Vegetation Succession in the Copper River Basin

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The land surface of the Copper River watershed is undergoing constant change. Every year some new land is exposed and some previously vegetated land is covered by ice, eroded by the river, or burned by wildfire. This regular reworking of the landscape creates a diverse assemblage of plant communities. The process of succession is always being reset somewhere in the watershed. As a result the vegetation is a mosaic of different successional stages set within a matrix of climax spruce forest. The major types of disturbance in the Copper River Basin include: insect infestation, fire, windstorms, fluvial processes, glaciers, deltaic processes, and herbivory. All of these processes are taking place within the larger context of tectonic uplift of the mountains and more recently global climate change. The purpose of this paper is to describe these physical and ecological disturbance processes and how the vegetation community of the Copper River basin responds to them. The Copper River starts in the interior of Alaska, cuts through the Chugach Mountains and spreads out into a large delta as it enters the ocean. The upper watershed is sheltered from the maritime influences and as a result is drier and colder. During the Pleistocene a large lake covered this region. Sediments deposited in this lake created a comparatively flat, poorly drained plateau. In the intervening 12,000 years glaciers have advanced and retreated from the plateau leaving behind a series of moraine deposits. The old lake deposits are now dominated by black spruce forest, and the drier, better-drained moraines are dominated by white spruce forest (Clark and Kautz 1998). Slope aspect and the depth of the active layer above the permafrost, which covers 75 to 80 percent of the area, control dominant forest type through out the interior of Alaska. Only floodplains and south facing slopes are free of permafrost (Viereck et al. 1986).

MATRIX SPRUCE FOREST

There are three species of spruce that form the matrix or climax forest in the Copper River basin. Black and white spruce are found in the upper basin and Sitka spruce dominates the area around the Copper River Delta. Although they intermix at the boundaries of their distributions and sometimes even hybridize these species have distinct physical requirements and are prone to different types of disturbance. Black spruce is found in low-lying boggy flats where permafrost is often only 30 to 50 cm below the soil surface during the summer growing season (Viereck and Johnson 1990). The poorly drained soils in these areas allow deep layers of mosses (e.g. *Spagnum spp*. and *Polytrichum commune*) to grow. These mosses in turn modify the soil nutrients and temperature. When air is warm and dry the mosses insulate the permafrost below. In the winter, however, they conduct the cold air and water down to the soil and cause the permafrost to expand towards the surface. The resulting cold soil conditions slow down nutrient cycling, decreasing the nutrients available to the black spruce. In addition these thick (up to 50 cm) continuous layers of moss also prevent important nutrients from reaching the tree roots below. A study on Washington Creek (in the interior near Fairbanks) showed that the annual uptake of nitrogen by the understory mosses was 3 times the nitrogen uptake by the black spruce overstory; and moss biomass production was 18% greater than black spruce (Oechel and Van Cleve 1986). On hill slopes black spruce forest dominate colder north facing slopes and areas at tree line with shallow soils. Despite the waterlogged soils in which these trees grow, the abundant lichens that cover their trunks and low branches make them extremely vulnerable to fire (Viereck and Johnson 1990). Black spruce release their cones gradually over a period of several years so that whenever there is a fire there will be cone on the trees to release seeds and begin the process of regeneration.

White spruce trees cannot tolerate the cold waterlogged soils created by the underlying permafrost. As a result their distribution is limited to well-drained uplands, primarily on warmer south facing slopes and floodplain forests underlain by sands and gravels. These forests also contain a moss layer, but it is much thinner and more discontinuous than in the black spruce forest (Viereck et al. 1986). On the floodplain white spruce forest may be a successional stage that is replaced eventually by black spruce as the forest traps the cold air, the understory layer of moss thickens, and the active layer above the permafrost decreases. Where the drainage is adequate white spruce can dominate indefinitely (Mann et al. 1995). The most significant cause of mortality among mature white spruce is the spruce beetle (Nienstaedt and Zasada 1990).

