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Ecological Considerations for the Sustainable Management of the North American Boreal Forests

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Foreword

The Sustainable Boreal Forest Resources Project at IIASA has the objectives:

- To generate quantitative input to a sustainable development concept for the boreal forest zone and specifically for Russia drawing on the work carried out earlier at IIASA. To achieve this objective, targeted analyses of existing forestry information available at the Institute and elsewhere with respect to forest utilization, and environmental and socieconomic importance will be used, and

- To use the quantitative information generated in an efficient policy mode. The information must be presented in an integrated and consistent format and directly integrated into the policy process regionally and internationally.

This report describes the features of the North American boreal forests and gives recommendations on how sustainability of these forests can be achieved. The report has been produced by Drs. J.C. Zasada (team leader, USA), A.G. Gordon (Canada), C.W. Slaughter (USA), and L.C. Duchesne (Canada).

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1. INTRODUCTION

The boreal forest is the largest forest region in North America, spanning 20 ° latitude, 110 ° longitude and covering 5.12 million km^2 (Botkin and Simpson 1990, Kuusela 1992). The renewable and nonrenewable resources within this region far outweigh the resources from other forest regions of North America, particularly because of the boreal forest's relative lack of human influence. Indeed, their presence and development are intertwined with all aspects of life in the region–economic, recreation, ecological and spiritual. Historically, the boreal region was considered remote and the resources inexhaustible. However, with increasing population and human demand for goods and services, advances in technology for resource extraction, improved transportation and communication, heightened concerns about the global environment, and decreases in availability of resources on a global scale, it has become obvious that boreal forests are a finite resource requiring proper stewardship.

The boreal forest means different things to different groups of people. Residents derive jobs, building materials, food, energy, spiritual well-being and recreation from the forests, lakes and rivers of the region. To others, the boreal forest is a remote uninhabitable region, rich in lumber and other building materials, pulp and paper, minerals, hydropower, oil and gas, water, food, and other natural resources needed to maintain their quality of life. For residents and visitors alike, the vast forests, free-flowing rivers, fish and wildlife populations and the vast open spaces provide unsurpassed opportunities for life and recreational experiences that are not available elsewhere in United States and Canada.

The needs of residents and non-residents who utilize boreal forest resources in consumptive and nonconsumptive ways determine the types of land use and rates of resource development and extraction. There are both common interests and significant differences among these user groups in the way they view the forest resource and its management. Owing to increased demands by the various interest groups, future management strategies must integrate social values of various user groups that are often incompatible. In practice, forest management must integrate demands on forests together with conservation needs in order to achieve sustainability and satisfy all present and future forest users.

Management of boreal ecosystems is an evolutionary process driven by people's perceptions, socioeconomic factors, politics, and biological and ecological realities. Because of the size and remoteness of the boreal forest, there was relatively little concern about the ecological impact of the extraction of renewable and nonrenewable resources from the boreal forest prior to the 1970's. However, we are entering a new stage in the way boreal forests are viewed locally and globally. Citizens at large and scientists alike now demand clear answers about concepts virtually unheard of within the last two decades: biodiversity and particularly genetic diversity, sustainable development, ecosystem management, forest health, global change–and whether or not short-term economic goals are compatible with these concepts which are by their nature difficult to apply in the short-term.

Sustainability in the boreal forest is a compromise as is the management of all natural resources upon which humans depend. There is an idealistic vision for "perfect" management of forest lands and associated resources, that must be tempered by the reality of compromise to accommodate actual local needs and conditions, national and international supply/demand conditions, and institutional and societal constraints and demands from local to global scales. Concern about sustainable forest ecosystems represents a highly idealized view of management and will only become a reality if adequate information is available and if social and economic conditions favor these practices–or with strict regulation and enforcement of practices to assure that sustainability is achieved and maintained. For a large part of the boreal forest, management is evolving from an era of exploitation where extraction of trees for lumber and paper was the primary concern to an era where there is a major effort to assure regeneration and an increasing interest in assuring the protection of other ecosystem values such as wildlife, aesthetics, recreation, and special forest products (Kimmins 1991).

The boreal forest is finite; its productivity is restricted within the bounds set by the physical environment and the ability of biota to survive and grow within that environment. Silvicultural activities can enhance productivity within the limits of biological constraints and economic realities. Understanding the biotic and abiotic characteristics of the present forest and its dynamics under current environmental conditions is necessary for determining the potential for biological productivity and resource management. The information is also critical for predicting future paradigms that will result from the evolution of environmental, socioeconomic, and political conditions.

The objective of our paper is two-fold. First we provide an overview of the physical and biological factors that determine the potential for sustainable development. Second, we describe some effects that humans have had on the resource and the implications of this use to sustainability of the resources. Although we provide a fairly broad overview of the boreal forest, this review does not cover all aspects of the boreal forest ecology. For other summaries of various aspects of the ecology of the North American boreal forest see Larsen 1980, 1982), Oechel and Lawrence (1985), Elliott-Fisk (1988), Society of American Foresters (1994), Packee (1995), Weber and Van Cleve (in press), Zasada and Packee (1995), Apps et al. (1995), Juday (1996), Pojar (1996), and Silva Fennica (1996), Heinselman (1996).

2. THE REGION

In this paper we will consider the boreal forest (*Figures 1 and 2*; Rowe 1972, Hare and Ritchie 1972, Botkin and Simpson 1990) and those portions of eastern Canada, the northern Great Lakes States and New England that have substantial areas dominated by species occurring across the boreal forest [e.g., trees such as aspen (*Populus tremuloides*), birch (*Betula papyrifera*), white spruce (*Picea glauca*)and black spruce (*P. mariana*) and associated biota], and a generally similar climate (Merz 1978, Burns and Honkala 1990). Environmental factors, e.g., growing season temperature, growing degree days, potential evapotranspiration, annual precipitation and seasonal distribution of precipitation, vegetative composition, used to define the limits of the boreal forest are discussed by Rowe (1972), Hare and Ritchie (1972), Botkin and Simpson (1990), and Hogg (1994).

There are over 500 million ha of boreal forest in North America (Botkin and Simpson 1990, Kuusela 1992). The physical environment varies substantially over this large area and has been described elsewhere (Hare and Ritchie 1972, Larsen 1980,1982, Hartman and Johnson 1984, Oechel and Lawrence 1985, Zoltai et al. 1988a,b, Van Cleve et al 1986, Canadian Journal Forest Research. 1983 and 1993, Bonan and Shugart 1989, Zasada and Packee 1994, Hogg 1994). From north to south, maximum day length during the growing season varies from about 24 to 15 hours and maximum sun angle varies from 45 to 67 degrees. At higher latitudes, shallow sun angle provides markedly longer periods of twilight than at lower latitudes. Precipitation ranges from 1400 mm in the relatively maritime areas of Newfoundland to 300 mm in areas characterized by continental climate; 50 percent or more of annual precipitation commonly occurs during the growing season.

Although all climatic attributes combined serve to distinguish boreal forests from more temperate areas, the temperature control over above- and below-ground biological processes and the characteristics of the snowpack are particularly important in differentiating boreal from temperate regions (Canadian Journal Forest Research 1983, 1993, Bonan and Shugart 1989). Long, cold winters are a characteristic feature of most boreal ecosystems. The minimum temperatures in areas with a well-developed continental climate commonly drop below -50 ^{o}C. Annual temperature range can exceed 80 ^{o}C as summer temperatures commonly peak at 30 to 35 ^{o}C. Cold soils and permafrost in some locations profoundly affect all aspects of soil biology and nutrient cycling (Canadian Journal of Forest Research 1983, 1993, Van Cleve et al. 1986). Forest floor conditions, overstory and understory density, and soil temperature conditions are closely related (Viereck 1973, 1989, Van Cleve et al. 1986, Dyrness et al 1988). Low air temperatures, i.e., a loimited amount of heat available for growth during the growing season, and frost events greatly influence phenology and development of vegetative and reproductive growth. Low rates of evaporation and periodic conditions of high water table and partly saturated soil conditions result in common occurrence of gleysolic soils and accumulation of organic matter and development of organic soils.

Snow covers the landscape for at least 6 to 7 months of the year and is an important component of the environment. Snow modifies local climate through its high albedo and low thermal conductivity. Insulating properties of a snow cover allow plants, small mammals, insects, and other organisms to survive on the forest floor beneath the snow despite extremely low air temperatures. Temperature modification by the snowpack has been described (Slaughter and Long 1974, Viereck and Lev 1983, Marchand 1991). Periods of unusually deep snow can severely limit the movement and distribution of large mammals such as moose and are often a significant factor in determining short-term population fluctuations. In western Alaska, snowpack distribution and density are important in determining availability of winter forage for domestic reindeer; the same applies to native caribou herds in Alaska and northern Canada (Brooks and Collins 1984, Pruitt 1981).

The physical characteristics of snow, coupled with the long duration of low temperatures in northern winters allow use of the snow in forest operations in ways not possible in more temperate areas. Snow reworking and compaction can significantly increase snow density. It is possible to construct snow roads and bridges (Johnson 1979, Johnson and Collins 1980) which can support heavy logging equipment including loaded logging trucks. Temporary snow-constructed transportation routes can be utilized during winter months to cross wetland and streams which to reach sites inaccessible (save for conventional road construction that may be economically and environmentally unfeasible) during the summer. A snow cover also provides physical protection for the understory and forest floor during forest management and harvesting operations, reducing direst impacts on vegetation and soils (Zasada et al. 1987). However disturbance and compaction of the snow during harvesting can cause drastic changes in the subnivian environment during the period of activity.

3. The Land and Water Base

The boreal forests are a mosaic of upland forests and wetlands with lakes and rivers interspersed. On some small-scale maps, “wetlands” and “boreal forest” are virtually synonymous (e.g., Zoltai 1988a). In Canada alone, there are 60 million ha of boreal wetland in Quebec, Ontario, Saskatchewan, Manitoba, Alberta, British Columbia Yukon and Northwest Territories and an additional 5 to 6 million ha in the boreal region of the Maritime provinces. Although wetlands occupy about 20% of the land area in the boreal region, they can dominate the landscape over large areas where physiographic conditions permit it (Zoltai et al. 1988a, Wells and Hirvonen 1988). Additionally, Zoltai et al. (1988b) indicate that about 30% (20 million ha) of the subarctic, a transition between the boreal forest and tundra, is wetland. In Alaska wetlands occupy about 44% of the boreal landscape or about 60 million ha; in some low-lying physiographic provinces 60 to 75% of the landscape is wetland (Hall et al. 1994).

The rivers and lakes of the boreal are an extremely important landscape element in terms of biodiversity and represent a major attraction for various forms of tourism. The dynamics of rivers are closely related to forest development and wood and litter inputs from the forest (Maser and Sedell 1994). The only remaining large free-flowing rivers in North America occur within the boreal forest. The Tanana, Kuskokwim, Yukon, Susitna, and Copper Rivers of Alaska and the MacKenzie, Peace, Nelson, Churchhill and La Grande rivers, to name but a few, in Canada are all several hundred to more than a thousand km long. Lakes of various sizes and cover approximately 12 % of the land surface (Lowe et al. 1994) and include some of the largest lakes in North America excluding the Great Lakes (For example Great Slave Lake, Great Bear Lake, Lake Arthabaska, and Lake Winnipeg). Lake Superior, the second largest body of fresh water on the planet, strongly influenced by boreal conditions.

4. SOILS AND PERMAFROST

In both the Canadian and United States systems of soil classification, boreal forest soils are usually described as “cold” or “frigid” relative to soils in bordering forest regions to the south (Soil Conservation Service 1975, National Cooperative Soil Survey 1979). Features commonly referred to in a discussion of boreal forest soils are low temperatures (with the formation of permafrost as the maximum expression of this characteristic), poor drainage, thick organic layers with deep organic soils in wetlands, low soil biological activity, and low nutrient availability. As a result of these features, productivity relative to the potential that a site has based on climate, soil physical properties, and potential vegetation, is often limited on some sites. This is particularly true as forests age and a relatively large proportion of site nutrients are held in undecomposed forest floor materials (Canadian Journal of Forest Research 1983, 1993, Ochel and Lawrence 1985, Van Cleve et al. 1986, Bonan and Shugart 1989).

There is no question that low soil temperatures, poor drainage and other limitations reduce productivity to varying degrees. However, disturbance, forest composition, and management practices significantly affect soil properties and can be manipulated to improve productivity within the limits imposed by ambient air temperature and solar radiation. Some of the most dramatic examples of soil warming are the result of clearing of forest land and conversion to agriculture. In one instance near Fairbanks, Alaska (an area of discontinuous permafrost), permafrost is at about 7 m below the surface in agricultural fields cleared 40 to 50 years earlier, while in the adjacent black spruce forest with a deep forest floor layer permafrost is near the surface and the active layer (zone of seasonal thawing) is shallow, typically 40-60 cm. Abandoned agricultural fields which prior to clearing supported slow-growing black spruce now commonly support relatively vigorous stands of aspen and paper birch, species that would not normally grow on these sites. Although changes due to natural disturbances are typically not as dramatic as those from the alterations resulting from agricultural clearing, Viereck and Lev (1983), for example, have shown significant increase in the depth of the active layer on burned black spruce sites. Dyrness et al. (1988) have shown significant changes in soil temperature following forest harvesting in interior Alaska.

Alteration of the forest floor has been shown to affect soil conditions throughout the boreal forest. Managing forest composition by promoting mixed stands of hardwoods and conifers is believed to maintain and improve soil properties compared to those in pure conifer stands.

In the following we will briefly discuss permafrost and development of organic soils. These are important aspects of boreal soils and ecology and illustrate some of the stand and landscape variability that has been described in the boreal forest soils.

Lower net solar radiation and lower mean annual air and soil temperature at higher latitudes and elevations can result in increasing persistence of frozen soil conditions. Under sufficiently cold conditions, the mean annual soil temperature may drop below 0 ^{o}C and soils remain frozen. Permafrost is earth material–mineral soil, organic material, parent material, bedrock, ice–which is perennially frozen. It is found in increasing amounts in more northerly, more continental, colder sectors of the boreal forest. Terrain that is underlain by permafrost still exhibits seasonal thawing and freezing at the surface; the “active layer”, or zone of seasonal thaw, may be as little as 20 to 30 cm in colder settings, or up to several meters in warmer discontinuous-permafrost landscapes. Most plant rooting and soil biological activity occurs in the “active layer” of permafrost terrain.

