Element Cycling in Taiga Forests: State-Factor Control

A framework for experimental studies of ecosystem processes

K. Van Cleve, F. S. Chapin III, C. T. Dyrness, and L. A. Viereck

Of the 136.8 million hectares comprising interior Alaska, approximately 31% is forested. The remainder of the area is made up of a mosaic of grassland, shrub, bog, and tundra vegetation. The interior Alaskan taiga is unique in that the structure and function of the forest is associated with an environment characterized by drastic seasonal fluctuations in day length and temperature, a short growing season, low soil temperatures, and permafrost (Van Cleve and Alexander 1981). The taiga is part of the circumpolar forest region near the latitudinal limit of tree growth.

The taiga occupies large areas of Alaska, Canada, Scandinavia, and the Soviet Union (Van Cleve and Alexander 1981). With changing climate, ecological relationships within the taiga could assume global importance, because this region contains 20% of the world's stored carbon and is a large but unexplored source of methane and carbon dioxide, two gases implicated in causing climate change (Billings 1987, McBeath 1984, Reeburgh 1990). Flux rates of these gases are expected to change

K. Van Cleve is professor of forest soils in the Agricultural and Forestry Experiment Station at the University of Alaska, Fairbanks, AK 99775. F. S. Chapin III is professor in the Department of Integrative Biology, University of California, Berkeley, CA 94720. C. T. Dyrness is a research soil scientist and L. A. Viereck is principal plant ecologist for the USDA Forest Service, Pacific Northwest Research Station, Fairbanks, AK 99775.

> An understanding of taiga ecosystem controls is important for predicting global responses to climate change

dramatically in the near future, because global changes in temperature will be most pronounced in polar regions. A solid conceptual understanding of controls over ecosystem function in the taiga is important to predictions of global responses to climate change.

In our research, which addresses not only the soils but also the ecosystem structure and function of the Alaskan taiga, we have found a useful paradigm in the state-factor approach of Jenny (1941, 1980). This approach provides ecology with a powerful conceptual framework for the study of ecosystem processes (Crocker and Major 1955, Dickson and Crocker 1953, Heilman 1966, Viereck 1970, Vitousek and Walker 1987).

The approach assumes that ecosystem properties, such as soil characteristics and patterns of energy and nutrient flow, are determined by five exogenous conditions, called state factors. These factors are: regional climate, the biota (potential flora), topography, soil parent material, and time (developmental stage). These

variables are independent of the ecosystem as it evolves, and they may or may not be independent of each other (Jenny 1980). State factors can be passive or static (e.g., relief, parent material, and time), or they can be active (e.g., climate and the biota) in that they supply energy to the ecosystem.

In using the state-factor approach, the challenge is to find conditions in nature where influence of the factors can be individually sorted out. Ecologists must choose ecosystems in which all state factors are constant except one (e.g., time) to explore how each factor independently governs the trend of some property (e.g., soil or vegetation).

In our research in the Alaskan taiga, we have found the state-factor approach useful in studying soils, energy flow, and element cycling (the distribution and dynamics of chemical elements in ecosystems). In this article, the term *element cycling* encompasses the flow of carbon and inorganic elements among compartments (trees, forest floor, and mineral soil) in forest ecosystems.

An experimental approach is essential to understanding the controls on ecosystem function. An explicit focus on state factors provides a framework that logically leads to formulation and experimental testing of hypotheses. In this article, we present an evaluation of controls on element cycling in taiga forests of interior Alaska as an example of how the state-factor concept has improved understanding of ecosystem phenomena in this biome.

Ecosystem controls

State factors are the general properties of a region; they determine the kinds of ecosystems that can exist there. The state factors condition the phenomena that directly affect ecosystem structure and function (Figure 1). These phenomena, or controls, include microclimate; the elevation, slope, and aspect components of topography; soil, including its physical, chemical, and biological characteristics; and successional phenomena, which reflect the time course of ecosystem development. The controls change during ecosystem development and can be manipulated either experimentally or by other human perturbations. To apply successfully the state-factor approach, it is necessary to understand the ecosystem controls and their interactions.

Differences among ecosystems in their energy or element flow can be explained by differences in state factors. However, in most ecosystems it is difficult to demonstrate this relationship, because human activity modifies natural cause and effect.

The taiga provides an excellent opportunity to test the state-factor approach. First, taiga ecosystems have been relatively undisturbed by man and therefore probably reflect natural environmental controls. Second, the small number of tree species (six in interior Alaska) in the taiga simplifies study of the impact of the biota on ecosystem function. Third, taiga eco-
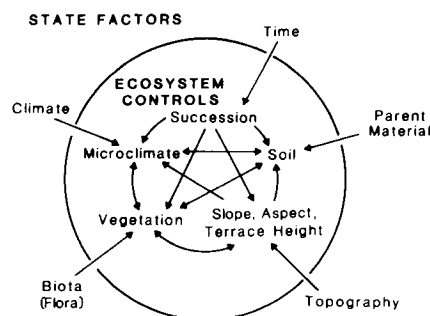
STATE FACTORS

Figure 1. State factors and ecosystem controls of element cycling in interior Alaskan forests.

systems show clear and repeatable patterns of distribution with respect to topography, soil parent material, and time, indicating that any controlling role of these state factors is not obscured by stochastic events. Finally, ecosystems more clearly display manifestations of environmental control on structure and element cycling when developing under the extreme environmental conditions encountered in the taiga.

Two decades of ecosystem research near Fairbanks in interior Alaska (Van Cleve and Viereck 1981, Van Cleve et al. 1983, 1986a) have focused on secondary succession after fire in the uplands and on primary succession after flooding on river floodplains. These studies provide field and laboratory evidence for the patterns described in this article and led to our hypotheses regarding

changing controls over element cycling during ecosystem development. We emphasize experimental analysis of those controls that are unique to the Alaskan taiga. However, we also point out other controls that operate in most ecosystems and reflect more general aspects of ecosystem function.

State factors in the Alaskan taiga

The general nature of state factors in the Alaskan taiga can be summarized as follows:

● Forest ecosystem development occurs in a cold-dominated environment.
● The topographic modification of regional climate has dramatic consequences for ecosystem processes.
● Parent materials differ between uplands and floodplains but are relatively uniform within these two landscape units.
● The distribution of potential plant colonizers is assumed to be relatively uniform across sites.
● The time during which ecosystem development can occur is limited by the length of the fire cycle in uplands and by fluvial processes on floodplains.

Climate. The coldness of this northern environment dominates all physical, chemical, and biological processes. At Fairbanks, snow covers the landscape from October through

Table 1. State factors and ecosystem controls for upland north, south, and floodplain ecosystems.