Sitka spruce grows in a strip along the north Pacific coast where maritime influences moderate the temperatures and increase precipitation. Throughout its range Sitka spruce is associated with western hemlock. The successional relationship between spruce and hemlock is unclear but it appears that hemlock invades existing spruce forest and may dominate the climax forest. In the Copper watershed the maritime climate is restricted to a narrow band along the coast by the steep rise of the Chugach Range. Sitka spruce and western hemlock grow on the well-drained soils of outwash plains and beach ridges. Blow down is the main source of mortality for mature Sitka spruce (Harris 1990).

MECHANISMS OF DISTURBANCE

Windstorms, insect infestation, and fires are the major catastrophic causes of widespread mortality in spruce. Each of these types of disturbance can impact thousands to millions of acres annually in interior Alaska. Even more important than the impact of any single disturbance event is the interaction between these three major sources of mortality. Either blow down or fire can make a forest susceptible to insect infestation. In turn a large insect outbreak leaves thousands of acres of standing dead trees that are extremely susceptible to fire or blow down which can then spread to live forests. Glaciers and fluvial processes are smaller scale chronic disturbances in this landscape impacting less acreage overall but on a more regular basis.

Spruce beetle

In recent years spruce beetle infestation has been by far the most important disturbance in the upper Copper River watershed and throughout much of south central Alaska. In the last seven years, 2.3 million acres of spruce forest in Alaska have been infested. After the most recent outbreak peaked in 1996, the acres of infestation have since declined due to a lack of host material in the most heavily impacted areas (Figure 1). Figures 2 shows the areas in the Copper basin that were impacted (Wittwer 2000). The remaining dead trees and the grasses that quickly invade the dead forests currently represent a substantial fire hazard to the remaining live trees in the area and the surrounding towns (Dyrness et al. 1986).

Infestations of spruce beetle begin in dead spruce trees on the forest floor. If populations get large enough they will infest large, slower growing live trees. Spruce beetles respond quickly to large scale blow downs and fire scorched trees, invading the dead tree and then spreading quickly to the surrounding forests. The resulting outbreaks can be quite extensive and have a large economic impact on the timber industry. Outbreaks are most common in white

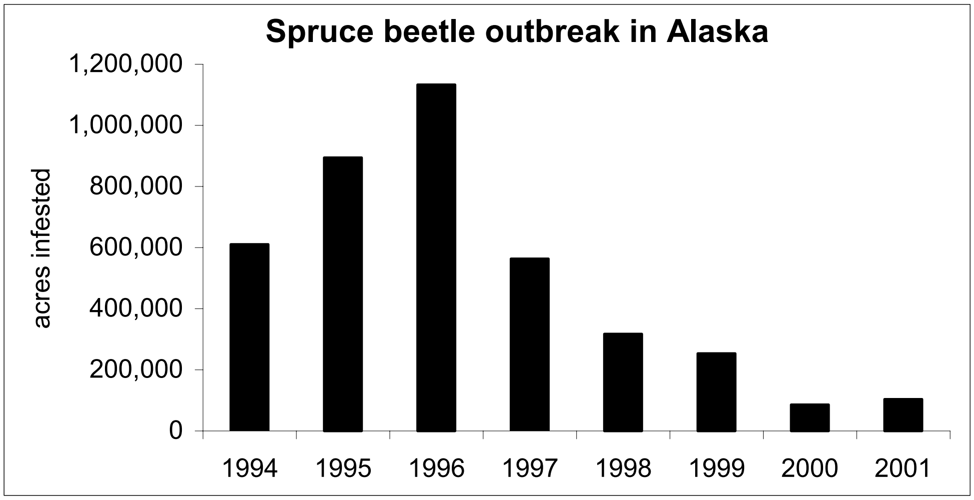

Figure 1. Timing and extent of the most recent spruce beetle outbreak in south central Alaska (Wittwer et al. 1999)

