Dynamic Interactions between Forest Structure and Fire Behavior in Boreal Ecosystems

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This paper reviews and synthesizes literature on fire as a disturbance factor in boreal forests. Spatial and temporal variation in the biophysical environment, specifically, vegetative structure, terrain, and weather lead to variations in fire behavior. Changes in slope, aspect, elevation, and soil affect site energy and water budgets and the potential plant community. These terrain features also have a major influence on fire-caused disturbance through their role in determining moisture conditions and flammability of fuels on hourly, seasonal, and successional time-scales. On fine time scales (minutes to hours), changes in weather, specifically wind and relative humidity, significantly affect a fire's intensity and aboveground effects. Normal seasonal changes in dryness and periodic drought influence fire intensity and severity principally by affecting the depth of burn and belowground effects. On decades-long time scales changes in vegetative structure affect the mass of fuel available for burning and therefore the potential energy that can be released during a fire.

The severity of fire varies in time and space depending not only on the biophysical environment, but also on the location on the fire's perimeter (head vs. flank vs. rear). Spatial and temporal variation in severity within a fire can have long-lasting impacts on the structure and species composition of post-fire communities and the potential for future disturbances. Characteristic temperature histories of ground, surface, and crown fires are used to illustrate variations in fire severity. A soil-heating model is used to illustrate the impact of varying depth of burn on the depth at which various fire effects occur in the soil profile. A conceptual model is presented for the effects of fire severity on fire-plant regeneration interactions. The conceptual model can be used by restoration ecologists to evaluate the differential effects of controlled or prescribed fires and wildfires and to plan and implement fire treatments to conserve biodiversity.

Keywords boreal forest, disturbance dynamics, fire behavior, fire severity, stand structure

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1 Introduction

Disturbances (White and Pickett 1985), and fires in particular, are important processes for maintaining community and landscape biodiversity in boreal ecosystems (Wein and MacLean 1983a, Johnson 1992, Shugart et al. 1992, Goldammer and Furyaev 1996). Excessive and often haphazard use of fire historically occurred and continues to occur in some areas (Malluik 1995, Parviainen 1996, Pyne et al. 1996, Östlund et al. 1997, Hörnberg et al. 1999, Pitkänen and Huttunen 1999). In many areas, natural resource managers have been largely successful at removing fire from the ecosystem, leading to major changes in species composition and stand structure (Gromtsev 1996, Hardy and Arno 1996, Parviainen 1996, Arno et al. 1997, Smith and Arno 1999). Both scenarios, excessive fire and fire suppression, constitute significant departures from the disturbance regimes that have prevailed through most of the Holocene (Tolonnen 1983, Clark and Richard 1996). Departures from long-standing disturbance patterns are widely believed to be major factors in the loss of biodiversity in many parts of the world (Gill and Bradstock 1995) and particularly in boreal forests (Granström 1996, Parviainen 1996). As a result, there is now considerable interest in reintroducing fire in many boreal ecosystems.

An understanding of the role and use of fire in restoring and maintaining biodiversity requires studies that integrate phytosociology, landscape ecology, ecophysiology, and wildland fire science (Johnson 1992, Shugart et al. 1992, Ryan 1998, 2000a). There is considerable literature on short-term changes in post-fire community ecology. In contrast, relatively few studies have quantified long-term community (Arno et al. 1997, Covington and Moore 1994, Östlund et al. 1997, Hörnberg et al. 1999) or landscape dynamics (Arno et al. 1993, Syrjänen et al. 1994, Gromtsev 1996, Minnich and Chou 1997, Turner et al. 1997, 1999, Hessburg et al. 1999, Kasischke et al. 2000a). Likewise, there have been few attempts to address the long-term consequences of fire on biogeochemical processes at the individual, community, or landscape levels (c.f. Shugart et al. 1992, 2000, Keane et al. 1997, 1998, 1999). Morphological characteristics, plant architecture, and life history attributes interact with heat transfer mechanisms during fires resulting in variable plant responses (Noble and Slatyer 1980, 1981, Gill 1981, Keeley 1981, Rowe 1983, Peterson and Ryan 1986, Trabaud 1987, Johnson 1992, Fischer et al. 1996). The physiological ecology of individuals and species affect their ability to respond favorably in the post-fire environment. How individuals and species resist fire injury, as well as their physiological response to injury, affect a number of cascading secondary disturbance and successional processes. For example, variations in fire behavior lead to variations in tree injury, which in turn, affect such ecosystem processes as which species of insects attack fire-damaged trees (Geiszler et al. 1984, Ryan and Amman 1994, 1996), fungal flora (Littke et al. 1986, Penttilä and Kotiranta 1996, Richter et al. 2000), stand decomposition (Lowell et al. 1992, Richter et al. 2000), snag retention, and insectivorous avian dynamics (Hutto 1995, Saab and Dudley 1998). Improved understanding of the role and use of fire in the restoration and maintenance of biodiversity requires greater recognition of fire's variability in space and time and how that affects pattern and process.

While climate has a dominant influence on the overall productivity and character of vegetation (Woodward 1987, Kasischke and Stocks 2000), disturbances have a major impact on community structure and function during stand development (Grime 1979, White and Pickett 1985). Landscapes are composed of communities with varying disturbance histories. A disturbance is a discrete event that has a significant affect on community composition, structure, or function (White and Pickett 1985). Over time, aggregate multiple disturbances lead to dynamic communities and shifting landscape mosaics (Fig. 1). Weather, insects, diseases, exotic species, and fire dynamically interact to affect the composition, structure, and function of the stand. The range and distribution of disturbance are just as important as the average and extreme events. Each type of disturbance has its own characteristic influence on community structure. For example, severe windstorms tend to thin the forest from above causing the greatest damage to the dominant overstory trees, which often are the earlier successional species (Foster 1988). In contrast, a surface fire thins the forest from below causing the greatest

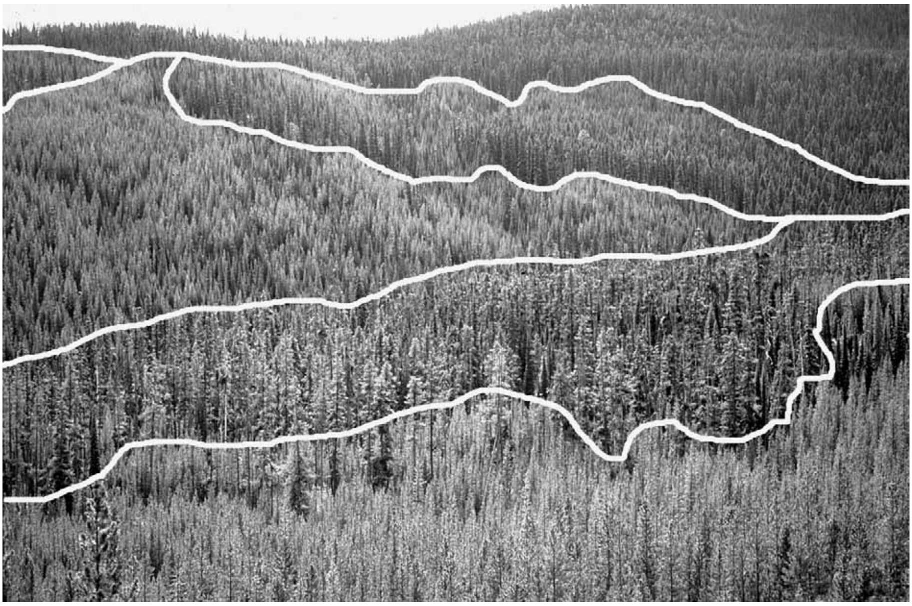

Fig. 1. Landscapes are aggregates of stands with multiple disturbance histories that affect the potential for future disturbances (from Arno et al. 1993). Photo by Steve F. Arno.

damage to smaller and younger trees, which tend to be the later successional species (Peterson and Ryan 1986, Ryan and Reinhardt 1988, Johnson 1992, Agee 1993).

Fire is a major disturbance in boreal ecosystems (Rowe 1983, Johnson 1992, Bonan and Shugart 1989, Shugart et al. 1992, Goldammer and Furyaev 1996, Kasischke and Stocks 2000). Fire science, the study of fire behavior and heat transfer mechanisms, provides a basis for understanding fire effects on individuals, landscapes and ecosystems (Albini 1976, Alexander 1982, Johnson 1992, Johnson and Miyanishi 2001). The purpose of this paper is to review fire as a disturbance process in boreal ecosystems, describe how spatial and temporal changes in the biophysical environment affect fire behavior and severity, and describe some relationships between fire severity, soil heating, plant survival, and regeneration.

