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Forest Ecosystem Structure and Disturbance Dynamics across the Circumboreal Forest

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14.1 INTRODUCTION

The northern circumpolar forest belt covers an area of 12 million km^2 (Burton et al., 2003), which is about one-quarter of the world's forested area. In countries in the circumboreal zone, the boreal forest accounts for a vast proportion of the total land area; such as in Finland where about 70% of the country is covered by boreal forest. Further east, the Russian boreal forest contains more than half of all the conifers found on the planet, 20% of the forested area and more than 10% of the world's forest biomass (Engelmark, 1999). Altogether the circumpolar boreal forests and peatlands are estimated to contain more than five times the amount of carbon found in the world's temperate forests and almost double the carbon in tropical forests (Goodale et al., 2002; Kasischke, 2000).

Unlike temperate and tropical forests, tree species richness is quite low in the boreal with only nine dominant forest-forming species in North America, five in Fennoscandia, and 12 across Eurasia (Table 14.1). There is, however, a larger number of minor tree species (e.g., 24 indigenous species in Finland). Although species differ, the dominant genera remain the same across this circumpolar region: *Abies, Larix, Picea, Pinus, Populus*, and *Betula*. Differences in species composition are due to postglacial migration history and variations in climate, topography, soil texture, and disturbance regimes.

Fire is an important part of boreal forest ecology (Zackrisson, 1977; Payette, 1992). However, it is currently understood that considerable variation in fire regimes exists within the boreal forest and that boreal forests with apparently no fire influence since the last glaciation can be found (Zackrisson et al., 1995; Pitkänen et al., 2003). In areas with long fire return intervals, nonfire disturbances (e.g., insect outbreaks, fungi, windthrow, senescence) become important (Kuuluvainen et al., 1998; McCarthy and Weetman, 2006). With short return intervals of stand-replacing fire, the forest is dominated by pyrogeneous tree species such as jack pine (*Pinus banksiana*), black spruce (*Picea mariana*), or trembling aspen (*Populus tremuloides*) in boreal North America. These species all have adaptations to crown fire, such as serotinous cones or the ability to resprout from root suckers. In Eurasia, species such as Scots pine (*Pinus sylvestris*) and larches (*Larix* spp.) have thick bark, which helps them resist low-intensity surface fires (Agee, 1998, Shorohova et al. 2009). Some tree species that are shade-intolerant (e.g., *Populus* and *Betula* spp.) benefit

Table 14.1 Some characteristics of major tree species dominating the canopy in the circumboreal forest

Continent	*Species*		*Regeneration strategy (pyrogeny)*	*Shade tolerance*	*Average longevity (years)*	*Main distribution/ typical site*
	Scientific name	*Common name*				
North America	*Pinus banksiana*	Jack pine	Serotinous cones	Very shade-intolerant	100–150	Nova Scotia to Alberta (exposed mineral soil)
	Picea glauca	White spruce	Wind dispersal	Mid-tolerant	200–300	Maritime provinces to Alaska (various soil types)
	Picea mariana	Black spruce	Semi-serotinous cones and layering	Shade-tolerant	200	Newfoundland to Alaska (various soil types)
	Picea rubens	Red spruce	Wind dispersal	Moderate to shade-tolerant	200–300	Eastern North America (southern boreal) (various soil types)
	Abies balsamea	Balsam fir	Wind dispersal (limited layering)	Very shade-tolerant	60–100	Newfoundland to Alberta (more dominant in east and in southern boreal) (various soil types)
	Larix laricina	Larch or tamarack	Wind dispersal	Very shade-intolerant	150–180	Newfoundland to Alaska (various soil types)
	Populus tremuloides	Trembling aspen	Root suckers and wind dispersal	Very intolerant	80–100	Newfoundland to Alaska, less abundant in far north (various soil types)
	Populus balsamifera	Balsam poplar	Root suckers and wind dispersal	Intolerant	60–200	Newfoundland to Alaska (various soil types)
	Betula papyrifera	Paper birch	Wind dispersal	Intolerant	70 (rarely past 140 yrs)	Newfoundland to Alaska (well-drained, sandy loams on cool, moist sites)
Eurasia	*Picea abies*	Norway spruce	Wind dispersal	Shade-tolerant	200–250	Scandinavia and Russia, west of Urals (fertile to medium fertile, well-drained sites)
	*Picea abies subsp. Obovata**	Siberian spruce	Wind dispersal, limited layering	Shade-tolerant	Up to 300	Northern Scandinavia to Northern China (various soil types)

Continued

Table 14.1 Cont'd

Continent	*Species*		*Regeneration strategy (pyrogeny)*	*Shade tolerance*	*Average longevity (years)*	*Main distribution/ typical site*
	Scientific name	*Common name*				
	Pinus sibirica	Siberian cedar, Siberian stone pine	Wind and bird dispersal	Moderately shade-tolerant	Up to 400	Siberia to Northern China (800–2500-m altitude) (moist sites)
	Pinus pumila	Dwarf Siberian pine, also known as Japanese stone pine	Animal and bird dispersal	Moderately shade-tolerant	150	Eastern Russia to Japan (1000–2300 m alt) (rocky acidic soils)
	Pinus sylvestris	Scots pine	Wind dispersal/ thick, fire-resistant bark	Shade-intolerant	300–400	Europe, Russia, and Southwest Asia (sandy well-drained sites, pine bogs)
	Larix Sukaczewii	Russian larch	Wind dispersal	Shade-intolerant	250	Central European Russia (various soil types)
	Larix gmelinii	Dahurian larch	Wind dispersal/ thick bark	Shade-intolerant	300	Central and eastern Siberia to Korea (various soil types)
	Larix sibirica, Larix russica	Siberian larch	Wind dispersal/ thick bark	Shade-intolerant	300	Eastern Urals to North China (lowland, great variety of soil)
	Abies sibirica	Siberian fir	Wind dispersal	Shade-tolerant	100	East of Ural to North China (various soil types)
	Betula pubescens	Arctic white birch	Wind dispersal and root suckering	Shade-intolerant	60–80	Scandinavia, European Russia, Western Siberia (especially peatlands and paludified sites)
	Betula pendula	Silver birch; European white birch	Wind dispersal and root suckering	Shade-intolerant	Up to 150	Scandinavia, European Russia, western Siberia (fertile to medium-fertile sites)
	Populus tremula	Eurasian aspen	Wind dispersal and root suckering	Shade-intolerant	Up to 200	All of boreal Eurasia (fertile, well-drained sites)

*In Western literature this is considered to be a subspecies, but in Russia it is considered to be an independent species.

from large areas with no overhead competition and mineral seedbeds on which to establish.

