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Carbon and nitrogen cycling in North American boreal forests.

I. Litter quality and soil thermal effects in interior Alaska

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Abstract. A model of boreal forest dynamics was adapted to examine the factors controlling carbon and nitrogen cycling in the boreal forests of interior Alaska. Empirical relationships were used to simulate decomposition and nitrogen availability as a function of either substrate quality, the soil thermal regime, or their interactive effects. Test comparisons included black spruce forests growing on permafrost soils and black spruce, birch, and white spruce forests growing on permafrost-free soils. For each forest, simulated above-ground tree biomass, basal area, density, litterfall, moss biomass, and forest floor mass, turnover, thickness, and nitrogen concentration were compared to observed data. No one decay equation simulated forests entirely consistent with observed data, but over the range of upland forest types in interior Alaska, the equation that combined the effects of litter quality and the soil thermal regime simulated forests that were most consistent with observed data. For black spruce growing on permafrost soils, long-term simulated forest dynamics in the absence of fire resulted in unproductive forests with a thick forest floor and low nitrogen mineralization. Fires were an important means to interrupt this sequence and to restart forest succession.

Introduction

Interactions among soil temperature, litter quality, and the forest floor are thought to control productivity and nutrient cycling in the boreal forests of interior Alaska (Flanagan & Van Cleve 1983; Van Cleve et al. 1983a; Van Cleve & Viereck 1981; Van Cleve & Yarie 1986). In particular, forest floor decomposition is positively correlated with soil temperature (Fox & Van Cleve 1983; Van Cleve & Yarie 1986). Cold soil temperatures in black spruce (*Picea mariana* (Mill.) B.S.P.) forests underlain with permafrost slow decomposition and nutrient mineralization (Van Cleve et al. 1981, 1983a;

Van Cleve & Viereck 1981; Van Cleve & Yarie 1986). This restricts tree growth while promoting the accumulation of a thick forest floor that further reduces soil temperature. In contrast, warm soil temperatures on permafrost-free sites enhance productivity and nutrient cycling through more rapid decomposition and nutrient mineralization (Van Cleve et al. 1981, 1983a; Van Cleve & Viereck 1981; Van Cleve & Yarie 1986).

Forest floor nitrogen and lignin concentrations are also correlated with decomposition rates (Flanagan & Van Cleve 1983), and substrate quality is thought to interact with soil temperature to enhance or restrict nutrient availability (Flanagan & Van Cleve 1983; Van Cleve et al. 1983a; Van Cleve & Yarie 1986). Cold, wet black spruce sites have forest floors with low nitrogen and high lignin concentrations, which further slow decomposition. Warm sites dominated by white spruce (*Picea glauca* (Moench) Voss), white birch (*Betula papyrifera* Marsh.), and trembling aspen (*Populus tremuloides* Michx.) have forest floors with higher nitrogen and lower lignin concentrations (Van Cleve et al. 1983a; Van Cleve & Yarie 1986).

The purpose of this paper was to use a simulation model of boreal forest dynamics to clarify the influence of forest floor substrate quality and the soil thermal regime on productivity and nitrogen cycling in interior Alaska. A 'gap' model of environmental and ecological factors controlling boreal forest dynamics and vegetation patterns (Bonan 1988, 1989b; Bonan et al. 1989; Bonan & Korzuhin 1989) was combined with compatible models of nitrogen and carbon cycling (Aber et al. 1982; Pastor & Post 1985, 1986). The model was modified to include fire regimes and empirical decomposition relationships specific to the upland forests of interior Alaska. Forests were then simulated using alternative substrate quality and soil thermal regime decomposition equations, and the simulated forests were compared to observed data.

Methods

The model

Botkin et al. (1972), Shugart & West (1977), and Shugart (1984) described the philosophy of gap models. Bonan (1988, 1989b) documented a boreal forest gap model that simulates interactions among forest dynamics, soil moisture, permafrost, moss, and fire. Bonan et al. (1990) used this model to examine the sensitivity of boreal forests in interior Alaska to climatic parameters. Bonan & Korzuhin (1989) examined the ecological consequences of interactions between mosses and trees. In this paper, I modified this

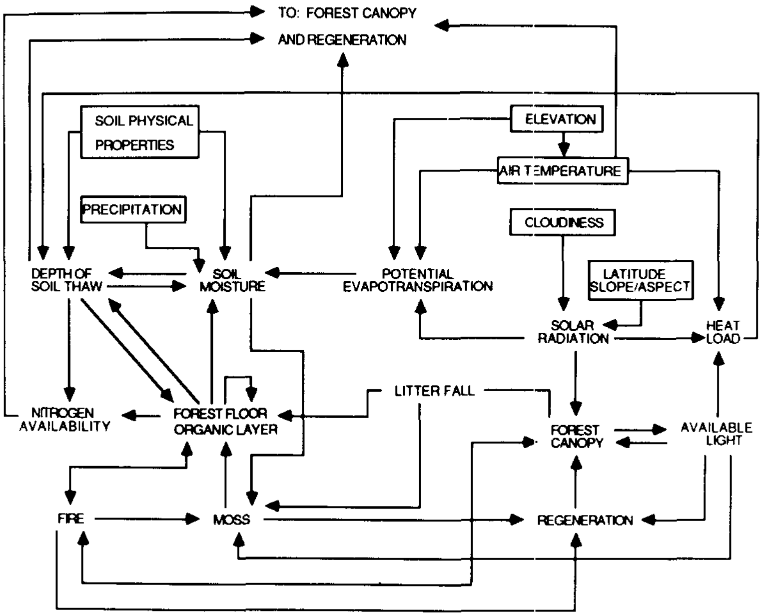

Fig. 1. Schematic diagram of boreal forest gap model. Boxes indicate required input parameters.

model to include carbon and nitrogen cycling in response to the soil thermal regime, forest floor substrate quality, and fire. General features of the model are outlined in Fig. 1 and are summarized below. Bonan & Shugart (1989) provided justification for including these factors in the model.

Bonan (1989a) described the algorithms that simulate the solar radiation, soil moisture, and soil thermal regimes. Solar radiation, soil moisture, and depths of soil freezing and thawing were calculated on a monthly time step to give annual and seasonal estimates of site conditions. Monthly solar radiation was calculated by attenuating incoming solar radiation for atmospheric effects, partitioning this into direct beam and diffuse components, and adjusting for slope and aspect. Monthly potential evapotranspiration was calculated from solar radiation and air temperature using a modified form of the Priestley–Taylor equation. Monthly water contents of the forest floor and mineral soil were based on precipitation, actual evapotranspiration, water released in soil thawing, and drainage. Depths of freezing and thawing in the mineral soil were calculated using Stephan's formula.

