

# Disturbance Ecology of North American Boreal Forests and Associated Northern Mixed/ Subalpine Forests

James K. Agee, College of Forest Resources  
Box 352100, University of Washington, Seattle, WA 98195

**Abstract**—Disturbance dynamics differ in the three subregions of the North American boreal forest (taiga, western United States, and eastern United States) where lynx are found, resulting in a range of potential effects on lynx populations. Fire severity tends to be high in most of the forest types where lynx habitat occurs, although subsequent succession will differ among the subregions. Other disturbance dynamics involve insects, disease, wind, and human ownership and use, such as logging, mining, agriculture, and fire suppression. The author addresses three general lynx management implications based on disturbance dynamics.

## Introduction

---

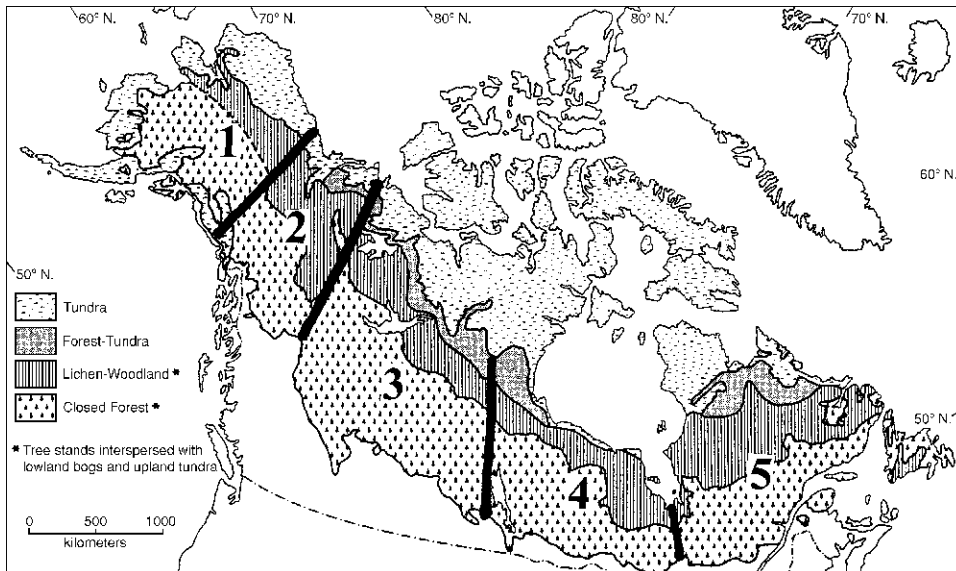
The distribution of the lynx in North America is closely associated with the distribution of the North American boreal forest. The range of the lynx extends south from the classic boreal forest zone, called the taiga, into the

subalpine forests of the western United States, and the boreal/hardwood forest ecotone in the eastern United States (Chapter 8). This chapter summarizes the forest ecology of lynx habitat within the boreal zone of North America, including the effects of a variety of disturbance agents.

## **Divisions of the North American Boreal Forest**

There are few, if any, forest classification schemes that have directly comparable boundaries for forest biomes. Criteria for classification often differ, and scientists often apply subjective rules. Even the acceptance of a zonal versus gradient classification spurs debate: Larsen (1980), in his classic treatment of the boreal ecosystem, describes the major types but favors a gradient approach so does not map his types. Yet of all the forest biomes, the boreal forest probably comes closest to a broadly accepted definition. The circumpolar boreal forest is commonly perceived as a set of homogeneous arboreal stands, dominated by conifers during later stages of succession, and by arboreal members of the birch and willow families in early succession. Many of the shrub species are circumpolar in distribution, but none of the tree species are (Solomon 1992). The northern border of the boreal forest is defined by tundra. While authors disagree slightly on where the boundary should be drawn along the gradient from closed-canopy forest to treeless tundra (Solomon 1992), this boundary is from one easily recognized type to another (Fig. 3.1). In North America, the southern boundary of the boreal forest is much more contentious, as the boreal forest changes to subalpine forest in the western continent, to prairie in mid-continent, and to a mixed coniferous/deciduous temperate forest in the east. These southern transitions are recognized in three broad groups, for the purposes of describing lynx habitat south of Canada, across an east-west gradient (map insert): Northeastern and the Great Lakes boreal forests that include eastern hardwoods and temperate conifers, as well as boreal conifers, and Western boreal forest, that includes subalpine forests similar to boreal forests.

Consistent and broadly recognized terminology is essential to effective presentation. I have chosen here to refer to the boreal forest as any forest with boreal features. This includes not only the taiga, but forests to the south such as the higher elevation portions of the Cascades, Sierra Nevada, and Rocky Mountains. Tree species are referred to by common name, with an appendix at the end of the chapter that includes Latin names; shrubs are mentioned by common and Latin name in the text. I have chosen here to refer to the northern boreal forest in general as taiga (e.g., Viereck 1983), with closed forest and the more open lichen-woodland as constituents. Other authors would disagree: taiga is variously defined as the “boreal forest” (Oechel and Lawrence 1985; Van Cleve et al. 1983) and “the great northern coniferous



**Figure 3.1**—Major divisions of the taiga, patterned after Larsen (1980). Descriptions of each zone are in Table 3.1. 1 = Alaska; 2 = The Cordillera; 3 = Interior Forest; 4 = Canadian Shield; 5 = Eastern Canada.

biome” (Larsen 1980) but is also defined as only the northern part of the boreal forest representing that portion from closed forest canopy to the forest-tundra treeless boundary (Sirois 1992). The closed-canopy boreal forest has been called the “main boreal forest” (Hare 1969). To delineate boreal forest to the north from the transitional boreal zones to the south, the northern zone will be referred to as taiga, with closed and open subdivisions. The transitional boreal regions will be called, in the west, Western boreal forests, and in the east, either Great Lakes or Northeastern boreal forests, recognizing each has elements of boreal character.

## The Physical Environment

The physical environment of the boreal forest is similar around the world. Unlike most other forest biomes, the boreal forest can be defined on the basis of structure as much as species composition (Hare and Ritchie 1972; Solomon 1992), and these structural characteristics are closely associated with climatic and edaphic factors (particularly permafrost). Climatic gradients across the type include decreasing radiation to the north, differing air mass trajectories that influence cloud cover and precipitation, topography, and maritime/continental location (Elliott-Fisk 1988). Long, bitterly cold winters, short and

cool summers, and brief springs and autumns are characteristic of the boreal climate (Trewartha 1968). Although the growing season is short, unusually long summer days compensate to some extent for the brief and cool summers. These summer periods include times with low fuel moisture and strong winds, associated with severe fire behavior (Schroeder and Buck 1970).

The northern limit of treeline in the Arctic generally occurs along the 13° July isotherm. Boreal forest is bounded on the north by 30 or fewer days with mean temperature above 10°C, and to the south by 120 days with mean temperature above 10°C. Mean yearly temperatures increase from a minimum of -6.2°C near the forest tundra ecotone to 2.5°C near the southern closed boreal forest boundary. Precipitation is concentrated in the summer months, and snow cover lasts more than half the year. Although North American boreal winters are not as severe as those of Siberia (due to a smaller land mass), large parts of the region are permanently frozen, and the depth of thaw of the permafrost layer during the summer has a great effect on rooting depth and nutrient availability (Trewartha 1968; Van Cleve et al. 1983).

Western boreal forest is primarily subalpine rather than a classically boreal climate. Most of these areas border temperate forest at lower elevation and alpine communities at higher elevation. This is analogous to the much wider borders of the taiga with tundra to the north and temperate forest to the south. Western boreal forests are found at elevations above 1,400 m in Washington (Agee and Kertis 1987), but the rainshadow effect of the coastal mountains raises the elevations of all the forest zones to the east, so that boreal forest is found at 2,700 m elevation in the Colorado Front Range (Peet 1981). The elevation of the Western boreal zone may shift with climatic change or disturbance (Agee and Smith 1984; Rochefort et al. 1994). Western boreal forests generally receive more solar radiation and have higher diurnal temperature fluctuations and warmer temperatures, as well as shorter growing season day lengths, than classic boreal environments of the taiga (Oechel and Lawrence 1985). Local topographic variation makes climatic information difficult to generalize for Western boreal environments. Water stress may affect photosynthesis at some locations, and severe winter winds, carrying snow and soil particles, have a significant detrimental effect on plants that emerge above the snow line in timberline environments.

The Great Lakes and Northeastern boreal forests tend to be warmer than the taiga, with mean annual temperatures from 1.6 to 7.2°C (Rowe 1972). They tend to have more available moisture than either the taiga or the Western boreal forests (Rowe 1972).

# Composition of the Major Boreal Forest Types

## The Taiga

Within the broad structural classes of closed boreal forest and lichen woodland that comprise the taiga are geographic variants. As one travels east or west, continuous change is present although not obvious over short distances (Larsen 1980). Larsen classified the taiga into various regions from west to east (Table 3.1), with each region having a south-north gradient from the closed boreal forest on the south to lichen woodland to forest tundra (Fig. 3.1).

Rowe (1972) defined eight major forest regions in Canada: the taiga is by far the largest. He subdivides the taiga into three parts: a “predominately forest” type, equivalent to closed boreal forest, a “forest-grass” type which fringes the plains in southern Alberta, Saskatchewan, and Manitoba, and a “forest-barren” type, that borders the “predominately forest” type to the north and is transitional to tundra. He defines roughly 33 geographically based “forest sections” within the taiga, with white and black spruce common across the spectrum. Eastern larch, balsam fir, and jack pine are common in the eastern portions, and subalpine fir and lodgepole pine are more common in the west, particularly in the transition to subalpine forest. Although primarily coniferous, the taiga does include white birch and its

**Table 3.1**—Major forest regions of the taiga, adapted from Larsen (1980) and Elliott-Fisk (1988).

Region and description
<p><b>1. Alaska</b> Upland and lowland forests dominated by white spruce, black spruce. Paper birch and quaking aspen are common pioneer species, with balsam poplar along streams and floodplains. Fire and permafrost important environmental factors.</p>
<p><b>2. The Cordillera</b> Mesophytic uplands dominated by white spruce and white birch. North aspects dominated by black spruce, with a different shrub understory. Southward, into the subalpine forest type, forest dominants are Engelmann spruce, subalpine fir, subalpine larch, and balsam poplar.</p>
<p><b>3. Interior Forest</b> This forest is composed of black spruce, white spruce, lodgepole pine, quaking aspen, and balsam poplar, extending from the Cordilleran foothills to the Canadian Shield. Black spruce is again common on north aspects, with white spruce typically dominant in the floodplains. The eastern portion of this zone also includes jack and/or lodgepole pine (ridges and sandy soils), and some eastern larch and balsam fir.</p>
<p><b>4. Canadian Shield</b> Both east and west of Hudson Bay, this forest is relatively uniform, with richer forests (more species) to the south. In the southerly regions, balsam fir/white spruce is dominant in valleys, with jack pine on uplands and black spruce in lowlands. To the north, black spruce, white spruce, and jack pine are common, with black spruce dominant near the northern forest border.</p>
<p><b>5. Eastern Canada</b> The Gaspé-Maritime forests are closely related to those of the Great Lakes–St. Lawrence region. Forests are primarily coniferous with balsam fir playing a prominent role; associated dominants are black spruce, white spruce, and paper birch. In Labrador-Ungava, black spruce and white spruce are often dominants, but balsam fir, eastern larch, paper birch, and balsam poplar are also found. Quaking aspen, jack pine, and white cedar are found to the south. Complex topography and geology has produced a complex mosaic of plant communities. Black spruce becomes more important to the north.</p>

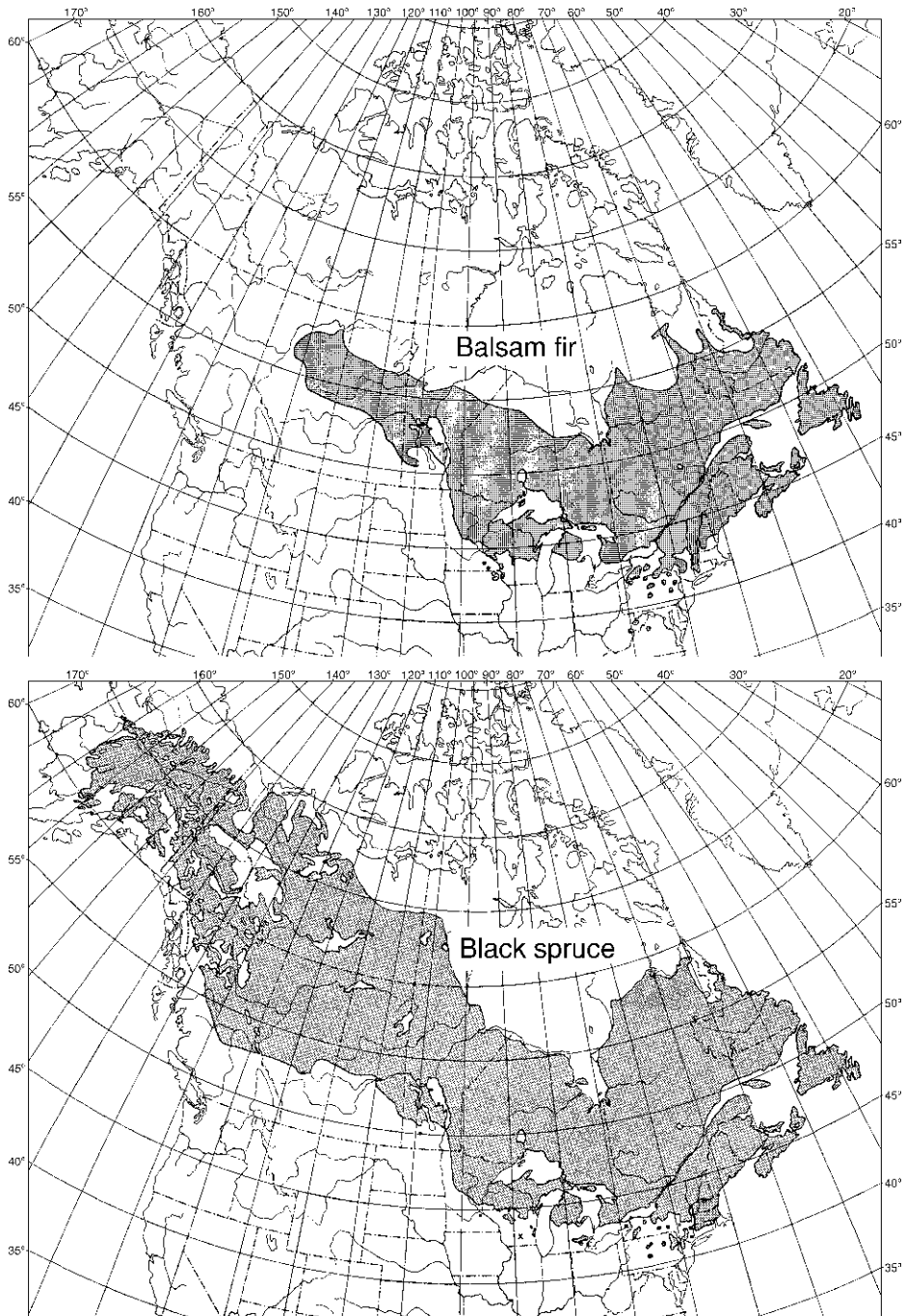
varieties, as well as quaking aspen and balsam poplar. The proportion of black spruce and eastern larch increases to the north. The eastern portion of the taiga includes an intermix of species that are summarized below under Great Lakes and Northeastern boreal forest. Viereck and Dyrness (1980) extend the taiga forest classification into Alaska and create a wide number of potential vegetation types aggregated into bottomland, lowland, and upland forests.