The boreal forest has a relatively low mammal and vascular plant diversity although the diversity of algae, moss, lichen, mushroom, and arthropod species is considered to be high (De Grandpré et al., 2003). Diversity must therefore be considered across taxa and various scales, both temporal and spatial. For example, due to the most recent glaciation (*c.* 11,000 years B.P.) most of the boreal tree species only arrived 2,000 to 9,000 years ago, making it one of the youngest forest biomes in the world. Glaciation also had different effects on different tree species. For example in boreal North-America white spruce found refugia in northern locations (Anderson et al., 2006), while other species were forced south and thus had long migration routes before recolonising boreal habitats (Davis, 1981). Barriers created between different populations also led towards speciation, as was the case for red spruce, which was probably originally a population of black spruce isolated by glaciers (Perron et al., 2000). Red and black spruce still readily hybridise, suggesting that the glaciation may not have lasted long enough to cause true speciation. In Europe the east-west orientation of the Alps prevented the southward migration of plants during glaciations and this led to the extinction of many plant and animal species (Stehlik, 2003).

At present the boreal zone contains some of the last and largest extents of nonexploited forests in the world outside of tropical forests in the Amazon (Aksenov et al., 2002). However, both regions share the same problem of increasing human pressure through logging and deforestation, and this is changing the structure and dynamics of these forests (Mery et al., 2010).

14.1.1 The boreal climate

The boreal zone is characterised by a cold climate in which during six to eight months of the year there are average minimum temperatures below 0°C and only three to five months have average temperatures greater than 10°C (Woodward, 1995). Daylength (with low sun angles) is quite variable, ranging from 15–24 hours in the summer to almost complete darkness in the winter. The boreal forest can thus be differentiated from other forest types by its climatic setting. As well as the short growing season, the high seasonality, and the long summer days this region can be characterised by the occurrences of permafrost and low biological productivity (Wein and MacLean, 1983). For example, it has been estimated that net primary productivity in the boreal forest ranges from 1.2 to 4.3 tons per hectare per year (t ha^{-1} yr^{-1}) whereas in temperate deciduous forests net primary production can be more than double the values (0.8 to 9.8 tons ha^{-1} yr^{-1}) found in the boreal (Landsberg and Gower, 1997). Despite the features that are general to the boreal climate, it is important to realize that considerable variability exists, from semi-maritime climates with cool summers and relatively mild winters (e.g., Fennoscandia, Russian Far East, eastern Quebec) to extremely continental ones with cold winters and short, hot summers (e.g., central Siberia and central Canada).

14.1.2 Disturbances

Throughout much of the western North American boreal forest, crown fires have long been considered to be the primary disturbance type (Bergeron, 1991; Heinselman, 1981; Johnson, 1992; Payette, 1992). In continental parts of the boreal forest with dry summer climates, such as in parts of Alberta or Saskatchewan, crown-fire cycles may be as short as 50 years (Heinselman, 1981; Hirsch, 1991) with large crown fires burning more than 100,000 hectares of forest. However, other disturbances such as surface fires, insect outbreaks, windthrow, and gap dynamics may also play important roles (Bonan and Shugart, 1989; Van der Maarel, 1993). In fact where crown-fire cycles are long, patch or gap disturbances drive forest dynamics.

It has been suggested that the role of fire may have been overemphasised in some boreal ecosystems (Engelmark, 1999; Kuuluvainen, 2002). In Scandinavia, China, and Russia there has been recognition of the importance of gap dynamics in boreal forests that are little affected by fire (Ban et al., 1998; Drobyshev, 1999; Kuuluvainen, 1994; Leemans, 1991; Liu and Hytteborn, 1991) as well as in pine forests affected by low-severity surface fires (Rouvinen et al., 2002; Shorohova et al., 2009). In North America this realisation has been longer in coming due to the pervasive nature of stand-replacing fire and fire research and the fact that only a handful of papers have been published in recent years (Coates and Burton, 1997; Cumming et al., 2000; Kneeshaw and Bergeron, 1998, 1999; McCarthy, 2001).

The main objectives of this chapter are thus to provide an understanding of the role and relative importance of different disturbances in boreal forests, to link the primary disturbances to species composition and climate, and to show how these interactions may have changed through time. In doing so, we will compare and contrast boreal forest dynamics amongst the different regions of the circumpolar boreal forest. The implications arising from the research we review are important for those who have advocated clear cutting as a surrogate for fire (which at least in one way imitates fire by opening large tracts of forest), and even-age forest management as a uniform recipe for forest management of the boreal forest.

14.2 DISTURBANCE REGIMES AND THEIR EFFECTS ON VEGETATION

14.2.1 Fire as a disturbance factor in the boreal forest

Forest fires differ in their severity, size, and return time. Indeed, fires are not all equal in their characteristics and impacts on forests. Most fires burn only a small area and have little impact at a regional scale, although at a local scale their effects may be important. Fire regimes (characterized in terms of fire frequency, severity, and area burned) in the boreal forest differ greatly between continents and across continents.

Climate affects forest fires directly by controlling lightning, fuel moisture levels, and wind regimes. Climatic effects can be observed from more maritime, coastal areas where the influence of fire is reduced compared to interior boreal forests where continental climate effects lead to drier summer conditions and larger and more severe fire events. However, the impact of climate is more complicated, because climate also affects the composition of the vegetation (i.e., the fuel that burns in these fires). Changes in fire regimes also occur through time as climate changes.

North America: The case of crown fire

With the exception of some pine stands for which nonlethal surface fires are locally reported (Smirnova et al., 2008; Bergeron and Brisson, 1990) fire regimes in the North American boreal forest are mainly characterised by stand-replacing fires (Johnson, 1992; Payette, 1992). This contrasts with Eurasian boreal forests where nonlethal surface fires are common (see below). Moreover, the landscape in Canadian boreal forests is mainly characterised by a small proportion of very large lightning-ignited fires. Fires greater than 200 ha represent 97 percent of the area burned in Canada (Stocks et al., 2002). These large fires control the fire interval (the time interval between fires burning the same point) and, inversely, the fire cycle (the time needed to burn an area equivalent to the total area being studied). This parameter is of major importance as it controls the proportion of the landscape, which is dominated by early successional postfire species (when fire cycles are short) and late successional species more associated with gap disturbances (when fire cycles are long).