2 Fire as a Disturbance Process

White and Pickett (1985) describe disturbance as a discrete event having attributes of kind or type, frequency, extent, seasonality, magnitude, and synergy. Fire is itself a dynamic process that varies in time and space, and each of these attributes has varying effects on the dynamics of boreal forests.

2.1 Fire Frequency

Fire frequency describes the number of fires in a given period of time. It is defined by such attributes as the mean fire return interval (the average number of years between successive fires in a given area over a given time period) and fire cycle (the time required to burn an area equal to the study area) (McPherson et al. 1990, Agee 1993, Brown 2000). Fire frequency is an important factor affecting species interactions because of age-to-reproductive-maturity considerations (Grime 1979, Noble and Slatyer 1980, 1981, Rowe 1983). Variations in fire frequency can also lead to variation in regeneration strategy within a species, e.g., proportion of cone serotiny (Muir 1993, Gauthier et al. 1996). Very frequent fires typically lead to dominance of species with short life-cycles, e.g., annual grasses and herbs

(Keeley 1981). Theoretically, frequent fires favor small patch size (Clark 1990, Malamud et al. 1998). On average the mass of burnable fuel, and therefore fire intensity, are inversely related to fire frequency (Olson 1981). An exception occurs when successive fires are much closer than the average fire return interval. For example, fire intensity and severity may be greater than normal when a stand replacement fire occurs in a mature coniferous forest and is followed by a subsequent fire in dense reproduction and heavy deadfall (Wellner 1970, Heinselman 1981, Hungerford et al. 1991, Gray and Franklin 1997). Variation in fire return intervals favors multiple species with varied life histories (Gill 1981, Keeley 1981, Noble and Slatyer 1981, Rowe 1983).

Several authors have reviewed fire frequency data for boreal forests (cf. Zackrisson 1977, Heinselman 1981, Wein and MacLean 1983b, Bergeron and Brisson 1990, Payette 1992, Wein 1993, Turner and Romme 1994, DeLong 1998, Brown 2000, Duchesne and Hawkes 2000). Fire frequencies vary from a few decades to several centuries depending on location. Fire frequency varies by climatic zone as seasonal patterns of precipitation (Johnson 1992, Payette 1992, Pojar 1996, Murphy et al. 2000, Flannigan and Wotton 2001) and lightning (Sannikov and Goldammer 1996, Latham and Williams 2001) vary. For example, on average, the frequency of fires decreases moving from the interior of Alaska and the Rocky Mountain Cordillera in the Northwestern part of the North American boreal forest toward the more humid boreal forest in southeastern Canada (Heinselman 1981, Johnson 1992, Pojar 1996, DeLong 1998, Murphy et al. 2000). Similar continental-scale patterns occur in the Eurasian boreal forest where fire frequency increases on average east of the Ural Mountains (Bonan and Shugart 1989). However, the minimum requirements for fires to occur are available dry fuel and a source of ignition. Because the energy and moisture constraints on combustion are spatially heterogeneous (Kunkel 2001), fire frequency is highly variable and short fire return interval vegetation types can be found on dry sites in more humid regions (Zackrisson 1977, Heinselman 1981, 1996, Rowe 1983, Bergeron and Brisson 1990, Engstrom and Mann 1991, Syrjänen et al. 1994). Within a climatic zone fire frequency varies by aspect because of its affect on the radiation balance (Kunkel 2001), by hillslope moisture gradients (Syrjänen et al. 1994, Samran et al. 1995, Kushla and Ripple 1997, Larsen 1997), and by proximity to human-caused ignitions (Syrjänen et al. 1994, Parviainen 1996, Swetnam 1996, Östlund et al. 1997, Hörnberg et al. 1999, Pitkänen and Huttunen 1999). Likewise, local drainage patterns (Larsen 1997) and landform (Zackrisson 1977, Hessberg et al. 1999, DeLong 1998) affect fire frequency. At the landscape scale fire movement may be viewed as somewhat analogous to the flow of a buoyant fluid. Natural barriers such as avalanche paths (Malanson and Butler 1984, Keane et al. 1997), lakes (Bergeron 1991, Gauthier et al. 1996), rivers, and barren ground reduce the likelihood of fire spreading into an area (Heinselman 1981, 1996, Turner and Romme 1994). Thus two sites that are otherwise similar can have different fire frequencies. Barriers that are effective in mild burning conditions (e.g., low fuel mass, high moisture content, and low wind speed) are ineffective under more severe conditions (e.g., high wind speed and spotting) (Heinselman 1981, Turner and Romme 1994, Schimmel and Granström 1997, Agee et al. 2000, Finney 2001). Thus, much of the boreal forest exhibits a pattern of periodic small fires with infrequent large fires that are associated with high wind and drought (Van Wagner 1983, Fryer and Johnson 1988, Larsen 1989, Bergeron and Brisson 1990, Johnson et al. 1990, Bergeron 1991, Johnson and Larsen 1991, Bessie and Johnson 1995, Korovin 1996, Murphy et al. 2000, Flannigan and Wotton 2001, Hess et al. 2001, Senkowsky 2001) and episodic climate variations (Clark 1990, Sirois and Payette 1991, Payette 1992, Campbell and Flannigan 2000).

The complexity of factors controlling the spatial and temporal distribution of dry, burnable fuel and ignition sources affect fire return intervals within and between vegetation types. Modal and extremes in the range of fire return have important implications on the species composition of stands (White and Pickett 1985). Attempts to restore or conserve biodiversity by reintroducing fire need to consider the natural range in variability of fire frequency for a given area (Hunter 1993, DeLong 1998, Lertzman et al. 1998).

2.2 Fire Size

The area within a fire's perimeter is often used to describe the extent of a fire, but the actual area burned, patch size, and burn mosaic should also be considered in bioconservation studies (Eberhardt and Woodward 1987, Turner and Romme 1994, Turner et al. 1997). Burn mosaic needs to be assessed in three dimensions: the pattern of area burned, i.e., green versus black within the overall fire perimeter, and the above- and belowground impacts within the burned area, i.e., the size-magnitude interaction within the disturbance. This interaction is important because the scale of the burn mosaic relative to species niche requirements and mobility can have major impacts on early floral and faunal dynamics (Noble and Slatyer 1977, 1980, 1981, Gill 1981, Heinselman 1981, 1996, Noble 1981, Rowe 1983, Eberhardt and Woodward 1987, Sirois and Payette 1991, Fischer et al. 1996, Smith and Fischer 1997, Turner et al. 1997, Kasischke et al. 2000a, Miller 2000, Smith 2000).

Heterogeneity in vegetation structure and microenvironment leads to heterogeneity in fire behavior and effects that can increase the heterogeneity of post-fire vegetation (Heinselman 1981, Rowe 1983, Mushinsky and Gibson 1991, Turner et al. 1994). Within the boreal forest, many sub regions have relatively few species adapted to a site (Nikolov and Helmisaari 1992), and the size of the burned area may be large relative to species mobility (Payette 1992). Thus, the increase in heterogeneity may not be readily apparent in the species present but may be manifest in the rates of numerous biogeochemical processes (Shugart et al. 1992, Kasischke and Stocks 2000). Heterogeneity occurs at all spatial scales within fires (Turner et al. 1994, 1997). Large patches of crown fire-killed forests often contain a mosaic of varying depths of burn into the soil due to spatial differences in the depth of the duff (mor) (i.e., the combined fermentation and humus soil horizons) and moisture content (Ryan and Noste 1985, Fryer and Johnson 1988, Zoltai et al. 1998, Kasischke et al. 2000a, 2000b, Miyanishi 2001). Lightly burned and unburned patches provide refugia for fire sensitive flora and fauna. Likewise, deep burning ground fires often occur with little surface flaming, resulting in large areas of deeply heated soil with minimal direct heat effects on aboveground tissues (Rowe 1983, Wein 1983, Ryan and Noste 1985, Ryan and Frandsen 1991). Because of subtle changes in the biophysical environment, fires often burn in combinations of intensity over short distances (Turner et al. 1994, Kafka et al. 2001). For example, creeping surface fires commonly transition into passive crown fires when they encounter low branches (Van Wagner 1977, 1983). These branches provide the vertical fuel continuity necessary to carry the fire into the crown. The torching of individual trees and small clumps of trees results in localized patches of high upward heat pulses. This type of fire is common in boreal forests burning under low winds and low relative humidity (Heinselman 1981, 1996, Rowe 1983). With increasing wind, these fires can transition into intense crown fires (Van Wagner 1977, 1993, Fryer and Johnson 1988, Scott and Reinhardt 2001) that result in heterogeneous fire treatments of varying size within the larger fire perimeter.