### **Great Lakes and Northeastern Boreal Forest**

The boreal forests of the Great Lakes and Northeast are southern extensions of boreal forest. These forests, as transitional types from boreal to temperate forest, are not well described in either the boreal forest (Elliott-Fisk 1988) or the deciduous forest (Greller 1988) descriptions of the North American terrestrial vegetation (Barbour and Billings 1988). While having the boreal species, this heterogeneous type also has many elements of the forests to the south (Pastor and Mladenoff 1992). Balsam fir is an important species, and appears to replace white spruce in an ecological sense. White pine, white cedar, and white birch are all more “important” than white spruce. Three species of *Populus* and three maples are also important members of the community. Black spruce and eastern larch are found in lowlands and nutrient poor sites (Larsen 1980). The distribution of both the Great Lakes and Northeastern boreal forest (map insert) closely resembles the range maps for balsam fir and black spruce (Fig. 3.2).

Balsam fir and northern white cedar are more important as soil moisture increases, with white pine and white spruce decreasing in importance. Sugar maple is important on mesic sites and jack pine, black spruce, and eastern hemlock distributions are bimodal, peaking at the extremes of the moisture gradient (Maycock and Curtis 1960; Pastor and Mladenoff 1992). Many of the understory species are circumpolar, but for trees, only genera are circumpolar, with significant species differences between the northern and southern parts of the mixed forest type.

In Wisconsin, the boreal forest can be divided into three somewhat distinct types: first, old stands of pure conifers with balsam fir and white spruce as major dominants, along with eastern white pine, red pine, or white cedar; associated hardwoods are paper birch, mountain ash, red maple, and mountain maple. Second, in mixed conifer-hardwood stands, found on inland mesic sites, shade tolerant hardwoods slowly replace the conifers; and third, dense stands of balsam fir or white spruce replacing a decadent canopy of white birch or aspen, with occasional balsam poplar (Curtis 1959). Some of these divisions represent successional sequences more than environmental heterogeneity.



**Figure 3.2**—The ranges of balsam fir and black spruce (Little 1971) south of the Canadian border closely parallel the distribution of boreal forest in the Great Lakes and Northeast.

## Western Boreal Forests

The extension of boreal features into the subalpine forests of the western United States where lynx are found is a southern modification of the boreal conifer forests, which are similar floristically and structurally (Peet 1988). Engelmann spruce, subalpine fir, and lodgepole pine, the primary dominants across the Western boreal forest, are genetically similar to, and sometimes hybridize with, the northern boreal species white spruce, balsam fir, and jack pine. Each species of the first group (Peet 1988) is genetically heterogeneous, and it is thought that the more genetically homogeneous boreal species of each pair may be derived from the more heterogeneous one (Taylor 1959; Parker et al. 1981; Critchfield 1985). North of about 54°N latitude, white spruce replaces Engelmann spruce. As one moves south, white spruce occurs at lower elevations than Engelmann spruce and hybridizes with it (Peet 1988). Boreal habitat becomes more fragmented to the south, with the Colorado Rockies separated from similar habitat in Utah and northwestern Wyoming (Findley and Anderson 1956).

The Western boreal forests where lynx habitat has historically occurred (map insert) are surprisingly uniform in their tree species composition: Engelmann spruce, subalpine fir, and lodgepole pine are found across the range. At the western edge of these relatively cold and dry forests, maritime influences allow mountain hemlock to be found on protected sites (Arno and Hammerly 1984; Agee and Kertis 1987). At timberline in the west, whitebark pine and subalpine larch replace spruce and fir (Arno and Habeck 1972). In Colorado, limber pine is a timberline species on xeric sites (Peet 1981; Veblen 1986), but across these subalpine forests, both Engelmann spruce and subalpine fir can be found to the margin of alpine tundra.

Other western boreal forests apparently do not support lynx. The boreal zones of the western Cascades of Washington and the Olympic Peninsula contain subalpine fir, but are dominated by Pacific silver fir and mountain hemlock. Winter snow often exceeds 3 m depth (Franklin and Dyrness 1973). The Oregon Cascades boreal zone has mountain hemlock and lodgepole pine mixed with noble fir, and noble fir is replaced by red fir in the southern Oregon Cascades. In the California Sierra Nevada, lodgepole pine and red fir constitute the primary boreal forest species. The winter snow accumulation can be quite deep in these areas, too (Barbour and Woodward 1985). In the southern Rocky Mountains, the boreal zone becomes a series of disjunct and isolated "islands" of mountaintops separated by wide areas of woodland or nonforest vegetation.

## Boreal Forest Disturbance Dynamics

---

Disturbance is common in boreal forests. In fact, the taiga has been referred to as a “disturbance forest” because of the ubiquitous nature of fire (Rowe 1961). Fires and insect epidemics are both major disturbance processes. Fire frequencies can range from 50 to 250 years (Viereck 1973; Heinselman 1981). Fire return intervals are longer (up to 500 years) in the Northeastern boreal forest (Foster 1983) and in some of the Western boreal forests (Romme and Knight 1981). Spruce beetles have killed white spruce across wide areas of south-central Alaska (Werner and Holsten 1983) and Engelmann spruce in the subalpine forests of the lower 48 states. Spruce budworm has been a major defoliating disturbance in eastern Canada and the northeastern United States (Blais 1968).

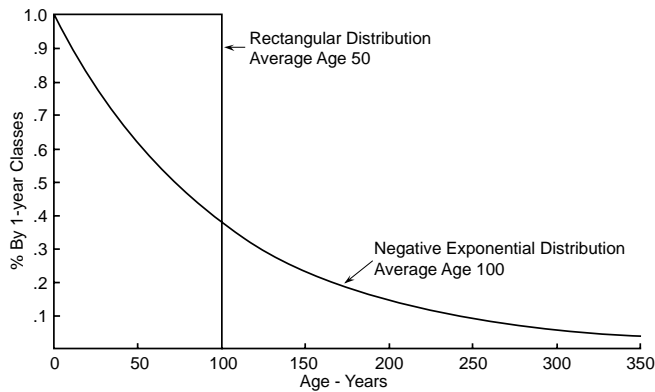
Forests are dynamic systems, and within a forest ecosystem, the only constant is change. For forest trees, change occurs through tree growth and death, and for boreal forest trees, natural disturbance has been a major factor in terminating the life of trees. There are a number of natural disturbance factors, including insects, wind, disease, and fire, but it is generally recognized that fire and insects were the most important disturbances across the boreal landscape. The *process* of disturbance creates variability in forest *pattern*, and it clearly varies in frequency by forest type. Landscape pattern over time will depend on whether the processes are *cyclic* or *stochastic*, and whether *equilibrium* or *non-equilibrium* systems result.

### Cyclic and Stochastic Properties of Disturbance

Editor’s note: Elements of the following discussion were drawn from a fire training lesson plan written by Kevin McKelvey, USDA Forest Service, Missoula, MT.

Any forest stand has a probability that a disturbance will enter and kill the trees in the stand. The nature of the probabilistic process can either be *cyclic* or *stochastic*, independent of the actual probability of disturbance. Consider a coin with heads (H) and tails (T) as the only possible outcomes. If it is turned alternatively from side to side, it will create a pattern of HTHHT, etc. The probability,  $p$ , is 0.5 for a head or a tail. This is a cyclic process, as it is very regular and predictable. If the coin is flipped in the air, the probability for a head or tail remains 0.5, but the pattern might be HHTTTH, so that subsequent tosses might produce runs of heads or tails. This is a stochastic process, even though the probability of head or tail is exactly the same as the cyclic process.

Now consider the distribution of forest stand ages as a cyclic or deterministic process (Fig. 3.3). The even-aged, area-regulated managed forest is a



**Figure 3.3**—Comparison of a cyclic age class distribution (the regulated forest) with a stochastic age class distribution (the negative exponential) (from Van Wagner 1978).

prime example of a cyclic system (assuming that natural disturbances are eliminated). The probability of age class  $x$  moving to age class  $x + 1$  is one ( $p = 1.0$ ), and the probability of being “recycled” to age 0 is zero ( $p = 0$ , assuming that all disturbances are controlled), until the rotation age is reached, at which time the stand is cut and it moves to age class 0 with  $p = 1$ . Forest stands operating under a cyclic process will have a rectangular age class distribution, truncated at the rotation age ( $R$ ). The average stand age is  $R/2$ , and there are no stands older than  $R$ .

Forests can also be “regulated” by stochastic processes. Boreal forests are the classic example of a natural forest regulated by fire acting in a stochastic manner (Van Wagner 1978; Johnson and Van Wagner 1985). The probability of any stand being burned in a given year is low, described by  $p$ . The probability of a stand of age  $x$  moving to age  $x + 1$  is then  $(1 - p)$ . If this process is carried out for a long time, then a negative exponential distribution like that shown in Figure 3.3 will result. The frequency of any age class  $x$  is

$$f(x) = pe^{-px}$$

This distribution assumes that the ignition pattern is random, that the area burned per year is roughly constant, and that stands of all ages are equally likely to burn (constant flammability). The average stand age is  $1/p$ , or  $C$ , and this is commonly called the fire cycle. Roughly one-third of the stands are older than the average stand age, and there is no maximum age for a stand, in contrast to the distribution created by cyclic processes. Of course, the number of older stands is small, and they are likely to be affected by disease or insects if protected from fire, but this disturbance is usually at

a finer grain than the landscape effects of fire. Another useful feature of this distribution is that if the proportion of the landscape above or below a certain age  $x$  is known, the entire age-class distribution can be defined:

$$\sum f(x) = 1 - e^{-px}$$

where  $\sum f(x)$  is the proportion of all age classes up to age  $x$ . The negative exponential model is simple and has a number of appealing characteristics (Rowe 1983). For example, about one-third of the stands are older than the mean age, or fire cycle, so that if structural characters by stand age are known, then habitat character can be inferred, although non-spatially, just by knowing the fire cycle.

The major criticism of the negative exponential model is its assumption of equal flammability of stands over time. Johnson and Van Wagner (1985) show that the negative exponential model is a simple case of the Weibull distribution where flammability, the shape parameter of the model,  $c$ , is constant at  $c = 1$ . Other options for flammability in the Weibull model are monotonic increases ( $c > 1$ ) or decreases ( $c < 1$ ) of flammability with stand age.

Stochastic models have become popular for describing fire history in a variety of forest types (Table 3.2; also, Lesica 1996). There is an implicit assumption that the fire regime is constant over time such that the age class data represent an ecosystem in equilibrium. Attempts have been made to disaggregate the age class data to analyze changes in fire frequency over time, and these are discussed below. The notions of stochasticity and equilibrium are relevant to the stability of adequate habitat over time for both lynx and its prey.

## Landscape Equilibria

If a given cyclic or stochastic process remains constant over time, then an equilibrium landscape is eventually produced, and the shape of the age-class distribution will remain constant over time, although quite different between the cyclic and stochastic models. However, if the probabilities of disturbance change over time, then a non-equilibrium state is introduced which may “ripple” through the age class distribution as a “blip,” or if the probabilities of disturbance are continually changing, there may be no predictable range of variability for any age class or the age class distribution as a whole. Assumptions about disturbance probabilities will have major implications for the management of lynx habitat.

