soil temperature. Increased substrate temperatures are generated by removal of insulating vegetation cover and surface organic layers, reduced heat loss from evapotranspiration, and lowering of the albedo from the burned surface. In time, the depth of the active layer decreases and reverts to prefire thickness as vegetation redevelops (Mackay 1995). Vegetation response to a warmer soil temperature regime can be dramatic, as shown in Figures 3 and 4. These photographs show how cotton grass (*Eriophorum vaginatum*), a circumpolar species, exploits improved substrate conditions (warmer soils, increased microbial populations, more rapid nutrient turnover, greater soil depth for root exploration), temporarily dominating postfire surfaces on cold soils near the northern treeline.

The importance of temperature control over boreal forest ecosystem processes has been repeatedly emphasized (Van Cleve et al. 1983, Anderson 1991, Van Cleve et al. 1991, Anderson 1992, Bonan 1992) and experimentally demonstrated by Van Cleve et al. (1986) for Alaskan taiga ecosystems. These workers produced substantial short-term changes to the physical and chemical nature of the substrate by artificial

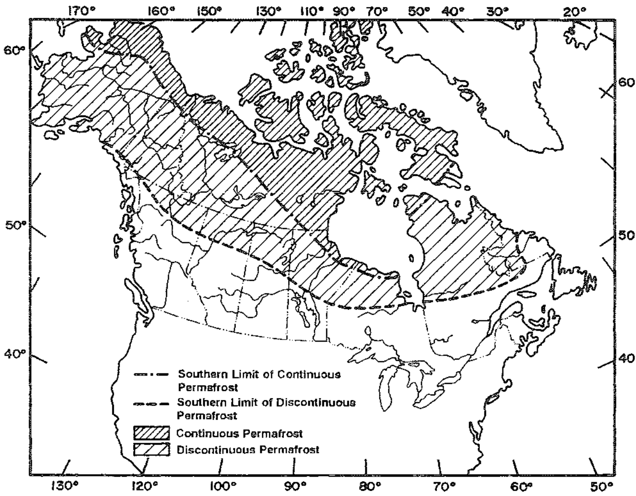

Fig. 2. Permafrost distribution in North America (from Weber and Flannigan 1997).

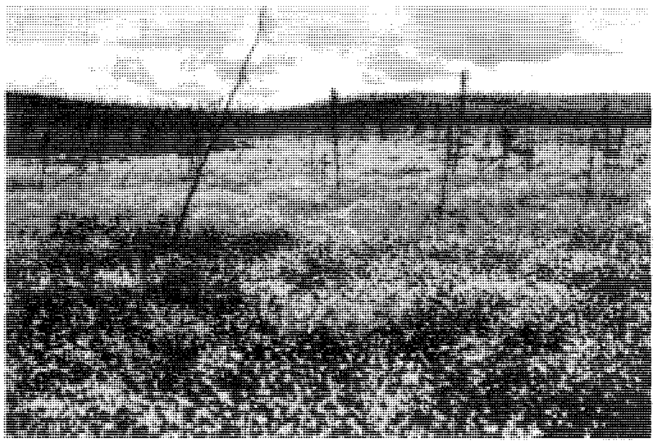

Fig. 4. Dramatic postfire proliferation of cotton grass in black spruce forests. Same area as Figure 3. (Photograph taken by M.G. Weber.)

Fig. 5. Even-aged, monoculture jack pine stand regenerating under burned jack pine overstory near Wood Buffalo National Park, Northwest Territories. (Photograph taken by M.G. Weber.)

soil heating. Forest floor weight declined by 20% during the 3-year experiment. Microbial respiration in the forest floor increased significantly, as did soil solution NH_4, available P, and total N. Higher nutrient and organic matter turnover rates and accelerated decomposition in the warmer soil reduced forest-floor mass and increased the concentration of available soil nutrients. 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).

