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INTERRELATIONSHIPS BETWEEN VEGETATION, SOIL DEVELOPMENT AND NITROGEN AND PHOSPHORUS CYCLING IN UPLAND CONIFEROUS FORESTS NEAR HONDO, ALBERTA

by

JAMES W. FYLES

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

OF DOCTOR OF PHILOSOPHY

DEPARTMENT OF SOIL SCIENCE
DEPARTMENT OF BOTANY

EDMONTON, ALBERTA

SPRING 1986

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To whom it may concern,

I hereby permit James Fyles to include our coauthored paper entitled "Litter production in *Pinus banksiana*-dominated stands in northern Alberta" in his Ph.D. thesis.

G.H. LaRoi

Robert A Ellis

R.A. Ellis

27 March 1986.

To whom it may concern,

I hereby permit James Fyles to include our coauthored paper entitled "Decomposition of boreal forest litters from central Alberta under laboratory conditions" as a chapter in his Ph.D. thesis.

W.B. McGill

THE UNIVERSITY OF ALBERTA

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7

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled INTERRELATIONSHIPS BETWEEN VEGETATION, SOIL DEVELOPMENT AND NITROGEN AND PHOSPHORUS CYCLING IN UPLAND CONIFEROUS FORESTS NEAR HONDO, ALBERTA submitted by JAMES W. FYLES in partial fulfilment of the requirements for the degree of DOCTOR OF PHILOSOPHY.

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ABSTRACT

Cycling patterns of nitrogen and phosphorus and their relationships to vegetation and soil characteristics were examined in eight upland coniferous stands near Hondo in central Alberta. The stands represented three forest types: jack pine/lichen woodland; closed canopy jack pine forest with green alder and feathermoss; and spruce forest with codominant jack pine and feathermoss groundcover. Each stand was characterized with respect to: age structure of tree species; soil profile development; micromorphology of selected soil horizons; quantity and distribution of secondary iron and aluminum, and inorganic P fractions in the soil profile; accumulation of C, N and organic P in LFH and mineral soil horizons; mineralization of N in LFH and mineral soil horizons; foliar N and P concentrations; resorption of N and P prior to leaf abscission; annual and seasonal production of various litter components; flux of N and P in litterfall; and turnover of N and organic P in LFH and mineral soil. Decomposition rates of major litter types were examined in the laboratory.

Age structure analysis of the eight study sites and 26 other stands suggested that, although successional processes appeared to be active in all stands, the dominant species on a site varied little over the life of a stand implying that vegetation patterns remain relatively static over many fire cycles. Differences among soils in the distribution of clay, and secondary iron and aluminum, and in profile weights of various forms of P, appeared to reflect historical differences in vegetation.

Nutrient cycling patterns differed among forest types apparently as a result of historical as well as present differences in vegetation. Relative to other forest types, pine/lichen stands had low levels of accumulated N and organic P in LFH and mineral soil, and lower N mineralization and flux of N and P in litterfall. These stands appeared to be N limited, particularly those in which green alder was absent. Litterfall nutrient flux and N mineralization were highest in pine/alder forest and these stands appear to cycle both N and P through the soil more rapidly than other vegetation types. High levels of accumulated N in soils beneath spruce stands supported high litterfall N flux and mineralization rates despite relatively slow cycling through soil. Turnover of organic P in these soils was rapid relative to

N, implying that spruce stands may be P limited.

Nutrient allocation and cycling patterns of individual species appear to be determined by genetic factors such that responses to changes in site fertility are expressed in biomass production but not in foliage or litter nutrient concentration. Nutrient cycling patterns are therefore controlled primarily by the relative abundance of species within a stand. A hypothetical model is presented which explains the apparent stability of vegetation, soil and nutrient cycling patterns in terms of feedback loops connecting fire frequency, forest type, forest floor characteristics and soil fertility and profile development.

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1. INTRODUCTION

The first goal of this research program, as it was originally conceived in the spring of 1982, was to examine nitrogen cycling in a series of stands representing points along an ecological gradient, so that differences in cycling patterns could be related to known ecological differences between sites. This objective was based on the impression that many nutrient cycling studies reported in the literature were empirical in nature and did not provide much information regarding controls on cycling patterns at an ecosystem level. Research on factors controlling N dynamics had generally examined a single process, such as litter decomposition or resorption from foliage prior to abscission, often without linking processes together in an ecosystem context. In contrast, theoretical treatments suggested that nutrient cycles are controlled by feedback mechanisms which result in correlations between quantity of nutrients cycled and site fertility, but in most studies causal processes were not specifically examined. It was apparent, however, that the hypothesized feedback mechanisms were related to linkage between individual processes: nutrient availability may control nutrient resorption from foliage prior to leaf abscission; resorption may control litter nutrient levels; litter nutrient levels may control decomposition rates; decomposition rates may control release of nutrients from litter and their availability to plants. Plant species may differ in nutrient demand and allocation patterns or in production of secondary compounds such as tannins and may differ in the quantity of litter produced and its resistance to decomposition. The second general goal of this research program was, therefore, to examine the interrelationships between N availability, foliar and litter N levels, N resorption from foliage, and N flux in litterfall in stands differing in species composition.

Four stands, established near Hondo, in central Alberta, as part of the ongoing SEADYN research program (Figure 1-1), appeared to provide an opportunity for research addressing the general objectives indicated above. These stands occupied upland sites in an area of sand ridges of aeolian origin, and were ecologically equivalent in terms of macroclimate and edaphic conditions. The stands represented stages of a successional sequence consistent with the prevailing view of successional development in forests of central and

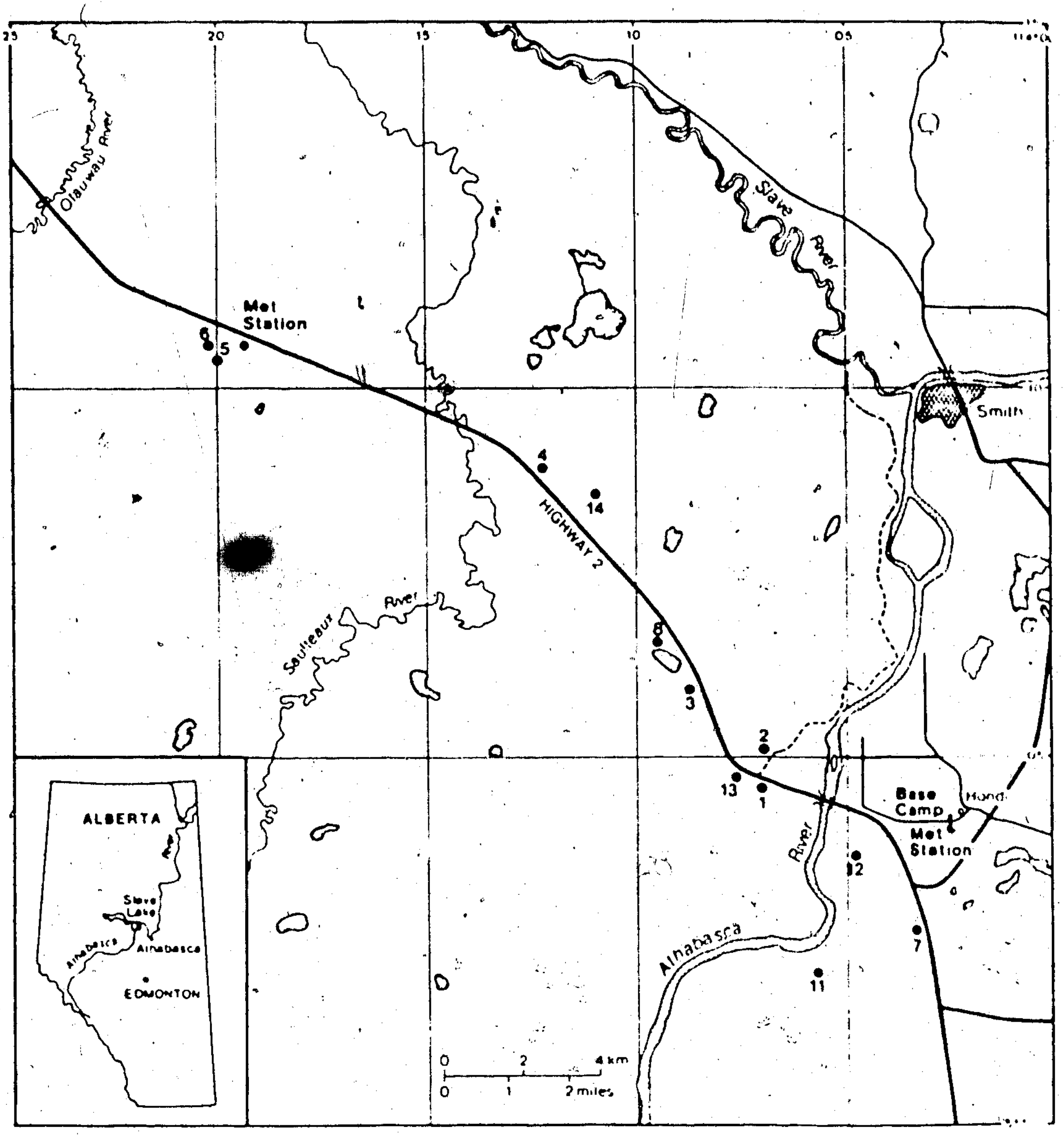

Figure 1-1. Locations of the eight SEADYN reference stands, and the four stands (11-14) established specifically for this study. This research is based primarily on data collected in stands 1, 2, 3, 4, 11, 12, 13, and 14.

northern Alberta: pine/lichen woodland succeeding to pine/alder/feathermoss forest followed by white spruce/balsam fir/feathermoss sub-climax or climax forest. Thus, the four stands appeared to represent points along a successional gradient and the specific research objective of comparing N cycling patterns between seral stages was adopted.

During the summer of 1982, the four stands were equipped to monitor N flux in litterfall and precipitation below the tree and shrub canopies. Samples were collected for laboratory analysis, estimation of total N and N mineralization capacity in the forest floor (LFH) and mineral soil horizons. Questions arose regarding successional relationships among the stands when preliminary soil characterization indicated that soil development differed between sites. It was reasoned that, if seral status of the vegetation was the only parameter which varied between sites, soil development should be the same in all locations. On the basis of these observations, the research objectives were divided, with one aspect of the program examining the ecological relationships among stands with respect to successional status and soil development and the other aspect examining N cycling patterns. Consideration of soil development introduced concepts of change in soil phosphorus chemistry with pedogenesis and the nutrient cycling objectives were expanded to include P dynamics in foliage, litterfall and soil. Four new stands were established in 1983 to enlarge the data base so that the research deals specifically with four pine/lichen stands, two pine/alder/feathermoss stands and two white spruce dominated stands. Data from additional stands, collected in conjunction with other aspects of the SEADYN program, are included in chapters 2 and 4 of this thesis.

In view of the two distinct aspects of the research program, the thesis is organized into two parts. Part 1 deals with questions relating to ecological relationships among stands and contains introductory material, including a discussion of general site conditions, a chapter dealing with tree age structure in boreal mixedwood stands, and a chapter examining profile development of soils in the eight Hondo stands. Part 2 deals with various aspects of the N and P cycling research including: litterfall dynamics, litter decomposition, N mineralization and N and P cycling processes. All chapters were written as relatively independent papers, each with its specific objectives. During the period of this research, a working hypothesis was developed from interpretations of collected data and field observations, and literature review, as a basis for organizing ideas and hypotheses regarding nutrient dynamics in boreal coniferous stands. This diagramatic model hypothesis is presented in the last chapter and used to synthesize the results of the entire research program and to identify future research objectives.

2. AGE STRUCTURE AND THE NATURE OF PLANT SUCCESSION

2.1 Introduction

Concepts of plant succession after fire, leading from pine or aspen dominated seral forest toward white spruce climax communities, were developed in the early published descriptions of vegetation in northern Alberta and adjacent areas of the Northwest Territories (Raup 1946, Moss 1953). Since that time, successional relationships among these prominent forest types have not been specifically examined in the boreal regions of Alberta. The patterns of vegetation change originally proposed appear, however, to have achieved a degree of general acceptance and, although seldom described in detail, are often alluded to in general vegetation descriptions (Rowe 1972, Kabzems *et al.* 1976, Strong and Leggat 1981).

In the Hondo area, casual observations of stand structure and species composition tend to support the view that jack pine/lichen woodland represents an early seral stage which leads to a gradual transition to pine/alder/feathermoss forest and eventually to white spruce/balsam fir/feathermoss communities. All stages in this progression are commonly observed in the mosaic of vegetation covering the landscape, including young jack pine (Pinus banksiana Lamb.) stands with lichen (mainly Cladina spp.) groundcover and scattered alder; older pine stands with alder (Alnus crispa (Ait.) Pursh.), with feathermosses (mainly Pleurozium schreberi (Brid.) Mitt.) beneath, forming patches in the lichen dominated areas; mature jack pine forest in which alder patches have coalesced to form, with small white or black spruce (Picea glauca (Moench.) Voss, P. mariana (Mill.) B.S.P.) a continuous shrub canopy and a feathermoss ground cover; and older spruce stands with large, decrepit jack pine, no alder and a continuous feathermoss (mainly Hylocomium splendens (Hedw.) B.S.G.) layer. On the basis of these sorts of observations and on literature reports, the successional sequence outlined above became a basic premise on which the original objectives of this research were founded.

Questions regarding the validity of the assumed successional relationships among forest types arose in the summer of 1982 because preliminary sampling suggested that soil profile development differed between forest types. It is generally accepted that soil development is a slow process in northern regions, requiring hundreds or thousands of years for major alterations in soil horizons to occur. In contrast, plant succession in the boreal forest is expected to be relatively rapid because stands are normally destroyed by fire at intervals rarely exceeding 200 years (Heinselman 1981). If plant succession is cyclical, with the vegetation of ecologically equivalent sites (drainage, topography, etc.) following the same cycle but representing different successional stages at any given time, soils would have developed under the same vegetation regime on all sites and therefore horizon development would not be expected to differ among forest types.

Three alternative explanations could account for the association of specific forest types with specific soil profile development: 1) the sites observed were not ecologically equivalent in terms of climate, topography, parent material or moisture regime, such that differences in soils and vegetation characteristics between sites related to overall differences in site conditions; 2) successional vegetation change did not follow the expected pattern such that the historical vegetation regime differed among sites; and 3) soil development did not differ between sites and conclusions based on preliminary sampling were in error. The hypothesis of lack of ecological similarity among sites was rejected for the following reasons:

1. All sites were within an 8 km radius such that macroclimate differences among them were negligible.
2. Air photo analysis indicated that all sites were located on the same landform which was an ancient glacial lake deltaic deposit modified by aeolian processes (St. Onge 1972).
3. Road profile surveys conducted at the time of the construction of Highway 2, which runs adjacent to most sites, indicated that all study areas were on the uppermost terrace level above the Athabasca River which suggests that the land surfaces were of equal age.
4. All sites exhibited undulating topography with subdued slopes typical of aeolian landforms in the area and although sites differed in overall slope and aspect, the differences were not consistent within forest types.
5. Water table depths, measured in pits, were found to fall within the same range of 1.5 m

>3 m in all sites.

6. Clay lenses, which have been observed in sandy soils in central Alberta (Kjearsgaard 1972) and which may influence site conditions by causing the development of a perched water table, were not observed in soil profiles in any of the study sites.

The nature of plant succession, as reflected in stand age structure, is examined in this chapter while a detailed discussion of soil development on the Hondo sites is given in Chapter 3.

Vegetation succession after fire in the Boreal Forest Region of northern Alberta was described in the early literature (Moss 1953, Raup 1946), as a sequential process involving initial invasion by jack pine or trembling aspen with later establishment of white spruce and possibly balsam fir, and the eventual development of a white spruce climax in which pioneers have died out. This view of succession is consistent with the relay floristics model of Egler (1954) and with the facilitation model of Connell and Slatyer (1977) in which pioneer species ameliorate environmental conditions to a degree which allows the establishment of later successional species.

An alternate hypothesis regarding succession in the boreal forest was described by Heinselman (1981) who cites earlier literature suggesting that species composition in existing stands is similar to that of pre-fire forest and does not change substantially over the life of the stand. This pattern of succession is consistent with the initial floristic model of Egler (1954) in which species composition is viewed as relatively static over time and dependent upon the composition of plant populations which occupy a site soon after disturbance. According to this view, changes in canopy characteristics arise from relative differences in the growth rates of different species rather than from species replacement.

These models of succession differ fundamentally in their predictions of timing, duration and pattern of establishment of different species in a forest. In the Mixedwood Section (B18A) of the Boreal Forest Region of Rowe (1972), if succession followed the relay floristics model, jack pine and aspen would be expected to be restricted to the oldest age-classes in a stand while white spruce should have increasing representation in the younger classes indicating gradual invasion and continued reproduction. If succession followed the inital floristics model, all species would be represented in the oldest age classes and have lower abundance in younger classes. The two models should, therefore, be distinguished by comparing the age distribution of component species in a stand. The objective of this research was to examine age structures of stands in the Hondo area of central Alberta to determine which model of succession best explains vegetation characteristics in the Boreal Mixedwood Section and then characterize the prominent tree species in terms of their successional attributes.

2.2 Methods

Age structure data were collected from 34 stands comprised of varying combinations of jack pine, trembling aspen, white and black spruce, balsam fir, paper birch and balsam poplar. Six stands (stands 1,2,3,4,5,6) were reference stands established as part of ongoing ecological research in the Hondo area, four of which (stands 1,2,3,4) were part of the nutrient cycling investigations associated with this study. Four other stands (stands 11,12,13,14) were established as part of the nutrient cycling research while the remaining 26 stands were selected specifically for a reconnaisance survey of age structure. In each stand a 25m x 25m (stands 11-14) or 50m x 50m (remaining stands) area was staked into 5m x 5m quadrats to facilitate sampling. Trees >2.5 cm dbh (diameter breast height, 1.3m) within the staked areas and smaller trees and seedlings in 5-10 randomly selected quadrats were counted to determine tree density. In the reference stands, all trees >2.5 cm dbh, and in stands 11-14, 30 trees of each species were cored using an increment borer 30 cm above the ground to determine age. The remaining stands were sampled in a more cursory manner by stratifying the tree population into 5 cm diameter classes and coring a total of 20 trees per stand distributed among the size classes according to the number of trees in each class. In all stands, diameters of trees < 2.5 cm dbh and seedlings were recorded and several individuals, spanning the range of diameters, were collected, sectioned and aged in the laboratory to allow estimation of age from diameter. Increment cores were glued to wooden holders in the field and, after drying in the laboratory, were sanded with fine sandpaper and annual rings counted.

under a dissecting microscope. Ages were corrected to account for time required to reach coring height (described below) and recorded in 5 year age classes. The proportion of the total number of cores in a stand within each class was multiplied by stand density to estimate the density of trees in each age class.

Young trees growing in a variety of sites were harvested to determine the number of years required to reach coring height (30 cm). Individuals of deciduous species, jack pine and black spruce were collected in the open while those of white spruce and balsam fir were collected under a closed canopy so that the ages obtained would be appropriate for the conditions expected during the establishment of each species within a stand. Once the age structure data had been collated it was apparent that white spruce commonly entered a stand immediately following fire so that correction factors obtained from individuals which became established under a canopy might be inappropriate. To investigate this possibility, 21 white spruce trees growing in six stands and ranging in age from 50 to 85 years, were uprooted and the root stock and lower bole returned to the laboratory for sectioning. Disks were cut at +30, +5, 0, -2, -5, -10 cm, with 0 cm indicating ground level, and sanded and annual rings counted to determine maximum and coring height ages.