The terms “continuous permafrost” and “discontinuous permafrost” refer to spatial distribution of frozen ground. In the continuous permafrost region, the entire landscape (except in the vicinity of geothermal energy sources and beneath major bodies of water) is underlain by perennially frozen ground. This is the condition of much of northeastern

Russia, the Canadian High Arctic, and the Arctic Coastal Plain of Alaska. In the discontinuous permafrost region, perennially frozen ground is found in colder settings–topographically shaded areas, north-aspect slopes, higher elevations, and poorly drained wetlands–while warmer locations such as south facing slopes are free of permafrost (*Figure 3*). The distribution of northern boreal forests generally coincides with the occurrence of discontinuous permafrost in central Alaska and Canada. In central and eastern Russia, large sectors of boreal forest occur on continuous permafrost landscapes; however, forests typically do not grow in the continuous permafrost settings of North America, except in the northernmost part of the Mackenzie River drainage (Northwest Territory). In Canada east of Hudson Bay, "sporadic discontinuous" permafrost underlies much of the boreal forest of Quebec and Newfoundland, with "widespread discontinuous permafrost" extending northward to Ungava Bay (Prowse 1990).

The proportion of the landscape that is underlain by permafrost, and the significance of permafrost to understanding and managing resources, increases with latitude, with continentality of the climate, with increasing northern aspect, and with greater soil moisture. There may be marked differences in climate of landscapes at the same northern latitude. Such differences are largely related to continentality of the climate and proximity to warm oceans. For example, the boreal forests of Finland at 65 °N lat. are free from permafrost, while the boreal forests of central Alaska, Yukon, and Northwest Territory at similar latitude lie in the discontinuous permafrost zone of northwestern North America, protected from the maritime influence of the Pacific Ocean by the Coast Range.

There is a close relationship between the occurrence of permafrost, depth of the active layer, and forest floor and overstory conditions. Floodplain sites in central Alaska provide a well-documented example of permafrost development as forest floor depth increases and solar radiation decreases due to increasing dominance of white spruce (*Figure 4*). On these sites, permafrost develops in isolated areas and eventually occupies the entire soil mass. Burning of the forest floor and spruce overstory on floodplain sites and on upland sites dominated by permafrost results in an increase in depth of the active layer and warming of the surface soil. Removal of forest overstory and the organic forest floor, as occurs in fire line construction with bulldozers or clearing for agricultural development, results in decreased albedo and surface insulation and rapid thawing of the permafrost and either disappearance from the site or establishment of permafrost at a much deeper soil depth. Fire line construction has caused soil instability and severe erosion; this can be prevented by replacing forest floor layers on the fire line after the fire has been controlled.

Peat accumulation is important in productivity in wetlands and varies among regions, wetland types and geographically within a region. In subarctic wetlands, Zoltai et al. (1988b) reported accumulation rates ranging from 0.29 (Cladina forest peat) to 8.32 cm/100 years (sphagnum riparian peat). In boreal wetlands, estimates ranged from 2.8 to 10.6 cm/100 years. Although rate of peat accumulation is only a crude measure of biomass production in wetlands it provides a general idea of the dynamics of the surface of this often dominating component of the landscapes. *Figure 5* provides an idealized illustration of bog development in the boreal region.

5. FOREST COMPOSITION AND DISTRIBUTION

To appreciate the boreal forest one has to understand the variability that exists at multiple scales within this vast region and the general relationship to bordering regions. La Roi (1967), Rowe (1972), Viereck and Little (1972), Oechel and Lawrence (1985), Elliott-Fisk (1988), Meidinger and Pojar (1991), Viereck et al. (1992), Zasada and Packee (1994), McNab and Avers (1994) and Hogg (1994) provide information on regional scale considerations (*Figures 1 and 2*).

Although the boreal forest is often viewed as one large cold-dominated area occupying the northern part of the continent, this simplistic view is far from reality. Rowe (1972) identifies 45 sections of the Canadian boreal forest based on climate, physiography, and tree species composition. Wiken et al. (1993) subdivided this same area into 7 ecoregions based on “vegetation, soil, water and fauna”. McNab and Avers (1994) identify 4 to 5 broad ecoregions in boreal forests of Alaska. Zasada and Packee (1994) suggest 5 major regional divisions for the Alaska northern forest based on climate, landform, and vegetation.

More detailed descriptions are found in classification work available in provincial and state publications (e.g., Yukon-Oswald and Senyk 1977; British Columbia–Meidinger and Pojar 1991; Alaska–Viereck et al. 1994; Alberta–Corns and Annas 1986; Ontario–Jones et al. 1983, Sims et al. 1989; Newfoundland–Meades and Moores 1994). In British Columbia, for example, there are four zones–boreal white and black spruce, sub-boreal spruce, sub-boreal pine-spruce, and spruce-willow-birch–with exclusively boreal or predominantly boreal characteristics. Within each zone there are 3 to 10 subzones delineated by temperature, and moisture conditions and within these subzones site associations incorporating vegetative composition are delineated.

At the scale of the stand (> 1 ha) there can be large stand-to-stand variation in species composition and structure. This has been well-documented in interior Alaska where changes in aspect result in major changes in forest composition; this is particularly true between permafrost-dominated areas and adjacent permafrost-free areas (Canadian Journal Forest Research 1983, 1993).

The southern boreal forest region has a common boundary with very different forest regions as one proceeds from east to west *(Figure 2).* The bordering forest regions vary from those with a strictly maritime influence in Nova Scotia and Newfoundland, to the northern hardwood-pine forests of the Great Lakes-St. Lawrence region, to the aspen parkland forest of the prairie provinces, to the montane forests of British Columbia and Yukon (Rowe 1972, Meidinger and Pojar 1991, Hogg 1994, Pojar 1995). The transitional zone in each area has distinct climatic features; in some areas temperature is a major growth-limiting factor while in others moisture tends to be growth-limiting (Hare and Ritchie 1972, Oechel and Lawrence 1985, Hogg 1994, Hogg and Hurdle 1995). In Alaska, the northern forest is divided by the Alaska Range with a maritime-influenced area to the south and an area dominated by continental climate north of the mountains and south of the Brooks Range (Viereck and Little 1972, Viereck et al. 1994, Zasada and Packee 1994). To the west and Southwest, Alaska's forest grades into alpine and moist tundra (Viereck and Little 1972, Viereck et al. 1994).

The northern transition (*Figure 1*) is probably not as complex as the southern because temperature is an overriding factor determining forest distribution (Oechel and Lawrence 1985). However vegetation patterns may be fairly complex even though species numbers are limited (Hansson 1992, Timoney et al. 1993). However, there is substantial variation in the transition from closed forest to tundra due to physiographic features such as mountains in the west and the Hudson Bay in the east. In the east, the transition tends to be relatively gradual because elevational change is not a major factor influencing climate, thus leading to a prevalent latitudinal effect. In Alaska closed forests follow some rivers northward to their headwaters in the Brooks Range and the transition to tundra often occurs over a distance of a few km or less. By contrast, the northward flowing MacKenzie River provides a corridor allowing trees to reach the highest latitudes in the boreal forest (Larsen 1980, Elliott-Fisk 1988). Generally speaking, boreal forests tend to occur further north or higher in elevation along rivers that extend into the tundra.

The northern forests have relatively few tree species. Paper birch, aspen, balsam poplar (*P. balsamifera*), white spruce, black spruce, and tamarack (*Larix laricina*) have a transcontinental distribution while the distribution of lodgepole pine (*Pinus contorta*) and subalpine fir (*Abies lasiocarpa*) is limited to the western boreal and jack pine (*P. banksiana*)and balsam fir (*A. balsamea*) to the central and eastern boreal (Elliott-Fisk 1988, Burns and Honkala 1992, Weber and Van Cleve in press, Gordon 1995, Packee 1995). Hybridization and introgression are relatively well-documented for the boreal forest. Some notable examples are hybrids of balsam poplar and black cottonwood, white and Sitka spruce, and white and Engelmann spruce (Gordon 1995). An interesting aspect of tree distribution is that lodgepole pine and subalpine fir occur in the Yukon, but neither occurs in neighboring Alaska boreal forest under similar climate conditions (Oswald and Senyk 1977, Viereck and Little 1972). Although distribution of species such as paper birch and tamarack is essentially transcontinental, there are some interesting gaps in their distribution that are unexplained. There are a number of species including e.g., white (*P. strobus*) and red pine (*P. resinosa*), red maple (*A. rubra*), black ash (*Fraxinus nigra*, red spruce (*P. rubens*), and northern white cedar (*Thuja occidentalis*) that have a limited range at the southern edge of the boreal region but play an important role in the transition zone, often offering unique old-growth stands as old as 500 to 900 years (Archambault and Bergeron 1992a, b).

The distribution of species within the landscape varies within the boreal region. The broadleaved species tend to occur on more nutrient rich, warmer, and better-drained sites along with white spruce and firs (*Abies*). The pines occur on drier sites often in mixture with white spruce or black spruce. Black spruce and tamarack are found on poorly drained and permafrost underlain soils throughout the boreal forest (Eyre 1980, Canadian Journal Forest Research 1983, 1993, Hills 1976).

Species composition, species diversity, and productivity of shrubs and herbaceous plants also vary within the region (LaRoi 1967). The number of genera present is lowest in the northernmost part of the boreal forest at all longitudes. The number of genera are also lower on the most productive sites in Alaska relative to similar sites farther south (La Roi 1967, Viereck and Little 1972, Viereck et al. 1994). Shrubs and herbs are extremely important colonizers following disturbance by fire, logging, flooding, and insect damage and can limit or exclude tree regeneration (Lieffers et al. 1993, Haeussler et al. 1990, Bell 1991, Lieffers 1995). Large areas of boreal forest may be dominated by shrubs both in sites where shrubs are transitional to tree-dominated systems [e.g., early stages of floodplain succession (*Figure 4*)] and sites where shrubs dominate indefinitely such as wetlands and open woodland areas north of the closed forest zone. Some of the common shrub genera are *Salix***,** *Betula*, *Alnus*, *Ledum*, *Vaccinium*, and *Empetrum* (Viereck and Little 1972, Larsen 1980,1982, Elliott-Fisk 1988, Zoltai et al. 1988a, 1988b, Meidinger and Pojar 1991, Viereck et al. 1992). Shrubs vary in growth form from low-growing dwarf shrubs to some of the willows and alders that have the stature of small trees when mature. These areas and species are key elements for wildlife habitat, providing both food and cover. Shrubs are also important because of the production of edible berries with high nutritional value.

Nonvascular plants such as mosses and liverworts are ecologically important boreal plants and often contribute more to plant species diversity in a stand than do vascular plants. La Roi and Stringer (1976) suggest that bryophytes should be an important component of ecosystem classification in the boreal forest. As components of the forest floor, they take on added significance because of their effect on soil temperatures, soil biological processes, nutrient availability, wetland development and carbon and nutrient cycling (LaRoi and Stringer 1976, Larsen 1982, Foote 1983, Viereck 1970, Oechel and Lawrence 1985, Van Cleve et al 1986, Elliott-Fisk 1988, Zoltai 1988a, 1988b). On black spruce sites of low productivity, annual moss production may exceed that of overstory trees (Oechel and Lawrence 1985, Van Cleve et al. 1986)

6. DYNAMICS

Forest ecosystems under natural controls are well-regulated functional systems that evolve toward stability and persistence. Stability may be loosely defined as the integrity of composition and productivity. In the boreal forest, many communities appear to operate in a form of cyclic stability. The boreal mixedwood is a very common association of vast dimensions. It's distribution is controlled by physiographic site and climate and it's dynamics by disturbance over time.

For example, the boreal mixedwood is comprised of white spruce in any combination with either or both trembling aspen or paper birch depending on site and/or disturbance history, and with balsam depending on the geographic region (Hills 1954, Rowe 1972, La Roi 1967, Viereck et al. 1992). In forests at lower latitudes, these species are successional to longer-lived and more tolerant species. However in the boreal, these species represent both early and late arboreal stages and essentially succeed themselves. There are no species to precede or follow them.

All species in these mixtures are not at the same stage of maturity at any given time because the longevities of each species are not the same. Regeneration and developmental dynamics may be initiated at the same or different times. These four species differ in shade tolerance and grow at different rates depending the stage of forest development relative to the others.

Trembling aspen and paper birch are relatively fast-growing, shade intolerant, and usually form even-aged forests. White spruce is partially shade tolerant and long-lived. Balsam fir is shade tolerant and short-lived. Both conifers can occur in pure even-aged stands (if free to grow) or develop in multiple cohort/species stands in which they grow in the moderate shade of the broadleaved species or in some cases themselves. Aspen and birch rarely are successful as understory species.

Soil sites of the boreal mixedwood (glacial till, lacustrine basins or plains, loess, and in the case of the related association, white spruce-balsam poplar, alluvial floodplains) tend to be moderate to rich in nutrient availability which in turn leads to a greater number of vascular plants, particularly shrubs and herbs. The rapid growth of these species in early stand development makes it difficult for black spruce and pine to become established. However these two species do occur within the mixedwood in site provinces of lower humidity where competition is reduced.

In contrast to the mixedwood species, black spruce, jack or lodgepole pine (depending on geographic area) and tamarack have different reproductive and growth strategies (Burns and Honkala 1992). They are generally less nutrient demanding and vary in shade tolerance with the pines and tamarack intolerant and black spruce moderately tolerant. The combination of their tolerance and growth rate makes it unlikely that they will succeed boreal mixedwood species. The exception is the replacement of white spruce by black spruce because of site change through time, i.e., paludification in which white spruce may no longer sustain growth, but less-demanding black spruce can (Viereck 1970, 1989).

The pines, black spruce, and tamarack commonly occur in pure stands on sites (shallow till over bedrock, outwash sands and gravels, or wetlands) which are relatively nutrient poor and low in water availability compared to mixedwood sites, but where these species can maximize their productivity. They may also occur in mixtures with one another along a soil moisture catena from wet to fresh. For example, tamarack and black spruce on wet to moist sites and black spruce with jack pine on moist to fresh sites.

Species life strategies based on long-developed tolerances such as shade tolerance mentioned above or, for example, tolerance for excess water (black spruce and tamarack), or the lack of water (jack pine), excess lime (white spruce) or the lack of it (red spruce), extreme cold temperatures (white spruce and black spruce) or the lack of it (red spruce and eastern hemlock) as well as other biotic and abiotic variation are genetically embedded through long-term selection during their evolution. Despite recent arguments for chaotic distribution and association that relay strongly on randomness of species response to perturbations such as fire, insect, disease, windthrow, flooding and other disturbances, speciation and composition appear to have remained fairly stable by site type for several thousand years.

Many species in the southern boreal forest have fairly broad ranges, but often grow only on particular sites in any abundance (for example black ash and white cedar). Other species are opportunistic generalists that grow on many sites (aspen and fir). Nevertheless, even superb generalists such as white spruce, whose range spans the continent, and can grow on wet to dry sites, moderate to rich, and from cool-humid to dry-cool climatic regimes, and with any of five common mixedwood species, cannot grow on acidic wet sites (common in throughout its range) where black spruce is common. Similarly, black spruce for all of its ability to tolerate wet sites cannot grow on alkaline wet sites where white spruce does relatively well.

