CARBON AND NUTRIENT AVAILABILITY EFFECT ON PLANT NUTRIENT SUPPLY FOR UPLAND FOREST SITES IN INTERIOR ALASKA

J. YARIE

Forest Soils Laboratory, Forest Science Department,
School of Agriculture and Land Resources Management, University of Alaska Fairbanks,
Fairbanks, Alaska 99775, United States

W. PULLIAM

Natural Resources Ecology Laboratory, Colorado State University,
Fort Collins, Colorado 80523, United States

K. VAN CLEVE and R. SCHLENTNER

Forest Soils Laboratory, Forest Science Department,
School of Agriculture and Land Resources Management, University of Alaska Fairbanks,
Fairbanks, Alaska 99775, United States

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ABSTRACT

The effects of microbial energy supply and low-level nitrogen fertiliser treatment on microbial respiration, nitrogen mineralisation, and tree foliar chemistry were addressed through field manipulations and modelling analysis. Sugar, sawdust, and nitrogen fertiliser were added to a series of upland successional communities in interior Alaska. Forest floor respiration and tree foliage chemistry were measured the year prior to treatment and for 2 years after treatment. LINKAGES and CENTURY were used in an attempt to duplicate the short-term field measurements and to extend the predicted effects to a longer time period. Ecosystem structure and function simulated by both models were consistent with field measurements of upland hardwood and mature *Picea glauca* (Moench) Voss (spruce) control stands. Neither model accurately predicted the effects of large-scale disturbance to the treated sites.

Keywords: nutrient availability; nitrogen; carbon; taiga forest growth; modelling.

INTRODUCTION

A model was presented by Bosatta & Berendse (1984) in which the effects of carbon or nitrogen treatments on microbial activity and nitrogen mineralisation could be described based on the primary limiting factor (carbon or nitrogen) of the microbial community. If the forest floor was carbon limited then microbial respiration decreased when nitrogen was added. If the forest floor was nitrogen limited then respiration increased when nitrogen was

added. Carbon addition resulted in the same general effects on nitrogen-mineralisation and microbial respiration when the community was either nitrogen or carbon limited, although the timing and the duration of the response differed. The initial nitrogen concentration and quality of the litter are the two primary factors that control the final nitrogen:carbon ratio of the eventual humus layer (Bosatta & Ågren 1985). The final nitrogen:carbon ratio of the humus layer is independent of the microbial efficiency of substrate utilisation and the rate of substrate utilisation.

Bosatta & Staaf (1982) suggested that low-quality litter will show a peak in nitrogen-mineralisation earlier in the decomposition process than litter of higher quality. In litter types with equal nitrogen concentrations but with differing quality, the litter with the lowest quality will have higher net mineralisation rates per unit weight loss during the first years of decomposition. On a range of sites with similar litter types this would result in more nitrogen recycling from litter on the lower decomposition sites. As a result, the quality of litter that does get transferred to humus will be much lower in low decomposition sites than on sites with higher decomposition rates. On the poor-quality sites the humus layer will supply less nitrogen to the trees than humus associated with high-quality sites.

The material that the microbial population processes develops in the plant prior to litterfall. The availability of both carbon and nitrogen to the plant results in the formation of either high- or low-quality litter materials. The range of litter quality through succession is controlled by the plant species present and the growing conditions that these plants experience. Environmental constraints, including nutrients and/or moisture, control the quality of materials that are recycled by specific plants. From a forest management perspective it is desirable to attempt to change the relationship between microbial decomposition of litter and the resulting decrease in litter quality through various management practices. The desired effect would be to improve litterfall quality or possibly the climatic environment.

The key factors in the above reasoning are the quality of litter that individual trees produce and the ability of the microbial community to process this material. The litter quality of taiga species varies (Horner *et al.* 1987b; Van Cleve *et al.* 1993). It has been suggested that microbial activity in taiga ecosystems is limited by energy supplies, and that fertiliser treatment of forest stands with available carbon may actually increase forest floor nutrient turnover and enhance tree growth (Flanagan & Van Cleve 1983). The microbial community was hypothesised to be limited by carbon availability because nutrient addition was not shown to increase microbial activity in forest floor samples during laboratory incubation studies (Flanagan & Van Cleve 1983; Flanagan 1986). However, a small response in inverted box respiration measurements was found as a result of annual, low-level fertiliser applications (unpubl. data).

The cycling of nutrients from tree to forest floor through litterfall was thought to respond to application of nitrogen fertiliser by the production of litter with higher carbon and nitrogen contents. This material should result in an increase in microbial activity which would temporarily immobilise more forest floor nutrients. Increased microbial growth leads to a reduction in available carbon and nitrogen for both trees and microbes as a result of immobilisation. This decrease limits microbial activity and a subsequent increase in available nutrients will result from microbial decomposition. This feedback process may

continue for a number of years until the nutrients are tied up in recalcitrant forest floor material or tree tissues that are slow to turn over (e.g., branch or stemwood) (Flanagan & Van Cleve 1983).

In the taiga of interior Alaska the greatest shift in foliar chemistry occurs as a result of species changes during vegetation succession (Yarie & Van Cleve in press). Early in succession plant litter is composed of material high in monomeric phenolics and carbohydrates but low in polymeric phenolics (lignin and tannin); late in succession the material is relatively low in carbohydrates and high in polyphenolics. In later successional stages or under nutrient-limited conditions, polyphenols in the soil react to produce increasingly complex and recalcitrant organic compounds, tieing up progressively larger portions of the soil carbon and nitrogen (Horner *et al.* 1987a). Thus both carbon and nitrogen become less available to the soil microbial and plant populations. The relative balance between accessible carbon and nitrogen controls whether the microbes are limited by energy, nitrogen, or some interaction of these.

The role of the physical environment in controlling soil organic matter dynamics is also complex in taiga systems. During summer, soil temperatures in early successional communities can be high enough to allow rapid microbial activity, while later in succession soils become insulated by moss cover and stay cold. The interior of Alaska is semi-arid with episodic summer rains. This may cause changes in microbial activity in direct response to changes in moisture, but may also alter the microbial population as drought stress and wetting events kill microbes. Microbial death releases nutrients (Kieft *et al.* 1987), potentially resulting in leaching, rapid microbial turnover, and/or nutrient uptake by trees.