Equilibrium is in part a function of scale, that in a cartographic sense decreases as the considered area increases. As scale decreases, the total area becomes larger, more fires will occur, and the average fire size as a proportion of the total landscape declines. As this occurs, the assumptions necessary to

**Table 3.2**—Fire frequency in the boreal forest. Each set is arranged west to east.

Biome and forest type	Fire return interval	Location <sup>a</sup>	Type of record <sup>b</sup>
	Yrs	--- Citation ---	
<b>Taiga (closed forest only)</b>			
Black spruce	49	Porcupine River, AK (1) (Yarie 1979)	Stand ages - NE, W
Black spruce	200	Alaska (1) (Viereck 1983)	Fire records
Black spruce	100	N. British Columbia (2) (Smith and Henderson 1970)	Stand ages
Subboreal black/white spruce	125	N. British Columbia (2)	BC Forest Service estimates
Subboreal pine-spruce	150	(Bunnell 1995)	
Subboreal spruce	125		
Spruce willow-birch	175		
Jack pine	30-70	Mackenzie River (2-3)	Stand ages
Black spruce	80-90	(Rowe et al. 1974)	
White spruce	300+		
Black spruce and others	130	S. Quebec (5) (Cogbill 1985)	Fire scars, reports, air photos
Black spruce	500	SE Labrador (5) (Foster 1983)	
<b>Western boreal forest</b>			
Subalpine fir	109-137	North Cascades (Agee et al. 1990)	Stand ages - NFR
Subalpine fir	250	Pasayten, WA (Fahnestock 1976)	Stand ages
Spruce-fir	250	British Columbia (Bunnell 1995)	Stand ages
Whitebark pine	30-300	N. Rocky Mtns. (Arno 1980, 1986) (Arno and Peterson 1983) (Morgan and Bunting 1990)	Fire scars
Spruce-fir	300-350	Yellowstone (Romme 1982)	Stand ages
Spruce-fir/upland	300	Medicine Bow, WY	Stand ages
Spruce-fir/drainages	300+	(Romme and Knight 1981)	
Spruce-fir	202	Colorado (Veblen et al. 1994)	Stand ages-NFR
<b>Great Lakes boreal forest</b>			
Northern pines	22	Itasca State Park, MN Frissell (1973)	Fire scars
Northern pines	100	BWCA Minnesota (Heinselman 1973)	Stand ages-NFR
Northern pines	50	BWCA, Minnesota <sup>c</sup> (Van Wagner 1978)	Stand ages - NE
Mixed forest	50-100	S. Ontario (Alexander and Euler 1981)	Stand ages
<b>Northeastern boreal forest</b>			
Red spruce/hemlock/pine	230	New Brunswick (Wein and Moore 1977)	—
Mixed Forest	200	Nova Scotia (Wein and Moore 1979)	—
Mixed forest	800	NE Maine (Lorimer 1977)	Land survey records

<sup>a</sup> Numbers 1-5 at taiga locations refer to Larsen's (1980) general subdivisions of the taiga summarized in Table 3.1 and Figure 3.1.<sup>b</sup> NFR = natural fire rotation method; NE = negative exponential; W = Weibull; blank = estimate that may or may not be quantitative.<sup>c</sup> The Heinselman and Van Wagner estimates use the same data but different techniques.

apply a model such as the negative exponential become more reasonable, and equilibrium landscape conditions are therefore more plausible. What is an appropriate scale? The scale must be such that fire is not “episodic” and individual fires do not burn “large” proportions of the landscape. Because individual fires can burn thousands of hectares, the total area necessary to consider can be quite large. The minimum equilibrium landscape size, called the “minimum dynamic area” (Pickett and Thompson 1978), contains representative age classes of the major stages of succession and will depend on the historic fire size distribution. The Yellowstone National Park, USA, landscape (2+ million acres) is a good example of a non-equilibrium landscape. It is a broad subalpine plateau that rarely burns, but much of it burned in the early 1700s (Romme 1982). The forest age classes created by those early fires created a very large age class that moved as a “wave” through the age class distribution over time, so that much of the park’s forest became old growth by the late 20th century, with lodgepole pine being replaced by subalpine fir on many sites. In 1988, the large fires that burned the national park killed much of the old growth age class, as well as stands of younger ages, too, and much of the park forest is now (1999) in the 10-year-old age class, which may move as a similar age class “wave” in the future or be broken up by other non-equilibrium fires. Obviously, for the past 300 years, and now for centuries to come, the Yellowstone forests have not and will not possess any equilibrium age class structure. If larger subalpine areas of the Rockies are considered, fire may well be more an equilibrium-maintaining process at that scale, particularly if topography is broken so that individual fires cannot burn large proportions of the landscape in any year.

Attempts to quantify changes in fire regimes using stochastic models is a work in progress. Johnson and Larsen (1991) developed a graphical technique to evaluate changes in slope of cumulative age class distributions over time. It has been criticized on three grounds: (1) different analysts would draw the subjectively placed “breaks in slope” of the lines in different places; (2) the use of empirical, sampled age class data effectively “censors” the oldest age classes and this “missing tail” of the distribution imparts a false trend to the graphical technique (Finney 1995); and (3) the actual standing age distribution, rather than the cumulative age class distributions, should be used to estimate the time-since-fire (survivorship) distribution (Huggard and Arnesault, in review). Most studies have incorrectly used the former rather than the latter distribution. The use of stochastic models remains a technique in development yet will remain important in analyzing disturbance in the boreal forest. For example, Ratz (1995) built a spatial simulation model and tested the flammability assumptions of the Weibull model. He found that an increasing flammability with time ( $c > 1$ ) fit real data sets from

Alberta (Eberhart and Woodard 1987) better than a constant flammability assumption.

Equilibrium models have been criticized on the basis that past climate change, in the presence of long-lived conifers, results in no single “natural” cycle expressed by age-class distributions on a landscape. The landscape mosaic is a reflection of a dynamic fire cycle and carries the memory of different past fire cycles (Johnson et al. 1998). Yet time-since-fire distributions necessary to draw such inference are rare, and the influence of climate change on disturbance frequency is difficult to estimate. These criticisms apply to setting the parameters, or form, of the models over time, more than a rejection of the models. Although climate change is likely to affect fire activity, the direction of the change is uncertain. Flannigan and Van Wagner (1991) projected an increase in fire activity across boreal landscapes with future global warming, while Flannigan et al. (1998) now suggest less fire activity in these landscapes with global warming.

The application of a concept such as landscape equilibrium implies that within limits, the forest landscape does possess equilibrium properties at some scale, yet we should be using such models to consider alternative states that might be more realistic. Such models might be best thought of as operational than actual, a way to conceptualize approaches to managing a landscape more than prescribing a precise equilibrium landscape as a desired future condition.

## Forest Fire Regimes

A fire regime is a generalized picture of the role fire plays in an ecosystem (Agee 1993). It is often simpler to describe the fire regime than to infer its effects on stand or landscape attributes, but the fire regime is clearly the starting point. Most of what we know about the fire regime of the boreal forest has been published in the last 25 years.

**Fire Frequency and Variability**—The fire frequency in forests where lynx habitat occurs varies by over an order of magnitude. Average fire return intervals using a variety of methods have been estimated for the taiga, as well as the Western, Great Lakes, and Northeastern boreal forests (Table 3.2). Variation is partly due to the method employed; for example, in the Great Lakes boreal forest, the Boundary Water Canoe Area estimates of 50 and 100 years use the same data but different analysis techniques. Nevertheless, useful trends emerge from these studies.

In the taiga, there is a trend of increasing fire return intervals (FRI) from west to east. The drier, continental portions of the closed forests have shorter FRIs than the more mesic eastern maritime boreal forests. Within local areas, ridgetops or sandy soil areas tend to have shorter FRI than bottomlands. The

Western boreal forests, with FRI ranging from 150-300 years, have generally longer FRI than the taiga, where FRIs tend to range from 50-150 years. Western boreal timberline variants such as whitebark pine, or isolated boreal “islands” surrounded by lower elevation types (Agee et al. 1990), may have shorter FRI. The Great Lakes boreal forest FRIs appear to be similar to the boreal forest to the north. The Northeastern boreal forest, with a greater maritime influence, tends to have longer FRIs, with fire becoming less important than wind and insects in coastal areas (Heinselman 1981) and to the north (Payette et al. 1989).

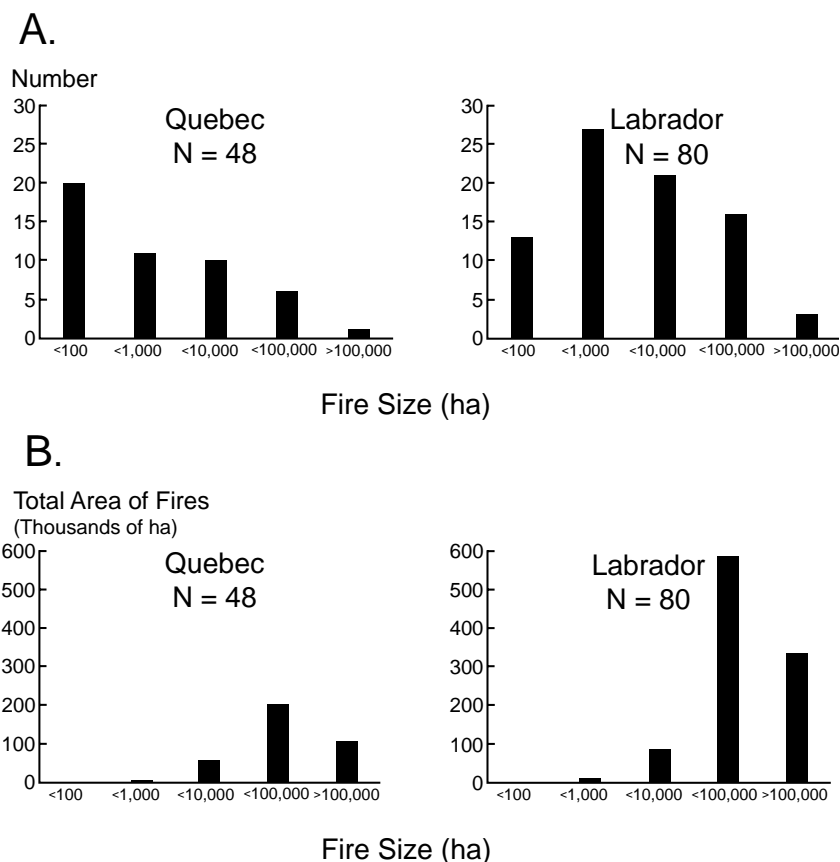
**Fire Spread and Intensity**—Fire intensity tends to be high in most of the forest types where lynx habitat is found. This creates conditions for extensive even-aged patches of regenerating conifer forest to occur. In boreal forest, fast-spreading, high-intensity fires are the ones that burn most of the area (Van Wagner 1983). Sustained fire spread rates over a day of 100 m/min with intensities of 50,000-100,000 kW/m (flame lengths of 13-18 m) have been measured (Kiil and Grigel 1969). Van Wagner (1983) summarizes the fire behavior in northern mixed and boreal forests. These fires spread during unusual weather conditions (e.g., Johnson and Wowchuck 1993) and under those conditions are essentially unmanageable. In the Great Lakes and Northeastern boreal forest, and portions of the Western boreal forests, fire behavior also tends to be intense (Lorimer 1977; Romme 1982; Agee 1993). The portions of southern boreal forests where lynx have not historically been found tend to have a more mixed fire intensity and a moderate-severity fire regime (Agee 1993). These may be more open timberline environments, such as the western boreal forest with whitebark pine, or lower elevation forest with more fire-tolerant conifers.

Although crown fires are common, fires of lower intensity do occur in boreal forests where lynx historically occurred, although they typically are a small proportion of the total fire area. Where trees with tall crowns or sufficiently thick bark occur (such as red, white, or jack pine), some residual trees may be expected (Johnson 1992). In areas where fuels are limited due to site conditions, moderate intensity fires may occur and multi-aged stands may result (Heinselman 1981; Gauthier et al. 1993; Roberts and Mallik 1994). Some isolated stands on poor soils may have non-serotinous forms of jack pine and all-aged pine structure (Conkey et al. 1995). Generally, fires in the taiga, Great Lakes and Northeastern boreal forests and the Western boreal forests are stand replacement events, either because of typically severe fire behavior or the inability of the trees to survive even moderate intensity events; these fires set the stage for open-grown regeneration. The successional dynamics of post-fire seres are discussed in this chapter in section “Successional Patterns After Disturbance.”

Different forest types have differing propensities to burn (Van Wagner 1983): jack and lodgepole pines have high flammability throughout the season; black spruce forest is less prone to surface fire but supports crown fire when weather conditions are severe; aspen and birch are highly flammable in spring when their litter layers are exposed and can dry quickly, but all hardwood stands are less flammable in summer because their shaded litter layers are compact and their crowns do not support crown fire; and lowland forests require a longer drought to become flammable than upland forests of pine or spruce.

**Fire Extent and Patchiness**—Fires in the taiga, as with most high-severity fire regimes (Agee 1998b), can become quite large. A typical pattern is to have the frequency of fire sizes skewed to the smaller fires while area burned is skewed to the larger fires (Fig. 3.4) (Foster 1983; Payette et al. 1989; Hunter 1993). A small number of fires is associated with the majority of the area burned; therefore, while average patch size created by fires is small, the landscape area is dominated by the less frequent but much larger patches. Topographic barriers in the taiga are often absent and severe weather conditions may drive the fires for days or weeks. Many fires may reach 50,000 ha, and fires of >200,000 ha are possible (Viereck 1983). In the maritime region of Northeastern boreal forests, fires of 80,000 ha have been recorded (Lorimer 1977). Where terrain is more heterogeneous, either because of mountains or lakes, fire spread may be interrupted (Bergeron 1991; Dansereau and Bergeron 1993; Bergeron et al. 1997). Average fire size in the Great Lakes boreal forest is about 360 ha (Baker 1994), but the average is a poor descriptor of the distribution. Heinselman's (1973) fire maps of the Boundary Waters Canoe Area in Minnesota show many fires that appear to have been stopped at lake edges. In Western boreal forests, fires may be quite large where few fire barriers are present (e.g., the Yellowstone Plateau) but in many areas the boreal zone abuts rock, alpine vegetation, ridgetops, or other barriers to limit fire size (Agee 1993).

Most fire studies have concentrated on disturbed areas, so that little is known about residual vegetation around and within the fires that may contribute substantial patchiness to the burn. Eberhart and Woodard's (1987) study of large fires in Alberta evaluated fires more than 20 ha in size and found that the unburned island area, shape index, and edge index increased with fire size (Table 3.3). Although the number of islands per 100 ha declined for the largest fires (E3), the unburned island area of this fire size class was much larger than for the other fire size classes. These islands covered less than 5% of the interior area of the fire. In interior Alaska, a 1985 fire had about 6% of its area in unburned islands (Paragi et al. 1997). Unburned area may occur because of higher foliar moisture, terrain, or



**Figure 3.4**—Typical patterns of frequencies of boreal fire sizes and area burned by fire size. A. Size-frequency distributions of fires in Quebec and Labrador. B. Total area of fires in each size class shown in A (from Hunter 1993).

