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Editors

Global Climate Change and Freshwater Ecosystems

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Climate Change and Alaskan Rivers and Streams

M.W. Oswood, A.M. Milner, and J.G. Irons III

Introduction

In this chapter, we explore the potential of Alaskan rivers and streams as exemplary systems for the study of effects of global climate change on high latitude freshwaters in northern regions. A wide range of climates and resulting ecosystem types are found in high latitudes. A major factor in the distribution of these ecosystem types is the latitudinal decrease in yearly input of solar energy and the latitudinal increase in its seasonal amplitude. In addition, the ameliorating effects of maritime influences (especially from warm ocean currents) produce regional differences in climate. Warming of northern Europe and much of Alaska by ocean currents (compared to frigid Greenland at a similar latitude) are classic examples (Young, 1989; Stonehouse, 1989). Alaska's climate includes maritime in the southeast panhandle, continental in the central interior, and arctic in the northwest and north. Likewise, distribution of permafrost and vegetation range from coastal Western Hemlock–Sitka Spruce forest with no permafrost to arctic tundra underlain by continuous permafrost. Any attempt to assess potential impacts of climate change in polar and subpolar regions must take into account both regional physiographic differences (e.g., distribution of permafrost) and changes in heat transfers from lower latitudes (e.g., Roots, 1989).

Climate modeling indicates that global warming may be amplified at high latitudes (Hall, 1988; Manabe and Wetherald, 1980; Mitchell, 1989). Regional and seasonal changes in precipitation are expected, particularly increased winter snowfall (Mitchell, 1989; Roots, 1989). Changes in the extent and duration of ocean ice cover will likely alter the availability of atmospheric moisture and contribute to these precipitation changes (Roots 1989). Comparison of precipitation changes from cold to warm years (over the past 50 years) shows increased precipitation at North American high latitudes, including Alaska (Wigley et al., 1980). Roots (1989) reviews several studies that indicate that warmer temperatures in the Pleistocene interglacial periods were associated with greater precipitation at high latitudes.

Climate warming at high latitudes seems likely to produce complex and far-reaching ecosystem changes in cold-dominated systems. Some changes (e.g., thawing and respiratory release of carbon from frozen peaty soils) have the potential to feed back positively to atmospheric carbon dioxide concentration (McElroy and Moore, 1988). The projected changes in temperature are proportionally greater (constitute a relatively greater change from existing temperature regime) for high latitude systems than for systems at lower latitudes (Roots, 1989). Thus environmental changes in polar and subpolar regions may provide "early warning" signals for the detection of global warming. The most obvious effects of high latitude climate change will likely involve changes in the cryosphere (snow, glaciers, permafrost, and ice cover) with consequent changes in biotic and biogeochemical processes of rivers and streams.

In this chapter, we first examine changes in the dynamics of glaciers (e.g., glacial advance or recession) and the associated complex changes in periglacial freshwater environments. We briefly examine potential changes in the contribution of glacial runoff to streams and the potential effects on biotic communities. The cryosphere also includes frozen soils (permafrost). Decomposition is slow in cold-dominated soils and soil carbon stores are consequently great. We suggest (with other authors) that warming of northern soils may increase the fluxes of carbon dioxide to the atmosphere (exacerbating global warming) and further suggest that transfer of dissolved organic carbon to streams will increase. The thermal environment of northern freshwater systems is generally severe, with lengthy ice cover, freezing of substrates, and low annual accumulation of thermal resources. We discuss the potential consequences of an ameliorating climate on the biogeography of freshwater organisms, including northward extensions in the distributions of lotic organisms. Finally, we speculate on some potential effects of climate change on ecosystem processes (herbivory, fire, light, and nutrient availability) and cascading effects on plant physiology of riparian trees (determining food quality of leaf litter) and, ultimately, detrital food webs in streams.

Throughout this chapter, we have combined current predictions of climate change in the high latitude region of North America with relevant aspects of our current knowledge of Alaskan lotic systems. Such an exercise immediately highlights the shortcomings of both the climate change models and our understanding of basic high latitude ecosystem structure and function. Perhaps the most important use of such predictions of ecosystem perturbations caused by climate change is to suggest critical ecosystem measurements and experiments to be carried out over the next few years and decades. Our ability to assess and manage anthropogenic changes in the biosphere may ultimately depend on the timely collection of this information.

