

ALASKA'S CHANGING BOREAL FOREST

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Introduction

Historically the boreal forest has experienced major changes, and it remains a highly dynamic biome today. During cold phases of Quaternary climate cycles, forests were virtually absent from Alaska, and since the postglacial re-establishment of forests ca 13,000 years ago, there have been periods of both relative stability and rapid change (Chapter 5). Today, the Alaskan boreal forest appears to be on the brink of further significant change in composition and function triggered by recent changes that include climatic warming (Chapter 4). In this chapter, we summarize the major conclusions from earlier chapters as a basis for anticipating future trends.

Forest Dynamics

Alaska warmed rapidly at the end of the last glacial period, ca 15,000–13,000 years ago. Broadly speaking, climate was warmest and driest in the late glacial and early Holocene; subsequently, moisture increased, and the climate gradually cooled. These changes were associated with shifts in vegetation dominance from deciduous woodland and shrubland to white spruce and then to black spruce. The establishment of stands of fire-prone black spruce over large areas of the boreal forest 5000–6000 years ago is linked to an apparent increase in fire frequency, despite the climatic trend to cooler and moister conditions. This suggests that long-term features of the Holocene fire regime are more strongly driven by vegetation characteristics than directly by climate (Chapter 5).

White spruce forests show *decreased* growth in response to recent warming, because warming-induced drought stress is more limiting to growth than is temperature per se (Chapters 5, 11). If these environmental controls persist, projections suggest that continued climate warming will lead to zero net annual growth and perhaps the movement of white spruce to cooler upland forest sites before the end of the twenty-first century. At the southern limit of the Alaskan boreal forest, spruce bark beetle outbreaks have decimated extensive areas of spruce forest, because warmer temperatures have reduced tree resistance to bark beetles and shortened the life cycle of the beetle from two years to one, shifting the tree-beetle interaction in favor of the insect (Chapter 9). At its altitudinal and latitudinal limits, the boreal forest is expanding into tundra because of tree recruitment beyond treeline during recent warm decades. At arctic treeline, spruce establishment in tundra depends at least partially on thawing permafrost and other disturbances. In summary, current trends show a slow expansion of forest into tundra in the north, retreat of boreal forest in the south, and impending major compositional changes in central portions of Alaska's boreal forest.

Some major Holocene vegetation transitions occurred over a time scale of a few centuries (e.g., deciduous to white spruce) to perhaps 1000 years (e.g., white to black spruce). Future changes in fire regime (Chapter 17) could trigger further widespread change by creating the potential for altered successional trajectories. Although self-replacement, in which the prefire tree species returns to dominance after fire, occurs in the coldest and warmest environments dominated by black spruce and aspen, respectively, successional sequences with multiple stages are more common in intermediate sites. Here, changes in a number of processes could alter vegetation composition and successional trajectory. Late-successional conifers establish during the first and second decades after fire, but their establishment success is sensitive to the depth of the organic mat remaining after fire, understory species composition, and seed availability from on-site serotinous cones (black spruce) or off-site seed sources (white spruce). Insect outbreaks can disrupt or redirect succession by reducing abundance of preferred hosts (Chapters 7, 9). Mammalian herbivores speed succession by eliminating early successional species and by shifting the competitive balance in favor of the less palatable, more slowly growing late-successional species (Chapters 8, 13). Changes in any of these processes could alter vegetation composition and successional trajectory.

After initial establishment, competition, facilitation, and herbivory interact to drive successional change (Chapter 7). Ecosystem controls change at key *turning points* (thresholds), where a shift in dominance of plant functional types radically alters the physical and chemical environments that govern ecosystem processes and disturbance probability (Chapter 1). In the floodplain, intense herbivory by moose initially constrains canopy development, creating an ecosystem dominated by physical controls over soil water movement, driving surface evaporation and gypsum accumulation at the soil surface (Chapters 7, 13). Colonization by thinleaf alder shifts the system from physical to biological control, adds 60–70% of the nitrogen that accumulates during succession, and causes herbivory to change from a deterrent to an accelerator of succession by eliminating palatable early successional species (Chapters 7, 13, 15). Other key turning points include (1) a shift to balsam poplar dominance, where changes in productive potential and litter chemistry enhance NPP and nitrogen cycling rates (Chapters 11, 14), and (2) a shift to white spruce dominance, where mosses grow rapidly in the absence of smothering broad-leaved litter, nutrient cycling rates are reduced by low temperature and the sequestering of nutrients in low-quality litter, and fire probability increases because fuels dry quickly and support fire spread (Chapters 6, 7, 14, 17).