2.3 Results

The intial survey of all tree species indicated that the number of years required for a tree to reach coring height (30 cm) differed among species as follows: trembling aspen 1, balsam poplar and paper birch 3, jack pine 5, white and black spruce and balsam fir 9. These values were used in generating the age structure data presented in this paper. Subsequent sampling of white spruce indicated that maximum tree age often occurred 5-10 cm below present ground level and that the time required for this species to grow to coring height varied considerably between individuals both within and between stands. Age at 30 cm ranged from 8 to 29 years with a mean of 12.8±5.5 (SD) years.

Fire is generally considered to be the primary cause of forest stand initiation in boreal regions (Heinselman 1981). Evidence of previous fire, in the form of charred wood, fire scars on living trees and charcoal in the forest floor and mineral soil, was commonly observed in all stand examined. Research on the fire history of the Hondo area is ongoing and has not been reported in this thesis. For the purposes of this study the timing of the fire which initiated an individual stand was interpreted from the age structure data. In burned stands, aspen generally suckers during the first growing season following fire and, therefore, the oldest cohort of aspen was considered to mark the fire date. Similarly, jack pine generally becomes established abundantly only after serotinous cones have been induced to open by fire such that the age of the oldest cohort of pine could be expected within the same age class as the date of the stand initiating fire.

The 34 stands sampled could be broadly divided into six forest types on the basis of species composition and differences in the ages of component species: jack pine/lichen (6 stands, Table 2-1); jack pine/alder (3 stands, Table 2-2); white and black spruce with codominant jack pine (6 stands, Table 2-3a,b); trembling aspen with subdominant spruce (6 stands, Table 2-4); trembling aspen with codominant spruce (5 stands, Table 2-5); and white spruce with codominant aspen or poplar (7 stands, Table 2-6a,b). In addition, a single stand was sampled which was dominated almost entirely by balsam fir and white spruce (stand 23, Table 2-6b).

In jack pine/lichen woodland (Table 2-1) the oldest age classes were invariably occupied only by jack pine. These individuals generally occupied a block of 3-4 age classes indicating that initial invasion after fire occurred over a minimum period of 7-12 years. Stand 1 contained several veteran trees which survived the fire that initiated the stand and occupied older age classes than the main group of dominant individuals. Stands 1 and 2 are in the same vicinity and comparison of their age structures suggests that they were both burned about 65 years before sampling and stand 1 was burned again about 20 years later. Establishment of jack pine in this foresr type has continued throughout the life of stand 1 and 2, to a lesser degree in stands 11 and 12, but in stands 21 and 24 occurred only at the time the stand was initiated. Individuals of other tree species in the pine/lichen stands were, in general, few in number and much younger than the dominant pines. Pine/alder stands varied in tree species

Table 2-1. Age structure of jack pine/lichen stands (trees ha⁻¹).
Species codes: J jack pine; A aspen; W white spruce; S black spruce; F fir;
P poplar; B birch; L larch.

Age Class (yrs)	Stand 1			Stand 2			Stand 11				Stand 12			Stand 21			Stand 24				
	J	A	W	J	A	W	J	A	W	P	J	A	W	J	W	S	J	W	S	B	L
2	0	8	0	0	12	0	128	255	0	0	0	0	0	0	0	0	0	0	0	223	119
5	152	32	0	20	24	4	765	255	0	255	0	64	0	0	32	0	0	40	0	64	8
10	200	64	0	64		8	1913		0		0		127	0	32	0	0	119	0	24	8
15	160		0	68		0	128		128		0		64	0	32	0	0	119	0	0	
20	48		0	92		0	0				0		0	0	95	32	0	56	0	0	
25	10		16	76		0	0				0		0	0	0	0	0	0	8	0	
30	48			26		0	26				0		72	0	0	0	0	0		0	
35	218			8		4	82				0		36	0	0	0	0	0		0	
40	475			25			845				0		72	0	0	0	0	16		16	
45	258			23			245				0			0	5	0	0	16		0	
50	19			56							21			0	0	0	0			0	
55	0			62							42			0	5	0	0			0	
60	6			275							21			0	5	0	0			16	
65	6			269							0			0	0	50	0				
70											21			0	5	31	0				
75											64			121		25	0				
80											106			260			360				
85											341			315			466				
90											64			826			455				
95																	97				

Table 2-2. Age structure of jack pine/alder stands (trees ha^{-1}). Species codes as in Table 2-1.

Age Class (yrs)	Stand 3						Stand 13		Stand 36		
	J	A	W	S	F	B	J	W	J	A	W
2	0	272	0	0	0	24	0	0	0	797	32
5	0	160	32	16	0	64	0	0	32	0	32
10	0	32	48	16	0	160	0	0	0	177	32
15	0	0	56	8	8	48	0	0	0	0	
20	0	0	48	0		8	0	0	0	0	
25	0	0	48	16		0	0	0	0	0	
30	0	0	32	8		0	0	16	141	0	
35	0	0	5	8		0	0	0	113	37	
40	0	0	6	0		0	17	16	1185	37	
45	0	0	7	4		8	0	0	113		
50	33	0	3				17	0	35		
55	33	0	1				137	32	0		
60	44	0	5				341		0		
65	44	0					188		0		
70	89	0							0		
75	111	0							0		
80	311	0							159		
85	278	12							53		
90	167	12							70		

Table 2-3a. Age structure of spruce stands with codominant jack pine and trembling aspen (trees ha^{-1}). Species codes as in Table 2-1.

Age Class (yrs)	Stand 4							Stand 14		
	[illegible]	A	W	S	F	P	B	J	A	W
2	0	40	40	0	80	80	0	0	0	0
5	0	240	120	0	600		0	0	0	0
10	0	0	0	0	960		0	0	0	0
15	0	0	0	0	240		0	0	0	0
20	0	0	0	0	40		0	0	0	32
25	0	0	0	0	40		0	0	0	32
30	0	0	0	0	120		0	0	0	64
35	0	0	0	0	200		0	0	0	0
40	0	0	0	0	72		0	0	0	0
45	0	0	0	0	32		0	0	0	0
50	0	0	5	0	135		0	0	0	0
55	0	0	16	0	169		0	0	0	123
60	0	0	5	0	301		0	0	0	741
65	0	0	5	0	249		0	0	0	494
70	0	0	5	0	322		7	14	0	247
75	0	0	27	0	265		0	57	0	123
80	0	0	67	18	122		0	142	304	
85	0	0	11	0	43		0	57		
90	0	0	16	0	53		0			
95	0	0	5	0	11		4			
100	0	0	5	0	0		0			
105	0	0	11	0	0		1			
110	0	22	28	0	0		0			
115	0	0	34	0	0		0			
120	0	0	68	18	0		0			
125	5	0	140	0	0		0			
130	0	0	169	36	16		0			
135	5	11	192	18			0			
140	9	11	45				0			
145	0	22					7			
150	0									
155	0									
160	9									
165	5									

Table 2-3b. Age structure of spruce stands with codominant jack pine and trembling aspen (trees ha⁻¹). Species codes as in Table 2-1.

Age Class	Stand 25						Stand 34				Stand 35						Stand 37					
(yrs)	J	A	W	S	F	B	J	A	W	S	J	A	W	S	F	B	J	W	S	F	B	L
2	0	0	0	0	0	249	0	1990	0	0	0	1095	0	0	0	0	32	95	0	0	32	0
5	0	0	199	0	0	50	0	1592	199	0	0	100	0	0	0	50	32	286	32	32	95	32
10	0	0	348	0	199	0	0	398	199	0	0	0	0	50	50		0	95	64		95	
15	0	0	99	0	50	0	0	0	0	0	0	0	50	100	0		0	0	32		0	
20	0	0	0	0		0	0	199	0	0	0	0	50	50	50		0	0	32		0	
25	0	0	0	99		0	0		199	0	0	0	0	0	0		0	0	0		0	
30	0	0	0	0		0	0		0	0	0	0	0	0	0		0	0	0		0	
35	0	0	0	0		0	0		0	0	0	0	36	0	0		0	0	0		155	
40	0	0	0	0		0	0		0	125	0	0	168	208	8		0	0	300			
45	0	0	69	0		0	0		0	0	0	32	0	416	0		0	43	150			
50	0	0	139	25		0	0		0	0	0	0	168	0	0		0	58	75			
55	33	0	46			0	0		0	0	0	0	50	0	0		0	24	0			
60	0	0	0			0	0		0	0	0	0	0	0	2		0	0	0			
65	0	0	46			0	0		0	0	0	0	0	104			0	0	0			
70	0	0	50			0	0		0	0	0	0	0	0			0	0	0			
75	0	0	33			0	0		0	0	0	0	0	0			0	0	0			
80	83	37				50	0		0	0	0	0	48	104			0	0	0			
85	307	0				25	0		0	0	0	0	0	0			250	0	0			
90		37					0		0	0	0	0	60	0			0	0	0			
95							0		0	0	0	0	168	0			110	0	0			
100							0		0	0	0	0	0	0			0	0	0			
105							0		0	0	0	0	60	0			0	0	0			
110							0		0	0	0	48	0	0			0	0	75			
115							0		65	0	28			0			100	0	0			
120							0		0	0	0		0	0			0	0	0			
125							0		0	0	28		0	32			100	0	0			
130							15		83	499	28						0	0	25			
135							398		122	1154							610	5	0			
140							214		130	499							250		25			

Table 2-4. Age structure of aspen stands with subdominant spruce (trees ha^{-1}). Species codes as in Table 2-1.

Age Class (yrs)	Stand 9				Stand 20			Stand 26				Stand 28		Stand 31			Stand 33		
	A	W	S	B	J	A	W	A	W	S	F	A	W	A	W	S	A	W	B
2	127	0	0	127	32	286	32	88	0	0	88	0	0	889	0	0	2388	0	0
5	255	0	0	255	32	486	127	88	0	0	442	0	0	286	0	0	199	0	0
10	0	0	0	637	95	95	127	0	0	0	177	0	0	0	64	0	0	0	0
15	0	0	0	127	0	32	0	0	0	0	0	0	0	0	0	0	0	0	0
20	0	0	0	0	0	0	0	0	88	0	177	0	0	0	0	0	0	32	0
25	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
30	0	0	0	0	0	0	0	0	88	0	0	0	32	0	0	0	0	26	0
35	0	0	0	0	0	0	0	0	88	0	0	0	32	0	0	0	0	0	0
40	0	0	0	42	0	0	0	0	0	0	88	0	32	32	0	0	0	0	0
45	155	13	0	0	0	0	0	0	0	0		0	95	0	40	0	0	26	0
50	182		38	117	0	0	0	0	88	0		0	283	0	0	0	0	20	0
55	155		0	0	0	0	38	0	394	0		0	375	0	0	0	0	20	16
60	537		22	0	0	0	42	0	175	0		0	436	0	0	0	0	0	0
65	1073			0	32	0	76	0	220	33		0	250	0	0	0	0	4	0
70	133			42	66	0		0	192			310	15	0	40	0	0		0
75					14	20		0				310		0	74	4	0		0
80						274		0				310		0	0		53		12
85						34		201				0		0	0		92		32
90								201				0		0	30		346		0
95								112				0		0	30		146		12
100								226				325		0	0		53		
105														0	0				
110														32	30				
115														0	88				
120														0					
125														58					
130														48					
135														0					
140														58					
145														68					

Table 2-5. Age structure of aspen stands with codominant spruce (trees ha⁻¹). Species codes as in Table 2-1.

Age Class (yrs)	Stand 5					Stand 15				Stand 17			Stand 22				Stand 27		
	A	W	F	P	B	A	W	S	B	A	W	B	J	A	W	F	A	W	S
2	216	0	0	0	0	0	0	0	0	32	0	254	0	0	0	0	0	0	0
5	240	8	0	0	16	32	0	32	0	32	0	64	0	0	0	0	0	0	0
10	80	4	4	0	0	0	0	32	0	0	0	32	0	0	0	0	0	0	0
15	24	0		0	0	0	0	64	32	0	0	0	0	0	0	0	0	0	0
20	8	8		0	0	0	0	95		0	0	0	0	0	0	0	0	0	0
25	0	4		0	0	0	0	0		0	32	0	0	0	0	0	0	0	0
30	0	16		0	19	0	0	0		0	286	0	0	0	0	0	0	0	32
35	0	4		0	0	0	0	0		0	95	0	0	0	0	0	0	95	32
40	0	16		0	0	0	0	18		0	32	0	0	0	0	0	0	127	0
45	0	115		0	0	0	91	16		0	0	247	0	0	0	0	0	95	0
50	0	195		0	0	0	43	18		0	96		0	0	68	0	0	95	50
55	0	305		0	0	0	75			96	422		0	0	0	0	0	238	50
60	0	599		0	0	143	32			420	343		0	0	0	0	0	393	218
65	16	615		[illegible]	0	92	32			258	199		0	0	273	0	0	437	300
70	48	329		11	0	286							0	47	68	50	0	103	82
75	434				0	184							0	0	273		0	129	
80	659				37								7	141	68		372		
85	32												13	188			73		
90														47					
95														47					

Table 2-6a. Age structure of spruce dominated stands (trees ha⁻¹). Species codes as in Table 2-1.

Age Class (yrs)	Stand 6				Stand 16				Stand 18		
	A	W	F	B	A	W	P	B	A	W	P
2	40	0	20	0	265	0	88	0	159	0	95
5	20	0	60	0	442	477	354	88	32	32	0
10	0	0	140	0	0	64		0	32	0	0
15	0	0	160	0	0	0		0	32	0	0
20	0	0	220	0	0	0		0		0	0
25	0	0	360	0	0	0		0		0	0
30	0	0	220	0	0	0		0		0	0
35	0	0	209	0	0	0		0		0	0
40	0	20	269	0	0	0		0		0	0
45	0	4	265	0	0	0		0		0	0
50	0	16	233	0	0	0		20		0	0
55	0	30	32	0	0	0				0	0
60	0	29	55	0	0	0				0	0
65	0	39	23	0	36	0				0	0
70	0	52	16	0	0	0				41	0
75	0	13	0	0	0	0				44	0
80	14	7	13	0	0	0				0	0
85	0	24	0	0	0	0				83	0
90	0	11	0	0	0	0				130	0
95	0	24	0	0	0	78				137	0
100	0	20	0	0	0	0				83	0
105	0	7	0	0	0	0				0	0
110	0	44	7	0	0	152				0	0
115	0	53		8	0	102				54	0
120	14	53		0	0	120				0	0
125	14	13		0	57	46				0	0
130	0	20		8	0					42	0
135	41	13		8	0					0	34
140	41	7			0					0	34
145	14	13			0					0	
150					0					0	
155					0					19	
160					0						
165					87						

Table 2-6b. Age structure of spruce dominated stands (trees ha⁻¹).

Age Class	Stand 19				Stand 29				Stand 30					Stand 32				Stand 23		
(yrs)	A	W	F	P	A	W	S	P	W	S	F	P	B	A	W	F	B	W	F	B
2	2805	510	893	0	509	0	0	32	0	0	199	0	0	0	0	354	0	0	0	0
5		128	2040	0	0	0	0	0	0	0	1592	0	0	0	354	4953	0	0	177	0
10		0	1275	0	0	0	0	0	0	0	597	0	0	0	0	4599	0	0	531	0
15		0	255	0	0	0	0	0	0	0	0	0	0	0	0	1769	0	0	531	0
20		0	0	0	0	0	0	0	0	0	199	0	0	0	0	708	0	0	88	0
25		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
30		0	0	0	0	0	0	0	0	0	0	0	0	0	0	354	0	0	0	0
35		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
40		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
45		0	0	0	0	32	0	0	0	0	0	0	0	0	0	0	0	0	0	0
50		0	0	0	0	95	0	0	0	0	135	0	0	0	0	0	0	0	0	0
55		0	0	0	0	0	32	0	199	0	98	0	0	0	0	0	0	0	75	0
60		0	85	0	0	112	0	0	749	0	135	0	0	0	64	0	0	0	0	0
65		0	0	0	0	594	0	0	600	0	135	0	0	0	0	0	0	0	0	0
70		0	85	0	0	474	0	0	0	0		226	0	102	83	0	0	0	0	0
75		0	0	0	0	548	140	44	210	0		0	0	0	0	0	0	25	0	0
80		0	0	0	60			0		0		0	0	172	0	85	0	50	67	0
85		0	85	0				0		0		54	16	165	403	78	33	50	0	0
90		0	0	0				49		0		129			184	29		0	108	0
95		0	85	0						0						17		0	157	0
100		38		0						0								25	90	0
105		0		0						0								0	87	0
110		124		113						0								0	0	0
115		74								0								0	0	0
120		341								0								0	0	0
125		38								0								0	0	0
130		148								0								25	0	0
135		74								0									0	0
140										0									42	0
145										0										25
150										0										
155										72										

composition and age structure (Table 2-2). The age structure of stand 3 followed the pattern predicted by the sequential invasion model with jack pine and some aspen becoming established immediately after fire followed by slow invasion of white and black spruce about 30 years later. This pattern was followed in stand 36 but not in stand 13 in which white spruce became established in small numbers soon after stand initiation.

In stands with white and/or black spruce and codominant jack pine most of the dominant species became established soon after the fire which caused stand initiation (Table 2-3a,b). In general, jack pine and aspen occurred primarily within the 3-4 oldest age classes with some representation at the seedling stage in aspen. A similar pattern was followed by white spruce in stands 14 and 34 with most individuals in these stands occurring in a discrete block in the oldest age classes. In contrast, in stands 4 and 35, white spruce became established initially at the same time as aspen and pine but continued to invade for 90 and 120 years respectively. Black spruce behaved in a manner similar to white spruce, occurring only in the oldest age classes in some stands and more evenly aged in others.

The mixed stands of trembling aspen and white spruce formed a continuum of age class distributions ranging from those in which the successful establishment of spruce was delayed up to 50 years after that of aspen (e.g. stands 9,31,33; Table 2-4) to stands in which both species became established at the time of stand initiation (stand 17, Table 2-5). In general, aspen was represented only in blocks in the oldest and youngest age classes while the age distribution of spruce varied from discrete blocks (stand 20, Table 2-4) to broader patterns spanning over 40 years (stands 5,27; Table 2-5, stand 28; Table 2-4). The age distribution of aspen, white spruce and jack pine in stand 20 (Table 2-4) may highlight the difficulties in comparing the times of seedling emergence or suckering of different species in the same stand. Trembling aspen regenerates from root suckers which generally sprout and grow vigorously immediately after fire, while jack pine cones are opened by heat and shed seed soon after fire but may have delayed germination (Thomas and Wein 1985) or may be suppressed as seedlings. The differences in the older age classes occupied by these two species in stand 20 probably relate to some mechanisms which retarded the growth of pine relative to aspen because it is unlikely that pine would have seeded into that stand only 5-10 years after its initiation. White spruce entered stand 20 over a discrete time period similar in length to that of pine and aspen but delayed by 4 age classes after aspen. Delayed emergence has not been studied in this species but it is possible that these phenomena, rather than sequential invasion may account for the observed delay in spruce establishment.