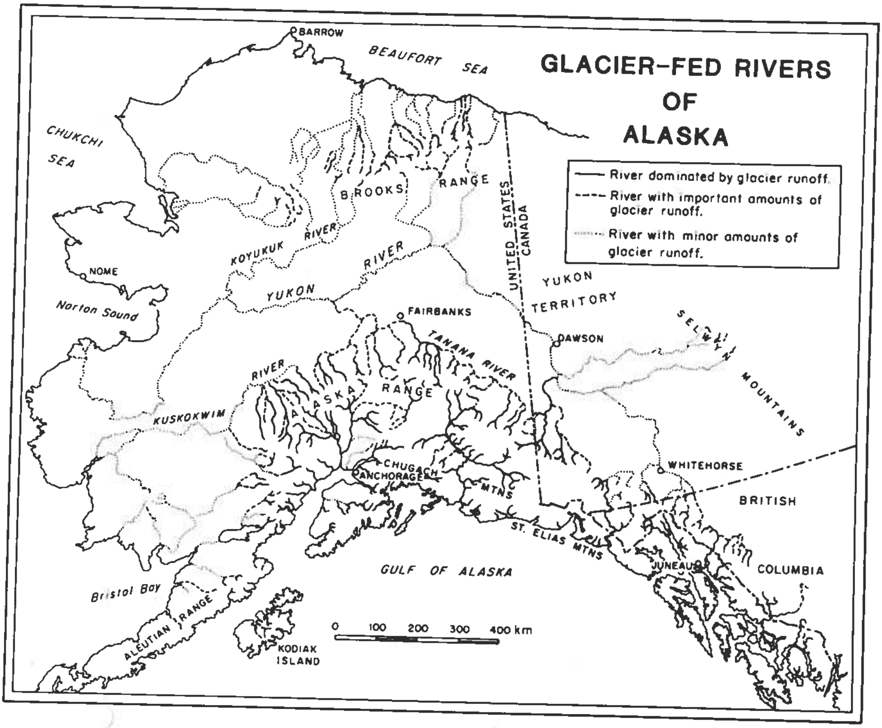

FIGURE 9.1. Influence of glaciers on Alaskan rivers.

Glaciers and Streams

Glaciers occupy approximately 73,000 km^2 or 5% of Alaska with an estimated average runoff rate of 220 km^3/yr; equivalent to 35% of the total runoff in Alaska, 14% of the runoff from the conterminous states and 10% of the total runoff in the United States (Mayo, 1986). Glaciers influence the flow and water quality of all the major Alaskan rivers. Rivers with substantial glacial influence flow from the Alaska Range, the Chugach Mountains, and the Wrangell St. Elias mountains (Figure 9.1). Overall, the effects of glacial runoff tend to diminish downstream as nonglacial flow is added.

A common hypothesis is that global warming will cause glaciers to recede due to increased melting and, as a result, sea levels will rise (Roots, 1989). However, this may be an oversimplification for Alaskan glaciers as the relationship between climatic change and glaciers is complex. The effect of climate change may be very different for glaciers that terminate on land compared to those that terminate at tidewater.

Terminus on Land

Recent records seem to indicate that climate change may cause glaciers to increase in mass and advance. Predicted temperature increases at high latitudes are more pronounced in winter than summer, causing increased precipitation, which elevates snow accumulation in the glaciated basin. For example, measurements of the Wolverine Glacier in southcentral Alaska and the Gulkana Glacier in the Alaska Range indicate that increased air temperatures since the early 1970s have resulted in an increase in glacial mass and glacial thickness (Mayo and Trabant, 1984; Mayo and March, 1990). The increase in glacial mass translates into glacial advance at the terminus after a time lag. Post (1969) identified over 200 glaciers in Alaska and the Yukon that periodically surge and retreat in cycles that range from 15 to 100 years. Although surging is indirectly linked to climate change, increased snow accumulation may enhance this phenomenon.

Terminus at Tidewater

Although climate is a first-order control on glaciers that terminate at saltwater or in large freshwater lakes, these glaciers can advance over long distances independently of climatic variations due to the forward movement of protective submarine moraines (Powell, 1990). A dramatic example was the Hubbard Glacier, the largest tidewater glacier in North America, which in 1986 advanced and blocked the entrance of Russell Fjord. Tidewater glaciers can also retreat rapidly by calving into deep fjords or lakes behind the moraines if they recede only a short distance from the protective moraines against which they were formerly grounded (Mayo, 1988). However, it is possible that climate variations are responsible for a glacier losing the ability to maintain itself on the protective moraine. Rapid recession of tidewater glaciers following retreat from a protective moraine has occurred at Glacier Bay in southeastern Alaska and Kenai Fjords in southcentral Alaska. In these areas, remnant ice sheets cut off from actively retreating glaciers feed new streams.

Glaciers and Runoff

The relationship between glacier movement and glacial runoff is complex for glaciers terminating on land. Predictions of runoff from the Wolverine Glacier have been made for various scenarios of climate change (Mayo, and Trabant, 1984). If glacier growth is due to warmer temperatures and increased airflow from the Pacific Ocean, runoff should increase due to a higher degree of summer melting and precipitation (Figure 9.2). If glacier growth is due to climatic cooling with predominant airflow from the arctic, then less melt runoff and precipitation are available. In general, runoff from glaciated basins in the Alaska Range has gradually increased during