**Table 3.3**—Mean values of percent disturbed area, median island area, number of islands per 100 ha, fire shape index, and edge index by fire size class for large fires in northern Alberta, 1970-83 (Eberhart and Woodard 1987). No similar data are available south of the Canadian border.

Variable	Fire size class <sup>a</sup>				
	C	D	E <sub>1</sub>	E <sub>2</sub>	E <sub>3</sub>
% disturbed area	100.0	99.3	96.3	96.6	94.8
No. of islands/100 ha	0.0	0.38	0.96	0.87	0.39
Median island area (ha)	—	2.29	2.50	2.59	9.39
Fire shape index <sup>b</sup>	1.79	2.40	2.36	2.96	3.78
Edge index <sup>b</sup>	2.17	3.29	3.48	5.11	7.47

<sup>a</sup> Fire size class: C = 20-40 ha; D = 41-200 ha; E<sub>1</sub> = 201-400 ha; E<sub>2</sub> = 401-2,000 ha; E<sub>3</sub> = 2,001-20,000 ha.

<sup>b</sup> Shape index is calculated as total exterior fire perimeter divided by the perimeter of a circle of equal area to the fire. Edge index is similarly calculated but perimeters of all islands are added to the exterior fire perimeter.

changes in fire weather such as a major wind shift. These unburned areas are also known as stringers (Quirk and Sykes 1971) or fire skips (Hunter 1993). In the boreal forests south of the Canadian border, little is known of the distribution of residual patches. Because lynx may be able to den in small patches of old growth, the presence of small fire skips may be critical for lynx habitat. In British Columbia, DeLong (1998) showed for the “dry cool boreal” and “moist very cold subalpine” forest types, transitional between taiga and Western boreal forest, that 40-60% of the area burned is in patches greater than 1,000 ha, and 60-85% in patches greater than 250 ha in size.

**Fire Seasonality and Synergistic Effects**—The major fire seasons vary across the boreal forest. In Alaska taiga, May, June, and July are the major fire months (Viereck 1983), with the latter part of June and early July the critical time (Barney 1971). Throughout much of the rest of the boreal forest, including the Western boreal forest, July and August are the months with the largest area burned (Johnson and Wowchuck 1993). Some fires that begin early in the season have the potential to burn into September, although most do not (Johnson 1992; Despain 1990).

Synergistic disturbance effects are defined as increased probability of one disturbance given the occurrence of another. A number of authors have suggested that spruce budworm-killed balsam fir may increase fire hazard, and refer to the Miramachi fire of 1825 in New Brunswick (Furyaev et al. 1983). Although most hurricanes lose strength before reaching the Northeastern boreal forest, these eastern seaboard hurricanes clearly create excessive fuel hazards from the creation of dead fuel from the windblown trees. Lorimer (1977) suggests a large fire in 1803 in northern Maine was fueled by a large blowdown that occurred within the previous decade. Surface fuels, and therefore fire hazard, will accumulate any time there is canopy mortality, but the hazard may exist for a short window of time. In Western boreal forest, Veblen et al. (1994) suggest that fires essentially “block out” spruce beetles for many decades until the trees in the recovering stands reach a size suitable for the beetles to attack. Conversely, Bergeron and Leduc (1998) suggested that when fire return intervals lengthen, basal area loss due to spruce budworm will increase because of the proportional increase in budworm-susceptible balsam fir in these stands.

## Other Natural Forest Disturbances

**Forest Insects**—The history of major insect outbreaks in the boreal forest is more difficult to track than the history of forest fire. Insects may kill only one species in a mixed stand, and they may remove either early successional (pine beetle on pines) or late successional (budworms on firs) species. While

fires usually thin a stand from below (kill smallest trees first, with the largest, thickest barked trees left), insects often take the largest trees and thin the stand from above. There are clearly some boreal forest areas where insects have a significant history as a disturbance agent, primarily where fire return intervals either are very long on average or an unusually long fire-free period has occurred. In Alaska taiga, spruce beetles have killed substantial white spruce (Werner and Holsten 1983). Spruce budworm appears to have a major effect on white spruce in the southern taiga, reducing the importance of spruce in late successional forests (Bergeron and Dubuc 1989). During the 1910-1920s outbreak, it is estimated that 40-50% of the total balsam fir volume in eastern Canada was killed (Furyaev et al. 1983).

In the Northeastern boreal forest, spruce budworm has defoliated balsam fir in outbreaks that have traced back over previous centuries (Blais 1968; Lorimer 1977). The most recent outbreak has occurred from 1970 to the early 1980s (Kettela 1983). Once a local outbreak exceeds a certain size, it can become self-propagating and spread much like a wildfire but more slowly (Holling 1992). Occasional spruce beetle epidemics have caused considerable mortality in red spruce stands (Hopkins 1901). In 1985, the boreal forest types of the northeastern United States had about 45% of the area in "light" damage (less than 10% dead trees), 28% of the area in "moderate" damage (11-30% dead trees), and 27% of the area in "heavy" (more than 30% dead trees) damage classes (Miller-Weeks and Smoronk 1993).

Significant insects of Western boreal forests are those that attack lodgepole pine (mountain pine beetle), Engelmann spruce (spruce beetle), and subalpine fir. While spruce budworm can become epidemic on lower elevation firs (Douglas-fir, grand fir) in the West (Swetnam and Lynch 1993; Despain 1990), it is less important in the subalpine zone, although it does attack subalpine fir and white spruce in the boreal zone (Van Sickle 1995). Lodgepole pine becomes more susceptible to mountain pine beetle as it ages, and a beetle attack will allow understory spruce and fir to release ingrowth (Agee 1993; Veblen et al. 1994). Where recent beetle attack has occurred, surface fuels will increase, but a fire is not necessarily guaranteed. Despain (1990) suggests that the loss of crown fuels reduces crown fire risk at the same time that surface fuels increase.

The spruce beetle attacks Engelmann spruce, and the additional surface fuels from this mortality have been implicated in severe fires in riparian zones (Agee 1998b). In Colorado, the return interval for spruce beetle is estimated at 116 years (Veblen et al. 1994). Attacks were dated by analyzing growth releases on firs and spruces too small to be attacked, indicating that beetle attacks in mixed species stands are usually not stand-destroying events like intense wildfires.

The dynamics of insect outbreaks are very complex. Although we may predict that older stands with target species of minimum size are more at risk than younger stands, the triggers for outbreaks are not well understood. Pine beetles often become epidemic during drought periods (Despain 1990), but western spruce budworm often erupts during periods of above-normal precipitation (Swetnam and Lynch 1993).

**Disease and Wind**—Forest ecosystems are affected by a wide variety of natural disturbances. We typically concentrate on the most important ones for a given forest type, such as fire or insects. Diseases are often ignored because they generally operate at long timeframes, and mortality may be gradual or associated with crown dieback (Hawksworth and Shigo 1980). Agents such as wind often remove the trees before they break or fall over from stem or root rot. Windsnap and windthrow can be important disturbances (Coutts and Grace 1995), but severe events are often widely spaced in time and not easily reconstructed. In boreal forests, wind as a disturbance event is poorly understood. There is little evidence that windthrow is a significant disturbance in the mature taiga.

In the Northeastern and Great Lakes boreal forest, wind can be a significant disturbance, especially for those types that burn infrequently (Canham and Loucks 1984; Seymour and Hunter 1992). Most frequently, small gaps are created in the Great Lakes boreal forest, with an annual gap creation rate of 1% of the forest area per year (Runkle 1982; Mladenoff 1987). Although catastrophic events may occur only once a millennium, these extreme events can alter forest dynamics over wide areas. In July 1977, about 15,000 ha of forest in eastern Minnesota and northern Wisconsin were devastated by a windstorm (Loucks 1983). The historic (1834-1873 era) forest patch blowdown size distribution in hemlock-hardwood forest of Wisconsin (excluding the southern, mature forests of the state) ranged from 1 to 6,000 ha with a mean size of 160 ha and median size of 30 ha (Loucks 1983). In these mature hemlock-hardwood forests, wind may be a more significant disturbance factor than fire (Canham and Loucks 1984). At least one large windthrow event occurred in northern Maine early in the 19th century (Lorimer 1977), but its effects were variable and localized. In New England, high-elevation balsam fir forests have a wave-like pattern largely due to persistent effects of wind on the forest (Sprugel 1976).

In the Western boreal forest, however, wind has profound physiological effects across open areas. Severe winter winds can retard succession above the winter snow line by abrading and desiccating foliage that emerges (Hadley and Smith 1983). In contrast to this annual disturbance, less frequent but powerful windstorms can result in large blowdown patches in western boreal forests, occasionally greater than 5,000 ha (Knight 1994).

## Land Ownership and Land Use History

Land ownership patterns and the history of land use vary considerably over the boreal forest, and particularly in the three areas of potential lynx habitat south of the Canadian border. This affects not only the condition of the land today but a variety of challenges in terms of future habitat management.

**The Taiga**—Much of the northern boreal forest habitat has been less affected by modern human influence than boreal forests to the south (Johnson et al. 1998). Low timber productivity, difficult access, and distance from markets has kept much of the boreal forest from being logged in the past, except around settlements. Fire suppression has been of limited effectiveness for the same reasons: values protected have been low, access for firefighters and equipment is poor, and even fire-detection capability is limited. The southern taiga has likely been affected more than the northerly parts, but in general, less modern human influence is detectable in the taiga than in the boreal forest types of the contiguous United States.

**The Northeast Boreal Forest**—European settlement in the Northeastern forest began in the early 1600s, and white pine was selectively harvested soon thereafter (Ferguson and Longwood 1960). Eastern hemlock was cut, its bark stripped for tanning purposes, and the logs left behind. Spruce was also selectively removed, and the pine and spruce harvest peaked in the 1850-1900 period (Ferguson and Longwood 1960). Pulp markets for hardwoods developed after 1900. The history of selective harvest for favored species (Barrett 1962) to some extent mirrored the pattern of natural disturbances by insects (particularly spruce budworm and spruce beetle) and wind. Stand-replacing harvests, like stand-replacing natural disturbances, were not the most common event (Seymour and Hunter 1992).

Forest lands were also cleared for agriculture. Land clearing and farming reached a peak in the mid-1800s. By 1880, forest covered only 27% of Connecticut, 74% of Maine, 40% of Massachusetts, 50% of New Hampshire, 34% of Rhode Island, and 35% of Vermont (Barrett 1962). Since that time, there has been a gradual increase in forest land in all of these states. Maine is now 87% forested (Ferguson and Longwood 1960) and Vermont is now 70% forested (Klyza and Trombulak 1994), in various stages of succession.

The forest today is somewhat different in character than it once was. Seymour and Hunter (1992) suggest at least three major differences. First, there appears to be less old growth, and in this boreal forest type old growth was more common than to the north because of extended natural disturbance intervals. Once-favored species such as eastern white pine and red spruce are less common, and recent land-use practices such as clearcutting

are imprinting a new landscape pattern. These land use practices are symptomatic of concerns about the future of what is locally called the “Northern Forest.”

The Northeastern forest area has the least amount of publicly owned forest of the three boreal forest areas south of the Canadian border. In Maine, for example, only 1-2% of the forest land is publicly owned, with 38% in forest industry ownership and about 60% in non-industrial ownership (Ferguson and Longwood 1960). The percentage of industrial forest ownership in Maine is the highest of the Northeastern states. In the Northeast, timberland area has continued to increase (about 9% since 1952), but ownership patterns suggest that fragmentation is also occurring. In 1958, about 25% of the land base of Maine was in ownerships less than 40 ha, 25% in ownerships of 40-20,000 ha, and 50% in ownerships greater than 20,000 ha. None of these were necessarily contiguous blocks of land. Changes over the past 25 years have resulted in further fragmentation of the ownership pattern (NRC 1998). Today, almost 32% of forestland area nationally, and 36% in the New England states exclusive of Maine (Brooks and Birch 1988), are in ownerships of less than 40 ha.

Recent concern has centered on changing forest industry ownership and management (Reidel 1994; Seymour and Hunter 1992). Industrial forest land began to be marketed for its development value in the 1980s, and the northern states affected were concerned enough to form a Northern Forest Lands Council (NFLC 1994). The intent was to stabilize the land ownership and management patterns that had characterized the region for decades, rather than to replace them with public ownership. Industrial forest management, particularly in Maine, was evolving to greater reliance on clear-cuts, with a first pass providing landscape diversity and second one within several years liquidating the remaining mature forest (Seymour and Hunter 1992).

**The Great Lakes Forest**—The Great Lakes area was the second major area of the boreal forest south of Canada to be settled by Europeans. Land clearing there relieved the pressure to farm the marginal lands of the Northeast forest, and as deforestation occurred in the Great Lakes, it was coincident with the process of reforestation in the Northeastern forest. Land settlement first began in the southern portions of Michigan, Wisconsin, and Minnesota and gradually moved northward (Barlowe 1983). Widespread, unregulated cutting and indiscriminate slash burning and clearing was rampant during the mid- to late-1800s. Some of the largest and most destructive forest fires in the lower 48 states occurred during this time, including the Peshtigo (Michigan, 1871) and Hinckley (Minnesota, 1884) fires.

Early logging was focused on pine, with large quantities of northern white-cedar also harvested (Sandberg 1983). By 1920, other species became dominant in the timber economy, and many of the hardwood species began to be utilized to produce charcoal. The charcoal industry was largely gone by 1930 and was replaced by a pulp industry with less exacting standards for size. Much of the new forest that replaced the early logged forest was aspen, and it remains a staple of the pulpwood industry. Jack pine and balsam fir are also used for pulp. Much of the Great Lakes forest is in an early successional state because of timber harvesting and farming over the past century (Curtis 1959).