However, natural fire frequency is difficult to estimate as it may vary greatly depending on the spatial and temporal extents considered. Table 14.2 presents current (over the last 50 years) and historical (last 300 years) fire frequency for Canada's boreal ecozones. The current burn rate was estimated from the Canadian government's large-fire database (Stocks et al., 2002); this includes all fires 200 ha and larger, which as mentioned earlier represent over 97% of all area burned. Historical burn rates were determined from a literature review (Bergeron et al., 2004a) using available forest fire history studies in the North American boreal forest (Figure 14.1). To estimate the historic burn rates, the average age of the forest (time since fire) or, if not available, the fire cycle before large clear-cutting activities began were used. The average age of the forest was preferred to the historic fire cycle because it integrates climatically induced changes in fire frequency over a long period and because it is easier to evaluate than a specific fire cycle (Bergeron et al., 2004a). The inverse of the average age (or fire cycle) was used as an estimator of the annual historic burn rate. An average for all studies belonging to a specific ecozone is presented in Table 14.2.

Historical data show a clear distinction between western Canada, which is characterised by short fire cycles, and eastern Canada, where fire cycles are longer. Differences are mainly due to a drier climate in the west, which leads to shorter intervals between fires and thus more aspen and spruce and less fir. Fire frequency also tends to decrease as one moves towards alpine or taiga environments, probably because of a decrease in fuel availability (Payette et al., 1989). Current fire frequencies show a similar trend but values are significantly lower for all ecozones, suggesting a common change affecting the entire North American boreal forest. In Quebec, the decrease in fire frequency has been related to a reduction in the frequency of drought events since the end of the Little Ice Age (Bergeron and Archambault, 1993; Lauzon et al., 2007). It is hypothesized that the warming that started at the end of the Little Ice Age is associated with an important change in the circulation of global air masses that may have affected boreal forest fire regimes (Girardin et al., 2006). This decrease has been exacerbated in the last part of the twentieth century by an increase in effective fire suppression (Lefort et al., 2003).

Table 14.2 Current and historical fire frequencies (percentage of a region burning expressed per year for Canadian boreal ecozones). Its inverse (the fire cycle) is indicated in parentheses

ECOZONES	*HISTORICAL %/year (fire cycle, yrs)*	*CURRENT %/year, (fire cycle, yrs)*	*% Changes*
Montane cordillera	0.99 (101)	0.058 (1724)	–95
Boreal cordillera	Unknown	0.392 (255)	
Taiga cordillera	Unknown	0.202 (495)	
Taiga plain	Unknown	0.702 (142)	
Boreal plain	1.48 (68)	0.418 (239)	–71
Taiga shield west	0.85 (118)	0.763 (131)	–10
Boreal shield west	1.92 (52)	0.761 (131)	–60
Hudson plains	Unknown	0.123 (813)	
Boreal shield east	0.77 (131)	0.145 (690)	–81
Taiga shield east	0.6 (166)	0.241 (415)	–60

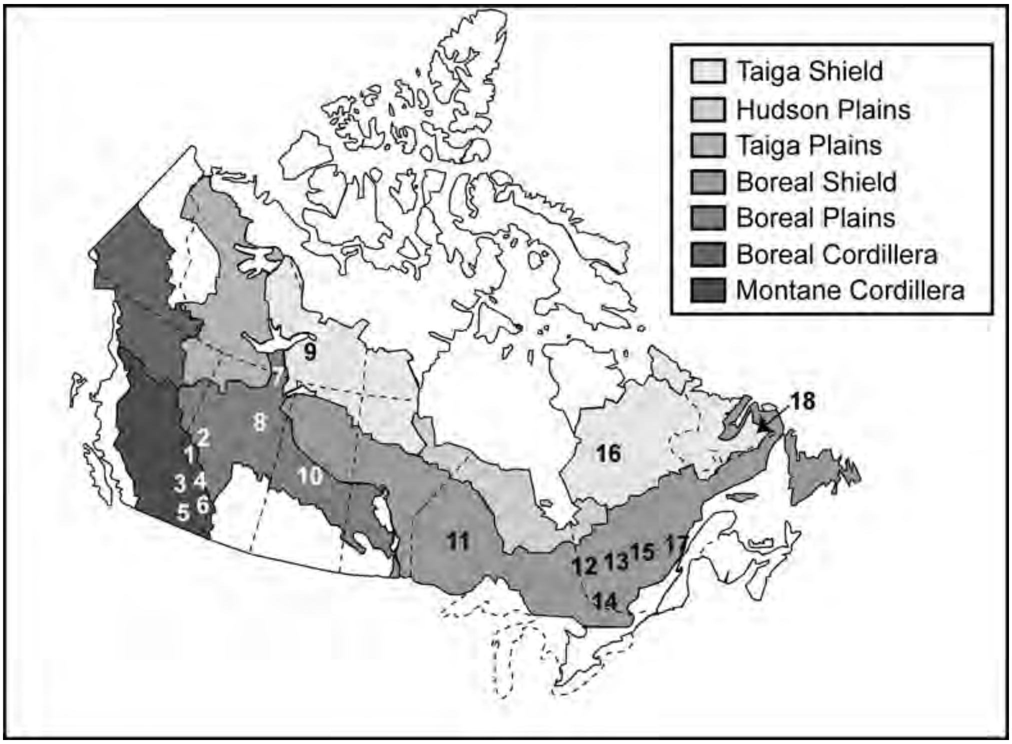

Figure 14.1 Location of the 18 study areas throughout ecozones of the Canadian boreal forests. Numbers refer to the following studies: 1. Tande (1979); 2. van Wagner (1978); 3. Johnson et al. (1990); 4. Johnson and Wowchuk (1993); 5. Masters (1990); 6. Johnson and Larsen (1991); 7. Larsen (1997); 8. Cumming (1997); 9. Johnson (1979); 10. Weir et al. (2000); 11. Suffling et al. (1982); 12. Lefort et al. (2003); 13. Bergeron et al. 2004b; 14. Cwynar (1977); 15. Bergeron et al (2001); 16. Payette et al. (1989); 17. Lesieur et al. (2002); 18. Foster (1983)

Eurasia: Dominance of surface fires

In general, in boreal Eurasia low- to medium-severity fires, such as surface fires, are the most common; although large-scale stand-replacing fires exist they are generally less prevalent (Wein and MacLean, 1983; Gromtsev, 2002; Lampainen et al., 2004, Shorohova et al., 2009). This applies especially to boreal Fennoscandia and western Russia but also to a large extent to Siberia and the Russian Far East (Sannikov and Goldammer, 1996; Gromtsev, 2002; Kondrashov, 2004. It has, for example, been reported that in European Russia 76–86% of fires are surface fires while crown fires account for 16–24% of the fires (Melekhov, 1947, cited in Gromtsev, 2002).