Because of the complexity of these interactions, not only in single site types but also across successional sequences, it was hypothesised that (i) micro-organisms in the forest floor are limited by energy which becomes less available as succession advances, and (ii) resource availability through succession controls plant growth and the distribution of carbon and nutrients among above-ground, below-ground, and forest floor components. The work presented in this paper addresses the effect of microbial energy supply and low-level nitrogen fertiliser treatment on microbial respiration, nitrogen-mineralisation, and tree foliar chemistry. Field measurements of tree foliar chemistry (Yarie & Van Cleve in press) and forest floor respiration were compared to model predictions. The models CENTURY (Parton *et al.* 1987, 1988, 1994) and a modified version of LINKAGES (Pastor & Post 1986) were used for long-term predictions of the effects of treatment.

MODEL DESCRIPTION

CENTURY

We are currently using Version 4.0 of the CENTURY model (Metherell *et al.* 1993). CENTURY is a stand level model; for a full description *see* Parton *et al.* (1987, 1988). In the soil organic matter (SOM) submodel, SOM is represented by active, slow, and passive SOM pools, above- and below-ground litter pools, and a surface microbial pool which is associated with decomposing surface litter. Above- and below-ground plant litter is divided into above- or below-ground structural and metabolic pools based on its lignin:nitrogen ratio. The structural pool receives the lignin and cellulose material, which decomposes at a much slower rate than the metabolic pool. Lignin is passed directly to the slow SOM pool.

Nonlignin material goes through either the active pool or the surface microbe pool. Decomposition of the SOM pools is assumed to be microbially controlled and has an associated loss of carbon dioxide as a result of microbial respiration. The actual decomposition process or change in carbon over time can be expressed as a function of a predetermined maximum rate augmented by three coefficients representing (1) a moisture effect, (2) a soil temperature effect, and (3) the amount of carbon available. The maximum decomposition rate is represented as a constant for all SOM pools except the structural and active SOM pools. For the structural pool it is a function of lignin content, and for the active pool it is a function of soil texture.

LINKAGES

LINKAGES (Pastor & Post 1986) is an individual tree growth model developed as part of the JABOWA (Botkin *et al.* 1972) series of models. LINKAGES is a further enhancement of FORTNITE (Aber & Melillo 1982). LINKAGES reduces individual stem growth from a theoretical maximum by calculating growth-limiting factors based on light, temperature, moisture, or nitrogen availability and then applying that factor based on Leibigøø's law of the minimum. In LINKAGES, resources other than nitrogen can be limiting. LINKAGES contains no feedback loop between nitrogen availability and tree growth, litterfall quality, or decomposition processes.

The movement of litter cohorts into the humus pool is based on the cohorts' initial lignin content (DeHann 1976). Nitrogen mineralisation is a function of the nitrogen:carbon ratio of the litter that forms the humus and a canopy gap factor. Climatic variables are indirectly included in the model through the canopy gap calculation. Carbon decomposition is then related to the nitrogen:carbon ratio of the humus pool.

Two changes were made to the LINKAGES model prior to running the control and treatment scenarios. Firstly, the program was modified to allow the inclusion of the treatments as a litter cohort in the year of treatment. The treatment dynamics were then controlled by the existing decomposition routines in the model. Secondly, foliar litterfall nitrogen concentration was allowed to change based on the calculated green foliar concentration. Previously, foliar litterfall nitrogen percentage was a constant regardless of the green foliar concentration. Foliar litterfall nitrogen was made a constant proportion of the green foliar concentration, and was not allowed to drop below 0.45% N for all species. The proportion of green foliar nitrogen returned as litterfall was a species-specific constant based on unpublished litterfall data (Forest Soils Lab, University of Alaska Fairbanks) and green foliar chemistry (Yarie & Van Cleve in press). This change incorporated a feedback between nutrient availability and litterfall quality.

Model Comparison

The two models differ in a number of ways. CENTURY is a stand growth model which includes below-ground vegetation components, while LINKAGES is an individual tree model that includes only certain aspects of below-ground vegetation dynamics, such as fine-root litter production. LINKAGES in general uses a yearly time step for process calculations while CENTURY runs on a monthly time step. The general philosophy for development of the decomposition routines in both models is based on the assumption that the microbial

community is carbon limited. However, the structure of the decomposition routines in CENTURY and in LINKAGES is quite different (Table 1). The total number of individual cohorts or groups of SOM pools has the potential to be much higher in LINKAGES, because LINKAGES follows each litter cohort separately until it is transferred to humus. However, the humus compartment of LINKAGES is a combination of all of CENTURY's forest floor

TABLE 1–Comparison of key components of the CENTURY and LINKAGES models

State factor or process	CENTURY Variable description or process function	LINKAGES Variable description or process function
Soil organic matter pools	STRUCC(1) - Surface structural METABC(1) - Surface metabolic STRUCC(2) - Below-ground structural METABC(2) - Below-ground metabolic SOM1C(1) - Surface microbe SOM1C(2) - Active organic SOM2C - Slow organic SOM3C - Passive organic	C(1,x) = Humus pool C(2-250, x) = litterfall cohorts based on foliage type or wood size class. Each cohort is handled separately until it is transferred to the humus pool (C(1,x)). The x value defines cohort characteristics which control decomposition and changes in chemistry on a yearly basis until transfer to humus pool.
Decomposition (dC/dt)	$dC/dt = K_i * M_d * T_d * C_i$ where C_i is the carbon quantity T_d = Soil temperature effect M_d = PPT/PET and K_i = Maximum decomposition rate. Constant for METABC(1), METABC(2), SOM1C(1), SOM2C, SOM3C. For STRUCC(1) and STRUCC(2), K_i is a function of lignin content. For SOM1C(2) K_i is a function of soil texture.	% Wt loss = {[(a+b*AET) - (c + d*AET) * (lignin/nitrogen)] * DECMLT} / 100 where a,b,c,d = constant coefficients for all species AET = actual evapotranspiration DECMLT = a factor based on stand density (gap presence). This is used for litter cohorts prior to movement to humus. Humus decomposition is a function of a constant nitrogen-mineralisation rate times an AET and GAP multiplier. Carbon is respired so that the C/N ratio of the humus does not change. Above- and below-ground wood has a constant decay rate based on size.
Litterfall nitrogen	Nitrogen returned in litterfall is a constant proportion of foliar nitrogen which does vary.	Nitrogen returned in foliar litterfall is a constant proportion of green leaf foliar nitrogen which does vary. Lower limit of 0.45% set for the foliar nitrogen concentration.
SOM compartment transfer functions	Litter becomes either STRUCC(*) or METABC(*) based on its lignin:nitrogen ratio. Transfer from STRUCC(*) to SOM1C(*) or SOM2C is based on fixed percentages of the decomposition (a portion is transferred and the rest is set equal to microbial respiration). Transfer between the other SOM compartments is handled in the same manner.	Transfer from the litter cohort to humus is based on a function of initial lignin . content