State Factors:	Topography			Time		Climate			Biota				Parent material	
Ecosystem controls	Position	Aspect	Elevation (m)	Successional stage	Age of surface since last disturbance (yrs)	Soil heat sum (DD)*	Summer throughfall (mm)	Incoming radiation (kj/m²d)	Vegetation type	Biomass[†] (kg/m²)	Annual[‡] production (g/m²)	Soil nitrogen (g/m²)	Soil texture
Characteristics	Upland	North	343–468	Early	0–30	1250–1000	—	488	Herb/shrub	0.01–0.07	—	—	Silt
				Intermediate	30–80	710	—	488	Black spruce	1.7–2.4	63–140	220	Silt
				Mature	80–250+	500–800	—	488	Black spruce	5.3–11.3	101–160	240–360	Silt
	Upland	South	200–400	Early	0–30	1150–1200	200	676	Herb/shrub	0.02–0.2	5–20	—	Silt
				Intermediate	30–130	970–1400	206	676	Deciduous tree (birch-aspen)	4.6–17.5	343–760	190–520	Silt
				Mature	100–250+	875–1120	150	676	Evergreen tree (white spruce)	23.2	353	200–300	Silt
				Early	0–2	—	194	697	Bare alluvium	0	0	30–100	Sand
					2–5	1611	198	697	Open shrub (willow-poplar)	0.2–0.6	200–300	80–200	Sand
					5–30	696	135	697	Closed shrub (alder-popular)	1.0–6.4	290–350	80–320	Sand-silt
	Floodplain	Level	120–177	Intermediate	30–130	1150–1300	148	697	Deciduous tree (popular)	4.1–18.0	264–952	150–470	Silt-sand
				Mature	100–200	800–1140	149	697	White spruce	14.6–22.7	331–540	200–700	Silt-sand
					130–250+	40–760	149	697	Black spruce	1.6–10.9	57–148	350–750	Silt-sand

*DD = Degree days above 0° C at 10 cm from the surface of the forest floor for the period May 20–September 10.
[†] Aboveground standing crop of tree biomass.
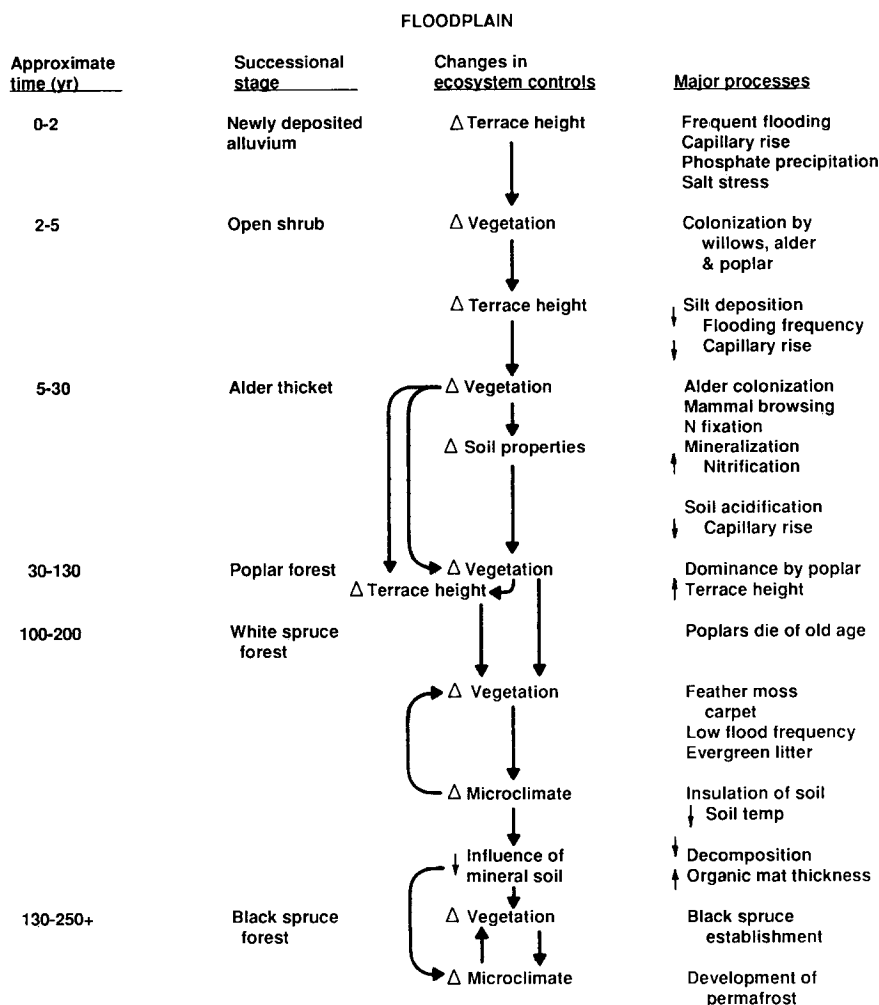[‡] Aboveground annual production for trees.

FLOODPLAIN

Approximate time (yr)	Successional stage	Changes in ecosystem controls	Major processes
0-2	Newly deposited alluvium	Δ Terrace height	Frequent flooding Capillary rise Phosphate precipitation Salt stress
2-5	Open shrub	Δ Vegetation	Colonization by willows, alder & poplar
		Δ Terrace height	Silt deposition Flooding frequency Capillary rise
5-30	Alder thicket	Δ Vegetation	Alder colonization Mammal browsing N fixation Mineralization Nitrification
		Δ Soil properties	Soil acidification Capillary rise
30-130	Poplar forest	Δ Vegetation Δ Terrace height	Dominance by poplar Terrace height
100-200	White spruce forest		Poplars die of old age
		Δ Vegetation	Feather moss carpet Low flood frequency Evergreen litter
		Δ Microclimate	Insulation of soil Soil temp
		Influence of mineral soil	Decomposition Organic mat thickness
130-250+	Black spruce forest	Δ Vegetation	Black spruce establishment
		Δ Microclimate	Development of permafrost

Figure 2. Changes in control of processes important in element cycling in floodplain ecosystems.

mid-April (an average of 214 days), leaving an average frost-free period of only 97 days (Slaughter and Viereck 1986). The average daily temperature ranges from −24.5° C in January to 17.5° C in July, with an average annual temperature of -3.5° C.

The dramatic seasonality of temperature is a reflection of changing solar angle and the incident radiation received at the ground surface. The solar elevation ranges from 2.5° in December to 49.5° in June (Seifert 1981). In summer, long days (21 hours in June) compensate for the relatively low solar angle. Consequently, during the snowfree period, radiation on a horizontal surface is 697 kj m^{-2}d^{-1}, a value similar to that received at temperate latitudes during the same time period (Chapin and Shaver 1985).

The interior Alaskan climate is semiarid. At Fairbanks, precipitation averages 285 mm, of which 65% falls during the growing season. Potential evapotranspiration is 475 mm, yielding a precipitation deficit of 190 mm (Patric and Black 1968, Slaughter and Viereck 1986). Reduced leaching of the soil profile and formation of caliche on the driest sites are consequences of the semiarid environment.

Topography. Topography plays a dramatic role in modifying regional climate in the taiga. Locally, elevations range from 120 m on the floodplain of the Tanana River to 470 m on adjacent ridgetops. On typical hillside slopes (30%) in our study area, south and north aspects receive 94% and 70%, respectively, of the radiation received on a horizontal surface (Seifert 1981). This difference in radiation regime translates into substan-

tial differences in soil temperature among forest types developing on different aspects in the taiga (Table 1; Viereck et al. 1983).

Soils on north aspects are cold and underlaid by permafrost, preventing downward water percolation. Evapotranspiration is markedly reduced compared with south aspects. Consequently, north-aspect soils are wet, and nutrients may leach below the rooting zone. Soils on south aspects are warm, dry, and free of permafrost. Because of high evapotranspiration, there is negligible leaching. Cold, wet permafrost soils also occur in lowland removed from active portions of the river floodplains.

Flora. Because both our upland and floodplain study sites occur within a relatively small geographic area, we assume that the same pool of plant species has the potential to disperse into all sites. We therefore treat the flora potentially available at each site as a constant. The vegetation that actually occupies each site is strongly influenced by topographic variations in microclimate, particularly soil temperature. The six tree species occurring in the Alaskan taiga have transcontinental ranges.