The general view that low-intensity surface fires are more common in Eurasia when compared to North America, where crown fires are common, has also been verified using infrared remotely sensed measurements (Moderate Resolution Imaging Spectroradiometer, MODIS) (Wooster and Zhang, 2004). The prevalence of low-intensity nonstand-replacing fires in boreal Eurasia is evidently related to climate, landscape characteristics, and the fire-resistant character of important tree species like pines (e.g., *Pinus sylvestris, P. sibirica*) and larches (e.g., *Larix gmelinii, L. sibirica*) (Helmisaari and Nikolov, 1989; Babintseva and Titova, 1996). Moreover, serotinity does not occur as a life-history strategy in Eurasian conifers, which suggests that nonlethal surface fire regimes have dominated in boreal Eurasia over evolutionary timescales.

Because boreal Eurasia covers a vast area, there are differences in fire regimes both at coarser geographic and finer spatial scales. In Siberia, large stand-replacing crown fires are relatively more common and associated with extended summer drought periods in the continental climate. In more humid areas with longer fire intervals, spruce (in Fennoscandia) and fir (in Russia east of the Ural Mountains) may dominate landscapes. However, since they have more fine fuel in the form of foliage they are more prone to stand-replacing fires during extreme drought periods than open pine or larch forests in which trees have less foliage and crowns are located high above the ground level (Ban et al., 1998; Engelmark, 1999).

In Fennoscandia and northwestern Russia (western Eurasia) natural fire regimes are variable also due to the diversity and heterogeneity of landscape conditions, which are characterised by mosaics of forests and peatlands and the semi-maritime climate (Gromtsev, 2002; Wallenius et al., 2005). Even the largest burnt areas are therefore generally relatively small due to climate and landscapes fragmented by natural fire breaks such as peat bogs and water bodies (Wallenius et al., 2004). However, fires larger than 100,000 ha have been documented before settlement in northern Sweden (Niklasson and Granström, 2000). In Siberia large fires are more common than in western Eurasia, where they can cover several hundred thousand hectares.

In Fennoscandia the fire frequency is generally higher in dry upland sites dominated by *Pinus sylvestris* than in moister lowland sites dominated by *Picea abies* (e.g., Zackrisson, 1977; Wallenius et al., 2004). There is also a general south-to-north gradient of decreasing fire frequency and area burned, due to increasing humidity and decreasing duration of the fire season (Granström, 1993; Sannikov and Goldammer, 1996; Larjavaara et al., 2004, 2005).

Recent studies indicate that natural fire return intervals in Fennoscandia are longer than hitherto assumed (Kuuluvainen, 2009; Wallenius, et al., 2010). For example, in eastern middle-boreal Fennoscandia, paleoecological studies show that before 1500 A.D., when human impact was low, upland dry *Pinus sylvestris*–dominated forests had a surface fire interval on the order of 150–250 years (Pitkänen, 1999, Pitkänen et al., 2002). However, on moister Norway spruce–dominated lowland landscapes the natural fire return interval was even longer, up to several hundred years and even over a thousand years (Pitkänen et al., 2003; Wallenius, 2002; Wallenius et al., 2005). Some sites having these environmental characteristics have not burned since the last glaciation over 10,000 years before (Pitkänen et al., 2003).

In Siberia, the climate becomes increasingly continental and natural fire return intervals in general decrease compared to western Russia (Sannikov and Goldammer, 1996). This is due to extended drought periods and the high number of lightning-ignited fires (Sannikov and Goldammer, 1996). In dry pine and larch forests the natural fire cycle (mostly surface fires) is on the order of 60–70 years, but it is longer (100–200 years) in forests characterised by *Abies sibirica* and *Picea obovata*: species that characterise the *dark taiga* as it is known in Russian terminology (Walter and Breckle, 1989). However, it has been suggested that some areas of the northern dark taiga experience fire cycles exceeding 400 years (Schulze et al., 2005). However in the Russian Far East, the climate again becomes more maritime and fire cycles become longer and resemble those found in Fennoscandia (Kondratshov, 2004).

During the past few hundred years fire regimes in many parts of boreal Eurasia have been strongly impacted by human activity that have increased ignitions (Sannikov and Goldammer, 1996; Niklasson and Granström, 2000; Wallenius et al., 2004), and this continues to be the case in European Russia and Siberia. In contrast, the impact of humans during recent decades in countries such as Sweden and Finland has been an exclusion of fires since suppression policies have been efficiently implemented. As a consequence a large number of fire-dependent species have declined or become threatened (Wikars, 2004).

In many parts of Eurasia the long-term human impact on fires makes it difficult to define natural fire regimes. For example, studies based on fire scars have shown that in middle-boreal Fennoscandia *Pinus sylvestris* forests commonly had a fire interval of 30–60 years during the nineteenth century (Pitkänen and Huttunen, 1999; Niklasson and Granström, 2000), at least three times shorter than the existing estimates for natural fire intervals (Pitkänen 1999, 2002). However, even during this period moist Norway spruce–dominated landscapes burned less frequently (Wallenius et al., 2005; Wallenius, 2002; Pitkänen et al., 2003).

14.2.2. Nonfire disturbances

In regions where fire cycles are long, nonfire gap disturbances (which are characteristic of old-growth forests) are important in controlling forest dynamics (Kuuluvainen, 1994; Kuuluvainen et al., 1998; Gromtsev, 2002; Kneeshaw and Gauthier, 2003). There is thus a general pattern of an increasing proportion of old forests as one moves from continental areas, such as central North America and central Siberia, to maritime areas, such as Alaska, Eastern Canada, and Fennoscandia. Such a pattern also occurs with latitude as shorter growing and shorter fire seasons in the north also lead to greater proportions of old-growth forest compared to south. Although old-growth forest landscapes may be fine-scale mosaics of different forest developmental stages, overall a greater continuous forest cover and fewer large openings are observed (Kuuluvainen et al., 1998; McCarthy and Weetman, 2006). It can be concluded that before significant human impact old-growth forests were a dominant feature of much of the boreal forest, especially in Eurasia where fire cycles are long and tree species longevity is greater than in North America (Table 14.1).

