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Landscape dynamics in crown fire ecosystems

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Abstract

Crown fires create broad-scale patterns in vegetation by producing a patch mosaic of stand age classes, but the spread and behavior of crown fires also may be constrained by spatial patterns in terrain and fuels across the landscape. In this review, we address the implications of landscape heterogeneity for crown fire behavior and the ecological effects of crown fires over large areas. We suggest that fine-scale mechanisms of fire spread can be extrapolated to make broad-scale predictions of landscape pattern by coupling the knowledge obtained from mechanistic and empirical fire behavior models with spatially-explicit probabilistic models of fire spread. Climatic conditions exert a dominant control over crown fire behavior and spread, but topographic and physiographic features in the landscape and the spatial arrangement and types of fuels have a strong influence on fire spread, especially when burning conditions (*e.g.*, fuel moisture and wind) are not extreme. General trends in crown fire regimes and stand age class distributions can be observed across continental, latitudinal, and elevational gradients. Crown fires are more frequent in regions having more frequent and/or severe droughts, and younger stands tend to dominate these landscapes. Landscapes dominated by crown fires appear to be nonequilibrium systems. This nonequilibrium condition presents a significant challenge to land managers, particularly when the implications of potential changes in the global climate are considered. Potential changes in the global climate may alter not only the frequency of crown fires but also their severity. Crown fires rarely consume the entire forest, and the spatial heterogeneity of burn severity patterns creates a wide range of local effects and is likely to influence plant reestablishment as well as many other ecological processes. Increased knowledge of ecological processes at regional scales and the effects of landscape pattern on fire dynamics should provide insight into our understanding of the behavior and consequences of crown fires.

Introduction

Crown fires result from complex interactions of weather, ignition, vegetation, and topography. Factors such as temperature, humidity, fuel moisture, species composition, and topographic relief, usually measured at relatively fine spatial scales (*e.g.*, for a particular stand or hectare), can exhibit substantial spatial and temporal variability. For example, the kinds and amounts of fuel vary considerably across the landscape, and each forest type may have a characteristic fuel mosaic (Brown 1985). Air temperature, humidity, and wind also have been shown to vary in relation to elevation and topography in mountainous areas (Mitchell **1976).** Finally, the probability of ignition may vary spatially, as demonstrated by the high frequency of lightning ignitions on ridgelines and south-facing slopes in Glacier National Park (Habeck and Mutch 1973). Because of these complex interactions, understanding and predicting crown fire behavior in the landscapes requires forging a linkage between the fine-scale mechanisms that control the ignition and spread of crown fires and the broad-scale factors that influence the spatial patterns of burning.

Crown fires also create patterns in vegetation by producing a patch mosaic of successional stages. This fire-mediated patch mosaic is superimposed upon underlying vegetation patterns resulting from the distribution of species along environmental gradients of moisture, temperature, nutrients, and other resources (Reiners and Lang 1979, Forman and Godron 1981, Romme and Knight 1982). These two patterns clearly interact, *i.e.*, the frequency and intensity of disturbance vary in relation to topographic and other gradients, and, disturbance parameters influence species richness and composition (*e.g.*, Huston 1979, Miller 1982, Malanson 1984). There is a rich literature on species distribution in relation to environmental gradients, but the disturbance-generated patch mosaic has received less attention (Pickett and White 1985).

In this paper, we address the implications of landscape heterogeneity for crown-fire behavior and the ecological effects of crown fires over large areas. Our objectives are to elucidate: (1) the role of landscape pattern in influencing the spread and behavior of crown fires; (2) the effects of crown fires in creating landscape patterns and maintaining the long-term dynamics of the vegetation mosaic; (3) the spatial heterogeneity of fire severities associated with crown fires and their effects on the vegetation; and (4) the potential influence of climate change on the crown fire dynamics and the associated implications for landscape change.

Approaches for predicting behavior of crown fires

Models of fire behavior generally have focused on fine-scale ignition and spread processes without incorporating landscape pattern. These analytical or mechanistic models simulate the combustion process based upon principles from physics and chemistry, and the models may include surface fuel parameters or the convective and radiative transfer of heat from an advancing flame front to the fuels in the crown (*e.g.*, Van Wagner 1977, Albini and Stocks 1986, Izbecki and Keane 1989). The objectives of these models are to predict the spread rate and intensity (*i.e.*, heat release) of fires based on measurable parameters of fuels and weather. However, the fire models used most widely in the USA were developed to predict ***surface*** fire behavior under any specified combination of weather and fuels parameters (*e.g.*, Rothermel 1972, 1983; Burgan and Rothermel 1984). The Rothermel model simulates the quasi-steady spread of a fire through a continuous surface fuel stratum (Rothermel 1972, Albini 1976) and was not developed for application to crown fires or fires that spread long distances through "spotting" (the transport of burning twigs and leaves by wind to sites ahead of the flaming front of the fire). The development of new mechanistic models for predicting crown fire behavior and incorporating nonuniform fuels and spotting has been identified as a research priority (Rothermel 1988).

The gradient modeling approach developed by Kessell (1976a, 1976b, 1979) was one of the first attempts to incorporate landscape pattern into a fire spread model explicitly. Kessell examined fire behavior at the landscape scale in Glacier National Park by combining the Rothermel model with estimates of fuel distributions. Gradient analysis of field data was used to predict the spatial distribution of fuels in 1-ha grid cells, and the model then predicted fire spread and intensity within all cells of interest. However, the objective of gradient modeling primarily was to predict the spread and intensity ofsurface fires, and crown fire behavior was recognized as being more difficult to predict.

The development of broad-scale probabilistic models that incorporate spatial patterns but do not include physical mechanisms represents a very different approach to predicting fire spread. These models are based on the probability of fire spreading from one site to an adjacent site. In particular, the models have been used to explore the conditions under which a fire spreading through a simple, homogeneous, two-dimensional space can become "critical", *i.e.*, can spread from one end of the space to the other (Albinet *et al.* 1986, Ohtsuki and Keyes 1986, Hirabayashi and Kasahara 1987, von Niessen and Blumen 1988). An explicit link between surface and crown fires also has been simulated in this manner by Von Niessen and Blumen (1988). That model consists of two horizontal spatial grids, the "top" grid representing the crown of the trees and the "bottom" grid the surface. A fire spreads in the top and bottom grid with different probabilities, but the two grids are coupled; the surface fire can ignite the crown, either directly or by heat transfer, or the crown fire can drop to the ground. Results demonstrate that both the crown and the surface fire can have relatively low probabilities of spread, but the total fire may still be able to spread from one end of the grid to the other.