components except the METABC(*) and the STRUCC(*) compartments. These four compartments (METABC(1), METABC(2), STRUCC(1), STRUCC(2)) (Table 1) are to some extent related to the individual litter cohorts of the LINKAGES model, but LINKAGES does not divide the lignin and nonlignin components of the litter cohorts.

METHODS

Field Work

The field methods have been described in detail by Yarie & Van Cleve (in press) and will be only briefly referenced here for the two sites chosen for simulation analysis. Of the seven successional stages used in the original study, only the UP2 and UP3 sites were chosen for this analysis. The UP2 sites represent the shift in the dominance of overstorey vegetation from deciduous to coniferous trees and the eventual establishment of a feathermoss layer. At this stage in succession the hardwood component of aspen (*Populus tremuloides* L.), birch (*Betula papyrifera* Marsh.), and poplar (*Populus balsamifera* L.) has reached maturity and is starting to give way to dominance by white spruce. The UP3 sites are represented by mature to overmature white spruce with a well-developed feathermoss layer and a significant lowering of soil temperature (Viereck *et al.* 1986).

Three nutrient amendment treatments were applied: sugar, sawdust, and nitrogen fertiliser (NH_4NO_3). The sugar and sawdust treatments were designed to increase the carbon:nitrogen ratio (C/N) of the forest floor to values typical of black spruce (*Picea mariana* (Mill.) Britt.) sites (C/N = 50). The nitrogen fertiliser treatment was designed to equal estimated yearly nitrogen mineralisation in an attempt to double plant-available nitrogen. Because the treatments were designed to make specific changes in factors that should alter nutrient availability of the site types, different levels of treatment addition were required for each site (Table 2). The sawdust treatment was applied during mid-summer of 1989 (late July and August). The sugar treatment was applied during May 1990, prior to tree growth. The fertiliser treatment was applied on a yearly basis in May prior to tree growth.

Tree and shrub foliage sampling was conducted prior to treatment in 1989 and again at approximately the same time period (mid July) in the 2 years after treatment (1990 and 1991). A total of five trees per dominant species on each plot replicate were randomly selected for sampling. Current foliage was collected in as short a time period as possible and

TABLE 2–Treatment levels for the UP2 and UP3 upland sites

Site and treatment chemistry	Sugar (kg/m^2)	Sawdust (kg/m^2)	Fertiliser NH_4NO_3 (g/m^2)
UP2 – A,B	7.38	7.60	17.67
C	5.98	6.20	17.67
UP3	5.58	5.80	14.71
Treatment chemistry*			
Carbon (%)	42.1	45.0	0.0
Nitrogen (%)	0.0	0.125	35.0
Lignin (%)	0.0	19.25	0.0

*The amount of carbon, nitrogen, or lignin added to each plot can be calculated by multiplying the percentage of carbon, nitrogen, or lignin by the amount of the treatment added.

returned to the laboratory on a daily basis. Foliage samples were collected as close as possible to peak season for tree growth. For white spruce only current years' tissue was collected. Foliar material was collected either by hand, with a pole pruner, or with the use of a shotgun, depending on the height of the sample tree.

Foliage samples were dried at 65°C; then ground for determination of total Kjeldahl nitrogen (Bremner & Mulvaney 1982), phosphorus, potassium, calcium, magnesium (Van Cleve & Viereck 1972), carbon (Nelson & Sommers 1982), percentage ash, lignin, cellulose, and holocellulose (Goering & Van Soest 1970). In addition, inverted box respiration (carbon dioxide) measurements (Schlentner & Van Cleve 1985) were taken for one 24-hour period every 2 weeks during the summers of 1990, 1991, and 1992.

Model Analysis

Because of the difficulty in setting up CENTURY for a successional sequence, the two upland scenarios that were chosen represent the development of an upland old-growth white spruce stand without a hardwood stage (UP3) and a mature hardwood stand (UP2). The treatments were applied during year 225 of white spruce development and year 70 of the hardwood stand development. LINKAGES was set up similarly to CENTURY, but on an individual tree basis, to develop a pure white spruce stand with no prior hardwood stage (UP3) and a mixed species hardwood stand to represent the UP2 site.

Control stands were simulated to evaluate the performance of both models. The long-term average climate was used for CENTURY, and a stochastic climate scenario based on the long-term average was used for LINKAGES. Both climate datasets were based on the average Fairbanks climate and its associated variability. The model treatments were imposed during years 225 and 70 for the UP3 and UP2 sites, respectively. Stand ages for the field study were estimated to be approximately 66 years for the UP2 site and 170 years for the UP3 site at the time of treatment. These ages were measured at breast height (1.3 m above ground-level) (Viereck unpubl. data). Using the 225-year time period in the model for the UP3 stands represents the breast height age plus the time it takes local spruce to growth to breast height (10 to 30 years) and the time required to develop regeneration at the site after the last disturbance.

Control model results were compared to measured values for taiga forests in the vicinity of Fairbanks, Alaska. Analysis of the treatment effects from both the modelling and field experiments followed the scheme outlined by White *et al.* (1988). Both the field data sets (foliar nitrogen percentage and inverted box carbon dioxide measurements) and the nitrogen-mineralisation, foliar nitrogen percentage, and carbon dioxide fluxes estimated by the model were compared to the control stand data sets. The control data set was subtracted from the treatment data set. Likewise, values for nitrogen-mineralisation, foliar nitrogen percentage, and carbon dioxide fluxes modelled for the control stands were subtracted from the values modelled for the treatment stands. The net result was then compared to the theoretical patterns of treatment effects presented by Bosatta & Berendse (1984).