Although forests that experience small-scale disturbances and openings are ubiquitous, nonfire disturbances that lead to even-aged conditions in relatively large openings can exist due either to severe drought, insect outbreaks or large blowdowns (Syrjänen et al., 1994, Aakala et al., 2011). These events can be generalised to specific forest conditions, with some events such as spruce budworm outbreaks being associated with eastern North America and others, such as windthrow, having important local effects but not being as easy to associate with a geographic region (Figure 14.2).

Nonfire disturbances that open up large areas

The first type of disturbance we consider in this section is insect outbreaks. In the boreal coniferous forests of western Eurasia there are no records of large-scale outbreaks of defoliators, comparable to those caused by the spruce budworm (SBW) in North America. Needle-defoliating insects such as pine sawflies (*Diprion pini, Neodiprion sertifer*) can cause significant damage locally, but no large-scale forest outbreaks have been reported. However, in the Fennoscandian monodominant mountain birch (*Betula pubescens* subsp. *czerepanovii*) forests, the autumnal moth (*Epirrita autumnata*) has occasionally triggered large-scale dieback in forests forming the treeline. Also in Siberia large-scale defoliation and forest dieback can occur, especially in southern boreal *Larix* forests due to the Siberian moth (*Dendrolimus spp.*).

Occasionally, bark beetles (mainly *Ips typographus*) can, in association with large-scale tree mortality, for example due to storms or extreme drought events, develop population densities high enough to attack and kill healthy trees across large areas. For example, there was an outbreak in Sweden and Norway in the 1970s, following extensive tree blowdowns in winter storms, in which millions of spruce trees died. A similar event associated with extreme drought has been documented in the Archangelsk region, North-Western Russia (Aakala et al., 2011). Other insects are important disturbance agents, but at scales that lead to small openings and single tree mortality or growth losses. Insects may also simply predispose trees to other agents of mortality.

The situation is different in North America, where large-scale outbreaks of species such as the Eastern spruce budworm (*Choristoneura fumiferana*) and the hemlock looper (*Lambdina fiscellaria*) occur in eastern forests and outbreaks of species such as the mountain pine beetle (*Dendroctonus ponderosae)* occur primarily in forests found in the Rockies. An evaluation of the relative importance of different disturbance types in the Canadian boreal forest shows that the average area affected by such outbreaks greatly exceeded the area affected by fire (Kneeshaw, 2001). The impacts of such disturbances are, however, very different. Fires kill most of the standing trees immediately while disturbances such as insect outbreaks may take years to kill trees, and some trees always survive (Kneeshaw and Bergeron, 1999; MacLean, 1980).

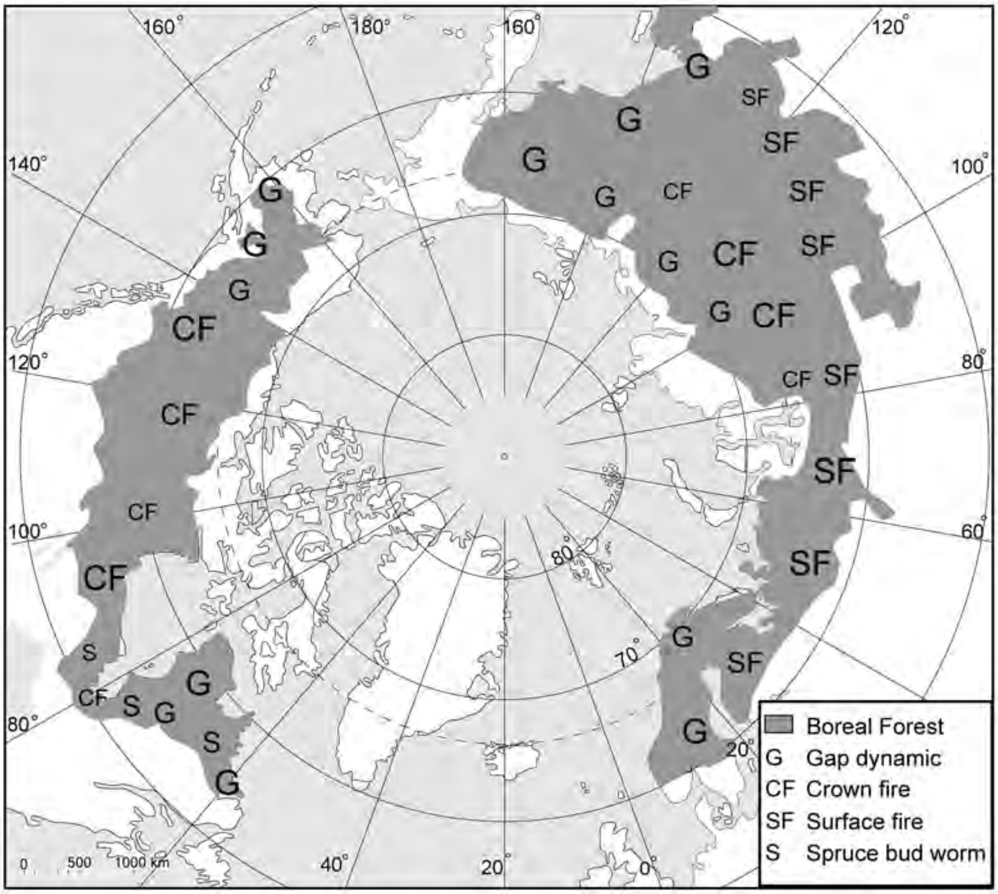

Figure 14.2 Illustration of the gradient of the main disturbances across the circumboreal forest. The main disturbances considered are surface fires, crown fires, and spruce budworm outbreaks

Furthermore, insects are often host-specific, attacking only one species or a small group of species. For example, the Eastern spruce budworm attacks only balsam fir and the spruces; thus outbreaks do not directly kill hardwood or cedar-dominated stands (Bouchard et al., 2005). At a landscape scale, mortality and thus age-class distributions are much patchier than those following fire.

Natural disturbances affect each other's probability of occurrence. For example there is a direct and obvious relationship between fire and insects such as the SBW so that in areas where fire is a frequent and dominant disturbance agent in the landscape, the primary host species (balsam fir) of the SBW is reduced since it is poorly adapted to fire. Temporally, outbreaks have been found to vary, perhaps in direct relationship to the fire cycle (Blais, 1983). For example, during the Little Ice Age, which finished around 1870 in the eastern North American boreal forest, the climate was generally colder and drier, leading to an increase and a greater occurrence of fires. SBW outbreaks were thus less important in continental areas with shorter fire cycles and more important in maritime regions of eastern Canada where a moister climate maintained an abundant supply of the host species, balsam fir.