Parent material. In the general vicinity of our study sites, soil parent material falls into two major classes. On the river floodplains, soils develop on well-drained sandy to silty alluvium. By contrast, in the uplands the parent material is micaceous loess, predominantly of silt texture. These deposits are 20 to 30 m thick on lower slopes adjacent to the Tanana River and become thinner to the north and on ridgetops (Péwé and Reger 1983, Viereck et al. 1986). Soil in lowlands is a mixture of alluvial deposits and colluvial material from the uplands. The research sites on which this article is based were located either on floodplain alluvium, lowland alluvium or colluvial deposits, or upland loess, thus simplifying our consideration of soil parent material as a controlling state factor. In the uplands, the mineral soil has normally developed through many fire cycles, so its characteristics reflect both the intensity of the most recent fire and previous cycles of vegetation development and destruction.

Figure 3. Primary succession on the Tanana River floodplain near Fairbanks, Alaska. Right foreground, bare alluvial surface; middle foreground, open shrub willow/poplar stage; left middle distance, closed shrub alder/poplar stage with poplar protruding through the crown canopy; middle right, mature white spruce.

continuous deciduous forest canopy (Figure 4).

● Further changes in the vegetation to white spruce (*Picea glauca*) and the development of a ground cover of bryophytes, alter microclimate and the rate of detrital decomposition, reducing rates of element cycling.

● Continued accumulation of forest floor organic matter (largely moss remains) causes additional modification of microclimate, the appearance of permafrost, further reduction in element cycling, and replacement of white spruce by black spruce (*Picea mariana*).

An additional disturbance stage, associated with river flooding and bank cutting, may occur at any time, reversing the process of succession and resetting the successional clock to time zero.

Initial stage. During the initial phase of ecosystem establishment, physical and chemical processes dominate the controls of element cycles. Newly formed surfaces have low terrace height (less than 1 m above mean river level; Walker et al. 1986), so the water table is close to the soil surface (Figure 2). Moreover, the particle size of the sediment in these youngest stages generally is sandy, reflecting

Time. In the uplands and nonfloodplain lowlands, the temporal control of ecosystem development is largely determined by fire frequency, which ranges from 50 to 200 yr (Dyrness et al. 1986). The mosaic of forest types that occurs in the uplands largely reflects the pattern of secondary succession after fire. In the floodplains, fluvial processes and their periodicity determine ecosystem age. Here, maximal surface ages approach several hundred years (Juday and Zasada 1984).

Controls of element cycling in floodplain ecosystems

Taiga floodplains of interior Alaska provide an excellent starting point for examining the importance of state factors, because regional climate, potential flora, and parent material are essentially constant, and the terrain is level. Therefore, we can evaluate how time influences controls of ecosystem processes. Time, manifest through succession, interacts with other controls which, in turn, are directly responsible for major changes in element cycling (Figure 1).

Our studies have enabled us to identify a number of points along

both the upland and floodplain successional trajectories that are of particular significance in the development of subarctic forests. We term these *turning points* in succession to emphasize that in relatively short time intervals (less than 50 years) critical changes in ecosystem structure are accompanied by functional changes that have far-reaching effects on ecosystem development.

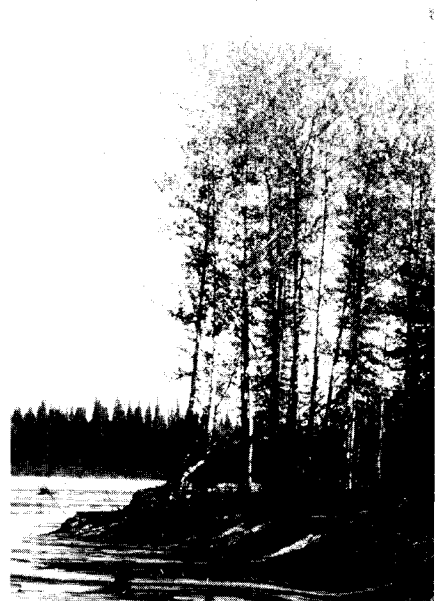There are six general stages in the course of primary succession on taiga floodplains (Table 1, Figure 2):

● Initially, soil, terrace elevation above river level, and microclimate exert almost exclusive control over element cycling. These bare alluvial surfaces occupy the lowest terraces and experience frequent intraseason flooding (Figure 3).

● Continued increase in terrace height and change in microclimate are closely related to development of plant communities.

● Changing vegetation (especially development of nitrogen-fixing alder, *Alnus tenuifolia*) at this time greatly modifies element cycling.

● Balsam poplar (*Populus balsamifera*) replaces alder as the dominant vegetation type, forming a

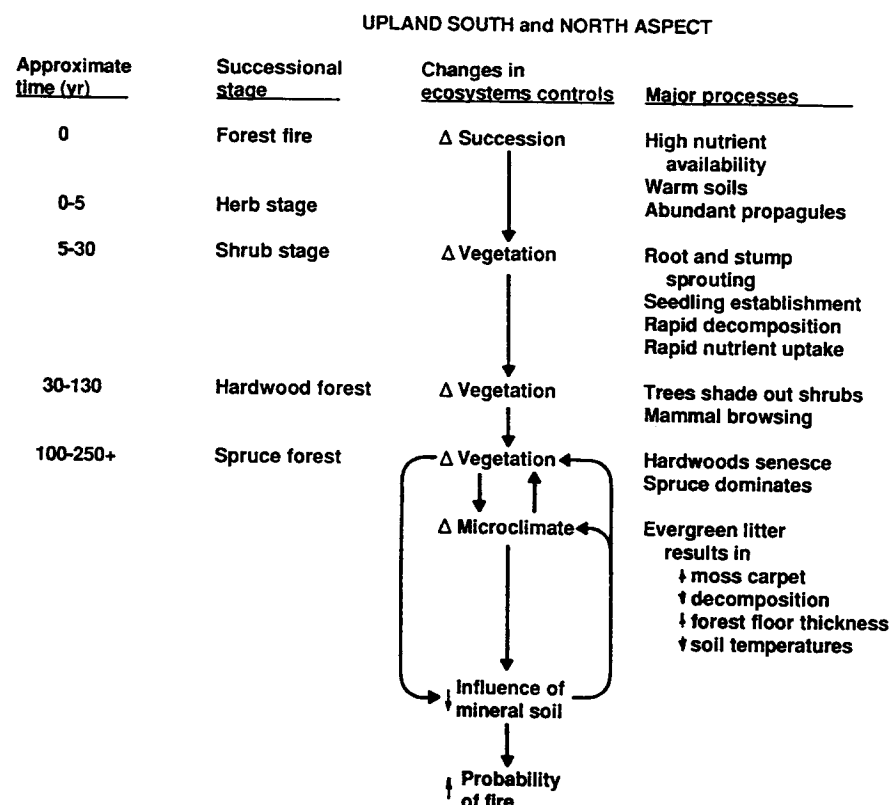Figure 4. Mature balsam poplar before dominance of white spruce. Some white spruce are visible in the understory.