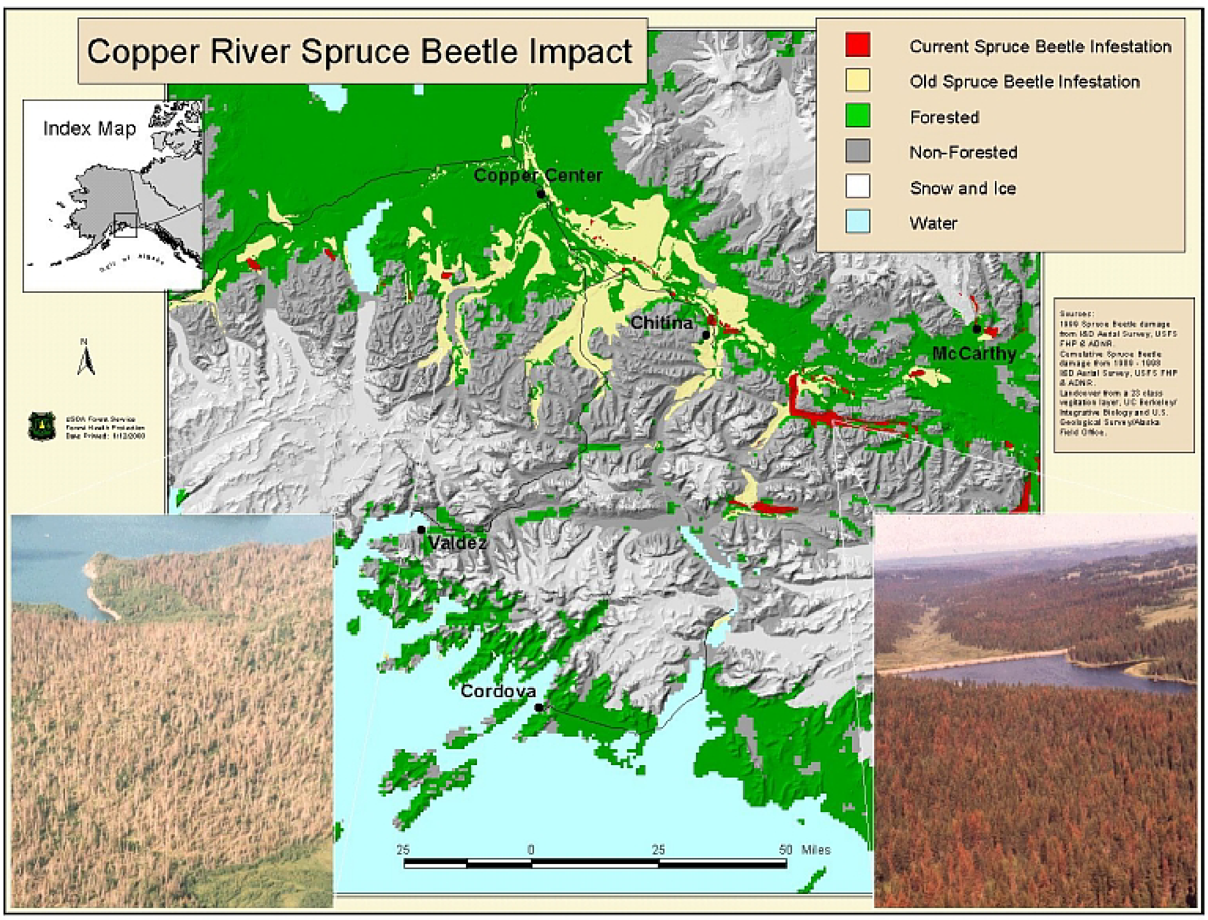

Figure 2. Map of spruce beetle infestation in the Copper River basin as of 1999 from (Wittwer et al. 1999)

spruce forest but a large outbreak can spread to black and Sitka spruce as well especially where they intermix with white spruce (Holsten et al. 2002). Tree ring evidence indicates that the spruce beetle has been part of the natural system at least since 1400 AD, and that climatic conditions appear to be one potential trigger for outbreaks (Zhang et al 1999). There is evidence that cold temperature in the past may have kept large outbreaks in check, and recent warming may have allowed outbreaks to cover a much larger area. As a result global climate change may have a substantial impact on the frequency and severity of spruce beetle outbreaks.