Species diversity is low in the boreal forest (Chapters 6, 13) and varies dramatically through succession, with peaks in early succession (e.g., fire-specialist plants, herbivorous insects, neotropical migrant birds, and mammals) and late succession (nonvascular plants and saprophagous insects).

Many boreal animals exhibit large population fluctuations. Moose and hare densities appear to be sensitive to food availability and predation, whereas vole densities correlate more strongly with climate (Chapter 8). Two native insects have changed from decadal outbreaks to consistently low populations (large aspen tortrix since 1985; spear-marked blackmoth since 1975), whereas other species that had negligible populations before 1990 now show large outbreaks (eastern spruce budworm, spruce coneworm, larch sawfly, and aspen leaf miner; Chapter 9).

Long-term forest harvest studies permit an assessment of potential future human impacts on Alaska's boreal forest. Low-intensity forest harvest (no scarification) reduces initial seedling establishment but maximizes long-term growth of tree seedlings (Chapter 18). Overstory retention treatments have no long-term effect on tree recruitment and growth. These studies suggest that low-intensity management after clear-cutting, an approach that mimics *certain* aspects of natural fire cycles, may maximize ecological recovery. Economics currently preclude widespread commercial forestry in interior Alaska, and future developments of this industry would require substantial changes in world markets and local infrastructure.

Biogeochemistry

Although most surfaces of interior Alaska have not been glaciated during the Quaternary, they exhibit properties of young soils, with minimal profile development being widespread on the landscape (Chapter 3). This occurs because weathering rates are slow because of the cold, and frequently anaerobic, environment and be-

cause surface loess deposition, frost-heaving, and/or erosion counteract these soil-forming processes (Chapters 3, 16).

Aboveground production varies by more than an order of magnitude among major forest types in interior Alaska, primarily due to variation in topography and successional age (Chapters 6, 11). It is greatest in midsuccessional stands on floodplains, where soil temperature and moisture are relatively high. On south-facing slopes, production is constrained by moisture and on north-facing slopes, by soil temperature. On temperature-limited sites, mosses account for half of aboveground production. Except on water-limited south-facing slopes, nitrogen appears to be the factor that directly limits growth, with temperature exerting indirect effects through its impacts on nitrogen cycling (Chapters 11, 12, 14, 15).

The critical controls over the productivity and nutrient cycling of Alaskan boreal forests occur belowground (Chapters 11, 12). Carbon and nutrient cycling rates in fine roots are several orders of magnitude faster than in aboveground tissues because of high belowground allocation and turnover (Chapter 12). Cold temperatures confine fine-root production to zones close to the soil surface, and the progressive extension of fine-root production into deeper soil horizons occurs slowly, as the soil warms through the season. Alaskan trees and shrubs have roots with morphological, phenological, and physiological traits that are similar to those of most forest biomes. Alaskan trees are unusual primarily in their large root allocation and in the large quantity and rapid turnover of fine roots (Chapter 12).

Ratios of aboveground litterfall to soil respiration in interior Alaskan forests are among the lowest recorded in North American forests, suggesting that a large proportion of boreal soil respiration originates in root respiration and the rapid turnover of fine roots (Chapter 12). For example, fine-root respiration constitutes about 60% of total soil respiration in black spruce forests. The soil carbon derived from fine roots is quite labile, so soil carbon stocks can decline rapidly in the absence of continued inputs, such as might occur after fire.

Mammalian herbivores play a key role in the biogeochemistry of the boreal forest. In the floodplain willow communities, they consume 40% of aboveground NPP (Chapter 13). When herbivores are experimentally excluded, biogeochemistry changes rapidly from a system dominated by inorganic C cycling and solubility equilibria to a biologically controlled pattern of cycling dominated by NPP and decomposition.