In contrast to fine-scale mechanistic fire models, the broad-scale probabilistic models are not designed to represent the deterministic causes of fire behavior nor to predict spread rates but rather to predict final burning patterns (*e.g.*, Green 1989). The arrangement, connectivity, and flammability of fuels and the spatial pattern of ignitions affect fire spread. By repeatedly running probabilistic models using the same or various combinations of spread probabilities, central tendencies can be established and the long-term consequences of subtle changes in the physical parameters that control fire spread can be explored, even if the details of those controles are not yet worked out. Probabilistic spread models have demonstrated that differing levels of fuel connectivity in the landscape may be responsible for a wide range of observed fire patterns and behaviors (Green 1983, 1989).

More generally, probabilistic disturbance models have been used to explore the interactions between landscape connectivity, probability of spread, and probability of initiation of disturbance (Turner *et al.* 1989). Results from simulations conducted on landscapes in which disturbance-susceptible habitat was distributed at random suggest that there is a qualitative difference in disturbance spread when the landscape is fragmented or connected (Fig. 1). When the susceptible habitat is fragmented (*e.g.*,

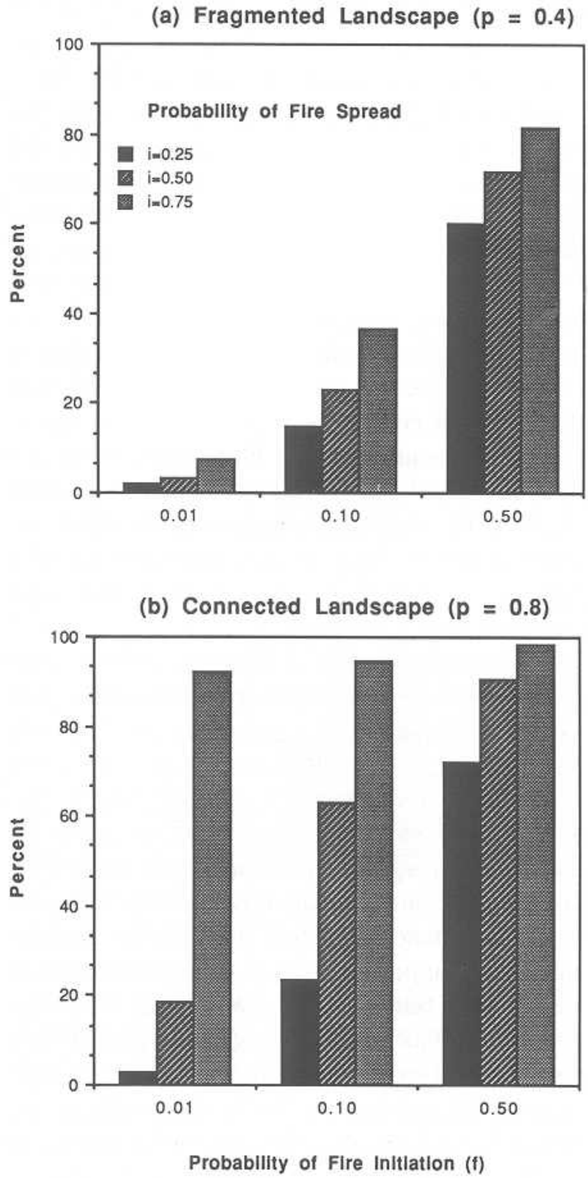

Fig. 1. The proportion of forest burned by fires simulated on random landscapes as a function of the probability of fire initiation (*f*) and the probability of fire spread (*i*) (Adapted from Turner *et al.* 1989). (a) Flammable forests occurred on 40% of the landscape, and the forest patches were fragmented. These conditions might be analagous to landscapes with rugged, dissected terrain during most years, or relatively flat landscapes during years in which burning conditions are mild. (b) Flammable forests occurred on 80% of the landscape, and the forest patches were highly connected. Similar fuel connectivity might be observed on relatively flat terrain during moderate or extreme burning conditions or even in rugged terrain if burning conditions are very extreme.

rugged, dissected terrain), the disturbance spread is constrained by the spatial pattern of the patches and is primarily a function of the number of initiation events (*e.g.*, lightning strikes). When the susceptible habitat is connected (*e.g.*, relatively flat terrain with contiguous forest), the disturbance can become "critical" and propagate across the entire landscape. This can occur with a single initiation if the probability of spread is sufficiently high (Fig. 1). In a random landscape constructed in a square grid, this qualitative change from fragmentation to connectivity occurs when approximately **60%** of the landscape contains susceptible habitat (Turner *et al.* 1989; see also Stauffer 1985). Such probabilistic models could be further developed to simulate realistic, heterogeneous landscapes in which the probability of fire spread varies among sites having different characteristics (*e.g.*, various fuel types and topographic features).

The preceding discussion leaves us with two questions that are important both from a theoretical and practical standpoint: (1) how can the fine-scale mechanisms that contribute to crown fire spread be extrapolated to the whole landscape, and **(2)** when is landscape pattern an important influence on crown fire spread? The question of how to build the linkage between fine-scale mechanisms of fire behavior and landscape-level fire patterns remains challengin. In our research in subalpine forests of Yellowstone National Park, Wyoming, we are attempting to link the mechanistic and probabilistic approaches. Developing a good probabilistic model of crown fire spread requires estimating the actual probability of fire spread from site to site under various combinations of weather, fuels, and topographic conditions. Ideally, mechanistic fire models would provide estimates of the probabilities of fire spread between forest patches for the broad-scale models. Burrows (1988) developed this approach by using the Rothermel model to predict spread rates of surface fires within individuals cells; if the rate exceeded a threshold value, then the fire spread to an adjacent cell. It may be possible to estimate the spread parameters for crown fires by developing empirical correlations between fire behavior and controlling factors. This technique is an important component of current fire research in Canada (*e.g.*, Stocks 1989) and elsewhere (Nelson and Adkins 1988). It might be possible to correlate the observed behavior of crown fires with meteorological parameters, forest successional stages, and topographic features to obtain appropriate values for the spread parameters used in a probabilistic model.

When is landscape pattern an important influence on the behavior of crown fires?

Landscape patterns may influence the behavior of crown fires in at least two ways. First, topographic and physiographic features in the landscape can influence the local probabilities of initial ignition and burning. For example, fires may burn more intensely on north and east aspects, where cooler and moister conditions may enhance tree growth and hence fuel accumuation (Barrett 1988). Natural fuel breaks such as lakes, streams, wetlands, and moist slopes have relatively low probabilities of burning and hence can alter fire spread (Loope and Gruell 1973; Heinselman 1973; Romme and Knight 1981). Fires also behave differently in rugged, highly dissected terrain than on broader slopes and more gentle topography (Arno 1980). Very steep topography promotes rapid spread of fires from canyon bottoms to ridgetops (Heinselman 1981, Barrett 1988).