As with fire, there is also a north-south gradient such that balsam fir decreases in abundance as one moves from Maine and New Brunswick into northeastern Quebec and Labrador. In these northern forested areas, the climate is less favourable to the development of the SBW and balsam fir, the primary host of the SBW, is a smaller component of the forest. Although species such as black spruce (a secondary host) are affected, the mortality caused by the SBW is much less than for fir. Even at a more regional scale, mortality caused by SBW outbreaks is also affected by stand composition in the surrounding landscape. Fir stands in mixedwood regions undergo a smaller degree of mortality than in landscapes that are primarily dominated by pure fir forests (Su et al., 1996; Bergeron et al., 1995).

Other insects have also had or continue to have an important impact on the boreal forest. In some cases they cause direct mortality as in the case of the hemlock looper but in other cases mortality is only minor and important effects are often reported only as volume losses (e.g., the jack pine budworm and the forest tent caterpillar). Each of these agents thus acts differently on the forest. A contrast can thus be made between insects that primarily cause volume loss (i.e., that slow tree growth) and those that cause mortality. Insects that do not cause mortality can accelerate successional processes if they cause foliage thinning in early successional stands. In such cases, late-successional shade tolerant species that are often slower growing may be able to more quickly attain the canopy. In the case of insects that cause tree mortality, compositional changes such as a shift to early or to late successional species may occur (Kneeshaw and Bergeron, 1998; Bouchard et al., 2006).

The second type of nonfire disturbance we consider is wind disturbance. A number of generalities about the effects of wind on boreal forest ecosystems are true on both continents. The effects of wind are most pronounced in species with long crowns (increasing the drag force of wind) and shallow root systems (e.g., balsam fir and Norway spruce) growing on shallow soils (such as shallow tills covering bedrock or on sites with a high water table). Topographic variables are also important as windthrow seems to occur morefrequently on strong slopes or when topography leads to wind-funnelling. Topographic factors, however, will have a smaller influence when winds have a downward component as in ‘derechos’ (widespread, long-lived windstorms associated with a band of rapidly moving showers or thunderstorms) and downbursts (Frelich, 2002). In western Eurasia most wind damage is caused by autumn and winter storm fronts, originating in the Atlantic Ocean These storms can cause large-scale damage in boreal Fennoscandia, but tree mortality tends to be partial and patchy. Large-scale stand-replacing wind storm damage has also been reported in the Ural Mountains (Syrjänen et al., 1994). In North America, strong wind damage occurs (or at least has been studied) in coastal regions in the east and west (i.e., nonboreal forest in British Columbia and Alaska). Boreal regions most affected by wind damage are found in coastal areas and where strong thunderstorms are frequent. Strong winds can also be expected where the polar jet stream and the subtropical jet stream meet in summer months (Frelich, 2002).

Based on available studies, the areas most affected by windthrow are around the Great Lakes in North America, in coastal areas of Fennoscandia and in the central part of Russia. Return intervals in the studied forests are quite long (1,000–2,000 years: Frelich and Lorimer, 1991; or 450 to 10,500 years for heavy windthrows: Schulte and Mladenoff, 2005). Schulze et al. (2005) suggest that return intervals of winds causing mortality can be on the order of about 150 years for parts of Russia’s dark taiga and Gromtsev (2002) suggests return intervals of 150–300 years. The size of windthrows is generally small, ranging from small gaps to openings of a few hectares. It has also been suggested that the size and severity of windstorms may be increasing due to climate change, although such an interpretation is tentative as we still do not have a good understanding of geographic wind disturbance patterns (Frelich, 2002).

Finally, we turn our attention to small-scale local level disturbances such as senescence, root rot, partial windthrow, and insect mortality. As well as causing relatively large openings, disturbances such as windthrow and insect outbreaks can also lead to partial mortality in a stand. In such circumstances, canopy gaps are small, corresponding to the growing space of single to multiple canopy trees. Some studies have suggested that insects and wind are responsible for a large proportion of the mortality observed in areas characterised by a continuous canopy interspersed with gaps (de Römer et al., 2007; Kneeshaw and Bergeron, 1998). However, such individual tree mortality often has multiple causes (Rouvinen et al., 2002; Reyes and Kneeshaw, 2008). For example, windthrown trees are often those close to their biological age and weakened by insects and wood-rotting fungi (Kuuluvainen, 1994; McCarthy, 2001).

Relatively little work has been conducted on the extent of mortality caused by fungi in the North American boreal forest. However, we suggest that in areas where neither fire nor insect outbreaks are important (e.g., Labrador, Canada) wind and fungal attacks would be important agents of disturbance (Lewis and Lindgren, 2000). Boreal trees are primarily affected by *Armillaria* spp. (primarily *Armillaria ostoyae*) (Mallett, 1992) and then secondarily by *Inonotus tomentosus* (Whitney, 2000). These two fungi cause both growth loss and tree mortality. Tree mortality is often caused in combination with other agents such as winds, which topple trees that have been structurally weakened by such fungi at the base of the tree or in their root system (Lännenpää et al., 2008). Death is usually greater in older trees (*I. tomentosus* generally kills trees greater than 50 years in age). There are also other decay fungi, primarily root and butt heartwood decayers, but these require damaged or dead roots with exposed heartwood to cause infection. However, since these fungi also cause structural failure they are important in increasing predisposition of trees to windthrow damage (Garry Warren, Canadian Forest Service, personal communication, 2005).

In Eurasia, common surface fires interact in a complex manner with disturbance factors such as bark beetles (e.g., *Ips typographus* and *Tomicus piniperda*) and wood-rotting fungi (e.g., *Phellinus pini, P. chrysoloma, Coniophora* spp.) (Rouvinen et al., 2002; Lännenpää et al., 2008) in contributing to gap formation. These agents kill individual trees or patches of trees, weakened by old age, surface fire, or wood-rotting fungi, so that gaps are formed due to wind or snow loads (Kuuluvainen, 1994). Occasionally after large-scale windthrow, bark beetles reproduce massively and attack and kill healthy trees at large scales.

Gap dynamics are best characterised by relatively small openings (Pham et al., 2004; Bergeron and Kneeshaw, 1998; Kuuluvainen, 1994) but often by a relatively high fraction of the forest being open. For example, many studies have found that the majority of gaps are smaller than 100 m^2 but that 40–50% or more of the forest is open (McCarthy, 2001; de Römer et al., 2007). Causes are often described as being due to senescence, which suggests that such mortality is most important in old stands (although see Hill et al., 2005) that have not been disturbed by major disturbances for periods exceeding the average life span of the dominant trees (Kneeshaw and Gauthier, 2003). These areas are found in northern sites, and in maritime areas which are little affected by fire or insect outbreaks. Nonetheless, large-scale blowdown may be important on some sites though it is usually a local phenomenon. Although Schulze et al. (2005) suggest that forests avoiding any type of disturbance are rare or do not exist they also state that many species in boreal forests are adapted to disturbance-free periods.