Approximate time (yr)	Successional stage	Changes in ecosystems controls	Major processes
0	Forest fire	Δ Succession	High nutrient availability
0-5	Herb stage		Warm soils / Abundant propagules
5-30	Shrub stage	Δ Vegetation	Root and stump sprouting / Seedling establishment / Rapid decomposition / Rapid nutrient uptake
30-130	Hardwood forest	Δ Vegetation	Trees shade out shrubs / Mammal browsing
100-250+	Spruce forest	Δ Vegetation ←	Hardwoods senesce / Spruce dominates
		Δ Microclimate ←	Evergreen litter results in ↑ moss carpet ↑ decomposition ↓ forest floor thickness ↑ soil temperatures
		Influence of mineral soil	
		Probability of fire	

Figure 5. Change in control of processes important in element cycling in upland-south and north-aspect ecosystems.

the greater energy of water associated with formation of the low-lying terraces (Van Cleve et al. 1971).

Open shrub stage. As terrace elevation increases with repeated flooding and sediment deposition, silt dominates the texture of surface soil layers. Because of the presence of small amounts of nitrogen and organic carbon in these early successional soils, the sequence is not strictly a primary succession in the sense of ecosystems developing on pristine glacial moraine or volcanic ash parent materials.

In addition, evaporation (caused by moisture deficits characteristic of the regional climate) drives capillary rise of water to the soil surface, depositing evaporites of gypsum ($CaSO_4 \cdot 2H_2O$) and calcite ($CaCO_3$; Patric and Black 1968, Slaughter and Viereck 1986). The low temperatures characteristic of regional climate limit rates of mineral weathering, so clay content and cation exchange capacity of the mineral soils are low. Because of this limited weathering and the low organic content of early successional soils, there is minimal potential storage of nutrients on the soil exchange complex.

Solubility phenomena and the balance between leaching and capillary rise determine the pool sizes of nutrients in the system. The soil solution is alkaline, mirroring the base-rich composition of the alluvium, upland loess, and glacial deposits at the river's headwaters. High calcium concentration and high pH in surface soils limit phosphorus availability through the low solubility of calcium phosphate under these conditions (Bohn et al. 1985).

Low soil organic-matter content and low phosphate availability and the osmotic effects of high salt concentrations may explain the low rates of nitrogen mineralization and nitrification observed in these early successional stages (Darrah et al. 1987). Surface evaporites may directly affect plant establishment through osmotic effects on seed germination and seedling growth (Krasny et al. 1988). Because seedling growth is slow on the low-nitrogen, low-phosphorus, high-

salt soils, the frequent flooding buries many seedlings, particularly those of more slowly growing late successional species. As a result of the relatively low plant biomass on these young alluvial deposits, element cycling through vegetation is minimal. Instead, cycles are dominated by evaporation-driven capillary rise, solubility equilibria, and flood events that deposit silt and leach accumulated salts.

Transition to the intermediate successional stage dominated by alder is a major turning point caused by a small but important change in ecosystem controls. Intraseason flooding and siltation raises terrace heights sufficiently to allow establishment of some seedlings. The early successional species (*Salix* spp. and poplar) are able to withstand additional sedimentation, because they produce new roots close to the soil surface.

The extensive root system stabilizes the soil against erosion, and root sprouting causes an increase in stem density. The high stem density of willow and poplar seedlings that establish on early successional alluvial bars slows the movement of floodwaters, promoting sedimentation and a gradual increase in terrace height (Figure 2). Moreover, the expanding plant root biomass helps to stabilize early successional surfaces against erosion. Heavy browsing by moose (*Alces alces*) and snowshoe hares (*Lepus americanus*) of seedlings that do establish on young silt bars limits the rate of biomass accumulation. Browsing may promote vegetative reproduction to increase stem density and thereby result in expanded root systems, allowing plants to utilize more efficiently the limited supply of available nutrients.

Alder stage. The subtle change in terrace height (less than 1 m elevation) increases the height of the ground surface above the water table, reduces flooding frequency, and promotes establishment of alder. These changes in terrace height and vegetation cause a shift from physical-chemical to biological control of element cycling.

Greater height above the water table, litter accumulation, and rapid transpiration by dense alder thickets all contribute to short-circuiting the

82

capillary rise of groundwater to the soil surface, thus preventing evaporite formation and the concentration of salts in surface soils. Experimental work in the open-shrub stage shows that litter accumulation creates an evaporation mulch that alone is sufficient to stop salt accumulation at the soil surface. Consequently, soil solution moves primarily from the water table to the rooting zone rather than to the soil surface. Despite the dry regional climate, there is adequate water transport to the rooting zone to support high rates of primary production, with no evidence of water stress (Van Cleve et al. 1983).

In this successional stage, nitrogen fixation, nitrogen mineralization, and nitrification are most rapid (Klingensmith 1988, Van Cleve et al. 1971). Processes come into play that gradually change the alkaline soil conditions of the earlier successional stages. These processes include neutralization by acids produced by nitrification and by organic acids from decomposition of the developing litter layer. Soil acidification increases the solubility of calcium phosphate. The increased phosphate availability generates a positive feedback that is essential to support observed high rates of nitrogen fixation and plant productivity.

During this stage, nitrogen fixation by alder adds 18g N m^{-2} yr^{-1} to these ecosystems, enough to account for 60–70% of the nitrogen accumulated by the system throughout succession (Van Cleve et al. 1971, 1983). Productivity in the alder thickets ranges from 2.9 to 3.8 t $ha^{-1}yr^{-1}$ (Van Cleve et al. 1971). There is a large increase in the element-storage (including nitrogen, phosphorus, potassium, calcium, and magnesium) capacity of the system in both the biota and the forest floor. The latter retains nutrients due to both organic binding and cation exchange (Van Cleve and Viereck 1972, Van Cleve et al. 1971, 1983). The nitrogen, total phosphorus, exchangeable potassium, calcium, magnesium, carbon, and cation exchange capacity of mineral soils also increase through this period of ecosystem development.

Deciduous forest stage. There is a gradual change from these alder thickets to deciduous forests dominated by poplar (Figure 2). This turning point arises primarily through a change in competitive balance between alder and poplar, the decreasing impact of salt-affected mineral soil on element supply for plant use, and the increasing influence of terrace height and microclimate on element cycles.

Poplar, which grows rapidly under the moist, fertile conditions characteristic of the alder thicket developing on lower terraces (Chapin et al. 1983, Van Cleve et al. 1983), gradually overtops and shades out alder. Productivity of poplar stands may reach 9 t $ha^{-1}yr^{-1}$. Snowshoe hares, which use the alder for cover, eliminate most early successional willows (Bryant and Chapin 1986). The tannin concentrations of poplar leaves are higher than those of willow or alder, perhaps explaining the dramatic decline in decomposition, nitrogen mineralization, and nitrification in the poplar forests (Vitousek et al. 1989). Thus the transition from alder thicket to poplar forest is caused by complex interactions among vegetation, animals, and decomposers.

Evergreen forest stage. The turning point from deciduous poplar to evergreen white spruce forest is reached through the gradual growth of the shade-tolerant spruce in the alder and poplar stages, combined with the short-lived nature of poplar (100–150 years) and the inability of poplar seedlings to establish in the forest floor of the alder or poplar stages (Van Cleve and Viereck 1981, Walker et al. 1986). This change in vegetation initiates a chain of events leading to a dramatic deterioration of microclimate (decline in soil temperature) and reduced rates of element cycling (Figure 2). This turning point is facilitated by a shift from deciduous (poplar) to evergreen (spruce) litter.