N_2 fixation inputs by green alder in the uplands and thinleaf alder in the floodplains account for the largest percentage of total N accumulated during succession (Chapters 14, 15). Fixation inputs appear to exceed plant N demand, and significant amounts of fixed N may be lost via leaching or denitrification, particularly in midsuccessional stages, where nitrification potential is high and soil microbial biomass is more C- than N-limited (Chapters 14, 16).

Despite the large quantities of organic N that accumulate in boreal soils, the vegetation is strongly N-limited, and conversion of insoluble organic N to plant-available forms appears to be the rate-limiting step (Chapters 11, 15). Once this organic N becomes soluble, it is quite dynamic. Amino acids turn over more rapidly than inorganic N and are a major source of N absorbed by both plants and microbes (Chapters 14, 15). The natural abundance of ^{15}N in vegetation suggests that uptake of organic N plays a significant role in the N nutrition of the boreal forest.

Landscape Processes and Disturbance

Presence or absence of permafrost is probably the single most important threshold regulating the structure and functioning of Alaska's boreal forest (Chapters 4, 16). Permafrost is discontinuous in most of interior Alaska, being generally present on north-facing slopes and in valley bottoms, where it leads to cold, water-logged soils, and generally absent on the upper parts of south-facing slopes, where soils drain freely. Permafrost temperatures are now typically warmer than -2°C and have warmed about 0.7°C per decade since 1970 in response to regional warming and changes in insulation by snow and vegetation (Chapter 4). Continued warming will likely lead to extensive permafrost degradation within 10 to 25 years. Currently 38% of the research watersheds that have been intensively studied by the Bonanza Creek LTER have unstable or thawing permafrost. Thus, permafrost is likely to be lost much more rapidly in the coming decades than during the past 90 years, over which span a 2.1% loss occurred.

Permafrost response to climate warming involves multiple ecosystem feedbacks that involve changes in insulation by snow, moss, the surface organic mat, and soil drainage (Chapter 16). Insulation declines dramatically after fire, increasing the depth of thawed soil from about 50 cm to 2–4 m. As permafrost recovers during postfire succession, an unfrozen layer (talik) forms between a seasonally frozen or newly developed upper permafrost layer and the lowered surface of original permafrost. In sloping terrain, water drains laterally through the talik, drying surface soils, whereas on flat terrain water may accumulate at the surface, forming ponds or waterlogged soil. In cases where this permafrost contains large volumes of ice, thawing may cause subsidence of the ground surface (thermokarst). Thus, the impact of climate warming on soil moisture in permafrost terrain depends strongly on topography, fire history, and other factors that control talik formation and drainage conditions.

Low-permafrost watersheds or watersheds with well-developed taliks have greater base flow (80% of discharge) and are less flashy (i.e., less likely to cause floods) than high-permafrost watersheds, in which base flow increases from 50% to 60% of discharge in early summer to values similar to those of low-permafrost watersheds in late summer, when mineral soils have thawed (Chapter 16). Areas with abundant groundwater flow also generate aufeis (areas of thick winter ice that forms when groundwater is forced to the surface by freezing soil) that kills most woody vegetation, substantially altering riparian dynamics. Groundwater flow also generates higher concentrations of base cations, inorganic nitrogen, and dissolved CO_2 and less dissolved organic carbon and nitrogen than in permafrost-dominated watersheds, where most water flows through the organic mat. Thus, permafrost and talik distribution strongly influence soil moisture, land-water interactions, and stream discharge and chemistry. In contrast to temperate ecosystems, nitrate losses in Alaskan boreal streams are four to five times greater than deposition inputs, a result that we cannot currently explain in light of the strong nitrogen limitation of watershed vegetation.