Fire

Although there have not been any large fires in the Copper River basin recently (Kasischke 1999), fire is an important form of disturbance in the northern coniferous forest particularly in the black spruce. In severe fire years 2.5 to 5 million acres burn in interior Alaska. Both white and black spruces are highly susceptible to fire. While spruce trees themselves are not adapted to survive fire, their cones release seeds on to the exposed soil after the fire where new trees can establish. Fire has an important impact on the soil nutrients and underlying permafrost. Nutrient cycling is extremely slow in the cold wet soils of the black spruce forest. Rates of decomposition do not keep up with deposition of organic matter so, despite some nutrient volatilization during the fire, soil nutrients generally increase after a moderate burn. Fires also result in a removal of the moss layer and a substantial decrease in albedo (Viereck et al. 1986). In a study near Fairbanks Viereck and Dyrness (1979) found that these changes resulted in an increase in the depth of the active layer that peaked nine years after the fire at 4 times the depth in the unburned control. This expanded active layer and increased soil temperatures results in increased nutrient cycling, which allows early successional trees to temporarily dominate.

Blow down

Windstorms are an important disturbance primarily near the coast where high winds can knock down large swaths of shallow rooted spruce. One recent windstorm in Minnesota flattened 400,000 acres of forest (Minnesota Department of Natural Resources 2001). This was clearly an extreme event but large blow downs are not uncommon. Older trees tend to be more susceptible to this kind of disturbance not only because they are taller, but also because they may already be weakened by insect or fungal infestation. Forest thinning also makes the remaining unlogged trees more vulnerable to blow down (Dale et al 2001). It is unclear how global warming will impact the frequency of blow downs, but there is some evidence that an intensification of weather patterns will make this sort of event more common.

Floodplain processes

Fluvial processes have two major impacts on the matrix spruce vegetation. First, active channel movement creates a dynamic landscape by destroying existing matrix vegetation and depositing new alluvium. The resulting moist silt and sand bars represent ideal sites for willow, poplar and birch establishment that cannot occur under thickly vegetated spruce forest (Walker et al. 1986). The more the river channel moves the more the banks are dominated by early successional plant species. Areas that are reworked every year are dominated by herbaceous species such as *Epilobium latifolium* and *Dryas sp*.

The other important impact of fluvial processes on vegetation results from the impact of the river on permafrost. The exposure of the riverbanks to solar radiation and comparatively warm water causes a receding of the permafrost. In addition, permafrost forms slowly in the coarse alluvium of newly deposited bars leading to much warmer soil conditions and increased microbial activity (Clark and Kautz 1998). These conditions allow white spruce to dominate in low lands along rivers where black spruce would ordinarily invade. Permafrost and other periglacial processes are discussed elsewhere in this volume (Rains 2002).

Glaciers

Glacial expansion and recession are the most extreme of all the forms of disturbance, but they only impact a small proportion of the landscape in a given year. The processes downstream of glaciers impact a much larger area. Glacial melt water creates large outwash plains below the toe of the glacier. This melt water has two important characteristics. 1) It carries large amounts of sediment that the glacier creates by grinding up the mountains as it flows down valley. 2) It melts off the glacier in pulses as water dammed behind the ice is released or as rain melts the large quantities of glacial ice. As a result, glacial streams spread sediment across wide areas dropping the biggest rocks near the glacier and spreading progressively smaller sediments across a large fan as the slope or the outwash plain flattens out. The rapid discharges of melt water cause drastic shifts in drainage pattern. These two factors combine to create a highly disturbed system where it is difficult for plants to establish. Some glaciers have lakes at their toe created by terminal moraines. These lakes mitigate some of this high disturbance rate by decanting much of the larger sediment. Glacial streams originating in these lakes tend to have a meandering rather than braided channel form giving vegetation a better chance to get established (Boggs 2000).