Effects of elevated soil temperature and improved nutrient conditions are less pronounced in more southerly locations of the boreal forest, but are nonetheless an important characteristic associated with periodic fires throughout the boreal forest. Duration of postfire effects and the successional trajectory upon which the vegetation will embark, are a function of fire regime and its components as defined above. Traditional concepts of secondary succession, including passage through several seral stages, leading to a climax stage of vegetation development, have been difficult to apply in most boreal forest landscapes because of the ubiquity of fire and the species' adaptation to its fairly regular recurrence. For example, in boreal forests of jack pine (*Pinus banksiana*), black spruce (*Picea mariana*), paper birch (*Betula papyrifera*), and aspen (*Populus tremuloides*), postfire recolonization is immediate and overwhelmingly by the same species present before the disturbance (Figure 5). In these cases there is no large-scale species displacement, and gradual recovery progresses over time through various plant community stages to the prefire forest cover type. The prefire area occupied by jack pine, for example, is retained after fire as a jack pine mosaic within the landscape. Jack pine stands are one of the best examples we have of large-scale, fire-evolved, natural monoculture forests in the boreal forest.

The case of jack pine provides the strongest case for adaptations of tree species to the periodic passage of fire. Without fire to open its serotinous cones, this tree species would actually disappear as a natural component of the boreal forest landscape in the absence of fire. Besides opening serotinous cones, fire fulfills 2 more important requirements for successful regeneration of this species. First, fire creates a mineral soil seedbed necessary for germination and survival of the young seedling. Second, fire temporarily eliminates overstory shade and other competition, allowing early seedling growth in full sunlight. Figure 6 illustrates this relationship by showing jack pine seedling height response to postfire overstory tree mortality and forest floor consumption (Weber et al. 1987). Black spruce (*Picea mariana*) has similar, if not as exacting, regeneration requirements. Prefire birch (*Betula papyrifera*) and aspen (*Populus tremuloides*) stands recolonize disturbed areas vegetatively from stem sprouts or root suckers, respectively.

It thus becomes apparent that the classical terms "succession" and "climax" seem inappropriate when applied to boreal forest ecosystem dynamics after fire. Exceptions that occasionally approach climax situa-

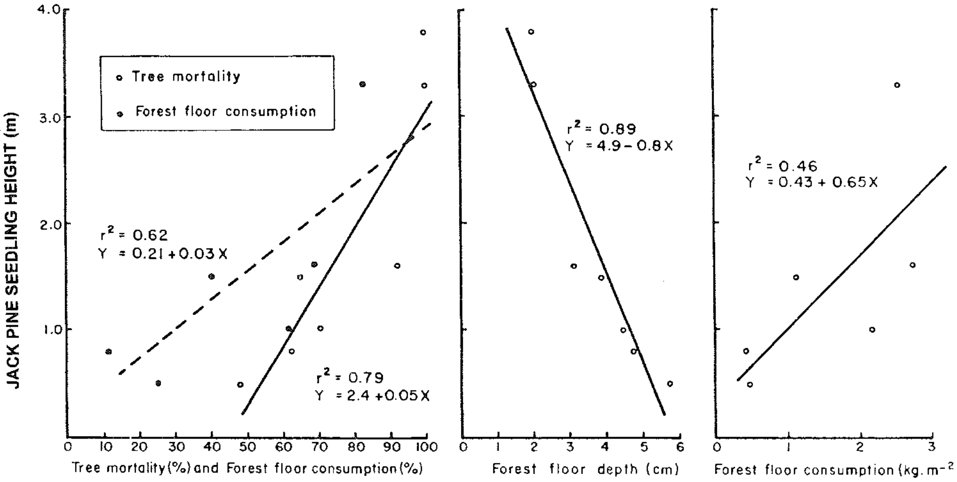

Fig. 6. Jack pine seedling performance in relation to overstory tree mortality, forest floor consumption, and depth reduction (from Weber et al. 1987).