There are other limitations. Again using white spruce as an example, it grows with shade-intolerant hardwoods surviving well under their shade and ultimately dominating the site because of greater longevity. However in the tolerant hardwoods of the adjacent and transitional “north temperate” forests, white spruce occurs as an emergent but is unable to regenerate well in these forests and often drops out of the species mix unless a severe disturbance occurs.

The paradigm goes further. A black spruce bog will not become a jack pin site as long as the bog exists. A dry outwash sand will not develop into a black spruce or tamarack stand regardless of perturbation. When a disturbance occurs, succession is set-back. The species replacement however is far from random. On any given physiographic site and in a given humidity and temperature regime, succession occurs in a predictable way.

Disturbance caused by harvesting may be different. Harvesting alone or in concert with other disturbances can take an ecosystem or population beyond its ability to recover in the normal sequence. Short of global catastrophes in geologic time, harvesting can remove a gene pool, reduce a species to the level of commercial extinction, or at least cause extensive losses of local, well-adapted populations. It is imperative that we use harvesting methods that have as a high priority the protection of gene pools and maintenance of species composition and productivity.

In the boreal forest, one species may replace another at given and reasonably predictable points in time. A local fire may destroy spruce but not harm poplar roots (Zasada et al. 1992, Viereck 1973). It may also enhance the establishment of aspen seedlings that ultimately form clones (Barnes 1966). Aspen forms the next stand through suckering and spruce may become established quickly or over a long time period (Youngblood 1993). The pattern of recovery is closely related to physiographic site type, apart from geology the most stable entity in northern terrestrial ecosystems and strongly related to local and regional climate (Hills 1954, 1959, Van Cleve et al. 1983). Sites of given physiographic types may support different successional pathways, an under different disturbance regimes temporarily lack some species. But they will ultimately contain the suite of species that will survive best and maximize productivity under those conditions. The maintenance of stability and species persistence in the boreal forest is not chaotic as some may interpret the mosaic pattern that is so common. Within the landscape patterns, stands are continually changing, but endlessly the same.

7. BIODIVERSITY IN THE BOREAL FORESTS

Biological diversity may be defined as the number, variety, and variability of living organisms on the earth (World Commission on the Environment and Development 1992), including the sum of diversities found at the genetic, species, ecosystem, and landscape levels (Wilson 1988). There are two major problems associated with determining the contribution of the North American boreal forest to biodiversity and species diversity. First, because biodiversity includes scales ranging from the cellular level to ecosystems making it difficult to measure its many components with certainty. Second, current species diversity estimates are confounded by the potential number of unknown species, a problem typical to organisms where the taxonomic effort is incomplete and is likely to remain so for the foreseeable future.

Although no census is available of the total number of all taxa in the boreal forest, recent estimates were made for Canada as a whole (Mosquin and Whiting 1992). To derive figures for the boreal forest we have determined that 40% of all Canadian mammals are found in the boreal forest. Therefore we have inferred the same ratio for abundance of other terrestrial organisms, with the exception of birds, reptiles, freshwater fishes, and amphibians present (*Table 1*). Additional information on biodiversity in Alaska and Canada has been summarized by Bunnell (1990) and Hansson (1992).

We estimate that the boreal forest contains over 100,000 species, 95% of which are arthropods and microorganisms. Interestingly, it is estimated that only 22 percent of the taxa contained in the boreal forest have been identified taxonomically. Viruses are particularly abundant with over 40,000 species because of the assumption that each higher species is infected by a unique viral species (Mosquin and Whiting 1992).

The large tracts of relatively undeveloped forests make the boreal forests unique in North America with regard to some aspects of biodiversity. For example, viable populations of forest carnivores (marten, fisher, lynx, and wolverine), which once had a broader North American range, now only occur to a major extent in Alaskan and Canadian boreal forests (Douglas and Strickland 1987, Strickland and Douglas 1987, Thompson 1991, Ruggerio et al. 1994) because of habitat fragmentation and destruction. Woodland caribou are also affected by effects of harvesting on their habitat (Stevenson 1990, Cummings and Beange 1993).

8. FOREST DEVELOPMENT

The boreal landscape is often described as a mosaic with the relatively few tree species arranged in pure and mixed stands of various sizes and shapes owing to site and soil conditions, distribution of lakes and rivers, species characteristics, and disturbance history (Lutz 1956, Oechel and Lawrence 1985, Elliott-Fisk 1988, Hansson 1992, Suffling 1993). Within any landscape, there are both long- and short-term processes that shape current vegetation and influence potential future vegetation (Larsen 1980, 1982 Elliott-Fisk 1988, Zoltai et al. 1988ab, Hollings 1992, Packee 1995). This paper emphasizes the relatively short-time frame factors acting at the scale of years to several centuries. Long-term events that occur at the time scale of centuries to millennia, to which the shorter time scale events are linked (Hollings 1992), include among other phenomena glaciation and deglaciation, climate change, the evolution of the many different wetland types occurring in different parts of the boreal forest, and floodplain dynamics. These processes can affect the distribution of upland and wetland forests, depth to water table and nutrient availability, all factors basic to determining plant species distribution and primary productivity in the landscape. An excellent description of long-term wetland dynamics for the Canadian boreal forest has been presented by Zoltai et al (1988a,b) and Wells and Hirvonen (1988) and an example is shown in *Figure 5*.

The primary short-term disturbance factors that influence landscape scale patterns in the boreal forest are fire and herbivory (particularly insects). Wind (Flannigan et al. 1989), snow breakage and diseases (Castello et al. 1995) can also be important but these tend to follow disturbances caused by the two factors mentioned above. Additionally, mammals such as beaver affect large areas by dam building and flooding (Naiman et al. 1994) and moose, hares and other species affect species composition and stand development through selective browsing (Bryant and Kuropat 1980). In other words, fire and insect epidemics are major ways in which succession is altered or reset over large areas; wind, snow, disease, and browsing affect successional pathways and rates of development differentially within this broader context of disturbance.

Fire is a ubiquitous feature of the boreal forest and although small fires (< 10 ha) are most common, wildfires often affect areas greater than 100,000 ha even with aggressive fire management policies (Lutz 1956, Viereck and Schandelmeier 1980, Van Wagner 1988, Hirsch 1991, Johnson 1992, Duchesne et al. 1995). Although virtually the entire boreal region is affected by fire, the fire return interval varies from 500 or more years to 50 or less; the longer intervals are characteristic of areas with a maritime-influenced climate and the shorter intervals are favored in areas with a well-developed continental climate (Duchesne et al. 1995, Viereck and Schandelmeier 1980). Fires in the boreal forests are best described as stand-replacing fires; however, fire intensity within a single, large burn can range from extreme to unburned, depending on the interaction between ambient weather, fire behavior, local site conditions, and vegetation type and pattern. It is important to note that adjacent stands within a landscape may have different fire return intervals because of forest type, topography, and prevailing winds. The microscale pattern (Friedman 1981, Zasada et al. 1983, Dyrness and Norum 1983, Van Cleve et al. 1986, Duchesne 1994) of forest floor created by fire, often apparent at scales of less than one square meter, is highly variable and is a significant factor in postburn vascular and nonvascular plant and microbial successions.

The spruce budworm (*Choristoneura fumiferana*) and spruce bark beetle (*Dendroctonus rufipenis*) have affected large areas and are important in determining landscape pattern and dynamics of the boreal forest (Miller 1975, Baskerville 1975, Hardy 1986, Holsten 1990, Packee 1995). We single these species out here because they often kill a major percentage of the trees attacked, while some other insects, such as the large aspen tortrix, spear-marked black moth, and forest tent caterpillar, affect large areas of aspen and birch but do not usually cause large-scale mortality.

The budworm has been most important in the eastern boreal forest where population fluctuations are well-documented. From 1954 through 1980 there was some defoliation every year with the maximum area affected in one year of almost 70 million ha (Hardy 1986). Spruce budworm was first reported in the Alaska boreal in the 1980’s and has been at outbreak levels since 1990 (R. Werner, Institute of Northern Forestry, Fairbanks Alaska. pers. com.). Currently, there are severe ongoing epidemics of bark beetle in Alaska’s northern forests and in parts of the Yukon. Since the 1920’s, approximately 720,000 ha have been affected by the bark beetle in south central Alaska and 70,000 ha in interior Alaska. There are other insects that also cause large scale defoliation–for example the aspen tortrix, spear-marked black moth, forest tent caterpillar, and larch sawfly–that have a significant effect on tree growth, stand development and species distribution, but a discussion of their impact is beyond the scope of this paper.

Forest succession patterns and factors affecting post-fire succession have been described for a number of ecosystem types across the boreal forest (e.g., Lutz 1956, Rowe 1961, Dix and Swan 1971, Rowe and Scotter 1973, Carleton and Maycock 1978, 1981, Viereck and Dyrness 1979, Larsen 1980, Viereck and Schandelmeier 1980, Van Cleve and Viereck 1981, Foote 1983, Van Cleve et al 1986, Youngblood 1993, Grigal and Ohmann 1975, Bergeron and Dubuc 1989, Duchesne et al. 1995, Zoltai et al. 1988a,b, Heinselman 1996). The following briefly summarizes some of the main points from these studies with regard to compositional and structural change of plant species. For consideration of the changes in the physical environment that drive vegetation change or are associated with changes in the plant community refer to the above-mentioned publications.

- Most boreal plant species have regeneration characteristics that provide the potential for rapid recovery even after severe fires. Tolerance to full sunlight and the ability to reproduce vegetatively give broadleaved trees and shrubs, and herbs an advantage over conifers in potential for rapid recolonization. With the exception of lodgepole and jack pine and black spruce, each having some degree of cone serotiny, colonization by other conifers can be limited by seed availability (Zasada 1986, Burns and Honkala 1990, Haeussler et al 1990, Bell 1991, Zasada et al. 1992). In treeline forests maintained by layering, fire can eliminate trees for long periods because seed years at these sites are infrequent and even in years of abundant cone production, cold weather may prevent seed maturation (Elliott-Fisk 1988, Zasada et al. 1992).

- The soil organic layers are an important factor in plant succession. They play a dominant role in the type of vegetative regeneration and the effectiveness of the seed bank and recently dispersed seeds in colonization. Depending on site conditions, organic surfaces may be a deterrent to immediate post-fire seed regeneration (upland sites) or may provide optimal seedbeds (lowland/wetland sites with organic materials derived from sphagnum mosses) (Canadian Journal of Forest Research 1983, Van Cleve et al. 1986, Burns and Honkala 1990, Jeglum and Kennington 1993, Herr and Duschesne 1995).

- The sequence of colonization by longer-lived conifers is variable and dependent on seed availability and site conditions. Youngblood (1992), for example, has documented simultaneous colonization of white spruce and paper birch on sites dominated by paper birch but a 20- to 30-year delay in white spruce colonization on aspen-dominated sites. Bergeron and Dubuc (1989) concluded that most pre-fire species in the southern boreal forest of eastern Canada were again present within 50 years of the fire, but that cedar and balsam fir continue to increase in post-fire frequency up to at least 200+ years. Late successional species, often called climax species, require the ability to germinate and establish on organic substrates such as various litter types and rotted wood. Serotinous-coned species with a canopy seed bank usually regenerate immediately unless extremely hot crown fires destroy cones.

- There is some argument regarding which of the generalized models proposed to describe succession [see review by Oliver and Larson (1990)] is most appropriate for the boreal forest. These models are variously referred to as relay floristics, initial floristics, facilitation, tolerance and inhibition. The initial floristics model describes much of what occurs in boreal succession when vascular plants are considered. However, there are certainly instances where succession at both the stand and landscape scales has features of all the other proposed models. There is a strong indication from the work of Viereck (1970), La Roi and Stringer (1976), and Foote (1983), for example, that the facilitation model is an important concept when considering the colonization of liverworts, mosses, and lichens–major components of diversity in boreal forests. These studies indicate that the trees and other vascular plants create the microclimatic conditions necessary for nonvascular plants and provide substrates for colonization.

- The development of boreal stands in the absence of fire is not as well-documented as are the first 50 to 100 years of post-fire development. The concept of a uniform climax vegetation across either the western or eastern boreal forest is completely erroneous because of the varying site conditions in the landscape and the widespread occurrence of wildfire in presettlement times (see for example Rowe 1961a, Larsen 1980, 1982). The following examples provide some idea of the variation that has been reported for older stands. Bergeron and Dubuc (1989) found fairly stable communities on drier sites in the southern boreal but continuing invasion of tolerant late-successional species on mesic sites. Rowe (1961) suggested that white spruce stands escaping fire for long periods in northern Alberta become open with a shrub-dominated understory and little sign of spruce recruitment. In interior Alaska, Foote (1983) indicated that little is known regarding the fate of white spruce forests protected from fire beyond the "normal" return interval. She suggested that the stands become more open and alder a more conspicuous component and in the absence of fire, black spruce might eventually occupy these sites. Throughout the boreal forest, black spruce present on lowland and wetland sites with relatively low productivity may come closest to a self-perpetuating forest type as it layers readily under these site conditions. That black spruce maintains itself for long periods by layering under some site conditions has been well-documented (Elliott-Fisk 1988, Burns and Honkala 1990). In terms of a steady-state condition, a variation of the shifting mosaic pattern described by Bormann and Likens (1979) might have applicability in the boreal forest, but at a larger scale than they suggest for the eastern North American northern hardwood forests (Heinselman 1996).

- Herbivores, such as moose and snowshoe hare, can significantly affect stand development and composition through selective browsing of the most desirable species. Boreal plants appear to have a well-developed chemical defense to reduce

> the impact of browsing (Bryant and Kuropat 1980). Additionally, they are well-adapted morphologically to recover from moderate levels of browsing.

Fire effects on wildlife components are not as well-documented as fire effects on plant succession. Fire affects wildlife in two general ways: modifies habitat and in extreme cases kills individuals. There is a consensus that birds and mammals evade fire and that deaths caused by direct fire are minimal for these species (Bendell 1974). Habitat losses caused by fire, particularly the more intense fires, cause greater losses for birds and mammals. Most other groups of organisms, particularly soil organisms, may be adversely affected by fire (Ahlgren 1974, Bendell 1974). Recovery time depends on fire intensity, depth of burn, size of burn, and microscale variations in post-burn ecosystems. Species, such as moose and snowshoe hares, are particularly well-adapted to utilize the habitat created by fire (Haggstrom and Kelleyhouse 1995).