Feather mosses can grow rapidly in the understory of poplar forests (Oechel and Van Cleve 1986), but their distribution is restricted to the few decaying logs and stumps where they are not shaded by the heavy deciduous litter fall. When spruce displaces poplar, feather mosses are no longer shaded by the deciduous litter, and they form a continuous carpet 10–20 cm thick. This moss carpet has a low thermal conductance, causing a

Figure 6. Early postfire secondary succession on upland south aspect, showing herbs, grasses, and standing dead white spruce.

drastic reduction in soil temperature and more gradual soil thaw in spring (Dyrness et al. 1988, Viereck 1970, Viereck et al. 1983).

The forest floors developing in white spruce ecosystems have a wide C:N ratio and may also have high concentrations of lignin and other polyphenolic compounds (Flanagan and Van Cleve 1983, Van Cleve et al. 1983, Chapin et al. 1986). The combination of low soil temperature and low litter quality greatly reduce the rates of decomposition and element cycling (Flanagan and Van Cleve 1983, Van Cleve et al. 1983), so that a thick mat of dead organic matter develops between the moss layer and the mineral soil. Because of low soil temperatures, deep root growth is slow (Lawrence and Oechel 1983,

Figure 7. Mature white spruce on upland south aspect.

Tryon and Chapin 1983), so that the spruce trees root almost entirely in the organic mat and depend largely on recycling of elements within the forest floor for their nutrient supply.

The gradual increase in terrace height through time separates the spruce from the groundwater source of either water or nutrients that moves along suction gradients to the rooting zone in lower terraces. Consequently, these forests may be susceptible to drought and nutrient stress. As the moss carpet and organic mat continue to develop, soils thaw progressively more slowly during summer, until eventually they remain permanently frozen at depth. Under these conditions, black spruce eventually replaces white spruce.

Flooding is the major source of disturbance in the floodplains. The probability of flooding is highest in early successional stages and declines as terrace height increases. However, the braided river is constantly changing its channel and destroys established communities, especially on the outside of river bends, for reasons unrelated to the successional stage of the community.

In summary, time, through successional processes, is important because it causes changes in ecosystem controls at the local level. Other state factors, including climate, parent material, flora, and topography, are

manifest through the ecosystem controls that include, respectively, microclimate, soil chemical and physical properties, the local vegetation, and terrace height (Figure 1). It is change in, and interaction among, the ecosystem controls, including microclimate, terrace height, and vegetation composition that is directly responsible for the successional progression in ecosystem structure and element cycling observed in floodplain succession.

Control of element cycling in south aspect uplands

South-aspect uplands are similar to the floodplain in regional climate and biota (flora), but they differ from the floodplain in parent material and topography (Table 1, Figure 5). Moreover, in the uplands, fire (an extension of regional climate) is the main disturbance that resets the successional clock. Estimates of the natural fire cycle in the taiga of Alaska range from 50 to 200 years (Dyrness et al. 1986, Heinselman 1978, Yarie 1981). Fire returns a large proportion of the nutrient capital of a mature forest to the soil, so there is greater nutrient availability in time-zero stands in the uplands than on the floodplain. Because of differences in initial site conditions, the interaction of successional time with other ecosystem controls is quite different between up-

land and floodplain ecosystems.

Five stages of ecosystem development in the uplands can be defined. In contrast with the floodplain, all stages reflect the strong influence of the vegetation. The vegetation, slope and aspect, and microclimate affect the first stage of succession by determining the severity of burn (the susceptibility of forest types to burning), composition of the nutrient pools remaining after fire, and the species composition of the immediate postfire herbaceous plant community (second stage; Figure 6).

In the third stage, continued recolonization of these upland sites is associated with a rapid development of deciduous shrub and tree species cover, increased phytomass, and increased element cycling. White spruce seedlings appear during this period and, as they mature during the fourth (hardwood forest) stage, are associated with a shift in dominance from deciduous to the fifth (spruce forest) stage, the rise of feather moss as ground cover, and changes in local climate that reduce rates of element cycling (Figure 7). The probability of fire increases with the accumulation of organic detritus, and especially with transition to the final successional phase.

Initial stage. Slope, aspect, microclimate, and successional time determine prefire forest type, which is a major determinant of burn intensity. South aspects are dominated by birch (Betula papyrifera) and aspen (Populus tremuloides) during mid-succession and by white spruce during late succession, whereas north aspects are dominated by black spruce in both mid- and late succession (Table 1, Figure 5). The forest floor in spruce stands is generally thicker than in hardwood stands due to slower decomposition of bryophyte and coniferous tree species detritus (Flanagan and Van Cleve 1983). Moreover, the retention of substantial amounts of dead branch biomass on standing trees, the resinous nature of spruce organic matter, and the combustible nature of moss remains make these stands more combustible than hardwood forests (Dyrness and Norum 1983).

The high fuel load and greater combustibility of spruce stands results in a

hotter fire and more complete combustion of the organic detritus than in hardwood stands (Viereck and Foote 1985). Because of better drainage and greater amounts of solar radiation reaching the ground surface on south aspects compared with lowland and north aspects, forest-floor organic layers tend to be drier and experience more complete combustion. Although as much as 50% of the original forest-floor nitrogen may be lost through volatilization on heavily burned areas, the availability of nitrogen and other mineral nutrients is high in the ash and can support rapid regrowth of vegetation (Dyrness et al. 1989, Van Cleve and Dyrness 1985). For example, three years after planting, significantly greater net biomass production, uptake of nitrogen, phosphorus, potassium, calcium, and magnesium and higher element concentrations were encountered in white spruce seedlings growing in heavily burned areas compared with control locations in white spruce forests.

Early postfire herb and shrub stages. The intensity of burn also controls the pool of potential colonizers after the fire. Complete ashing of the forest floor destroys seeds, rhizomes, and root stock of herbs, grasses, and woody plants that under less severe conditions comprise the early and mid-successional plant community. In these situations, invasion of light-seeding species is favored. Moderately intense fires allow regeneration to communities with a mixture of willow, birch, aspen sprouts, and spruce seedlings intermixed with early successional woody and herbaceous species. The relative abundance of seedlings and sprouts depends on proximity of seed sources, species composition of the preburn forest, and fire intensity. Birch and aspen forests, partly because of low fire intensity, tend to regenerate with a dense cover of herbaceous species derived from buried seed, rhizomes, or root stock, and with a canopy of either birch stump sprouts or aspen root suckers (Viereck and Foote 1985, Zasada 1986).

As a result of the loss of the overstory canopy and reduced albedo of the forest floor, surface soil temperatures (at ten-centimeter depth) are 2–4.5° C warmer than in unburned spruce and aspen stands, speeding the decomposition of any remaining unburned forest floor (Van Cleve and Dyrness 1985, Viereck and Foote 1985). The high nutrient availability after fire supports rapid regrowth of vegetation, which minimizes leaching losses (Slaughter 1985), as observed on most postfire successions (Chapin and Van Cleve 1981). These conditions contrast strikingly with those of the floodplain, where physical rather than biological factors dominate patterns of element cycling for the first two to ten years, until alder invades.

Hardwood forest stage. The turning point that encompasses this early postdisturbance phase to the hardwood forest stage depends largely on the initial biota (Figure 5). Stand establishment proceeds more rapidly from sprouts because of the use of established root systems and their stored reserves to support growth. If seed sources exist and mineral soil sites are available for germination, white spruce may become established. However, heavy litterfall, shading, and root competition from the dominant deciduous overstory reduces growth of spruce in the early decades of forest development (Gregory 1966).