RESULTS

Control Runs

Stand structure simulated by both models was consistent with field measurements of upland hardwood and spruce stands found in the interior of Alaska (Table 3). The differences

TABLE 3–Comparison of predicted values (UP2 at 70 years and UP3 at 200 years) for selected system parameters with measured values for comparable stands in interior Alaska.

Item	Model prediction at year of treatment for both sites		Range of observed values
	LINKAGES	CENTURY	
Above-ground biomass (kg/m^2)			
UP2	15.5	8.0	4.6–17.5*
UP3	14.1	18.4	6.2–24.6*
Total SOM (kg/m^2)			
UP2	9.3	9.43	12.0–17.2†
UP3	14.0	10.2	13.4–19.0†
N-mineralisation (g/m^2• year)			
UP2	3.0	3.59	1.5–5.5‡
UP3	3.1	2.34	1–2‡
CO_2 efflux (kg CO_2/m^2• year)			
UP2	0.28	0.33	1.02*
UP3	0.24	0.27	0.96*
Litterfall (foliage and small branches) (g/m^2• year)			
UP2	320	NA	27–265†
UP3	250	NA	95–316†

NA: Values are not available in the current version of CENTURY.
References: * Unpubl. data
† Van Cleve *et al.* (1983)
‡ Flanagan & Van Cleve (1983)

in the simulated values for above-ground biomass were related to differences in nitrogen-mineralisation and the vegetation structure of both models. In LINKAGES the early stand growth based on individual trees was higher than the stand growth predicted by CENTURY; this resulted in higher stand biomass values predicted by LINKAGES for the UP2 site. Fine tuning the input parameters in both models would result in a closer correspondence of the predicted output values. However, values for both of these variables were within the range of reported values (Table 3), and further parameter changes would merely change predicted output, not the functional relationships in both models.

The carbon dioxide respiration values reported from field measurements were based on inverted box soda lime measurements for these two sites. The field values were larger than those reported for the simulation models because the field values also included root respiration from the area under the box. The models predicted only 20 to 30% of the measured values which is in the range for microbial respiration compared to total soil respiration (R.Ruess pers. comm.).

It was assumed that the response to treatment would be accurately simulated by both models as a result of being able to simulate a number of important variables for control stands. However, major differences can be seen in the response of the models to the sawdust, sugar, and fertiliser treatments for both the hardwood (Fig. 1 and 2) and pure spruce (Fig. 3 and 4) stands for predicted nitrogen-mineralisation and carbon dioxide respiration from the forest floor. Simulated nitrogen-mineralisation actually decreased below control levels as a result of fertiliser application for the first 2 or 3 years in the CENTURY model (Fig. 1b and 3b). Sawdust and sugar decreased mineralisation in CENTURY, but only sugar decreased

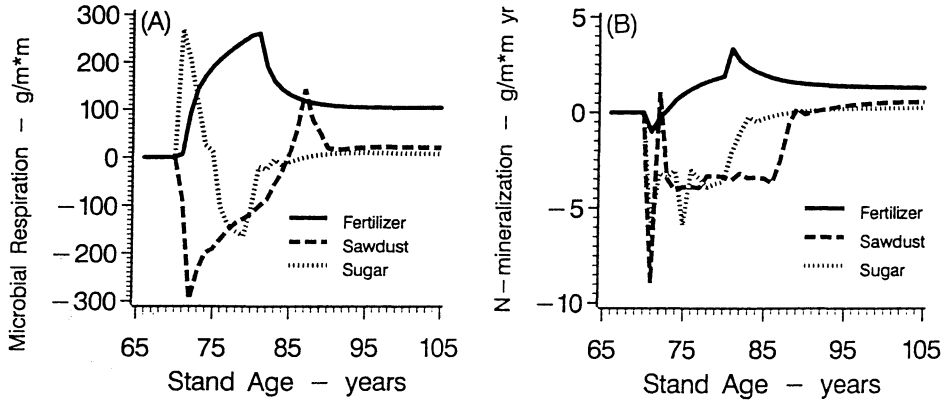

FIG. 1–Comparison between the simulated fertiliser, sawdust, and sugar treatments and the simulated control results using CENTURY for microbial respiration (A) and nitrogen-mineralisation (B) for upland hardwood stands (UP2). The lines represent the difference between treatment and control values.

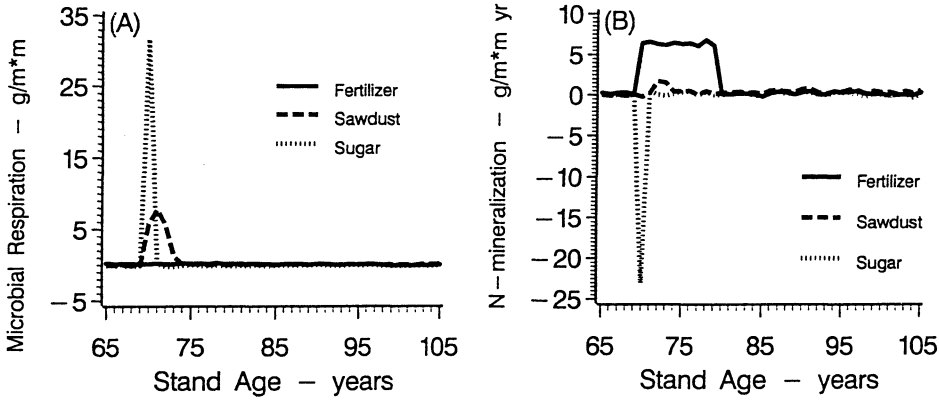

FIG. 2–Comparison between the simulated fertiliser, sawdust, and sugar treatments and the simulated control results using LINKAGES for microbial respiration (A) and nitrogen-mineralisation (B) for upland hardwood stands (UP2). The lines represent the difference between treatment and control values.

mineralisation in LINKAGES. Some of these differences can be explained by the manner in which the treatments were handled by the models. Fertilisation in LINKAGES was included as a litter cohort and was mineralised (or decomposed) in the year of application. In CENTURY fertiliser was added to the mineral nitrogen pool which could subsequently influence the active organic, slow, or passive organic nitrogen and carbon pools. The net effect was an increase in microbial activity and nitrogen concentration and an increase in foliar nitrogen (Fig. 5).