The running waters of the boreal forest derive most of their physical and biological characteristics from a cold climate syndrome. Extreme seasonality induces

formation of several kinds of ice in streams and drainage basins. Long-lasting ice cover can limit gaseous exchanges between water and the atmosphere, frazil and anchor ice can disturb substrates, and permafrost in the drainage basin increases transport of dissolved organic carbon and makes streams hydrologically flashy in response to runoff and precipitation (Chapters 10, 16). Glaciers in headwaters transport cold water and sediments during summer melt, reducing substrate diversity and stability and so limiting biotic diversity. As is the case elsewhere, autumnal leaf litter is the major source of food to stream foodwebs and a connection between riparian and aquatic ecosystems. The cascading effects of herbivory on soil systems (changes in species composition of vegetation and chemical characteristics of leaf litter; Chapter 13) affect stream foodwebs via autumnal leaf litter. High-latitude limitations on primary production by both periphytic microbes (attached to streambed sediments) and riparian vegetation make running waters nutrient-poor. Therefore, the uphill transport of marine-derived nutrients by spawning salmon provides a key source of nutrients for stream and riparian consumers. Even so, limited food resources and cold waters slow growth rates and maturation of stream consumers, so many major taxa are absent or in low abundance in Alaskan running waters, compared to their presence in temperate streams. Extreme seasonality renders some habitats uninhabitable in winter, forcing vertical migrations of benthic invertebrates and longitudinal migrations of fishes. The arctic grayling, a ubiquitous fish in boreal forest streams, has a complex life history that maps the seasonal availability of habitats for spawning, juvenile rearing, adult feeding, and overwintering.

Fire is the dominant disturbance agent in interior Alaska but is highly variable in space and time. In the average year, the fire season lasts only three weeks, sandwiched between early summer, when soils are wet from snowmelt, and late summer, when precipitation increases (Chapter 17). However, 55% of the total area burned between 1961 and 2000 burned in just 6 years, when the fire season lasted much longer, giving rise to very large fires. Thus, the fire regime is dominated by unusual years, rather than by average conditions. The 7% increase in area burned in Alaska in the past 40 years is much less than the doubling reported for western Canada. Fire return time varies regionally from <50 years to more than 100 years. It correlates positively with temperature and vegetation cover and negatively with precipitation. Lightning, which accounts for 90% of the area burned, is controlled by both synoptic processes related to El Niño and by local factors such as topography and presence of forest vegetation. Human ignitions, which account for 60% of the fires in Alaska, generally produce small fires because they are lit at times and places where fire does not readily spread.

Recent and projected changes in the boreal forest could feed back to the climate system. The lower albedo and greater sensible heat flux of spruce compared to deciduous forests or nonforested wetlands (Chapter 19) suggest that northward forest expansion could be a positive feedback to regional warming but that loss of forests to the south or net conversion from conifer to deciduous forests resulting from fire could have a net cooling effect, one of the few negative feedbacks to high-latitude warming that has been identified. Boreal forests contain approximately 27% of the world's vegetation carbon inventory and 28% of the world's soil carbon inventory (equivalent to 75% of the total atmospheric carbon), so warming effects on net

ecosystem production (NPP minus respiration) or on fire regime could substantially alter the global climate system. Warming appears to enhance carbon release in dry areas, enhance uptake in wet areas, and enhance methane release in wet areas. The net effect of fire depends on fire severity and on changes in fire frequency. All of these effects on trace-gas feedbacks hinge on permafrost and hydrological changes, which are poorly known. The recent shrinkage of lakes and wetlands in interior Alaska suggests, however, that the CO₂ efflux is increasing and methane efflux is decreasing.

Preparing for the Future

Although the boreal forest is the northernmost outpost of forested biomes, whose current distribution is clearly linked to temperature, its immediate future appears to be more sensitive to projected changes in moisture than to temperature. If warming leads to surface drying, as suggested by recent trends and many climate projections, drought could enhance soil drying and cause more frequent insect outbreaks and fires, triggering rapid changes in vegetation, permafrost, soils, and streams. Alternatively, a more ice-free ocean upwind of Alaska could increase precipitation (Chapters 2, 4), with quite different ecosystem consequences. Although our crystal ball does not allow a clear choice between these alternative futures, it seems quite likely that the Alaskan boreal forest will change dramatically from its current state and that future planning must account for this eventuality (Chapter 20). Only with long-term research, such as that conducted by the Bonanza Creek LTER program, can we understand the controls and patterns of long-term change adequately to prepare society for the choices that it must face.