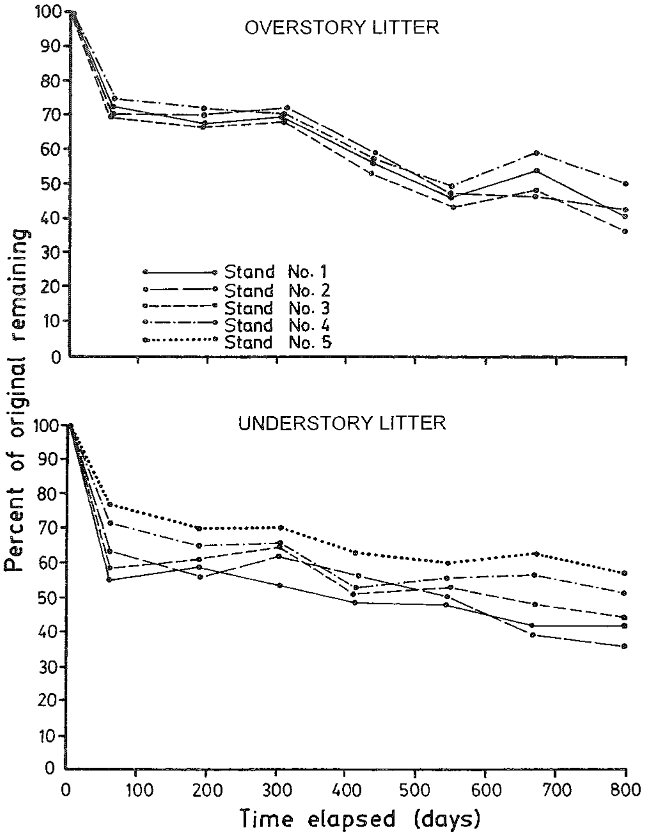

Fig. 7. Overstory (needles) and understory litter mass loss from litter bags placed on forest floor surfaces of five jack pine stands in eastern Ontario. Stand No. 1—age 65 years; No. 2—understory burn; No. 3—understory burn; No. 4—age 21 years; No. 5—age 8 years. Note lack of overstory litter on Stand No. 5, due to regeneration failure after burning of an immature age class on this site (from Weber 1987).

tions in the classical sense include lake and river floodplain islands, maritime areas, or higher elevations where successional trends may be clearly discernible (Wright and Heinselman 1973).

Fire adaptation of the ecosystem as a whole, not just of tree characteristics, can be demonstrated by examining ecosystem processes, such as organic matter decomposition or litter nutrient dynamics, on a series of jack pine stands of different ages and disturbance histories (Weber 1987). Thus, ecosystem stability in the presence of fire can be inferred from the rapid recovery of ecosystem processes at the soil surface (litterbag dynamics) in stands of various age classes and fire histories (Figures 7a-b, 8a-b). Nutrient and organic matter dynamics in the mature, 65-year-old jack pine forest ecosystem (Stand No. 1), are approximated by stands of younger age classes after fire (Stand No. 4), as well as stands subjected to repeated understory burning (Stand Nos. 2, 3, and 5).

Soil respiration is another vital ecosystem attribute that has been used to assess the recovery and hence resilience and stability of fire-adapted forest types (Weber 1985, 1990). For example, aspen forests have been shown to recover their soil respiration patterns quickly after disturbance such as fire or cutting (Figure 9), indicating that these ecosystems are adapted to periodic disturbance, prescribed or natural, if properly spaced in time (Weber 1991).

Besides fire's vital association with individual tree species, the other important role of fire in the boreal forest is maintaining the vegetation mosaic in the landscape. The boreal forest landscape mosaic constitutes the underlying basis for plant and animal biodiversity within this biome. The landscape mosaic, and hence biodiversity, is safeguarded by the dynamic nature of fire. Fire is more than a straightforward binary event; it does more than simply occur or not occur. Once a forest fuel complex has been ignited, fire spreads in non-uniform fashion across the landscape. The resulting patchwork of vegetation types and age classes in the landscape is therefore much more than a function only of fire-return interval or fire frequency. Figure 10 shows that even a single fire does not provide uniform burned area coverage. Each of the patches, differentially affected by fire, will take a different pathway to preburn recovery with respect to vegetation dynamics, ecosystem processes, and immigration and emigration of animal species. There are infinite possible landscape diversity scenarios when superimposing such variables as fire-return intervals, fire intensities, phenological state of the vegetation (time of year of the fire), and postfire local climatic conditions over the occurrence of a single fire. Only fire can provide the resource mix required by various wildlife populations or the habitat requirements for a single species at different times during the year and for different stages in its life cycle (Weber and Stocks 1998).

THE USE OF FIRE IN BOREAL FOREST ECOSYSTEM MANAGEMENT

If fire is a crucial boreal forest ecosystem process, then interference with its natural role or alteration of its long-term regulatory function can be expected to have pronounced effects at both the local level and biome scales. Conversely, acknowledgment of fire as a natural agent helps to validate its use as a management tool in contemporary forest ecosystem management practice.