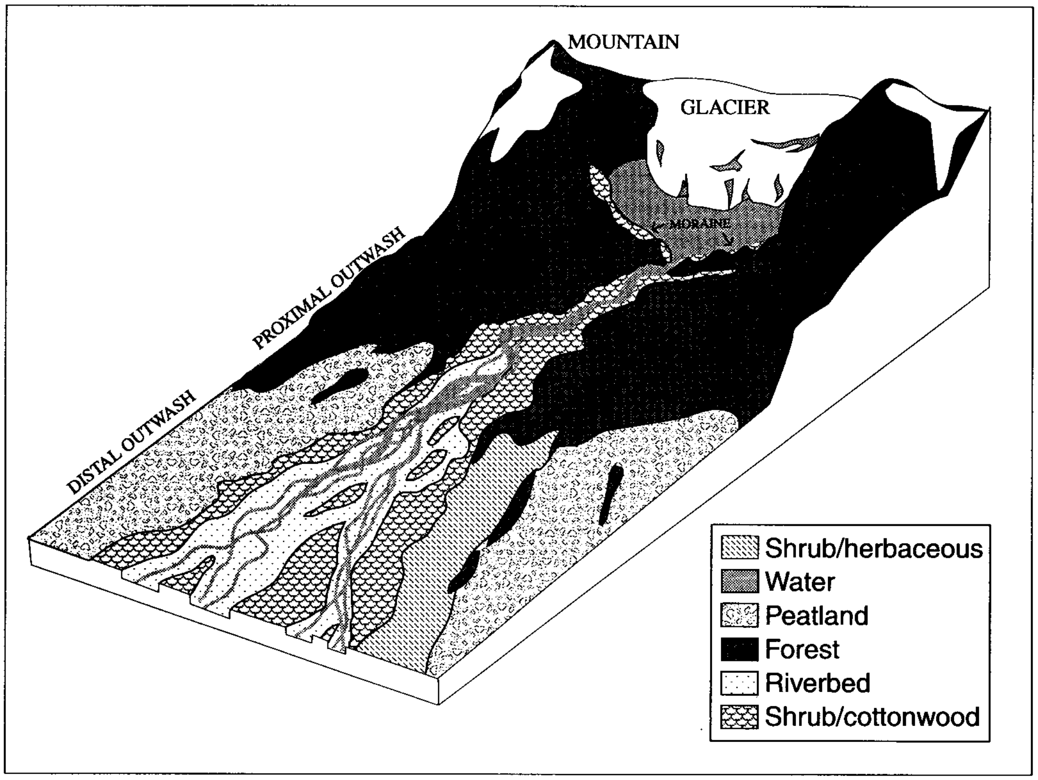

Figure 2: Oblique view of an idealized glacial outwash plain (from Boggs 2000)

Near the glacier, the melt water streams are often incised leaving high, less disturbed terraces that are forested with white spruce or Sitka spruce and western hemlock near the coast. Further away, as the fan spreads out and disturbance increases, the vegetation on the banks never makes it beyond the early shrub stage of succession (willow and alder) before it is disturbed and succession is reset (see figure 2). There are also numerous ponds in this lower fan area created by abandoned channels. These for the most part eventually fill in with peat (Boggs 2000).

Deltaic processes

For the purposes of this paper I am primarily interested in terrestrial processes and vegetation types. I will not discuss tidal marsh, barrier island, or coastal dune landscapes because the processes that control these landscapes are primarily maritime rather than terrestrial processes and the vegetation communities that colonize them are fundamentally different. In 1964, however, there was a large earthquake that uplifted former tidal marsh creating a new uplift marsh landscape that is no longer tidally influenced. This is now a freshwater system of levees, small channels, and ponds. Uplift has allowed shrub and tree species that could not survive in the tidal marsh to colonize the levees. On these upland areas the sequence of dominance is similar to the successional sequence on the upstream outwash plains (Boggs 2000).

Away from the levees beavers, which were previously excluded from the marsh by the salt water, play an important role in this landscape by damming small channels and creating ponds and wetlands where herbaceous vegetation dominate. Within this system of wetlands and ponds, gradients of water depth, nutrient, pH and salt concentration drive the species distributions. These gradients are, in turn, controlled by groundwater inputs. A completely different suite of plants dominates shallow ponds that receive nutrient rich input from groundwater and stream flow than bogs whose main water source is nutrient poor precipitation. Sedge rich ponds often build up so much peat that they choke off their source of nutrient rich water and are converted to sweetgale/crowberry bogs (Boggs 2000). As the surface ages the amount of open water decreases, as does the pH. (Boggs and Shephard 1999).

POST DISTURBANCE SUCCESSION

Succession of plant species along the Copper River is generally considered autogenic, meaning that the sequence of ecological changes that allow one dominant group of plants to be replaced by another is driven by changes that the plants themselves make to their environment. In this case life history traits of the dominant tree species such as dispersal ability, growth rate, and shade tolerance drive succession. For the most part, these successional processes follow the same general pattern regardless of the type of disturbance. Once the ground surface has been cleared of litter and competing plants, seeds blow in from the surrounding areas setting primary succession in motion (Walker et al. 1986). Figure 3 shows some examples of the species involved on the Copper River.