In white spruce stands with codominant trembling aspen and balsam poplar (Table 2-6) white spruce invariably made up a large proportion of the tree population which became established at the time of stand initiation. As found in other forest types, the period of spruce invasion ranged from 20 to over 100 years among stands. Balsam fir was represented in the oldest age classes of stands 30 and 32 and was dominant in stand 23 in contrast to other stands in which fir is found only in the younger classes. The oldest individuals in stands 18 and 30 appear to be veterans from a previous stand which survived the fire which initiated the present stand. These veterans include white spruce, suggesting that white spruce was represented in the previous stand.

2.4 Discussion

Interpretation of tree age data

The accuracy of estimates of total tree age from ring counts on increment cores is dependent largely on the accuracy of the estimated age at coring height. In species which sprout from root stocks and grow vigorously immediately after a fire, such as trembling aspen, the age at coring height can be accurately estimated because it seldom exceeds one or two years. In species which regenerate from seed, however, estimates will be less accurate because seedlings may be suppressed to varying degrees by other vegetation or by weather conditions during the growing season. The effect of varying growth rates within and between stands is demonstrated in the wide variation in age at 30 cm observed in white spruce. Estimation of coring height age is further complicated because the present ground surface, from which coring height is measured, may not be the same as that on which the seedling germinated such that maximum age may be below present ground level particularly in la trees

Thomas and Wein (1985) observed delayed emergence of jack pine and black spruce seedlings from burned seedbeds in New Brunswick and cite research demonstrating that germination of jack pine seed may occur up to five years after seeding. Similar research has not been conducted on white spruce. In the age structure of a mixed stand, species with delayed emergence will appear to have entered the stand later than species which establish without delay.

In this paper, age data have been expressed in five-year classes for simplicity of presentation and to enhance distribution patterns in stands in which relatively few trees were aged. Five years was arbitrarily selected as a compromise between broader classes, which may obscure discrete age differences, and narrower classes, which result in numerous empty classes and make patterns difficult to discern. The difficulties in pattern distinction in distributions with empty classes can be observed in the older stands with even age distributions sampled in this study (e.g. stands 35,37; Table 2-3). When interpreting apparent age differences in distribution patterns based on age classes it must be kept in mind that ages vary within classes. For example, the actual difference in ages of two groups of individuals separated by a single age-class may range from 6 to 14 years while individuals in adjacent classes may differ in age from 1 to 5 years.

The age structure of stand 20 (Table 2-4) highlights the difficulties in comparing age distributions, and particularly the relative times of entry of different species in the same stand. Jack pine, aspen and white spruce all became established over discrete time periods suggesting that propagules of each species were available for a limited time. Pine and aspen are similar in that their reproduction is triggered by fire through release of root sprouts in aspen and the opening of serotinous cones in pine. These species would therefore be expected to enter a stand within the same time period. Apparent differences in the older age-classes occupied by these species in stand 20 probably relate to some of the delay mechanisms discussed above rather than representing actual differences in the time of entry. The establishment of white spruce in stand 20 is further delayed but several interpretations of this delay are possible: spruce may have entered the stand through the germination of seedbank seeds at the same time as pine and aspen but the seedlings were strongly suppressed and therefore apparent ages are underestimates; spruce may have seeded into the stand from surviving individuals in the vicinity after the stand had become established; or spruce may have seeded into the stand continuously but establishment was inhibited initially be harsh conditions soon after the fire and later, possibly because of smothering by aspen leaves. These alternatives cannot be distinguished on the basis of present stand conditions or information currently available on the behaviours of these species during establishment and early growth.

It is apparent, on the basis of the above discussion, that uncertainty is inherent in any age structure based on increment core data and that the degree of this uncertainty differs among species. To accomodate data uncertainty during interpretation, conventions were adopted for this study such that groups of individuals in adjacent age-classes or separated by a single class did not differ significantly in age while ages of groups separated by four or more classes were significantly different. Differences spanning two or three classes such as those described in stand 20 above were interpreted with caution.

Characteristic age distribution of species

Age distributions of jack pine were typical of a pioneer species, with individuals restricted to the oldest age-classes in most stands. In three pine/lichen stands, however, jack pine had an age distribution indicating continued regeneration suggesting that this species may be considered to be an edaphic climax on some sites. Regenerating pine occurred in the youngest age-classes in some stands indicating that initial establishment under a canopy is possible but that survival is limited. Trembling aspen also followed an age distribution expected of pioneer species being represented in most stands only in the oldest and youngest age classes. Aspen regeneration was observed in most stands irrespective of whether mature individuals were present or not, indicating that this species is easily dispersed and often establishes successfully in mature stands but seedlings do not survive.

White spruce age distributions varied substantially among stands including patterns expected of pioneer species (stand 34, Table 2-3; stand 16, Table 2-6), broader patterns indicating continued establishment for several decades after stand initiation but without continued regeneration in younger classes (e.g. stand 4, Table 2-3; stand 6, Table 2-6), even age distributions suggestive of climax conditions (stand 35, Table 2-3) and patterns indicating sequential invasion of established stands (stand 3, Table 2-2). This variety in age distribution patterns indicates that the establishment of white spruce in a stand is not as restricted by the degree of canopy closure as pine and aspen appear to be, although a dense subcanopy of fir appears to terminate successful regeneration. White spruce is known to regenerate on rotten logs (Zasada and Gregory 1969) which may account for increased or maintained establishment as stands mature and logs from trees killed by the initial fire decompose. Age structures of black spruce were similar to those of white spruce, varying widely among stands. In many cases the age distribution of black spruce appeared to be fragmented but whether this reflects periodicity in reproduction or availability of appropriate seed beds is not known.

Balsam fir was commonly restricted to younger age-classes, in which it was often abundant, forming a distinct subcanopy as would be expected of a late seral species. In some stands, however, fir became established at the time of stand initiation and had an age structure more similar to jack pine and aspen indicating that it is able to tolerate a wide range of light conditions. Delayed emergence of balsam fir germinants was not observed in the study by Thomas and Wein (1985) implying that early establishment of this species was not the result of buried seed which survived the fire. Fir is often observed as small, suppressed or heavily browsed individuals in the forest floor of mature stands. A canopy fire at a time when the ground was moist would have killed the dominant trees without harming these small individuals allowing their release from suppression and subsequent growth into the new canopy.

Balsam poplar and paper birch had scattered occurrence in the stands sampled and appeared to follow no distinct age distribution pattern. Individuals or groups of these species were commonly found in several age classes with establishment spread out at intervals throughout the life of a stand. These results may suggest that invasion of these species is dependent on the periodic occurrence of factors such as specific weather conditions, which influence seedbed suitability or seed production.

Successional processes

Age structures observed in stands in the Hondo area suggest that plant succession in the Boreal Mixedwood Section does not follow a fixed pattern. In several stands, the age distributions of the component species were clearly consistent with the relay floristics model while in other stands, distributions were better predicted by the initial floristics model. In addition, many stands followed a "mixed model" pattern in which white spruce and pine or aspen established initially with fir invading at a later date.

In jack pine/lichen woodland, the wide difference in age between pine and white spruce is indicative of a relay floristics pattern of succession. In these stands, however, spruce was generally of low abundance relative to jack pine such that even if stands attained a great age it is unlikely the spruce would replace pine as the dominant canopy species. Most pine/lichen woodlands cannot be considered to be fire climax forests because jack pine age distributions remain strongly dominated by the oldest age classes and invasion of white spruce does occur. Successional change, in terms of species replacement, is so slow, however, that this vegetation type probably remains stable over many fire-initiated generations of forest because abundant pine seed would always be available for stand regeneration after fire.

Age structures of pine/alder stands are also generally consistent with the relay floristics model with jack pine establishing initially and white spruce seeding in later (Table 2-2). This is particularly evident in stand 3 in which spruce invasion in appreciable numbers came about 60 years after stand establishment and has continued since.

White spruce would be expected to become codominant in the canopy of stand 3 as they approach maturity in about 50 years, but complete replacement of pine would require a much longer period and may never occur because of the short life-expectancy of stands in the Hondo area which appears to be less that 150 years. Thus, pine/alder stands probably remain dominated by jack pine through much of their existence which, unless they survive to be very old, will ensure an abundance of seed following fire and result in the reestablishment of pine forest in the next stand generation.

Age structures in mixed stands of aspen and white spruce (Tables 2-4 and 2-5) indicated that the relay floristics pattern of succession was not consistently followed in this forest type; because, in many stands, aspen and spruce became established at about the same time. In some stands, age distributions were consistent with the initial floristics model, with ages of most individuals falling within a discrete block in the oldest classes, but white spruce frequently continued to invade for several decades after initial establishment. Age distributions seldom indicated that spruce regeneration was continuous as would be expected if this species was to eventually form the climax stand. The oldest aspen stand (31, Table 2-4) was about 150 years in age and still maintained a codominant population of aspen; indicating that a long period of time would be required for spruce to become completely dominant in this forest type.

In stands dominated by spruce, white spruce occurred invariably and often abundantly in the oldest age classes. Many of these stands were very old and it is difficult to know whether individuals in the oldest age classes became established at stand initiation or represent a sequential invasion in which older individuals of the pioneer species have died off. The presence of relatively young stands in which white spruce codominated the oldest classes with jack pine or aspen (stands 14, 25, Table 2-3; stands 29,32, Table 2-6) suggested that spruce was initially present in most spruce stands.

The age structures of several spruce stands indicated that regeneration by any species after initial invasion was limited and are thus consistent with the predictions of the initial floristics model. In other stands, balsam fir began invading long after initial establishment of white spruce, pine or aspen which is more consistent with the relay florisitic model. In addition, in many spruce dominated stands, white spruce was observed to have become established continuously for several decades beginning at the time of stand initiation, a behavior which is inconsistent with either model. These results suggest that neither of the proposed models fully describe successional processes in spruce forests in the Boreal Mixedwood Section.

This research has shown that the processes which control successional change in the vegetation of the Mixedwood Section differ markedly among sites and forest types. Age structures consistent with the relay floristics model were observed in some aspen, pine/alder and pine/lichen stands although in the latter, species replacement appeared to be occurring so slowly that it probably had little significance in vegetation dynamics. Age structures indicating initial floristics successional patterns were observed in all forest types but were most common in spruce stands. It was clear, however, that age distributions of many stands did not follow either hypothetical model suggesting that another conceptual model, possibly dealing with spatial and temporal controls on seedling establishment and the ecological characteristics of species which influence reproduction, dispersal, germination and early growth, will be required to fully explain successional patterns in these stands. In general, however, it appears that the fire return interval in the study area is short relative to the rate of successional change such that, many stands change very little during their life-span. Vegetation patterns in the landscape may, therefore, remain relatively static for long periods.

2.5 References

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3. CHARACTERIZATION OF SOILS AND THEIR RELATIONSHIP WITH FOREST TYPE

3.1 Introduction

The development of a soil profile in unweathered geologic parent material is the result of the combined effects of biological, chemical and physical processes which control additions to, losses from and transformations and translocations within the solum. The expression of these processes in soil properties is determined by the factors of climate, biota, topography and parent material and differences in these factors between sites lead to differences in soil profile characteristics (Jenny 1980). As indicated in Chapter 2, preliminary examination of upland sites on sand ridges near Hondo suggested that these areas were uniform in climate and topography, were located within the same landform and probably were of similar age, implying that differences in soil profile development between sites related to differences in parent material properties or vegetation history. Age structure analysis of forest stands in this area has suggested that vegetation patterns in the landscape may be relatively static, with individual sites occupied by similar forest stands for extended periods. Under these conditions, sites presently occupied by different forest types would also be expected to differ in soil horizon development. The objectives of this study were: 1) to characterize and compare soils in forest stands differing in species composition; and 2) to determine the extent to which differences in soil characteristics between sites reflected differences in vegetation.

Soils may be characterized and compared on the basis of a wide variety of morphological, chemical, mineralogical and physical criteria. In this study, soils at each site were initially described in the field and subsequent laboratory analysis was used to validate field observations and to measure chemical properties which reflect soil development. Preliminary observations indicated that clay content and distribution in the profile differed among sites. Laboratory analyses were conducted to 1) quantify clay contents of all horizons in all soils; 2) calculate the fine sand:total sand ratio in all horizons, as an index of parent material uniformity within a profile, to determine whether high-clay horizons were depositional or pedogenic; and 3) determine whether clay in high-clay horizons was illuvial in origin by micromorphological observation. Color differences among horizons observed in the field suggested that soils differed in their contents of C and iron oxides, leading to laboratory analyses for these components. Field observations also indicated that the degree of horizon differentiation differed among stands implying differences in overall soil development. This possibility was investigated by comparing the proportions of P in organic and various inorganic fractions as indices of pedogenesis (Walker and Syers 1976).

3.2 Methods

Eight sites representing three forest types were examined. Four stands (1,2,11,12) represented pine/lichen woodland dominated by jack pine with a ground cover of fruticose lichen and low shrubs. Two stands (3,13) represented closed canopy jack pine forest with an extensive shrub canopy of green alder and a continuous ground cover of feathermoss. An additional two stands (4,14) were dominated by white spruce with codominant jack pine and trembling aspen and had a feathermoss ground cover. Species composition and stand characteristics are described in detail in Chapter 4.

Soil profiles were described in 3 to 4 pits (1.5 m deep) in each stand. In four stands (1,2,3,4) soil samples for laboratory analysis were collected by horizons [illegible]pth of 40 cm at 16 randomly selected locations in each stand using a 7.6 cm diameter co[illegible] tube. LFH and Ahe or Ae horizons were collected from these cores in their entirety while 5 cm sections were collected from deeper horizons. Samples of horizons deeper than 40 cm were collected from three pits on each site using 5 cm x 4.7 cm diameter coring tubes inserted horizontally into the pit face. Five or more cores were taken from different locations across the pit face within a horizon and composited for analysis. In the remaining stands, a composite sample comprised of five 7.6 cm diameter cores was collected from LFH and A horizons at each of four pit locations in each stand and deeper horizons were sampled using the smaller tubes as described above.

All soil samples were oven-dried at 100°C and weighed immediately after collection, crushed by hand and passed through a 10 mesh (2 mm) sieve. Fragments coarser than 10 mesh were negligible in all soils. Subsamples were ground to pass a 100 mesh sieve prior to chemical analysis. The following chemical analyses were carried out according to McKeague (1978): particle size using the pipette method with peroxide destruction of organic matter in A horizon samples only; pH in 0.01 M $CaCl_2$, 2:1 solution:soil ratio; total carbon using a Leco automatic C analyser; iron and aluminum complexed with organic matter using Na-pyrophosphate; amorphous iron and aluminum using acid ammonium oxalate; and extractable phosphate using 0.03 M NH_4F + 0.025 M HCl. Sand particle size distribution was measured by dry sieving oven-dried sand using nested sieves in an Allen-Bradley Sonic Sifter, following ultra-sonic dispersion and wet sieving to remove silt and clay. Shaking times and amplitudes were maintained constant among samples to ensure uniform separation conditions.

Phosphorus in samples bulked within horizons in each stand was fractionated by chemical components using the sequential extraction procedure described by Olsen and Sommers (1982). This technique distinguishes three phosphorus fractions including acid-soluble calcium phosphates, base-soluble aluminum and iron phosphates (non-occluded), and reductant-soluble aluminum and iron phosphates considered to be occluded within secondary mineral grains or coatings on other minerals. Organic P was measured in the same samples using the ignition method (Olsen and Sommers 1982).

Slides for micromorphological observations were collected, as sections of undisturbed 7.6 cm diameter cores, in the two spruce stands (4,14), one pine/alder stand (3) and one pine/lichen stand (2). Core sections were taken at 15 cm - 25 cm and 25 cm - 35 cm. These depths represented the Bm horizon and straddled the Ae2/Bt1 interface, respectively, in the spruce stands, and the Bm1 and Bm2 or Bj horizons respectively in the other stands. Cores were air-dried and impregnated under vaccuum with 3M epoxy resin prior to slicing and polishing. Micromorphological characteristics were identified under a microscope with reference to Brewer (1964), Brewer and Pawluk (1975) and Pawluk and Brewer (1975).

Statistical comparisons among stands employed one-way analysis of variance (Zar 1974) followed by Duncan's multiple range test (Chew 1976).

Weights of clay redistributed with and added to a 75 cm profile in each stand were calculated as follows. Present weight of total soil, silt and clay were calculated from bulk densities, thickness and constituent percentage in each horizon to a depth of 75 cm. This depth was chosen because it represented the majority of the developed profile and soil above this depth appeared to have developed from uniform parent materials while discontinuities in parent material occurred below 75 cm in some sites. In addition, bulk density was near maximum at 75 cm in all soils indicating that any expansion of the solum which occurred during soil development affected only shallower horizons. In the calculation of clay redistribution it was assumed that clay was originally evenly distributed in the profile as would be expected in uniform parent materials. Mean clay content was calculated as weight of clay/total soil weight and used to calculate the weight of clay expected to be found in each horizon. Redistribution was calculated as the difference between actual and expected values, and must be considered approximate because additions of clay to the profile could not be taken into account. The calculation of clay additions was based on the assumption that clay contents in C horizons were equal to those in the original parent materials and that the total weight of soil in a 75 cm profile had not changed during soil development. Constant weight would be expected in the weakly weathered soils under consideration. Clay contents of the C horizon were used to calculate the original weight of clay in the profile which was subtracted from the present weight to determine the weight of clay added during soil development. Ranges of values based on clay contents of BC and C horizons were calculated for soils of stands 4 and 14 because C horizon contents may not have been representative of original contents throughout the profile while BC horizons may have been slightly augmented with translocated clay.

3.3 Results

Horizon development

Horizon development in soils under pine/lichen stands (Table 3-1) was similar to that under pine/alder stands (Table 3-2) with the latter having generally thicker horizons of slightly finer textures. Transitions across B horizon boundaries were gradual in all of these soils resulting in profiles with few distinct pedogenic features apart from a general increase in color chroma in the upper B relative to lower horizons. Soils of the spruce stands differed in horizon development from other soils, having thick Ae and distinct textural B horizons. The boundary between the Ae2 and Bt1 horizons was always abrupt and was generally marked by a 0.5 - 2 cm thick involute band which was slightly darker in color than adjacent material. Soil textures were consistently finer under spruce stands than in other soils.

Physical Properties

Total sand content was highest in soils under pine/lichen stands (Table 3-3), lowest in those under spruce stands (Table 3-4) and intermediate in those under pine/alder stands. Silt content was higher in soils under spruce stands than on other sites and was similar in pine/lichen and pine/alder stand soils. Clay contents were highest in soils under spruce stands and lowest under pine/lichen woodland. Enrichment in clay was apparent in the lower B horizons of all soils but was most pronounced under spruce forest.

The ratio of fine sand:total sand was relatively uniform throughout most profiles but, in C horizons of soils in stands 11, 4 and 14 this ratio differed from that of horizons above. In the latter two stands, BC horizons also differed from shallower horizons. With the same exceptions, the content of clay-free sand increased uniformly with depth in the profile while silt content decreased.

Micromorphological observations

In thin section, most soils appeared uniform across the 5 cm slide with no distinct organization of particles or changes in fabric type. In the deeper samples in both spruce

Table 3-1, Description of soil profiles under pine/lichen stands.