An instructive example of the effects of altering local fire regimes can be found in some of Canada's national parks. As elsewhere, national parks are set aside, presumably in perpetuity, to preserve ecological or aesthetic aspects of the natural environment. Until recently, fire was not recognized as an ecosystem process in any of Canada's national parks and therefore suppressed as undesirable whenever it occurred within park boundaries. This lack of recognition of fire as an integral part of boreal forest ecosystem structure (e.g., vegetation patterns) and function (e.g., biogeochemical cycling) caused changes in the vegetation characteristics and landscape mosaics that had served as the rationale for designating these areas as parks in the first place. Even after fire was recognized as a key organizing factor in forest ecosystem dynamics, it took some time to develop the policy framework that al-

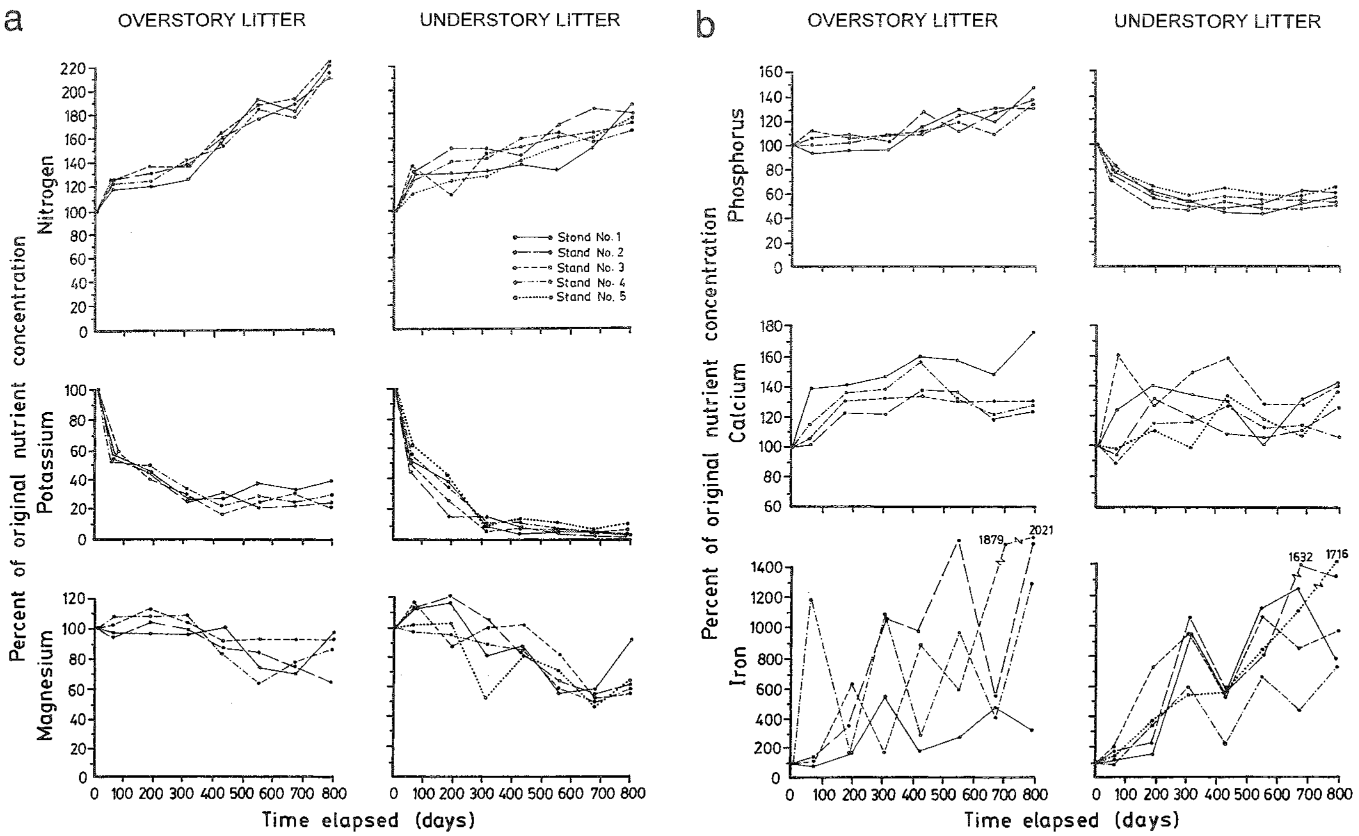

Fig. 8. (a) Overstory and understory litter nutrient dynamics (N, K, Mg) on the same stands as Figure 7 (from Weber 1987). (b) Overstory and understory litter nutrient dynamics (P, Ca, Fe) on the same stands as Figure 7 (from Weber 1987).

lowed restoration of fire to those plant communities requiring it for their perpetuation (Alexander and Dubé 1983, Day et al. 1990, Weber and Taylor 1992). The Canadian Parks Service had 3 options to manage large parks containing fire-dependent vegetation: (1) use fire as a management tool, (2) permit artificial means of vegetation renewal, or (3) accept drastic changes in park vegetation and wildlife with time (Van Wagner and Methven 1980). Parks Canada policy makers chose the first option and initiated an ambitious fire management program for several of their parks, particularly in the west (Lopoukhine 1983).