The response in predicted microbial respiration was similar for sugar treatments in both sites in both models, the major difference being in the duration of the response. LINKAGES predicted a single-year increase in respiration, while CENTURY indicated that the increase should last for 5 years before resulting in a decrease (Fig. 1a and 3a). LINKAGES predicted

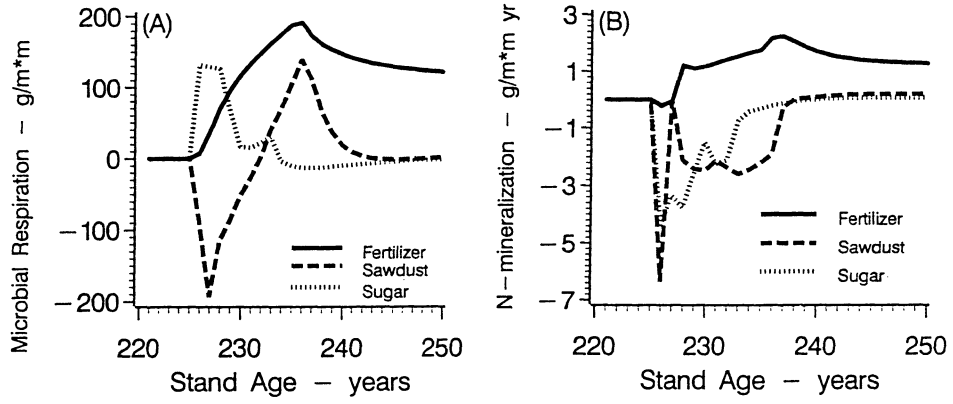

FIG. 3–Comparison between the simulated fertiliser, sawdust, and sugar treatments and the simulated control results using CENTURY for microbial respiration (A) and nitrogen-mineralisation (B) for upland pure spruce stands (UP3). The lines represent the difference between treatment and control values.

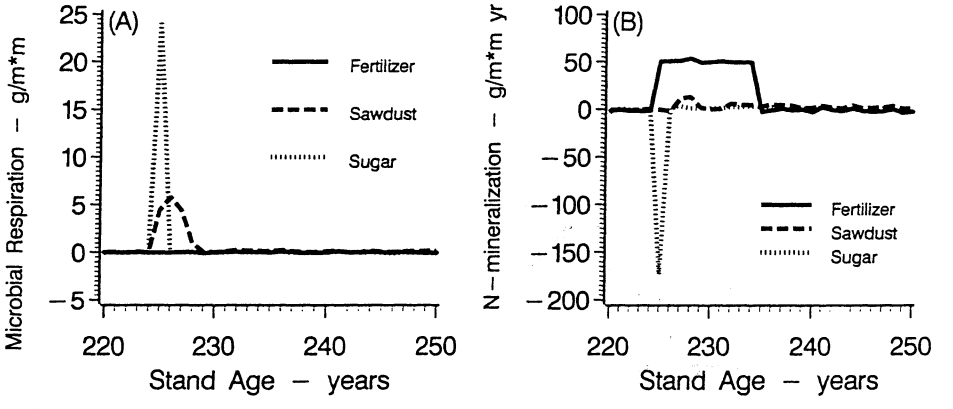

FIG. 4–Comparison between the simulated fertiliser, sawdust, and sugar treatments and the simulated control results using LINKAGES for microbial respiration (A) and nitrogen-mineralisation (B) for upland pure spruce stands (UP3). The lines represent the difference between treatment and control values.

virtually no effect on microbial respiration from the fertiliser treatment (Fig. 2a and 4a). CENTURY showed a significant increase in microbial respiration (Fig. 1a and 3a) starting in the second year after treatment and lasting for over 30 years from the start of treatment. The predicted increase in microbial respiration as a response to sawdust treatment started in the year after treatment in LINKAGES and lasted for 5 years, while CENTURY predicted a long-term decrease in microbial respiration in both sites before an increase in respiration (Fig. 1a and 3a) as a result of sawdust application.

The number of years in which all treatments have an effect on ecosystem function was predicted to be longer by CENTURY than by LINKAGES. LINKAGES indicated a 1-year response for both nitrogen-mineralisation and microbial respiration while CENTURY indicated that the response should last for 10 years or longer, depending on the predicted parameter and the simulated site.

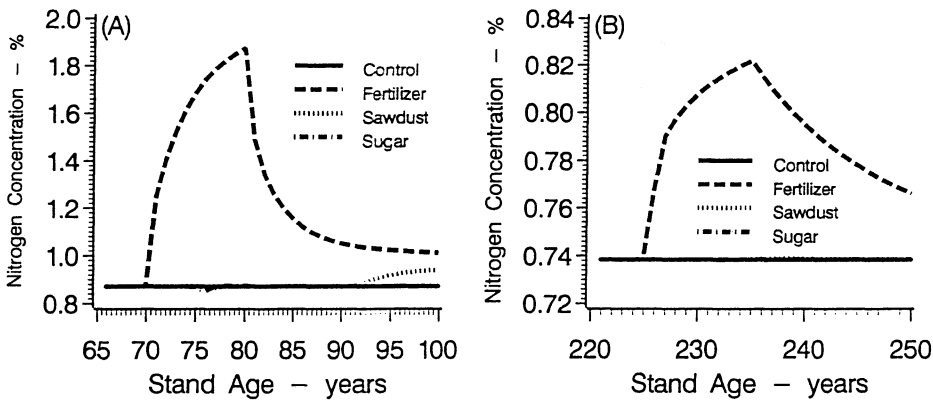

FIG. 5–Changes in foliar nitrogen concentration predicted by CENTURY for the upland hardwood (A) and upland pure spruce (B) simulation runs. The hardwood site is UP2 and the pure spruce site is UP3.