Stand	Horizon	Thickness (cm)	Color (dry)	Texture	Structure	Consistence	Boundary
1	Ahe	2	10YR4/2	S	single grained	loose	clear, wavy
	Bm1	24	2.5Y4/6	S	"	"	gradual, wavy
	Bm2	23	2.5Y5/6	S	"	"	gradual, wavy
	BC	45	2.5Y4/4	S	"	"	clear, wavy
	Ck		2.5Y4/4	S	"	"	
2	Ahe	2	2.5Y3/2	S	single grained	loose	clear, wavy
	Bm1	22	2.5Y4/4	S	"	"	gradual, wavy
	Bm2	31	2.5Y4/6	S	"	"	gradual, wavy
	BC	40	2.5Y4/4	S	"	"	clear, wavy
	Ck		2.5Y4/4	S	"	"	
11	Ahe	4	2.5Y3/2	S	single grained	loose	clear, wavy
	Bm1	19	2.5Y4/6	S	"	"	gradual, wavy
	Bm2	32	2.5Y5/6	S	"	"	gradual, wavy
	BC	38	2.5Y4/4	S	"	"	clear, wavy
	Ck		2.5Y4/4	S	"	"	
12	Ahe	3	2.5Y3/2	S	single grained	loose	clear, wavy
	Bm1	25	2.5Y4/6	S		"	gradual, wavy
	Bm2	34	2.5Y5/6	S		"	gradual, wavy
	BC	32	2.5Y5/4	S		"	clear, wavy
	Ck		5Y4/4	S		"	

Table 3-2. Description of soil profiles under pine/alder (3, 13) and spruce (4, 14) stands.

Stand	Horizon	Thickness (cm)	Color (dry)	Texture	Structure	Consistency	Boundary
3	Ahe	4	2.5Y4/2	LS	single grained	loose	clear, wavy
	Bm	23	2.5Y4/6	LS	"	v. friable	gradual, wavy
	Btj	44	2.5Y4/4	LS	"	v. friable	gradual, wavy
	BC	30	2.5Y5/4	S	"	loose	clear, wavy
	Ck		2.5Y5/6	S	"	loose	
13	Ahe	5	2.5Y2/1	LS	single grained	loose	clear, wavy
	Bm	26	2.5Y4/6	LS	"	v. friable	gradual, wavy
	Btj	50	2.5Y5/6	LS	"	v. friable	gradual, wavy
	BC	30	2.5Y4/4	S	"	loose	clear, wavy
	Ck		5Y4/4	S	"	loose	
4	Ae1	7	2.5Y4/4	LS	single grained	v. friable	clear, wavy
	Bm	15	2.5Y3/3	SL	"	v. friable	clear, wavy
	Ae2	8	2.5Y4/4	SL	"	v. friable	abrupt, wavy
	Bt1	20	2.5Y4/6	SL	"	firm	gradual, wavy
	Bt2	17	2.5Y4/6	SL	"	friable	gradual, wavy
	BC	33	2.5Y4/4	LS	"	v. friable	clear, wavy
	Ck		2.5Y4/4	LS	"	v. friable	
14	Ae1	6	2.5Y4/4	SL	single grained	v. friable	clear, wavy
	Bm	13	2.5Y4/4	SL	"	v. friable	clear, wavy
	Ae2	9	2.5Y5/4	SL	"	v. friable	abrupt, wavy
	Bt1	18	2.5Y4/6	SCL	"	firm	gradual, wavy
	Bt2	28	2.5Y5/6	SL	"	friable	gradual, wavy
	BC	25	2.5Y5/4	SL	"	v. friable	clear, wavy
	Ck		5Y5/3	LS	"	v. friable	

Table 3-3. Physical properties of soils under pine/lichen stands.

Stand	Horizon	Depth (cm)	Sand Coarse	Sand Medium	Sand Fine	Sand V. Fine	Total Sand %	Silt %	Clay - %	Ratio of fine sand/ total sand	Clay-free total sand %	Bulk density ($g \cdot cm^{-3}$)
			----------------	%	----------------							
1	Ahe	0-2	1.8	30.2	50.5	7.6	90.3	7.5	2.2	.56	92	0.57
	Bm1	2-26	1.0	25.1	55.3	8.9	90.4	7.3	2.3	.61	93	1.37
	Bm2	26-49	0.7	23.2	60.9	8.3	93.2	2.7	4.1	.65	97	1.59
	BC	49-94	-	--	--	-	--	-	-	-		--
	Ck	94+	0.5	22.7	64.3	8.4	96.0	1.4	2.6	.67	99	1.51
2	Ahe	0-2	0.5	19.7	60.1	8.7	89.0	8.8	2.2	.66	91	0.61
	Bm1	2-24	0.7	20.4	58.9	9.3	89.5	8.2	2.3	.66	92	1.26
	Bm2	24-55	0.5	18.1	62.0	10.3	90.7	5.2	4.1	.68	95	1.56
	BC	55-95	-	--	--	--	--	-	-	-	-	--
	Ck	95+	0.5	20.3	66.6	7.7	95.2	2.2	2.6	.70	98	1.51
11	Ahe	0-4	0.4	15.6	68.5	7.6	92.2	4.0	3.8	.74	96	0.45
	Bm1	4-23	0.2	13.3	70.6	8.5	92.6	4.3	3.1	.76	96	1.40
	Bm2	23-55	0.1	14.2	73.5	6.0	93.8	1.5	4.7	.78	98	1.49
	BC	55-93	0.2	17.6	70.7	7.1	95.7	1.2	3.1	.74	99	1.51
	Ck	93+	0.2	24.9	58.1	10.6	93.8	3.0	3.2	.62	97	1.50
12	Ahe	0-3	0.8	20.1	55.4	11.7	88.0	6.6	5.4	.63	93	0.60
	Bm1	3-28	0.7	20.6	54.7	11.1	87.3	9.2	3.5	.63	90	1.44
	Bm2	28-62	0.3	17.2	62.1	11.1	90.7	4.0	5.3	.68	96	1.48
	BC	62-94	0.3	16.4	62.2	14.2	93.1	2.6	4.3	.67	97	1.51
	Ck	94+	0.4	16.7	59.9	15.9	93.0	2.7	4.3	.64	97	1.46

Table 3-4. Physical properties of soils under pine/alder (3, 13) and spruce (4, 14) stands.

Stand	Horizon	Depth	Sand				Total Sand	Silt	Clay	Ratio of fine sand/ total sand	Clay-free total sand	Bulk density
			Coarse	Medium	Fine	V. Fine						
			---------------	%	---------------		%	%	%		%	(g•cm⁻³)
3	Ahe	0-4	0.5	11.2	57.9	15.3	84.8	11.4	3.8	.68	88	0.88
	Bm	4-27	0.3	10.3	58.7	16.8	86.2	9.4	4.4	.68	90	1.28
	Btj	27-71	0.1	8.7	63.2	15.7	87.6	5.8	6.6	.72	94	1.55
	BC	71-101	-	-	--	--	--	-	-	-		--
	Ck	101+	0.2	11.5	63.5	17.4	92.6	3.0	4.4	.68	97	1.48
13	Ahe	0-5	0.8	14.6	48.0	20.0	83.5	9.7	6.8	.58	90	0.60
	Bm	5-31	0.7	13.2	48.5	23.3	85.6	9.8	4.6	.57	90	1.39
	Btj	31-81	0.5	11.3	53.3	22.4	87.5	4.6	7.9	.61	95	1.48
	BC	81-111	0.3	11.3	61.5	19.2	92.2	2.9	4.9	.67	97	1.48
	Ck	111+	0.3	12.8	58.3	22.5	93.9	2.0	4.1	.62	98	1.48
4	Ae1•	0-7	0.2	1.2	36.0	38.1	75.5	20.0	4.5	.48	79	0.86
	Bm	7-22	0.2	1.9	37.0	38.4	77.5	11.9	10.6	.48	87	1.28
	Ae2	22-30	-	-	--	--	--		--	-	-	--
	Bt1	30-50	0.1	1.0	35.9	37.8	74.8	12.0	13.2	.48	86	1.47
	Bt2	50-67	0	0.8	44.0	34.2	78.9	12.6	8.5	.56	86	1.47
	BC	67-100	-	-	--	--	--	--	-	-	-	--
	Ck	100+	0.1	1.2	51.4	32.5	85.2	7.8	7.0	.60	92	1.37
14	Ae1	0-6	0.1	0.2	9.2	51.2	60.8	31.2	8.0	.15	66	0.81
	Bm	6-19	0.1	0.3	13.7	46.9	61.0	25.2	13.8	.22	71	1.23
	Ae2	19-28	0.1	0.2	10.1	49.3	59.6	26.6	13.8	.17	69	1.23
	Bt1	28-46	0.1	0.2	8.4	52.6	61.1	16.7	22.2	.14	79	1.35
	Bt2	46-74	0	0.2	10.9	63.7	74.7	10.9	14.4	[illegible]	87	1.36
	BC	74-99	0	0.2	17.6	55.4	73.2	14.4	12.4	.24	84	1.36
	Ck	99+	0	0.3	26.5	50.3	77.2	12.3	10.5	.34	86	1.32

stands, however, the abrupt upper boundary of the Bt1 horizon, marked by a distinct brown band, was readily apparent. The dominant soil fabric in all soils was matrichlamydic, comprising skeletal sand grains with thin, generally continuous, light brown coatings. These coatings were isotropic and rarely formed bridges between grains in samples from both depths in the pine/lichen stand soils and in the 15 cm - 20 cm sample in the pine/alder stand soil. Occasional, weakly anisotropic coatings and more frequent bridging were observed in the lower sample of the pine/alder stand soil and in the upper samples of the spruce stand soils. Sections from the lower B horizon samples in both spruce stand soils exhibited moderately to strongly anisotropic coatings which commonly bridged between grains. This was particularly apparent within the brown bands observed in these horizons where strongly anisotropic coatings bridged between most skeletal grains forming a chlamydic-plectic or plectic fabric.

Chemical properties

Soil pH was generally similar within equivalent horizons in all stands (Tables 3-5, 3-6). Carbon contents of A horizons and, to a lesser degree, Bm1 and Bm horizons ranged widely with few distinct differences between forest types. In lower B horizons, however, C concentration was consistently highest in soils under spruce stands and lowest in soils under pine/lichen stands. Concentrations of pyrophosphate extractable Fe and Al were generally highest in the upper B horizon of all soils and did not differ greatly among sites (Tables 3-5, 3-6) although concentrations were higher in the lower solum of spruce and pine/alder than in pine/lichen stands. Oxalate extractable Fe decreased with depth in pine/lichen stands with the exception of stand 2. In contrast, a distinct increase in oxalate extractable Fe occurred between the A and Bm horizons of pine/alder and spruce stands. Concentrations of oxalate extractable Fe and Al in Bm1 and Bm horizons were similar in all soils except in those of stands 11 and 12 in which they were lower. In Bm2, Btj and Bt1 horizons, concentrations of oxalate extractable Fe differed significantly among stands (one-way anova, $P<.01$) with stands 3, 4 and 14 having higher concentrations than stands 1, 11 and 13. Oxalate extractable Al also differed significantly among these horizons, with those under spruce and the oldest pine/alder stand (3) having higher concentrations than other stands.

Table 3-5. Chemical properties of soil under pine/lichen stands.

Stand	Horizon	Depth	pH	Carbon	Pyrophosphate		Oxalate	
					Fe	Al	Fe	Al
		(cm)		(%)	-----%	-----	-----%	-----
1	Ahe	0-2	3.75	3.66	.06	.03	.32	.10
	Bm1	2-26	4.78	0.58	.08	.05	.32	.11
	Bm2	26-49	5.40	0.05	.02	.01	.16	.06
	BC	49-94	5.45	0.03	-	-	-	-
	Ck	94+	7.25	--	.01	.01	.11	.04
2	Ahe	0-2	4.55	3.21	.05	.03	.26	.07
	Bm1	2-24	5.00	0.90	.11	.06	.37	.13
	Bm2	24-55	5.35	0.10	.02	.01	.20	.07
	BC	55-95	5.50	0.04	-	-	-	-
	Ck	95+	7.40	--	.01	.01	.12	.04
11	Ahe	0-4	5.45	1.37	.04	.03	.19	.09
	Bm1	4-23	4.96	0.16	.05	.03	.19	.07
	Bm2	23-55	5.21	0.02	.01	.01	.14	.05
	BC	55-93	5.38	0.05	.01	.01	.11	.04
	Ck	93+	7.35	--	.01	.01	.13	.03
12	Ahe	0-3	5.19	2.32	.06	.04	.23	.08
	Bm1	3-28	4.93	0.19	.05	.02	.22	.06
	Bm2	28-62	5.30	0.11	.02	.02	.18	.05
	BC	62-94	5.39	0.10	.02	.01	.15	.04
	Ck	94+	7.50	--	.01	.01	.15	.04

Table 3-6. Chemical properties of soil under pine/alder (3, 13) and spruce (4, 14) stands.

Stand	Horizon	Depth	pH	Carbon	Pyrophosphate		Oxalate	
					Fe	Al	Fe	Al
		(cm)		(%)	-----%-----		-----%-----	
3	Ahe	0-4	4.65	2.56	.06	.02	.21	.06
	Bm	4-27	4.85	0.77	.12	.05	.38	.12
	Btj	27-71	5.33	0.16	.04	.02	.26	.09
	BC	71-101	5.87	0.07	-	-	-	-
	Ck	101+	6.88	--	.01	.01	.24	.03
13	Ahe	0-5	4.58	3.55	.08	.05	.21	.07
	Bm	5-31	4.94	0.27	.09	.05	.27	.09
	Btj	31-81	5.42	0.15	.03	.02	.15	.06
	BC	81-111	5.81	0.17	.02	.01	.14	.04
	Ck	111+	7.15	--	.01	.01	.15	.03
4	Ae1	0-7	5.10	[illegible]	.08	.03	.20	.07
	Bm	7-22	4.83	[illegible]	.08	.04	.36	[illegible]
	Ae2	22-30	4.80	[illegible]	-	-	-	-
	Bt1	30-50	5.35	0.58	.03	.04	.24	.09
	Bt2	50-67	5.50	0.34	.04	.02	.17	.08
	BC	67-100	5.75	0.45	.04	.02	.17	.06
	Ck	100+	6.95	--	.01	.01	.15	.03
14	Ae1	0-6	4.72	0.93	.07	.03	.27	.08
	Bm	6-19	4.40	0.58	.10	.04	.42	[illegible]
	Ae2	19-28	5.07	--	-	-	-	-
	Bt1	28-46	5.34	0.29	.02	.02	.24	.11
	Bt2	46-74	5.71	0.28	.03	.01	.18	.08
	BC	74-99	6.20	0.29	.03	.01	.20	.06
	Ck	99+	7.45	--	0	0	.15	[illegible]

Forest types differed in the chemical forms of phosphorus in the upper 50 cm of the solum (Table 3-7). Pine/alder stands had a lower proportion of total inorganic P in Ca phophates (Ca-P) and tended to have a higher proportion in non-occluded Fe phosphates (Fe-P) and Al phosphates (Al-P) than other forest types. Spruce stands characteristically had a lower proportion of inorganic P in non-occluded Fe-P and Al-P than other stands. Acid ammonium fluoride extractable P was highly correlated with non-occluded Fe-P and Al-P ($r = .815, P < .01$) amd inversely correlated with Ca-P ($r = -.761, P < .01$) in a data set including individual horizon samples from all stands. The signficantly lower levels of ammonium fluoride P (Table 3-7) in soil under spruce stands relative to other soils is, therefore, consistent with the low levels of non-occluded P in spruce stand soils indicated by bulked sample analysis. Differences between forest types were observed in the weight of organic P in a 50 cm profile, with pine/lichen stand soils consistently lower and spruce stand soils consistently higher than other soils.

Redistribution of clay

The weight of clay redistributed in a 75 cm profile (Table 3-8), was highest in soils under spruce stands and lowest in those under pine/lichen stands and was highly correlated with total clay in the profile ($r = .978, P < .01$), although the significance of this correlation was dependent upon values from the spruce stand soils. The weight of clay added to a 75 cm profile during soil development was also highest in the spruce stand soils and lowest in pine/lichen stand soils. Clay addition was significantly correlated with total weights of silt and clay ($r = .943$ and $.961$ respectively, $P < .01$), and with weight of clay redistributed ($r = .973$ $P < .01$) but the significance of these correlations depended on values from the spruce stand soils. The ratios of clay added:original clay and clay added:silt+clay added were highest in the spruce stand soils and, in general, lowest in soils of the pine/lichen stands (Table 3-8).

Table 3-7. Chemical forms of phosphorus in soils under three forest types. Total inorganic P calculated as the sum of individual inorganic fractions. All values except acid NH_4F-P from analysis of bulked samples. Weights refer to a 50cm profile depth. Means followed by the same letter do not differ significantly ($P > .05$).

Stand	Forest Type	Total inorganic P	Ca-P	Non-occluded Fe-P	Occluded Fe-P	Organic P	Acid NH_4F P
		($g \cdot m^{-2}$)	---------% of total	-------------------	------------	($g \cdot m^{-2}$)	($g \cdot m^{-2}$)
1	pine/lichen	284	27	54	19	20.1	18.1a
2	"	232	30	53	17	25.1	16.6a
11	"	160	32	44	23	28.2	17.9a
12	"	167	35	39	26	25.5	15.8a
3	pine/alder	242	20	65	14	30.3	15.9a
13	"	212	22	56	20	33.1	20.7a
4	spruce	222	33	42	25	43.4	10.6b
14	"	167	35	33	31	41.1	8.2b

Table 3-8. Weight of constituents in a 75cm profile in each stand and calculated parameters relating to clay redistribution.

Stand	Total Soil ($g \cdot cm^{-2}$)	Silt ($g \cdot cm^{-2}$)	Clay ($g \cdot cm^{-2}$)	Mean Clay Content (%)	Clay Redistr. ($g \cdot cm^{-2}$)	Original Clay ($g \cdot cm^{-2}$)	Clay Added ($g \cdot cm^{-2}$)	Clay Added / Orig. Clay (%)	Clay Added / Silt & Clay Add. (%)
1	111.9	4.3	3.6	3.3	0.46	2.9	0.73	25.2	[illegible]5
2	108.1	6.0	3.7	3.4	0.34	2.8	0.84	30.0	12.3
11	106.3	2.3	4.0	3.8	0.41	3.4	0.77	22.6	25.1
12	115.3	6.1	5.2	4.5	0.42	5.0	0.23	4.6	3.6
3	107.2	7.4	6.3	5.8	0.52	4.7	1.54	32.7	17.2
13	92.2	7.6	5.2	5.7	0.66	3.8	1.44	37.8	15.9
4	102.2	12.7	10.4	10.1	1.04	7.1-7.9	2.5-3.2	35.2-40.5	16.5-20.1
14	95.3	16.8	15.2	15.9	1.58	10.0-11.9	3.3-5.2	33.0-43.3	16.4-23.6

3.4 Discussion

Uniformity of parent materials

Sand ridge soils in the Hondo area have developed from parent materials which were originally deposited as deltaic sediments in a glacial lake (St. Onge 1972) and have subsequently been modified by aeolian processes. These geomorphological processes may result in soil parent materials which differ with depth in the profile because of differences in timing and characteristics of deposition. Assessment of the uniformity of parent materials within the solum was necessary to permit accurate interpretation of soil profile development. Parent material uniformity is generally determined by comparing ratios of resistant minerals between horizons because such ratios can be expected to remain constant in uniform materials (Barshad 1955). In weakly weathered soils having sand fractions high in minerals resistant to weathering, such as quartz and potassium feldspar, the ratio of fine sand:total sand and the content of clay-free sand have been used as indices of parent material uniformity (Wang and McKeague 1982). Pawluk and Dudas (1982) found little evidence of weathering in a sandy aeolian soil near Edmonton which was similar in many respects to the Hondo area soils suggesting that the use of sand-based indices of uniformity is probably valid in the present investigation. There appear to be no established criteria for evaluating the constancy of fine sand:total sand ratios down a soil profile. In this study, ratios falling within a 10 % range were considered to indicate uniformity of parent materials. This value is consistent with the interpretation of fine sand:total sand ratios by McKeague and Wang (1982).