With a new directive produced in 1986 and a comprehensive fire policy review, Parks Canada embarked on a new relationship with fire and restored it to its natural role by active management. Unregulated wildfire was considered an unacceptable alternative in most parks because of the implied lack of control over its effects and perceived threats to public safety, property, rare species, and delicate habitats (Woodley 1995). The many years of fire exclusion in parks had resulted in fuel accumulation and changes in fuel complexes that would have resulted in fire behavior completely different from pre-suppression conditions. The only course of action to deal with the modern fuel realities was deemed to be through planned-ignition prescribed fires. Thus, prescribed burning of several thousand hectares annually is not unusual to maintain desired ecosystem attributes in fire-adapted ecosystems of Canada's national parks (Weber and Taylor 1992).

A special application of fire for ecosystem maintenance and restoration has taken place at least every 2 years since 1983 in southern Ontario. There, fire is used for the restoration and maintenance of one of the last remnants of the tallgrass prairie biome in eastern North America. Not strictly a boreal forest ecosystem, it is nonetheless of interest here because of its geographic proximity to the boreal forest and the example it provides within the context of fire and ecosystem management. The tallgrass prairie ecosystem, now preserved as an 85-hectare provincial park, can be maintained only by regular fires (Hayes and Seastedt 1989). In the absence of fire, succession to dense woodland takes place over time, with a rapid reduction in biodiversity (Bevan 1977, Sulston and Bruin 1985, Knapp and Seastedt 1986).

One of the more traditional uses of prescribed fire is for site preparation, which is applied extensively in the boreal forests of Canada. Prescribed burning is considered a lower-cost alternative to mechanical site preparation, although it cannot be applied in all situations because of various operational, environmental, and social constraints (Weber and Taylor 1992). One of the important differences between the 2 site preparation techniques is that fire can be manipulated in such a way as to remove varying amounts of surface organic material compared with mechanical means, such as disk trenching, which simply leave behind a mineral soil furrow of fairly constant depth. Both methods of site preparation are assuming greater im-