Substantial public ownership exists for the Great Lakes boreal forest. National forests began to be reserved in 1908 (later than in the West), and new national forests were created in the 1920s and 1930s. Lands added between then and 1948 almost tripled the size of national forest ownership, from about 800,000 ha to 2,500,000 ha (Barlowe 1983). National Park system lands were added (Pictured Rocks and Sleeping Dunes National Lakeshores), among the over 400,000 ha that has been added to public ownership since World War II. The north-central region of the United States has the largest absolute area, and greatest percentage, of State and County/Municipal timberland in the country. This is primarily due to reversion of tax-delinquent land, almost 7,000,000 ha by 1950 (Barlowe 1951). In the eastern area of the Great Lakes boreal forest, in northern Michigan, about 20-40% of the land base is now publicly owned, and this percentage increases to about 40-60% in northern Wisconsin and more than 60% in northern Minnesota (Barlowe 1983).

Continued fire suppression has allowed development of more complex forest structure in previously farmed/logged areas but has also disrupted the fire regime in unlogged areas. Baker (1989, 1994) suggests that restoration of the natural fire regime, where desired, will restore natural pattern without additional restoration measures. Continuation of current suppression policies has significant implications for the boreal forest, discussed in section "Successional Patterns After Disturbance" (Frelich and Reich 1995).

**The Western Boreal Forest**—The western boreal forest region has never had the human-created forestland impact experienced by the other two boreal forest regions south of the Canadian border. This region was the last settled by Europeans in the expansion to the Pacific Coast, and development and exploitation occurred around the fringe of these areas or along narrow corridors passing through them. These areas were the focus of the first land reservations for forest reserves, and today much of the National Park System and National Wilderness System is centered on these western boreal forests. The distribution of these boreal forests is patchier than in the other two

boreal regions described in this chapter, so that land use in the intervening lands can affect lynx migration, but the human history of land use that changed area of forestland, disturbance patterns, and dominant tree species is much less prevalent in the West than in the Great Lakes or the Northeast boreal forest.

Mining was the first large-scale land use practice to affect the western boreal forest, and it had significant impacts on a local scale. Where mining occurred, not only was there surface soil disruption, but extensive human-caused forest fires were set to provide easier access to local timber for firewood, mining timbers, etc. Larger scale timber harvest practices did not begin until after World War II, and the boreal forest areas were cut only when the more accessible lands were cutover. The carving of national parks from the forest reserves, and later from national forests, preserved much of this land from cutting, and the creation of the Wilderness Act in 1964 further preserved much of the western boreal forest. Of all the western forest types, it has the highest proportion of reserved land, largely because it is primarily in public ownership and is the least productive timberland, making the land-use tradeoffs between preservation and extraction less controversial than for other public lands. In the Western boreal forest zone, fire suppression has been in effect for much of this century, but the long natural fire return intervals (Table 3.2) suggest that removal of fire has not been as significant as in the lower severity fire regimes of the West (Agee 1998b).

## Successional Patterns After Disturbance

---

Across much of the range of the lynx in North America, a high severity fire regime occurs, and succession follows a series of paths from early- to late-successional communities. Within a given forest type, many potential sequences may be possible: a function of fire duration and soil heating, species composition at the time of the fire, post-fire climate, biotic interactions, and other factors. The rate of succession will also vary depending on site conditions. In this section, the common successional sequences in each of the four major boreal forest divisions (taiga, Northeast, Great Lakes, and Western) are summarized.

After a stand replacement event, the post-fire sere will include a herbaceous stage, a shrub/sapling stage, a dense, small tree stage, a transition stage (in many cases a hardwood to conifer transition, but in others just a shift in conifer species), and a mature/old growth stage. Depending on the fire return interval, the mature stage may never develop far before it is disturbed. The timing of these stages will depend on the adaptations of the species that will possibly grow on the site (Table 3.4). Where a tree or shrub

**Table 3.4**—Responses of common tree species of the boreal forests to disturbance. The “Rowe Class” is a set of life history characters associated with response to disturbance (Rowe 1983), and the specific adaptations are listed for each of the species.

Tree species	Rowe class <sup>a</sup>	Thick bark	Cone serotiny	Sprouter	Light seeds
Black spruce	Evader		X		
White spruce	Avoider				
Aspen	Endurer, Invader			X	X
Paper birch	Endurer, Invader			X	X
Balsam poplar	Endurer, Invader			X	X
Jack pine	Evader, Resister		X		
Red pine	Resister	X			
Eastern white pine	Resister	X			
Balsam fir	Avoider				
Red spruce	Avoider				
Lodgepole pine	Evader		X		
Engelmann spruce	Avoider				
Subalpine fir	Avoider				

<sup>a</sup>Invasers = highly dispersive pioneering species with short-lived disseminules

Evaders = species with long-lived propagules stored in soil or canopy

Resisters = shade-intolerant species whose adult stages can survive low-severity fires

Endurers = sprouting species with shallow or deep buried perennating buds

Avoiders = shade tolerant, late successional species that slowly reinvade burned areas

species is able to sprout or develop new plants from a soil or canopy seed bank, succession is likely to progress more rapidly. Most of the species listed in Table 3.4 are well-adapted to disturbance. A simple collation of the life-history strategies of the common species of a site will give an indication of the likely rate of recovery. Where evaders and endurers are common, the post-fire sere will likely begin with those same species. Where avoiders are the norm, transformation to non-forest vegetation is likely until tree reestablishment is eventually successful, a function of seed source and post-fire climate (Agee and Smith 1984).

Where the disturbance removes the overstory but leaves the understory relatively intact, as in a typical blowdown, the successional sequence will be similar but the species composition will be heavily weighted to the shade-tolerant understory trees, either conifers or hardwoods, that were able to persist in the shade of the overstory trees. Because of the high-severity fire regime, the live trees on the site become snags and eventually logs as the snags fall. In a typical post-fire sequence of this nature, there will be (1) a large post-fire increase in coarse woody debris, (2) a mid-seral decline as the initial input is over, existing coarse woody debris decays, and the new stand is not yet large enough to produce more coarse woody debris, and then (3) a slow increase in late succession as large trees occasionally die or are killed by insect outbreaks (Harmon et al. 1986).

## The Taiga

The taiga has two major environmental gradients that affect species composition and successional patterns. The first is a set of local gradients from dry/warm to wet/cold, and the second is an east/west continental gradient that affects both climate and the biogeography of species mixes. In the Alaskan taiga, the local gradients create a complex mix of successional pathways (Fig. 3.5A) (Viereck 1973; Lutz 1956; Rowe and Scotter 1973). One of the common themes in taiga forest ecology is that the species mixes are relatively stable, replacing themselves after disturbance, so the major successional stages are structural in nature. In most cases the disturbance intervals by fire are short enough that the later successional sequences, shown at the top of the diagram, are rarely reached. Tree colonization occurs rapidly, but tree dominance may take 50+ yrs due to early dominance by shrubs and generally low productivity.

In Alaska, Foote (1983) summarized the major stages on closed-forest white spruce and black spruce sites. Many of the species are common to both white and black spruce sites, although relative dominance will differ. On white spruce sites, the newly burned stage lasts only a few weeks, and sprouts of rose, highbush cranberry, and willow emerge, along with fireweed. Sprouts of aspen emerge as well, with seedlings of both aspen and paper birch. White spruce is rarely present immediately after the fire. Within one to five years post-fire, these plants expand cover and several species of mosses dominate the ground layer at the site (up to 30% cover). Tall shrubs and tree saplings dominate the tall shrub-sapling stage (three to 30 years post-fire). The dense tree stage (26-45 years post-fire) is dominated by the young trees that initially established, rose, highbush cranberry, mountain-cranberry, and Labrador-tea. Lichens are best developed at this time, and feathermosses are now established. Willows, herbs, and the seral mosses are no longer important. The hardwood stage is a further development of the hardwood tree layer, with similar understory shrubs to the dense tree stage and *Hylocomium splendens* on the forest floor. As the hardwood trees die (150+ years), white spruce, which has persisted (but rarely as a dominant), becomes the dominant overstory species. It will persist until the next disturbance.

On mesic black spruce sites, the initial patterns are similar (Foote 1983) but bog blueberry and Labrador-tea are dominant shrubs in early succession, and black spruce is present rather than white spruce. Black spruce may average 18,000 stems ha<sup>-1</sup>, and quaking aspen 11,000 stems ha<sup>-1</sup>. Hardwood dominance is usually less than on white spruce sites. In the tall shrub-sapling stage, willows dominate at densities up to 15,000 stems ha<sup>-1</sup>, herbaceous



species decline, and the tree layer continues to expand. The dense tree stage (30-55 years post-fire) is dominated by trees, with low shrubs, feathermosses, and lichens below. Black spruce density averages 2,500 stems ha<sup>-1</sup>. A mixed hardwood-spruce stage occurs 56-90 years post-fire, but hardwoods usually are not dominant. In the spruce stage (90 years post-fire +), a thick feathermoss-Sphagnum ground cover allows permafrost to increase from 80+ cm depth to about 60 cm. Fire usually burns these sites before they reach 200 years old.

The first three successional stages (newly-burned, moss-herb, and tall shrub-sapling) last about 20-25 years on white spruce sites and 30-35 years on black spruce sites. The hardwood stage is better defined and lasts longer on white spruce sites. Vegetative and *in situ* seed (such as serotinous cones) is greater on black spruce sites (Black and Bliss 1978; Foote 1983). Succession on lichen-woodland sites is similar to the closed-forest black spruce, except that crown closure rarely occurs and the sequence of stages is usually prolonged (130+ years for mature woodland [Maikawa and Kershaw 1976]).

In the central and eastern taiga, a similar set of successional sequences is postulated (Fig. 3.5B) (Viereck 1983). Balsam poplar, although present, is less a component of the sere, jack pine is added, and balsam fir appears where fire return intervals are longer. To the north, jack pine is the first species to disappear, followed by balsam poplar, eastern larch, and black spruce (Payette et al. 1989), a pattern supported by the rooting depth of the species and shallower permafrost (Larsen 1980). Balsam fir and white spruce are the late successional species on mesic sites, while succession toward black spruce is the trend on more xeric sites (Bergeron and Dubuc 1989). A majority of the post-fire seedlings become established in a three- to 10-year period (Lavoie and Sirois 1998). On the xeric sites, low productivity and the presence of species like red pine, jack pine, or white pine can result in multi-aged stands, although this appears to be most common in the transitional mixed northern forest (Heinselman 1981). On more mesic sites without these pines, quaking aspen and paper birch are common early successional species (Bergeron and Dubuc 1989) after stand-replacing disturbances, particularly if the fire exposes substantial areas of bare ground (Payette 1992). The succession of black spruce stands to balsam fir occurs in some stands (Dammon 1964) but does not appear to happen on other sites (Carleton and Maycock 1978).

Coarse woody debris trends differ between white and black spruce stands. Black spruce sites are poor, and large stems will never be found on these sites. In Alaska, the average diameter at breast height for 51-year-old upland and lowland stands was 2-3 cm, and there were no logs greater than 5 cm diameter on the forest floor (Barney and Van Cleve 1973). If these stands burned, there would be almost no snags or logs created that would be more

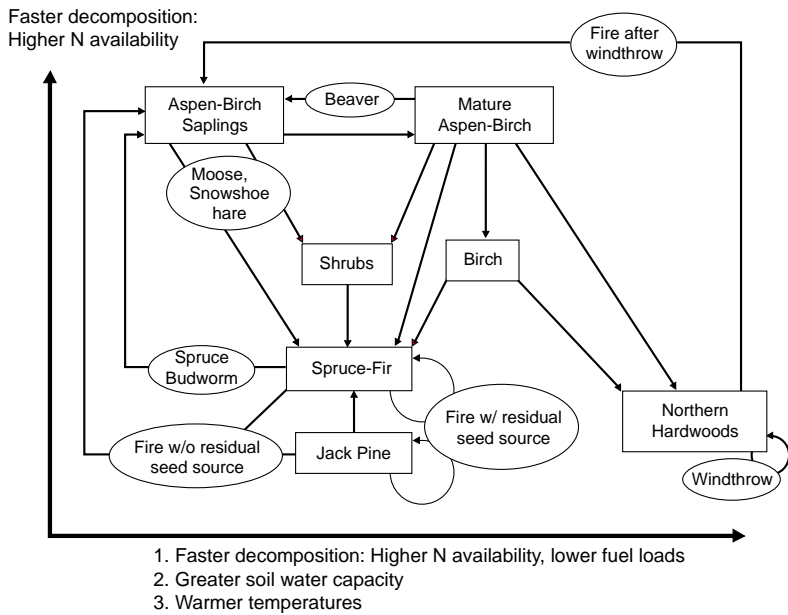
than 5 cm. More productive black spruce sites of greater age (130 years old) had five to 10 times the mass of live stem wood (Van Cleve 1981) that would become coarse woody debris if the site burned. By 25 years post-fire, all snags had been converted to logs in a black spruce stand (Paragi et al. 1997). In white spruce stands, the same post-fire increase will be seen, but generally more significant. Coarse woody debris cover in black spruce sites ranged from 2 to 6% compared to 5 to 16% for a white spruce sere (Foote 1983). Because more of the coarse woody debris in white spruce stands will be hardwoods, decay rates are more rapid for coarse woody debris in white spruce stands (Harmon et al. 1986).

## Northeastern and Great Lakes Boreal Forests

Successional sequences after disturbance in the Northeastern and Great Lakes boreal forests represent a mix of species common to the deciduous forest and boreal biomes and a mix of disturbances common to both. Therefore, the successional dynamics are covered together here. As noted earlier, fire tends to be more important in the Great Lakes boreal forest than the Northeastern boreal forest. In the Great Lakes, windthrow and insects may become locally as important as fire, creating a complex series of successional pathways (Fig. 3.6) (Pastor and Mladenoff 1992). In the Northeastern boreal forest, longer fire return intervals (Lorimer 1977) and higher frequencies of insect outbreak (spruce budworm) and wind (Seymour 1992) resulted in many disturbances that were less than stand-replacing in severity. The Northeastern forest, also called the Acadian forest, had greater potential diversity and age structure as a result (Seymour and Hunter 1992).

Boreal conifers are more frequent on cooler sites or at the extremes of the moisture gradient (Larsen 1980), while northern hardwoods follow the early successional species on more mesic and warmer sites (Maycock and Curtis 1960). Like the more northerly boreal forest, tree establishment on stand replacement burns is rapid. The hardwoods sprout, some like paper birch have light seeds that disperse widely, and jack pine reproduces from a seed bank in serotinous cones. On poorly drained sites, black spruce reproduces from semi-serotinous cones that retain at least part of the seed production.