The effects of fire on the more prominent animal species has been discussed by Hunter (1990) and Ruggerio et al. (1994), among others. Several examples of changes in insect composition illustrate some aspects of the dynamics of less well-known fauna after fire. Duchesne (1994) reported that the species composition of carabid beetles was different among burned and unburned sites in a study conducted in Ontario. Others have found similar trends in jack pine stands in Manitoba (Richardson and Holliday 1982, Holliday 1991). Werner (1997) concluded, regarding the effects of fire on wood borers and bark beetles associated with white spruce forests in the eastern interior of Alaska: “Fire removes the majority of host trees inhabited by cerambycid and scolytid beetles but provides excellent habitat for buprestid species the first year after burning. The effects of fire are long-lasting and few wood borer or scolytid species are found inhabiting burned areas 5-10 years after the initial disturbance because burned spruce ecosystems usually convert to hardwood species. The effects of fire, however, are beneficial in providing habitat for populations of cerambycids and scolytids in the fringe areas surrounding the severely burned areas. Partially burned trunks and roots of spruce are intensively infested with these beetles during the first year after burning and continue to maintain high populations up to 15 years after burning, but not scolytids and cerambycids.”

The spruce budworm and spruce bark beetle affect forests by killing overstory trees but leaving some trees alive. Although each outbreak has different effects on the trees, the following examples provide some idea of their impact. Budworm outbreaks in eastern Canadian forests affect all size classes of white spruce and balsam fir in mixed stands, but generally kill and severely damage more of the fir in all size classes. In a study in Ontario, Gordon (1985) reported that about one-third of the overstory fir were killed and another one-third sustained 90-100 % defoliation, while only about 20 % of the spruce were similarly affected. Although fir maintained dominance in this stand, the reduction in fir density allowed spruce to remain on these sites where it might otherwise be eliminated under a dense fir overstory. In Alaska, white spruce is the only significant conifer in productive forests and the impact of budworm will be different than in the eastern boreal forest. In white spruce forests of southcentral Alaska, spruce beetles killed about 50 % of trees during a 16-year period. Mortality was concentrated in the larger diameter classes, so that 90 % of the commercially valuable trees were killed (Holsten et al. 1995).

There are few similarities between post-fire and post-insect forest development. Several differences are mentioned below to illustrate why rates of development and successional pathways usually differ between these disturbances. The timing of death of the overstory is more prolonged in areas affected by insects. With most fires, death occurs within a matter of minutes or at most several months, while an insect outbreak kills trees over a period of years. The slower process can have advantages and disadvantages. Advantages are that regeneration can become established during the period of decline if seed is available. What often occurs, though, is rapid clonal expansion of understory species which, in turn, may retard tree regeneration by physically preventing seed from reaching the soil, crushing seedlings or through competition for resources. This is particularly limiting when aggressive colonizers like *Calamagrostis* sp. are present in the stand before disturbance (Holsten et al. 1995). Seedbed conditions are altered through shading by standing trees but mineral soil exposure may not occur until trees are uprooted because of decomposing root systems. If seedlings and trees in the intermediate and suppressed size classes and seedlings are present in insect-affected areas they may occupy the site relatively quickly.

Pathogens have an important influence on forest development and we do not have the space to provide even a brief summary of their role in forest succession. They obviously affect seed production, foliage quantity and quality, root systems, stem condition and general overall forest health in both positive and negative ways. Pathogens interact with other factors to create the mosaic of vegetation pattern and must be considered as an important part of the economics and ecology of boreal forests.

A final example of a disturbance with lasting effects on forest development is breakage related to snowfall events that depart significantly from the norm. These events may be the result of combined snow and ice storms (Van Cleve and Zasada 1970) or much greater than normal snowfall (Sampson and Wurtz 1994). On a highly productive upland site in the eastern interior zone of Alaska, relatively severe snow breakage events occurred in 1969 and 1992-93 in a stand that was 180-years-old in 1969. The first event resulted in breakage of about 25 % of the trees in the stand and the second produced an additional 18 % breakage (Van Cleve and Zasada 1970, Sampson and Wurtz 1994); stand density was reduced from 845 to 480 trees/ha by these two events.

Floodplain and riparian forests occupy a relatively small percentage of the boreal landscape, but are extremely important because of their higher productivity relative to the majority of adjacent upland forest. At higher latitudes, forests on active river floodplains are the only forests that produce trees large enough for products such as house logs and lumber and are thus very important to local inhabitants. In addition, floodplain and riparian forests link upland and aquatic systems and are critical to wildlife habitat and water quality considerations. The northmost conifer forests in North America are associated with riparian areas in the Mackenzie River watershed and the rivers draining the north slope of the Brooks Range in northern Alaska (Viereck and Little 1972, Pearce et al. 1988).

Forest development on floodplains (primary succession) has received considerable research, particularly in the western boreal forest (Viereck 1970, 1989, Nanson and Beach 1977, Juday and Zasada 1984, Van Cleve et al 1986, Walker et al. 1986, Pearce et al. 1988, Dyrness et al. 1988, Krasny et al. 1988, Canadian Journal Forest Research 1993). *Figure 4* illustrates the generalized developmental stages of the primary successional sequence showing changes in soil properties as well as tree and shrub composition. The transition from the white spruce stage to the black spruce dominated stage is of particular note because the white spruce on these sites attains greater age (300 to 400 years) than the same species occurring on upland sites. The time required for this process is not well-documented, but the following occurs during the transition: i) white spruce stands deteriorate and a multi-aged white spruce stand may develop; ii) replacement by black spruce is gradual with a mixed stand of the species present for an extended period of time; and iii) forest floor depth increases and soil temperature decreases and, in the discontinuous permafrost zone, permafrost gradually develops. Secondary succession on these sites, particularly in the older spruce forests, occurs following fire, insect-related mortality, and snow breakage.

Succession in wetlands follows the general patterns as in uplands following fire, but the formation of wetlands is unique (Larsen 1982, Zoltai et al. 1988a,b). The natural evolution of wetlands is toward the establishment of treed bogs (Zoltai et al. 1988a). Although wetlands of various types are initiated in depressions, the type of wetland formed depends on the source of the water (precipitation only or a combination of rain, snowmelt and ground water), quantity and mineral content of water, slope of the terrain, size of the depression, and drainage characteristics of the depression (*Figure 5*). Peat accumulates in these depressions at varying rates and succession may span thousands of years depending on the site. Although the general tendency is toward a treed bog, local environmental factors may arrest development before this condition is attained. In bog formation, water quantity and quality, soil (organic), surface form, flora and fauna are the main constituents determining development and a change in any of them can change the developmental pattern. Fire is important in affecting vegetation pattern and composition but only in extreme cases affects peat depth (Zoltai et al. 1988a,b, Wells and Hirvonen 1988).

To summarize, disturbances caused by fire and herbivory (large-scale insect epidemics) can kill or severely damage forests over large areas and occur to varying degrees throughout the boreal forest. Other disturbances (for example, wind and snow breakage, browsing, and diseases) tend to affect smaller areas within the larger landscape affected by fire and insects. Disturbances all have different return intervals or frequencies of occurrence. They may interact to create unique situations on a site-by-site basis. For example, Schulz (1995) described the changes in standing and down, dead trees caused by bark beetles; these dead materials could affect the probability of fire occurrence and fire intensity. In beetle-killed stands, flammable understory vegetation, particularly grass, develops rapidly. Similarly, breakage from snow and wind increases dead tree biomass and may make the residual trees more susceptible to insect attack. The significance of these interactions on upland, wetland and floodplain sites is that they ultimately affect successional pathways and rates of development. Thus, both individually and collectively, they are important in determining the mosaic pattern so characteristic of boreal landscapes and important to structure and function in these ecosystems.

9. FOREST PRODUCTIVITY

There are many elements to consider when estimating ecosystem productivity in the boreal forest. Although primary productivity is generally lower than more temperate North American forests, there are many tangible and intangible products and values that humans derive from the North American boreal forests. All of these values should be accounted for when evaluating productivity in order to place it in the broadest context possible. The most easily quantified aspect of productivity is trees and associated plant standing crop–long- and short- productivity of trees has been a major concern of forester managers and ecologists. Within limits, it is possible to predict the rate of growth of trees and associated vegetation and how growth rate is affected by natural disturbance and human activities. It is more difficult to assess the productivity of primary and secondary consumers in the boreal forest. Populations of consumers, regardless of size, depend on the distribution, structure, and composition of primary productivity at all scales of resolution and not simply the standing crop and annual growth rate of primary producers. Other tangible values of these ecosystems, such as water for human use and maintenance of aquatic ecosystems, are closely linked to terrestrial productivity and human activities affecting that productivity. Furthermore, the maintenance of conditions important to tourism, aesthetics, and spiritual values depends on spatial and temporal conditions of terrestrial and aquatic ecosystems and these are usually difficult to quantify. We will cover what we believe are some important aspects of productivity–mainly considering tree dynamics and productivity. For other discussions of various aspects of productivity we refer to Bryant and Kuropat (1980), Larsen (1982), Oechel and Lawrence (1985), Elliott-Fisk (1988), Canadian Journal of Forest Research (1983, 1993), Zoltai et al. (1988 a,b), Peterson and Peterson (1992), and Ruggerio et al (1994).

Forest biomass and annual productivity of the boreal forest have been of particular interest recently because of the importance of the boreal forest in the global carbon budget (Botkin and Simpson 1990, Apps et al. 1993, Kurz and Apps 1993) and the effects that climate change are predicted to have on carbon cycling in the boreal forest (Slaughter 1992). Biomass estimates for the entire boreal forest ranged from 4.2 to 17.5 kg/m^2 (Botkin and Simpson 1990). The variation among estimates probably occur because of differences in study design and sampling methods. For example the estimate of 4.2 kg/m^2 (Botkin and

Simpson 1990) was for trees and shrubs only and did not include the green moss layer and forest floor–major components of the biomass in some forest types (Van Cleve et al. 1986) General estimates of annual primary productivity are from 400 to 2000 $g/m^2/yr$ (Whittaker and Likens 1975). Soil types are a major factor determining primary productivity in the boreal forest.

There are some general trends in primary productivity that are important to understanding boreal forests. Stability may be defined as the integrity of composition and productivity. It can be postulated that if the world were a smooth ball, productivity would decline uniformly from the equator to the pole. It is however not so simple. Mass topography, proximity to water, continental directions of isotherms, and humidity regimes modify this simple model greatly. However, productivity in general in the boreal forest is indeed less than that of the north temperate forests to the south of the Boreal Zone (Burgess 1981). Notwithstanding the foregoing, the agents of evolution (selection and speciation) also play an important role in productivity.

The relationship of productivity to latitude differs between the eastern and western regions. Productive forests in the west extend to much higher latitudes than in the east due to the influence of Hudsons Bay (*Figures 1 and 2*). In the east, primary productivity is more clearly inversely related to latitude than in the western area. In the west, the relationship is confounded by elevational effects due to the presence of mountains and the presence of rivers along which forest development and growth is much better than on adjacent upland treeline sites. For example, Alaskan forests on productive sites north of the Alaska Range in a warm-summer, continental climate have productivity equal to or greater than that on similar sites south of the mountains, in an area with a cool, summer maritime climate. Productive forests extend to higher latitudes in the western than the eastern boreal forest because of differences in climate. There are also large differences in productivity between north and south aspects, and wetland, upland and riparian zones (Canadian Journal Forest Research 1983, 1993, Van Cleve et al 1986, Oechel and Lawrence 1985, Elliott-Fisk 1988).

Boreal species have been selected throughout eons for higher latitudes with their shorter growing seasons, longer days and lower temperature regimes. Aspen at lower latitudes may not be able to sustain productivity as sugar maple or still more southern species such as yellow poplar (*Liriodendron tulipifera*). However, as sugar maple reaches its northern borders, productivity declines to zero while that of aspen increases into the boreal. It is, presumably, maintained by a cline or graduated succession of genotypes adapted for increasingly higher latitudes. Final reduction in the north occurs as conditions become sufficiently severe that intra-specific variation may not accommodate further extension.

In summarizing information on aspen productivity for the Canadian boreal forest, Peterson and Peterson (1992) concluded that there was good evidence that more northern areas of Alberta and British Columbia have the highest annual growth rates of aspen. Thus the general trend of decreasing growth with increasing latitude appears to hold more for the forest-tundra and lichen woodland regions than for the closed forest boreal zone (*Figure 1*).

Productivity in a classical forestry sense has been measured by the construction of growth and yield tables of volume increment. Such tables based on previous growth accurately predict yield for forest management. They have been associated historically with current levels of utilization and customarily disregard components on non-commercial materials such as stumps, small branches, etc. Since utilization has increased with time, and as wood supply has diminished, full and whole-tree harvesting and utilization require adjustment in yield tables.

Net primary productivity is the rate of dry matter (biomass) production, expressed as annual accumulation in kg/ha. It is estimated by measuring the annual litterfall, and the mean or current annual increment of all components of a forest: the trees by components (boles, branches, foliage, fruits and flowers, roots) and above and below ground growth of shrubs, herbs, and non-vascular plants. There are many papers in the literature (Stanek and State 1978) presenting various estimates of forest production. However many of these catalogue biomass of the standing crop and not annual biomass production.

While there is considerable information on biomass (standing crop) in the boreal forest there is much less on actual productivity. *Table 2* presents above-ground productivity (PA) estimates for some principle boreal species. Comparison is provided in *Table 3* for some species from comparable sites in the Scandinavian and Russian boreal forest. Both tables also provide comparisons with a few samples for related species growing farther south in the north temperate and higher elevation forests of Minnesota and Oregon, Ontario, Sweden, Germany, Rumania and Japan.

These data illustrate the trend toward higher productivity at lower (north temperate) latitudes, with those of transitional areas being intermediate. This concurs with the findings of O’Neill and DeAngelis (1981) that above ground net primary production increases directly with heat sum. In almost all cases, Broadleaved species exhibit greater productivity than coniferous species of similar age on comparable sites (Malkonen 1974, 1977, Ellenburg et al. 1981, Gordon 1981a, Nihlgard 1981, Ando et al. 1981, Shedei et al. 1981, and Van Cleve et al. 1983).

Productivity is the measure of a species response to site conditions. However, variation, apart from site and species composition, will be apparent. A number of factors such as age, basal area, stand density, and site index, among others, can affect productivity and make strict comparison difficult. Productivity should be measured when stands are in a “steady state”, essentially when crown coverage has stabilized whether in a closed forest or forest parkland stand structure. Ovington and Pearsall (1956) noted that when canopy closure was complete, annual increase in dry weight was at a maximum and more or less constant. They deemed annual dry matter increase the best measure of comparative efficiency in different British forests and recommended its evaluation 20 to 40 years after stand establishment. Yarie and Van Cleve (1983) selected 45 as the minimum age for sampling white spruce productivity in interior Alaska. Post (1970), working in northern New Brunswick, found that mountain maple (*Acer spicatum*), a short-lived shrub, mean annual increment increased up to age 8 and remained constant until age 26. In tree species, juvenile growth initially proceeds very slowly, becoming exponential before crown closure. In addition there are many differences in juvenile growth patterns depending on shade tolerance and growth characteristics. Apart from shrub species, comparisons of productivity of immature stages should be avoided.