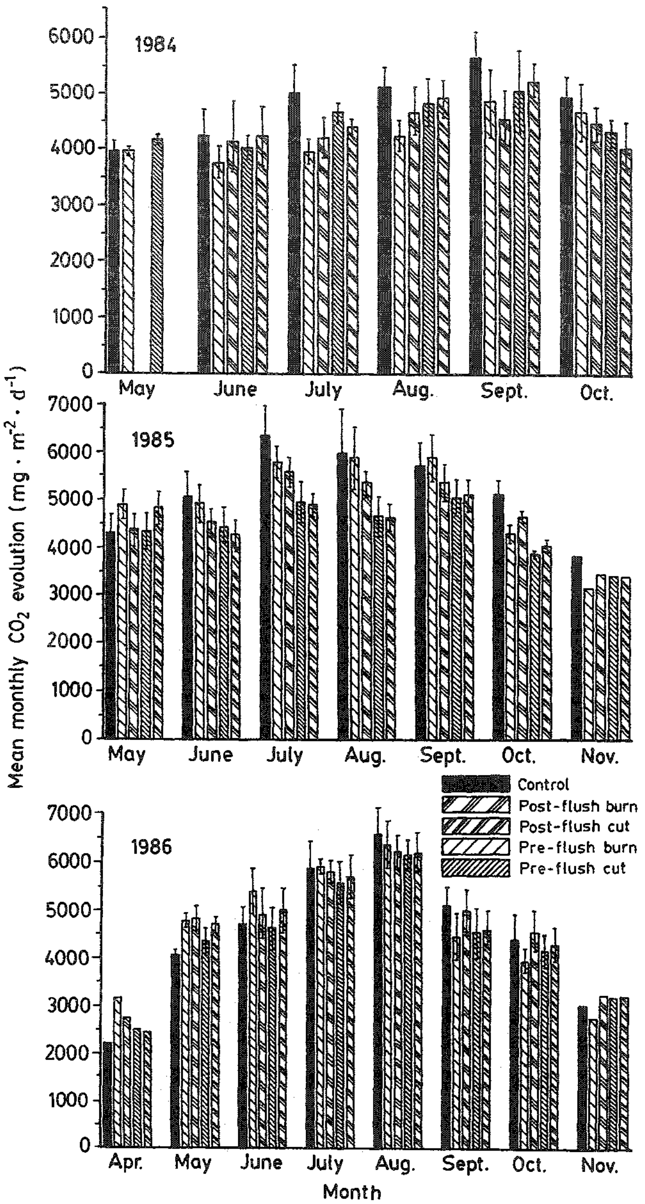

Fig. 9. Soil respiration (CO_2 evolution) from aspen stands burned or cut before and after vernal leaf flush in eastern Ontario. Note lack of significant respiration differences on all treatments after 3 years (from Weber 1990, 1991).

portance in Canada as alternatives to herbicides for vegetation management (Weber et al. 1995).

The requirement of some sort of site preparation as a prerequisite for successful plantation establishment has been demonstrated experimentally for early development of white pine (*Pinus strobus*) and red pine (*P. resinosa*) in eastern Ontario. Thus, lack of site preparation on clear-cut areas resulted in unacceptably high seedling mortality of either pine species (Figure 11) due to excessive growth of competing vegetation, especially bracken fern (*Pteridium aquilinum*). The warmer substrate temperature regime on the burn and disk trenching treatments, especially at rooting depth (Figures 12, 13), can be expected to have contributed to the observed increase in biomass production and nutrient use efficiency on site-prepared plots (Table 1).

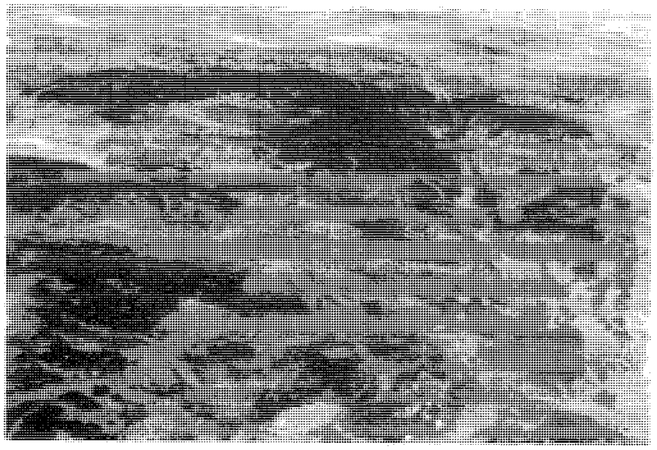

Fig. 10. Postfire mosaic of burned, partially burned, and unburned boreal woodland in Ontario (photograph taken by B.J. Stocks).

Extension of the growing season, in spring or fall, on site-prepared treatments of cold boreal soils, may be of critical importance because low soil temperature has been shown to restrict conifer regeneration in a variety of forest regions by delaying budburst, reducing root or shoot growth, increasing water flow resistance of roots, increasing water stress, impeding nutrient uptake, and decreasing photosynthetic rates (Coates et al. 1991).

ECOSYSTEM MANAGEMENT AND THE NATURAL DISTURBANCE PARADIGM

Growing concern about the impacts of intensive forestry on biodiversity, aesthetics, and long-term pro-