Based on uniformity of fine sand:total sand ratios, and a gradual increase in clay-free sand with depth, parent materials appeared to be uniform throughout the profiles of all soils under pine dominated stands with the exception of stand 11 in which the Ck differed from other horizons. Surface (A and B) horizons of spruce stand soils appeared to have developed from a uniform parent material but C horizons in both soils were distinctly different. The parent material in the lower part of the profile did not differ greatly in texture from that of the upper solum, however, and would not be expected to have influenced development of surface horizons. Comparison of lower soil horizons among stands indicated that the parent materials of spruce stand soils were finer in texture than those of other soils. Parent materials under pine/alder and pine/lichen stands were more coarse in texture because of their proximity to the river channel. Both spruce stands were located in areas at the periphery of the original deltaic deposit where sediments would be expected to be of finer texture than closer to the river channel because of differential sedimentation rates among particle sizes.

Clay distribution and addition

The uniformity of parent materials through the A and B horizons of all soils indicated that the increased clay contents of B relative to A horizons was the result of eluviation or *in situ* clay formation rather than initial deposition. The dominance of eluvial processes is supported by the micromorphological observations which identified anisotropic coatings and bridges between skeletal sand grains, diagnostic characteristics of illuvial horizons, in B horizons under spruce and pine/alder stands. Illuvial horizon development, as indicated by the difference in clay contents between eluvial and illuvial horizons and the frequency of anisotropic sand grain coatings in thin sections, was greatest in spruce stand soils, slight in pine/alder stand soils and almost negligible in pine/lichen stand soils. Calculated values of clay redistribution (Table 3-8) are consistent with this pattern.

Differences in illuvial horizon development between sites cannot be attributed unequivocally to differences in forest type because of differences in parent material texture among soils. Although several factors which influence clay translocation have been identified, controls on the degree of development of illuvial horizons are poorly understood (Birkeland 1974). Clay translocation may be higher in a soil with a high clay content than in one low in clay simply because more clay would be available to be translocated. Alternatively, clay eluviation may be regulated by water flow and clay dispersion processes related to organic compounds entering the soil (Bloomfield 1957) or wetting/drying cycles (Soil Survey Staff 1975). Clay translocation would then be expected to be more dependent on factors such as vegetation, which control soil climate and organic matter production, than on total clay content. Detailed examination of sites differing in vegetation but with more similar parent material textures will be necessary to determine the relative role of vegetation and clay content in controlling eluviation in these soils.

Clay addition followed a pattern among stands similar to that of clay redistribution and illuvial horizon development, being highest in spruce and lowest in pine/lichen stands. Increases in total clay in soil profiles in New Brunswick examined by McKeague and Wang (1982) were attributed to clay formation during pedogenesis while Pawluk and Dudas (1982) concluded that aeolian drift had caused the increase in clay observed in a profile near Edmonton. Although the Hondo soils are similar to the soil studied by Pawluk and Dudas (1982), the results of this study are inconsistent with addition of clay by aeolian drift. Calculated additions differed between stand 13 and stands 1 and 2 even though they are located within 1 km of each other and would thus be expected to have received similar additions by drift. However, formation of crystalline clay or of clay-sized non-crystalline material would be expected to be low in weakly weathered soils under boreal climate conditions. Detailed physical and mineralogical analyses are required to distinguish between the possible processes which have resulted in addition of clay to these soil profiles. If the observed increases in clay relative to predicted values are the result of clay formation, controls on this process are confounded by the parallel patterns of soil texture and vegetation. Higher concentrations of C and secondary Fe and Al in soils under spruce imply that these stands may produce a soil environment high in organic matter which increases the rate of mineral weathering and, potentially, clay formation. Conversely, weathering and clay formation would be expected to be higher in fine than in coarse textured soils because of the higher surface area available for weathering. The ratios of clay added:original clay and clay added:silt+clay added suggest that clay addition relative to original parent material texture differed among forest types implying, at least, a contributory influence of vegetation.

Phosphorus, iron and aluminum chemistry

Soil characteristics related to the chemical consitituents of P, Fe and Al can be expected to be independent of soil texture so that their interpretation relative to vegetation is more straight forward. Both P and Fe are essential nutrients and their dynamics in soil must therefore be controlled, in part, by cycling through vegetation. In addition, Fe and Al are highly reactive with various organic compounds and are closely linked to organic matter in many soil processes, such that differences in these soil components might be expected to relate to differences in vegetation. The results of this study suggest that secondary Fe and Al compounds occur in higher concentration and are eluviated to a greater degree in soils under pine/alder and spruce stands than in pine/lichen soils. In spruce stand soils, Al-P and Fe-P appear to be depleted relative to other soils while in soils of pine/alder stands, Ca-P appears to be depleted. Whether these patterns are related to P or Fe cycling patterns which are specific to these vegetation types is unknown at present and warrants further investigation.

In conclusion, sand ridge soils in the Hondo area differ with respect to content and distribution of clay, secondary iron and aluminum and phosphorus compounds within the solum. Differences between soils in several of these properties appear to reflect differences in vegetation between sites. Changes in most soil physical and chemical properties are considered to be slow processes such that differences in soil development only result when differences in site conditions have been maintained over an extended period. The observed correlations between forest type and soil characteristics are therefore consistent with the age structure data, suggesting that vegetation patterns in the Hondo area landscape have been relatively stable over time. Further research is necessary, however, to clarify relationships between vegetation, soil texture, and the development of illuvial horizons in these soils and to identify functional differences between vegetation types which have led to the observed differences in soil properties among sites.

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4. LITTER PRODUCTION IN PINUS BANKSIANA-DOMINATED STANDS IN NORTHERN ALBERTA[1]

4.1 Introduction

Litter production in terrestrial ecosystems represents one of the primary links between producer and decomposer organisms in studies of organic matter and nutrient cycling, and is one of the few system fluxes which can be accurately measured. In boreal forest ecosystems, litterfall rates have been reported by various authors both in individual studies of specific forest types (Foster 1974, Cragg *et al.* 1977, Malkonen 1977, Flower-Ellis and Olsson 1978, Van Cleve *et al.* 1981, Gordon 1983, Van Cleve *et al.* 1983) and in syntheses of data on a global scale (Bray and Gorham 1964, Cole and Rapp 1981). To date, no litterfall data specific to boreal regions in Alberta have been published.

In general, litter data have been presented as annual production rates, often with broad divisions into functional litter-types (foliage, bark, branches etc.). Very few studies (Bray and Gorham 1964, Flower-Ellis and Olsson 1978) have provided data on the contribution of individual species or specific litter types to total litter production rates. In addition, seasonal patterns in litter production have seldom been reported. While measurements of annual transfer of litter in broad categories are required and appropriate for the construction of nutrient budgets, more detailed information is necessary when considering the ecological behavior of individual species and their role in the community and ecosystem. Plants may control nutrient fluxes in litter through the allocation of nutrients during growth and their resorption prior to litterfall. The extent to which plant physiological processes can influence general nutrient cycling patterns depends on the relative importance of physiological and environmental factors in controlling the rate and timing of litter production.

This paper describes litter production over a one to two year period in 12 jack pine (Pinus banksiana Lamb.) and 2 white spruce (Picea glauca (Moench) Voss) stands located in two areas of northern Alberta. The specific objectives of the study were: 1) to determine

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production rates of photosynthetic, reproductive and structural litter and the relative contribution of different species and litter components to total litterfall; 2) to examine controls on litterfall through correlation of production rates with stand characteristics; and 3) to interpret seasonal patterns in litter production with respect to possible controls on litterfall within stands.

4.2 Study Area

Data were collected from seven stands located in the Hondo-Slave Lake area (HSL) of north-central Alberta and from eight stands in the Athabasca Oil Sands area (AOS), in northeastern Alberta. Both study areas are found within the Boreal Mixedwood Section of Rowe (1972). Characteristics of the monitored stands are summarized in Table 4-1.

The seven stands in the HSL area are located in an area of sand ridges with interspersed wetlands, (55° 00'-10' N; 114° 00'-15' W) adjacent to the Athabasca River and about 55 km southeast of the town of Slave Lake. The sands originated as fluvial deposits in post-glacial lakes (St. Onge 1972) and have subsequently been modified by aeolian processes.

The upland vegetation of this area is a mosaic of open jack pine/lichen woodland, closed canopy jack pine or trembling aspen (Populus tremuloides (Michx.)) forest and scattered stands of white spruce with pine and aspen. Among the stands monitored in this study, four (HSL1, 2, 11, 12) represent the open woodland type dominated by jack pine with a shrub layer composed mainly of bearberry (Arctostaphylos uva-ursi (L.) Spreng.), lingonberry (Vaccinium vitis-idaea L.) and blueberry (Vaccinium myrtilloides Michx.) with occasional green alder (Alnus crispa (Ait.) Pursh.). Ground cover is strongly dominated by lichens, particularly Cladina mitis (Sandst.) Hale & W. Culb. Small white spruce are occasionally observed in stands of this type. HSL3 represents a closed canopy jack pine forest with a well-developed shrub canopy of green alder and a continuous feathermoss groundcover dominated by Pleurozium schreberi (Brid.) Mitt.. Scattered, subdominant or suppressed white and black (Picea mariana (Mill.) B.S.P.) spruce occur in this stand. Mixed pine-spruce forest is represented by HSL4 and 14. In HSL14 white spruce and jack pine form a codominant tree

Table 4-1. Vegetation type and age and structural characteristics of the tree stratum in the fifteen monitored stands.

Stand	Stand Type	Age	Basal Area				Density				Tree BA Increment	
			Pine	Spruce	Aspen	Fir	Pine	Spruce	Aspen	Fir	Pine	Spruce
		(yr)	--------(m^2ha^{-1})--------				--------(#ha^{-1})--------				($cm^2tree^{-1}yr^{-1}$)	
HSL1	Pine/bearberry/lichen	45	11.9				924				2.862	
HSL2	Pine/bearberry/lichen	65	20.3				736				4.243	
HSL3	Pine/alder/feathermoss	85	33.3	0.9			1016	124			3.856	0.854
HSL4	Spruce/fir/pine/feathermoss	140	3.5	28.7	2.1	4.2	28	716	52	421	8.929	2.863
HSL11	Pine/bearberry/lichen	40	17.8				1216				3.660	
HSL12	Pine/bearberry/lichen	85	27.9	0.1			660	72			4.973	0.163
HSL14	Spruce/pine/feathermoss	80	17.4	18.3	4.[illegible]		272	2368	336		7.996	0.996
AOS3	Pine/bearberry/lichen	41	11.7				1004	4			2.842	
AOS3N	Pine/bearberry/lichen	37	9.9				1604				1.668	
AOS4	Pine/bearberry/lichen	38	9.4				1068				2.316	
AOS4N	Pine/bearberry/lichen	75	18.4				1184				2.072	
AOS5N	Pine/black spruce/feathermoss	131	16.8	1.6			608	128			2.107	0.954
AOS8	Pine/bearberry/lichen	38	6.3				712				2.323	
AOS10	Pine/bearberry/lichen	75	20.1				1604				1.671	
AOS15	Pine/black spruce/feathermoss	39	20.9	0.1			1944	8			2.757	0.321

canopy along with scattered aspen. The shrub layer consists only of scattered low shrubs including Lonicera involucrata (Richards) Banks and Viburnum edule (Michx.) Raf. with a few young balsam fir(Abies balsamea (L.) Mill.). The feathermoss groundcover is almost continuous, being composed mainly of Hylocomium splendens (Hedw.) B.S.G. and Pleurozium schreberi. The tree canopy of HSL4 consists primarily of white and occasionally black spruce, with scattered aspen and paper birch (Betula papyrifera Marsh.). Balsam fir forms a well-developed sub-canopy. As in HSL14, the shrub layer is poorly developed while the groundcover of feathermoss is extensive.

Soils of the HSL area have developed from aeolian parent materials and are predominantly orthic and eluviated dystric brunisols. Orthic and brunisolic gray luvisols occur in some locations.

The eight stands of the AOS area are located on a lowland plain east and west of the Athabasca River (57°-58° N; 111° 10'-30' W) 30-120 km north of Fort McMurray. Six of the stands are found on sandy outwash materials modified by aeolian processes while the remaining two stands occur on glacial till.

The vegetation of the AOS area, similar to that of the HSL area, is comprised of a mosaic of upland forest among wetland fen, bog and bog forest. Upland areas are predominantly open jack pine/lichen woodland with areas of more closed-canopy forest and trembling aspen or mixed pine and aspen stands. The six stands with sandy soils (AOS-3, 3N, 4, 4N, 8, 10) are typical of the open woodland type with Pinus banksiana tree canopy, a dwarf shrub layer of bearberry, lingonberry, and blueberry and an extensive cover of Cladina mitis. The two stands on glacial till represent jack pine-dominated forest in which black spruce forms a strongly (AOS5N) or weakly (AOS15) developed subcanopy. The shrub layer is dominated by Labrador tea (Ledum groenlandicum Oeder) and Pleurozium schreberi forms an extensive groundcover. Soils of the AOS stands are predominantly eluviated dystric brunisols.

4.3 Methods

The plot layout used in stands HLS1-4 and the AOS stands consisted of a 50 x 50 m macroplot divided into 5 x 5 m plots with alternate rows designated for sampling. Ten plots were randomly selected and equipped with a 0.5 x 0.5 m wood and fiberglass screen (2 mm mesh) litter trap, positioned in the center of the plot, 0.3 m above the forest floor. The plot layout in stands HSL11, 12, and 14 consisted of a 25 x 25 m area with 10 traps positioned at random locations. Traps in AOS4 and AOS8 were repeatedly destroyed by bears and were replaced in mid-summer with 0.1 m^2 traps made from steel drums.

Litter was collected from traps at monthly or biweekly (AOS stands, September and October) intervals during the snowfree season. Traps were placed on the ground prior to the first snowfall and emptied the following spring to measure litter production during winter. Litter was monitored on a May to May annual cycle, 1982-1984 in HSL1-4 and 1983-1984 in the other 11 stands.

Once collected, the litter was oven-dried at 65°C and sorted, prior to weighing, into foliage by species, male cones, and structural material. The structural category combined bark, twigs, and attached lichen. Branches larger than 1 cm diameter were not collected because small litter traps were considered to be inappropriate for measuring the production of such large litter. Female cones were separated and excluded from the litter because, in many cases, this material had been deposited in the trap by squirrels and did not represent actual litterfall. The fine particulate bark and insect frass generally passed through the mesh of the traps and therefore could not be measured. Small amounts of large particulate frass were excluded prior to weighing. All individuals of each tree species in each stand were counted and measured (dbh) to allow calculation of density and basal area. Dominant trees were aged by coring 30 cm above the base. Mean annual basal area increment was calculated on an individual tree (BA/Density/Age) basis. Litterfall was calculated on the basis of stand area and tree basal area (litter weight/BA, foliage litter by species). Daily litter producton rates were calculated by dividing the weight of litter collected in a given collection period by the number of days in the period.

Preliminary data analysis revealed considerable variation in homogeneity of variance and normality among stands and litter types, such that parametric statistics could not be uniformly applied throughout the data set, even with transformations. In order to ensure uniformity of criteria among analyses, the Kruskal-Wallis nonparametric analysis of variance and the multiple comparison technique of Conover (1980) were used. Simple linear correlation (Zar 1974) was used to correlate litter production with stand variables because assumptions of parametric tests were met by these data.

Most data have been presented as median values rather than means because many of the data sets were markedly skewed by the patchy distribution of vegetation within stands (e.g. alder clumps in HSL1 and 2). In data sets with normally distributed observations, the median will equal the mean, while in skewed sets, the median is more descriptive of the field situation as it is less sensitive to extreme values.

4.4 Results

Annual litter production in the HSL and AOS stands ranged from 42 to 344 g m^{-2} with mean production in 1983 equaling 147 g m^{-2} (Table 4-2). Foliage litter predominated, representing 62% to 96% of total litterfall. In stands with an alder shrub canopy, alder leaves made up less than 15% of total foliage litter despite high abundance of this species in HSL3. Male cones had a maximum contribution of 12% of total litter and averaged much lower (4%). Structural litter, including bark, twigs and associated material, made up, on average, 15% of the total but represented as much as 35% in some cases.

Summer weather condtions differed markedly between the two years monitored with May-June rainfall in 1982 less than 25% of normal and June-July rainfall in 1983 more than three times normal. These differences in weather conditions may have been reflected in the general increase observed in pine needle and structural litter production between 1982 and 1983. Parallel increases were not observed in foliage litter from other species.

Litter production was significantly correlated with stand or species basal area (pine needle litter vs pine BA $r=0.81$ $p<0.01$; spruce needle litter vs spruce BA $r=0.99$ $p<0.01$;

Table 4-2. Median annual production of different litter types in [illegible] monitored stands. Within each litter type stands with the s[illegible] following d[illegible] not differ significantly (P>.05).

Stand	Pine	Spruce	Fir	Aspen	Alder	Foliage	Male Cones	Structural Material	Total
					gm^{-2}				
HSL3-83	184.7a	0.1cd	0.0b	0.0c	19.2a	220.3a	11.6abc	106.7a	344.4a
HSL4-82	3.7gh	135.0a	23.2a	6.2bc	0.0e	196.4ab	13.4ab	34.2abcde	[illegible]
HSL14	95.1de	78.1b	0.0b	25.7a	0.0e	215.4ab	4.0efg	37.5abc	[illegible]
HSL4-83	2.6h	93.8ab	30.1a	11.4b	0.0e	136.0bc	7.7cd	53.7ab	[illegible]
HSL12	180.7ab	0.0d	0.0b	0.0c	0.0e	180.8bc	6.1de	42.4abcd	[illegible]
HSL2-83	133.1bc	0.0d	0.0b	0.0c	2.9abc	143.1c	5.9de	[illegible]	[illegible]
HSL3-82	108.9cd	0.0d	0.0b	0.0c	18.7ab	133.0cd	13.6a	[illegible]	[illegible]
HSL11	139.2abc	0.0d	0.0b	0.0c	0.0e	139.2c	2.3hi	[illegible]	[illegible]
HSL1-83	124.2cd	0.0d	0.0b	0.0c	0.2bcd	125.3cd	3.5fgh	[illegible]	[illegible]
HSL2-82	90.8de	0.0d	0.0b	0.0c	3.2abc	95.1de	8.1bcd	[illegible]	[illegible]
HSL1-82	108.9de	0.0d	0.0b	0.0c	0.2cd	114.7de	4.8ef	[illegible]	[illegible]
AOS3	77.3ef	0.0d	0.0b	0.0c	0.0d	80.6ef	5.0efg	[illegible]	[illegible]
AOS5N	70.4ef	7.3c	0.0b	0.0c	0.0e	77.7efg	3.9fghi	17.1ef	[illegible]
AOS10	83.0ef	0.0d	0.0b	0.0c	0.0e	83.0ef	2.9ghi	[illegible]	[illegible]
AOS4	75.0ef	0.0d	0.0b	0.0c	0.0e	75.0efg	0.3j	[illegible]	[illegible]
AOS4N	62.1fg	0.0d	0.0b	0.0c	0.0e	62.1fg	1.5ij	[illegible]	[illegible]
AOS3N	69.7fg	0.0d	0.0b	0.0c	0.0e	69.7fg	1.2ij	[illegible]	[illegible]
AOS15	65.8fg	0.0d	0.0b	0.0c	0.0e	65.8fg	1.0ij	[illegible]	[illegible]
AOS6	38.3gh	0.0d	0.0b	0.0c	0.0e	38.3g	[illegible]	[illegible]	[illegible]

total, male cone, structural litter vs total BA $r=0.69-0.83$ $p<0.01$). As a result, values of litter weight expressed in relation to basal area (kg litter m^{-2} BA) generally fall within a narrow range (Table 4-3). Litterfall per square meter basal area was not correlated with stand density or age. The abnormally high value for structural litter in HSL3 probably reflects the action of the July 1983 hailstorm which affected only this stand. Values for pine and male cone litter in this stand do not differ greatly from those of other stands indicating that the storm affected only structural litter. The low values of litter m^{-2} BA obtained for pine and aspen foliage in HSL4 suggest that the productivity of these large old trees is very low relative to the codominant spruce, implying that pine and aspen may be dying out of this stand. In pine, this effect does not appear to be strictly related to age because pines in AOS5N, which are of similar age to those in HSL4, have much higher litter m^{-2} BA values.