The model simulated the annual regeneration, growth, and depth of individual trees on a 1/12-ha forest plot in response to these and other site conditions. Individual tree growth under optimal site conditions was a function of a species-specific growth rate, tree diameter, and tree height and was decreased multiplicatively to the extent that site conditions (available light, growing season air temperature sum, soil moisture, depth of thaw, nitrogen availability) were less than optimal. Regeneration was constrained by these same site conditions and by other effects such as a thick moss ground cover, seed availability following forest fires, and vegetative reproduction. Mortality was a function of potential longevity, stress, and forest fires. As in other gap models, trees were subjected to stress mortality when their diameter increment was less than 1 mm for two consecutive years. This critical diameter increment was reduced to 0.1 mm for black spruce, a slow growing species with annual growth rates as low as 0.1–0.2 mm (Hustich 1951, 1954; Zoltais 1975; Clyde & Titus 1987).

The forest floor consisted of foliage and twig litter and a humus layer. If present, moss and moss litter were added to the forest floor. Annual moss productivity was the difference between carbon assimilation and respiration and decay and was reduced for deleterious effects of deciduous litter, dessication under canopy openings, and shading by trees. Simulated fire intensity was a function of fuel buildup. Fire severity (i.e., depth of burn in the forest floor) was a function of forest floor moisture content and pre-burn thickness.

Relative growth multipliers were used to scale optimal tree growth in response to available light and air temperature (Botkin et al. 1972; Shugart & West 1977; Shugart 1984), soil moisture (Pastor & Post 1985, 1986), and available nitrogen (Aber et al. 1982). Bonan (1988, 1989b) developed a depth-of-thaw growth multiplier for boreal forest trees. However, permafrost and nutrient availability are highly interdependent (Van Cleve et al. 1983a; Van Cleve & Viereck 1981; Van Cleve & Yarie 1986), and Bonan's (1988, 1989b) depth-of-thaw growth multiplier combined the effects of cold soil temperature on tree metabolism with the effects of cold soil temperature on decomposition and nutrient availability. Because the nitrogen availability growth multiplier simulated the effects of soil temperature on nutrient availability, the depth-of-thaw growth multiplier was reformulated to simulate only the effects of soil temperature on plant metabolism.

Yarie's (1983) stand yield data revealed that black spruce and white spruce biomass increased as a linear function of depth to permafrost (black spruce: $R^2 = 0.86$, $n = 8$, $p < 0.001$; white spruce: $R^2 = 0.75$, $n = 11$, $p < 0.001$). In neither case was the intercept significantly different from zero. These equations were divided by the maximum reported stand biomass in interior Alaska (black spruce: $100\,\mathrm{t\,ha^{-1}}$; white spruce $250\,\mathrm{t\,ha^{-1}}$ [Van Cleve et al. 1983a]) to give the relative stand biomass response to permafrost. Because tree biomass is approximately a square function of

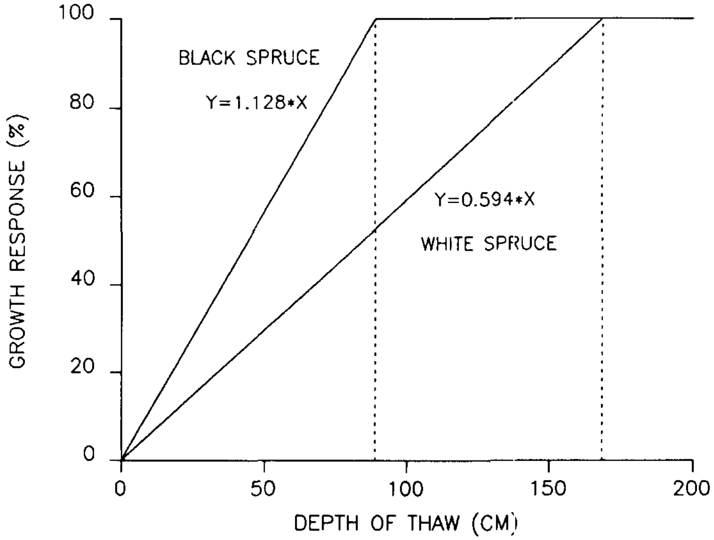

Fig. 2. Individual tree growth response to depth of soil thaw.

diameter, the individual tree growth response to permafrost was represented by the square root of the stand response (Fig. 2) These equations indicated that optimal white spruce growth occurs on soils where depth of thaw is greater than 170 cm. Stoeckeler (1952) stated that optimal white spruce growth occurs on soils unfrozen to a depth of at least 150–180 cm.

For black spruce growing on permafrost, the growth factor estimated from Fig. 2 corresponded with Aber et al.'s (1982) nitrogen availability growth factor calculated with Van Cleve & Yarie's (1986) nitrogen availability data. I assumed, therefore, that the growth of black spruce, a permafrost-tolerant species, was not limited by the direct effects of soil temperature on plant metabolism, but was limited by low nitrogen availability associated with cold soils. White spruce was assumed to respond to both low metabolism and low nutrient availability associated with cold soils. Low metabolism was simulated by the depth-of-thaw growth multiplier, which was assumed to be the ratio of the white spruce growth response to the black spruce growth response (Fig. 2). These equations were generalized by assuming that black spruce represents permafrost-tolerant species and white spruce represents species less tolerant of permafrost.

Nitrogen and carbon cycling

Nitrogen and carbon cycling were simulated using the approach developed by Aber et al. (1982) and Pastor & Post (1985, 1986). Annual litterfall entered a litter pool where all individual litter cohorts except fresh wood

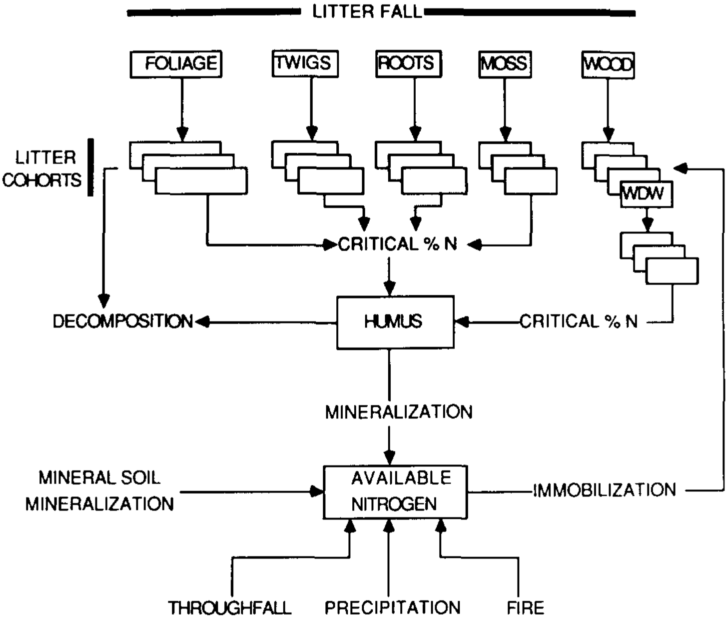

Fig. 3. Simulated carbon and nitrogen cycling in the absence of fire.