Homogeneous environments lead to larger, more uniform fires. When fuels, weather, and terrain are relatively uniform within a region, a large portion of the area will be receptive to ignition and burnout at one time (DeLong 1998). Once ignited, fires will burn until a significant change occurs in either the weather or fuels (Johnson 1992, Bessie and Johnson 1995). Patch size is then determined by how far the fire can spread before encountering a significant change in burning conditions. Dry continental air masses, strong persistence patterns such as blocking high-pressure ridges, and the strong wind events associated with passing of dry cold fronts create conditions suitable for rapid fire growth and extended severe fire weather (Johnson 1992, Johnson and Wowchuk 1993, Flannigan and Wotton 2001). Thus, most of the area burned in the boreal Alaska, Canada, and Siberia is burned by a relatively small number of large fires that burn for several days in relatively dry years (Johnson et al. 1990, Johnson and Larsen 1991, Johnson 1992, Bessie and Johnson 1995, Korovin 1996, Valendik 1996, Flannigan and Wotton 2001, Hess et al. 2001).

2.3 Seasonality

Fires may burn during the pre-growing dormant period, the active growing season, or the post-growing dormant season with variable results that may be related to differences in the fire's energy release characteristics, plant susceptibility to injury, or physiological response to injury.

Seasonality is important because of direct changes in fuel moisture that affect flammability (Albini 1976, Van Wagner 1983, Andrews 1986, Stocks et al. 1989, Johnson 1992). Crown fire potential increases with decreasing foliar moisture (Van Wagner 1977, 1993, Alexander 1998, Scott and Reinhardt 2001). Foliar moisture content is lowest in the spring prior to bud-break when soils are still at or near freezing (Chrosciewicz 1986). Early in the fire season low relative humidity and high wind can combine to yield high crown fire potential while the forest floor is still too wet to sustain combustion (Artsybachev 1983, Stocks et al. 1989). Even though it is somewhat more difficult to initiate and sustain a crown fire when foliar moisture content is higher in the mid and late summer, high intensity crown fires still occur when relative humidity is low, wind speed is high, and fine fuels are abundant (Stocks et al. 1989, Johnson 1992). In contrast to spring fires, these later-season fires often are accompanied by deep depth-of-burn ground fires due to the lower duff moisture content (Kasischke et al. 2000a, 2000b, Miyanishi 2001). The depth of meristematic tissues varies by species (Flinn and Wein 1977, Schimmel and Grandström 1996, Fischer et al. 1996, Smith and Fischer 1997, Miller 2000). Thus, species susceptibility varies with the depth of heat penetration during burning, which can be expected to increase with seasonal dryness of the duff leading to a species-dependent seasonal effect on survival of meristematic tissues. Given its influence on fire severity, the most significant seasonal effect in boreal forests is related to duff moisture content (Heinselman 1981, Johnson 1992).

Independent of the duff moisture effect on combustion, species-dependent variation should be expected in responses due to seasonal changes in phenology (Wright and Bailey 1982, Flinn and Pringle 1983, Peterson and Ryan 1986, Agee 1993, Miller 2000). These differences may be due either to morphological factors affecting heat transfer to meristematic tissues (Peterson and Ryan 1986) or seasonal variations in plant water relations and the availability of stored carbohydrates (Flynn and Pringle 1983, Ryan 1990, 1998, 2000a, Rigolot et al. 1994, Ducrey et al. 1996). For example, in controlled laboratory studies Flinn and Pringle (1983) found that rhizomes of eight boreal species varied in their heat tolerance. All were most sensitive to injury during the summer, and all but one species exhibited better growth following spring heating as compared to fall heating. Several species from lower latitudes have been shown to respond most favorably, e.g., by flower production, following fires that occur in the 'natural' fire season as opposed to those contrived for cultural purposes (c.f. Fischer et al. 1996, Miller 2000). Thus, seasonally-dependent species responses likely exist in boreal areas dominated by early vs. mid vs. late season fire occurrence.

Other seasonal effects likely occur. For example, large boreal forest fires are commonly associated with drought (Johnson 1992, Bessie and Johnson 1995, Korovin 1996, Murphy et al. 2000, Flannigan and Wotton 2001, Hess et al. 2001, Senkowsky 2001). Drought affects tree physiology in a variety of ways, including reduced carbon allocation to stem growth and host resistance to bark beetles (Larsen and MacDonald 1995, Ryan 1998, 2000a). There is little direct evidence of seasonal effects on host resistance to insect attack because of the lack of research. However, one would anticipate that fire injury prior to bark beetle flight would subject a tree to an increased likelihood of attack as opposed to fire injury that occurred after beetle flight. There are likely a number of seasonally-dependant fire effects other than the obvious ones related to fire behavior, but these remain to be elucidated

2.4 Fire Magnitude

In fire ecology there is no universally accepted definition for the magnitude of fire. White and Pickett (1985) give examples of intensity and severity as two measures of magnitude. Accordingly, intensity pertains to the '…physical force of the event per area per time period (e.g., heat released per time period for a fire…)' and severity pertains to the 'impact on the organism, community or ecosystem (e.g., basal area removed).'

Fire managers have long recognized that the amount of available fuel, weather conditions, and terrain steepness have a dominant effect on a fire's energy release characteristics and fire suppression capabilities (cf. Rothermel 1972, 1991, Albini 1976, Stocks et al. 1989, Pyne et al. 1996, Grishin 1997). This triplet, fuels, weather, and terrain, is referred to in the North American fire science community as the fire environment concept. Of more interest in bioconservation and restoration studies is the understanding that the energy released by fire has the potential to do ecological work, i.e., to change a host of ecosystem state variables. Thus, quantification of the energetics of fires is desirable in ecological studies (Johnson 1992, Johnson and Miyanishi 2001). However, fire behavior is highly variable in non-uniform fuels, instrumentation is costly, and it is often impractical to sample fire behavior except on small experimental plots, making it difficult to quantify the magnitude of fire treatments in ecological studies and restoration projects.

The fire environment concept can be extended from its suppression-derived simplicity to a more ecological construct (Fig. 2a). The extension of the fire environment concept to ecological studies requires that fuels be considered in the broader context of the structure of biomass on the site. Structure includes the quantity, distribution, and horizontal and vertical arrangement of live and dead trees, understory vegetation, woody debris, litter, and humus (Artsybashev 1983, Brown and Bevins 1986, Johnson 1992). Structure defines the total amount of biomass that can be burned, and therefore the total energy that can be released in a fire. The size distribution of the structural components defines the rate at which energy will be released during favorable burning conditions. The rates at which fuels wet, dry (Nelson 2001), and burn (Anderson 1969) are functions of particle surface-area. These rates can be approximated from diameter for most fuels above the duff layer.

As a fire burns across the landscape, it encounters different communities with different disturbance histories that result in varying stand structures and flammability. For example, stands with a high open crown and low understory fuels have poor vertical fuel continuity. They have an increased likelihood of burning due to increased sunlight and wind at the surface (Albini 1976, Stocks et al. 1989, Kunkel 2001) but have a low crown fire potential (Van Wagner 1977, 1993, Artsybashev 1983, Grishin 1997, Scott 1998, Scott and Reinhardt 2001). In contrast, stands with a dense understory of shrubs or immature trees have high vertical fuel continuity. If they have a patchy overstory, i.e., poor horizontal fuel continuity in the canopy layer, they are less likely to burn because of the typically moister microenvironment but readily support passive crowning (torching) and spotting under low relative humidity. Stands with high vertical and horizontal fuel continuity have the highest crown fire potential (Van Wagner 1977, 1993, Alexander 1998, Finney 1998, 1999, Scott 1998, Scott and Reinhardt 2001). The availability of these fuels varies not only in space, but also in time with changes in weather, principally relative humidity, temperature, and drought (Johnson 1992, Bessie and Johnson 1995).