Seasonal variation in litter production is described by daily litterfall rates (Figure 4-1). Patterns shown for each litter type are typical of all stands with one exception (AOS 4, needle litter). As expected, the deciduous species (alder, aspen) showed marked seasonality in foliage litter production, with high rates of litterfall observed only in the autumn. Among the coniferous species, pine and spruce also had distinctly seasonal patterns, with litterfall rates being significantly higher in the autumn than at other times of the year. Among several studies on European coniferous forests reviewed by Bray and Gorham (1964) seasonality in litter production was commonly observed in pine (Pinus) species but was not observed in spruce (Picea). Foliage litter production by balsam fir (HSL4) differed from that of the other conifer species in that production rates did not differ significantly between sampling dates over the two year period.

Production of male cone litter followed a regular, predictable pattern with observed rates being high in the spring and diminishing as the seasons progressed, to low levels in fall and winter. Bark and twig litterfall appeared to have no consistent pattern among sites or across seasons. The high daily rate of structural litter production in July 1983 in HSL3 reflects the influence of local storm activity during that month as indicated above.

Table 4-3. Annual production of foliage litter expressed relative to basal area of each species and male cone and structural litter expressed relative to total stand basal area.

Stand	Pine	Spruce	Aspen	Cones	Structural Material
	kg BA m^{-2}				
HSL1	104.4			2.9	6.9
HSL2	65.7			2.9	11.5
HSL3	55.5	1.1		3.4	31.1
HSL4	7.4	32.7	2.9	2.0	13.9
HSL11	78.2			1.3	5.6
HSL12	64.8			2.2	15.1
HSL14	54.7	42.7	62.7	1.0	9.4
AOS3	66.1			4.3	11.5
AOS3N	70.4			1.2	7.4
AOS4	79.8			0.3	7.2
AOS4N	33.8			0.8	10.8
AOS5N	41.9	45.6		2.1	9.3
AOS8	60.8			0.2	1.1
AOS10	41.3			1.4	4.9
AOS15	31.5			0.5	4.8

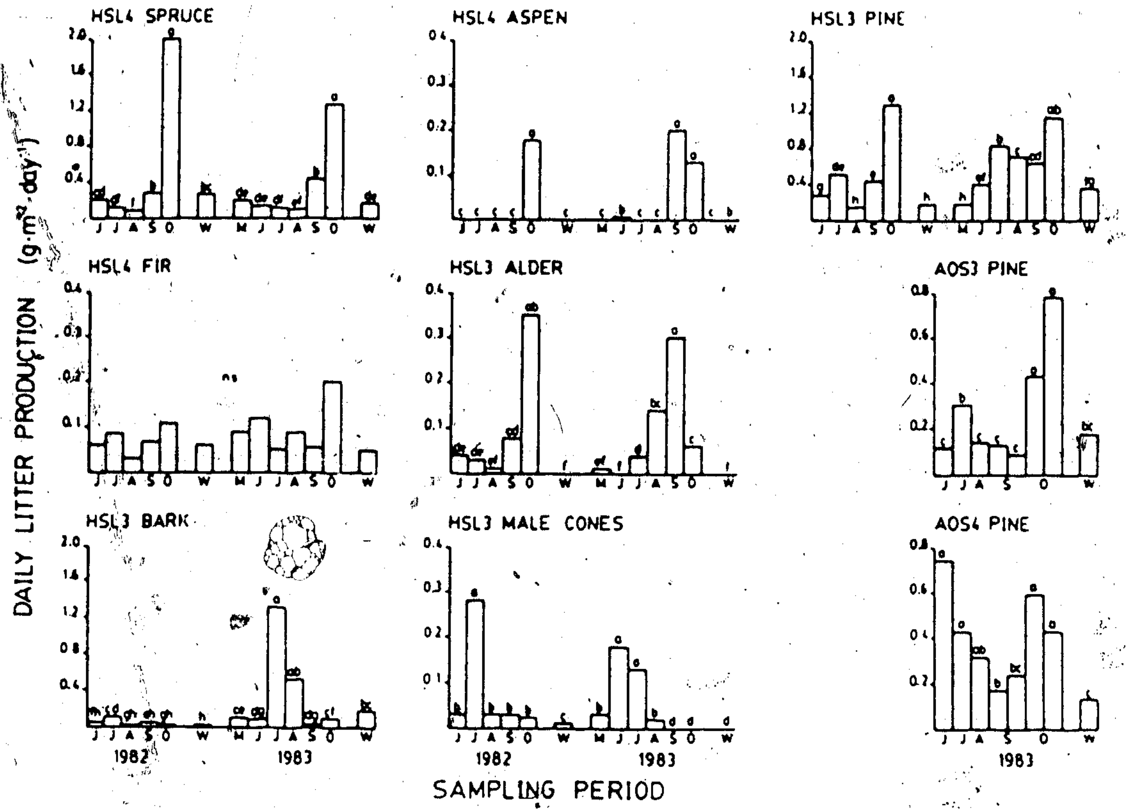

Figure 4-1. Daily production of various litter types by sampling period in selected stands. W denotes the winter period. Periods with the same letter do not differ significantly ($P > 0.05$). Nonconsecutive letters indicate an inclusive range.

Stand AOS4 was remarkable for its lack of seasonality and atypical pattern of foliage-litter production (Figure 4-1). During the sampling season it was observed that this stand was undergoing a severe infestation of bark beetle. Insect-induced stress probably accounts for the unusual pattern of needle litterfall. Production of male cone and bark litter did not appear to be similarly affected.

4.5 Discussion

Litter production in coniferous forests of the boreal region of western Canada has not been reported in the literature. Comparative data, however, are available from boreal forests of Alaska and Sweden. The litterfall rates of 95-136 g m^{-2}yr^{-1} measured in upland white spruce stands in central Alaska (Van Cleve *et al.* 1983) are within the range of our Alberta data, as are the rates obtained from many upland deciduous and lowland coniferous forests in the same area (Van Cleve *et al.* 1983, Van Cleve and Noonan 1975), despite the large difference in latitude. Litterfall rates in Scots pine (Pinus sylvestris L.) stands in Sweden ranged from 58-170 g m^{-2}yr^{-1}, very similar to the range observed in our jack pine/lichen stands (Flower-Ellis and Olsson 1978).

The central Ontario jack pine stand examined by Foster (1974) was located in the Great Lakes-St. Lawrence Forest Region (Rowe 1972) at a latitude of 46° N. While not strictly boreal, this stand was similar to HSL3, growing on sandy soils with a jack pine canopy and feathermoss forest floor but without green alder. The central Ontario stand produced more litter (370 g m^{-2}yr^{-1}) with half the basal area of HSL3, suggesting that higher litter production is to be expected in milder hemiboreal than in southern boreal climates, despite close similarities in stand composition. Similarly, Perala and Alban (1982) found that jack pine plantations with basal areas similar to HSL3 and growing on sandy and loamy soils in Minnesota (lat. 47° N) produced twice as much litter as HSL3 annually (530-620 g m^{-2}yr^{-1}). These data are consistent with the general increase in litterfall biomass with decreasing latitude observed by O'Neill and DeAngelis (1981) and Van Cleve *et al.* (1983).

Litter production varied widely among northern Alberta jack pine stands with over an eight-fold difference between stands of lowest and highest productivity. Much of this variation could be attributed to differences in basal area among stands. In tree species of the Mixedwood Section, basal area is directly proportional to the biomass of various tree components including that of small branches plus foliage (Singh 1982). Observed relationships between litterfall and basal area probably reflect the control of stand biomass on litter production. Ultimately, therefore, differences in litter production among stands must arise from differences in climatic and site factors which control plant growth and overall stand productivity.

The relationships between litterfall and basal area suggest that the contribution of an individual species to total litter production in a mixed stand is related to its proportional contribution to stand basal area. The relative importance of species in a mixed stand depends largely on interspecific interactions during stand growth and ecology of the species involved. This is illustrated by HSL14 in which the contribution of jack pine to total stand litterfall and basal area is high, despite the low density of this species, because of the high mean growth rate (annual BA increment) of individual jack pine in this stand (Table 4-1). This high growth rate is probably the result of lack of competition with slower growing spruce early in stand history and it is likely that the relative contribution of jack pine to total litterfall was higher when the stand was younger. Similarly, although the present contribution of green alder to litterfall in HSL1, 2 and 3 is relatively small, because this species sprouts from root stocks after fire while jack pine must establish from seed (Heinselman 1981), the relative contribution of this species was probably higher in younger stands. Thus, detailed examination of growth rates of species in mixed stands can provide information which are of value in understanding long-term litterfall and organic matter dynamics.

Seasonal patterns in daily litter production rates provide insight into the factors which control litterfall within a stand on a seasonal or annual basis. Structural litter production followed no distinct pattern but, on some occasions, was clearly influenced by weather conditions. This suggests that bark litterfall, was primarily controlled by random processes such as storm activity. The pattern of foliage litter production outside the autumn period was similar to that of bark and twigs but, in many cases, daily litterfall rates were much less variable between months. In addition, foliage litter did not appear to be strongly influenced by storm activity. This implies that the controlling factors were much less random, perhaps implicating chronic, low-level herbivory or disease activity. If such factors are active, leaf abscission may represent a protective plant response. Winter foliage litterfall may be affected by snow or ice loading but the significance of these factors could not be independently determined.

The high autumn litter production rates observed in all species except balsam fir indicate that a proportion of foliage litterfall, typically 30-50% of annual foliage litter, is not controlled by random events, but by predictable, seasonal physiological changes which occur in individual plants. A similar situation is apparent in the pattern of male cone litterfall which was high only in the early summer following pollen release. The lack of a distinct autumnal peak in foliage litter in insect-infested AOS4 suggests that the controlling physiological conditions can be altered by external stress. It is possible that the lack of seasonality in fir needle litter in HSL4 is indicative of a stressed condition in the fir trees which may be subjected to adverse light or moisture conditions because of their subcanopy position beneath the dense crowns of the dominant white spruce. In this situation, seasonal patterns might be overridden by physiological processes (e.g. carbon, nutrient allocation) involved in maximizing the utilization of resources distributed unevenly in space or time. The tendency toward an autumn peak in fir litterfall in 1983 (Figure 4-1), a year in which water stress would be minimized by high rainfall, may support this contention. It would be interesting to measure seasonal litterfall in stands in which fir formed the dominant canopy to determine whether the aseasonality in litter production related to its stressed subcanopy position. If litter production patterns reflect the general physiological state of plants as influenced by individual stress factors as well as by synergistic effects among factors, monitoring of litterfall and calculation of daily litter production rates may provide a means of detecting the impact of man-made stresses, such as pollutants, on forest stands. Such monitoring would necessarily be long-term in nature in order to accomodate cyclic processes such as pollen or seed cone production.

We recognize that short-term litterfall monitoring can provide only approximate estimates of production rates because the full range of annual variablility in weather conditions cannot be sampled adequately in only a few years. In addition, relationships between litterfall and longer term cyclic processes such as leaf turnover or cone production cannot be identified during short monitoring periods. Although the present study was short in duration, the general conclusions are based on a large and structurally and geographically diverse group of stands and thus are probably regionally applicable. The results suggest that differences in litter production between jack pine stands in northern Alberta relate primarily to differences in basal area and, by implication, stand biomass. These parameters are controlled by stand age and climatic and site factors which determine stand productivity. Within a stand, controls on litterfall differ among litter components. Structural litterfall is controlled by random processes associated primarily with weather. In contrast, foliage and male cone litterfall appear to be mainly under plant control, representing responses to seasonal changes in physiological state or to pathogen activity. The cycling of organic matter and nutrients through plant litter, and the characteristics of accumulated organic matter on the forest floor therefore potentially reflect physiological characteristics of the species which dominate a stand.

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5. DECOMPOSITION OF BOREAL FOREST LITTERS FROM CENTRAL ALBERTA UNDER LABORATORY CONDITIONS[1]

5.1 Introduction

Decomposition of litter in boreal forest ecosystems directly or indirectly affects a variety of ecosystem and community processes. The cycling of organic nutrients (N, S, P), and site fertility in general, are strongly influenced by the rate of litter decomposition and concomitant nutrient release (Melillo and Gosz 1983). Rates of litter production and decomposition control the accumulation of fire fuels on the forest floor, and therefore influence the susceptibility of a stand to fire and fire intensity (Rowe and Scotter 1973). The regeneration of boreal forest stands depends upon sprouting of plants from rhizomes, germination of seeds from the forest floor seed bank, and establishment of seedlings from post-fire seed fall (Heinselman 1981), all of which are dependent to a large degree on pre- and post-fire forest floor accumulations and thus on litter decomposition rates.

While decomposition processes are primarily controlled by climatic conditions, specifically temperature and moisture availability, the chemical composition of litter is known to be a strong modifying factor (Swift *et al.* 1979). Decomposition rate has been found to be correlated with lignin content, C:N ratio, Ca, P (Van Cleve 1974), lignin:N ratio (Melillo *et al.* 1982), soluble carbohydrates (Moore 1984) and tannins or other polyphenolic compounds (Swift *et al.* 1979).

This laboratory study of litter decomposition was conducted as part of a broader investigation of the ecological relationships among three forest stand types which commonly occur on sandy soils in the Hondo-Slave Lake region of north-central Alberta. The forest types under investigation are: 1) open jack pine/lichen woodland dominated by Pinus banksiana Lamb., with a sparse dwarf shrub layer of Arctostaphylos uva-ursi (L.) Spreng. and Vaccinium vitis-idaea L. and an extensive ground cover of fruticose lichen, primarily Cladina mitis (Sandst.) Hale and W. Culb.. ; 2) closed jack pine forest with scattered white

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[1] A version of this chapter has been submitted for publication. Fyles, J.W. and W.B. McGill. Canadian Journal of Forest Research.

spruce (Picea glauca (Moench) Voss), a continuous tall shrub layer of green alder (Alnus crispa (Ait.) Pursh.) and a feathermoss groundcover dominated by Pleurozium schreberii (Brid.) Mitt..; and 3) mixed pine/spruce forest with codominant Picea glauca and Pinus banksiana, a well developed subcanopy of balsam fir (Abies balsamea (L.) Mill.) and a continuous feathermoss ground cover dominated by Hylocomium splendens (Hedw.) B.S.G.

The objectives of the study were: 1) to determine whether litter from the dominant species in these stands decomposed at different rates under controlled conditions; 2) to identify chemical characteristics of litter which controlled decomposition rates; and 3) to try to relate any observed differences in decomposition rates to the structure and function of the forest stands under study and the ecological roles of individual species within them.

5.2 Methods

Pine, white spruce, fir and alder foliage litter were collected in wood and screen litter traps during September and October 1983 and oven-dried at 60°C for storage prior to the study. Pleurozium, Hylocomium, and Cladina were collected from the ground in appropriate stands during the same period and sorted to remove vascular litter and attached, previously decomposed, parts of the collected plants. Since bryophytes and lichens are known to be resistant to severe desiccation and might, therefore, remain alive for some time into the decomposition study, the bryoid material was autoclaved for 30 minutes prior to oven-drying and storage. This material therefore was not litter in the strict sense but was plant material killed by autoclaving rather than by natural senescence. It was assumed that bryophytes and lichens, which lack well-developed vascular tissue, would not be capable of translocating nutrients out of senescing tissue so that natural litter would not differ greatly from killed tissue. An additional litter type was prepared by cutting pine needles into 1 cm sections in order to observe the effect of comminution on decomposition. Samples of each litter type were soaked in distilled water for one hour, allowed to drain freely and weighed to calculate a wet moisture content which could be maintained during the incubation.

Five or ten samples (± 2 g), were drawn from mixed containers of each litter type and weighed to the nearest 0.1 mg. Each sample was placed in a 7 cm diameter plastic cup containing 100 g of sand obtained from the soil B horizon of one of the litter collection sites. Seven cups containing sand but no litter were used as controls. The sand was used to support the litter while providing a reservoir to buffer moisture fluctuations in the litter during the incubation. Each sample was innoculated with 10 ml of a soil suspension (5:1 distilled water:forest floor, filtered through 2 mm mesh and glass wool), to ensure uniformity of decomposer populations among samples. An amount of water equivalent to that required to bring the litter to its wet weight and the sand to field capacity was added to each cup. Each cup was covered with a thin polyethylene sheet perforated with small holes to maintain humidity. Distilled water was added twice weekly in a fine spray to maintain wet weight.

The samples were incubated in the dark at 23 ± 1°C for seven, five week periods to give a total decomposition time of 35 weeks. At the end of each period, the cups were air-dried at room temperature and then allowed to equilibrate in a sealed cabinet over saturated $CaCl_2$ solution (32.5% relative humidity (Slavik 1974)) prior to weighing to the nearest 0.1 mg. The litter usually dried within 24 hours but a three week period was required to obtain adequate drying of the sand and equilibration at constant humidity. Oven-drying at elevated temperatures would have speeded the process but would have subjected microbial populations to unna[illegible]l desiccation. It was assumed that decomposition was negligible during the drying period. After weighing, the samples were remoistened gradually, using distilled water added in a fine spray to allow the water to soak into the litter.

The P3R non-linear least squares regression of the BMDP statistical analysis package (Dixon 1983) was used to fit decay equations to weights obtained at the end of each five week incubation period for each sample. In its general form, the equation used was:

$$A_t = A_{01}e^{kt} + A_{02}e^{kt} + A_{03}e^{-kt} \ldots \qquad [1]$$

in which A_t is the percent of the litter remaining at time t. The right side of the equation represents a series of components, each having an initial ($t=0$) concentration (A_0) in the litter and having a unique decomposition rate constant (k). In the simplest case decomposition of a homogeneous substrate is described by a one component model (Olson 1963):

$$A_t = A_0 e^{kt} \qquad [2]$$

In this study, equations with more than two terms could not be fit to the data probably because of the small number of data points per sample. Therefore, only one and two component (single and double exponential) models have been discussed. The use of these and other mathematical equations to model litter decomposition has been reviewed by Wieder and Lang (1982). The residual sums of squares (RSS) calculated using the two equations were compared to determine their relative goodness of fit to the data.