immobilized nitrogen during decomposition (Fig. 3). Fresh wood did not immobilize nitrogen during decay until some fraction of its initial mass was lost, at which point it was transferred to a well-decayed wood cohort where nitrogen immobilization occurred. The mass and nitrogen concentration of each litter cohort was updated annually, and when nitrogen reached a critical concentration, the litter cohort was transferred to the humus pool, where mineralization occurred (Fig. 3). Aber et al. (1982) assumed nitrogen mineralization from humus was a constant fraction of the total humus nitrogen pool. Pastor & Post (1985, 1986) calculated humus nitrogen mineralization from the current year's litter C:N ratio, adjusted for site conditions. In contrast, I followed the example of Van Cleve et al. (1981), Flanagan & Van Cleve (1983), and Van Cleve & Yarie (1986) and calculated nitrogen mineralization as humus mass loss times the nitrogen concentration.

Net nitrogen mineralization was the difference between litter immobilization and humus mineralization. Following Pastor & Post (1985, 1986), precipitation added 5 kg ha^{-1} yr^{-1} nitrogen to the soil, and nitrogen addition from throughfall was 16% of the foliage litter nitrogen. Aber et al. (1982) assumed mineral soil nitrogen mineralization was 10 kg ha^{-1} yr^{-1}. I used this value for soils where depth of thaw was greater than one meter; otherwise mineral soil nitrogen mineralization was directly proportional to depth of

Table 1. Prediction of individual tree foliage biomass from diameter at breast height (DBH). Crown width (m) = $a + b\,\mathrm{DBH}\,[\mathrm{cm}]$; Foliage weight (kg) = $c\pi/4$ (crown width)^2.

a (m)	b ($\mathrm{m\,cm^{-1}}$)	c ($\mathrm{kg\,m^{-2}}$)	Genera
8.04	0.69	0.01320	Spruce
8.04	0.69	0.00248	Birch

thaw. Fires, when they occurred, also mineralized nitrogen contained in the forest floor and above-ground biomass.

Litter production

Five main litter classes were simulated: foliage, roots, twigs, wood, and moss. Woody litter was divided into fresh wood and well-decayed wood. Foliage litter was divided into genera-level subclasses. For dead trees not killed during fire, all the foliage biomass entered the foliage litter pool. For live trees, foliage litter was proportional to the annual turnover in foliage biomass. Foliage biomass was simulated using Aber et al.'s (1982) and Pastor & Post's (1985, 1986) equations and parameters (Table 1). Fine-root litter was 1.3 times foliage litter (Aber et al. 1982; Pastor & Post 1985, 1986). Fresh wood litter for dead trees not killed in fire was 60% of individual tree biomass (Aber et al. 1982; Pastor & Post 1985, 1986). Twig litter was directly proportional to stand basal area (Aber et al. 1982; Pastor & Post 1985, 1986). Moss litter was calculated from moss growth.

Litter and humus decay

Three different equations were used to examine forest floor decomposition as a function of substrate quality, the soil thermal regime, and their interactions.

1. Forest floor substrate quality. Flanagan & Van Cleve (1983) found that the annual forest floor decomposition rate in interior Alaska was a linear function of nitrogen concentration

$$\%\ \text{mass loss} = -0.7 + 2.8\,\%\text{N}.$$

2. Soil thermal regime. Data from Viereck et al. (1983), Van Cleve & Yarie (1986), and Bonan (1989a) were used to develop decay rates as a function of depth of thaw. Van Cleve & Yarie's (1986) equation relating forest floor decomposition to soil temperature was used to estimate decomposition rates for several forest sites in interior Alaska (Viereck et al. 1983). Bonan's (1989a) model of site conditions was then used to estimate depth of thaw for

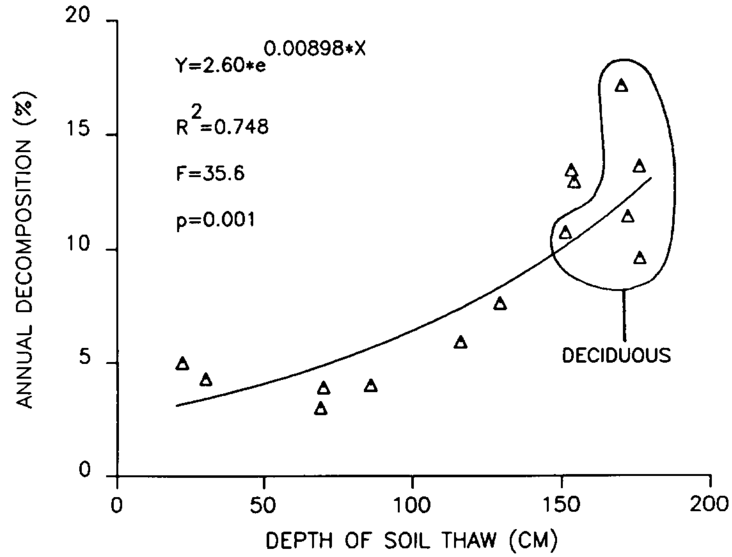

Fig. 4. Relationship between annual forest floor decomposition and depth of soil thaw for deciduous and coniferous forests.

each site. Annual decomposition was highly correlated with depth of thaw (Fig. 4).

3. Interactive effects. These two equations were combined to examine the joint effects of substrate quality and the soil thermal regime. Overall, decomposition predicted from depth of thaw was unbiased for deciduous forest types, but tended to overestimate the observed decomposition for spruce forests (Fig. 4). Consequently, the decay equation for the soil thermal regime was multiplied by a substrate quality factor. This factor was estimated from the substrate quality decay equation, scaled to a factor of one when nitrogen concentration was 1.5% (i.e., the maximum reported nitrogen concentration in deciduous forests [Van Cleve et al. 1983a]).

The three decay equations are compared in Fig. 5. At shallow depths of thaw, all three equations gave similar forest floor decomposition. For deeper depths of thaw, the substrate quality equation indicated lower annual decay compared to the soil thermal regime equation. Decomposition estimated by the interactive effects equation varied greatly with nitrogen concentration.

These equations were used to simulate annual decomposition for all litter cohorts and humus. Following Aber et al. (1982) and Pastor & Post (1985, 1986), wood and twigs had maximum annual decay rates of 6% and 20%, respectively. These equations were not meant to be causal, but merely reflected empirical forest floor turnover relationships in interior Alaska.