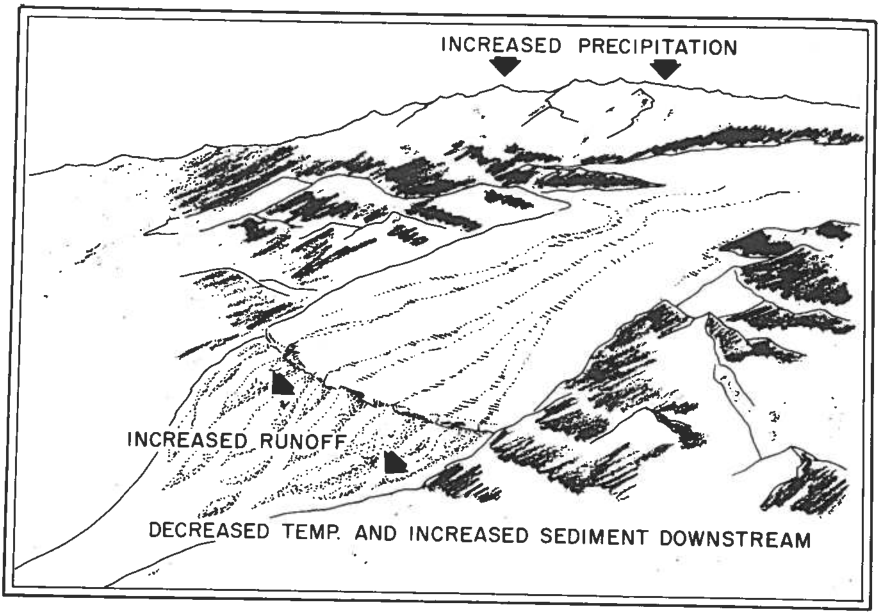

FIGURE 9.2. Potential effects of climate change on a glacier (and associated rivers and streams) with terminus on land.

the past 10 to 15 years (Mayo and Trabant, 1986). Increased runoff has not yet been recorded during the thickening of the Wolverine Glacier but is anticipated (L.R. Mayo, U.S.G.S., personal communication). However, sustained temperature increases above 0°C may eventually lead to glacial recession, which will initially also result in increased runoff. Continued glacial recession will, however, produce less runoff as the glacier decreases significantly in mass (Benson et al., 1986). Surging glaciers may dam up rivers and streams, which, when the glaciers retreat, causes catastrophic flooding.

The relationship of tidewater glacier movement and glacial runoff is even more complex (Figure 9.3). Rapid glacial recession can cause the creation of new freshwater streams that are colonized by biotic communities. The rapid advance of tidewater glaciers may form a glacier-damned lake that can overflow into streams, significantly increasing their flow.

Effect on Biotic Communities

Increased glacial runoff may have a significant effect on flow, temperature, and sediment regimes in downstream areas. Changed runoff patterns and altered sediment loads may influence channel morphology and stability, substrate composition, and habitat complexity (Williams, 1989). Reduced

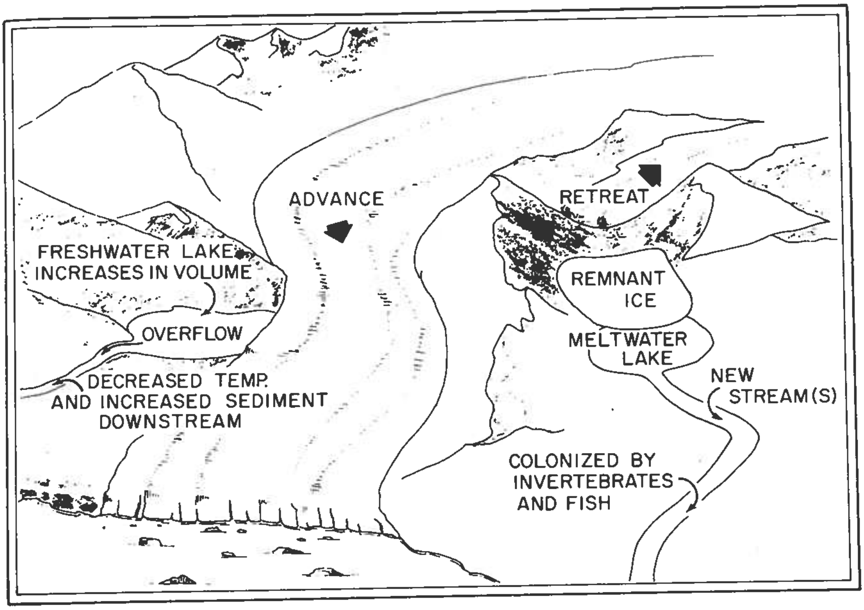

FIGURE 9.3. Potential effects of climate change on a tidewater glacier (and associated rivers and streams).

temperatures from increased contributions of glacial meltwater near glaciers may eliminate certain invertebrate taxa or increase the length of their life cycles. Salmonid developmental rates, in terms of egg incubation, fry emergence and growth, and time of smoltification, may be altered. Turbidity, caused by suspended inorganic particles, results in decreased primary production, reduced abundances of invertebrates, and lower fish production (Lloyd, 1987; Lloyd et al., 1987). Of particular concern for macroinvertebrates may be the extent of sediment deposition on the streambed (filling the cobble interstices and restricting access to the underside of stones) rather than turbidity induced by suspended sediment. Clearly, potential impacts of increased glacial runoff would be greatest if they were to affect streams that have, at present, relatively clear water with unembedded substrate.