Second, the spatial arrangement of fuels on the landscape can influence burning patterns (Brown 1985). The flammability of the adjacent fuel complex determines, to some extent, the likelihood that any particular patch in the landscape will burn (Knight 1987). In the Jackson Hole area of Wyoming, crown fires developed only in areas of exceptionally heavy fuels where the heat of the fire generated substantial convection currents; the crown fires died down in lighter ground fuels (Loope and Gruell 1973). If flammability is related to stand age (*e.g.*, through stand density and the dead woody fuel mass), the spatial distribution of old and young stands may constrain or enhance fire spread (see Fig. 1). In California, for example, fires in chaparral were observed to burn well in old stands and become diminished as they spread toward patches of younger vegetation (Minnich 1983). A similar phenomenon was observed in Yellowstone National Park between 1972 and 1987, when fires burned intensely in 300-yr-old forests but failed to be carried through the canopy when they reached 100-yr-old stands, even though weather conditions remained favorable for fire (Despain and Sellers 1977). Thus, in most years, the juxtaposition of stands of different ages classes appears to reduce the flammability of the landscape as a whole (Knight 1987, Romme and Despain 1989), and the probable path and maximum run of fires might be predicted by mapping the spatial distribution of susceptible stands downwind from a point of ignition (Heinselman 1985). These examples demonstrate that, except under extreme burning condition, fires are likely to respond to variations in fuel availability and moisture conditions aross the landscape.

Landscape pattern may have little influence on crown fire behavior when burning conditions are extreme, however. Under conditions of extreme drought and high winds, all fuels across the landscape become highly susceptible to burning and may render the occurrence of large stand-replacing fires inevitable (Fryer and Johnson 1988). For example, the 1988 weather conditions in Yellowstone Park were sufficiently severe that the fires burned through all forest age classes in proportion to their availability on the landscape (Despain 1991), and landscape features that traditionally served as fuel breaks (*e.g.*, younger forests, and even rivers and wetlands) surprisingly were not effective. Thus, landscape pattern did not appear to constrain fire spread in Yellowstone during the 1988 fire season, in striking contrast to the patterns documented from 1972 to 1987.

We suggest that fine-scale mechanisms of fire spread can be extrapolated to make broad-scale predictions of landscape pattern by coupling the knowledge obtained from mechanistic and empirical fire behavior models (which treat variables of weather and the fuel characteristics of various vegetation types) with probabilistic models of the spread of disturbance through heterogeneous landscapes (which incorporate the spatial effects of ignition and the connectivity of the mosaic of fuel types). One way of developing this linkage is to hypothesize that there may be thresholds both in landscape pattern and in meteorological conditions that interact to produce large-crown fires (Fig. 2). Above some fuel moisture threshold (*e.g.*, 1000-hr time lag fuel moisture, generally measured in large dead logs and branches), stand-replacing crown fires cannot occur because the fuels are too wet, and

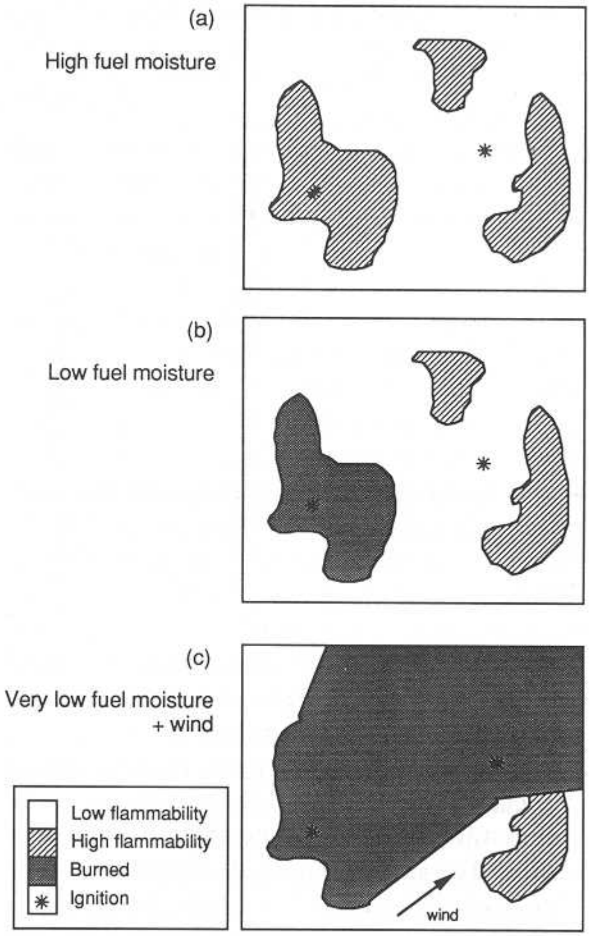

Fig. 2. Interaction between hypothesized thresholds in both meteorological conditions and landscape pattern that interact to produce large-scale crown fires. (a) If fuel moisture is high, lightning strikes are unlikely to initiate a fire even when the strikes occur in highly flammable forests. Landscapes pattern is not important in controlling fire spread. (b) If fuel moisture is low, but burning conditions are not extreme, then crown fires are likely to be constrained by the spatial distribution of highly flammable forest stands. (c) If fuel moisture is extremely low and there are high winds, crown fires are likely to burn in a variety of fuel types. The landscapes essentially becomes connected, and the patterning of highly flammable forest stands does not constrain fire spread.

Table 1. Area burned from 1972 to 1988 in Yellowstone National Park, Wyoming. [Data from Diaz (1979) and courtesy of the **U.S.** National Park Service.]

	% Mean Precipitation (1889–1977)			
Year	July	August	Number of fire starts	Area burned (ha)
1972	119	178	21	2
1973	106	126	33	59
1974	73	139	38	529
1975	141	67	26	2
1976	148	160	30	650
1977	195	163	29	27
1978	99	46	24	6
1979	115	151	55	4548
1980	143	199	25	2
1981	103	25	64	8338
1982	118	163	20	0
1983	269	88	7	0
1984	297	121	11	0
1985	160	84	53	13
1986	212	75	33	1
1987	303	122	35	390
Total (1972–1987)	–	–	503	14,566
1988	79	10	24	292,00

the spatial distribution of fuels is not important (Fig. 2a). Below some threshold of extremely low fuel moisture, and especially when coupled with high wind speed, large crown fires will be inevitable if ignition occurs (Fig. 2c). Landscape pattern is also not important under these extreme conditions because virtually all fuel classes can burn, and the landscape essentially is fully connected. When fuel moisture is between these hypothesized upper and lower severity thresholds, landscape pattern constrains the crown fire behavior (Fig. 2b). Large crown fires can occur if the proportion of flammable forests stands on the landscape exceeds a critical threshold of connectivity and there is either a large number of ignitions or a long period of time for the fire to spread. In this case, crown fire behavior is primarily a function of time and landscape structure, *i.e.*, the spatial pattern of the fuel categories that are most flammable.