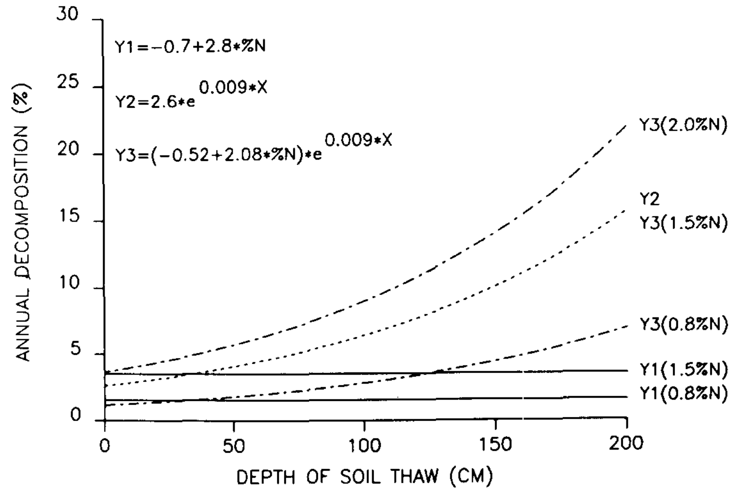

Fig. 5. Substrate quality (Y1), soil thermal regime (Y2), and interactive effects (Y3) decay equations evaluated for different depths of soil thaw and nitrogen concentrations.

Indeed, though nitrogen controls initial litter decay (Aber & Melillo 1980; Staaf & Berg 1982), lignin may be more important in later stages of decomposition (Berg 1986; Berg & Staaf 1980, 1981). This does not, however, mitigate the usefulness of empirical forest floor decomposition relationships.

Annual decay was also adjusted for canopy openings. Aber et al. (1982) used a function of foliage biomass. Pastor & Post (1985, 1986) used a function of foliage litter biomass and soil water holding capacity. I used Aber et al.'s (1982) decay multiplier, adjusted to leaf area. When the leaf area index (LAI) was less than 2.5, annual decomposition for all litter cohorts and humus was increased by a factor

$$y = 1.0 + 1.5(1.0 - LAI/2.5)^{1/2}$$

Fire

Recurring forest fires are common in interior Alaska, and forest vegetation reflects the effects of fires on site conditions and seed availability (Dyrness et al. 1986; Lutz 1956; Viereck 1973, 1983; Viereck & Schandelmeier 1980). The direct effects of fire on carbon and nitrogen cycling include consumption of biomass, mineralization of organically-bound nitrogen, and loss of nitrogen through volatilization or as smoke and ash (MacLean et al. 1983). Indirect effects following fire include return of nitrogen lost in smoke and ash, leaching of mineralized nitrogen into the soil profile, loss of mineralized nitrogen in overland flow, and increased decomposition and mineralization brought about by changes in the soil thermal regime (MacLean et al. 1983).

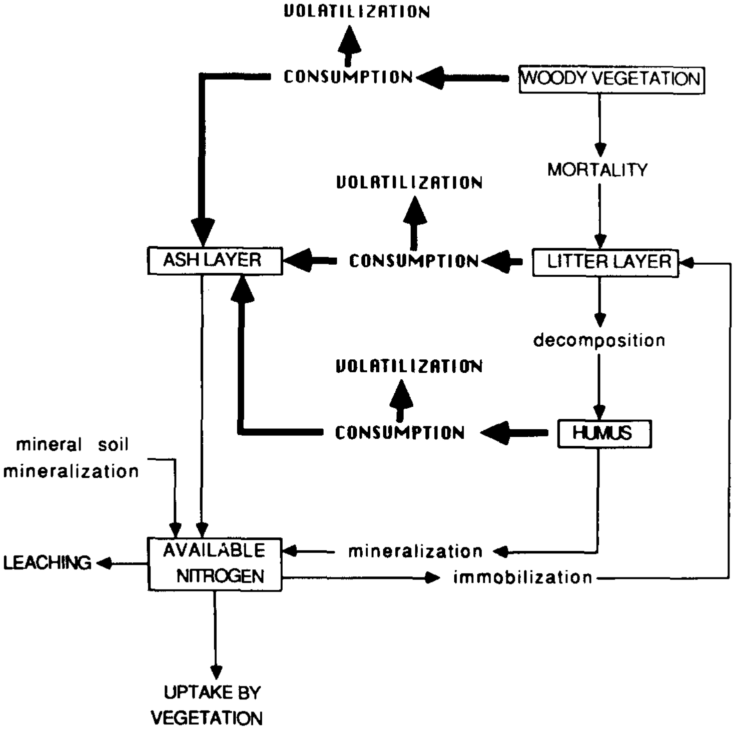

Fig. 6. Simulated carbon and nitrogen redistribution during (boldface lettering) and following (normal lettering) fire. Lower case lettering indicates post-fire processes influenced by the soil thermal regime.

These relationships were included in the model to simulate the effects of fire on nitrogen and carbon cycling (Fig. 6).

Data from MacLean & Wein (1980) were used to simulate the consumption of carbon in trees killed during fire as a function of simulated fire intensity (Table 2). The biomass not consumed by fire was added to the annual litter pool. Decaying wood on the forest floor burned similarly to woody biomass.

In the black spruce forests of interior Alaska, fire burns the forest floor unevenly, leaving behind a patchy mosaic of burn types (Viereck 1973; Viereck & Schandelmeier 1980; Zasada et al. 1983). Viereck & Schandelmeier (1980) recognized three fire severity classes based on the amount of area in light, moderate, and heavy burn types. These classes were combined with estimates of the amount of forest floor consumed per burn type (Dyrness & Norum 1983) to simulate the reduction in forest floor thickness in response to fire severity (Table 3). Five severity is a direct linear function of moisture content and pre-burn thickness (Dyrness & Norum 1983).

Table 2. Percent consumption of biomass components for trees killed during fire. Nitrogen volatilization is the percent of nitrogen in the various biomass components that is volatilized during fire.

	Fire intensity		
	Light	Moderate	Severe
Wood	10%	30%	50%
Foliage	60%	80%	100%
Twigs	20%	40%	60%
Roots	50%	70%	90%
N volatilization	10%	40%	70%

Consequently, simulated fire severity was a function of forest floor moisture content and pre-burn thickness.

Nitrogen in plant tissue is volatilized at temperatures above 200 °C (Dubreuil & Moore 1982; Knight 1966). Reported loss of nitrogen from plant tissue ranges from 25% at 300 °C to 63% at 700 °C (Knight 1966). Dubreuil & Moore (1982) reported losses of 7–18% at 200 °C and 52–88% at 500 °C. Under natural conditions mean temperatures during fires range from 300–400 °C (Smith & Sparling 1966), 200–375 °C (Smith & Bowes 1974), and 250–300 °C (Sims 1976). Extreme temperatures are as high as approximately 500 °C (Sims 1976; Smith & Bowes 1974) or 600 °C (Smith & Sparling 1966). These data were used to derive the amount of nitrogen in burned plant tissue lost through volatilization (Table 2). These values were applied to all tree biomass components, to decaying wood accumulated on

Table 3. Fire severity statistics.