New streams in Glacier Bay formed by glacial recession have been rapidly colonized by chironomid larvae that may initially reach large densities (Milner, 1987). After a number of years other groups colonize, including stoneflies and mayflies. The long time for development (>10 years to maximum species diversity and species equilibrium and >25 years for noninsect species to colonize) is attributed to the different dispersal and colonizing abilities of the immigrating species and distance from source areas (Gore and Milner, 1990). In less than 30 years, streams may develop salmonid runs of commercial importance. Streams are initially colonized by Dolly Varden charr (*Salvelinus malma*) but as flow and sediment influences ameliorate, other salmonids become more numerous (Milner and Bailey, 1989). In these developing streams the retention of flow-buffering lakes within the watershed is important to act as a sediment trap and prevent detrimental effects on downstream areas. Two stream systems with lakes in Kenai Fjords, less than 80 years old, support a commercial fishery for sockeye salmon (*Oncorhynchus nerka*). Hence, in a short time period rapid recession of tidewater glaciers can have an important socioeconomic effect on an area by creating streams that support a commercial salmon fishery.

It is expected that another advance of the Hubbard Glacier will occur within the next few years and, if the dam does not burst, cause Russell Lake to fill to a height of 39 m over a 1.1- to 1.5-year period. This would cause an overflow of Russell Lake southward into the Old Situk Creek and would increase the present average discharge of 10 to 15 $m^3\ s^{-3}$ to an estimated 220 $m^3\ s^{-1}$, with peak discharges about five times greater (Mayo, 1988). The physical characters of Old Situk Creek and the lower Situk River would be drastically altered, with the water becoming glacial, turbidity increasing (Mayo, 1988), and water temperatures likely decreasing (Thedinga et al., 1990). These high discharges will cause the Old Situk Creek and a portion of the Situk River to become a cool, fast, turbid river and will reduce salmon spawning and rearing to stream margins (Thedinga et al., 1990).

Permafrost, Soil Carbon, and Stream Ecosystems

Permafrost is ground that is continuously at or below 0°C during at least 2 years and is found in high latitudes and altitudes (Brown and Andrews, 1982; Young, 1989). Nearly one-fourth of the earth's surface is influenced by permafrost (Brown and Andrews, 1982; Bruemmer, 1987). Permafrost may be continuous, i.e., underlying all soil except under larger aquatic systems. In somewhat warmer regions, permafrost is discontinuous and is found in locally cold microclimates (e.g., north-facing slopes and low-lying poorly drained peaty soils). The presence of permafrost is responsible for much of the character of northern ecosystems. Permafrost is generally impervious to the percolation of water (Young, 1989) and is the basis for the "paradox of the arctic," i.e., the generally water-logged summer soils and relatively high diversity of plant life in spite of very low annual precipitation (Bruemmer, 1987). The depth of summer thaw (the "active layer") in part determines the kind of vegetation that can exist in a particular location. White spruce requires approximately 1 m of seasonally thawed soil, while black spruce requires only about 0.5 m. The only trees that tolerate active layers less than 0.5 m are the prostrate dwarf birches and dwarf willows characteristic of arctic tundra (Bruemmer, 1987).

Soil carbon density (kg C m^{-2}) is high in boreal forest, tundra, and, especially, wetlands (Post et al., 1982; Schlesinger, 1977). Soil carbon densities reflect the balance between input (organic matter production) and decomposition. In the cold and often water-logged soils common at high latitudes, decomposition is reduced and soil carbon accumulates. In consequence, boreal forest and tundra soils contain a disproportionate share of world carbon stores compared to their surface area. Several authors (e.g., Billings, 1987; Billings et al., 1982; Chapin, 1984; Post et al., 1982; Roots, 1989) have pointed out that climate warming may decrease high latitude carbon stores via thawing of frozen peat, warming and drying of these cold, waterlogged soils, and subsequent production of carbon dioxide via soil microbial respiration. However, given the uncertainties of precipitation and soil moisture predictions, the alternative scenario of increasingly waterlogged soils from a wetter climate, with increased carbon accumulation and increased release of methane (McElroy and Moore, 1988), must be recognized. Another route of increased carbon flux from high latitude soils is via increased transfer of dissolved organic carbon (DOC) from soils to streams and rivers, with subsequent respiration to carbon dioxide (Figure 9.4) in lotic, lentic, or near-shore marine systems (Coutant, 1981). Increased flux of carbon dioxide or DOC from high latitude soils is important for two reasons: (1) such changes may transform high latitude soils from net sinks for carbon to net sources and so contribute to increasing atmospheric carbon dioxide, and (2) increasing ecosystem output of carbon may serve (along with changes in other high latitude phenomena such as permafrost depth) as a sensitive early indicator of ecosystem effects of global climate change.