In our current research, we are testing these ideas in Yellowstone National Park, Wyoming. Summary data on the amount of forest burned for different years suggest the existence of thresholds in both weather conditions and in connectivity of the forest. During wet or normal summers, very small areas burned in Yellowstone (Table 1), and fires were generally limited to stands that were 300+ yrs in age. During extreme burning conditions, as experienced in 1988, the area burned was extensive (Table 1) and included stands of all ages (Despain 1991). The identification of thresholds at which the broad-scale dynamics of crown fire behavior change qualitatively (Fig. 2) may permit the extrapolation of fine-scale mechanisms of fire spread to the landscape level.

Landscape patterns created by crown fires

Ecologists have long recognized the importance of landscape-level patch mosaics (*e.g.*, Cooper 1913; Leopold 1933; Watt 1947), but rigorous, quantitative description of landscape pattern has been attempted only recently. Two general types of approaches have been used in the analysis of fire-created landscape mosaics: spatially aggregated methods and spatially explicit methods. Each has certain advantages and problems, and each gives a somewhat different view of the landscape.

Methods for describing pattern in fire-dominated landscapes

In the spatially aggregated approach, one determines the statistical distribution of stand age classes, time intervals between successive fires, or of similar parameters related to disturbance history (*e.g.*, Van Wagner 1978; Johnson 1979; Yarie 1981; Johnson and Van Wagner 1985). The negative exponential and Weibull models are commonly used to describe these distributions. Although a stand-age map may be generated during the analysis, the proportion of the landscape within each age class is considered without regard to the spatial arrangement of age classes in the landscape.

With this approach, the quantitative measures of fire return interval and stand age class distribution can be obtained using basic forest inventory data. This is possible even in regions where fire-scarred trees are absent or rare, which is commonly the case in crown fire ecosystems because the tree species are often fire-sensitive, and fires tend to be severe (Van Wagner 1978; Yarie 1981). Moreover, the spatially aggregated models explicitly acknowledge the stochastic nature of fire, *e.g.*, by producing a probability density function for fire intervals of varying length (Johnson and Van Wagner 1985).

A problem with this method is that it assumes that the distribution of fire intervals and stand age classes remains more or less constant through time. This assumption is difficult to test directly, but most evidence suggests that crown fire ecosystems are not characterized by equilibrium or steady-state conditions (Romme 1982; Baker 1989a, b; Clark 1989). Nevertheless, the descriptive parameters of the spatially aggregated models are useful because they provide a general picture of the fire regime and the stand age class distribution, and they allow at least semi-quantitative comparisons of different landscapes.

The second approach to describing fire-mediated landscape pattern, spatially explicit methods, involves making a map of the patch mosaic within a defined geographic area. The patch units commonly are stand age classes. The classic work of this type is the series of stand-origin and fire-year maps produced by Heinselman (1973) for the Boundary Waters Canoe Area in northern Minnesota. Similar studies also have been conducted in other areas (*e.g.*, Hawkes 1979; Tande 1979; Hemstrom and Franklin 1982; Foster 1983; Johnson and Fryer 1987; Suffling *et al.* 1988; Romme and Despain 1989). Quantitative measures of landscape pattern then can be derived from a spatially explicit map of a patch mosaic (Turner 1989).

An advantage of this approach is that it requires no assumptions about the stability of the patch mosaic (*i.e.*, constancy in the proportion of the landscape occupied by different stand age classes). Furthermore, spatially explicit maps provide an empirical basis for analyzing of the spread of fire and other ecological phenomena in which spatial relationships are important. These include, for example, nutrient and energy fluxes between patches, wildlife habitat preferences and movement patterns, and the spread of other disturbances such as insect outbreaks (Turner 1989).

A spatially explicit depiction of landscape pattern is applicable only to a discrete moment in time; it does not by itself yield any of the temporal and stochastic parameters of the disturbance regime and the patch mosaic as are produced by the statistical models that use a spatially aggregated approach. However, temporal variation in landscape pattern can be examined by reconstructing spatially explicit patch mosaics that existed at discrete times in the past (*e.g.*, Hemstrom and Franklin 1982, Romme 1982, Turner and Ruscher 1988).

Variation in landscape patterns among crown fire ecosystems

Published information on fire regimes and resulting stand age class distributions in crown fire ecosystems throughout North America and Eurasia is summarized in Table 2 (also see Heinselman 1981; Wein and MacLean 1983). Because of the great variety of methods, concepts, and terminology employed by different researchers, these results are not comparable in any quantitative fashion. However, they do suggest qualitatively that there are least three broad-scale gradients in fire regime and landscape structure, as well as numerous finer scale patterns.

Table 2. Variation in landscape patterns and fire regimes along three major gradients in North America and Eurasia. Data are for periods with minimal fire control and are based on tree-rings or written records. The fire "cycle" is the estimated number of years required for an area equal to the entire study to burn; however, some sites may burn more than once and others not at all. Some authors use other terminology to express what appears to be the same or an equivalent concept. To facilitate comparison, all apparently comparable estimates are reported here as fire cycles. The particular terminology of each author is indicated in the footnotes whenever it is different; see the individual references for further explanations and details.

Location	Fire cycle (yr)	Comments
	I. CONTINENTAL GRADIENTS	
	Alaska and Northwestern Canada	
Nortwestern Territories, Canada	**37–102**	observed no stands **>350** yr old in subarctic forests (Johnson **1979)**[1]
Northwest Territories, Canada	–	spruce-feathermoss forests rarely escape fire for **>200** yr (Kershaw **1977: 398)**
MacKenzie River. northwest Canada	100	upland forests of jack pine , black, and white spruce (Rowe ***et al.*** **1974,** cited in Heinselman **1981)**
interior Alaska	**26–113**	<1% of sampled stands >200 yr old (Yarie **1981)**
interior Alaska	–	nearly all of interior Alaska has burned within last **200** yr; most sampled stands **< 150** yr old (Viereck **1973: 474)**
northwest Alberta	*50*	pine-spruce forests (Van Wagner **1978)**
	Eastern Canada and Northeastern United States	
northern Quebec	**100**	subarctic forest zone (Payette ***et al.*** 1989)[2]
Laurentian Highlands, central Quebec	**59–200**	nearly all stands **<150** yr old in three study areas (Cogbill **1985: 253, 260)**[3]
Algonquin Park, southern Ontario	**70**	fire burned at least half of the study area every **45** yr (Cwynar 1977)[3]
Quebec, northwestern Ontario and Labrador	**100–150**	pine and black spruce forests (Heinselman **1981)**
northwestern Ontario	–	all sampled stands **<173** yr old (Suffling **1983)**
Boundary Waters Canoe Area, northern Minnesota	100	oldest documented stand **375** yr old (Heinselman 1973)[3]
northern Michigan	**83–130**	in pine forest types (Whitney 1986)[4]
Nova Scotia	**200**	(Wein and Moore **1979,** Wein and MaclLean *1983)*[2]
southeastern Labrador	500	(Foster 1983)[3]
Maine	**470**	(Wein and MacLean 1983)[2]
northeastern Maine	**800**	**88%** of landscape covered by "climax" stands in ca. **1800** AD (Lorimer 1977)[5]
	Pacific Northwest	
Mount Rainer National Park, Washington	**434**	many stands **>1000** yr old (Hemstrom and Franklin **1982)**
	Eurasia	
north Sweden	**100**	mean interval between successive fires on the same site was **80** yr (Zackrisson 1977)[3]
northern European Russia	**130–200**	one fire each **40–68** yr in pine-dominated stands (Vakurov **1975,** cited in Tolonen **1983: 28)**[6]
	II. ROCKY MOUNTAINS: LATITUDINAL GRADIENT	
	Canadian Rockies	
Jasper National Park, Alberta	**74**	in subalpine forests (Tande 1979)[7]