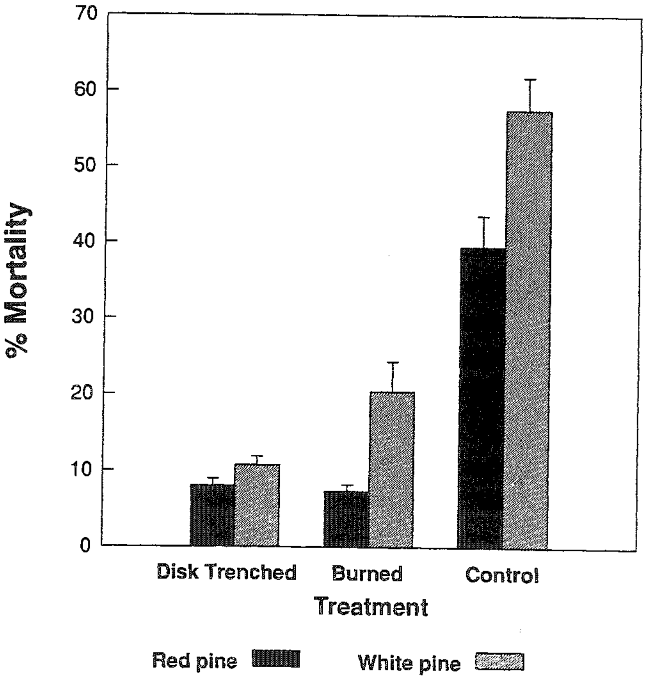

Fig. 11. Red and white pine seedling mortality on prescribed burned, disk trenched, and untreated clear-cut substrates after the first growing season in eastern Ontario (from Weber et al. 1995).

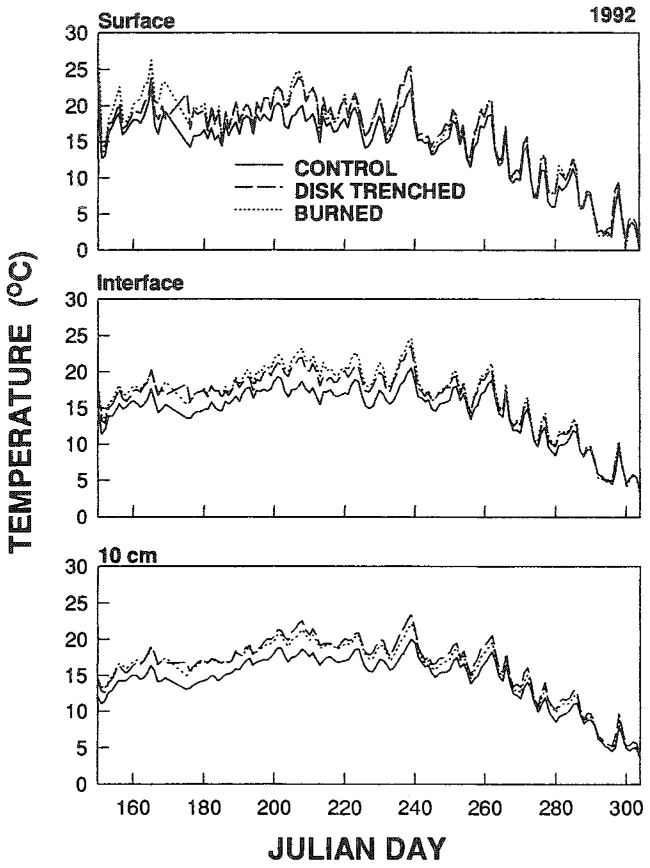

Fig. 12. Soil temperature profiles for 3 depths on prescribed burned, disk trenched, and untreated clear-cut substrates during the first growing season after treatment application (from Weber et al. 1995).

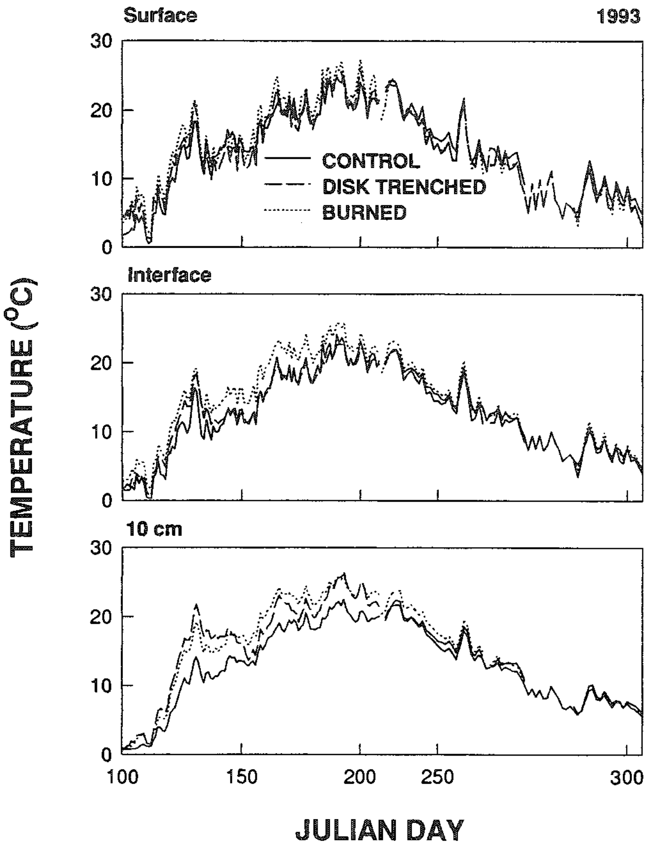

Fig. 13. Soil temperature profiles for 3 depths on prescribed burned, disk trenched, and untreated clear-cut substrates during the second growing season after treatment application (from Weber et al. 1995).