Similarly, a cut-off age of about 130 years is appropriate for many species, but could be less for intolerant species. For long-lived intolerant species, such as red spruce, an older age may be more appropriate. Mixed stands of tolerant species of several age classes may also be analyzed at older ages.

Productivity measures are also related to other stand descriptors such as basal area and stand density index (SDI). Basal area is useful since, after rising, it maintains a relatively constant flat profile for an extended time falling off at older ages. SDI relates usefully in some instances but in understocked stands does not remain constant, gradually increasing toward normalcy. Current and mean annual increment are directly related to productivity. Mean annual increment (IMA) is commonly used but because total age is used this measure incorporates the very slow period of juvenile growth. Current annual increment (ICA) is very useful in expressing productivity, but as Ovington points out is not constant. ICA can be calculated from periodic annual increment (IPA) at any point in the growth of a tree.

Anomalies in productivity may be projected through the use of data that includes juvenile growth. Improper comparisons may occur if a mix of IMA and ICA are used particularly when ICA is calculated from the wrong segments of IPA. Not all anomalies in comparisons of growth over some gradient are incorrect. The data presented in *Tables 2* and *3* are reasonable with few anomalies. A small number of data sets based on juvenile data were, of necessity, omitted.

Another important trend is the change in productivity that can occur during forest development. One of the best examples for the North American boreal forest is the work on floodplain ecosystems in the eastern interior zone of Alaska (Canadian Journal of Forest Research 1983, 1993, Van Cleve et al. 1986, Zasada and Packee 1994). Briefly summarized, this work shows that annual productivity of early stages in primary succession dominated by shrubs (alder and willow) and broadleafed trees (balsam poplar) is equal to or greater than that in both the white spruce stage and far exceeds annual productivity in the late stages of white spruce stand development and the transition to black spruce forests (see *Figure 4* for stages of development). Total forest biomass increases during succession with larger percentages of the biomass contained in the moss and forest floor layers during the white spruce stages of succession.

Productivity trends in secondary succession on upland and lowland sites also vary with successional stage. The magnitude of these differences depends on site quality and soil conditions. Black spruce sites with permafrost often show increased productivity following fire when they are dominated by shrubs and herbs and the active layer is deeper, soils warmer, and nutrients more available. One of the best documented examples of the rapid return to high levels of productivity following disturbance is for stands containing a significant component of aspen (Peterson and Peterson 1992).

Total biomass, distribution of biomass and productivity differs depending on site conditions, species composition and stand age. In Alaska, Van Cleve et al. (1983) found that forest floor biomass in black spruce forests was greater than above ground biomass, but not in other forest types; mean annual productivity was higher in forests dominated by broadleaved species than in white and black spruce forests. Gordon (1981, 1983) studied mixed hardwood-conifers and pure conifers in the Ontario boreal forest. He found that there was substantial variability in productivity and distribution of biomass due to age of stands and site conditions.

Although there is a tendency to think more in terms of production of woody biomass on sites in a tree-dominated region, trees may not be the most productive part of the system. This is particularly true on cold sites with low tree productivity. Here the moss component may have levels of annual productivity equal to or greater than that of the overstory woody species. Oechel and Lawerence (1985), Zoltai et al. (1988a, 1988b), and Van Cleve et al. (1986) provide more information on these aspects of boreal forest productivity.

10. SUSTAINABILITY OF THE BOREAL FORESTS

Sustainability of forests and forest ecosystems throughout the world and related concerns for forest health, long-term site productivity, ecosystem management, and “new forestry”, have been dominant issues in forestry, ecological, and political debates during the past decade (see for example Lubchenco et al. 1991, Kimmins 1992, Canadian Council of Forest Ministers 1992, Maini 1992, Hansson 1992, Gow 1992, Biodiversity Science Assessment Team 1994, Northern Forest Lands Council 1994, Gordon 1994, Natural Resources Canada 1994, Rowe 1992, Vitousek 1994, Kaufmann et al. 1994, Lackey 1994, Standing Committee on Natural Resources 1994, British Columbia Forest Practices 1993ab, Arrow et al. 1995). Sustainability of all of the values derived from forest ecosystems is a complex issue that is exacerbated by the fact that sustainability means different things to different people. However the core definition implies that management should provide for the needs of people within the constraints of ecosystem productivity and economic realities (Rowe 1992, Maini 1992, Gow 1992, Arrow et al. 1995). In practice, sustainability is an idealistic concept that has applicability only after people's basic needs are met and when people are generally satisfied with their quality of life (Gow 1992). One only needs to read accounts from Africa, Serbia, Bosnia, Chechnya, Bangladesh, and other places in the world where people are under stress from overpopulation, war, poverty, disease, and hunger to realize that concerns about sustainability, and ecological resilience and values of forests are secondary to the concern for basic needs of people. For concepts of sustainable forest ecosystem management to come to general application in the North American boreal forest, people in Alaska, Canada, and the contiguous United States must have a sense of stability in their lives and be a part of the evolutionary process that brings the concepts to reality.

Why should we be concerned about sustainability of the North American boreal forest? There are both pragmatic and idealistic reasons. The pragmatic answer is that the boreal forest is an important source of jobs as a result of forest harvesting, manufacture of forest products, and tourism, and it is a source of food, fiber, water, and special forest products upon which people depend. In Canada the forest products industry is the backbone of the national economy, being responsible for 10% of the gross national product, and much of the industry depends on the boreal forest. In Alaska, forests have always played an important role in the lives of the residents, but the forest products industry in the boreal forest has been a relatively minor component of the Alaskan economy as compared to Canada's economy. Tourism has become a major industry in Alaska and the aesthetics and wildlife viewing provided by the forested landscape are an important aspect of this industry. In the upper Great Lakes region and New England, forest products, tourism, and hunting and fishing are based on forest ecosystem values and are vital to the economy of these areas (Shands 1992, Kuusela 1992, Northern Forest Lands Council 1994, Standing Committee on Natural Resources 1994).

The more idealistic or long-term concerns about sustainability are of an ecological nature. These concerns include the role the boreal forest plays in the global carbon budget and global warming resulting from a build up in CO_2 and other greenhouse gases, and the resiliency of boreal forests to disturbance and change (Maini 1992, Slaughter 1992, Apps et al. 1993, Kurz and Apps 1993, Vitousek 1994, Arrow et al. 1995, Apps et al. 1995, Silva Fennica 1996, Gordon 1999). (Maintenance of genetic diversity, wilderness, wildlife habitat and spiritual values also fall under this category.) Although there is a substantial amount of ecological evidence and a theoretical basis for these concerns, they are difficult to substantiate to the satisfaction of the general public, politicians, and policy makers. In many instances, there is a direct conflict between ecological issues and pragmatic issues at the scale of the individual communities situated in the boreal forest. The resolution of such conflicts is critical to achieving sustainable management in the boreal forest.

How will sustainability be achieved? Sustainability of ecosystem values at local and regional scales will be affected by factors that are controlled at both the local and global scales (Maini 1992, Arrow et al. 1995). The focus of our discussion will be at the local and regional scale. However, the larger context cannot be ignored as it often directly affects what happens at the smaller scales, particularly through policy and regulations (Maini 1992).

11. Global and National Issues Affecting Sustainability

A major global concern is the rapidly expanding world population and our basic needs for living (Kimmins 1992, Maini 1992, Gow 1992). As people seek to find places to live, land for food production and industrial development, and areas for disposal of wastes, forest land is eliminated and more pressure is placed on the remaining forest land. Thus, there is increased demand for forest products from places like the tropics and the North American boreal forest, areas with relatively large undeveloped forests and low population density.

Global change is another issue vital to the productivity of terrestrial and aquatic ecosystems at the level of individual lakes or forest stands (Apps et al 1995, Silva Fennica 1996). Unfortunately the use of fossil fuels for power generation, manufacturing and transportation is causing global change and these sources of atmospheric pollutants are not subject to local regulations. In addition to adding large quantities of CO_2, CH_4 and other greenhouse gases to the atmosphere, they are also the source of sulfur and nitrogen compounds that contribute to acid rain that has been shown to affect lake chemistry and productivity (Schindler 1988, Schindler et al. 1996). Heavy metals like mercury and lead in elemental or organic forms are known to adversely affect productivity of terrestrial and aquatic ecosystems directly or through bioaccumulation in fish and wildlife species (Verry and Vermette 1992). While local, regional, national, and international regulations and agreements exist to reduce or eliminate these problems, more has yet to be accomplished to reduce the impact of global factors.

The point is that there are many factors outside the boreal forest that are inextricably linked to the issue of sustainability of the North American boreal forest. Local and regional planning that does not recognize the influence of these external factors may have limited success or may fail regardless of well-conceived ideas and well-executed operations.

Regional and Local Issues Relating to Sustainability of Forest Ecosystems

Many complex factors determine how sustainability will be achieved (Rowe 1961, 1992, Maini 1992, Kaufmann 1994, Vitousek 1994). We will discuss three areas that play a major role in sustainability in the North American boreal forest: land ownership, forest management, and biological diversity.

12. LAND OWNERSHIP/TENURE

The ownership or control of the land significantly influences the type of management practiced, land ethics of the manager, land use regulations, and the ease with which forest land is converted to other uses (Gow 1992). Ownership determines to a large degree the stability of the land base over periods relevant to management in the boreal forest. Within the boreal forest, there are significantly different ownership and tenure situations.

In the northern contiguous United States having a boreal forest element as defined earlier, private landownership predominates (Merz 1978, Northern Forest Lands Council 1994). On average, 65 to 75 percent of the land is privately owned with about two-thirds of the area in non-industrial ownership (Smith et al. 1994). Although all levels of public ownership are represented, state and county ownership is more common than federal ownership. Thus, land ownership is dominated by relatively small private holdings. Public lands were in large part purchased by governments or returned to state and county governments as a result of non-payment of taxes. The majority of this land was abandoned after all of the forest was removed and an unsuccessful attempt to farm it. The history of federal lands in the eastern U.S. is substantially different from that in the west, where large areas of public domain lands were reserved for the establishment of national forests.

Tenure of Canadian lands is significantly different from that for the northern United States. Excluding the Yukon, where most of the land remains under the jurisdiction of the federal government, private and federal ownership comprise about 6 and 2 %, respectively, of inventoried forest land whereas the remaining 92 % is owned by the provinces. In the boreal region, provincial ownership may exceed 95 % of forest land. Private land holdings are greatest in New Brunswick, Nova Scotia, and Prince Edward Island where 48, 70 and 90 %, respectively, is privately held (Haley and Luckert 1990). However, as Pearse (1987) pointed out “the preference of Canadians for public ownership of forest lands is not matched by an enthusiasm for big (federal) bureaucracies to manage them”. Haley and Luckert (1990) have reviewed the system of forest tenures in Canada. They state “one of the foremost forest policy questions....throughout Canada.....has been the transfer of timber harvesting rights and forest management responsibilities from the public to the private sector while ensuring that public resource management and development objectives are achieved." Common features in the evolution of tenure systems have been a transfer of regeneration responsibilities to the forest company doing the harvesting, and a general increase in the size of land tenures granted to forest companies. For example, one tenure in Alberta is 55,000 km^2. One of the more serious drawbacks of the tenure system results when the conifer resource is allocated to one company and the broadleaved (usually aspen) resource allocated to another (Lieffers and Beck 1994). Clearly, stand management goals of one company may be at odds with the goals of the other.

In Alaska, 98 percent of the land was under the jurisdiction of the federal government until 1959. The partitioning of Alaska began with passage of the Statehood Act in 1958. This legislation entitled the newly formed state to select 41.2 million hectares (103 million acres) of land. The Alaska Native Claims Settlement Act of 1971 created village and regional corporations which were entitled to select 16.2 million hectares (40 million acres) from the federal lands and from some of the lands selected by the state. The criterion for selection by both the State and Native corporations was high renewable and nonrenewable resource values. A further important aspect of Native land entitlement was the intent to provide land for villages to maintain a subsistence lifestyle. The Alaska National Interest Lands Conservation Act of 1980 added about 41 million hectares (104 million acres) to federal conservation systems, mainly national parks, preserves, monuments, and fish and wildlife refuges. The remaining federal lands are in the public domain and administered by the USDI Bureau of Land Management and USDA Forest Service. Lands were transferred to private ownership through homesteading, mining, special use (trade and manufacturing sites), and state recreational and residential land lottery programs. State programs also allowed individual communities to select land for development.

The ramifications of these land ownership patterns are significant in terms of the landscape patterns that would result from natural processes, e.g. fire, and human activities, e.g., forest harvesting. A predominance of small privately held parcels of land may result in good management at the stand level, but landscape management and regional objectives may be difficult to achieve. One alternative is to manage the large public land holdings (e.g., national forests) to meet ecosystem objectives and the private lands, where ownership may change frequently, to meet commodity needs. Large areas under single ownership or control establish a high degree of potential that landscape level management will occur.

Substantial areas of North America's boreal forest are reserved as parks and wildlife preserves (Zasada and Packee 1994, Weber and Van Cleve 1995). In Canada, there are approximately 83,000 km^2 located in 10 national parks. In Alaska, there are approximately 129,000 km^2 in 5 parks and 20,000 km^2 in Fish and Wildlife Preserves. The Wrangell-St. Elias National Park in Alaska and the adjacent Kluane Park in Yukon have a common boundary and the combined area is 71,000 km^2. For the most part natural disturbances, such as fire and insect outbreaks, are not controlled in parks and preserves.

In some parks and refuges, there are active prescribe burn programs to maintain the landscape mosaic for wildlife habitat.

A continuing issue in the North American boreal forest is the settlement of land claims of indigenous peoples (Natives). In Alaska, federal legislation has resolved most of the landclaims issues whereas in Canada many land claims have not been resolved. In the northern Great Lakes region of the United States, rights of Natives to utilize fish, wildlife and some of the plant resource established by treaties in the 1800’s and early 1900’s have created significant conflicts among Natives and non-natives.

Conversion of lands to agriculture, community development, mining, and oil and gas development have all affected forest land in the past and will continue to be competing uses. The effects of these other land uses go beyond land conversion. For example, oil and gas exploration and development greatly increase access through road development and seismic activity. In the past, land clearing practices that resulted in a substantial amount of trees being cut and left have been associated with bark beetle outbreaks.

13. FOREST MANAGEMENT

The forest management activities that have most influenced the boreal forest as a whole are fire management and forest harvesting. Both of these activities change forest dynamics at all scales of resolution from altering landscape structure to microsite characteristics.