Table 2. Continued.

Location	Fire cycle (yr)	Comments
Kananaskis Provincial Park, Alberta	**90–153**	(Hawkes **1979,** cited in Arno **1980)**[7]
Kananaskis Valley, Alberta	**150**	(Johnson and Fryer **1987)**[8]
Crowsnest Forest, southern Alberta	–	**77%** of stands sampled in **1931** were **<100** yr old; few stands **>250** yr old escape fire (Day **1972)**
	Northern U.S. Rocky Mountains	
western Montana, northern Idaho	90–150+	in subalpine forest types (Arno **1980)**[7]
northwestern Montana	125–300+	Gabriel **(1976),** cited in Arno **(1980)**[7]
Yellowstone National Park, Wyoming	**200–400**	**40%** of subalpine landscape composed of forests >200 yr old in **1985** (Romme **1982,** Romme and Despain **1989)**
	Central and Southern Rockies	
Medicine Bow Mountains, southeastern Wyoming	–	many stands >200 yr old; some >500 yr old (Oosting and Reed **1952,** Romme and Knight **1981)**
Front Range, northern Colorado	–	many stands >200 yr old; some >500 yr old (Peet **1981,** Veblen **1986,** Aplet ***et al.*** **1988)**
	111. ROCKY MOUNTAINS: ELEVATIONAL GRADIENT	
Kananaskis Provincial Park, Alberta	**90** **153**	at lower elevations; at higher elevations (Hawkes **1979,** cited in Arno **1980)**[7]
western Montana, northern Idaho	**22–130** **63–> 150**	in lower subalpine zone; in upper subalpine zone **(Arno 1980)**[7]
Jasper National Park, Alberta	–	sites with no history of fire located only at higher elevations (Tande **1979)**
Northern Rocky Mountains	–	climax stands more common at high elevations than at low elevations (Habeck and Mutch **1973)**
northwestern Wyoming	–	**1** fire per **50** yr at low elevations; fewer fires at higher elevations (Loope and Gruell **1973)**
Medicine Bow Mountains, Wyoming	–	predominantly younger stands at lower elevations; older stands at higher elevations (Romme and Knight **1981)**
Front Range, Colorado	–	fires at intervals ***of*** **50–150** yr at low elevations; longer intervals at high elevations (Clements **1910;** Peet **1981, 1988)**

[1] "expected fire recurrence interval"
[2] "fire rotation period"
[3] "fire rotation"
[4] "average return time"
[5] "average fire recurrence interval"
[6] "mean fire interval"
[7] "mean fire return interval"
[8] "average fire interval"

The first gradient is continental. Effective summer precipitation across northern North America varies from generally drier conditions in interior Alaska and northwestern Canada to wetter conditions in eastern Canada and the northeastern United States (Heinselman **1981).** Western and central regions appear to have relatively frequent fires and patch mosaics dominated by younger stands, whereas the eastern region (especially in Labrador and Maine) is characterized by longer intervals between fires and a greater representation of older stands (Table **2).** The eastern Canadian coastal region has a cool, moist climate (Foster 1983), whereas the interior regions are subject to recurrent drought (Heinselman 1981). The northwest Pacific coast also is characterized by high precipitation (Franklin 1988), and fire intervals are long in that region (Table 2). The limited information available on fire regimes in boreal Eurasia suggests that this region is similar to interior boreal North America (Table 2).

There also are regional-scale patterns in fire regime and landscape structure in boreal North America that are not evident in the continental scale of comparison in Table 2. These patterns are controlled by regional-scale climatic processes. For example, the expected fire recurrence interval in northwestern Canada ranged from 102 years near the northern tree line to 37 years at a site 400 km southwest of the tree line (Johnson 1979). The more southerly sites also were characterized by generally younger stands and more fire-resistant features such as serotinous cones. This gradient is related to the penetration and duration of the Pacific air mass, *i.e.*, weather conditions conducive to fire occur more frequently with increasing distance from the tree line (Johnson 1979).

Another example of regional-scale pattern within the interior boreal forest zone was reported by Suffling (1988), who calculated landscape diversity using the Shannon index along a 300-km transect in northwestern Ontario. He reported maximum diversity in areas having intermediate rates of disturbance, with lowest diversity in areas of either very low fire occurrence (< 0.05% of the area burned per year) or very high fire occurrence (> 0.75% burned per year).

At even finer scales throughout the boreal forest zone, one finds considerable variation in fire intervals and stand age class distributions in response to local topography, vegetation, and microclimate. For example, white spruce forests > 300 yr old are common in Alaska and Canada on moist sites that burn less frequently and possibly less intensely than surrounding upland sites (*e.g.*, Quirk and Sykes 1971; Viereck 1973; Heinselman 1981). Similarly, concave topographic surfaces and north-facing slopes generally support older stands than convex surfaces and south-facing slopes in Sweden (Zackrisson 1977). The local distribution of lakes and wetlands, or of relatively non-flammable vegetation types, may result in different fire regimes upwind and downwind of these barriers to fire spread (*e.g.*, Heinselman 1973; Foster 1983; Whitney 1986).

The second major gradient evident in Table 2 is a latitudinal gradient in fire regime and landscape structure in the coniferous forests of the Rocky Mountains. The Canadian Rockies appear to be characterized by a fire regime similar to that of the boreal forest, *i.e.*, relatively frequent fires and a preponderance of younger stands. In contrast, the Rocky Mountain subalpine forests in the western United States show much longer fire intervals and very extensive, old upland forests. The major reason for longer fire intervals to the south probably is the reduction in fire hazard produced by moist air mass from the Gulf of Mexico that tend to move into the southern Rocky Mountain region, especially New Mexico, Arizona, and Colorado, during late summer (Mitchell 1976; Arno 1980).