Melting of permafrost (i.e., thermokarst processes) can create thaw lakes and beaded streams. Beaded streams consist of more-or-less rounded pools connected by narrow interconnecting channels. Pools of beaded streams form where a stream flows over and partially melts an ice wedge (Young, 1989). Two of us (M.W.O. and J.G.I., in collaboration with Dr. D. Schell, University of Alaska Fairbanks) have investigated the carbon dynamics of a beaded stream (Imnavait Cr.) on the North Slope of Alaska. Imnavait Cr. contains high concentrations of dissolved organic carbon (Oswood et al., 1989) consistent with derivation of stream water from the shallow, carbon-rich active layer (Figure 9.4). Annual transport of carbon from Imnavait Cr. (adjusted for watershed area and annual runoff) is very similar to transport from an adjacent watershed (Peterson et al., 1986) and seems high compared to data from small watersheds from other biomes. Brinson (1976) and Mulholland and Watts (1982) each provides equations predicting annual watershed output of organic carbon (per unit watershed area) from annual runoff. Predicted carbon transport from Imnavait Cr. is 0.756 g TOC m^{-2} yr^{-1} based on Brinson's (1976) equation and 1.99 g TOC m^{-2} yr^{-1} based on Mulholland and Watts' (1982) equation. The actual value for 1987 was 3.013 g TOC m^{-2} yr^{-1}, a value among the higher

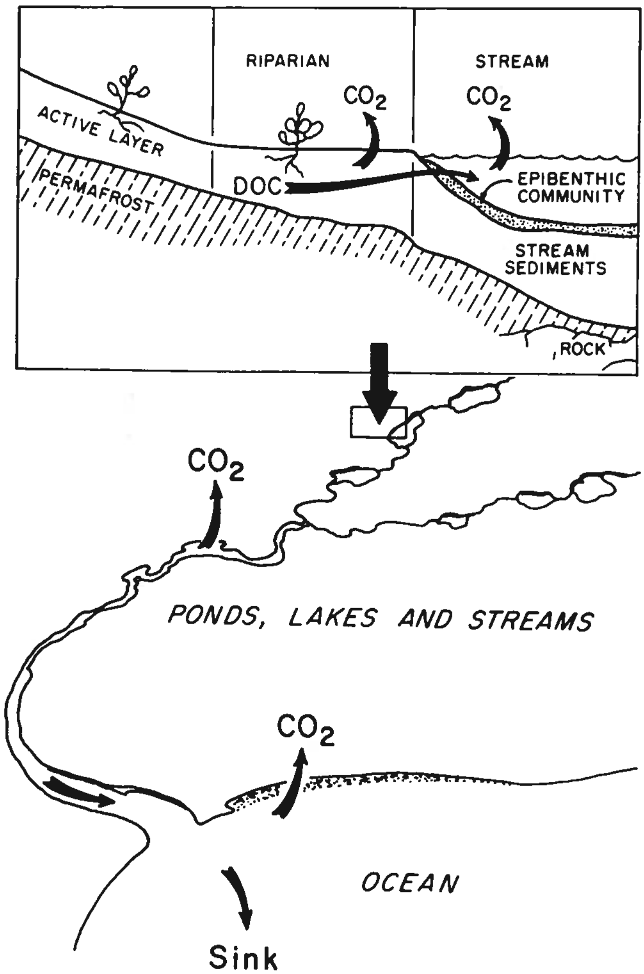

FIGURE 9.4. Diagrammatic cross section of an arctic tundra stream. Increased temperatures would likely result in a deeper active layer and increased respiratory fluxes of CO_2 to the atmosphere and increased hydrological transport of dissolved organic carbon to the stream (with subsequent respiratory processing to carbon dioxide).

deviations from the regression lines of annual TOC output vs runoff (compare with Figure 5 in Brinson, 1976 and Figure 2 in Mulholland and Watts, 1982). There are several alternative, but not mutually exclusive, hypotheses suggested by these findings: (1) relatively high watershed outputs of carbon are due to short-term regional fluctuations in climate unrelated to any global climate changes, (2) high carbon output is characteristic of high latitude watersheds and predictive equations (Brinson, 1976; Mulholland and Watts, 1982) may require modification as more data for high latitude systems become available, and (3) these fluxes are the early result of long-term climate warming and the resultant release of ancient carbon from arctic soils via permafrost warming. Data on yearly watershed carbon fluxes (along with associated data on any changes in regional climate and permafrost characteristics) are necessary to distinguish among these hypotheses. Consistent with the hypothesis of permafrost warming (and consequential release of carbon) is the finding that the upper permafrost in northern Alaska has warmed 2–4°C over recent decades to a century (Lachenbruch and Marshall, 1986).

Is hydrologic transport of carbon from arctic watersheds significant in terms of potential contribution to atmospheric carbon stores (following respiration of dissolved organic carbon to carbon dioxide in aquatic systems) compared to efflux of carbon dioxide to the atmosphere from arctic soils? A crude comparison is possible by examining hydrologic transport of carbon (and assuming that all such carbon reaching a stream is eventually respired to carbon dioxide in downstream rivers, lakes, or in the ocean) with carbon dioxide evolved from soils directly to the atmosphere. Transport from Imnavait Cr. (3.013 g TOC m^{-2} yr^{-1}) is modest but significant compared with output of carbon dioxide from tundra soils (mean = 95 g C m^{-2} yr^{-1}, $n = 3$ from Table 4 in Schlesinger, 1977).