Weather, specifically relative humidity, wind, and drought, define the fraction of the total fuel that is available to be consumed in a given fire. The short-term weather history is the primary determinant of the flammability of the moss and lichen layers, loose litter, foliage, and fine twigs (Albini 1976, Stocks et al. 1989). Long-term weather determines the moisture content and combustibility of deeper organic layers and surface logs (Stocks et al. 1989). Wind is perhaps the single most important cause of spatial and temporal variation within boreal forests. Fires frequently pulsate between intense surface fires and crown fires with only modest changes in wind speed (Van Wagner 1977, 1993, Finney 1998, Scott 1998, Scott and Reinhardt 2001). The result is a mosaic of small crown fire patches instead of the large expanses that occur in sustained wind-driven fires.

In ecological studies terrain needs to be considered in the broader context of how it affects not only the site water and energy budgets that dominate site productivity, but also fuel moisture (Rothermel 1972, Albini 1976, Andrews 1986, Miyanishi 2001) and wind flow patterns (Pyne et al. 1996). Thus, terrain includes slope angle, aspect, elevation, hill-slope drainage, and land-

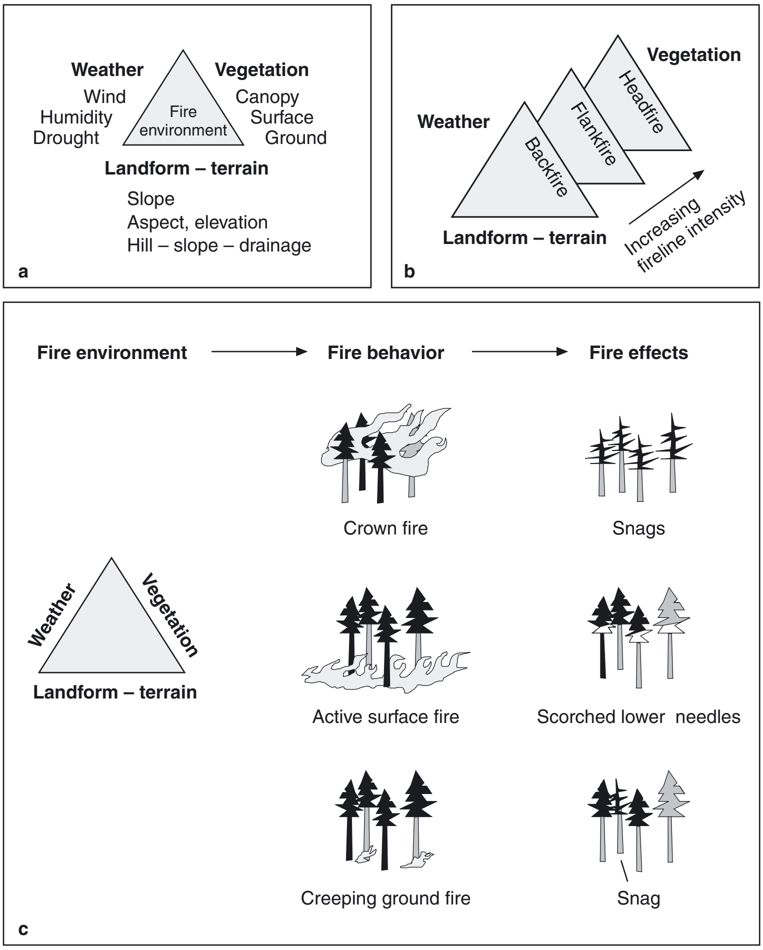

Fig. 2. Fire behavior varies in time and space with a) changes in the terrain, weather, and vegetative structure and with b) whether or not the area experiences a head fire, flank fire, or backing fire. c) As the fire behavior changes so do the effects.

form. An additional aspect of terrain is that terrain features can present barriers to fire spread. Barriers have two general effects. Either the area's fire frequency is reduced due to its reliance on local ignitions as discussed in fire frequency above, or at scales smaller than the typical fire's size, the fire flanks or backs into the area with a reduced intensity and severity (Catchpole et al. 1982, 1992, Agee et al. 2000, Finney 2001).

Taken collectively, the vegetation structure, weather, and terrain constitute the biophysical fire environment (DeBano et al. 1998) (Fig. 2a). Independent of the biophysical environment in which the fire is burning, major differences in fire behavior are associated with the location on the fire's perimeter, that is whether an area is burned by a heading fire, flanking fire, or backing fire (Catchpole et al. 1982, 1992) (Fig. 2b). The heading portion of the fire burns with the wind or upslope. The backing fire burns into the wind or down slope. The flanking fire burns perpendicular to the wind's axis. The direction of fire spread is a function of the slope and wind vectors, with the latter dominating except at low wind speeds

(Rothermel 1972, Albini 1976, Finney 1998). The greater the wind speed or slope, the greater the difference between the intensity of the heading fire and backing fire. Commonly, fireline intensity in a backing fire is on the order of 0.1 to 0.2 times that of a heading fire in a given biophysical environment, while flanking fires are about 0.4 to 0.6 times the headfire intensity (Catchpole et al. 1992). Variations in the fire environment and location on the fire perimeter lead to significant variations in the fire behavior and effects (Fig. 2c). For example, it is common to see fires spread across a slope running with the wind when the vegetation structure is not sufficient and continuous enough for the fire to carry up the slope. The ignition pattern that is used in a restoration burn can also be expected to affect the pattern of fire behavior.

2.4.1 *Fire Intensity*

Byram's (1959) definition of fireline intensity has become a standard quantifiable measure of intensity (cf. Alexander 1982, Van Wagner 1983, Johnson 1992, Agee 1993, DeBano et al. 1998). Fireline intensity (kW/m) is the product of the fuel value, i.e., the fuel's heat content (kJ/kg), the mass of fuel consumed (kg/m^2), and the rate of spread (m/s) (Byram 1959). It is proportional to the flame length in a spreading fire and is a useful measure of the potential to cause damage to aboveground structures (Van Wagner 1973, Alexander 1982, Ryan and Noste 1985). Rothermel (1972) defined a somewhat different measure of fire intensity, heat per unit area, which is commonly used in fire behavior prediction in the United States (Albini 1976, Andrews 1986, Scott 1998, Scott and Reinhardt 2001). Likewise, the Canadian forest fire danger rating system calculates the intensity of surface fires and crown fires (Stocks et al. 1989). One problem with using current fire behavior prediction systems in ecological studies is that they do not predict all of the combustion, and therefore all of the energy released, over the duration of the fire (c.f. Johnson and Miyanishi 2001).

Fires burn throughout a continuum of energy release rates (Table 1) (Artsybashev 1983, Rowe 1983, Van Wagner 1983, Rothermel 1991). Ground fires burn in compact fermentation and humus layers and in organic muck and peat soils (Fig. 3a). Ground fire spread is predominantly by smoldering combustion. Such fires typically burn for hours to weeks, exhibit forward rates of spread in the range of decimeters to meters per day, and exhibit temperatures in excess of 300 °C for several hours (Frandsen and Ryan 1986, Ryan and Frandsen 1991, Hartford and Frandsen 1992, Agee 1993) (e.g., Fig. 3b). The conditions necessary for ground fires are organic soil depth greater than about 4 to 6 centimeters and extended drying

Table 1. Representative ranges for fire behavior characteristics for ground, surface, and crown fires.

Fire type	Dominant combustion	General description	Fire behavior characteristics		
			Rate of spread (meters/minute)	Flame length (meters)	Fireline intensity (kW/meter)
Ground	Smoldering	Creeping	3.3E–4 to 1.6E-2	0.0	< 10
Surface	Flaming	Creeping	< 3.0E–1	0.1 to 0.5	1.7E0 to 5.8E1
		Active/spreading	3.0E–1 to 8.3E0	0.5 to 1.5	5.8E1 to 6.3E2
		Intense/running	8.3E0 to 5.0E1	1.5 to 3.0	6.3E2–2.8E3
Transition	Flaming	Passive crowning (Intermittent torching)	Variable a)	3.0 to 10.0	Variable a)
Crowning	Flaming	Active crowning	1.5E1 to 1.0E2	5.0 to 15 b)	1.0E4 to 10.0E5
		Independent crowning	Up to ca. 2.0E2	Up to ca. 70 b)	Up to ca. 1.3E6

a) Rates of spread, flame length and fireline intensity vary widely in transitional fires. In subalpine and boreal fuels it is common for surface fires to creep slowly until they encounter conifer branches near the ground, then individual trees or clumps of trees torch sending embers ahead of the main fire. These embers start new fires, which creep until they encounter trees, which then torch. In contrast, as surface fires become more intense, torching commonly occurs prior to onset of active crowning.

b) Flame lengths are highly variable in crown fires. They commonly range from 0.5 to 2 times canopy height. Fire managers commonly report much higher flames but these are difficult to verify or model. Such extreme fires are unlikely to result in additional fire effects within a stand but are commonly associated with large patches of continuous severe burning.