The predicted effect on foliar chemistry was also different between CENTURY and LINKAGES. CENTURY predicted near-term changes to foliar chemistry from the fertiliser application on the hardwood sites (UP2, Fig. 5a). The increased foliar nitrogen content was maintained for up to 20 years after treatment stopped in year 80. There was also a small increase in foliar chemistry 22 years after the sawdust application on the hardwood sites (Fig. 5a). LINKAGES also showed near-term changes due to fertiliser application that lasted until fertiliser application was discontinued (Fig. 6a). LINKAGES predicted a decrease in foliar nitrogen concentrations due to sugar application for the first 2 years after treatment, and an increase in foliar concentrations for years 3 through 5 after sawdust treatment (Fig. 6). The general response was similar in both hardwood and pure spruce stands, with the only differences occurring in timing and magnitude of the trends.

Field data collected for carbon dioxide efflux and foliar chemistry showed different treatment effects from those predicted by CENTURY and LINKAGES (Table 4). CENTURY

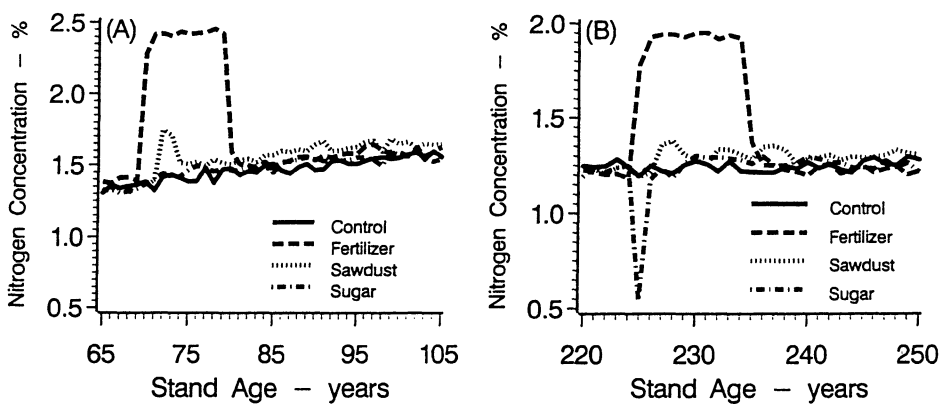

FIG. 6–Changes in the foliar nitrogen concentration predicted by LINKAGES for birch (A) in the upland hardwood site (UP2) and for white spruce (B) in the upland pure spruce (UP3) site. Aspen and spruce in the hardwood site displayed the same trends as birch.

TABLE 4–Expected (Bosatta & Berendse 1984), observed, and simulated changes in nitrogen-mineralisation, soil respiration, and foliar chemistry due to effects of treatment on nitrogen or carbon-limited nutrient turnover in the forest floor.

Site	Treatment	Theoretical result of treatment (from Bosatta & Berendse 1984)				Observed change in complementary parameters on treated sites compared to control		Changes predicted by CENTURY and LINKAGES in treated sites compared to control sites			
		Carbon-limited systems		Nitrogen-limited systems				CENTURY		LINKAGES	
		N-min	CO_2 efflux	N-min	CO_2 efflux	Foliar nitrogen (%) (Yarie & Van Cleve in press)	Forest floor respiration	N-min	CO_2 efflux	N-min	CO_2 efflux
UP2	Sugar	–	+	– –	0 --> +	– (birch 90)* + (spruce 90, 91)	+ (UP2A 90)†	– (NC)‡	+	–(–)	+
	Sawdust	–	+	– –	0 --> +	+ (spruce 91)	+ (UP2A 90? 91? 92)	– (NC)	–	NC (NC)	+
	Fertiliser	+	–	+	+	+ (spruce 90, 91)	+ (UP2A 91? 92?) + (UP2B 91?)	– (+)	+	+ (+)	NC
UP3	Sugar	–	+	– –	0 --> +	– (alder 90)	+ (UP3A 90)	– (NC)	+	– (–)	+
	Sawdust	–	+	– –	0 --> +	NC	NC	– (NC)	–	NC (NC)	+
	Fertiliser	+	–	+	+	NC	NC	– (+)	+	+ (+)	NC

* Species and year of change reported. All treatments were applied in 1989.

† Site (UP2), rep (A), and year of reported effect. A ? indicates a measured increase that is small and may not be significantly different.

‡ Values in parentheses indicate predicted change in foliar nitrogen conmcentration; NC = No change.

predicted a decrease in nitrogen mineralisation for all treatments, no change in foliar nitrogen as a result of sugar and sawdust treatment, and an increase in foliar nitrogen as a result of fertiliser treatment. The actual measured response showed an increase in foliar nitrogen as a result of all treatments in the UP2 site except for birch in 1990 as a result of sugar treatment (Yarie & Van Cleve in press), and a decrease in foliar nitrogen for alder in the UP3 site as a result of sugar treatment (Table 4). Microbial respiration was predicted by CENTURY to increase as a result of fertiliser and sugar treatments and decrease as a result of sawdust treatment. All measured values tended to increase as a result of treatment on both sites except for the sawdust and fertiliser treatment in the UP3 site. This was consistent with the trends predicted by LINKAGES.

DISCUSSION

Model Analysis

Both models simulated a response to the sugar treatment in the direction predicted by Bosatta & Berendse (1984). This was consistent with the changes in deciduous foliage nitrogen concentration measured in the field (Table 4). CENTURY predicted a response of microbial respiration opposite to that hypothesised for the sawdust treatment. The inverted box field measurements were consistent with the hypothesised response. CENTURY also predicted an opposite response of nitrogen-mineralisation to the fertiliser treatment (Table 4), but the predicted change in foliar nitrogen was consistent with field measurements. LINKAGES did not show this inconsistency. No response was predicted by LINKAGES for nitrogen-mineralisation resulting from the sawdust treatment. There was no change in microbial respiration predicted by LINKAGES due to the fertiliser treatment. These results indicate that these models do not accurately represent forest floor and mineral soil decomposition dynamics of a boreal forest system. Similar results for the simulation of high lignin- or nitrogen-containing litter have also been reported (Parton *et al.* 1994), but those authors did not report a problem with dynamics of high carbon amendments such as sugar.