Potential Effects of Climate Change on the Thermal Environment of High-Latitude Streams

The thermal environment of streams and rivers is a key determinant of many aspects of the ecology of lotic organisms. Thermal features of the aquatic environment, such as minimum and maximum temperatures, accumulated degree-days, and rates of temperature change partially determine organismal growth and maturation, fecundity, and survival (Oswood et al., 1991; Sweeney et al., Chapter 7, this volume; Vannote and Sweeney, 1980; Ward and Stanford, 1982). Rivers and streams at high latitudes share a rigorous thermal environment with adjacent terrestrial systems. Ice cover is lengthy (generally 6–8 months) and annual accumulated Celsius degree-days are low (approximately 400–1000). As in terrestrial ecosystems, the amplitude of seasonal thermal changes increases with latitude so that polar aquatic systems are ice-covered for most of the year but may have very high summer water temperatures (Oswood et al., 1989b). Predicted changes in surface air temperatures in response to doubling of atmospheric carbon dioxide are significantly greater for high latitudes than for lower latitudes. Predictions by Manabe and Wetherald (1980) indicate a warming of approximately 4 to 8°C from 60–80° latitude. Such a temperature change would have several likely effects on stream thermal characteristics although predictions for systems receiving substantial runoff from glaciers are difficult (see above). The most obvious consequence (at least for nonglacial streams) is a significant increase in the annual accumulated degree-days, via increased water temperatures over a longer ice-free season. Although temperature increases are likely to be most pronounced in winter (Mitchell, 1989), a 4°C increase in water temperature over a 4-month ice-free season would constitute an increase of approximately 500 degree-days, or roughly a 50–100% increase in yearly accumulation of degree-days. Changes in winter air temperature would increase the length of the ice-free season and decrease freezing to the substrate in shallow margins of high latitude freshwaters (overwintering of benthic invertebrates in relation to freezing is reviewed by Oswood et al., 1991). Hall (1988) reviews the use of remote sensing to monitor changes in freeze-up and break-up of lakes. The timing of freeze-up and break-up of riverine and lake ice appears to be a very sensitive measure of climate change. In addition, long-term historical records exist for some northern rivers. For example, the time of break-up of the Tanana River (interior Alaska, near Fairbanks) is the focal point of the Tanana Ice Classic held since 1917 (the lotic equivalent of a football pool). In sum, it seems likely that the thermal environment of polar and subpolar streams is likely to become much more benign under current climate change scenarios.

The most likely consequence of a less rigorous thermal environment is a substantial change in the biogeography of high latitude freshwater organisms. Compared to lower latitude lotic systems, Alaskan systems are dominated by Diptera and many taxa are absent or very scarce (Oswood, 1989a). Although the ecological constraints to distributions of northern organisms likely involve complex interactions between low availability of organic carbon (see below) and severe thermal regimes, amelioration of thermal regimes seems likely to allow northward movement of mobile organisms, e.g., fishes and insects. Both increased water temperatures and decreasing permafrost (producing year-round groundwater flow) may make streams more suitable for salmonines (Meisner et al., 1988). There is the potential for complex adjustments of benthic invertebrate communities with the arrival of new competitors or predators (e.g., Megaloptera). Conversely, it is possible that some cold water stenotherms may lose habitat (Coutant, 1981). Changes in the biogeographic distributions of vagile organisms may be the aquatic equivalent of changing tree-line and may serve as an excellent early indicator of climate change (Coutant, 1981; Roots, 1989). We agree with Coutant (1981) that historic biogeographic records should be summarized and changes in organismal ranges monitored, and that the joint roles of temperature and carbon resources in determining the distributions of organisms should be investigated.

Potential Changes in Leaf Litter Food Quality and Quantity due to Climatic Change

Leaf litter is a major energy source for streams with substantial riparian canopies. It has been known for over 20 years that the leaf litter from trees of different species may differ in quality as food for shredding stream invertebrates, and that litter from different species is processed (decomposed) at different rates in streams (Kaushik and Hynes, 1968, 1971; Petersen and Cummins, 1974). There is a large body of literature on this topic, reviewed by Anderson and Sedell (1979) and Webster and Benfield (1986). The general consensus is that species high in nitrogen are processed more rapidly than species low in nitrogen. The prevailing theory is that leaves with more nitrogen have more available protein, which increases their value as food to shredders, and perhaps allows more rapid colonization by microbes, which are also used as food by the shredders.