(*A*) Percent reduction in forest floor thickness per burn type

	Burn type		
	Light	Moderate	Heavy
Forest floor reduction	21%	63%	76%

(*B*) Percent reduction in forest floor thickness per fire severity class

Fire severity	Area per burn type			Forest floor reduction
	Light	Moderate	Heavy	
Light	85%	15%	0%	27%
Moderate	45%	45%	10%	46%
Severe	0%	80%	20%	66%

the forest floor, and to the forest floor. The nitrogen in burned plant tissue that remained after volatilization was made available to plants.

Nutrients contained in smoke or convected ash may be deposited following a fire (Clayton 1976; Lewis 1974; Smith & Bowles 1974). For example, up to 30% of the nutrients lost from plants during burning can be recovered in downwind deposits of ash (Smith & Bowles 1974). Others, however, have found that little of the volatile loss is returned to the surface (Clayton 1976; DeBell & Ralston 1970), and in their review of the effects of fire on nutrient cycling, MacLean et al. (1983) concluded that the return of nutrients in post-fire ash deposition is unlikely to be a major factor.

Nutrients in the ash layer will be leached into the soil profile or lost in runoff, generally in the first year following fire (MacLean et al. 1983). In this model, available nitrogen was not accumulated from year-to-year. Thus, I assumed that the nitrogen made available during a given year was taken up by plants, and any remaining nitrogen was lost to runoff.

Changes in surface albedo and removal of the forest canopy and the forest floor increase soil temperatures, and this can increase decomposition and mineralization rates (Lutz 1956; MacLean et al. 1983; Viereck 1973, 1983; Viereck & Schandelmeir 1980; Dyrness et al. 1986). Increased depth of soil thawing also enlarges the soil nutrient pool. These effects were incorporated into the model by post-fire changes in the simulated depth of thaw caused by complete or partial removal of the forest canopy and the forest floor.

Simulation analyses and model testing

For each decay equation, forests were simulated for three different sites: black spruce growing on a poorly-drained north slope, black spruce growing on a well-drained, permafrost-free south slope terrace, and a successional sequence of birch and white spruce forests growing on a well-drained, permafrost-free south slope terrace. These forests were chosen to span the range of observed site conditions in the uplands of interior Alaska (Viereck et al. 1983, 1986). Following an initial fire, forest dynamics for each site were simulated for 500 years with recurring fire. Because processes such as mortality, reproduction, and fire occurred stochastically, each simulated forest was replicated for 30 1/12 ha plots to give an expected range of forests. All replicate forest plots received the same climate and soil conditions, but fires occurred independently among the replicate plots.

After 500 years of simulation, equilibrium conditions were obtained and the 30 simulated forest plots provided an estimate of the expected distribution of forests found on each site. Simulated plots with ages comparable to the observed data were then compared to the observed distribution

Table 4A. Required species parameters.

AGEMAX	–	maximum age of species (yr)
DBHMAX	–	maximum diameter at breast height (cm)
HTMAX	–	maximum height (m)
G	–	growth parameter
LITE	–	shade tolerance classification (1: tolerant, 2: intermediate, 3: intolerant)
SMOIST	–	the maximum percentage of the growing season that the species can tolerate soil moisture below the wilting point
Sprouting		
N	–	the tendency for stump sprouting
DBHMIN	–	the minimum diameter at breast height for sprouting (cm)
DBHMAX	–	the maximum diameter at breast height for sprouting (cm)
KTOL	–	fire tolerance (1: tolerant, 2: intermediate, 3: intolerant)
NUTR	–	nutrient stress tolerance class (1: tolerant, 2: intermediate, 3: intolerant)
IPFR	–	ability to grow on permafrost (1: good, 2: poor)
ALC	–	light level at which reproduction is inhibited
GDDMIN	–	minimum degree-days above 5.56 °C in the species' range
GDDMAX	–	maximum degree-days above 5.56 °C in the species' range
FRT	–	foliage retention time (yrs)
CDI	–	critical diameter increment for stress mortality (mm)
SWTCH	–	reproduction switches [SWTCH(1) is true if the species has serotinous cones. SWTCH(2) is true if the species has copious, light, wind dispersed seeds. SWTCH(3) is true if the species can reproduce by layering].

of forest types. Model testing compared simulated above-ground tree biomass, basal area, density, litterfall, moss biomass, and forest floor mass, turnover, thickness, and percent nitrogen with observed data. Parametric tests of differences between observed and simulated data were not appropriate because for each forest type, the available field data describing black spruce, birch, and white spruce forests were obtained from forests growing on several different soils and topographies (Viereck et al. 1983). Instead, overlap between the ranges of observed and simulated data was considered the relevant test. However, parametric tests were appropriate to assess differences in simulated forests due to the different decay equations.

Except for foliage retention time, which was estimated from field observations of foliage biomass and litterfall (Van Cleve et al. 1983a), species parameters (Table 4) were taken from Bonan (1988, 1989b). Foliage, root, and twig litter parameters (Table 5) were taken from Pastor & Post (1985, 1986). Pastor & Post's (1985, 1986) fresh wood parameters cause fresh wood to be transferred to well-decayed wood when 40% of the initial woody litter

Table 4B. Species parameters. Dashes indicate extraneous parameters.

	Age Max	DBH Max	HT Max	G	Sprouting									GDD Min	GDD Max	SWTCH	FRT	CDI
					LITE	SMOIST	N	DBH Min	DBH Max	KTOL	NUTR	IPFR	ALC					
White birch	140	76	30	187.2	3	0.30	1	10	32	3	1	2	0.6	280	2036	FTF	1	1.0
White spruce	200	76	34	147.3	1	0.30	–	–	–	3	1	2	–	280	1911	FFF	8	1.0
Black spruce	250	46	27	93.5	1	0.30	–	–	–	3	1	1	–	247	1911	TFT	13	0.1

Table 5. Required litter parameters.

Litter type	Initial % N	Mass N immobilized per unit weight loss	Critical % N	Ash-free correction
Foliage				
Birch	0.88	0.0092	2.00	0.92
Spruce	0.46	0.0215	0.72	0.97
Wood				
Fresh	0.30	0.0000	1.50	0.99
Well-decayed	1.50	0.0113	2.00	0.99
Twigs	0.30	0.0113	0.90	0.96
Fine-root	0.93	0.0108	1.50	0.98
Moss	0.46	0.0215	0.72	0.97

biomass has been lost. In contrast, Aber et al. (1982) assumed this transfer occurs when 80% of the initial biomass has decayed. I followed Aber et al.'s (1982) assumption and adjusted the fresh wood and well-decayed wood parameters accordingly (Table 5).