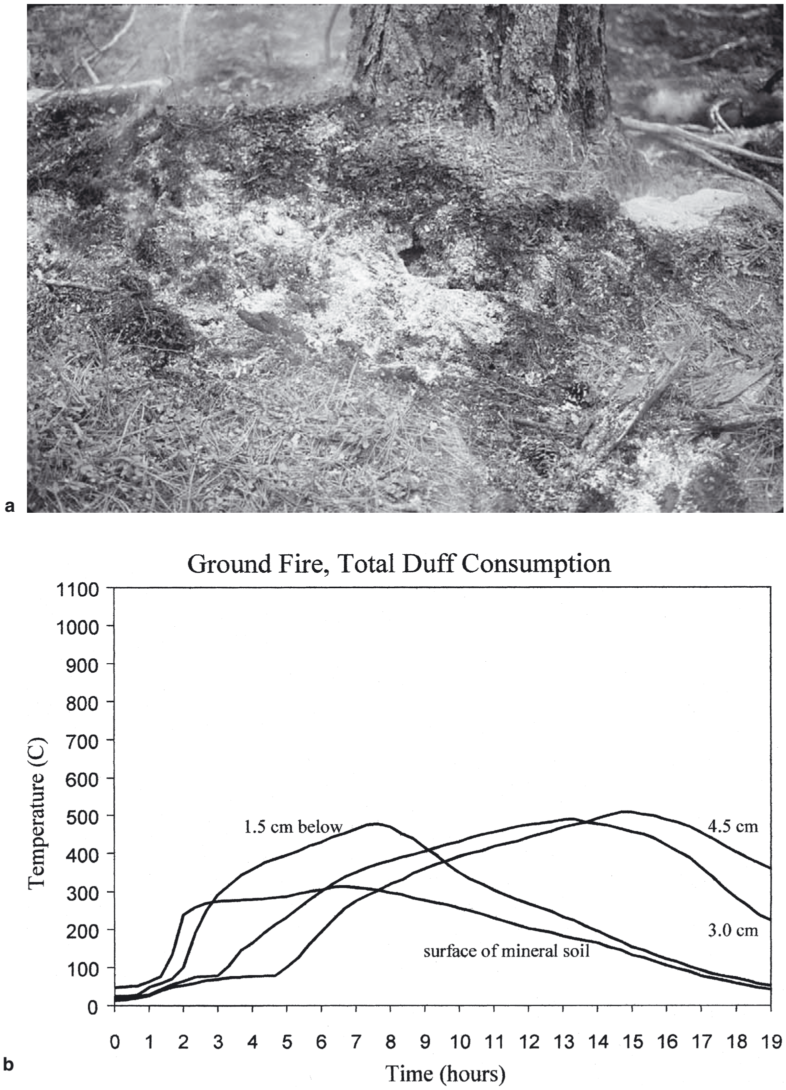

Fig. 3. a) Example of smoldering ground fire in deep duff (average 17 cm) (from Ryan and Frandsen 1991). b) Such fires typically produce temperatures in excess of 300 °C for several hours. Duff depth = 6.5 cm, moisture content = 18.3% (from Hartford and Frandsen 1992). Photo by Kevin C. Ryan.

(Reinhardt et al. 1997, Miyanishi 2001). Surface fires spread by flaming combustion in loose litter, woody debris, and understory herbaceous and shrubby plants typically less than two meters tall. Under marginal burning conditions surface fires creep along the ground at rates of decimeters per hour with flames less than five decimeters (Table 1). As fuel, weather, and terrain conditions become more favorable for burning, surface fires become progressively more active with spread rates ranging from tens of meters to kilometers per day. The duration of surface fires is on the order of one to a few minutes (Vasander and Lindholm 1985, Frandsen and Ryan 1986, Hart-

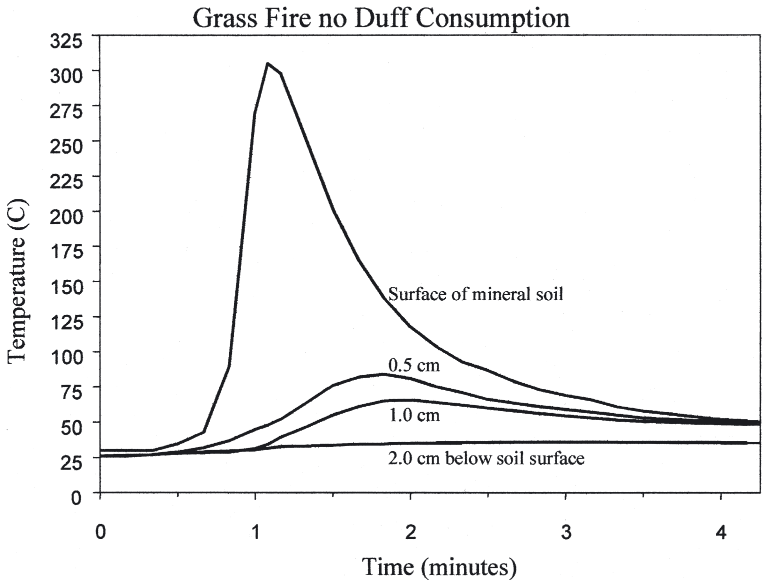

Fig. 4. Example of an active flaming surface fire in grassland. Such fires typically produce surface temperatures in excess of 300 °C but only for 1 to 2 minutes.

ford and Frandsen 1992) except where extended residual burning occurs beneath logs or in concentrations of heavy woody debris (e.g., Fig. 4). Here flaming combustion may last a few hours resulting in substantial soil heating (Hartford and Frandsen 1992). If canopy fuels are plentiful and sufficiently dry, surface fires begin to transition into crown fires (Van Wagner 1977, Scott and Reinhardt 2001). Crown fires burn in the foliage, twigs, and epiphytes of the forest or shrub canopy above the surface fuels (Fig. 5a). Such fires exhibit the maximum energy release rate but are typically of short duration, 30 to 80 seconds (Fig. 5b). Fires burn in varying combinations of ground, surface, and crown depending on the local conditions at the specific time a fire passes a point. Ground fires burn independently from surface and crown fires and often occur some hours after passage of the flaming front (Artsybashev 1983, Rowe 1983, Van Wagner 1983, Hungerford et al. 1995). Changes in surface and ground fire behavior occur in response to subtle changes in the microenvironment, stand structure, and weather leading to a mosaic of fire treatments at multiple scales in the ground, surface and, canopy strata.

2.4.2 Fire Severity

Within the fire effects literature, there is increasing acceptance of the use of the term fire severity to describe the ecological impacts of fires (Rowe 1983, Ryan and Noste 1985, Moreno and Oechel 1989, Turner et al. 1994, Schimmel and Granström 1996, Smith and Fischer 1997, DeBano et al. 1998, Feller 1998, Neary et al. 1999, Kafka et al. 2001). Given the many ecological components and their peculiar metrics, it is not possible to come up with a single system to quantify fire severity (DeBano et al. 1998). Consistent criteria for classifying fire severity have yet to emerge. Numerous authors have used measures of the depth of burn into the organic soil horizons or visual observation of the degree of charring and consumption of plant materials to define fire severity (cf. Rowe 1983, Schimmel and Granström 1996, DeBano et al. 1998, Feller 1998, Pérez and Moreno 1998). However, focusing severity only on ground-based processes ignores the aboveground dimension of severity implied in the definition of White and Pickett (1985). This is especially important because soil heating is commonly shallow even when surface fires are