However, foliar nitrogen is not the only component of leaf chemistry that affects the quality of leaves as food for invertebrates. Many plants make secondary compounds that deter feeding on their leaves and twigs by insect and vertebrate herbivores. There is growing evidence that condensed tannin concentration in leaves may play a negative role in shredder palatability (Irons et al., 1988) and leaf litter processing rates (Stout, 1989; Irons et al., 1991). Preliminary evidence suggests that other plant secondary compounds, e.g., phenolic glycosides in *Populus balsamifera*, pinosylvan in *Alnus crispa* (Bryant et al., 1983b), germacrone in *Ledum groenlandicum* (Reichardt et al., 1990), may play important roles in leaf litter decomposition dynamics (Irons and Oswood, unpublished data). Bryant et al. (1983a) proposed that plant secondary chemistry is controlled, at least in part, by the balance between endogenous carbon (photosynthate) and nutrient (usually nitrogen) concentrations. The premise behind this carbon–nutrient balance theory is that when a plant has an excess of nutrients, most of the photosynthate produced will be used for increased growth of plant tissue. Conversely, when a plant has an excess of photosynthate over nutrients, the excess cannot be used for growth and will instead be shunted into secondary chemical pathways that result in such defensive compounds as condensed tannins or phenolic glycosides.

Following defoliation of leaves by an insect herbivore in summer, the amount of nutrient in the plant as a whole is reduced more than is the amount of carbon, as there are often large belowground reserves of carbohydrate (Bryant et al., 1983a). The following year, the plant will produce leaves that are smaller, tougher, and contain more secondary compounds and less nitrogen. Conversely, browsing of twigs by a vertebrate in winter (e.g., by moose) removes some of the next season's leaf buds and increases the relative amount of nutrient (which is stored in the roots at this time and is not affected by browsing) for each remaining bud. The leaves

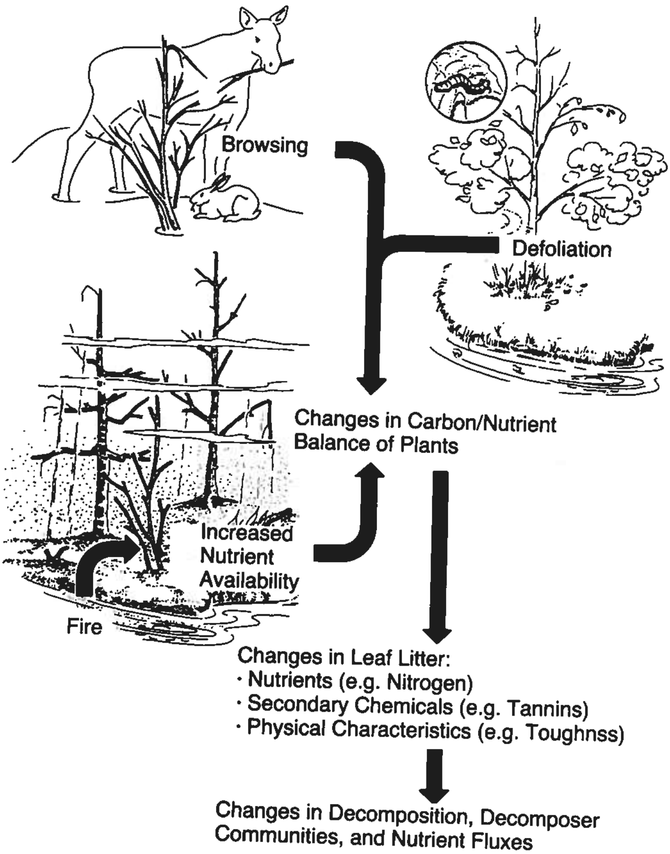

FIGURE 9.5. Cascading effects of disturbance to riparian vegetation. Changes in carbon–nutrient balance of plants is correlated with chemical and physical changes in leaf litter and hence detrital dynamics in streams. Interactions among likely ecological responses (e.g., browser and defoliator abundance, fire frequency, moisture stress) to climate change make predictions of impacts to biotic systems extremely complex.

that grow the next summer will be larger, less tough, and contain fewer secondary compounds and more nitrogen. Winter browsing of twigs by vertebrates and summer defoliation of leaves by insects thus have opposite effects on the physical (e.g., leaf toughness, leaf area, and leaf specific weight) and chemical (e.g., nitrogen, phosphorus, and secondary metabolites such as tannin and phenol glycosides) characteristics of leaves grown in the following summer. Fertilization of trees results in leaves similar to those of browsed trees, i.e., higher food quality of leaves for invertebrates.

Many environmental factors (Figure 9.5) have the potential to change the quality of leaf litter as food for stream shredders. These factors can be anthropogenic (e.g., fertilization by urban or agricultural runoff) or natural (e.g., forest fire or herbivory). Increased concentrations of carbon dioxide may directly increase carbon fixation, elevating carbon–nitrogen ratios of leaves and likely decreasing litter quality (McElroy and Moore, 1988). Wide-scale climate change at high latitudes has the potential to produce an extraordinarily complex array of ecosystem changes, which, in turn, may also produce changes in quality of leaf litter. Increased temperature and changes in amount and seasonal distribution of precipitation (the predicted scenario for climate change at high latitude) are likely to cause changes in cloud cover, growing season, herbivore populations, soil nutrient availability (e.g., through changes in fire frequency or microbial regeneration of nutrients), and water availability for plants. While the consequences of single effects may be predictable from current understanding of plant ecophysiology, interactions among these effects (e.g., simultaneous changes in nutrient availability and populations of defoliating insects) make prediction of net changes in leaf litter food quality impossible at present.