Annual uptake of nitrogen, phosphorus, potassium, calcium, and magnesium is substantially higher than in early succession because of the greater plant mass. The original ashed or burned forest floor and the surface layers of the mineral soil are gradually acidified through their leaching by end products of decomposition from the new forest floor, by nitrification of mineralized nitrogen, and by ion uptake by the established plant community. The pH of the forest floor in birch and aspen ecosystems ranges from 5.5 to almost 6.0 during this stage of forest development. The heavy litterfall also prevents establishment of a bryophyte ground cover because of the shading effect of the litter (Oechel and Van Cleve 1986).

Evergreen forest stage. The turning point from deciduous aspen or birch forest to evergreen white spruce forest, characteristic of the fifth stage of ecosystem development on south-facing aspects, is similar to the poplar-spruce transition observed on the floodplain. As on the floodplain, the change from dominance by hardwoods to spruce is partly a consequence of the shorter life-span and shade intolerance of these species. Moreover, hardwood seedling regeneration does not occur on these forest floors, and vegetative reproduction does not occur except after more substantial disturbance that stimulates dormant bud stump or root sprouting.

The change from broad-leaved to needle-leaved litter permits development of a complete moss ground cover. Declining litter quality (largely moss remains) results in reduced rates of decomposition, organic matter accumulation on the forest floor, and reduced soil temperature, nutrient availability, and tree growth (Flanagan and Van Cleve 1983). Annual nitrogen, phosphorus, potassium, calcium, and magnesium uptake and return in litterfall in white spruce is only 20–40% of rates encountered in the earlier hardwood stage of succession (Van Cleve et al. 1983). White spruce dominance is also associated with increased probability of fire. The fire return interval on south-aspect uplands is 100–150 years, the interval during which spruce dominance is attained.

In summary, succession on south-aspect uplands differs dramatically from that on the floodplain because of the differential operation of the state factors climate, flora, topography, and time and of their associated ecosystem controls (Figure 1). A large pool of nutrients and plant species inoculum is available at time zero in upland ecosystems. Consequently, the vegetation quickly assumes dominance of element cycles, rapidly utilizing this resource and preventing leaching loss. On the floodplain, terrace height controls susceptibility to flooding and plant access to additional supplies of water and nutrients from the groundwater. Because of level terrain, solar radiation received at the ground surface is constant. On south-aspect uplands, radiation received at ground surface depends on slope and aspect. As succession proceeds, the influence of the vegetation causes convergence in the control and pattern of element cycling between

Figure 8. Black spruce, in foreground and left middle distance (dark patches), occupies cool north aspects in contrast to birch and aspen, which occur on south aspects.

upland and floodplain ecosystems because of dominance of the same tree species, white spruce.

Controls of element cycling on north-aspect uplands

North-aspect uplands are similar to south-aspect uplands in the state factors parent material, biota, and regional climate (Figures 1 and 5). However, the difference in aspect (topography) results in at least a 25% reduction in solar radiation. This difference in local climate has a dramatic impact on the vegetation and the processes that control element cycling. There are five successional stages on north-aspect uplands. These stages are quite similar to those described for south aspects. Therefore, we emphasize the differences between north and south aspects rather than provide a complete description of north-aspect succession (Figure 8).

After fire, community structure and function depend on the vegetation present before fire, as described for south-aspect uplands. However, on north aspects, succession to spruce occurs more rapidly than on south aspects, so highly combustible fuels are common and fires occur frequently (approximately every 70 years). On the other hand, the cool, moist conditions that prevail on north aspects result in

higher fuel moisture content and less complete combustion than on south aspects, reducing the extent of nutrient release by fire. The semiserotinous cones of black spruce provide a ready seed source on north aspects. Spruce regeneration usually is abundant after fire.

As on south aspects, the second through fourth successional stages include herb-shrub-hardwood forest communities that regenerate rapidly from roots and rhizomes in uncombusted forest floor material and from local seed input. However, the smaller initial pulse of nutrients released by fire and the lower radiation input (and consequently cooler soil temperatures) cause slow growth of herbs, shrubs, and deciduous trees. Therefore, the turning point to spruce forest occurs more rapidly than on south aspects.

In the fifth stage, black spruce displaces early successional species and, along with developing moss ground cover, reduces soil temperatures by increasing forest floor thickness. This process is similar to that described for floodplain and south-aspect ecosystems. However, the lower radiation input on north aspects results in colder soils, slower decomposition, greater accumulation of an insulating forest-floor layer, and, therefore, the development of permafrost. This

change in local climate prevents drainage and physically isolates the biota from the underlying mineral soil. Thus tree productivity is more dependent on element redistribution within the plant, and trees use elements more efficiently than on south aspects.

State-factor approach and hypothesis testing

The state-factor approach can provide an organizational, hypothesis-testing framework for examining cause-effect relationships with regard to environmental control of ecosystem processes. Four examples illustrate this approach.

Control over element cycling. We hypothesized that a change from physical to biological controls on nutrient cycling was a key turning point in floodplain succession. In this case, the experimental framework was established with the state factors regional climate, potential flora, and parent material essentially constant and the terrain level. In early succession, the presence of crusts of calcite ($CaCO_3$) and gypsum ($CaSO_4 \cdot 2H_2O$) on the soil surface suggest that soil solution rises by capillary action, moving along moisture suction gradients to evaporate at the soil surface.

Tests of these ideas, using injections of concentrated solutions of NaCl at the 25 cm soil depth, demonstrated upward movement of the salt to the soil surface. The absence of salt crusts in alder thickets, even though they were located on terraces where the surface mineral soil is still influenced by groundwater, suggested that the vegetation somehow prevented salt crust formation. Application of leaf litter to the early successional mineral soil surfaces prevented NaCl movement and salt crust formation.

These experiments demonstrated a turning point from physical to biological control of ecosystem function (element cycling). Interaction among ecosystem controls (microclimate, soil, and terrace height) resulted in formation of salt-affected soil. The demise of this condition is controlled by interaction among successional processes—soil, terrace height, and vegetation (Figure 1). This example also illustrates that in relatively short time intervals (less than ten years) major

86

changes may occur in control of ecosystem processes.

Deciduous to evergreen forest. A second major turning point is the transition from deciduous to evergreen forest and associated development of the feather-moss ground carpet. This turning point is associated with a change in several potential ecosystem controls (vegetation, microclimate, and mineral soil), which probably interact in a complicated fashion. Again, the state-factor approach suggested a series of experiments, some of which have been completed.

By recognizing different ecosystem controls, we are forced to design experiments that attempt to separate the controls or that explore the nature of their interactions. Warming of the soil to reverse the change in microclimate associated with this turning point dramatically enhances decomposition, nutrient availability, and tree growth (Hom 1986, Van Cleve et al. 1983). However, manipulation of root temperature in laboratory experiments where nutrient availability was held constant had relatively minor effects on growth of tree seedlings (Tryon and Chapin 1983).

This finding suggests that the change in microclimate caused by vegetation change is important mainly through its effects on decomposer organisms rather than through direct effects on the vegetation. We intend next to manipulate the type of litter input to the forest floor in deciduous and evergreen forests and examine the response of moss growth.

Vegetation and element cycling. In a third example, we examined the effect of vegetation on ecosystem-level phenomena such as element cycling. Examples of mature forests were selected for each type encountered in interior Alaska (Viereck et al. 1983). We hypothesized that black spruce would display the lowest rates of element turnover because of low productivity and nutrient limitation to tree growth.