Fire Management

Effective fire protection began in the 1930’s and 40’s throughout the boreal forest and is most intensive where forests are of relatively high value or where there are valuable homes and other structures requiring protection, and where road access is good. In spite of these efforts, however, fire still affects large areas. Van Wagner (1988) reported that area burned in the Canadian boreal forest reached a high in the early to mid 1980’s despite more sophisticated detection and suppression capabilities than in previous decades. His work suggests that climatic conditions still determine to a large degree the amount of acreage that may burn in a specific year in the boreal forest. Hirsch (1989) described the 1987 fire season in Manitoba when 4 million ha burned, the worst fire season in 70 years. As we write this paper, there are hundreds of thousands of hectares of land burned or burning in the Canadian boreal forest while there is little fire activity in Alaska.

Because of the unpredictable nature of fire, efforts to reduce its impact are divided into presuppression, those activities that maintain the ability to suppress fires and education, and suppression, those activities dealing with fire control, activities. Presuppression activities are relatively similar from year to year, while suppression efforts vary wildly annually. For example from 1991 to 1993, the Alaska Department of Natural Resources spent about $5 million annually in presuppression activities. During the same period the cost of suppression varied from $10.8 to 51 million annually. During the 5-year period from 1988 to 1992, the total cost of fire suppression in Alaska was about $114 million and the acreage burned about 18 million ha. In Manitoba, suppression costs were about $50 million (Canadian) in a year in which 5 million ha burned (Hirsch 1991). Suppression activities are often important sources of income for rural communities and thus have played a role in community stability.

Currently, fire management and suppression activities are undergoing review and change in the boreal forest. This is due in part to the recognized ecological importance of fire at all scales in this forest region and in part to the high cost of attempting to control fires in remote areas where timber values may be marginal and other values, such as wildlife habitat, may benefit from burning. The outcome of this review in most provinces and in Alaska has been to delineate zones with varying resource values and to suppress fires where values are highest. In some cases, for example parks and wildlife refuges, natural fire can achieve management objectives and when possible they are left to burn uncontrolled. There are also increasing efforts to introduce large-scale prescribed fire in parks and wildlife preserves to reestablish succession to desired stages. Because of the large size and remote location of some parks and reserves, they are ideal places for the use of prescribed fire to achieve management objectives.

Although fire will always have the potential to burn large areas in any given year, its importance as a major influence in the landscape relative to other disturbances, particularly timber harvesting, varies across the boreal forest. In interior Alaska, a total of 5,000 to 8,000 ha of forest were harvested from 1980-93 while 3.1 million ha burned (L. Fortune, Alaska Dept. Nat. Resources, Fairbanks AK, pers. comm.). In Alberta, about 724,000 ha were harvested from 1966-92 while fires burned about 3.5 million ha. In northern Ontario, harvesting exceeded fire as a disturbance factor from 1950-90. In a 30.3 million ha area, harvesting (disturbances > 200 ha) occurred on 12.8 % of the area while fire burned 4 % (Perara et al. 1994). The northern United States represents the extreme end of the spectrum in that forests were largely cutover and burned several times in the early 1900’s. These forests were regenerated both naturally and artificially. Fire has been virtually eliminated in the second-growth forests and harvesting and other human development activities are the dominant disturbances (Stearns 1988). With the increased utilization of aspen in western Canada (Ondro 1990) and increased harvesting in Alaska and the Yukon, harvesting will continue to grow in importance relative to fire as a shaper of the landscape. Therefore in the future it will be critical to develop forest harvesting practices that emulate the role of fire at all scales (Duchesne 1994).

Over time fire may affect all components, i.e., lands with relatively low and high primary productivity, of the landscape within a given area. In contrast harvesting only directly affects stands having adequate wood volume to cover costs of operations and provide useable wood. If fire control is effective in eliminating fire from the unharvested areas of lower productivity, there will be substantial portions of the landscape that will not be disturbed or the disturbance interval will become much longer than the natural fire cycle, thus affecting forest longevity and the temporal scale of succession.

Harvesting and Silvicultural Practices

Harvesting and silvicultural practices have passed through several well-defined stages as they have evolved to their current state (Kimmins 1991, Pollard 1991, Bisset et al. 1993, Weetman 1995, Wurtz and Gasbarro 1995). Because of settlement history, the timing of these stages differed between the eastern and western boreal forest. The following discussion briefly summarizes the earliest stages as they provide insight into the current condition of parts of the forest and the values that are placed on these forests.

Before the arrival of Europeans in the boreal forest, Native peoples obtained all of the necessities of life from the plants and animals of these forests (Nelson 1983, MacKinnon et al. 1992, Meeker et al. 1993, Viereck 1987). Although they utilized virtually all species for various purposes, some species, for example white spruce in Alaska, appear to have had relatively higher utility than other species (Nelson 1983). The impact that the Natives had on the forest varied with the region, but they practiced management to meet specific needs (see review by Weber and Van Cleve 1995).

Settlement by European immigrants had different effects on the forests. Forests were cleared to provide wood for all purposes and where agriculture was possible, the lands were farmed for varying lengths of time up to the present day. Where farming was not possible, people stayed for a while but ultimately moved on leaving the forest to recover to some degree. A particularly well-described case of intense use of the forest was along the Yukon River in Alaska and Yukon. Forests along the river were utilized for everything from fuel to provide steam to power sternwheelers, to mine timbers to construction and heating of homes during the gold rush era. Following the gold rush these forests were largely left to recover and have never since had the same level of use (Bisset et al. 1993).

Following the early settlement and gold rush period, the forests were utilized to provide many products for use by residents and for export from the region. However, a particularly defining moment for each region of the boreal forest, except central Alaska, was the establishment of pulp and paper mills. This greatly increased the level of utilization and brought the shift from various forms of partial cutting and high-grading to clearcutting (Bernsohn n.d., Weetman 1995). From this point on the size of tree that could be utilized decreased as technology improved and wood became more difficult to get.

Local wood shortages, the cost of transportation and the lack of adequate regeneration on many harvested areas resulted in establishment of intensive silviculture programs during the late 1960's, 70's and 80's following the agricultural "model" in order to maximize fiber yield. Clearcutting was the major silvicultural method and all reforestation activities were aimed at regenerating conifers in clearcuts as rapidly as possible. The rationale for clearcutting was partially ecological with the argument that the effect was similar to that of stand replacement fires. Although there are some broad similarities, it has become obvious that this comparison was over-generalized and that there are many significant biotic and abiotic differences between the effects of fire and clearcutting (Keenah and Kimmins 1993).

Regeneration was the main silvicultural concern and giant strides were made in seedling production, handling and planting of nursery stock, site preparation technology, application and efficacy of herbicides and understanding effects of competition and organic layers on seedling survival and growth (Stiell 1976, Walstad and Kuch 1987, Doucet and Weetman 1990, Burns and Honkala 1990, Coates et al. 1994). A major goal was to reforest land with relatively rapid-growing superior genotypes of pine and spruce where possible.

There was significant success with some species on some sites, most notably with artificial regeneration and natural regeneration of the serotinous coned pines and black spruce on nutrient-poor sites with relatively low levels of competition from grasses and vegetative regeneration of broadleaved trees and shrubs. In mixedwood forests that are relatively high in nutrients, regeneration of conifers, mainly white spruce, was very difficult because of rapid regrowth and competition from aspen, grass (*Calamagrostis* sp.), in particular, and raspberry (*Rubus idaeus*). During this period forest values such as wildlife, aesthetics, and special forest uses were viewed as constraints to management and few, if any, concessions were made for managing for these other values. However, some species of wildlife, such as moose, deer and grouse, benefited from clearcutting whereas other species, such as woodland caribou and marten, species requiring older forest stands, were adversely affected (Thompson 1991, Hunter 1990, Hansson 1992, Ruggerio et al. 1994).

During this period, controversies regarding sustained yield of wood centered around impacts of harvesting on soil compaction, nutrient availability, stocking levels to achieve maximum production and the effects of competing vegetation (Kimmins 1992). As a result of these controversies, ongoing operations, and research activities, a great deal was learned about these impacts, how harvesting and silvicultural activities could be used to eliminate or reduce them, and what remedial action was necessary to restore impacted sites (Keenah and Kimmins 1993). Although many questions remain concerning these practices, the state-of-the-art advanced significantly and good results were possible given adequate resources to use all available technology and information.

Public and scientific concern regarding the impact of forest management practices on all forest values became more obvious in the 1970’s and rapidly increased in the 1980’s (Kimmins 1992). The main reasons for concern were the expanding use of clearcutting and the practices used in stand regeneration, particularly use of herbicides and some forms of site preparation. Sustained fiber yields were possible for some species and sites, but there remained substantial areas of poorly stocked clearcuts despite expensive regeneration efforts. In addition, there were questions about the ecological impacts on wildlife, stream habitat, water quality, aesthetics, tourism, soil stability and other values.

Thus ecosystem management, which had its roots decades earlier, was proposed as a basic guiding management concept for considering all forest values (Rowe 1961, 1992, Hansson 1992, Gordon 1994, Ruggerio et al. 1994). Key elements of the concept are: 1) management of landscapes and rather than individual stands; 2) silvicultural practices which simulate natural disturbance more closely; 3) maintenance of forest structure in the form of living trees and standing and down dead trees; and 4) adoption of the concept of adaptive management (that is adjusting management practices as new knowledge and experience become available).

Boreal forests are at a significant crossroads in forest ecosystem management; the shape of things to come is not clear. It took 30 or more years to develop the systems currently being used to manage the boreal forest and large-scale change will not occur immediately. However there is a wealth of experience from which to draw and there are significant operational and research trials under way that will provide information to adapt practices in the future (Jeglum and Kennington 1993, Navratil et al. 1994, Coates and Steventon 1995).

The strengths from past forest land management experience on which we can draw to achieve these forest conditions include: The mechanized technology for extracting trees from the forest is very advanced. We are rapidly learning to use this technology to partially cut forests and the limits of this technology are relatively well understood (Keenah and Kimmins 1993). One of the first types of partial cutting that has been adopted is the protection of advance regeneration in the understory of mature broadleaved and conifer stands. Excellent examples of this are removal of aspen overstory with retention of white spruce understory in Alberta (Navratil et al 1994) and saving black spruce regeneration when removing a black spruce overstory (Jeglum and Kennington 1993). A significant variation in the way stands are clearcut is also being used. This takes the form of leaving groups or individual trees to provide structure and habitat diversity in areas that would normally be clearcut. Coates and Steventon (1995) and Standing Committee on Natural Resources (1994) suggest leaving groups of trees on about 5 % of the cutblock. Classical silvicultural systems such as the shelterwood also hold promise for white spruce regeneration (Lees 1964, Zasada 1990, Youngblood and Zasada 1992).

We have learned through operational trial and error to create an almost infinite variety of microsite conditions utilizing various site preparation techniques (Orlander et al. 1990). These techniques combined with different types of overstory manipulation could significantly change the way in which forests are regenerated.

A final example is the tremendous amount of knowledge regarding the production, handling, planting and tending of seedlings. These methods used in conjunction with natural regeneration on cut blocks with various types of residual overstory can reduce reforestation costs while not reducing regeneration success.

Some major areas needing more operational experience and research are briefly considered. From a stand level point-of-view, alternatives to clearcutting are needed. Particularly we should emphasize systems that can be used to: 1) produce mixed species stands using combinations of natural and artificial regeneration, 2) develop stands with different and predictable vertical and horizontal structure, 3) create different successional trajectories on similar sites and 4) create acceptable wildlife habitat. From a landscape perspective we need to know more about the implications of alternative stand patterns for wildlife populations (metapopulations), forest development, stream habitat, and aesthetics.

Putting all of this together to achieve ecosystem management will require an unprecedented level of integration between fiber production and wildlife conservation goals. This integration comes in several forms. One form is better integration among practices comprising the silvicultural system developed for a given site. The concept of integrated forest vegetation management (Wagner and Zasada 1991, Wagner 1994) is only one example of how information and practice must be organized to achieve well-stated goals. Another important form of integration is among disciplines.

The shape which forest management appears to be taking is one which will include both extensive (semi-natural) and intensive management on selected lands (Rowe 1992, Lieffers and Beck 1994). Such an approach should help meet the industrial needs for fiber on a smaller portion of the land base, allowing the remainder to be actively managed for preservation of biodiversity or other values. However for this approach to succeed, there must be a careful selection of the lands devoted to intensive fiber production, and substantial incentives for the conservation of forests.

14. Maintaining Biodiversity

Conservation of biodiversity is a key issue not only with regard to maintaining current wildlife species but also because of the need to preserve the adaptive potential of boreal forests to changing environments, for example global warming. Maintaining biodiversity of the boreal forest will require great scientific, political and economic effort. Here we propose three complementary approaches:

1. Maintain the broadest possible genetic base in all organisms. For trees this means encouraging natural regeneration of conifers on all sites, as well as using artificial regeneration. For animals this means providing all types of conditions necessary for movement, feeding, and reproduction.
2. In order to have resilient ecosystems, we must maintain a variety of forest conditions that are consistent with the natural spectrum that existed prior to European settlement (Duchesne 1994).
3. Coordinate management of forests at the landscape and regional levels between all forest users to insure maintenance of wildlife components that select their habitat at these scales (Duchesne and Thompson 1995).

The North American boreal forest provides unique opportunities to achieve these biodiversity goals. A primary reason is that large areas remain undeveloped and the main effect of management activities has been to lengthen the fire return interval. In comparison to the rest of North America, the boreal forest is still relatively pristine and there are large areas in which the natural forest can be studied.

15. CONCLUSIONS

1. *Forest Values*. The view that the boreal forest should be harvested as quickly as possible is no longer acceptable because of clashing demands. The boreal forest has many values in addition to solid wood and wood fiber. Instead, clean water, carbon sinks, aesthetics, tourism, and wildlife habitat are frequently underrated and there is an increasing sense of urgency as population increases and these values become limited or non-existent elsewhere in the world.

2. *Ecological Management.* Sustaining the multitude of values of the boreal forest requires a much broader view of management than past practices (Nordin 1996). Based on the assertion that it is not feasible to protect all ecosystems in the boreal forest, ideal management may be conducted using a mix of extensive (semi-natural) (Rowe 1992) and intensive management. We believe that this would be achieved developing management methods that emulate natural disturbance regimes encountered in boreal ecosystems in primeval times. With this, planners should be able to leave large areas in a near natural state to sustain natural ecosystem functions and distributions. Semi-natural management must include wildlife management and management for other values as an objective of equal importance to wood production.

Intensive management would be conducted on sites near mills. Intensive management does not imply the elimination of wildlife and other values but rather the management for high fiber production in order to satisfy industrial needs. However, within intensive management zones, attention must be given to the protection of rare species and/or ecosystems. As well, we would expect the application of intensive silvicultural techniques within intensive management zones.