Simulated data were used to determine whether experimental error in data representing simple exponential decay, could have increased the RSS of the one component model relative to that of the two component model and lead to incorrect conclusions regarding the relative fit of the models. The single component equation [2], with a rate constant chosen from within the ranges of those obtained from the experimental data ($k = 0.05$ wk^{1}), was used to generate the simulated data sets. Error was introduced by calculating percent weight remaining (A_t) for the time intervals used in the incubation and adding a randomly determined residual to each value. The residuals were normally distributed with a mean of zero and a standard deviation of 1, 3 or 5%. One hundred simulated samples were generated and a two component model was fit to each data set. Equation parameters, correlations between parameters and residual sums of squares were compared between the two component equations of the experimental and the simulated data.

Rate constants were compared using the procedure for comparison of slopes and the Newman-Kuels multiple range test described by Zar (1974) to test for differences among the slopes (k) of linearized one component equations (ln(% weight remaining) vs time). Comparison among litters and within litters among time periods used hierarchical and simple designs respectively. Simple linear correlation was used to correlate rate constants with litter characteristics.

Chemical analysis of litter was carried out as follows: total carbon by dry combustion using a LECO automatic C analyser (McKeague 1978); total N using a sulfuric acid/peroxide digestion (Thomas *et dl,* 1967) followed by NH_4^+ determination using standard autoanalyser techniques (Technicon Industrial Method #334-74W/B+ 1977); soluble tannins using the Folin-Denis reagent and a tannic acid standard (Allen *et al.* 1974); and lignin following Effland (1977).

5.3 Results

Most litter types followed the expected curvilinear pattern of weight loss over the 35 week incubation period (Figure 5-1), with the exception of Cladina which appeared to have an initial time lag before the onset of rapid weight loss. The one component model, describing simple exponential decay [2], fit well to data from all litter types, including Cladina, giving mean coefficients of determination (r^2) of 0.900-0.983 (Table 5-1). The mean rate constants (k) calculated using this model ranged from 0.0044 wk^{-1} for Pleurozium to 0.0118 wk^{-1} for Cladina with no discernible pattern relating to natural groupings of litter types (e.g. vascular vs nonvascular). Values of the equation coefficient (A_0) (Table 5-1) were approximately equal to 1.0 in all litter types as would be expected in a model which describes a homogeneous substrate which is all decomposing at the same rate.

The litter types used in this study represented a wide range of litter quality which was expected to be reflected in decomposition rates. However, no significant correlation was found between k and any of the chemical parameters measured (Table 5-1). Although the correlation between k and lignin:N ratio (Figure 5-2) was non-significant when all points were considered, a significant correlation, ($r = .940$, $p<.001$), was obtained when the coniferous needle litter data were excluded. Relative to the other litter types, the decomposition rate of coniferous litters was higher than would have been predicted by their lignin:N ratio.

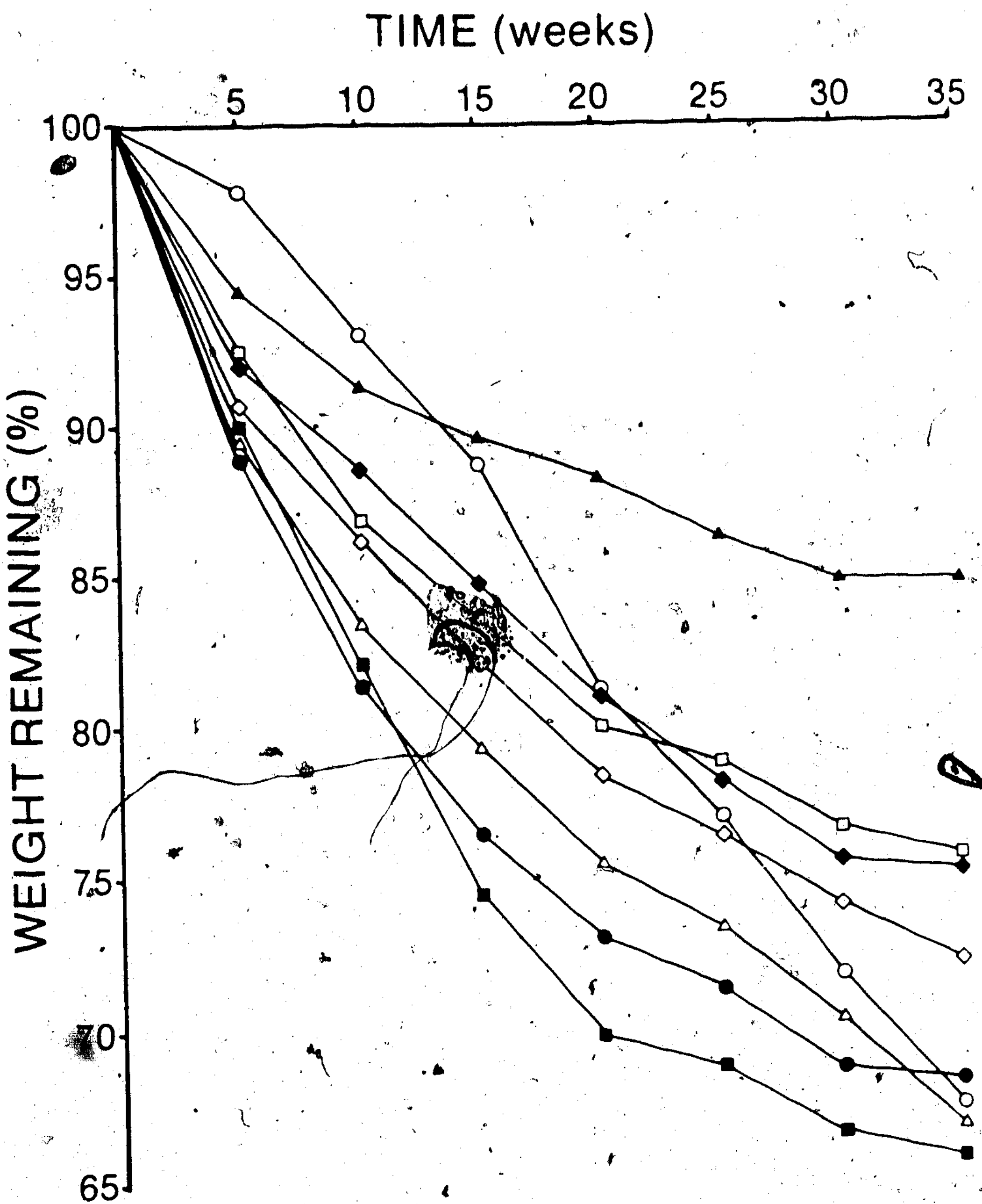


Figure 5-1. Percentage of original weight of eight litter types remaining after different periods of decomposition. o Cladina, ▲ Pleurozium, □ Pine, ◆ Hylocomiumn, ◇ Fir, ■ cut Pine, △ Spruce, ● Alder.

Table 5-1. Rate constants and coefficients of determination obtained for each litter type using the one component model and chemical characteristics of the litters. Litter types with k followed by the same letter do not differ significantly in decomposition rate.

Litter Type	k(SD)	A_0(SD)	Mean r^2	n	Total Carbon	Total Nitrogen	C/N	Soluble Tannins	Lignin	Lignin/N
	$weeks^{-1}$				%	%		%	%	
Pleurozium	.0044(.0002)a	.970(.007)	.913	10	45.5	0.70	65.0	0.4	22.6	32.3
Pine	.0072(.0002)b	.961(.015)	.948	10	52.2	0.51	102.8	4.0	29.3	57.7
Hylocomium	.0082(.0003)c	.967(.016)	.944	10	44.3	1.06	41.7	0.3	25.5	24.0
Fir	.0088(.0004)c	.958(.008)	.950	5	49.8	0.59	84.7	3.8	27.6	46.9
Spruce	.0102(.0003)d	.948(.006)	.943	10	48.3	0.41	116.7	4.7	24.9	60.1
Alder	.0104(.0006)d	.934(.008)	.900	5	48.1	1.09	44.1	6.9	24.6	22.6
Cladina	.0118(.0002)e	.969(.016)	.983	10	41.3	[illegible]33	126.3	0.1	3.6	11.0
Cut Pine	.0122(.0008)e	.942(.025)	.902	5	52.2	0.51	102.8	4.0	29.3	57.7

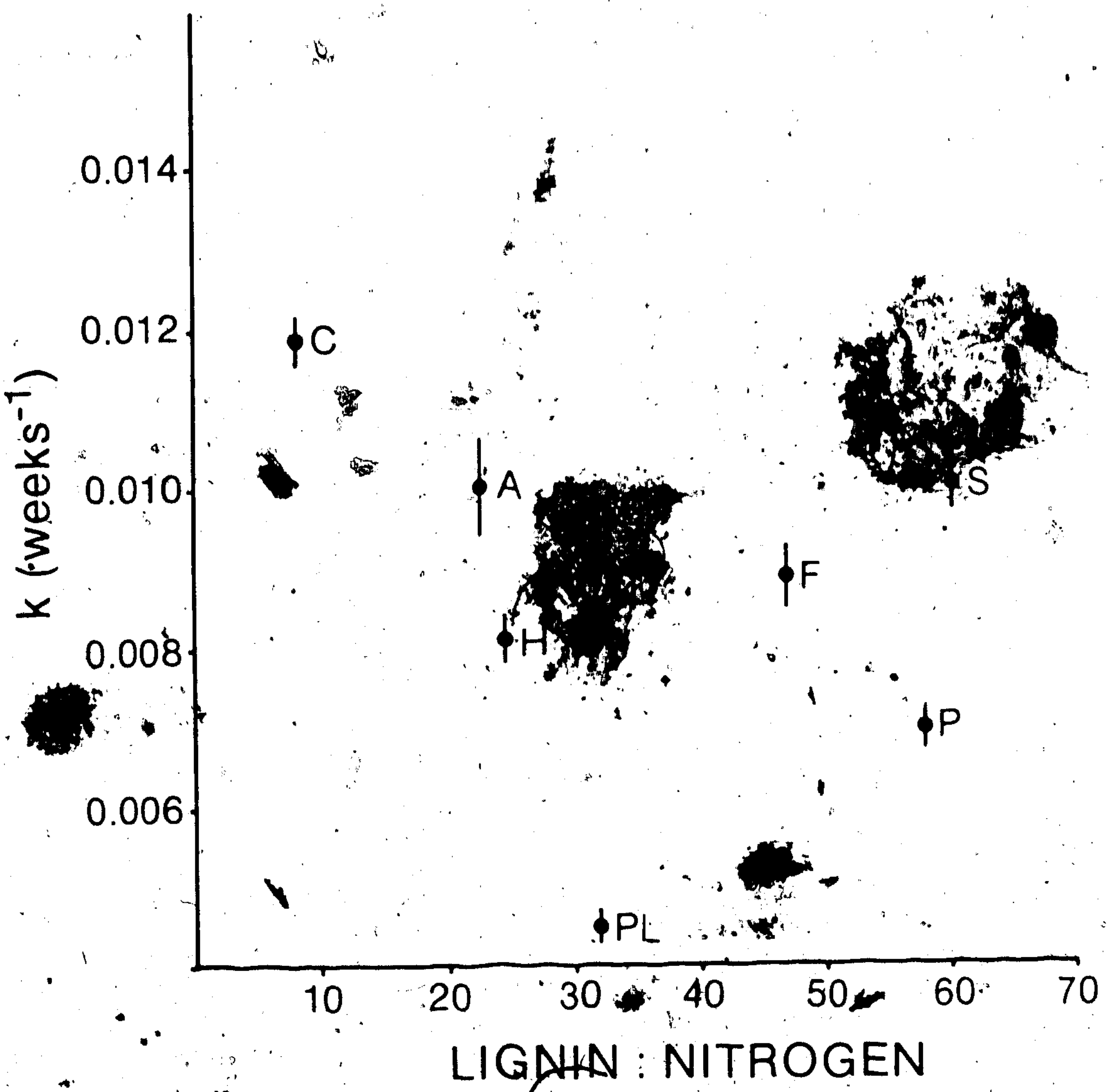


Figure 5-2. Decomposition rate constant (k) (mean = SD) as a function of lignin : N ratio. Alder A, Cladina C, Fir F, Hylocomium H, Pine P, Pleurozium PL, Spruce S.

The high coefficients of determination obtained using the one component model indicated a good fit of the data, but plots of ln(%litter remaining) vs time, the linear form of the model, were in many cases distinctly curvilinear. In simple exponential decay, k, the slope of the above line, is constant throughout the course of decomposition. In the experimental data, however, significant changes were observed in k calculated for different periods of the 35 week incubation. Over time, k decreased in most litter types but increased in Cladina (Figure 5-3). The rate of decrease of k with time appeared to be highest in litters with high inital k values and decreased with decreasing inital k. Cutting pine needles into 1 cm pieces caused a significant increase in both inital k and the rate at which k decreased. These results suggested that although the one component model described the data with acceptable precision, it did not describe the functional relationship between decomposition and time. The decrease in k with time observed in most litter types indicates that at least two components must be involved in the decomposition process.

In all litter types except Cladina, the two component model reduced the residual sum of squares by one to two orders of magnitude indicating a better fit of the data than the one component model. The RSS of Cladina samples were approximately equal in the two models.

Fitting two component equations to the simulated data generated using the [illegible] component model demonstrated that with low levels of introduced error (< 5%), the two component model did not reduce the RSS relative to the one component model. At higher error levels, however, the two component equation had a significantly reduced RSS. The magnitude of individual residuals generated at these higher error levels was, however, much larger than that of residuals associated with two component equations of the experimental data which, in general, were similar in magnitude to those of the SD 1% error residual distribution. This indicates that experimental data error was low and suggests that the improved fit of the two component model was not the result of random error in data which actually represented a one component relationship. The better fit of the two component model is consistent with the decline in k over time observed in most litter types which implies that easily decomposed materials became depleted relative to more resistent materials in the litter.

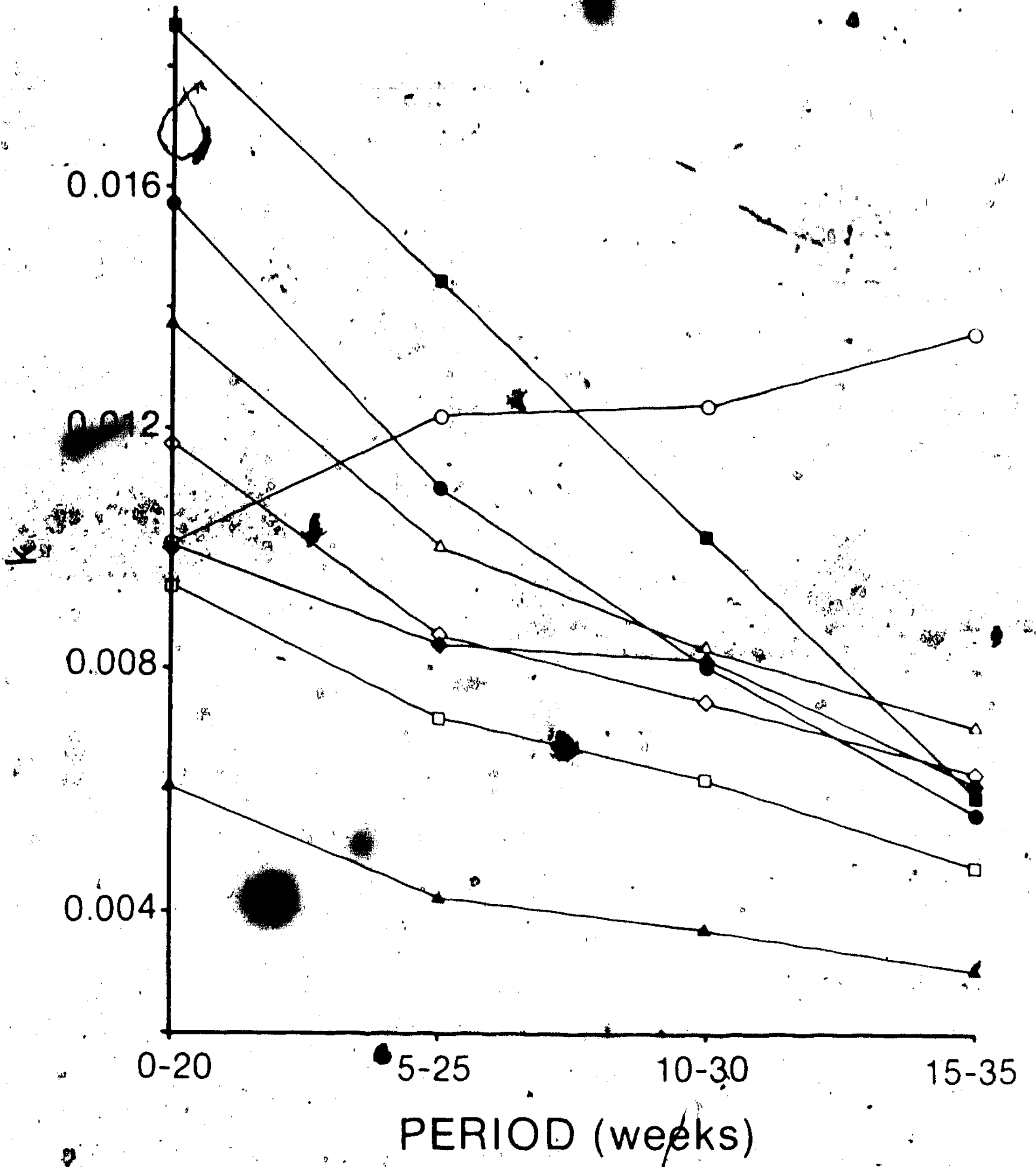


Figure 5-3. Decomposition rate constant (k) calculated for different periods during the 35 week incubation illustrating change in k over time. ○ Cladina, ▲ Pleurozium, □ Pine, ◆ Hylocomium, ◇ Fir, ■ cut Pine, △ Spruce, ● Alder. Comparison between periods within each litter type, analysis of variance P<0.01**, P<0.05*, not significant (P>0.05) ns.

While these observations do not demonstrate that the relationship between decomposition and time involves specifically two components, they do suggest that more than one component must be considered to adequately describe the decomposition process. The absence of a decrease in k during Cladina decomposition and the similarity of RSS in the two models suggests that the weight loss of this litter type is most precisely described by the one component model.

The parameter estimates and associated statistics derived by fitting the two component model to the five fir litter samples (Table 5-2) are representative of those obtained from all other litters. The parameter estimates varied considerably among replicate samples and standard deviations of individual estimates were generally high relative to the estimated value. Within each equation parameter estimates were highly correlated. The magnitude of standard deviations appeared to increase with increasing correlation among parameters such that equations with high internal correlation had very low precision in parameter estimates. Lack of precision in highly correlated parameters is to be expected because a single estimate is influenced by the estimates of other parameters and their associated variability as well as by variability related directly to that parameter.

In the two component model, A_1 and A_2 are considered to represent the initial concentrations of two litter constituents, often referred to as the labile and recalcitrant fractions (Wieder and Lang 1982). According to theory, $A_1 + A_2 = 1$ so that A_2 may be replaced in the equation by $(1-A_1)$ (Hunt 1977) thus constraining the possible values of A_1 and A_2. In this study, the iterative procedure could not converge on parameter estimates for a majority of samples when constrained equations were used. Using unconstrained equations, however, the sum of A_1 and A_2 was always approximately equal to one (mean of all samples of all litters .99±.05(SD)). Exact adherence to the $A_1 + A_2 = 1$ relationship should not be expected because litters always contain inert "ash" in addition to labile and recalcitrant fractions. As well, if the two component equation is used as an approximation of a multi-exponential model as suggested by Minderman (1968), a precise fit is unlikely. The use of a constrained model may lead to loss of information because parameter estimates which

Table 5-2. Parameters with standard deviations, asymtotic correlation coefficients (r) and residual mean squares (RMS) from two component equations for five replicate samples of fir litter.