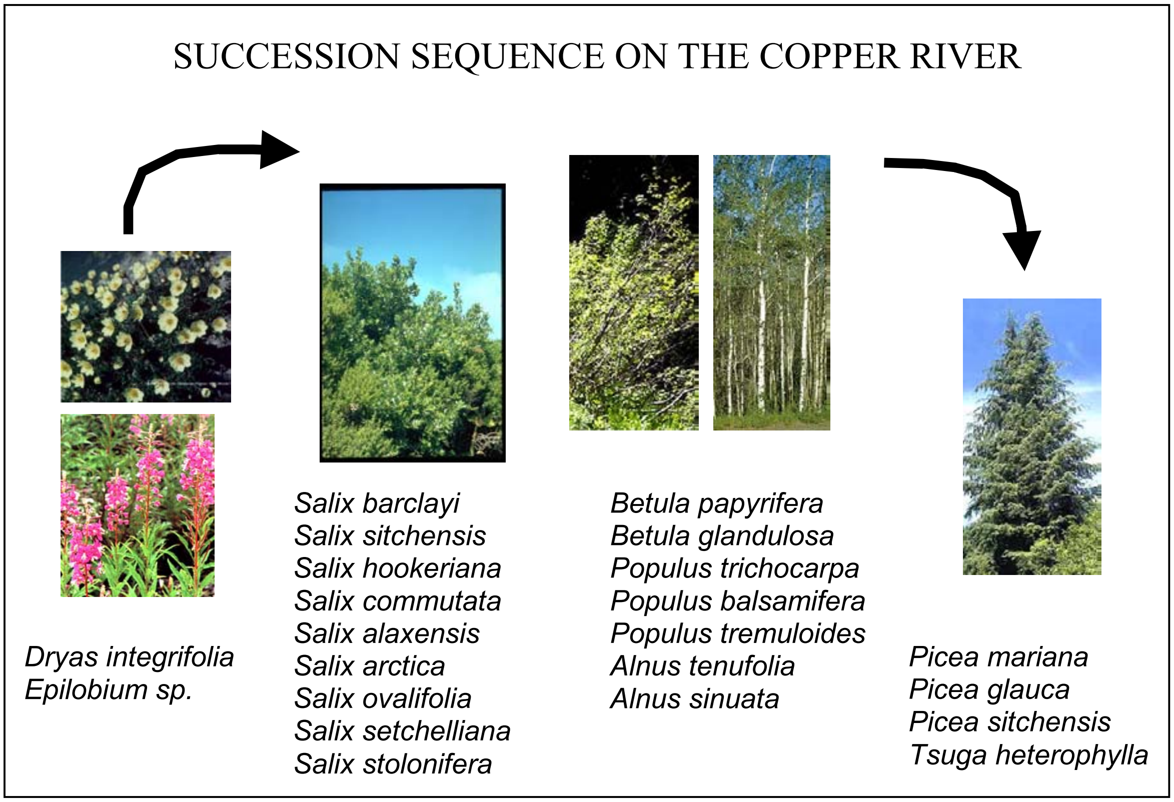

Figure 3. Flow chart of the post disturbance successional sequence including examples of the species that are found on the Copper River.

Plants with light seeds that can disperse long distances and arrive in large numbers have a temporary advantage. Seeds of all the tree species can and do sprout on this new surface, but in the early years after disturbance fast growing herbs and shrubs dominate. Fireweed and other *Epilobium* species usually dominate the first year after a disturbance. In the years that follow, willow shrubs start to grow up through the herb layer. Alder has slightly larger seeds so they arrive more slowly after a disturbance, but they are fast growing and spread quickly once they become established. As the alders and other tree saplings grow taller than the willows, they begin to dominate the site. Eventually the sapling poplar, aspen, and birch shade out even the alder and create a dense forest where little light makes it to the forest floor. Throughout this early successional series spruce have been slowly growing in the understory. Spruce is the only tree in this area that can establish in the thick litter and moss layer and continue to grow in the shade created by this increasingly dense forest. As the fast growing species begin to die out creating gaps in the canopy spruce can take advantage of the increased light conditions and grow to eventually become the dominant tree (Walker et al. 1986).