It is important to consider that nonfire disturbances play a major role in shaping large parts of the boreal forest. Stand-replacing disturbances, although important in some regions of the boreal forest, especially in North America, are not the only factor driving the dynamics of boreal forests. Many forests are naturally old and punctuated by smaller partial disturbances, creating complex heterogeneity in stand structures (Rouvinen et al., 2002; McCarthy and Weetman, 2006).

14.2.4 Effects of disturbance regimes on ecological communities

Where crown-fire cycles are short the effects of other disturbances will be minor and the boreal landscape will be controlled by the recurrence of large fire events. Under such cycles entire stands of trees are killed before trees attain their longevity (Dix and Swan, 1971) and the North American boreal landscape is often thought of as large patches of trees recovering from burns. The long-term cumulative effect of short fire cycles has been to limit not only successional processes but also the presence of trees with late successional characteristics such as shade tolerance and recruitment from seedling banks (Kenkel et al., 1997). Such species in fact dominate in regions of the boreal forest where fire cycles are long. It has, however, been argued that many dominant boreal trees have what can be considered pioneer characteristics, with frequent fires favouring species that are able to regenerate from aerial seed banks (stored in serotinous cones), root or basal sprouting, long-distance dispersal of small seeds and from underground seed banks (e.g., pin cherry or ephemeral herbs). In areas where surface fires are common, thick fire-resistant bark and a high branching habit (since low branches act as fuel ladders conducting fire to the crown) are important characteristics. Many of the pine species (e.g., *Pinus sylvstris, P. strobus, P. resinosa*) as well as the larches (e.g., *Larix gmelinii*) have such characteristics. In both continents many boreal tree species (e.g., *Picea* spp, *Populus* spp. *Salix* spp. and *Betula* spp.) that regenerate from seeds require a mineral seed bed for successful establishment (Greene et al., 1999). Such a mineral seed bed is often found in severely burnt areas where both surface fires and crown fires consume accumulated organic litter (Johnson, 1992).

Rowe (1983) used Noble and Slatyer's (1977, 1980) vital attributes theory to demonstrate the effectiveness of many regeneration strategies for boreal forest tree species in relation to recurrent disturbances such as fire. In this model, the important elements used for predicting forest composition are determined from the vital attributes of individual species. These tree attributes are longevity, age at reproduction, and method of reproduction. Trees will thus disappear from an area if they are not able to regenerate given the current conditions or when a local population is eliminated before it attains a reproduction age. Thus trees dependent on wind-dispersed seed must have an unburnt seed source in close proximity if they are to regenerate. Galipeau et al. (1997) have also demonstrated that colonisation of shade-tolerant balsam fir and white spruce can occur over time as individuals regenerate in an ever-expanding concentric wave from the initial seed source. In other terms once individuals that have established surrounding a fire-preserved zone have attained an age at which they can begin producing seeds, recruitment will occur at an ever-increasing distance from the original source (Galipeau et al., 1997). In large burns, with few remnant islands of surviving trees, colonisation by such species can require excessively long time periods and may not occur before the next fire event. This may thus be one of the important factors ensuring the mono-specific nature of many boreal stands (Carleton and Maycock, 1978).

Species that are able to regenerate in situ following canopy fire (i.e., from seeds conserved in serotinous cones or from sprouting) are thus able to maintain themselves following a crown fire. Species such as jack pine would only be predicted to disappear from a site if recurrent fires occurred before the jack pine became sexually mature (i.e., there was no seed source) or if fire intervals were so long that all individuals died out without having the opportunity to release seed onto a favourable substrate (Rowe, 1983). In Eurasia, crown fires may change a landscape from one with trees resistant to surface fires to those adapted to long-distance dispersal, such as birch and aspen. More shade-tolerant species, such as Norway spruce, which may also have established shortly after fire will wait in the understorey for the overstorey to die off. Thus compositional change may be linked more to species growth rates and longevity than to recruitment-mediated replacement processes (Bergeron, 2000; Schulze et al., 2005). Aspen or birch when regenerated in abundance, often dominate stands for up to 100 years following fire (Aakala and Keto-Tokoi, 2011), but gradually these stands take on a mixed character during the following century before being dominated by conifers after approximately 200 years. Many authors have thus linked compositional dynamics primarily to time since fire (Bergeron, 2000; Kneeshaw and Bergeron, 1998). In monospecific black spruce forests it is stand structure rather than composition that changes with time since fire (Harper et al., 2005; Boucher et al., 2006).

Following windthrow or insect outbreaks, tree species composition may not shift as it does after fires. Thus instead of a return to dominance by intolerant species, it is often the shade-tolerant species that have formed a seedling bank thatare recruited. *Abies balsamea* and *A. sibirica* have both been shown to follow cyclical patterns, with preestablished seedlings replacing canopy dominants following windthrows or insect outbreaks (MacLean, 1980; Schulze et al., 2005).

A great body of evidence demonstrates that fire is the agent that greatly controls the dynamics of boreal forests when crown-fire cycles are shorter than the life span of the dominant tree species. In the case of surface fires, compositional change has also been noted when fires are excluded for long periods (Frelich, 2002). Communities that are dependent on surface fires often require relatively short intervals between fires. In cases where fire intervals are increasing, later successional species often invade (Lilja and Kuuluvainen, 2006). The maintenance of branches along the stem facilitates fire access to the canopy and the destruction of the seed source of former canopy dominants in forest stands in North America and Siberia. Changes in disturbance regimes can thus have large effects on tree species composition (Romme et al., 1998).

In moister maritime and semi-maritime climates fire intervals are often quite long and shade-tolerant species like balsam fir, Norway spruce, or Siberian fir dominate. These species often have larger seeds and form dense seedling banks that are well adapted to respond to overstorey canopy disturbances (Baskerville, 1975; MacLean, 1980). There is also research showing that these species have greater moisture requirements when establishing conditions that are often found in shaded understorey environments as well as in more humid maritime climates (Kneeshaw and Bergeron, 1999).