ductivity has led foresters throughout the world to reevaluate practices aimed solely at the maximization of wood fiber production. The paradigm has shifted for forestry, as strategies for the management of ecosystems instead of just trees are developed in a way that more closely approximates natural disturbance patterns in space and time (Spence et al. 1999, Volney et al. 1999). Silvicultural approaches are being brought into line with the widespread demand to leave a lighter footprint on the landscape.

Contemporary forestry practice focuses on ecosystem management, whereby individual forest stands should not be managed in isolation from the landscape in which they are embedded. Ecosystem management, regardless of which definition is employed, must address protection of the structural and functional complexity of the forests, such as the abundance and distribution of habitats, keystone organisms and attributes, and the cycling and storage of elements. Ecosystem management therefore involves a shift of emphasis from what is taken during harvest to what is left (Perry 1994).

In Canada, policy demands for the development of an ecosystem approach to forest management have energized the scientific wing of the profession. The scientific challenge consisted of the need to design and implement a large-scale field experiment to test the hypothesis that forestry operations can approximate natural disturbance by fire in the boreal forest. A large-scale, multidisciplinary, cooperative study has been initiated in northern Alberta to provide some answers to the question of comparability of partial harvesting with fire disturbance in the boreal forest. The experiment is referred to as EMEND (Ecosystem Management by Emulating Natural Disturbance) and represents the only hypothesis-testing, experimental approach currently underway to shed light on the controversy of forest harvesting as an approximation to natural disturbance.

Table 1. Biomass production and foliar nutrient use efficiency of white and red pine after 2 growing seasons (Weber et al. 1995).

	Biomass production[a]		Nutrient use efficiency[b]	
Treatment	White pine	Red pine	White pine	Red pine
Burn	145	434	49	79
Disk trenched	183	427	61	78
Control	17	88	5	44

[a] Percent difference in total seedling weight from t = 0 to end of second growing season.

[b] Weight of total seedling biomass produced since planting (grams per gram of total plant N).

The experiment is described in detail at *http://www.biology.ualberta.ca/emend/emend.html* with progress reported periodically at that website. Briefly, the overall objectives of EMEND are: (1) to determine which forest harvest and regenerative practices best maintain biotic communities, spatial patterns of forest structure, functional ecosystem integrity in comparison with mixed-wood landscapes that have originated through wildfire and other inherent natural disturbances, and (2) to employ economic and social analyses to evaluate these practices in terms of economic viability, sustainability, and acceptability to society. The experimental design is fully replicated, involving 3 experimental burning treatments of increasing surface fire intensity, 5 harvesting treatments, and appropriate controls in 4 forest ecosystem types from pure conifer to pure aspen with 2 intermediate mixed woods. Cooperators from various disciplines find EMEND particularly attractive because of the size of individual treatment plots (10 hectares) and the duration of the experiment (1 rotation, i.e., 80–100 years). The experimental design and treatments also have proven to be highly desirable to global change researchers interested in creating field-derived data sets to drive their models of harvesting and wildfire impacts on carbon sequestration in boreal forest substrates under climate change.

CONCLUSIONS

Fire is, and always has been, an integral part of the boreal forest landscape of North America. In spite of managers' sophisticated fire-management capabilities, it is neither economically feasible nor ecologically desirable to eliminate all fires from the boreal forest. On the contrary, in Canada, realization of the natural role of fire in the boreal forest has led to the reintroduction of fire into those national parks from which it had been excluded. Restoration of fire to its original role as an organizing factor in ecosystem structure and function is an ongoing process in designated Canadian parks and conservation areas.

Adoption of the natural disturbance paradigm for contemporary ecosystem management activities in the boreal forest represents challenges and opportunities for operational agencies, the forest industry, and researchers working in the boreal forest environment. The attempt to tailor forestry operations to approximate natural disturbances demands intensive, multidisciplinary research in the natural and social sciences to provide the scientific underpinnings required for ecosystem management of the boreal resource in a changing environment.

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