The third gradient in Table 2 is an altitudinal gradient in the Rocky Mountains. Fire frequency appears to decrease with increasing elevation, probably because of higher precipitation and cooler temperatures. Indeed, the oldest stands in the central and southern Rocky Mountains are generally found at high elevations. As in the boreal region, there also is local variation in fire frequency and stand age distribution in relation to topographic effects. For example, older forests commonly are found in valley bottoms (Loope and Gruell 1973; Romme and Knight 1981; Hemstrom and Franklin 1982) or near large lakes because of less frequent fires in these sheltered sites.

Johnson and Fryer (1987) reported the size distribution of fires in the Kananaskis Valley, Alberta, from 1783 to 1972. Most fires were small, but just four large fires accounted for most of the total burned area. This appears to be the usual pattern in crown fire ecosystems (Baker 1989a, b; Heinselman 1973, 1981; Hemstrom and Franklin 1982; Romme and Despain 1989), that is, large fires create the vegetation mosaic that dominates the landscape until the next extensive fire.

***Are crown fire dominated landscapes in equilibrium*?**

Crown fire ecosystems are repeatedly referred to as "disturbance forests'' (*e.g.*, Rowe 1961, Peet 1988). Ecologists have long suggested, however, that despite continual disturbance and succession in every small stand, there may be some broader spatial or temporal scale at which there exists a stable configuration of stand ages or successional stages. For example, Cooper (1913) proposed that the forests of Isle Royale maintained a more or less stable composition despite periodic fires, because as forests were being destroyed by fire in one part of the island, they were being replaced by succession in other areas that had burned previously. Shugart and West (1981) explored the effects of spatial scale through modeling experiments, and concluded that a quasi-steady state landscape was likely only where the average size of disturbances (*e.g.*, fire) was small relative to the total extent of the landscape. Specifically, they predicted that a stable patch mosaic is likely only where the land area is more than 50 times the size of individual patches. Bormann and Likens (1979) and Pickett and White (1985) also concluded that landscapes characterized by small, frequent disturbances may be in some sort of equilibrium, whereas large, infrequent disturbances usually lead to non-equilibrium conditions.

The equilibrium question is complicated by inconsistent terminology and criteria among investigators. The terms ''equilibrium'' and ''steady-state'' appear to be roughly synonymous when applied to landscapes, and so we use the term equilibrium here. Exactly what constitutes an equilibrium state is much less clear. Some of the definitions that have been applied include persistence of all species (DeAngelis and Waterhouse 1987), no net change in biomass accumulation over time (Bormann and Likens 1979), and distributions of stand age classes or successional stages that show little or no change over time (Romme 1982; Baker 1989a, b). In this discussion we use the latter definition for equilibrium at the landscape level.

Two detailed studies have explicitly tested the idea of equilibrium in crown fire ecosystems. One was by Romme (1982), who reconstructed patch mosaics for the last 250 years in a 7300-ha watershed in Yellowstone National Park and found that the relative area covered by each successional stage varied continuously throughout that time because of succession on extensive areas that burned in the 1700s and an absence of large fires since 1800. Romme and Despain (in prep.) expanded this study to an area of 129600 ha but still found constant fluctuation in the patch mosaic over the last 250 years, again because of extensive fires in the 1700s. They concluded that Yellowstone National Park is a non-equilibrium landscape even at the scale of the entire Park because fires burn very large areas at long intervals.

A second test of landscape equilibrium was conducted by Baker (1989a, b) in the 404000-ha Boundary Waters Canoe Area in northern Minnesota. Baker subdivided the entire area into a series of progressively smaller, nested subunits. He then reconstructed past age class distributions and determined parameters of the Weibull distribution within the entire study area and within each subunit. He found no evidence of a temporally stable patch mosaic at any scale because of spatial heterogeneity in age-class distributions and the persistent effects of a few very extensive fires.

It is possible that both the Yellowstone and the Boundary Waters landscapes would be characterized by an equilibrium distribution of stand age classes if we viewed them over a longer temporal scale than the 200–300 years examined in these two studies, However, with time frames longer than about 400 years the fire regime may be altered by climatic changes (Johnson and Van Wagner 1985; Swetnam and Betancourt 1990). It is possible also that equilibrium conditions prevail in a few crown fire ecosystems, such as the forests of the southern Rocky Mountains or the Pacific northwest where stands persist for centuries without fire. However, the necessary data to test this hypothesis are not presently available.

We conclude, therefore, that crown fire ecosystems probably are best regarded as non-equilibrium systems, because extensive, infrequent fires tend be very large relative to the total landscape area. Smaller fires also occur, perhaps frequently, but they have far less influence on stand age class distribution, and their effects are generally overshadowed by the rare large fires.

Landscape patterns of burn severity associated with crown fires

Over a long period of time, most of the burned area in a crown-fire landscape is usually the result of relatively few intense conflagrations (Baker 1989a, b; Heinselman 1973, 1981; Hemstrom and Franklin 1982; Romme and Despain 1989). These large crown fires rarely consume the entire forest, however, because of the influence of wind variations, topography, vegetation type, natural fire breaks, and the time of day that the fire passed through (Rowe and Scotter 1973; Wright and Heinselman 1973; Van Wagner 1983). Thus, crown fires contain areas of low as well as high intensity fire, usually in a complex mosaic (Van Wagner 1983). These variable fire intensities result in a heterogeneous pattern of burn severities (effects of fire on the ecosystem) as well as islands of unburned vegetation. This heterogeneity is quite obvious, for example, in the 1988 fires that occurred in Yellowstone Park (Christensen *et al.* 1989). The influence of burn severity on plant reestablishment following fire is well documented (*e.g.*, Ahlgren and Ahlgren 1960; Lyon and Stickney 1976; Rowe 1983; Viereck 1983; Ryan and Noste 1985), and the importance of the effects of limited burns and low-intensity fires on the vegetation mosaic has also been recognized (Habeck and Mutch 1973; Rowe and Scotter 1973). However, the spatial heterogeneity of burn severities in the landscape has not been studied explicitly.