Results of our field studies showed that there were substantial differences in element cycling among forest types. In general, rates of annual tree element uptake, recycling in litterfall, and supply from the forest floor for tree use declined in the order aspen

greater than birch greater than white spruce greater than black spruce (Flanagan and Van Cleve 1983, Van Cleve et al. 1983).

Laboratory incubation and bioassay studies were conducted on forest floor organic matter to estimate nitrogen and phosphorus supply for birch seedling growth under conditions of constant temperature, moisture, and light. Rates of nitrogen and phosphorus supply were greater in birch than in aspen. The supply of these elements in white spruce was the same as in aspen, whereas the supply was smallest in black spruce (Van Cleve and Harrison 1985, Van Cleve et al. 1986b).

Topography and element cycling. The influence of topography on forest element cycling was examined across the array of site types discussed in the paragraph above and between almost contiguous white spruce and black spruce stands occurring on adjacent south and north aspects. The topographic analysis showed that black spruce primarily occurred on cold, wet permafrost sites that arise on north-trending aspects. These microenvironmental conditions resulted in reduced organic matter decomposition and element recycling for plant growth, compared with forest types developing on warmer aspects (Van Cleve et al. 1983, Van Cleve and Yarie 1986). Moreover, heating the soil in one of the black spruce sites resulted in substantial increase in forest floor decomposition and element supply to the black spruce (Hom 1986, Van Cleve et al. 1983).

Conclusions

Jenny (1980) recommended that the influence of each state factor be studied by choosing ecosystems in which all but one factor is held nearly constant. As he pointed out, and as our studies in the taiga indicate, this experimental design is not always feasible because of the complex interaction among state factors at the local level. Nonetheless, dramatic differences in structure and function of the taiga forest ecosystems in interior Alaska, as viewed through the study of element cycling, can be explained by steep gradients in state factors across the landscape. Wise manage-

ment of the large renewable forest resource of interior Alaska ultimately depends on these considerations.

References cited

Billings, W. D. 1987. Carbon balance of Alaskan tundra and taiga ecosystems, past, present and future. *Quat. Sci. Rev.* 6: 165–177.

Bohn, H., B. McNeal, and G. O'Connor. 1985. *Soil Chemistry.* John Wiley & Sons, New York.

Bryant, J. P., and F. S. Chapin, III. 1986. Browsing–woody plant interactions during boreal forest plant succession. Pages 213–225 in K. Van Cleve, F. S. Chapin III, P. W. Fanagan, L. A. Viereck, and C. T. Dyrness, eds. *Forest Ecosystems in the Alaska Taiga: A Synthesis of Structure and Function.* Springer-Verlag, New York.

Chapin, F. S. III, and G. R. Shaver. 1985. Individualistic growth response of tundra plant species to environmental manipulations in the field. *Ecology* 55: 564–576.

Chapin, F. S. III, P. R. Tyron, and K. Van Cleve. 1983. Influence of phosphorus supply on the growth and biomass distribution of Alaska taiga tree seedlings. *Can. J. For. Res.* 13: 1092–1098.

Chapin, F. S. III, and K. Van Cleve. 1981. Plant nutrient absorption and retention under differing fire regimes. Pages 301–321 in H. A. Mooney, T. M. Bonnicksen, N. L. Christensen, J. E. Lotan, and W. A. Reiners, eds. *Fire Regimes and Ecosystem Properties.* General Technical Report WO-26, USDA Forest Service, Washington, DC.

Chapin, F. S. III, K. Van Cleve, and P. R. Tryon. 1986. Relationship of ion absorption to growth rate in taiga trees. *Oecolgia (Berlin)* 69: 239–242.

Crocker, R. L., and J. Major. 1955. Soil development in relation to vegetation and surface age at Glacier Bay, Alaska. *J. Ecol.* 43: 427–448.

Darrah, P. R., P. H. Nye, and R. E. White. 1987. The effect of high solute concentrations on nitrification rates in soil. *Plant Soil* 97: 37–45.

Dickson, B. A., and R. L. Crocker. 1953. A chronosequence of soils and vegetation near Mt. Shasta, California. *J. Soil Sci.* 4: 142–154.

Dyrness, C. T., and R. A. Norum. 1983. The effects of experimental fires on black spruce forest floors in interior Alaska. *Can. J. For. Res.* 12: 879–893.

Dyrness, C. T., K. Van Cleve, and J. Levison. 1989. The effect of wildfire on soil chemistry in four forest types in interior Alaska. *Can. J. For. Res.* 19: 1389–1396.

Dyrness, C. T., L. A. Viereck, M. J. Foote, and J. C. Zasada. 1988. The effect on vegetation and soil temperature of logging flood-plain white spruce. Research Paper PNW-RP-392, USDA Forest Service, Pacific Northwest Forest and Range Experiment Station, Portland, OR.

Dyrness, C. T., L. A. Viereck, and K. Van Cleve. 1986. Fire in taiga communities of interior Alaska. Pages 74–88 in K. Van Cleve, F. S. Chapin III, P. W. Flanagan, L. A. Viereck, and C. T. Dyrness, eds. *Forest Ecosystems in the Alaska Taiga: A Synthesis of Structure and Function.* Springer-Verlag, New York.

Flanagan, P. W., and K. Van Cleve. 1983. Nutrient cycling in relation to decomposition and organic matter quality in taiga ecosystems. *Can. J. For. Res.* 13: 795–817.

Gregory, R. A. 1966. The effect of leaf litter upon establishment of white spruce beneath paper birch. *For. Chron.* 42: 251–255.

Heilman, P. E. 1966. Change in distribution and availability of nitrogen with forest succession on north slopes in interior Alaska. *Ecology* 47: 825–831.

Heinselman, M. L. 1978. Fire intensity and frequency as factors in the distribution and structure of northern ecosystems. Pages 7–57 in H. A. Mooney, T. M. Bonnicksen, J. L. Christensen, J. E. Lotan, and W. A. Reiners, eds. *Fire Regimes and Ecosystem Properties.* General Technical Report WO-26, USDA Forest Service, Washington, DC.

Hom, J. L. 1986. Investigations into some of the major controls on the productivity of a black spruce (*Picea mariana* (Mill.) B.S.P.) forest ecosystem in the interior of Alaska. Ph.D. dissertation, University of Alaska-Fairbanks, Fairbanks.

Jenny, H. 1941. *Factors of Soil Formation.* McGraw-Hill, New York.

_____. 1980. *The Soil Resource: Origin and Behavior.* Springer-Verlag, New York.

Juday, G. P., and J. C. Zasada. 1984. Structure and development of an old growth white spruce forest on an interior Alaska flood-plain. Pages 227–234 in W. R. Meehan, T. R. Merrell Jr., and T. A. Hanley, eds. *Fish and Wildlife Relationships in Old Growth Forests.* Proceedings of a symposium held in Juneau, AK. American Institute of Fisheries Research Biologists. John W. Reintjes, Moorehead City, NC.

Klingensmith, K. M. 1988. Nitrogen dynamics in primary successional soils on the Tanana River of interior Alaska. Ph.D. dissertation, University of Alaska, Fairbanks.

Krasny, M. E., K. A. Vogt, and J. C. Zasada. 1988. Establishment of four Salicaceae species on river bars in interior Alaska. *Holarct. Ecol.* 11: 210–219.

Lawrence, W. T., and W. C. Oechel. 1983. Effects of soil temperature on the carbon exchange of taiga seedlings. I. Root respiration. *Can. J. For. Res.* 13: 840–849.