Due to lack of data, I assumed moss litter parameters were similar to spruce litter (Table 5). The limited available data indicated that this was an appropriate assumption. The estimated initial nitrogen concentration (0.46%) was consistent with observed nitrogen concentrations in green moss foliage (0.2–1.2% [Weetman 1968; Weetman & Timmer 1967]). Moreover, in a study of nutrient cycling in mature black spruce forests, Weetman (1968) and Weetman & Timmer (1967) estimated that it takes 5–12 years for dead moss to decompose to the point where it is no longer distinguishable. For a comparable mature, black spruce forest growing on permafrost-free soil in interior Alaska, the parameters in the current study, when used with the interactive effects decay equation, resulted in 5–6 years of decay before a moss litter cohort was transferred to humus.

Required edaphic parameters (Table 6) for the poorly-drained, north-facing site and the well-drained south slope terrace sites were taken from Bonan (1988, 1989b). The relative fire intensity parameter was set to a low level so that the simulations included severe fires that regenerated the forest plot. In addition, the litter and humus pools and nitrogen availability following the initial fire are required parameters. For each site, the model was initialized with representative above-ground woody biomass and forest floor mass and nitrogen concentrations for a mature forest (Van Cleve et al. 1983a). A severe fire was assumed to occur, and the litter and humus pools and nitrogen availability were initialized accordingly. Required climate

Table 6. Required edaphic parameters.

	Black spruce		Birch/white spruce
Aspect	N	S	S
Slope	30%	0%	0%
Elevation	350 m	133 m	133 m
Volumetric soil moisture			
Saturation	53%	35%	35%
Field Capacity	38%	20%	20%
Wilting point	6%	6%	6%
Fire regime			
Annual probability (yr^{-1})	0.01	0.01	0.0067
Relative intensity ($kg\,m^{-2}$)	5	10	10
Above-ground biomass ($kg\,m^{-2}$)	5	10	17
Forest floor			
Biomass ($kg\,m^{-2}$)	8	7	7
Nitrogen	0.8%	0.8%	0.8%

parameters were taken from Bonan (1988, 1989b). To facilitate statistical comparisons, climate parameters were not allowed to vary stochastically from year-to-year.

Results

For the north slope black spruce forest, the interactive effects decay equation simulated significantly less above-ground tree biomass, basal area, and litterfall than the other decay equations (Table 7). However, each equation simulated forests within the range of observed data. Moss biomass and available light varied significantly among decay equations, but each equation produced results that were consistent with observed forests. Forest floor mass, residence time, and thickness simulated by the soil thermal equation were significantly less than those simulated by the other equations (Table 7). However, all three decay equations simulated forest floors that overlapped to various degrees with the range of observed data. Depth of thaw is not necessarily the same as depth to permafrost (Bonan 1989a), but each decay equation resulted in shallow depth of thaw, which was consistent with the observed shallow depth to permafrost (Table 7).

For the permafrost-free black spruce forest, the substrate quality equation simulated less tree biomass and basal area than the other equations, but all three equations simulated tree biomass, basal area, and litterfall that were consistent with productive black spruce forests (Table 8). All three decay

Table 7. Simulated range of mature black spruce forests growing on a north slope. Common superscripts indicate simulated variables not significantly different ($p = 0.05$).

	Observed data	Decay equations		
		Substrate quality	Soil thermal regime	Interactive effects
Age[c] (yr), Sample size	60–140	62–135 (12)	64–134 (10)	66–140 (9)
Tree biomass[a] (t ha^{-1})				
Above-ground	25.9–109.8	43.7–64.6*	50.8–62.5*	40.7–51.9
Litter	0.2–1.4	0.8–1.0*	0.8–1.0*	0.7–0.9
Basal area[b] (m^2 ha^{-1})	7–27	12–15	13–16	11–13
Density[b] (ha^{-1})	1400–4000	3000–5724*	2664–4476*	3048–4536•
Forest floor				
Mass[e] (t ha^{-1})	44.7–92.2	77.2–141.3*	47.2–73.0	75.3–148.4*
Residence time[h,d] (yr)	36–64, 99–111	59–63	26–31	68–73
Depth[c] (cm)	12–38	17–28*	10–14	17–29*
Nitrogen[h] (%)	0.74–0.92	0.83–0.86	0.87–0.90	0.79–0.83
Moss biomass[g] (t ha^{-1})	3.5–10.1	4.7–5.0	4.7–4.9	4.9–5.0
Permafrost thaw depth[c] (cm)	16–55, none	20–27*	30–52	20–27*
Available light[f] (%)	33–60	35–48	35–42	43–50

Observed data from:

[a] Van Cleve et al. (1983a)

[b] Viereck et al. (1986)

[c] Viereck et al. (1983)

[d] Van Cleve et al. (1981)

[e] Van Cleve et al. (1983b)

[f] Slaughter (1983), permafrost site

[g] Oechel & Van Cleve (1986)

[h] 95% confidence interval, Van Cleve et al. (1983a)

Table 8. Simulated range of mature black spruce forests growing on a permafrost-free site. Common superscripts indicate simulated variables not significantly different ($p = 0.05$).

	Observed data	Decay equations		
		Substrate quality	Soil thermal regime	Interactive effects
Age[c] (yr), Sample size	60–140	61–135 (9)	70–139 (7)	66–140 (8)
Tree biomass[a] ($t\,ha^{-1}$)				
Above-ground	25.9–109.8	72.3–132.4	115.1–155.8	91.5–138.3
Litter	0.2–1.4	1.1–1.5*	1.1–1.6*	1.2–1.4*
Basal area[b] ($m^2\,ha^{-1}$)	7–27	18–27	26–31*	23–29*
Density[b] (ha^{-1})	1400–4000	2928–4752*	2736–3588†	2424–4008*,†
Forest floor				
Mass[e] ($t\,ha^{-1}$)	44.7–92.2	97.4–167.9	25.9–27.6	55.9–71.9
Residence time[g,d] (yr)	36–64, 99–111	61–64	9–10	25–26
Depth[c] (cm)	12–38	20–31	5–6	11–14
Nitrogen[g] (%)	0.74–0.92	0.82–0.84	0.89–0.94	0.80–0.82
Moss biomass[f] ($t\,ha^{-1}$)	3.5–10.1	4.0–4.6	3.9–4.2*	4.0–4.3*
Permafrost thaw depth[c] (cm)	16–55, none	32–111	165–166	136–145

Observed data from:

[a] Van Cleve et al. (1983a)

[b] Viereck et al. (1986)

[c] Viereck et al. (1983)

[d] Van Cleve et al. (1981)

[e] Van Cleve et al. (1983b)

[f] Oechel & Van Cleve (1986)

[g] 95% confidence interval, Van Cleve et al. (1983a)

equations simulated nitrogen concentrations that were consistent with observed data. However, if the lowest observed forest floor mass and residence time are representative of warm sites, then the forest floor mass simulated by the substrate quality equation was much too large (Table 8). The insulative effect of this thick organic layer caused depth of thaw to be as low as 32 cm in some cases, which was not consistent with the observed permafrost-free conditions. Conversely, the forest floor mass simulated by the soil thermal equation was too small and residence time was too short. Forest floor mass simulated by the interactive effects equation was more consistent with observed data, though residence time was slightly underestimated. The thinner forest floors simulated with the soil thermal and interactive effects equations resulted in deep depth of thaw, which was consistent with the observed permafrost-free conditions.