Jack pine is a common dominant on drier sites where morainal, coarse-textured soils predominate (Conkey et al. 1995). After fire, jack pine and quaking aspen form dense stands. In the 5-15 year period, jack pine may reach 10,000-30,000 stems  $\text{ha}^{-1}$ , with 500-13,000 stems  $\text{ha}^{-1}$  of aspen (Roe and Stoeckler 1950; Cayford and McRae 1983; Agee 1998a). At 40+ years, the pine-aspen overstory has a black spruce, balsam fir, and shade tolerant hardwood understory (sugar maple and paper birch). By age 75, the overstory begins a decline, with subsequent release of the understory species,



**Figure 3.6**—Multiple successional sequences in the Great Lakes boreal forest (Pastor and Mladenoff 1992).

and by age 165, the jack pine and aspen are largely replaced by a multi-storied black spruce-balsam fir-hardwood forest, unless an intervening fire creates another even-aged pine-aspen stand. Heinselman (1973) projected that spruce would become more dominant over time but found remnant jack pines to live more than 200 yrs. Mixed pine stands (red pine, eastern white pine, jack pine) are often indicative of the limited boreal forest area in a moderate-severity fire regime. These sites will commonly have fire-scarred pines and represent a succession of multi-aged stands on poor sites. Where the fire thins few trees, more shade-tolerant species will regenerate, while hotter fires that kill more trees may create another age class of shade-intolerant pines.

Fire suppression in the Great Lakes area has changed the dominant successional pathways (Frelich and Reich 1995). Many stands are undergoing a transition from even-aged stands of catastrophic origin to uneven-aged stands due to small scale openings. Jack or red pine or aspen stands are moving toward an old-growth mix of black spruce, balsam fir, paper birch, and white cedar, in patches of 10-30 m created by wind, insects, and disease (Frelich and Reich 1995). At scales of 1-16 ha, succession leads to a convergence on a mixture of species. It is not clear whether reintroduction of

catastrophic disturbance will lead back to the original landscape character of this region. In the heavily altered landscapes at the southern edge of the boreal forest, the historic landscape character is probably permanently altered. Second-growth forest landscapes caused by harvest have generally smaller forest patches and are significantly simpler in shape; important ecosystem juxtapositions (such as old-growth hemlock adjacent to lowland conifers) have been largely eliminated (Mladenoff et al. 1993).

While the jack pine type is of interest to fire ecologists, many of the forests of the Great Lakes and Northeastern boreal forest burn less frequently. On mesic sites, with longer fire intervals (Table 3.2), hardwoods typically occupy a more important niche, and as the conifer component decreases, so does the flammability of the forest (Van Wagner 1983). Other disturbances such as wind (Pastor and Mladenoff 1992) or insects (Baskerville 1975) become more important disturbance agents. Replacement of resinous, multi-year evergreen foliage with deciduous foliage that maintains a higher average foliar moisture content reduces the probability of intense fire. Seed source for jack pine may be gone by the time a site burns. In Maine, a search of old records showed pine to be a minor component of the forest in most areas (Lorimer 1977). In these areas, aspen and birch tend to be the dominant early successional species. White and gray birch composed >70% of early successional (younger than 25-year-old) stands, at densities of 1,500-7,600 stems ha<sup>-1</sup> (Lorimer 1977). Wet sites tend to be dominated by black spruce and eastern larch boreal species. Successional trends tend to follow those of the more classical boreal forest (Damman 1964).

Coarse woody debris loads are significantly greater in the Great Lakes and Northeastern boreal forest than the taiga, due to higher productivity, longer disturbance intervals, and minor disturbances such as gap-creating wind events that periodically replenish the log supply. Unburned stands up to 250 years old had bole mass of 190 to 344 t ha<sup>-1</sup> (Gordon 1981), while young jack pine stands (younger than 60 years old) had less than 20 t ha<sup>-1</sup> of stem biomass (Green and Grigal 1979). Young balsam fir stands from 12 to 52 years old had coarse woody debris mass decreasing from 35 to 13 t ha<sup>-1</sup> (Lambert et al. 1980). Snag biomass decreased from 27 to 0.25 t ha<sup>-1</sup> over the same sequence.

## Western Boreal Forests

The Western boreal forests within the range of the lynx are dominated by three tree species: lodgepole pine, Engelmann spruce, and subalpine fir. Like the remainder of the forests with boreal features, these ecosystems are subjected to disturbance by fire on a periodic basis. Yet there are numerous characteristics of the subalpine forests that distinguish them from their more

northerly boreal neighbors: longer intervals between major disturbances (Table 3.2); species that are less fire-adapted (Table 3.4), implying a longer post-fire recovery period; absence of a tall shrub component following disturbance, except where aspen is present; and more post-fire coarse woody debris.

Many of the forest types below the boreal zone in western forests have more frequent disturbance by fire than the boreal zone (Agee 1993) and contain the serotinous-coned lodgepole pine allowing dense, young lodgepole stands to develop after severe fire. However, these stands have occasional lower intensity fires or more representation of fire-tolerant species more typical of lower elevations (western larch and Douglas-fir). These species may be representative of a moderate-severity fire regime (Agee 1993), and multiple age classes may occur in these stands (Arno 1976; Arno 1980; Arno et al. 1993). Where residual density is high, post-fire regeneration is likely to be sparse and dominated by shade-tolerant species. Where residuals are absent, the dense lodgepole pine stands common to higher elevations will be found in a mosaic with the residual-dominated stands.

Across the range of western boreal forests, many fire return intervals are long enough that relatively short-lived lodgepole pine may be removed from the stands by mountain pine beetles before another fire event occurs. In such cases, the old-growth dominants Engelmann spruce and subalpine fir may compose the dominant tree component, but when burned, the spruce and fir are killed and the species do not quickly re-establish. The seeds of both species are large, so they are not easily dispersed by wind, and they do not easily establish on freshly burned sites. Tree colonization may take decades to centuries (Stahelin 1943, Agee 1993), although occasionally spruce or fir will immediately regenerate (Loope and Gruell 1973; Habeck and Mutch 1973; Doyle et al. 1998). During the interim period, vegetation cover is a herbaceous-low shrub meadow (Stahelin 1943). Near timberline the trees may return in a "ribbon forest" pattern (Billings 1969), where linear strips of forest are interspersed with meadow as a result of snow accumulation patterns.

Seventeen years after the Waterfalls Canyon fire in Wyoming, sedges provided the most vegetative cover, with total shrub cover at 4-6% and a seedling-sapling density of 2,000-5,000 ha<sup>-1</sup>, dominated by Engelmann spruce (Doyle et al. 1998). On the Yellowstone Plateau, on the less productive end of the western subalpine forest productivity gradient, Romme (1982) simulated forest succession after fire in two plant associations (Table 3.5) and estimated the longevity of each stage as a function of plant association, restocking rate, and lodgepole pine mortality from bark beetles. The immature pine stage (closed canopy) in all cases began at a minimum age of 40 years post-fire.

**Table 3.5**—Postfire successional stages (years) in the Yellowstone Plateau area of northwestern Wyoming (adapted from Romme 1982).

Successional stage	Lodgepole pine/sedge				Subalpine fir/huckleberry		
	“Typical” stands	Slow restocking	Early pine canopy mortality	Late pine canopy mortality	“Typical” stands	Early pine canopy mortality	Late Pine canopy mortality
Herbaceous	0-20	0-40	0-20	0-20	0-20	0-20	0-20
Seedling-sapling	20-40	40-80	20-40	20-40	20-40	20-40	20-40
Immature pine	40-150	80-200	40-150	40-150	40-150	40-150	40-150
Mature pine	150-200	200-250	150-170	150-300	150-300	150-180	150-350
Transitional	200-300	250-350	170-240	300-400	300-400	180-280	350-450
Climax forest <sup>a</sup>	300+	350+	240+	400+	400+	280+	450+

<sup>a</sup>Climax forest is defined as the potential vegetation on the sites. For the lodgepole pine/sedge plant association (infertile sites) it is lodgepole pine, and for the subalpine fir/huckleberry plant association it is subalpine fir and Engelmann spruce.

Where wind is the disturbance agent, or bark beetles remove an overstory of lodgepole pine or whitebark pine, Engelmann spruce and/or subalpine fir, released from the understory, are likely to be the post-disturbance dominants (Morgan and Bunting 1990; Agee 1993). They may or may not develop as dense stands of small (and usually not young) conifers.

Coarse woody debris in western subalpine forests follows a U-shaped trend after stand-replacing disturbances, with snags and logs most common in the young stands, declining to a low in mid-succession (Clark et al. 1998). Not all the pre-fire log biomass is consumed, and post-fire log biomass is fed by the fall of snags created by the fire. Unburned spruce-fir forests in Colorado had 120-135 t ha<sup>-1</sup> of stem mass (Landis and Mogren 1975) that would become coarse woody debris if the stand burned. On old-growth spruce-fir sites, where lodgepole pine mortality adds a new cohort of coarse woody debris, log biomass may exceed 100 t ha<sup>-1</sup> (Brown and See 1981), and much of that will remain after fire passes through the stand. In these environments, decay is slow, so that 50-100 years after the fire, some snags and many logs still reflect the fire evidence (Agee and Smith 1984). During the successional stages, there is clearly a substantial mass of coarse woody debris on site (Huff et al. 1989).

## Landscape Management Implications

The natural landscapes of the boreal forest within which the lynx has successfully existed have been profoundly affected by disturbance, primarily by fire. Although most of the lynx range is included in the high-severity fire regime, there is considerable range in the frequency with which fire occurred on these landscapes, and because of that a wide variation in

successional stages present. Further variation has occurred due to local site conditions, intensity and duration of the fire, forest age at the time of fire, and post-fire climate. Mimicking this pattern of natural disturbance has been suggested as a way to maintain biodiversity in managed forests (Hunter 1990; Bunnell 1995).

For the boreal forest, there are several general principles that must be addressed in landscape management plans if harvesting or fire disturbance is to be incorporated:

1. The habitat will be a product of the cumulative effect of all disturbances. The substitution of logging for fire, for example, is only meaningful if fire can be successfully removed from the environment, and even then, logging will not totally mimic fire as a disturbance process because of roading and coarse woody debris differences.

2. Typical models used for fire history studies suggest that fire selected a range of stand ages to burn. Harvesting only the oldest ages will decrease the average stand age of the landscape and will remove the complex boreal stand structure that may be critical for lynx denning. Young and old stands need to be part of any landscape disturbance plan.

3. Size and juxtaposition of stands is critical. Most fires are small. Most of the landscape, however, is affected by larger fire patches, with unburned areas inside the fire perimeter (stringers, islands, fire skips).

There are a range of prescriptions for lynx or lynx habitat that have quite different implications for management. Koehler and Aubry (1994), addressing the “southern latitude” habitat (equivalent to Western boreal forest), suggest that although approximating the natural disturbance frequency and spatial patterns will provide the best habitat for lynx, large openings (greater than 100 m across) may create barriers to lynx movement and travel corridors are needed for cover for lynx. Typical spatial patterns of historic fires in this type suggest much larger patches were the norm in boreal forests and that there are no guaranteed “travel corridors” or connectivity between fire patches or among unburned islands within fires. The discrepancies within Koehler and Aubry’s (1994) recommendations probably represent the difference between what is “natural” and what may be optimum for one species that occupies this natural environment. An example of problems caused by openings smaller than the natural scale is discussed by Hunter (1993). Small openings by cutting in boreal forest were ideal for moose but less so for caribou; wolf populations increased and thereby depressed caribou populations, a result of creating openings smaller than what historic fires had done.

## Summary

---

It is clear that boreal forests, in addition to covering a wide geographic area, contain many unusual combinations of species and disturbance regimes. Few generalizations beyond broad climatic conditions apply over the large geographic range of boreal forests. Fire has been the primary natural disturbance in boreal forests, although its influence decreases in the eastern boreal region. Stand replacement disturbances are common and are often large with few islands. Across much of the boreal forest, insects and other disturbances generate small scale heterogeneity, although spruce budworm can create widespread epidemic mortality in the eastern boreal forest region. Fire disturbances tend to fit stochastic models well, although the specific parameters of the models may be difficult to fit. These models suggest that large proportions of young forest were characteristic of the boreal region but that fair amounts of quite old forest were part of the mosaic as well. These natural landscapes diverged significantly from even-aged silvicultural systems: fewer roads, more coarse woody debris, older age structures, and complex juxtaposition of different-aged stands. Post-fire successional sequences are very different in the taiga, eastern, midwest, and western forest types, particularly in the proportion of deciduous vegetation.

Ecology is a science of place, and scientific recommendations for lynx will have to take the natural and cultural features and history of each boreal subregion into account.

## Literature Cited

---

- Agee, J. K. 1993. Fire ecology of Pacific Northwest forests. Island Press, Washington, DC.
- Agee, J. K. 1998a. The ecological role of fire in pine forests. Pages 193-218 in Richardson, D. M., ed. The genus *Pinus*. Cambridge University Press, Cambridge.
- Agee, J. K. 1998b. The landscape ecology of western forest fire regimes. Northwest Science 72 (special issue): 24-34.
- Agee, J. K., M. Finney, and R. deGouvenain. 1990. Forest fire history of Desolation Peak, Washington. Canadian Journal of Forest Research 20: 350-56.
- Agee, J. K. and J. Kertis. 1987. Forest types of the North Cascades National Park Service Complex. Canadian Journal of Botany 65: 1520-1530.
- Agee, J. K. and L. Smith 1984. Subalpine tree reestablishment after fire in the Olympic Mountains, Washington. Ecology 65: 810-19.
- Alexander, M. E., and D. L. Euler. 1981. Ecological role of fire in the uncut boreal mixedwood forest. Pages 42-64 in Proceedings of the boreal mixedwood symposium. Canadian Forest Service Pub. COFRC Symp. Proc. O-P-9.