Despite the overall similarities listed above, each type of disturbance clearly creates different physical starting conditions for primary succession. Soil depth, nutrient availability, and soil temperature are the major physical determinate of the rate of succession. Spruce beetle infestation and moderate fires do not volatilize all the soil nutrients and depending on the timing and conditions may cause the spruce to release seeds. This clearly speeds up the successional sequence because it eliminates the dispersal limitation that often slows spruce colonization. At the other extreme glacial retreat exposes bare rock that is unsuitable for colonization by even willows and herbs without substantial modification by lichens and then herbaceous species such as *Dryas sp.*. Hot fires and fluvial processes represent a middle ground where nutrient poor soils are available for colonization (Viereck et al. 1986).

Throughout the course of succession the physical conditions at the site and the stresses that the resident plants must tolerate change. In the beginning, soil nutrients are low (except after a low intensity fire), there is plenty of available light, and soil is warm (increased active layer due to a change in albedo). As the sapling trees get taller and eventually dominate the site, soil nutrients increase (due to increased litter, nitrogen fixation by alders, and soil microbial action), available light at the understory decreases substantially, and the soil active layer becomes smaller. The final spruce stage is a more open forest so there is more available light in the understory, but the cold soil conditions make nutrient cycling slow, so available nutrients decrease dramatically (Bryant and Chapin, III 1986).

Herbivory

These physical changes throughout succession have important implications for herbivory in the forest. Both moose and snowshoe hare can have substantial impact on young trees in the understory. The specific ecology of moose is discussed elsewhere in this volume (Hammersmark 2002). Plants have two main strategies to cope with herbivory. They can use defensive chemicals and structures to discourage animals from eating their leaves or they can just grow quickly and replace damaged tissue. The relative effectiveness of these strategies changes as conditions change with succession. Chemical and structural defenses in Alaska are generally made using carbon, which plants get from the air using photosynthesis. These defenses are easy and metabolically cheap for the plant to make when there is plenty of available light. In the early and final stages of succession light for photosynthesis is not limiting plant growth, soil nutrients are. New leaves are difficult to make because plants have limited access to important soil nutrients such as nitrogen and phosphorus, but carbon based leaf defenses require only light, air and water, which are plentiful. Once the poplar, aspen and birch trees reach maturity, however, conditions change. There is much less light in the understory where willows and herbs are trying to hang on and an increase in soil nutrients. Now carbon based defenses are expensive to make. Plants respond to these changing conditions by making fewer defensive chemicals and structures. As a result herbivory increases and when plant growth can no longer keep up with the rate of herbivory, low growing early successional species such as willows are eliminated from the forest (Bryant and Chapin, III 1986).

CONCLUSIONS

The dynamic nature of the Copper River landscape maintains diversity in a harsh, nutrient poor system that would otherwise be dominated by a few shade tolerant species that can survive cold soil temperatures and low nutrient levels. The main impact of disturbance in this system is to alter the soil nutrient, temperature and light conditions to allow a suite of less tolerant species to persist. The resulting mosaic of forests of different ages is direct evidence of a history of disturbance that in some cases is clear, but in others is more obscure. A patch of willow and alder shrubs growing along a river is obvious evidence of recent channel movement, whereas an even age stand of birch on a hill slope is more ambiguous. The interaction of different forms of disturbance also plays an important role on the landscape, but can be difficult to interpret. A large wildfire that starts in a forest of dead trees that were previously killed by an insect infestation erases the evidence of the earlier disturbance. These problems contribute to difficulties in predicting the impact of global warming. However, it does seem likely that large-scale disturbance may have already increased and will continue to increase in the future. One study of climate change suggested that increased levels of CO_2 and temperatures may lead to increased drought stress and actually decrease rather than increase tree growth rates in Fairbanks (Barber et al. 2000). While another suggested that temperature and precipitation will increase together causing an increase in growth rates in Anchorage (Juday 2000). The impact of climate change may vary throughout the state but it is clear that in the late 1970's all of Alaska experienced a sudden change in climate and the vegetation is still adjusting (Juday 2000).

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