For the mixed birch and white spruce forests growing on a south slope terrace, simulated ages since fire for the 30 replicate plots ranged from 3 to 353 yr, 2 to 444 yr, and 3 to 351 yr, respectively, for the substrate quality, soil thermal, and interactive effects decay equations. Of the 30 plots, 14, 14, and 16 plots, respectively, were classified as birch stands based on relative species biomass. For the simulated plots with ages within the range of the observed data, above-ground tree biomass, density, and litterfall simulated by each decay equation overlapped with the range of observed data (Table 9). Each equation underestimated basal area. The forest floor simulated with the substrate quality equation was not consistent with observed data; the mass was too large, the residence time was too long, and the organic matter was too thick. Nitrogen concentration and residence time simulated by the soil thermal and interactive effects decay equations were consistent with observed data, but forest floor mass was too little (Table 9). Each decay equation resulted in deep depth of thaw, which was consistent with the observed permafrost-free conditions.

The remaining south slope plots were classified as white spruce forests. All decay equations simulated similar above-ground tree biomass, density, and litterfall, and all were consistent with observed data (Table 10). However, simulated basal area was underestimated. Each decay equation simulated forest floor nitrogen concentration that was consistent with observed data. Forest floor mass simulated by the substrate quality equation was significantly greater than those simulated by the other equations, and though consistent with observed data, the residence time was too long (Table 10). The soil thermal equation simulated too little forest floor mass and too rapid turnover. Forest floor mass and residence time simulated by the interactive effects equation were more consistent with observed data. Each decay equation resulted in deep depth of thaw, which was consistent with the observed permafrost-free conditions.

Table 9. Simulated range of mature birch forests growing on a south slope terrace. Common superscripts indicate simulated variables not significantly different ($p = 0.05$).

	Observed data	Decay equations		
		Substrate quality	Soil thermal regime	Interactive effects
Age[c] (yr), Sample size	60–130	91–114 (4)	65–124 (4)	62–132 (7)
Tree biomass[a] ($t\,ha^{-1}$)				
Above-ground	91.9–147.1	93.5–135.2*	137.4–171.7†	123.3–167.2*,†
Litter	0.3–2.2	0.9–1.1	1.3–1.6*	1.3–1.6*
Basal area[b] ($m^2\,ha^{-1}$)	30–35	16–21	22–29*	21–27*
Density[b] (ha^{-1})	2000–3000	684–1500	1164–2436*	984–2892*
Forest floor				
Mass[d] ($t\,ha^{-1}$)	43.7–68.4	86.5–98.8	14.8–21.0	27.6–36.2
Residence time[f] (yr)	6–20	43–47	8	12–14
Depth[c] (cm)	4	13–15	3–4	4–6
Nitrogen[f] (%)	0.94–2.06	1.00–1.07*	1.23–1.43	1.00–1.15*
Moss biomass[e] ($t\,ha^{-1}$)	0.0–0.1	0*	0*	0*
Permafrost/thaw depth[c] (cm)	None	130–137	172–175	164–169

Observed data from:

[a] Van Cleve et al. (1983a)

[b] Viereck et al. (1986)

[c] Viereck et al. (1983)

[d] Van Cleve et al. (1983b)

[e] Oechel & Van Cleve (1986)

[f] 95% confidence interval, Van Cleve et al. (1983a)

Table 10. Simulated range of mature white spruce forests growing on a south slope terrace. Common superscripts indicate simulated variables not significantly different ($p = 0.05$).

	Observed data	Decay equations		
		Substrate quality	Soil thermal regime	Interactive effects
Age[c] (yr), Sample size.	70–250	71–129 (3)	121–214 (4)	103–242 (10)
Tree biomass[a] (t ha^{-1})				
Above-ground	61.5–245.8	116.8–149.6*	103.8–165.8*	73.2–170.9
Litter	0.1–3.2	1.2–1.5*	0.5–1.4*	0.6–1.4*
Basal area[b] (m^2 ha^{-1})	30–60	21–28*	18–30*	14–28*
Density[b] (ha^{-1})	550–1000	1068–2460*	240–2136*	168–2640*
Forest floor				
Mass[d] (t ha^{-1})	47.1–105.3	99.5–102.4	16.2–31.1	32.0–61.8
Residence time[e] (yr)	19	44–50	8–10	16–23
Depth[c] (cm)	5–18	16–17	3–6	6–12
Nitrogen[a] (%)	0.66–1.04	0.97–1.07*	0.94–1.23*	0.83–0.96
Moss biomass[f] (t ha^{-1})	4.5	0.0–3.4*	1.0–4.4*	2.3–4.6
Permafrost/thaw depth[c] (cm)	None	122–127	163–174	143–164

Observed data from:

[a] Van Cleve et al. (1983a)

[b] Viereck et al. (1986)

[c] Viereck et al. (1983)

[d] Van Cleve et al. (1983b)

[e] Estimated from Van Cleve et al. (1983a)

[f] Oechel & Van Cleve (1986)

Discussion

No one decay equation produced simulated forests that were entirely consistent with observed data. However, over the range of forest types that were examined, the decay equation that combined the effects of both substrate quality and the soil thermal regime simulated forests that were more consistent with observed data than the other two equations. Differences among forests simulated with the various decay equations were negligible on the north slope permafrost site, where all equations gave similar estimates of decay rates (Fig. 5). Differences in simulated forests were much more apparent on the permafrost-free south slope sites with deep depths of thaw, where estimated decay rates differed greatly among equations (Fig. 5). For these sites, the substrate quality equation did not produce forest floor characteristics that were consistent with observed data. In particular, slow rates of decay resulted in too large an accumulation of forest floor mass. Conversely, the soil thermal equation simulated faster rates of decay that resulted in too little forest floor mass. Simulations that estimated decomposition from combined substrate quality and soil thermal effects resulted in more appropriate estimates of forest floor mass and turnover rates.