- Arno, S. F. 1976. The historical role of fire on the Bitterroot National Forest. Res. Pap. INT-187. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station.
- Arno, S. F. 1980. Forest fire history of the northern Rockies. *Journal of Forestry* 78: 460-65.
- Arno, S. F. 1986. Whitebark pine cone crops: A diminishing source of wildlife food. *Western Journal of Applied Forestry* 1: 92-94.
- Arno, S. F. and J. R. Habeck. 1972. Ecology of alpine larch (*Larix lyallii* Parl.) in the Pacific Northwest. *Ecological Monographs* 42: 417-450.
- Arno, S. F. and R. P. Hammerly. 1984. *Timberline: mountain and Arctic forest frontiers*. The Mountaineers. Seattle, WA.
- Arno, S. F. and T. D. Peterson. 1983. Variation in estimates of fire intervals: a closer look at fire history on the Bitterroot National Forest. Res. Pap. INT-301. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station.
- Arno, S. F., E. D. Reinhardt, and J. H. Scott. 1993. Forest structure and landscape patterns in the subalpine lodgepole pine type: a procedure for quantifying past and present conditions. Gen. Tech. Rep. INT-294. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station.
- Baker, W. L. 1989. Landscape ecology and nature reserve design in the Boundary Waters Canoe Area, Minnesota. *Ecology* 70 (1) 23-35.
- Baker, W. L. 1994. Restoration of landscape structure altered by fire suppression. *Conservation Biology* 8: 763-769.
- Barbour, M. G. and W. D. Billings, eds. 1988. *North American terrestrial vegetation*. Cambridge University Press, Cambridge.
- Barbour, M. G. and R.A. Woodward. 1985. The red fir forest of California. *Canadian Journal of Forest Research* 15: 570-576.
- Barlowe, R. 1951. Administration of tax-reverted lands in the Lake States. Michigan Agricultural Experiment Station Tech. Bull. 225.
- Barlowe 1983. Changing land use and policies: The Lake States. Chapter 10 in Flader, S. L., ed. *The Great Lakes Forest: an environmental and social history*. University of Minnesota Press, Minneapolis, MN.
- Barney, R. J. 1971. Selected 1966-69 interior Alaska wildfire statistics with long-term comparisons. Res. Note PNW-154. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station.
- Barney, R. J. and K. Van Cleve. 1973. Black spruce fuel weights and biomass in two interior Alaska stands. *Canadian Journal of Forest Research* 3: 304-11.
- Barrett, J. W. 1962. The Northeast Region. Chapter 2 in Barrett, J. W. ed. *Regional silviculture of the United States*. John Wiley and Sons, New York.
- Baskerville, G. L. 1975. Spruce budworm: super silviculturist. *Forestry Chronicle* 51: 138-140.
- Bergeron, Y. 1991. The influence of island and mainland lakeshore landscapes on boreal forest fire regimes. *Ecology* 72: 1980-92.

- Bergeron, Y. and M. Dubuc. 1989. Succession in the southern part of the Canadian boreal forest. *Vegetatio* 79: 51-63.
- Bergeron, Y. and A. Leduc. 1998. Relationships between changes in fire frequency and mortality due to spruce budworm outbreaks in the southeastern Canadian boreal forest. *Journal of Vegetation Science* 9: 492-500.
- Bergeron, Y., A. Leduc, and L. Ting-xian. 1997. Explaining the distribution of *Pinus* spp. in a Canadian boreal insular landscape. *Journal of Vegetation Science* 8: 37-44.
- Billings, W. D. 1969. Vegetational patterns near alpine timberline as affected by fire-snowdrift interactions. *Vegetatio* 19: 192-207.
- Black, R. A. and L. C. Bliss 1978. Recovery sequence of *Picea mariana-Vaccinium uliginosum* forests after burning near Inuvik, Northwest Territories, Canada. *Canadian Journal of Botany* 56: 2020-30.
- Blais, J. R. 1968. Regional variation in susceptibility of eastern North American forests to budworm attack based on history of outbreaks. *Forestry Chronicle* 44: 17-23.
- Brooks, R. T. and T. W. Birch. 1988. Changes in New England forests and forest owners: implications for wildlife habitat resources and management. *Transactions of the 53rd North American Wildlife and Natural Resources Conference*: 78-87.
- Brown, J. K. and T. E. See. 1981. Downed dead woody fuel and biomass in the northern Rocky Mountains. Gen. Tech. Rep. INT-117. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station.
- Bunnell, F. 1995. Forest-dwelling vertebrate faunas and natural fire regimes in British Columbia: patterns and implications for conservation. *Conservation Biology* 9: 636-644.
- Canham, C. D. and O. L. Loucks. 1984. Catastrophic windthrow in the presettlement forests of Wisconsin. *Ecology* 65: 803-09.
- Carleton, T. J. and P. F. Maycock. 1978. Dynamics of the boreal forest south of James Bay, Canada. *Canadian Journal of Botany* 56: 1157-1173.
- Cayford, J. H. and D. H. McRae. 1983. The ecological role of fire in jack pine forests. Pages 183-199 *in* Wein, R. W. and D. A. MacLean. *The role of fire in northern circumpolar ecosystems*. John Wiley and Sons, New York.
- Clark, D. F., D. D. Kneeshaw, P. J. Burton, and J. A. Antos. 1998. Coarse woody debris in sub-boreal spruce forests of west-central British Columbia. *Canadian Journal of Forest Research* 28: 284-90.
- Cogbill, C. V. 1985. Dynamics of the boreal forests of the Laurentian Highlands, Canada. *Canadian Journal of Forest Research* 15: 252-61.
- Conkey, L. E., M. Keifer, and A. H. Lloyd. 1995. Disjunct jack pine (*Pinus banksiana* Lamb.) structure and dynamics, Acadia National Park, Maine. *Ecoscience* 2: 168-176.
- Coutts, M. P. and J. Grace. 1995. *Wind and trees*. Cambridge University Press. Cambridge, England.
- Critchfield, W. B. 1985. The late Quaternary history of lodgepole and jack pines. *Canadian Journal of Forest Research* 15: 749-772.
- Curtis, J. T. 1959. *The vegetation of Wisconsin*. University of Wisconsin Press, Madison.

- Dammon, A. W. H. 1964. Some forest types of central Newfoundland and their relations to environmental factors. *Forest Science Monographs* 8.
- Dansereau, P.-R. and Y. Bergeron. 1993. Fire history in the southern boreal forest of northwestern Quebec. *Canadian Journal of Forest Research* 23: 25-32.
- DeLong, S. C. 1998. Natural disturbance rates and patch size distribution of forests in northern British Columbia: implications for forest management. *Northwest Science* 72 (special issue): 35-48.
- Despain, D. G. 1990. *Yellowstone vegetation*. Roberts Rinehart. Boulder, CO.
- Doyle, K. M., D. H. Knight, D. L. Taylor, W. J. Barmore, Jr., and J. M. Benedict. 1998. Seventeen years of forest succession following the Waterfall Canyon fire. *International Journal of Wildland Fire* 8: 45-55.
- Eberhart, K. E., and P. M. Woodard. 1987. Distribution of residual vegetation associated with large fires in Alberta. *Canadian Journal of Forest Research* 17: 1207-12.
- Elliott-Fisk, D. L. 1988. The boreal forest. Pages 33-62 in Barbour, M. G. and W. D. Billings, eds. *North American terrestrial vegetation*. Cambridge University Press, Cambridge.
- Fahnestock, G. R. 1976. Fires, fuel, and flora as factors in wilderness management: The Pasayten case. *Tall Timbers Fire Ecology Conf.* 15: 33-70.
- Ferguson, R. H. and F. R. Longwood. 1960. *The timber resources of Maine*. USDA Forest Service, Northeastern Forest Experiment Station, Upper Darby, PA.
- Findley, J. S. and S. Anderson. 1956. Zoogeography of the montane mammals of Colorado. *Journal of Mammalogy* 37: 80-82.
- Finney, M. A. 1995. The missing tail and other considerations for the use of fire history models. *International Journal of Wildland Fire* 5: 197-202.
- Flannigan, M. D. and C. E. Van Wagner. 1991. Climate change and wildfire in Canada. *Canadian Journal of Forest Research* 21: 66-72.
- Flannigan, M. D., Y. Bergeron, O. Engelmark, and B. M. Wotton. 1998. Future wildfire in circumboreal forests in relation to global warming. *Journal of Vegetation Science* 9: 469-476.
- Foote, M. J. 1983. Classification, description, and dynamics of plant communities after fire in the taiga of interior Alaska. Res. Pap. PNW-307. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station.
- Foster, D. R. 1983. The history and pattern of fire in the boreal forest of southeastern Labrador. *Canadian Journal of Botany* 61: 2459-71.
- Franklin, J. F. and C. T. Dyrness. 1973. *Natural vegetation of Oregon and Washington*. Gen. Tech. Rep. PNW-8. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station.
- Frelich, L. E. and P. B. Reich. 1995. Spatial patterns and succession in a Minnesota southern-boreal forest. *Ecological Monographs* 65: 325-346.
- Frissell, S. S. 1973. The importance of fire as a natural ecological factor in Itasca State Park, Minnesota. *Quaternary Research* 3: 397-407.

- Furyaev, V. V., R. W. Wein, and D. A. MacLean. 1983. Fire influences in *Abies*-dominated forests. Pages 221-234 in Wein, R. W. and D. A. MacLean. The role of fire in northern circumpolar ecosystems. John Wiley and Sons, New York.
- Gauthier, S., J. Gagnon, and Y. Bergeron. 1993. Population age structure of *Pinus banksiana* at the southern edge of the Canadian boreal forest. *Journal of Vegetation Science* 4: 783-790.
- Gordon, A. G. 1981. Woodlands data set: Ontario site Region 5 sites 1-4. Pages 576-79 in Reichle, D. E., ed. Dynamic properties of forest ecosystems. International Biological Programme 23. Cambridge University Press, Cambridge.
- Green, D. C. and D. F. Grigal. 1979. Jack pine biomass accretion on shallow and deep soils in Minnesota. *Soil Science Society of America Proceedings* 43: 1233-37.
- Greller A. M. 1988. Deciduous forest. Pages 288-316 in Barbour, M. G. and W. D. Billings, eds. North American terrestrial vegetation. Cambridge University Press. Cambridge.
- Habeck, J. R. and R. W. Mutch. 1973. Fire-dependent forests in the northern Rocky Mountains. *Quaternary Research* 3: 408-424.
- Hadley, J. L. and W. K. Smith. 1983. Influence of wind exposure on needle desiccation and mortality for timberline conifers in Wyoming. *Arctic and Alpine Research* 15: 127-35.
- Hare, F. K. 1969. Climate and zonal divisions of the boreal forest formation in eastern Canada. Pages 7-23 in Nelson, J. G., and M. J. Chambers eds. Vegetation, soils, and wildlife. Methuen Publications, Toronto.
- Hare, F. K. and J. C. Ritchie. 1972. The boreal bioclimates. *Geographical Review* 62: 333-65.
- Harmon, M. E., J. F. Franklin, F. J. Swanson, P. Sollins, S. V. Gregory, J. D. Lattin, N. H. Anderson, S. P. Cline, N. G. Aumen, J. R. Sedell, G. W. Liemkaemper, K. Cromack, Jr., and K. W. Cummins. 1986. Ecology of coarse woody debris in temperate ecosystems. *Advances in Ecological Research* 15: 133- 302.
- Hawksworth, F. G. and A. L. Shigo. 1980. Dwarf mistletoe on red spruce in the White Mountains of New Hampshire. *Plant Disease Reporter* 64: 880-992.
- Heinselman, M. L. 1973. Fire in the virgin forests of the Boundary Waters Canoe Area, Minnesota. *Quaternary Research* 3: 329-82.
- Heinselman, M. L. 1981. Fire intensity and frequency as factors in the distribution and structure of northern ecosystems. Pages 7-57 in Mooney, H. and others, eds. Fire Regimes and Ecosystem Properties. Gen. Tech. Rep. WO-26. Washington, DC: U.S. Department of Agriculture, Forest Service.
- Holling, C. S. 1992. The role of forest insects in structuring the boreal landscape. Pages 170-91 in Shugart, H. H., R. Leemans, and G. B. Bonan, eds. A systems analysis of the global boreal forest. Cambridge University Press, Cambridge.
- Hopkins, A. D. 1901. Insect enemies of spruce in the Northeast. USDA Forest Service, Bureau of Entomology Bull. 28.
- Huff, M. H., J. K. Agee, M. Gracz, and M. Finney. 1989. Fuel and fire behavior predictions in subalpine forests of Pacific Northwest National Parks. USDI National Park Service Rep. CPSU/UW 89-4. College of Forest Resources, University of Washington. Seattle.