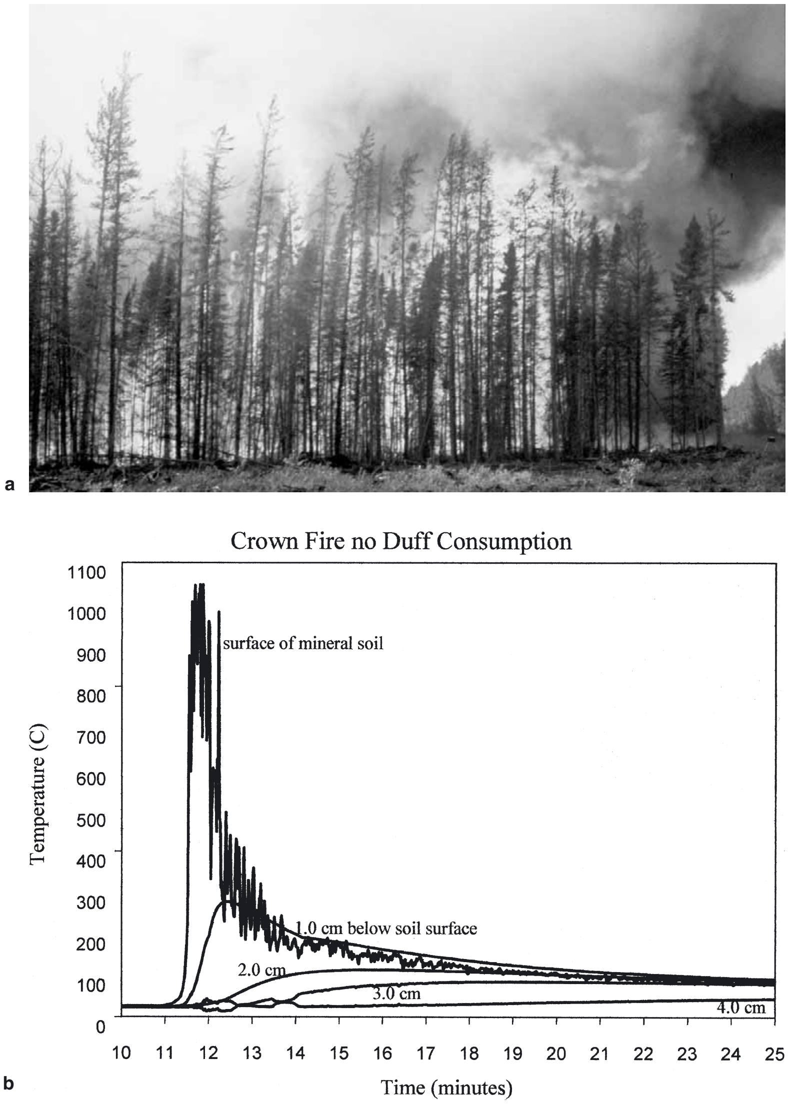

Fig. 5. a) Example of a crown fire in jack pine (*Pinus banksiana*) in the Northwest Territories, Canada. b) Such fires typically produce temperatures in excess of 1000 °C for about 1 minute. Photo by Kevin C. Ryan.

intense (Wright and Bailey 1982, Frandsen and Ryan 1986, Hartford and Frandsen 1992) (Fig. 4). Ryan and Noste (1985) summarized literature on depth of burn and charring of plant materials and developed descriptive characteristics. A condensed and revised (Moreno and Oechel 1989, Pérez and Moreno 1998, DeBano et al. 1998, Feller 1998) description of their characteristics is provided for clarification of subsequent discussion of fire effects.

Unburned: Plant parts are green and unaltered, there is no direct effect from heat.

Scorched: Fire did not burn the area but radiated or convected heat caused visible damage. Mosses and leaves are brown or yellow but species characteristics are still identifiable. Soil heating is negligible.

Light: In forests the surface litter, mosses, and herbaceous plants are charred to consumed but the underlying forest duff or organic soil is unaltered. Fine dead twigs are charred or consumed but larger branches remain. Logs may be blackened but are not deeply charred except where two logs cross. Leaves of understory shrubs and trees are charred or consumed but fine twigs and branches remain. In non-forest vegetation plants are similarly charred or consumed, herbaceous plant bases are not deeply burned and are still identifiable, and charring of the mineral soil is limited to a few millimeters.

Moderate: In forests the surface litter, mosses, and herbaceous plants are consumed. Shallow duff layers are completely consumed and charring occurs in the top centimeter of the mineral soil. Where deep duff layers or organic soils occur they are deeply burned to completely consumed resulting in deep charcoal and ash deposits but the texture and structure of the underlying mineral soil are not visibly altered. Trees of later successional, shallow-rooted species are often left on root pedestals or topple.

Fine dead twigs are completely consumed, larger branches and rotten logs are mostly consumed, and logs are deeply charred. Burned-out stump holes and rodent middens are common. Leaves of understory shrubs and trees are completely consumed. Fine twigs and branches of shrubs are mostly consumed (this effect decreases with height above the ground), and only the larger stems remain. Stems of these plants frequently burn off at the base during the ground fire phase leaving residual aerial stems that were not consumed in the flaming phase lying on the ground. In non-forest vegetation plants are similarly consumed, herbaceous plant bases are deeply burned and unidentifiable. In shrublands charring of the mineral soil is on the order of 1.0 centimeter but soil texture and structure are not clearly altered.

Deep: In forests growing on mineral soil the surface litter, mosses, herbaceous plants, shrubs, and woody branches are completely consumed. Sound logs are consumed or deeply charred. Rotten logs and stumps are consumed. The top layer of the mineral soil is visibly oxidized, reddish to yellow. Surface soil texture is altered and in extreme cases fusion of particles occurs. A black band of charred organic matter 1 to 2 centimeters thick occurs at variable depths below the surface. The depth of this band is an indication of the duration of extreme heating. The temperatures associated with oxidized mineral soil are associated with flaming rather than smoldering. Thus, deep depth of burn typically only occurs where woody fuels burn for extended duration such as beneath individual logs or in concentrations of woody debris. In areas with deep organic soils deep depth-of-burn occurs when ground fires consume the root-mat or burn beneath the root-mat. Trees often topple in the direction from which the smoldering fire front approached.

The moderate depth of burn class is a broad class. Some investigators have chosen to divide the class into two classes (c.f. Feller 1998). In practice I have found it difficult to do so on the basis of post-hoc examination of the mineral soil alone but rely on the preponderance of the evidence, which includes reconstructing the prefire vegetative structure. The depth-of-burn characteristics are appropriate for quadrat-level descriptions. At higher spatial scales logic needs to be developed for defining fire severity on the basis of the distribution of depth of burn classes (c.f. Ryan and Noste 1985, DeBano et al. 1998).

Ryan and Noste (1985) combined fire intensity classes with depth of burn (char) classes to develop a two-dimensional matrix approach to defining fire severity. The basis for these characteristics is that fire-intensity classes qualify the relative energy release rate for a fire, whereas depth-of-burn classes qualify the relative duration of burning. Their concept focuses on the ecological work performed by fire both above ground and belowground. The matrix provides an approach to classifying the level of fire treatment or severity for ecological studies at the scale of the individual and the community. The approach has been used to interpret differences in plant survival and regeneration (Willard et al. 1995, Smith and Fischer 1997) and to field-validate satellite-based maps of burned areas (White et al. 1996).

2.5 Synergy

Synergism occurs when multiple disturbance factors interact (White and Pickett 1985). There are numerous examples of synergy related to fire-caused disturbances. For example, fire injury in conifers leads to increased incidence of insect attack on both short (Ryan and Amman 1994, 1996) and long (Geiszler et al. 1984, Gara et al. 1985) time scales. Insect-caused mortality leads to increased fuel and fire potential (Lotan et al. 1985). High winds periodically blow down large forest tracts. The increased solar drying, surface wind, and the heavy fuel that result increase the likelihood and potential severity of subsequent wildfire (Stocks 1975, Ryan 2000b, Finney 2001). Perhaps the best example of synergy is the fire/flood cycle common to mountainous areas of the world. The potential for erosion increases with depth of burn, surface fire intensity, and slope steepness (Wright and Bailey 1982, DeBano et al. 1998, Gresswell 1999, Pannkuk et al. 2000).