Though the interactive effects decay equation produced simulated forests that were most consistent with observed data, there were some exceptions. Forest floor mass for the permafrost-free black spruce site was consistent with observed data, but the turnover rate was slightly faster than observed values. Simulated birch forests were consistent with observed data except for too little forest floor mass; basal area was also slightly underestimated. Simulated white spruce forests were also consistent with observed data except for basal area. However, the observed maximum basal area ($60\,m^2\,ha^{-1}$) occurred in a commercial forest and may not be indicative of natural stands (Viereck et al. 1983). Overall, considering the wide range in site conditions and forest variables tested, the interactive effects decay equation yielded simulated forests that were remarkably similar to observed data.

These results support empirical observations of the effect of soil temperature on decomposition in interior Alaska. For example, soil temperature is significantly correlated with forest floor respiration within particular forest types (Flanagan & Van Cleve 1977; Schlentner & Van Cleve 1985). Experimental heating of a black spruce forest floor resulted in a 20% reduction in forest floor mass, greater nutrient availability, higher foliage nutrient concentrations, and higher foliage photosynthesis (Van Cleve et al. 1983a).

These results also indicate the importance of litter quality on nutrient availability. Indeed, seedling yield is strongly affected by forest floor chemistry (Flanagan & Van Cleve 1983; Van Cleve et al. 1983a; Van Cleve & Yarie 1986), and presumably, this indicates different nutrient availability among forest types. Moreover, litter decay rates vary greatly among tree species in interior Alaska (Flanagan & Van Cleve 1983). However, reciprocal transplants of birch and black spruce litter between birch and black spruce forest floors revealed no influence of site conditions on decomposition even though soil temperature was significantly colder on the black spruce site (Flanagan & Van Cleve 1983). More reciprocal transplants are needed to clarify these data.

The results of this study support the hypothesis that productivity and nutrient cycling in the uplands of interior Alaska are affected by interactions among soil temperature and permafrost, soil moisture, the forest floor, litter quality, and fire (Van Cleve & Viereck 1981; Van Cleve et al. 1983a; Van Cleve & Yarie 1986). On the warm, permafrost-free south slope, decomposition rates were high in birch forests with good litter quality. This, combined with an absence of mosses, resulted in a thin forest floor. However, as white spruce began to dominate the forest, the forest floor mass increased because of the growth of mosses and the poor litter quality.

In the black spruce forests growing on permafrost soils, cold soil temperatures resulted in little organic matter decomposition and nitrogen mineralization. This reduced tree growth and promoted the accumulation of a thick forest floor composed of moss and humus. Because bulk density and thermal conductivity of the forest floor are low, soil temperature declined, creating a cold soil with a shallow depth of thaw that prevented drainage. The poor quality of black spruce litter further reduced decomposition rates. Over time, the forest floor became the principal reserve of nitrogen and biomass.

Fires are thought to interrupt this sequence by consuming the forest floor, increasing post-fire soil temperature and depth of thaw, and mineralizing nutrients contained in the forest floor (Dyrness et al. 1986; Lutz 1956; Van Cleve & Viereck 1981; Viereck 1973, 1983; Viereck & Schandelmeier 1980). To test this hypothesis, north slope black spruce simulations with the interactive effects decay equation were repeated, but this time all plots burned every 100 years. Fire significantly affected above-ground tree biomass, forest floor mass, depth of thaw, and nitrogen availability (Fig. 7). The occurrence of fire partially consumed the thick forest floor and opened the canopy. Consequently, post-fire depth of thaw increased and decomposition and mineralization rates increased accordingly. Fire also mineralized nitrogen contained in the forest floor and woody biomass. The improved thermal and nutrient regimes created conditions favorable for stand regeneration.

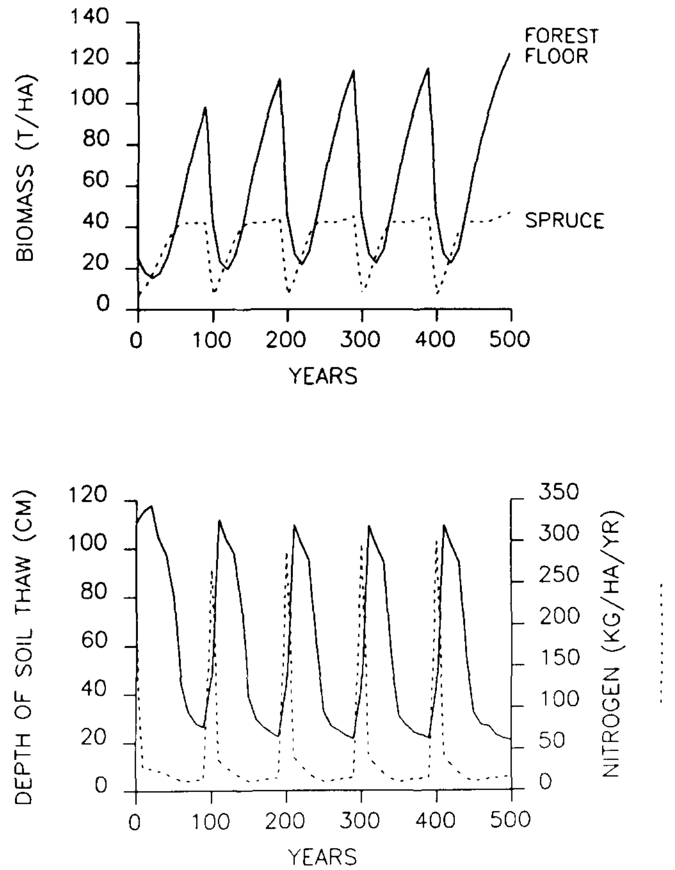

Fig. 7. Above-ground tree biomass, forest floor mass, depth of soil thaw, and available nitrogen for a poorly-drained north slope black spruce forest with all plots burning every 100 years.

The importance of substrate quality, the soil thermal regime, and fire for carbon and nitrogen cycling is a recurring theme in boreal forest literature (Bonan and Shugart 1989). Moore (1980, 1981, 1984) has indicated the importance of these factors in the lichen woodlands of northern Quebec, though the post-fire nutrient flush may be less than in other forests (Moore 1980; Auclair & Rencz 1982; Dubreuil & Moore 1982). Pastor et al. (1987) have suggested that strong feedback between litter quality and nutrient availability may result in cyclic dynamics between birch and spruce in the southern boreal forest region. The results of this study clearly showed the importance of these factors in the upland boreal forests of interior Alaska. The degree to which these relationships, quantified for the forests of interior Alaska, can be applied to other biogeographic regions of the boreal forest biome should be explored.

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