Thus, changes in the carbon–nutrient balance (whether from anthropogenic sources or from ecosystem changes affecting the natural internal availability of nutrients) can affect the physiological status of a tree, which can affect the quality of its leaves as food for aquatic detritivores (Figure 9.5). In an experiment on the feeding preferences of a shredding caddisfly, leaf disks from four Alaskan tree species that had been fertilized were preferred over leaves from unfertilized trees (Irons et al., 1988). In three cases, the nitrogen plus phosphorus treatment was preferred; however, in balsam poplar, the nitrogen only treatment was preferred (Irons et al., 1988). In all cases, the preferred treatment had higher nitrogen, and except for poplar, lower tannin. Leaves from naturally browsed (by moose) birch trees were higher in nitrogen, had rapidly leached tannin, and were processed faster in a stream than unbrowsed controls (Irons et al., 1991).

There is a great deal of uncertainty in the current climate models regarding cloudiness: where, how much, and of what type (e.g., ice or water) (Mitchell et al., 1989). Evidence is accumulating that shading may affect the carbon–nutrient balance of a tree. When the leaves are shaded, less photosynthate is produced, most of which is used for further growth, resulting in leaves with low tannin and high nitrogen. For example, in southeast Alaska, forbs and shrubs that grow in clearcuts are higher in tannin and lower in nitrogen than the same species in the adjacent old growth forest (Hanley et al., 1989). Bryant (1987) found that tannin and soluble carbohydrate were lower in leaves from experimentally shaded *Salix alaxensis* trees than in those from controls. An increase in regional cloudiness may result in leaves with higher nitrogen and lower tannin concentrations, while a decrease may result in just the reverse. Jonasson et al. (1986) found year-to-year variations in foliar nitrogen and tannin associated with cloudiness (measured as accumulated degree-days during the growing season) in a long-term study of forage plants of microtine rodents in Finland.

Soil moisture is another important constraint likely to be affected by climate change, affecting both tree species composition (Pastor and Post, 1988) and foliar chemistry (Mattson and Haack, 1987). Summer precipitation is predicted to decrease in interior Alaska (Bowling, 1984), which will probably increase plant moisture stress (Sveinbjornsson, 1984). Although secondary compounds are often higher under moisture stress (Gershenzon, 1984; Sharp et al., 1985), defoliating insects seem to grow better on such foliage (Mattson and Haack, 1987). Some effect is likely; however, it is impossible to predict the magnitude and direction of the effect of changes in soil moisture on leaf litter food quality, especially for riparian trees that may have adequate water.

Frequency and intensity of wildfire are predicted to increase due to decreased summer precipitation resulting in drier foliage and leaf litter (Bryant and Reichardt, 1991). This may have the effect of fertilizing the forest floor (if the fire intensity is not so great that the organic layer is volatilized) resulting in stimulation of the early successional deciduous trees that grow back rapidly after such a fire. Such trees are of higher food quality to stream shredders. However, if the intensity is too great, the organic layer will be burned off, and the nutrients released by the fire may be lost to the system (Chapin and Van Cleve, 1981).

It also seems possible that organic inputs to freshwater food webs will increase with increasing temperatures. Leaf litter deposition is a negative function of latitude (Schlesinger, 1977). Leaf litter input to two Alaskan subarctic streams is low (approximately 37–60 g AFDW m^{-2} yr^{-1}) compared to usual values (approximately 300–700 g AFDW m^{-2} yr^{-1}) for locations at lower latitudes (Cowan and Oswood, 1983; Oswood et al., 1989a). Although periphyton primary production in Alaskan streams is fairly high in summer (about the same as northern temperate region streams), winter primary production is very low (LaPerriere et al., 1989) so that yearly primary production is low. As discussed above, it is difficult to predict the consequences of anticipated high latitude climate changes to terrestrial plants; however, a warmer climate with a longer growing season may increase leaf litter input to streams. Increased temperatures and changes in amount and seasonality of precipitation and cloudiness, combined with changes in depth and moisture content of the active layer in permafrost areas, are likely to produce very complex changes in both the quantity and quality of leaf litter input to freshwaters.

Conclusion

Global climate warming in response to increased atmospheric carbon dioxide and other greenhouse gasses is likely to have major impacts on subarctic and arctic streams. Sediment and flow regimes are likely to change as a result of changing mass balance of glaciers. Thermal regimes of streams are also likely to change, resulting in biogeographic changes in freshwater organisms. Release of carbon (as carbon dioxide or as dissolved organic carbon in hydrologic transport) may be a major effect of warming carbon-rich soils, potentially exacerbating climate warming. Quality of food for stream invertebrates is likely to change as a result of complex interactions of many climatic and biotic variables. Some of these changes may be synergistic (increasing the impact) or antagonistic (ameliorating the impact); however, given the current state of the climate models, prediction is uncertain at best.

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