3 Fire Severity and Fire Effects

Fire severity changes as vegetation structure changes (Olson 1981, Van Wagner 1983, Turner and Romme 1994, Schimmel and Granström 1997, Kafka et al. 2001). At least at a coarse scale, predicted or observed fire severity can be integrated with plant vital attributes (Noble and Slatyer 1977, 1980, 1981, Noble 1981, Rowe 1983) to postulate which individuals are likely to survive and which species are likely to increase vs. decrease following a fire. It is possible to predict survivorship of trees based on knowledge of fire behavior, tree morphology, and species' life history attributes (c.f. Peterson and Ryan 1986, Ryan and Reinhardt 1988, Ryan 1990, 1998, Johnson 1992, Agee 1993, Fischer et al. 1996, Reinhardt et al. 1997, Dickinson and Johnson 2001). In general, the probability of crown injury decreases with increasing plant height and height of the live-crown-base, at roughly the two-thirds power of the fireline intensity (Van Wagner 1973, Ryan 1998, Dickinson and Johnson 2001). Resistance to stem injury increases with the square of the bark thickness, which increases approximately linearly with tree diameter (c.f. Sofronov and Volokitina 1977, Peterson and Ryan 1986, Ryan and Reinhardt 1988, Johnson 1992, Agee 1993). The diameter-to-bark-thickness ratio is a species-specific parameter commonly available in the forest mensuration literature. Thick-barked trees frequently survive active surface fires, whereas thin-barked trees only occasionally survive creeping fires. Survival of thin-barked trees usually only occurs when the fire is patchy and does not circumnavigate the entire stem or where only fine, light, flashy surface fuels (e.g., lichens and grasses) are quickly consumed. Thick-barked and deep-rooted trees commonly survive ground fires several centimeters deep (Ryan and Frandsen 1991) but not deep peat fires (Artsybashev 1983). Shallow-rooted species rarely survive ground fires (Wein 1983, Johnson 1992, Smith and Fischer 1997).

In contrast to Eurasian boreal forests that contain a number of thick-barked fire resistant trees (Sofronov and Volokitina 1977, Nikolov and Helmisaari 1992), only red pine (*Pinus resinosa*) is fire resistant in the North American boreal (Heinselman 1981, Engstrom and Mann 1991). Red pine is a minor component of the North American boreal forest (Heinselman 1981). In the North American boreal crown fires are more common than in the Eurasian boreal (Shvidenko and Nilsson 2000), apparently because of different stand structure. Due to thin bark, active surface fires kill most trees in North American boreal fires regardless of depth-of-burn (Johnson 1992). In contrast, mortality in similar fires in pine and larch forests in the Russian boreal is approximately 20 percent in light depth-of-burn fires (Shvidenko and Nilsson 2000). Although surface fires and crown fires both cause high mortality in thin-barked species, their effects on other ecosystem processes can be expected to be quite different. For example, the surface microenvironment, shaded vs. exposed, in surface fires vs. crown fires can be expected to affect post-fire species dynamics (Rowe 1983). Needles are killed by heat rising above the fire (Van Wagner 1973, Dickinson and Johnson 2001), thereby retaining their nutrients. Thus, litterfall of scorched needles vs. no litterfall in crown fire areas can be expected to affect nutrient cycling. Rainfall simulator experiments have shown litterfall also

Table 2. Species attributes relative to early post fire revegetation (modified from Rowe 1983).

Mode of regeneration and reproduction –
first vital process (Noble and Slatyer 1980)

Vegetative-based
V species – able to resprout if burned in the juvenile stage
W species – able to resist fire in the adult stage and to continue extension growth after it (although fire kills juveniles)

Disseminule-based
D species – with highly dispersed propagules
S species – storing long-lived propagules in the soil
C species – storing propagules in the canopy

Communal relationships –
second vital process (Noble and Slatyer 1980)

T species – tolerants that can establish immediately after a fire and can persist indefinitely thereafter without further perturbations
R species – tolerants that cannot establish immediately after fire but must wait until some requirement has been met (e.g., for shade)
I species – intolerants that can only establish immediately after a fire. Rapid growth pioneers, they tend to die out without recurrent disturbances

reduces erosion on sites where duff was completely consumed (Pannkuk et al. 2000). Thus, a lethal stand replacement crown fire, i.e., one that kills the dominant overstory (Brown 2000) represents a more severe fire treatment than a lethal stand replacement surface fire.

Many non-tree species in boreal forests rely primarily on vegetative reproduction from belowground tissues to survive fires (Flinn and Wein 1977, Flinn and Pringle 1983, Granström and Schimmel 1993, Schimmel and Granström 1996). Noble and Slatyer (1977, 1980) described plant adaptive traits affecting fire survival. Rowe (1983) summarized these traits. Survival of species that rely on vegetative reproduction, the V and W species in Rowe (1983) (Table 2) depends on the depth of burn relative to the depth of the meristematic tissue (Flinn and Wein 1977, Wein 1983, Schimmel and Granström 1996). Organic soils are excellent insulators (Uggla 1974, Vasander and Lindholm 1985, Hungerford et al. 1991, Hartford and Frandsen 1992). Unburned residual organic soil effectively protects deeper levels from significant temperature rise. Survival of species with V and W reproductive strategies is relatively independent of surface fire intensity, as aboveground organs are nearly uniformly killed by all fire intensities (Granström and Schimmel 1993, Schimmel and Granström 1996, Feller 1998).

Reproduction from seeds, either from on-site seed banks (S and C species) or from off-site dissemination (D species) (Table 2) is also differentially affected by fire severity (Granström and Schimmel 1993, Schimmel and Granström 1996). Similar to V and W species the deeper the depth of burn, the greater the destruction to the soil seed bank (S species). A number of S species store seeds for decades to centuries awaiting the next fire (Heinselman 1981, 1996, Keeley 1981). Low depth of burn may or may not favor soil seed bank species (S species) depending on the depth of the stored seed (Granström 1982, Rydgren and Hestmark 1997). The fate of S species is relatively unaffected by surface fire intensity except when such seeds are exposed on the surface. In contrast, canopy-stored (C species) seed bank survival is reduced by severe heating in intense surface and crown fires (Despain et al. 1996). Even species storing seeds in serotinous cones experience reduced survival in crown fires (Ellis et al. 1994, Despain et al. 1996). However, C species are relatively insensitive to the depth of burn because the lethal temperature height above ground fires is insignificant. Fire severity affects

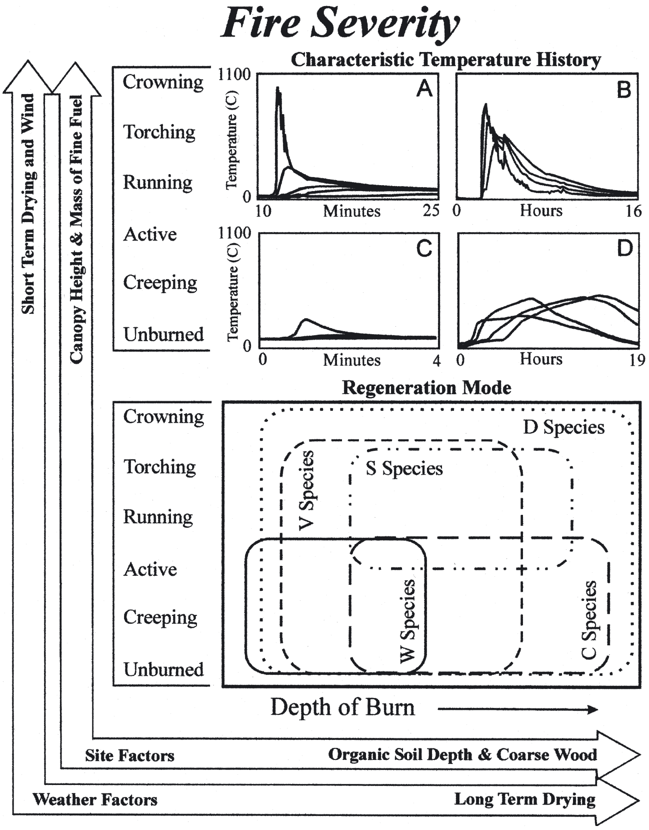

Fig. 6. Representative temperature histories (top) for fires of varying severity: A-crownfire/low depth of burn (DOB), B-crownfire/moderate DOB, C-active surface fire/low DOB, D-creeping surface fire/moderate DOB. (See text and Table 1 for fire intensity and DOB descriptions). Relationship between fire severity and the mode of regeneration following fire. (See Text and Table 2 for description of plant regeneration attributes). Changes in site variables, including terrain and vegetative structure, and weather variables lead to fires of differing peak temperature and duration. Arrows indicate increasing site and weather potential. Both site and weather conditions must be met to affect fire severity.

regeneration of D species by determining the quality of the seedbed and the amount of early post-fire competition.