3. *Forest Management/Silviculture.* Natural disturbances such as fire and insects will continue to be important and largely unpredictable because of the stochasticity of fire and pest occurrences. Although forest management practices can improve forest health and reduce losses caused by wildfire, it must be understood that unpredictability will remain an intrinsic component of forest management.

The technology exists to harvest forests more rapidly now than at any time in the past. However, our past experience suggests that high rates of harvest do not equate to good forestry. In fact, the opposite may be true if we are unable to assure adequate forest renewal on the harvested lands. Good forest practices are achievable when ecological requirements for sustainable forests are adequately integrated with technology to create silvicultural systems that produce not just stands of trees but stable ecosystems. Regeneration in post-disturbance forests should resemble previous pre-disturbance associations and be optimized for site conditions. Sustainability also requires maintenance of the genetic integrity of the harvested stands in the regeneration cohort, a factor often overlooked in conservation plans.

For a variety of social, political, and ecological reasons, there are high levels of uncertainty associated with the prescription and use of standard forest management and silvicultural practices, e.g., clearcutting, herbicides, prescribed burning, and mechanical site preparation. Because of this uncertainty, an integrated approach to silviculture is essential. This approach requires that land managers be proactive, that is able to anticipate problems rather than reacting to problems after they occur. Essential elements of a proactive strategy are: multifactor land classification systems; detailed information on the biology and effects of disturbance on all plant species; an understanding of cumulative effects of forestry practices as they relate to soil productivity and biodiversity; an understanding of genetic diversity as a prerequisite for maintaining speciation and fitness; an understanding of the effect of forestry practices on species other than trees; and, an understanding of sustainability as related to extensive and intensive management. With such insights we believe that the boreal forest will continue to provide to North Americans in a sustainable manner.

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Figure 1. General subdivisions of the North American boreal forest (Elliott-Fisk 1988).

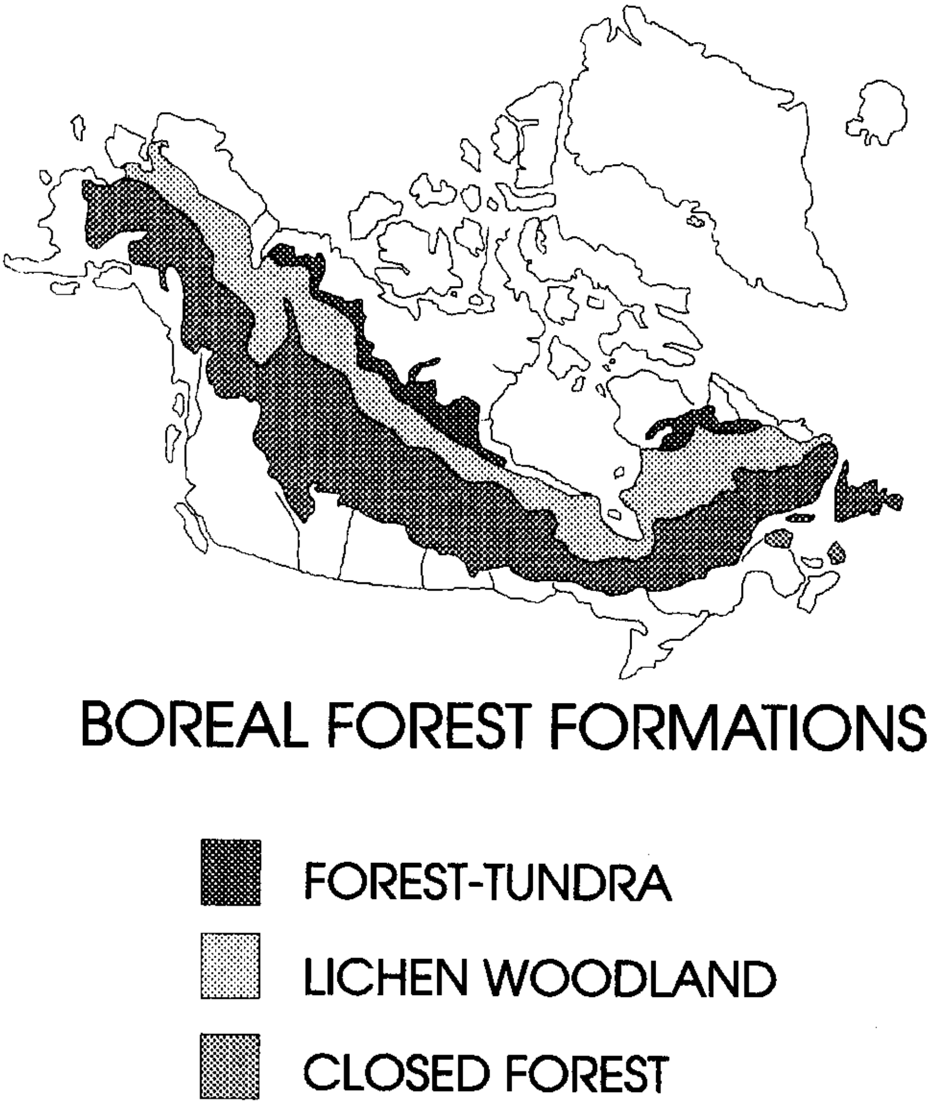


Figure 2. Regions of the North American boreal forest and adjacent forest zones (adapted from US Environmental Protection Agency/Environment Canada map).

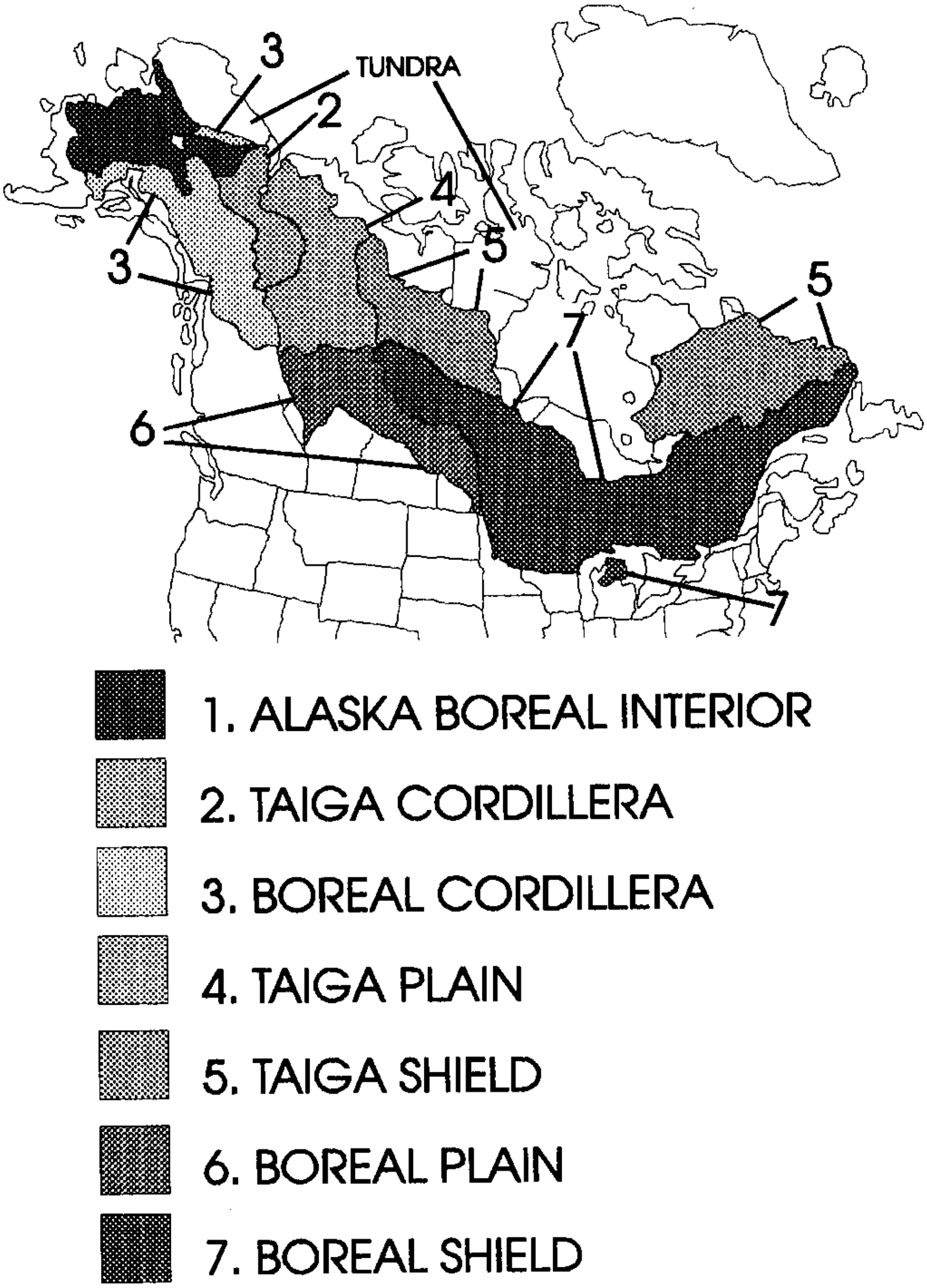


Figure 3. Idealized transect for the eastern interior zone of Alaska showing distribution of permafrost as affected by aspect, elevation, and overstory condition. Note for example the absence of permafrost on south slopes at low elevations and presence on south slopes at higher elevations. See Fig. 4 for a more detailed example of permafrost distribution on floodplains (Figure developed by Long-Term Ecological Research program University of Alaska/USDA Forest Service).

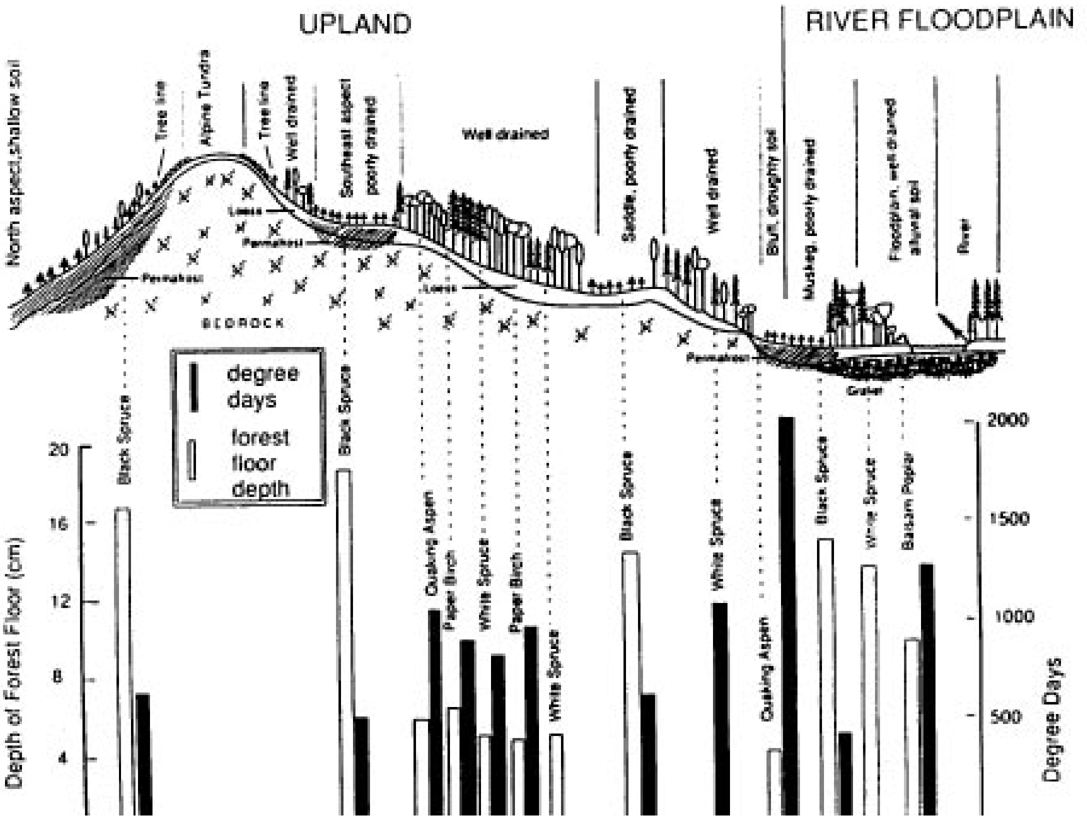


Figure 4. Idealized sequence of forest development on the Tanana River floodplain in interior Alaska. Note soils are composed of alternating layers of buried forest floor and flood deposited silt. Permafrost develops as white spruce becomes dominant and forest floor layers increase in depth, insulating the mineral soil (Viereck 1989).

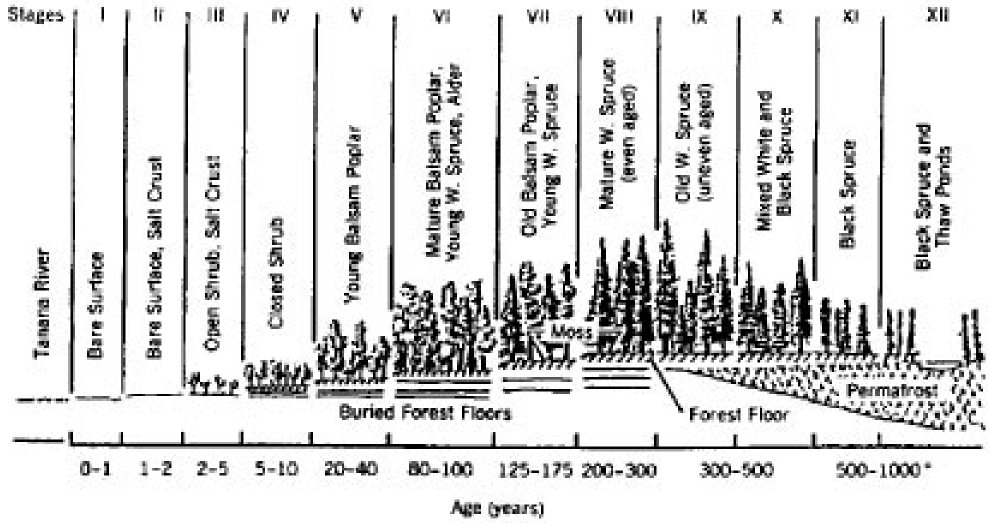
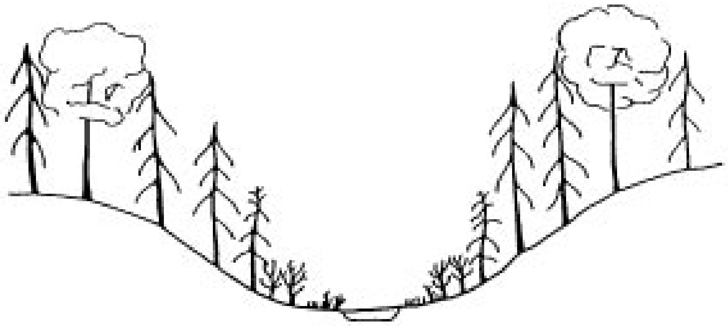
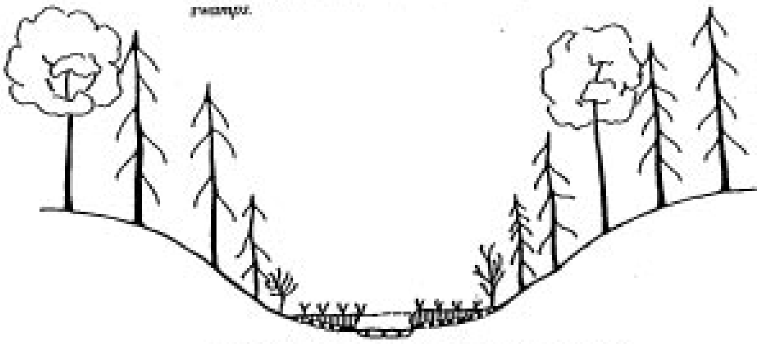


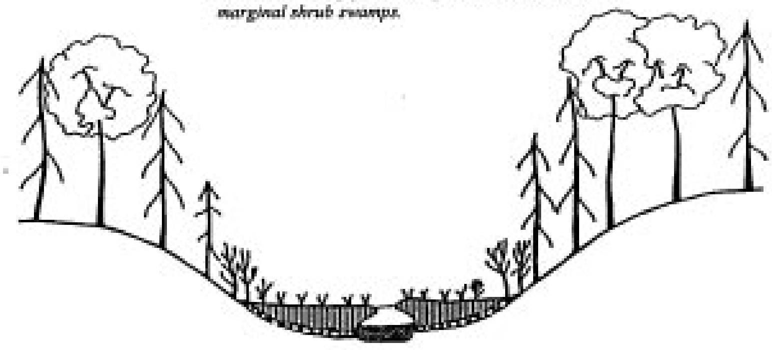
Figure 5. Generalized sequence of bog development in North American boreal zone. Time frame for sequence shown here covers hundreds of years or more (Zoltai et al. 1988a, 1995).