In CENTURY decomposition is a function of soil temperature, precipitation, and an estimated maximum decomposition rate. This maximum decomposition rate is a constant for five of the eight soil organic matter pools represented in the model (Table 1). These five pools represent the largest combined quantity of soil organic matter. Once the treatment moves into one of these pools its decomposition rate will remain constant unless the model is run with variable weather. For the active organic pool the maximum decomposition is a function of soil texture and so it will remain unchanged for the model runs unless different soil types are used. Only the surface and below-ground structural pools have a maximum decomposition rate that is related to substrate chemistry, in this case lignin content. The treatments can be seen to enter different pools based on the treatment chemistry. The sugar treatment moves into the surface metabolic pool, the sawdust enters the surface structural pool, and fertiliser enters the mineral nitrogen pool and then affects vegetation growth which affects the size of the surface structural and slow organic pools (Fig. 7).

The treatment effect of sugar was considered correct; however, because the surface metabolic pool has a constant decomposition rate, the sugar pulse did not move through the system as quickly as field measurements indicated (unpubl. data). Within CENTURY the sugar treatment moves from the surface metabolic pool to the slow organic pool and a substantial portion is released as respiration during the same time period (Fig. 1a and 7a). The

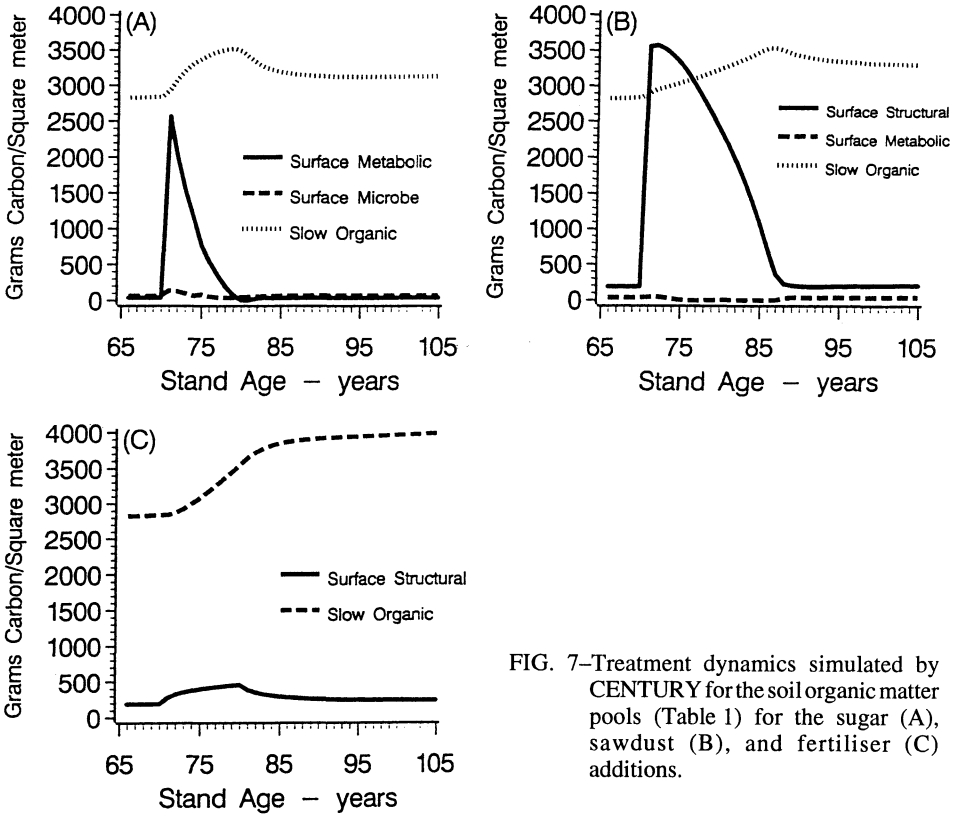

FIG. 7–Treatment dynamics simulated by CENTURY for the soil organic matter pools (Table 1) for the sugar (A), sawdust (B), and fertiliser (C) additions.

sawdust treatment starts in the surface structural pool which does have a decomposition rate influenced by the lignin content. This pool actually decomposes at a higher rate than the sawdust added in the field experiment. This drives the model into a nitrogen-limited situation which significantly reduces microbial activity, resulting in simulated decreases in both nitrogen-mineralisation and microbial respiration compared to the control plot (Fig. 1 and 7b). The fertiliser treatment also has an effect on the surface structural and slow organic SOM pools (Fig. 7c). Fertiliser increases vegetation growth and subsequent litterfall in the forest stand; it also has the effect of changing the C/N ratio of some of the SOM pools which may speed their movement into the slow organic pool.

In LINKAGES there were no large inconsistencies encountered for the effects of treatment compared to the theoretical results of Bosatta & Berendse (1984). However, some of the effects were less than those measured in the field. All treatments were added as a litter cohort in the LINKAGES model. Their individual chemistry resulted in the initial decomposition parameters for the simulation. The respiration response for sugar ended in the first year after application. None of the sugar was transferred to the humus pool because sugar contains no lignin. All decomposition of the sugar took place as a litter cohort in LINKAGES. The sawdust treatment was treated as a small wood cohort. Wood within LINKAGES decomposes at a constant rate and will eventually end up in the humus component. At this point it will not have an effect on nitrogen-mineralisation and respiration because decay in

the humus layer is a constant function of nitrogen-mineralisation that is affected by actual evapotranspiration (AET) and a decay multiplier based on the ratio of litterfall to estimated closed canopy litterfall (Pastor & Post 1986). The carbon removed is in the same proportion as the nitrogen removed, resulting in a constant C/N ratio after decomposition. Fertiliser is treated as a cohort that goes into the available nitrogen pool during the year of application. It does not affect the humus C/N ratio in the current version of LINKAGES; with the low level of fertiliser application that is being simulated this is a valid assumption.

Both models handle the microbial dynamics of decomposition in a very simplistic fashion. The microbial dynamics are represented as functions of lignin to nitrogen ratios or maximum decomposition values, both of which are augmented based on physical factors such as temperature and moisture. Pools that directly represent microbial biomass, dead microbial tissue, etc., are not present in either model. Our current knowledge of the function of these components is greater than the current representation in these two models. The most likely improvement in both models would be to include the microbial community and model its function based on our knowledge of microbial ecology similar to that presented by Grant *et al.* (1993a, b). It is not clear if the time step used in modelling the microbial dynamics needs to be reduced. The work presented by Grant *et al.* (1993a) uses an hourly time step but it may be possible to use a longer one if the representation of small time step (hour) dynamics can be adequately summarised in longer ones (e.g., week to month).