- Huggard, D. and A. Arsenault. In review. Mistakes in fire frequency analysis.
- Hunter, M. L. 1990. *Wildlife, forests, and forestry, principles of managing forests for biological diversity*. Prentice Hall, Englewood Cliffs, NJ.
- Hunter, M. L. 1993. Natural fire regimes as spatial models for managing boreal forests. *Biological Conservation* 65: 115-120.
- Johnson, E. A. 1992. *Fire and vegetation dynamics: Studies from the North American boreal forest*. Cambridge University Press, Cambridge.
- Johnson, E. A. and C. P. S. Larsen. 1991. Climatically-induced change in fire frequency in the southern Canadian Rockies. *Ecology* 72: 194-201.
- Johnson, E. A., K. Miyanishi, and J. M. H. Weir. 1998. Wildfires in the western Canadian boreal forest: landscape patterns and ecosystem management. *Journal of Vegetation Science* 9: 603-610.
- Johnson, E. A. and C. E. Van Wagner. 1985. The theory and use of two fire history models. *Canadian Journal of Forest Research* 15 (1): 214-220.
- Johnson, E. A. and D. R. Wowchuck. 1993. Wildfires in the southern Canadian Rocky Mountains and their relationship to mid-tropospheric anomalies. *Canadian Journal of Forest Research* 23: 1213-22.
- Kettela, E. G. 1983. A cartographic history of spruce budworm defoliation 1967-81 in Eastern North America. Canadian Forest Service Information Report DPC-X-14. Ottawa, Ontario.
- Kiil, A. D. and J. E. Grigel. 1969. The May 1968 forest conflagrations in central Alberta. Canadian Forest Service Information Rep. A-X-24.
- Klyza, C. M. and S. C. Trombulak. 1994. *The future of the Northern Forest*. Middlebury College Press. Hanover, NH.
- Knight, D. H. 1994. *Mountains and plains: the ecology of Wyoming landscapes*. Yale University Press, New Haven, CN.
- Koehler, G. M. and K. B. Aubry. 1994. Lynx. Pages 74-98 *in* Ruggiero, L. F., K. B. Aubry, S. W. Buskirk, L. J. Lyon, and W. J. Zielinski, eds. *The scientific basis for conserving forest carnivores: American marten, fisher, lynx, and wolverine in the Western United States*. USDA Forest Service Gen. Tech. Rep. RM-254.
- Lambert, R. C., G. E. Lang, and W. A. Reiners. 1980. Loss of mass and chemical change in decaying boles of a subalpine balsam fir forest. *Ecology* 61: 1460-73.
- Landis, T. D. and E. W. Mogren. 1975. Tree strata biomass of subalpine spruce-fir stands in southwestern Colorado. *Forest Science* 21: 9-12.
- Larsen, J. A. 1980. *The boreal ecosystem*. Academic Press, New York.
- Lavoie, L. and L. Sirois. 1998. Vegetation changes caused by recent fires in the northern boreal forest of eastern Canada. *Journal of Vegetation Science* 9: 483-492.
- Lesica, P. 1996. Using fire history models to estimate proportions of old growth forest in northwest Montana, USA. *Biological Conservation* 77: 33-39.
- Little, E. L. 1971. *Atlas of United States trees. Volume 1. Conifers and important hardwoods*. USDA Forest Service Miscellaneous Publication 1146.

- Loope, L. L. and G. E. Gruell. 1973. The ecological role of fire in the Jackson Hole area, northwestern Wyoming. *Quaternary Research* 3: 425-443.
- Lorimer, C. G. 1977. The presettlement forest and natural disturbance cycles of northeast Maine. *Ecology* 58: 139-148.
- Loucks, O. L. 1983. New light on the changing forest. Chapter 2 in Flader, S. L., ed. *The Great Lakes Forest: an environmental and social history*. University of Minnesota Press, Minneapolis, MN.
- Lutz, H. J. 1956. Ecological effects of forest fires in the interior of Alaska. *USDA Technical Bulletin* 1133.
- Maikawa, E. and K. A. Kershaw. 1976. Studies on lichen-dominated systems. XIX. The post-fire recovery sequence of black spruce-lichen woodland in the Abitau Lake region, N.W.T. *Canadian Journal of Botany* 54: 2679-2687.
- Maycock, P. F. and J. T. Curtis. 1960. The phytosociology of boreal conifer-hardwood forests of the Great Lakes region. *Ecological Monographs* 30: 1-35.
- Miller-Weeks, M. and D. Smoronk. 1993. Aerial assessment of red spruce and balsam fir condition in the Adirondack Region of New York, the Green Mountains of Vermont, the White Mountains of New Hampshire, and the mountains of western Maine, 1985-86. *USDA Forest Service, Northeastern Area Report NA-TP-16-93*, Durham, NH.
- Mladenoff, D. J. 1987. Dynamics of nitrogen mineralization and nitrification in hemlock and hardwood treefall gaps. *Ecology* 68: 1171-80.
- Mladenoff, D. J., M. A. White, J. Pastor, and T. R. Crow. 1993. Comparing spatial patterns in unaltered old-growth and disturbed forest landscapes. *Ecological Applications* 3: 294-306.
- Morgan, P. and S. Bunting. 1990. Fire effects in whitebark pine forests. Pages 166-170 in Schmidt, W. C. and K. J. McDonald, comps. *Proceedings: Symposium on whitebark pine ecosystems: Ecology and management of a high-mountain resource*. Gen. Tech. Rep. INT-270. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station.
- National Research Council. 1998. *Forested landscapes in perspective: prospects and opportunities for sustainable management of America's nonfederal forests*. National Academy Press, Washington, DC.
- Northern Forest Lands Council (NFLC). 1994. *Finding common ground: conserving the Northern Forest*. Northern Forest Lands Council. Concord, NH.
- Oechel, W. C. and W. T. Lawrence. 1985. Taiga. in Chabot, B. F. and H. A. Mooney, eds. *Physiological ecology of North American plant communities*. Chapman and Hall, New York.
- Paragi, T. F., W. N. Johnson, D. D. Katnik, and A. J. Magoun. 1997. Selection of post-fire seres by lynx and snowshoe hares in the Alaskan taiga. *Northwestern Naturalist* 78: 77-86.
- Parker, W. H., J. Maze, and G. E. Bradfield. 1981. Implications of morphological and anatomical variation in *Abies balsamea* and *A. lasiocarpa* (Pinaceae) from Western Canada. *American Journal of Botany* 68: 843-854.

- Pastor, J. and D. J. Mladenoff. 1992. The southern boreal-northern hardwood forest border. Pages 216-240 *in* Shugart, H. H., R. Leemans, and G. B. Bonan, eds. A systems analysis of the global boreal forest. Cambridge University Press, Cambridge.
- Payette, S. 1992. Fire as a controlling process in the North American boreal forest. Pages 144-169 *in* Shugart, H. H., R. Leemans, and G. B. Bonan, eds. A systems analysis of the global boreal forest. Cambridge University Press Cambridge.
- Payette, S., C. Morneau, L. Sirois, and M. Despons. 1989. Recent fire history of the northern Quebec biomes. *Ecology* 70: 656-73.
- Peet, R. K. 1981. Forest vegetation of the Colorado Front Range. *Vegetatio* 45: 3-75.
- Peet, R. K. 1988. Forests of the Rocky Mountains. Pages 63-102 *in* Barbour, M. G. and W. D. Billings, eds. North American terrestrial vegetation. Cambridge University Press, Cambridge.
- Pickett, S. T. A. and Thompson, J. N. 1978. Patch dynamics and the design of nature reserves. *Biological Conservation* 13: 27-37.
- Quirk, W. A. and D. J. Sykes. 1971. White spruce stringers in a fire-patterned landscape in interior Alaska. Pages 179-197 *in* Proceedings of the symposium, fire in the environment. Portland, OR: U.S. Department of Agriculture, Forest Service.
- Ratz, A. 1995. Long-term spatial patterns created by fire: a model oriented towards boreal forests. *International Journal of Wildland Fire* 5: 25-34.
- Reidel, C. 1994. The political process of the Northern Forest lands study. Chapter 6 *in* Klyza, C. M. and S. C. Trombulak. 1994. The future of the Northern Forest. Middlebury College Press. Hanover, NH.
- Roberts, B. A. and A. V. Mallik. 1994. Response of *Pinus resinosa* in Newfoundland to wildfire. *Journal of Vegetation Science* 5: 187-196.
- Rochefort, R. M., R. L. Little, A. Woodward, and D. L. Peterson. 1994. Changes in sub-alpine tree distribution in western North America: a review of climatic and other factors. *The Holocene* 4(1): 89-100.
- Romme, W. H. 1982. Fire and landscape diversity in subalpine forests of Yellowstone National Park. *Ecological Monographs* 52: 199-221.
- Romme, W. H. and D. H. Knight. 1981. Fire frequency and subalpine forest succession along a topographic gradient in Wyoming. *Ecology* 62: 319-326.
- Roe, E. I. and J. H. Stoeckler. 1950. Thinning over-dense jack pine seedling stands in the Lake States. *Journal of Forestry* 48: 861-865.
- Rowe, J. S. 1961. Critique of some vegetational concepts as applied to forests of northwestern Alberta. *Canadian Journal of Botany* 39: 1007-17.
- Rowe, J. S. 1972. Forest regions of Canada. Canadian Department of Environment. Canadian Forestry Service Publication 1300. Ottawa.
- Rowe, J. S. 1983. Concepts of fire effects on plant individuals and species. Pages 135-154 *in* Wein, R. W. and D. A. MacLean. The role of fire in northern circumpolar ecosystems. John Wiley and Sons, New York.

- Rowe, J. S., J. L. Bergsteinsson, G. A. Padbury, and R. Hermesh. 1974. Fire studies in the Mackenzie Valley. Canadian Department of Indian Affairs and Northern Development. ALUR Rep. 73-74-61. 123 p.
- Rowe, J. S. and G. W. Scotter. 1973. Fire in the boreal forest. *Quaternary Research* 3: 444-64.
- Runkle, J. R. 1982. Patterns of disturbance in some old-growth mesic forests of Eastern North America. *Ecology* 63: 1533-46.
- Sandberg, L. 1983. The response of forest industries to a changing environment. Chapter 12 in Flader, S. L. ed. *The Great Lakes Forest: an environmental and social history*. University of Minnesota Press, Minneapolis, MN.
- Schroeder, M. and C. Buck. 1970. Fire weather. USDA Agricultural Handbook 360.
- Seymour, R. S. 1992. The red spruce-balsam fir forest of Maine: evolution of silvicultural practice in response to stand development patterns and disturbances. Pages 217-244 in Kelty, M. J. et al., eds. *The ecology and silviculture of mixed-species forests: A festschrift for David M. Smith*. Kluwer Publishers, Norwell, MA.
- Seymour, R. S. and M. L. Hunter, Jr. 1992. New forestry in eastern spruce-fir forests: Applications to Maine. Maine Agricultural Experiment Station Misc. Pub. 716.
- Sirois, L. 1992. The transition between boreal forest and tundra. Pages 196-215 in Shugart, H. H., R. Leemans, and G. B. Bonan, eds. *A systems analysis of the global boreal forest*. Cambridge University Press, Cambridge.
- Smith, J. H. G. and R. C. Henderson. 1970. Impact of fire control practices on ecosystem development. pp 86-98 in *Role of fire in the Intermountain West*. University of Montana, Missoula.
- Solomon, A. M. 1992. The nature and distribution of past, present, and future boreal forests: lessons for a research and modeling agenda. Pages 291-307 in Shugart, H. H., R. Leemans, and G. B. Bonan, eds. *A systems analysis of the global boreal forest*. Cambridge University Press, Cambridge.
- Sprugel, D. G. 1976. Dynamic structure of wave-regenerated *Abies balsamea* forests in the Northeastern United States. *Journal of Ecology* 64: 889-91.
- Stahelin, R. 1943. Factors influencing the natural restocking of high altitude burns by coniferous trees in the central Rocky Mountains. *Ecology* 24: 19-30.
- Swetnam, T. W. and A. M. Lynch. 1993. Multicentury, regional-scale patterns of western spruce budworm outbreaks. *Ecological Monographs* 63: 399-424.
- Taylor, T. M. C. 1959. The taxonomic relationship between *Picea glauca* (Moench) Voss and *Picea engelmannii* Parry. *Madrono* 15: 111-115.
- Trewartha, G. T. 1968. *An introduction to climate*. 4th Edition. McGraw-Hill, New York.
- Van Cleve, K. 1981. Woodlands data set: black spruce feathermoss and muskeg sites 1-2. Pages 648-650 In Reichle, D. E., ed. *Dynamic properties of forest ecosystems*. International Biological Programme 23. Cambridge University Press, Cambridge.
- Van Cleve, K., C. T. Dyrness, L. A. Viereck, J. Fox, F. S. Chapin, III, and W. Oechel. 1983. Taiga ecosystems in interior Alaska. *Bioscience* 33, 1: 39-44.

- Van Sickle, G. A. 1995. Forest insect pests in the Pacific and Yukon region. Pages 74-89 *in* Armstrong, J. A. and W. G. H. Ives, eds. Forest insect pests in Canada. Natural Resources Canada, Canadian Forest Service, Science and Sustainable Development Directorate.
- Van Wagner, C. E. 1978. Age-class distribution and the forest fire cycle. *Canadian Journal of Forest Research* 8: 220-7
- Van Wagner, C. E. 1983. Fire behavior in northern conifer forests and shrublands. Pages 65-80 *in* Wein, R. W. and D. A. MacLean. The role of fire in northern circumpolar ecosystems. John Wiley and Sons, New York.
- Veblen, T. T. 1986. Age and size structure of subalpine forests in the Colorado Front Range. *Bulletin of the Torrey Botanical Club* 113: 225-40.
- Veblen, T. T., K. S. Hadley, E. M. Nel, T. Kitzberger, M. Reid, and R. Villalba. 1994. Disturbance regime and disturbance interactions in a Rocky Mountain subalpine forest. *Journal of Ecology* 82: 125-135.
- Viereck, L. A. 1973. Wildfire in the taiga of Alaska. *Quaternary Research* 3: 465-95.
- Viereck, L. A. 1983. The effects of fire on black spruce ecosystems of Alaska and Northern Canada. Pages 201-220 *in* Wein, R. W. and D. A. MacLean. The role of fire in northern circumpolar ecosystems. John Wiley and Sons, New York.
- Viereck, L. A. and C. T. Dyrness 1980. A preliminary classification system for vegetation of Alaska. Gen. Tech. Rep. PNW-106. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Station.
- Wein, R. W. and J. M. Moore. 1977. Fire history and rotations in the New Brunswick Acadian Forest. *Canadian Journal of Forest Research* 7: 285-294.
- Wein, R. W. and J. M. Moore. 1979. Fire history and recent fire rotation periods in the Nova Scotia Acadian Forest. *Canadian Journal of Forest Research* 9: 166-178.
- Werner, R. A. and E. H. Holsten. 1983. Mortality of white spruce during a spruce beetle outbreak on the Kenai Peninsula in Alaska. *Canadian Journal of Forest Research* 13: 96-101.
- Yarie, J. 1979. A preliminary analysis of stand age distribution in the porcupine inventory unit (abstract). Page 12 *in* Proceedings 30th Alaska Science Conference, Fairbanks, Alaska.