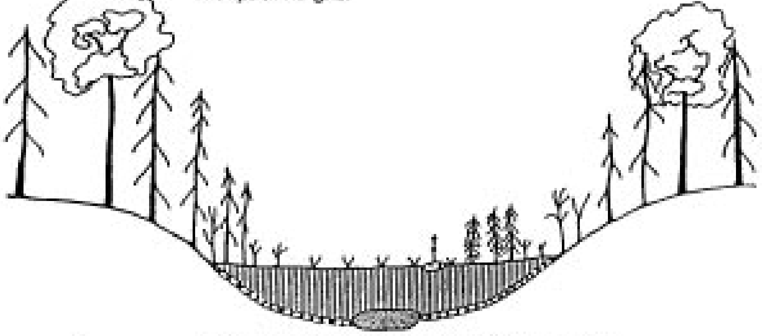
A. Initial stage: small pool, marsh, and marginal shrub swamps.



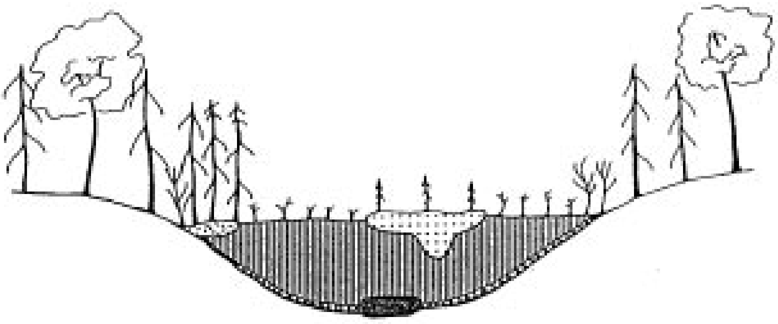
B. Initiation of fen development around pool, with marginal shrub swamps.



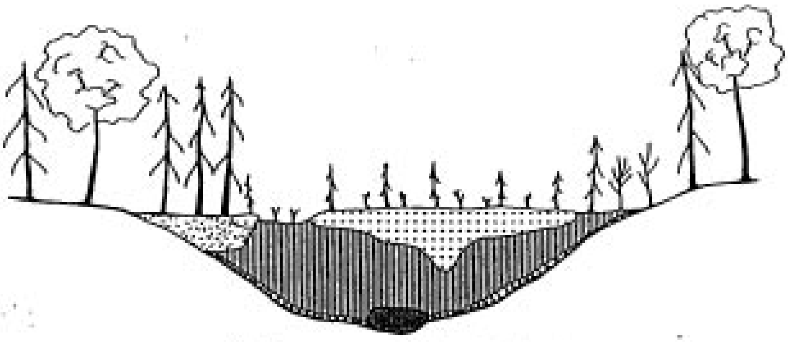
C. Pool nearly overgrown by open fen, with tall shrub swamps on margins.



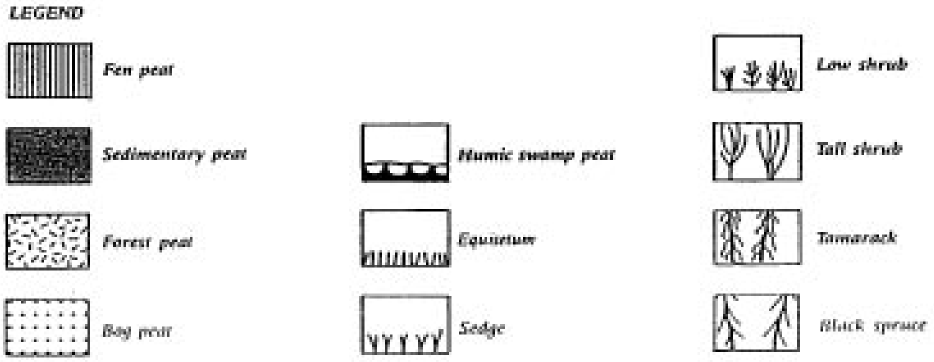
D. Fen occupies depression, differentiating into open shrub and treed fens. Small bog islands may be initiated. Marginal shrub or coniferous treed swamps are present.



E. Bog develops on portion of diversified open shrub and treed fens. Marginal tall shrub and coniferous treed swamps are present.



F. Bog covers most of the wetland, but fens may be present as narrow strips draining surplus water. Coniferous treed and tall shrub swamps are present on margins.



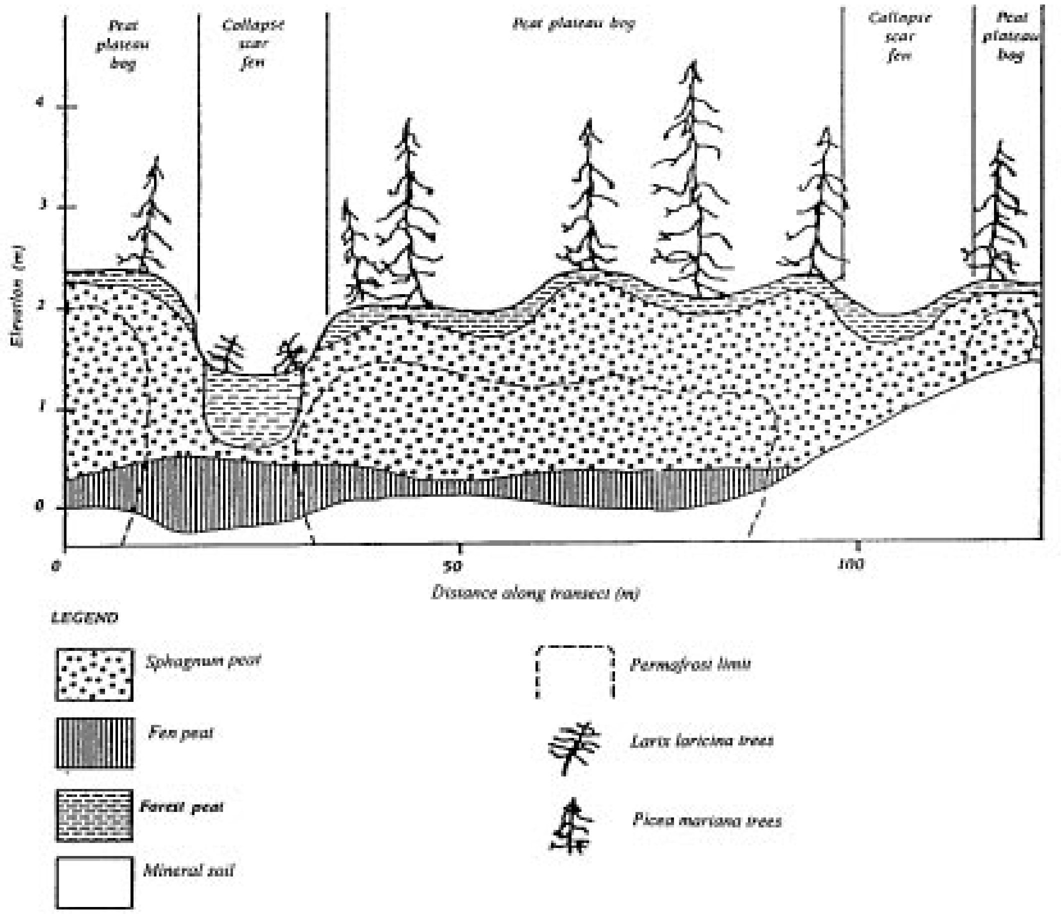

Peat plateau bog
Collapse scar fen
Peat plateau bog
Collapse scar fen
Peat plateau bog
Elevation (m)
4
3
2
1
0
0
50
100
Distance along transect (m)
LEGEND
Sphagnum peat
Fen peat
Forest peat
Mineral soil
Permafrost limit
Larix laricina trees
Picea mariana trees

Table 1. Species diversity of the North American boreal forest

GROUP	NUMBER OF TAXA		SOURCE
	Known	Uknown*	
VIRUS	40	40000	Inferred from Mosquin and Whiting 1992**
BACTERIA	520	4200	Inferred from Mosquin and Whiting 1992
ALGAE	2400	480	Inferred from Mosquin and Whiting 1992
FUNGI	5000	450	Inferred from Mosquin and Whiting 1992
HIGHER PLANTS	2100	30	Inferred from Mosquin and Whiting 1992
ARTHROPODS	14000	11000	Inferred from Mosquin and Whiting 1992
BIRDS	310	0	Godfrey 1966
MAMMALS	92	0	Banfield 1977
FRESH WATER FISHES	115	0	Scott and Grossman, 1973
AMPHIBIANS AND REPTILES	40	0	Conant 1975
OTHERS	500	733	Inferred from Mosquin and Whiting 1992
TOTAL	23217	80000	

*: unknown species are undescribed species presumed to exist

**: see text

Table 2. Biomass, Total and Average Annual Production for Above-ground Tree Component, for Forests Dominated by the Indicated Species in the Eastern Interior Alaska Forest Zone.

	Standing Crop (tons/acre)		
Forest type	Aboveground	Forest floor/soil	Annual Production
Black spruce	22.7	34.1	0.50
White spruce	77.8	33.1	1.63
Aspen	49.2	21.2	2.52
Birch	49.5	25.5	2.10
Balsam poplar	53.9	9.5[a]	2.46

[a] This accounts for the forest floor that has accumulated since the last flood, which buried previously deposited layers.

Table 3. Above-ground productivity estimates of steady-state immature and mature Eurasian taiga and cool temperate forest stands.

Forest region/Veg. Type+	**Species**	**Site**	**Age**	**Product-ivity $(kgha^{-1}yr^{-1})$**	**Lat.**	**Long.**	**Elev. (m)**	**Source**
Bo/BL	hairy birch, warty birch	Oxal.a.; Vac.myrt.; Rub.s; Calam.e	40	8,470	61°37’N	24°09’E	160	Malkonen E. 1977
Bo/Co	Scots pine	Pleur.s; Vac.v-i.	28	3,325	60°31’N	23°53’N	135	Malkonen, E. 1977
		Pleur.s; Call.v.	47	4,864	61°40’N	24°19’E	140	
		Pleur.s; Vac.myrt.	45	6,325	60°31’N	23°51’E	125	
Bo/Co	norway spruce	Vac.myrt.,v-i; Hylo.s; Pleur.s	260	4,208	66°22’N	29°E	270	Havas, P. 1981
Te/Co	norway spruce	Vac.myrt., v-i, Hylo.p	125	5,370	64°40’N	47°30’E		Rudneva *et al.* 1981
Bo/Co	norway spruce	Clad.;Rub.S.	37	2,870	62°N	34°E	200	Kazimirov, N.I. and R.M. Morozova 1981
		Vacc.	45	4,780			170	
		Polit.	42	3,680			100	
		Vac.u.; Herb	42	4,320			80	
		Oxal.a; Vac.myrt.	43	7,160			150	
		Vac.myrt.	54	6,210			130	
			98	4,810			110	
			109	4,090			110	
			126	3,090			120	
			138	2,550			130	
Bo-Te/Co	norway spruce	Vac.myrt.; Lin.b.; Oxal.a.	110	5,300	56°30’N	32°40’E	200	Karpov, V.G. 1981
Te/Co	norway spruce	Oxal.a.; plantation	60	13,700	55°59’N	13°10’E	120	Nihlgard, B. 1981
Te/BL	european beech	Stell.n.;Lam.g.; Oxal.a	45-130	15,400	55°59’N	13°10’E	120	Nihlgard, B. 1981
Te/Co	norway spruce	plantation	34	8,492	51°45’N	9°35’E	390	Ellenberg, H. *et al.* 1981
			87	9,358	51°49’N	9°35’E	505	
			115	7,470	51°44’N	9°34’E	440	
Te/BL	european beech	Luz-Fag	59	12,244	51°45’N	9°36’E	430	
Te/Co	european silver fir	Oxal.a.; Pleur.s.	110	11,300	45°23’N	23°15’E	985	Bindiu, C. 1981
Te/BL-Co	european beech-silver fir	Pulm.r.; Oxal.a.	1-450	9,250	45°23’N	23°15’E	950	Popescu-Zeletin, I. *et al.* 1981
Te/Co-BL (subalpine)	northern J.hemlock, Maries fir, birch		290	6,100	36°40’N	138°30’E	1790	Kitazawa, Y. *et al.* 1981
Te/Co	southern J.hemlock, Hinoki cypress, J.red pine	Cley.j.; Eury.j.	120-443	8,037	33°20’N	133°E	720	Ando, T. *et al.* 1981
Te/BL	Japanese beech	Viol.v; Oxala.a.	150	10,100	35°20’N	135°45’E	680	Shedei, T. *et al.* 1981