It is also suggested that both models should contain algorithms that can handle the change in quality of substrates as they decompose. The box-transfer scheme of both LINKAGES and CENTURY should be sufficient if the appropriate quality index for each box is chosen (Bosatta & Ågren 1991). The changes in quality should be related to the species composition in the forest stand and to the change in quality of individual litter as it progresses through the decomposition process. Soil organic matter quality will need to be related to both nitrogen and carbon limitations for microbial activity. Bosatta & Ågren (1991) present a general description of carbon and nitrogen dynamics using a changing carbon quality distribution which is unimodal in structure; this same analysis should be formulated using a bimodal distribution that could include changes in both the carbon- and nitrogen-related quality of the litter cohort.

What are the Models Telling Us About Plant Nutrient Supply in the Taiga of Alaska?

As these models are not accurately predicting the effects of disturbance to the treated sites, we can suggest that they do not accurately represent all processes influenced by such a treatment. The simulations of the untreated stands do give reasonable results when compared with actual field measurements; however, it is possible that the structure of the models was such that even incomplete representation of the decomposition process could yield results comparable to field studies. The parameters and relationships used for the decomposition routines are, in general, based on data sets derived from natural stands.

The decomposition routines for both models have been derived from literature and field studies that generally assume the decomposition process is carbon limited. Bosatta & Berendse (1984) suggested that the way to investigate the microbial limitation for decomposition is through the addition of fertiliser and its influence on microbial respiration. However, it may be easy to add sufficient nitrogen to the organic layer to create a carbon

limitation in the forest floor. Because low levels of nitrogen fertiliser (equal to the estimated mineralisation rate) were added to the plots, the fertiliser treatment probably did not drive the microbial community into carbon limitation. Treatment effects observed in additional successional plots support the idea that the decomposition process in taiga forests is nitrogen limited (Table 5). One problem with the inverted box respiration measurement is that it will also measure an increase in root respiration as a result of improved nutrient status through fertiliser application. However, it is difficult to assign all of the respiration effect to root activity. LINKAGES currently handles the fertiliser application as available nitrogen and as such it does not affect the decomposition process except through the production of litter with a lower C/N ratio. Three of the six sites treated showed an increase in foliar nitrogen concentrations and inverted box respiration (Tables 4 and 5), indicating a potential increase in microbial nitrogen-mineralisation and respiration as a result of fertiliser treatment.

TABLE 5–Observed changes in foliar chemistry (Yarie & Van Cleve in press) and soil respiration due to effects of treatment on nitrogen- or carbon-limited nutrient turnover in the forest floor. Expected changes were the same as indicated in Table 4.

Site	Treatment	Observed change in foliar nitrogen and forest floor respiration on treated sites compared to control	
		Foliar nitrogen (%)	Forest floor respiration
UP1	Sugar	- (birch '90, 91/2)* - (aspen '90)	+(UP1A 90, 91/2)†
	Sawdust	NC‡	NC
	Fertiliser	NC	NC
FP2	Sugar	- (poplar '90)	+ (FP2A 90, 91/2)
	Sawdust	NC	+ (FP2A 90, 92?) + (FP2B 91?)
	Fertiliser	+ (poplar '91)	+ (FP2B 91?)
FP3	Sugar	- (spruce '90)	+ (FP3A 90)
	Sawdust	NC	NC
	Fertiliser	+ (alder '90) + (spruce '90 '91)	+ (FP3A 90?)
FP4	Sugar	NC	+ (FP4A 90/2)
	Sawdust	NC	NC
	Fertiliser	NC	NC

* Species and year of change reported. All treatments were applied in 1989.

† Site (UP2), rep (A) and year of reported effect. A ? indicates a measured increase that is small and may not be significantly different.

‡ NC = no change

The primary limitation of the microbial community can be estimated by comparing the forest floor C/N ratio (r = C/N) to the microbial C/N ratio and microbial efficiency ($r_c = f_c/(f_n e)$ where f_c is microbial carbon content, f_n is the microbial nitrogen content, and e is microbial efficiency in carbon uptake) (Bosatta & Berendse 1984). If $r_c > r$ the microbial community is carbon deficient. If $r_c < r$ the microbial community is nitrogen limited. Based on laboratory results for three different substrates added to the UP2 and UP3 forest floor samples (Sugai & Schimel 1993), it is indicated that the microbial community will be carbon limited if decomposing materials such as salicylic acid (SAL), while they can be nitrogen

limited if decomposing materials such as glucose or p-hydroxy benzoic acid (PHY) (Table 6). Both SAL and PHY are common in water leachates from birch, willow, and poplar and PHY is also common in spruce leachates (Kuiters & Sarink 1986). Values for the f_c/f_n ratio range from 7.8 (Grant *et al.* 1993b) to 12.5 (Bosatta & Berendse 1984). The implication is that plant litter and possibly throughfall leachates can be a combination of material that will result in both carbon and nitrogen limitations in the microbial community.

TABLE 6–Calculation of the r and rc values for the UP2 and UP3 sites based on different added substrates, from Sugai & Schimel (1993).

Site	Substrate	r	e	Critical f_c/f_n (if < nitrogen-limited; if > carbon-limited)
UP2	glucose	32.3	0.74	23.9
	PHY*		0.58	18.7
	SAL†		0.23	7.4
UP3	glucose	32.3	0.74	23.8
	PHY		0.58	18.7
	SAL		0.23	7.4

* p-hydroxy benzoic acid
† salicylic acid

Our understanding of how to influence the nutrient supply of the forest floor will revolve around influences on the efficiency of the microbial community, changes in the quality of the substrate for microbial activity, and factors that are related to the process inertia of the current substrate. If we want to manage a long-term change in the nutrient dynamics of the forest floor we have to identify the important quality factors that must be manipulated in the current forest floor to allow for greater nutrient turnover in the "new" forest floor. The critical issues that are important for understanding nutrient supply are then related to microbial efficiency, microbial growth rate, and changes in the quality of the substrate through the decomposition process (Bosatta & Ågren 1991).

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