Species responses following fire may vary with different kinds and severities of disturbance and with the larger spatial and temporal context of the disturbance (also see Pickett 1976; Johnson 1977; Loucks *et al.* 1980, 1985; Rowe 1983; Finegan 1984). When differential plant mortality and reestablishment folllowing crown fires is considered, the spatial mosaic of burn severities becomes important. Extensive areas that experienced fires of high severity are likely to have few resprouting individuals, and may even have had much of the seedbank (in both the soil and canopy) destroyed. Many

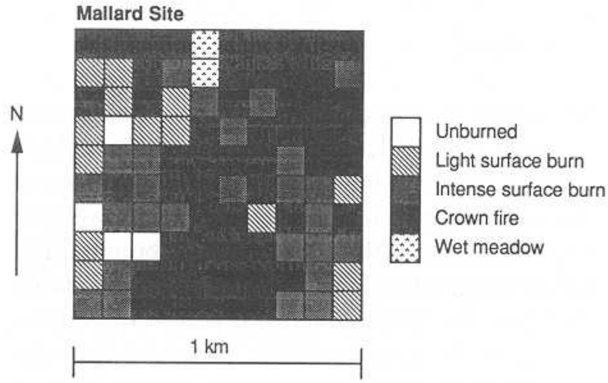

Fig. 3. The spatial pattern of burn severities in a 1-km × 1-km area in Yellowstone National Park that burned during the summer of 1988. The site is located approximately 2 km northeast of Old Faithful and was sampled during the summer of 1989.

forest herbs, for example, resprout vigorously in lightly burned areas but must reestablish from seed in severely burned patches. Remnant unburned or lightly burned patches within a severely burned area (as shown in Fig. 3, for example) can provide a seed source that might considerably increase the rate of plant reestablishment. Thus, we might hypothesize that the burn mosaic will differentially influence plants depending on the modes of reproduction. The rate of reestablishment of plants that depend on the dispersal of propagules will be influenced by the size of the burned patch, the distance to the nearest unburned forest patch, and the amount and spatial distribution of burn severities within the patch. In contrast, the rate of reestablishment of resprouting species may be controlled primarily by burn severity, regardless of the size of the burned patch or the distance to an unburned forest patch.

The spatial heterogeneity of burn severity patterns is also likely to influence a variety of other ecological processes. For example, the amount of edge habitat created by an extensive crown fire will vary with burn patterns – a patchy distribution of severely burned areas and lightly burned or unburned stands is likely to increase the browse available for wild ungulate populations (Christensen *et al.* 1989). Landscape-level burn patterns will also affect watershed dynamics (Minshall *et al.* 1989) because the removal of vegetation by fire alters the relative amounts of water lost through evapotranspiration, surface flow, and subsurface flow (Knight *et al* 1985). For a given proportion of burned area, a high degree of patchiness in burn severity may ameliorate the effects of fire on streamflow and water quality (Knight and Wallace 1989).

The effects of crown fire patterns on ecological processes are scale-dependent, that is, the effects are different when observed or quantified at different spatial scales. Responses at particular locations, which may have experienced a severe burn, are likely to be qualitatively different than the response of the whole landscape, across which there is a mosaic of burn severities. For example, lower order watersheds may be entirely burned, and hence fine-scales effects on stream ecosystems may be substantial (Minshall *et al.* 1989). In contrast, higher order watersheds are likely to exhibit a mosaic of burn severities, and thus broad-scale effects on stream dynamics may be less severe than at the finer scales. Scale-dependence is also important when the potential for a steady-state mosaic is considered; landscapes may be in equilibrium at some spatial or temporal scales, but not at others. However, as the temporal scale is expanded, we cannot necessarily assume that other broad-scale environmental conditions remain constant. This becomes increasingly important as we consider the potential for climatically-induced changes in crown fire dynamics (Swetnam and Betancourt 1990).

Crown fire dynamics in a changing climate

The interaction between climate change and disturbance regimes, which can rapidly alter landscape structure, potentially could be as important as the direct effects of global warming in controlling shifts in species distributions and local extinctions (Johnson and Sharpe 1982; Solomon *et al.* 1984; Davis and Botkin 1985; Nielson *et al.* 1989; Graham *et al.* 1990; Franklin *et al.* 1992). The predictions of current general circulation models (*e.g.*, Hansen *et al.* 1988; Wetherald and Manabe 1988; Schlesinger and Zhao 1988; see also review by Dickinson 1986) suggest a global warming in the coming century. Current projections are for an average rise in global temperature of 1.5 to 4.5 °C with increased warming at higher latitudes and decreased summer precipitation and soil moisture in middle latitudes of the northern hemisphere. Although considerable uncertainty remains about the magnitude, rate, and spatiotemporal characteristics of the potential climate change, the ecological implications are of sufficient importance that serious consideration of possible effects is warranted.

A probable effect of global warming is an increased frequency of dry years and a consequent increase in the risk of large fires (Sandenburgh *et al.* 1987), perhaps increasing the likelihood of fires of the magnitude observed in the northern hemisphere in 1987 (*e.g.*, China and North America) and 1988 (*e.g.*, Yellowstone and elsewhere in North America). Fire regimes may be more sensitive to climate change than other forest processes (Clark 1990a) because fire is responsive to fuel moisture, which depends in turn on precipitation and relative humidity. The direct effects of climate change on forest production and decomposition (Meentemeyer 1978; Meentemeyer *et al.* 1982; Pastor and Post 1988) might be overshadowed by more drastic effects of climate on fire regimes (Clark 1990a).

Past climate changes of small magnitude have caused substantial changes in fire regimes (*e.g.*, Clark 1988, 1990b). In northwestern Minnesota, for example, fire was most frequent (~ 8.6-yr return interval) during the warm dry 15th and 16th centuries and less frequent (~ 13.2-yr return interval) during the cooler moister periods from 1240–1440 AD and during the “little ice age” (Clark 1990b). In Mt. Rainier National Park, Washington, all but two episodes of major fires since 1300 A.D. correspond with major droughts that were reconstructed for regions east of the Cascade Range Hemstrom and Franklin 1982). Fire regimes are sensitive to both the “average” climate over decades to centuries as well as the interannual variability of water balance (Clark 1990b). In northwestern Minnesota, fires were clustered during times of extended low effective precipitation and soil moisture storage in the 1880s and 1910s (Clark 1989). Similarly, the duration of dry periods is one of the best predictors of the area burned in contemporary Canadian forests (Haines and Sando

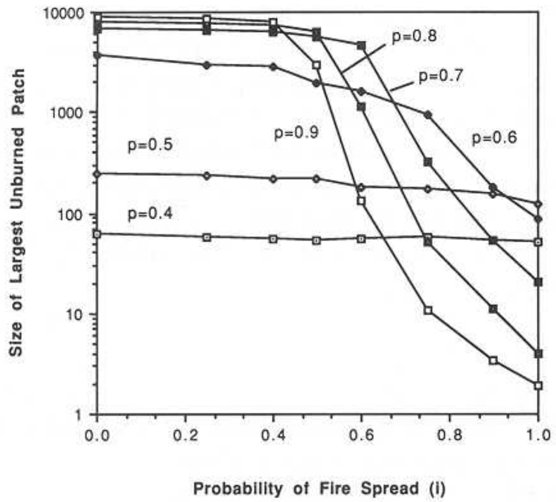

Fig. 4. Size of the largest unburned forest patch remaining following fires simulated with increasing probabilities of spread. Simulated landscapes have varying proportions (p) of flammable forest distributed at random. (Adapted from Turner *et al.* 1989).