The mode of regeneration and reproduction (i.e., the first vital process) and the communal relationship (i.e., the second vital process) (Noble and Slatyer 1977, 1980, Noble 1981), can be evaluated in the context of the fire severity matrix (Fig. 6) and Table 2. Three examples can be used to illustrate differential responses. First, fires with low depth of burn favor vegetative regeneration by V and W species. However, the surface fire intensity will tend to favor one mode over another. A V species that establishes immediately after a disturbance (VT species) can be expected to respond more favorably than a species that requires shade (e.g., VR species) following low depth of burn crown fires. Second, deep depth of burn fires favor species that regenerate from canopy-stored seed (C species) or species with highly dispersed seeds (D species). C species should be favored over D species in low flame length-deep depth-of-burn fires because they are already present on the site. Shade tolerant, late successional, CR species should be favored over early successional, shade intolerant CT species. Third, fires of high heat pulse up (Table 1) and high heat pulse down (i.e., deep depth of burn) eliminate the maximum amount of the on site seed and vegetative material and favor regeneration of highly disseminated species that are intolerant and only establish following disturbance (DI species). An integrated analysis of the different species attributes and how they are affected by fires of varying severity would likely lead to a greater understanding of fire's role in maintaining biodiversity.

Variability in fire severity affects both the amount and depth of seed and belowground organs that survive fire, as well as the communal relationships. These lead to spatial variability in the initial post-fire floristics. Secondary successional processes increasingly dominate population dynamics with time since fire. However, a mechanistic understanding of fire severity can be coupled with knowledge of species attributes to further understand the role of fire as a disturbance process. Clearly, more integrated field studies are needed to better understand how complex phytosociological, ecophysiological, and fire science relationships affect biodiversity.

Models exist for predicting the energy output of fires in relatively homogeneous stands (cf. Albini 1976, Andrews 1986, Stocks et al. 1989, Van Wagner 1998) and for multiple stands across landscapes (Finney 1998). However, fire behavior models predict rates of spread (m/s), fireline intensity (kW/m), heat per unit area (kW/m^2), and flame length (m) (Table 1), whereas fire effects on flora, fauna, and soils are typically described in terms of temperature histories (c.f. Wright and Bailey 1982, Hungerford et al. 1991, DeBano et al. 1998). The energy output of a fire cannot be directly related to the temperature history of an entity within a fire. The temperature reached by an entity in a fire depends not only on the fire's behavior but also the heat transfer mechanism and the thermal properties of the heat transfer medium. The only fire effect that has been clearly demonstrated to relate to the existing fire behavior model outputs is crown scorch which is defined as the height of the 60 °C lethal isotherm (Van Wagner 1973). Empirical measurements of the temperature history associated with fires of varying behavior provide insights into the type of effects to be expected (Fig. 6). Active surface fires with no secondary burning (i.e., no organic soil or coarse woody fuel consumption) are of sufficient temperature (310 °C) and duration to kill foliage, thin-barked stems, and exposed seeds near the surface but not those in the forest canopy or deeper than 2 centimeters in the mineral soil (Fig. 4, Fig. 6 lower left temperature history). Crown fires burning over wet organic soil horizons produce substantially higher surface temperature (1060 °C) but the depth of lethal heat penetration (60 °C) is only 4 centimeters (Fig. 5, Fig. 6 upper left temperature history). In contrast, a smoldering ground fire in the absence of an active surface fire causes few effects above the ground level but temperatures in excess of 300 °C persist for several hours at depths greater than 4 centimeters (Fig. 3, Fig. 6 lower right temperature history). The combined effect of a crown fire followed by a ground fire provides the maximum potential to kill aboveground and belowground tissues (Fig. 6 upper right temperature history). These representative temperature histories can be related to the fire severity matrix developed by Ryan and Noste (1985). This illustrates the combined effect of the heat pulse up, represented by the flame length class, and the heat pulse down, represented by depth of burn class. As the flame length increases, the fire's ability to cause ecological change to aboveground ecosystem components increases. Likewise, as the depth of burn increases, the fire's ability to cause ecological change to belowground ecosystem components increases.

Active growing tissues die at lower temperatures or exposure times than dormant tissues (Wright and Bailey 1982, Peterson and Ryan 1986). Seeds are more resistant to temperature than active growing tissues (Wright and Bailey 1982, DeBano et al. 1998). Killing of plant tissues is, however, only one of a number of fire effects related to high temperatures (Hungerford et al. 1995, DeBano et al.1998). Campbell et al. (1994, 1995) developed and Albini et al. (1996) tested a model for predicting temperature histories in the

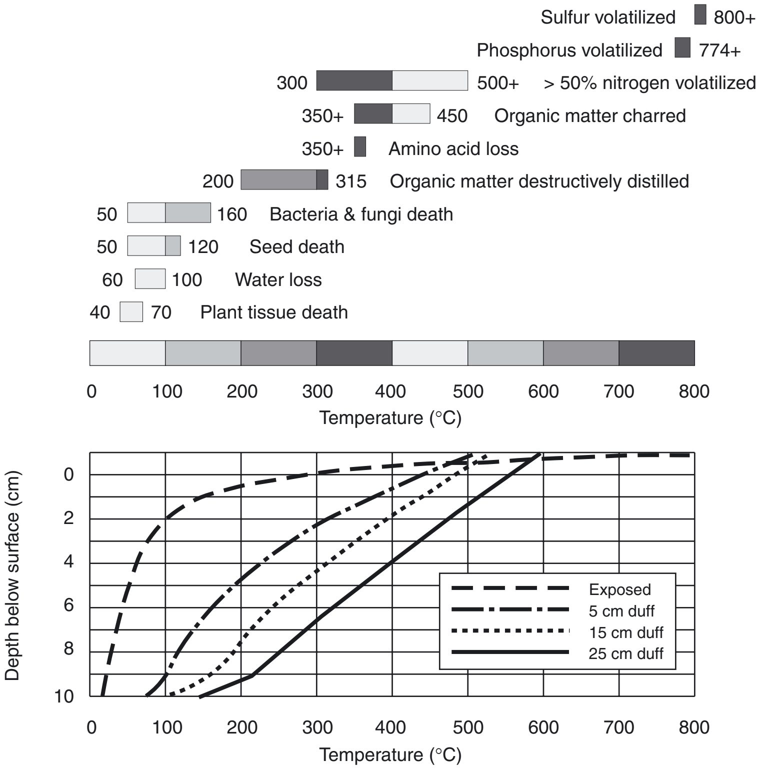

Fig. 7. Temperature ranges associated with various fire effects (top) (from Hungerford et al. 1991) compared to the depth of heat penetration into mineral soil (bottom) for a crown fire over exposed mineral soil (observed in jack pine *Pinus banksiana* in the Canadian Northwest Territories) or for ground fire burning in 5-, 15-, and 25-cm of duff (predicted via Campbell et al.1994, 1995). Conditions are for coarse dry soil, which provides the best conduction (i.e., a worst-case scenario).

soil given fires of different energy release rates and durations. The model predicts the effects of varying soil texture and moisture content on temperature history. The model can be used to predict the maximum temperature for varying depths of burn (Fig. 7). An increase in the depth of burn increases the depth at which any temperature-related effect will occur. This further illustrates that the greater the depth of burn, the more severe the disturbance. Models are available to predict the depth of burn in many North American vegetation types (Reinhardt et al. 1997, Johnson 1992). These empirical models provide a first approximation for predicting the effects of fire on belowground ecosystem components. By coupling these predictions with fire behavior models (Andrews 1986, Stocks et al. 1989, Finney 1998, 1999, Scott and Reinhardt 2001), ecologists engaged in restoration burns can predict the severity of disturbance in advance and can compare the expected disturbance to historical reference conditions. It is important, however, to account for spatial variation in model input parameters.

4 Conclusions

Fires are a dominant force in shaping boreal landscapes. The severity of these fires varies in time and space depending on the vegetation structure, terrain, short- and long-term weather, and location on the fire's perimeter (head vs. flank vs. rear). Fire behavior and effects models can be used to understand this variation. Individual plants and species vary in their resistance to fire injury in predictable ways. A combined understanding of plant attributes and fire severity concepts can be used to predict or evaluate the effects of wildfires on biodiversity and for defining restoration goals. In order to understand the effects of fire-caused disturbances on bioconservation and restoration more emphasis is needed on field studies that integrate complex phytosociological, ecophysiological, and fire science relationships.

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