McBeath, J. H., ed. 1984. The potential effects of carbon dioxide-induced climatic changes in Alaska: proceedings. Miscellaneous publication 83–1, School of Agriculture and Land Resources Management, University of Alaska, Fairbanks.

Oechel, W. C., and K. Van Cleve. 1986. The role of bryophytes in nutrient cycling in the taiga. Pages 121–137 in K. Van Cleve, F. S.

Chapin III, P. W. Flanagan, L. A. Viereck, and C. T. Dyrness, eds. *Forest Ecosystems in the Alaskan Taiga: A Synthesis of Structure and Function.* Springer-Verlag, New York.

Patric, J. H., and P. E. Black. 1968. Potential evapotranspiration and climate in Alaska by Thornthwaite's classification. Research Paper PNW-71, USDA Forest Service, Pacific Northwest and Range Experiment Station, Portland, OR.

Péwé, T. L., and R. D. Reger. 1983. *Richardson and Glenn Highways, Alaska: Guidebook to Permafrost and Quaternary Geology.* Guidebook 1, Division of Geology and Geophysical Survey, Alaska Department of Natural Resources, Fairbanks.

Reeburgh, W. S., and S. C. Whalen. 1990. The role of tundra and taiga systems in the global methane budget. Page 102 in *Abstracts from International Conference on the Role of Polar Regions in Global Climate Change.* June 11–15, Fairbanks, AK. Geophysical Institute, University of Alaska, Fairbanks.

Seiferet, R. D. 1981. A solar design manual for Alaska. Bulletin of the Institute of Water Resources. vol. I. University of Alaska, Fairbanks.

Slaughter, C. W. 1985. Soil movement associated with the Rosie Creek fire. Pages 5–6 in G. P. Juday and C. T. Dyrness, eds. *Early Results of the Rosie Creek Fire Research Project 1984.* Miscellaneous publication 85–2, Agricultural and Forestry Experiment Station, School of Agriculture and Land Resources Management, University of Alaska, Fairbanks.

Slaughter, C. W., and L. A. Viereck. 1986. Climatic characteristics of the taiga in interior Alaska. Pages 9–21 in K. Van Cleve, F. S. Chapin III, P. W. Flanagan, L. A. Viereck, and C. T. Dyrness, eds. *Forest Ecosystems in the Alaskan Taiga: A Synthesis of Structure and Function.* Springer-Verlag, New York.

Tryon, P. R., and F. S. Chapin III. 1983. Temperature control over root growth and root biomass in taiga forest trees. *Can. J. For. Res.* 13: 827–833.

Van Cleve, K., and V. Alexander. 1981. Nitrogen cycling in tundra and boreal ecosystems. *Ecol. Bull. (Stockholm)* 33: 375–404.

Van Cleve, K., F. S. Chapin III, P. W. Flanagan, L. A. Viereck, and C. T. Dyrness, eds. 1986a. *Forest Ecosystems in the Alaskan Taiga: A Synthesis of Structure and Function.* Springer-Verlag, New York.

Van Cleve, K., and C. T. Dyrness. 1985. The effect of the Rosie Creek fire on soil fertility. Pages 7–11 in G. P. Juday and C. T. Dyrness, eds. *Early Results of the Rosie Creek Fire Research Project 1984.* Miscellaneous publication 85–2, Agricultural and Forestry Experiment Station, School of Agriculture and Land Resources Management, University of Alaska-Fairbanks.

Van Cleve, K., C. T. Dyrness, L. A. Viereck, J. Fox, F. S. Chapin III and W. Oechel. 1983. Taiga ecosystems in interior Alaska. *BioScience* 33: 39–44.

Van Cleve, K., and A. F. Harrison. 1985. Bioassay of forest floor phosphorus supply for plant growth. *Can. J. For. Res.* 15: 156–162.

Van Cleve, K., O. W. Heal, and D. Roberts. 1986b. Bioassay of forest floor nitrogen supply for plant growth. *Can. J. For. Res.* 6: 1320–1326.

Van Cleve, K., and L. A. Viereck. 1972. Distribution of selected elements in even-aged alder (*Alnus*) ecosystems near Fairbanks, Alaska. *Arct. Alp. Res.* 4: 239–255.

_____. 1981. Forest succession in relation to nutrient cycling in the boreal forest of Alaska. Pages 185–211 in D. West, H. Shugart, and D. Botkin, eds. *Forest Succession: Concepts and Application.* Springer-Verlag, New York.

Van Cleve, K., L. A. Viereck, and R. L. Schlentner. 1971. Accumulation of nitrogen in alder (*Alnus*) ecosystems near Fairbanks, AK. *Arct. Alp. Res.* 3: 101–114.

Van Cleve, K., and J. Yarie. 1986. Interaction of temperature, moisture, and soil chemistry in controlling nutrient cycling and ecosystem development in the taiga of Alaska. Pages 160–189 in K. Van Cleve, F. S. Chapin III, P. W. Flanagan, L. A. Viereck, and C. T. Dyrness, eds. *Forest Ecosystems in the Alaskan Taiga: A Synthesis of Structure and Function.* Springer-Verlag, New York.

Viereck, L. A. 1970. Forest succession and soil development adjacent to the Chena River in interior Alaska. *Arct. Alp. Res.* 2: 1–26.

Viereck, L. A., C. T. Dyrness, K. Van Cleve, and M. J. Foote. 1983. Vegetaion, soils, and forest productivity in selected forest types in interior Alaska. *Can. J. For. Res.* 13: 703–720.

Viereck, L. A., and M. J. Foote. 1985. Effects of the Rosie Creek fire on selected environmental factors in the Bonanza Creek Experimental Forest. Pages 1–4 in G. P. Juday and C. T. Dyrness, eds. *Early Results of the Rosie Creek Fire Research Project 1984.* Miscellaneous publication 85–2, Agricultural and Forestry Experiment Station, School of Agriculture and Land Resources Management, University of Alaska, Fairbanks.

Viereck, L. A., K. Van Cleve, and C. T. Dyrness. 1986. Forest ecosystem distribution in the taiga environment. Pages 22–43 in K. Van Cleve, F. S. Chapin III, P. W. Flanagan, L. A. Viereck, and C. T. Dyrness, eds. *Forest Ecosystems in the Alaskan Taiga: A Synthesis of Structure and Function.* Springer-Verlag, New York.

Vitousek, P. M., P. A. Matson, and K. Van Cleve. 1989. Nitrogen availability and nitrification during succession: primary, secondary, and old-field series. *Plant Soil* 115: 229–240.

Vitousek, P. M., and L. R. Walker. 1987. Colonization, succession, and resource availability: ecosystem-level interactions. Pages 207–223 in A. Gray, M. Crawley, and P. J. Edwards, eds. *Colonization, Succession, and Stability.* Blackwell Scientific, Oxford.

Walker, L. R., J. C. Zasada, and F. S. Chapin III. 1986. The role of life history processes in primary succession on an Alaskan flood-plain. *Ecology* 67: 1243–1253.

Yarie, J. 1981. Forest fire cycles and life tables: a case study from interior Alaska. *Can. J. For. Res.* 11: 554–562.

Zasada, J. 1986. Natural regeneration of trees and tall shrubs on forest sites in interior Alaska. Pages 44–73 in K. Van Cleve, F. S. Chapin III, P. W. Flanagan, L. A. Viereck, and C. T. Dyrness, eds. *Forest Ecosystems in the Alaskan Taiga: A Synthesis of Structure and Function.* Springer-Verlag, New York.