14.3 DISCUSSION

The boreal forest is often thought of as a relatively homogeneous biome due to the dominance of a few plant and animal species over large areas. For example, tree species such as black spruce in North America and Scots pine in Eurasia have continent-wide distribution ranges and are almost synonymous with the public image of the boreal forest. Furthermore, many of the tree species form large, intact blocks of forest with similar structure and composition. Animals such as woodland caribou, lynx, and snowshoe hare have continentwide distributions while some lichens and mosses have circumboreal ranges. However, there is substantial regional variation, which, at a biogeographical scale, shows up as patterns in species dominance related to variations in dominant disturbance regimes and climatic patterns. These differences are important for ecosystem processes, levels of biological diversity and the degree to which a region's ecological integrity is at risk due to often similar and repetitive (across the landscape) types of resource management.

More than 90% of forest management in the boreal forest is based on clear-cutting and even-aged forest management. Justification for this approach has often been linked to the perception that large-scale disturbances such as fire dominate boreal forests and that relatively young even-aged stands are the rule rather than the exception. However, as seen throughout this chapter, disturbance regimes vary between and across continents (Figure 14.2) and this in turn is reflected as variations in forest structure and composition. Variations in the dominant types of disturbance and the intervals between disturbances have important consequences on structure and the species compositions of forests. Short return interval fires are relatively dominant only in the central parts of the continents where drier climates occur. These are thus the regions with fewer late successional shade-tolerant species.

In North America, crown fires have a dominant influence on the forest from Quebec through to eastern British Columbia and southeastern Alaska. However, the intervals between fires become longer as continental climate conditions are replaced by more maritime conditions. However, even in more maritime regions of the boreal zone (i.e., closer to the coasts), dry conditions, which are positively related to fire occurrence, still occur and lead to large burns, although these are infrequent. This in turn leads to large tracts of forest that are of similar composition, age, and structure. In maritime and northern regions with long fire cycles this is translated as old forest with a complex vertical and horizontal structure. Such a complex structure is not maintained when foresters favour only short-rotation (80–100 years), even-aged management.

In Eurasia, the greater prevalence of surface fires often leads to multi-cohort stands. Such fires lead to a pulse in postfire recruitment and thus to a stand structure that is dominated by large fire-resistant trees with a mix of multiple age cohorts recruited following different fire events. It may thus be expected that in such stands relatively continuous cover was the rule rather than the exception (Pennanen, 2002) and that clear-cut techniques, which favour a single cohort, change the natural forest structure. Much of the natural forest was dominated by old-growth conditions with mixed ages and structures in both continents but especially in Eurasia (Shorohova et al., 2009; Kuuluvainen, 2009).

As previously noted, there is also an important north-south variation in disturbances in the boreal forest. In both North America and Eurasia the natural interval between fires is shorter in the south than in the north, meaning again that there should be a greater proportion of older stands in the north. In North America, spruce budworm outbreaks also create more mortality and larger openings in the southern part of the boreal forest than in the northern part. The reduced influence of these disturbances is in part explained by climate. The shorter snow-free period limits fire and the shorter growing season limits SBW growth and expansion. Lower productivity in these northern regions also means that fuel or food sources may not always be continuous. Although forest management rotations may thus be somewhat longer to account for the lower productivity and longer period of time taken to grow, they do not approximate the multiple centuries that stands may develop in the absence of large-scale disturbance in natural conditions.

Many boreal tree species are thus generalists with adaptations to fire and nonfire disturbances. Black spruce is perhaps the best example, as it is adapted to fire, nonfire disturbances, and old-growth forest conditions through a combination of cones that are serotinous, cones that are not, and through vegetative layering. *Populus* species are able to maintain themselves in disturbed areas through vegetative sprouting and clonal growth but also by dispersing long distances to colonise favourable seedbeds. Other species such as Dahurian larch have also been shown to be able to regenerate in both old-growth conditions and following fire (Ban et al., 1998). Recent work also shows that shade-intolerant species that were once considered fire obligate are able to recruit second or third cohorts (Cumming et al., 2000; Bergeron, 2000). Even characteristics such as cone serotiny have been shown to decrease under long fire cycles in favour of open cones (Gauthier et al., 1996).

Under natural conditions a large proportion of the boreal forest would have been considered old-growth (Pennanen, 2002; Kneeshaw and Gauthier, 2003). Thus, small-scale disturbances such as gap dynamics are important in much of the boreal forest (Vepakomma et al., 2010). This should be most apparent in maritime and humid northern regions. For example, Labrador in northeastern North America has been reported to have a fire cycle of greater than 500 years (Foster, 1985). However, even in regions where fire cycles are generally short a proportion of old-growth stands can be expected to occur as not all areas burn with equal frequency and because surface fires may only have minor effects on stand structure.

It has been proposed that differences between past and current fire frequencies could be used to determine the proportion of clear-cutting that could be used to emulate the distribution of a proportion of stands originating from stand-replacing fires in the landscape (Bergeron et al., 2006). However, the exclusive use of clear-cut systems (or variants, e.g., variable retention or harvesting that protects advance regeneration) cannot be justified by historical fire frequencies. In most cases, the reported historical fire frequencies are less than the current harvest rotation; or in other terms a large proportion of the preindustrial landscape was composed of forests older than the typical 80- to 100-year commercial forest rotation (Kuuluvainen, 2009). Already, compositional changes due to harvesting are being observed (Carleton and MacLellan, 1994). Alternative silvicultural systems that include extended rotations or a variety of silvicultural treatments have been proposed to maintain a proportion and characteristics of overmature and old-growth forests in the managed landscape (Bergeron et al., 1999; Burton et al., 1999). We may also need to revise the line of thinking that focuses only on optimising timber supply through forest regulation, since this may, under many scenarios, put us into direct conflict with biodiversity objectives and lead to problems should fire cycles become shorter in the future (Bergeron et al., 2004a).

14.4 SUMMARY

The boreal forest is not as homogeneous as once thought. Considerable variation in disturbance regimes due in part to climatic influences can be found throughout Eurasia and North America. Continental regions in central Eurasia and North America have shorter fire intervals than in more maritime regions. Similarly fires, and spruce budworm in North America, are naturally more important in the southern part of the boreal forest than in the northern part. Such variation has led to a greater dominance of pyrogeneous, shade-intolerant species in the interior of each continent and the dominance of more shade-tolerant species nearer to the coasts. Important differences also exist between continents, due in part to species characteristics but also to climate and disturbance regimes. In North America large-scale disturbances include both the spruce budworm in eastern forests and crown fire whereas in Eurasia surface fires are more prevalent than crown fires. Old-growth forests are thus a dominant feature of many natural boreal forests, a condition that has been and is being rapidly modified by human intervention.

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