1969; Flannigan and Harrington 1988). However, the projection of changes in fire frequency, intensity, and severity with a changing climate remains challenging because of the complex relationship between weather, fuel availability, and ignition.

A simple probabilistic model of the kind described earlier in this chapter may provide insight into the potential effects of climatically-induced changes in fuel patterns, fire frequency, and the probability of fire spread on landscape patterns (*e.g.*, Turner *et al.* 1989, 1991). Consider, for example, a simple model in which a forested landscape is represented in grid cell format as a 100 × 100 array. The proportion of the landscape that is flammable can be represented at various levels (*e.g.*, 0.1, 0.5, etc.) by using a probability, p. Fire frequency, f, can be represented as the probability of ignition occuring on a flammable cell, and fire propagation across the landscape can be simulated as the probability, i, of fire spreading from a burning cell to an adjacent flammable cell. By varying these three parameters, the implications of an altered fire regime can be explored. For example, consider the size of the largest unburned patch that remains on the landscape following a simulated fire. Patch size may be of great importance for the persistence of particular species in disturbed landscapes. In a series of ten Monte Carlo simulations, fires were simulated with a fixed frequency of ignition ($f = 0.1$) but with increasing probabilities of spread, as might occur under warmer and drier conditions. The size of the largest unburned patch was influenced by an increased probability of fire spread (i), with qualitative differences above and below the critical threshold of connectivity, p_c (approximately 0.6 for random square arrays) (Fig. 4). The size of the largest unburned patch was not affected by the probability of fire spread when the flammable forest was disconnected on the landscape, *i.e.*, occurring below p_c (spotting behavior was not included in this simulation). When the flammable forest was connected on the landscape (*i.e.*, above p_c), the size of the largest undisturbed patch decreased rapidly when the probability of spread was greater than 0.5. The decline in patch size was sharpest for the highest values of p. That is, when the flammable forest was very common and connected, it was easily fragmented by fires that had moderate to high probabilities of spreading. Simulation experiments such as these, in which parameters such as probabilities of initiation or spread can be varied to represent climatically-induced changes, can also be linked with succession models. These models may provide useful heuristics to explore the effects of climatically-altered crown fire regimes on the landscape mosaic by providing testable predictions of potential changes in landscape pattern.

In a changing climate, the plant communities that become established after large crown fires may be different in composition from the communities present before the fire. On Mt. Rainier, for example, Dunwiddie (1986) demonstrated that fires that occurred during the mid-1800s burned through an *Abies amabilis* and *Tsuga mertensiana* forest that had persisted for centuries. The mid-1800s were characterized by warming temperatures that caused earlier seasonal snowmelt and longer growing seasons. These climate conditions allowed *Tsuga heterophylla* to become abundant briefly after the fires, and *T. heterophylla* was then replaced by *Abies lasiocarpa*. Because long-lived mature trees may survive short-term climate fluctuations, species that are best adapted to the current climate may only be able to enter the forest in open habitats following severe fires, and forest composition may respond to climatic changes primarily after disturbance (Dunwiddie 1986). A study by Cwynar (1987) also suggests that, although the ultimate cause of postglacial vegetation change in the Pacific Northwest was climate change, the proximate cause of some postglacial vegetation changes was an altered fire regime. A small change to a drier climate probably triggered a relatively large change in the disturbance regime by increasing fire frequency (Cwynar 1987).

Potential climatically-induced alterations in crown fire regimes may therefore lead to substantial landscape changes, in terms of both the characteristic vegetation mosaic and the species composition of particular regions. Landscape dynamics may shift along the gradients described in Table 2, with associated changes in the frequency of stand-replacing fires. An increase in fire frequency in forests of the Pacific Northwest, for example, would likely decrease the abundance of older forest stands on the landscape, thereby accentuating the effects of logging by further reducing the habitat available for obligate old-growth species. Thus, additional research is warranted regarding the sensitivity of crown fire regimes to climatological shifts along continental, latitudinal, or elevational gradients.

Conclusions and research needs

There is a two-way interaction between crown fires and the spatial patterning of a landscape. Crown fires create broad-scale patterns in vegetation by producing a patch mosaic of stand age classes, but the spread and behavior of crown fires also may be constrained by spatial patterns in terrain and fuels across the landscape.

We suggest that fine-scale mechanisms of fire spread can be extrapolated to make broad-scale predictions of landscape pattern by coupling the knowledge obtained from mechanistic and empirical fire behavior models with spatially-explicit probabilistic models of fire spread. Climatic conditions exert a dominant control over crown fire behavior and spread, especially during extreme climatic events, *i.e.*, very wet or very dry conditions. Between these extreme climatic conditions, however, both topographic and physiographic features in the landscape and the spatial arrangement and types of fuels have a greater influence on fire spread. Research is needed to more clearly delineate the range of conditions under which landscape pattern is important and to identify possible thresholds at which fire behavior changes qualitatively.

General trends in crown fire regimes and stand age class distributions can be observed across continental, latitudinal, and elevational gradients. Crown fires are more frequent in regions having more frequent and/or severe droughts, and younger stands tend to dominate these landscapes. The projected changes in global climate during the next century may alter fine regimes, with major implications for landscape structure and ecological processes. Additional research is needed to clarify the mechanisms by which regional-scale climatic variables interact with local conditions of terrain and fuels to produce characteristic fire regimes and patch mosaics.

Crown fires rarely consume the entire forest because of the influence of wind variations, topography, vegetation, and natural fire breaks. Crown fire always contain areas of both high and low intensity fires and create a complex mosaic of burn severity across the landscape. The spatial heterogeneity of burn severity patterns creates a wide range of local effects and is likely to influence plant reestablishment as well as many other ecological processes. Potential changes in the global climate may alter not only the frequency of crown fires but also their severity, with important implications. Research is needed to better document the ways in which these spatial patterns influence the responses of organisms having different life history characteristics and of ecosystem-level processes such as nutrient cycling.

Landscapes dominated by crown fires appear to be nonequilibrium systems (Romme 1982; Baker 1989a, b). This nonequilibrium condition presents a significant challenge to land managers, particularly when the implicatons of potential changes in the global climate are considered. There may not be easy answers to questions of how large an area must be to encompass the ''natural'' fire regime, or how likely extensive crown fires will be in the future. However, increased knowledge of ecological processes at regional scales and the effects of landscape pattern on fire dynamics should provide insight into our understanding of the behavior and consequences of crown fires.

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