Sample	A_1	k_1	A_2	k_2	Mean r_a	RMS
1	.10(.03)	.15(.12)	.88(.05)	.008(.002)	.9003	1.3×10^{-5}
2	.43(.63)	.05(.06)	.54(.64)	-.006(.022)	.9977	2.7×10^{-5}
3	.17(.83)	.06(.21)	.81(.84)	.006(.020)	.9976	3.7×10^{-5}
4	.28(.25)	.06(.05)	.69(.27)	.001(.008)	.9960	1.3×10^{-5}
5	.63(1.09)	.03(.04)	.34(1.00)	-.010(.048)	.9988	1.9×10^{-5}

indicate that the sum of A_1 and A_2 is not approximately equal to one may provide insight into the quality of the original data or the nature of decomposition.

The low residual mean square values, typified by those in Table 5-2, and the close adherence to the $A_1 + A_2 = 1$ criterion, suggest that the two component model precisely describes the relationship between weight loss and time for most litters. While it can be concluded that the two component model is appropriate, variability and imprecision in estimates make the development of general predictive equations and correlation of parameters with litter properties impossible.

5.4 Discussion

A major objective of this research was to determine whether differences in the rates of decomposition of different litter types could be attributed to differences in specific chemical characteristics of the litter. Although no general relationship was found between decomposition and any of the chemical parameters measured, it was apparent that litter composition was reflected in the decomposition process. Cladina was the [illegible] type with a negligible lignin content and, in addition to having the highest decomposition rate, was the only litter with decomposition which could be adequately described by the single component model. Lichen tissue is composed mainly of various polysaccharide compounds similar to cellulose and starch (Hale 1974) which, while differing in molecular structure, probably have similar decomposition characteristics and thus might act as a homogeneous substrate during decomposition.

Decomposition of the remaining litter types was more precisely described by the two component than by the one component model. It is possible that these litters might have been fit better by a model with more than two components but the small number of data points per sample precluded the testing of multicomponent models.

In the experimental data, k from the one component equations calculated for different periods of the 35 week incubation decreased significantly in all litter types except Cladina. (Figure 5-3). This supports the conclusion, indicated above, that decomposition of most litter types is not accurately described by the one component model but follows the two component model more closely. A decrease in k over time implies that an easily decomposed component is being depleted relative to a persistent component so that the substrate as a whole becomes increasingly dominated by slowly decomposing materials as decomposition progresses. This is consistent with the rapid loss of cellulose and hemicellulose relative to lignin observed by Berg and Staaf (1980) during pine needle decomposition. A decrease in k would also be expected if the availability of a limiting nutrient, such as nitrogen, decreased over time. The formation of N-lignin complexes, suggested by Melillo *et al.* (1982), might lead to such a situation but the formation of these complexes and their influence on nitrogen availability has not been adequately demonstrated. Incorporation of nitrogen into microbial biomass could also reduce its availability, making litter decomposition rate dependent on biomass turnover rate.

In contrast with the other litter types, k for Cladina litter increased over time (Figure 5-3). An increase in k over time would be expected during the decay of a chemically homogeneous tissue if physical phenomena such as tissue thickness or surface area restricted microbial access to potentially decomposable materials. Cladina thallus has a dense and relatively thick inner layer (Figure 5-5b) which may have acted in this way to decrease the rate of initial decomposition. Disintegration or separation of strands during decay would increase the surface area available for microbial colonization, and resulting in faster decomposition.

Melillo *et al.* (1982) demonstrated a linear relationship between k and the ratio of initial lignin concentration to initial nitrogen concentration in hardwood leaf litters from New Hampshire and deciduous and coniferous tree litter from North Carolina. Recalculation of data presented by Daubenmire and Prusso (1963) demonstrated that a similar, although curvilinear, relationship (power function) existed in the decomposition of needle and leaf litter under laboratory conditions (100 days, 10°C, constant moisture). Figure 5-4, based on data from the present study (105 days, 23°C, Figure 5-1), Mikola (1954) (100 days, 25°C) and Daubenmire and Prusso (1963) (100 days, 25°C), supports the existence of a general relationship between decomposition and lignin:N ratio. This data set represents a diverse

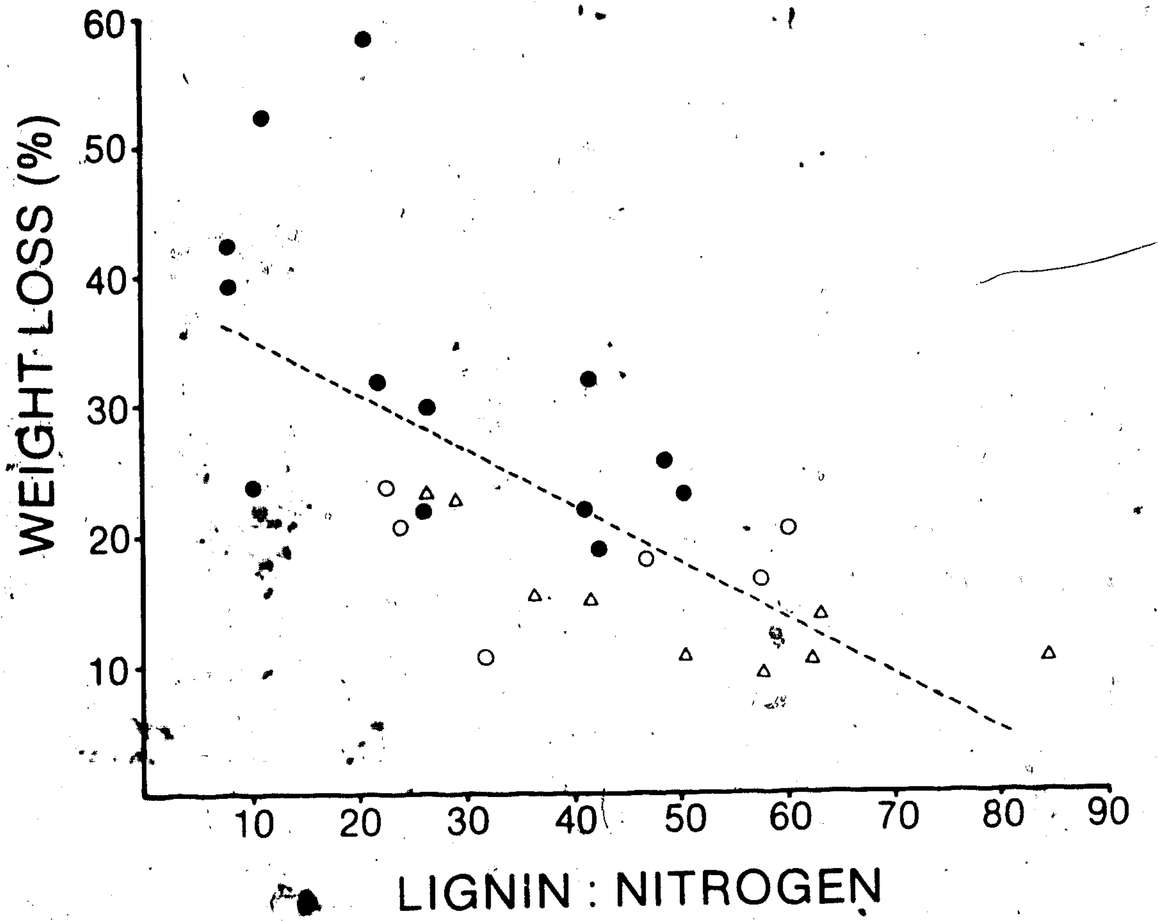
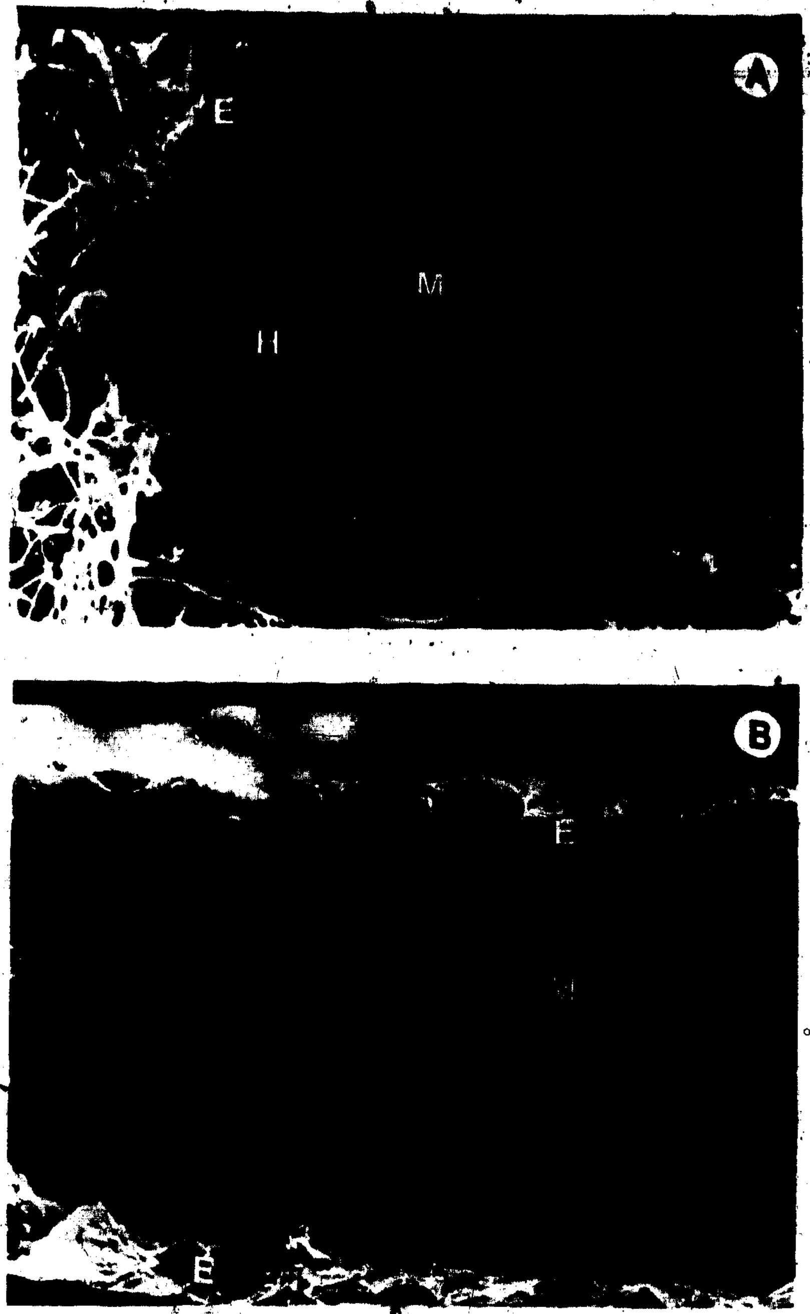


Figure 5-4. Percentage of litter weight lost over 100-105 days of incubation as a function of lignin:N ratio. Data are from: Daubenmire and Prusso (1963) (△), Mikola (1954) (●), and this study (○). Cladina (this study) was excluded because of an initial lag in decomposition (Figure 1). Several points from Daubenmire and Prusso (1963) were excluded because of apparently aberrant values. Plotted line: y=40.9-0.472x r²=0.456.



igure 5-5a. Electron micrographs of litter after 35 weeks of decomposition. A. Cross-section of a jack pine needle. Epidermal cells (E) and hypodermal fibers (H) are seen in cross-section while collapsed mesophyl cells (M) are seen in face view because of separation along an intercellular space. Fungal mycelium covers the external surface of the epidermis and, to a lesser degree, the mesophyl tissue. B. Cross section of alder leaf showing thin walled epidermal (E) and mesophyl (M) cells.

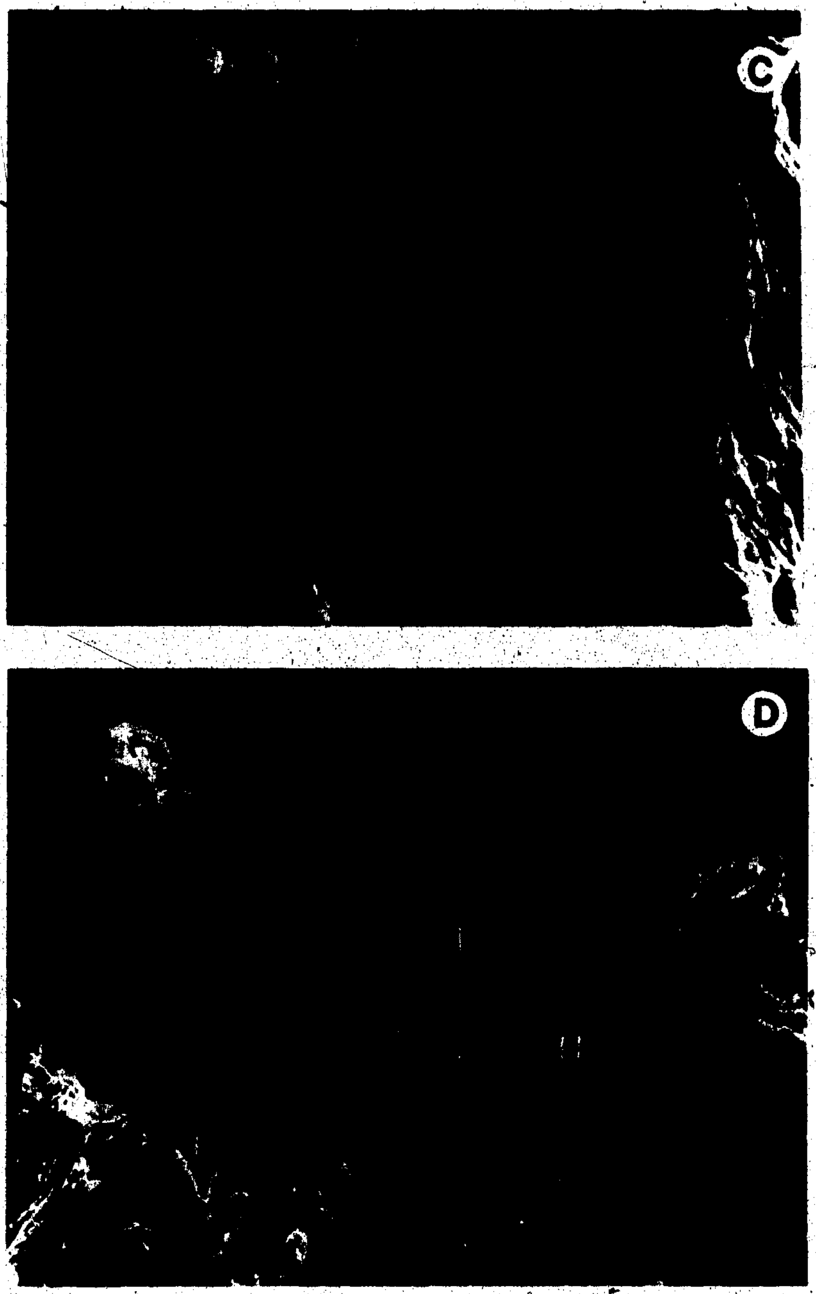


Figure 5-5b. Electron micrographs of litter after 35 weeks decomposition (C) or after an undetermined period in the field (D). C. Cross section of Cladina thallus. D. Spruce needle from a forest floor F layer. Epidermal (E) and hypodermal (H) layers remain intact relative to mesophyl cells which are represented only by remnants (arrow) adhering to outer tissue layers.

group of litters including a lichen, a grass, bryophytes, conifers and deciduous shrubs and trees. Regressions of the combined data were significant with both linear ($r = .675$, $p < .001$) and power ($r = .720$, $p < .001$) functions. These correlation coefficients do not differ significantly (z statistic $z = 0.310$ $z_{.05} = 1.96$, $P > 0.50$, Zar 1974) indicating that while a relationship exists, the specific function involved is open to question. Removal of possible outliers did not alter the explained variability greatly ($r^2 = .443$-$.543$) indicating that the observed correlation was not strongly influenced by outlying points but was general throughout the data set.

In the present study, k was significantly correlated with lignin:N ratio only among the non-coniferous litters. While these litter types form a phylogenetically diverse group, their tissues would be expected to be made up largely of thin-walled cells or, in the case of Cladina, bundles of fungal hyphae, with a relative lack of sclerified cells with thick lignified walls (Figures 5-5a, b). This would be especially true for litters from non-vascular species because of their low degree of tissue specialization (Bold *et al.* 1980). Lignin in the non-coniferous litters would be expected to be distributed relatively uniformly throughout the tissue, with higher concentrations in the walls of supportive or conductive cell types. In contrast, most coniferous needles have a high degree of cellular specialization. Many, including those used in this study (Figure 5-5a), have a hypodermal layer of heavily sclerified fibers as well as fibers associated with the vascular tissue (Esau 1977). Epidermal cells of conifer needles tend to have extremely thick outer walls which are cutinized in addition to being lignified. Together, these specialized cells probably contain a large proportion of the total lignin in conifer litter tissue. Lignin contained in thick, secondary wall accumulations, particularly those of epidermal cells which are perfused with waxy cuticular materials, is probably inaccessible to microbial enzymes except on the cell surface and therefore would not participate in biochemical decomposition reactions until cellular integrity had been lost. Analysis of total lignin in coniferous litter probably overestimates the amount of lignin actually involved in decomposition processes. Nitrogen compounds included in the structure of thick, lignified cell walls also would be isolated from decomposition reactions but, because most leaf nitrogen is associated with photosynthetic rather than structural tissue, overestimation of active nitrogen by total analysis would not be as great as for lignin.

If lignified structural tissue is resistant to microbial attack, the inital decomposition of conifer tissue is probably dependent on degradation of non-sclerified mesophyl and vascular tissue (Figure 5-5b) and is therefore controlled by the characteristics of these cell types rather than those of the litter as a whole. All litter types except Cladina had similar lignin contents (Table 5-1) but the high proportion of conifer lignin which is in sclerified cells suggests that conifer mesophyl tissue is less lignified than equivalent tissue in non-coniferous litter. This may explain the relatively rapid rate of weight loss of coniferous litters despite the presence of lignified tissue resistant to initial breakdown.

The effect on weight loss of cutting pine needles into 1 cm lengths is further evidence of the influence of litter micro-structure on decomposition. While particle size is known to affect litter decomposition through its influence on surface area (Swift *et al.* 1979), the increase in needle surface area caused by cutting needles was negligible and would not account for the observed increase in decomposition (Table 5-1, Figure 5-1). Cutting would, however, increase the access of micro-organisms to internal surfaces, including those of non-lignified mesophyl tissue, by removing the barrier of epidermal and hypodermal tissue which would have to be penetrated in uncut needles. In this situation, decomposition would be expected to increase because of an increase in accessibility and the rate of colonization of the leaf interior by microorganisms.

In summary, with the exception of Cladina lichen, decomposition of the boreal forest litter types examined was best described using a two component model. The exact nature of the litter constituents and structures which were reflected in the two component model could not be determined although the existence of components which differed in their persistence, was suggested by the data. While the components may differ in chemical composition (e.g. polysaccharide vs lignin), they are probably also distinguished by micro-structural differences (e.g. mesophyl vs sclerified tissue).

Differences in decomposition rates among boreal forest litters could not be explained by differences in litter chemistry alone and a major role of litter structure in controlling decomposition was strongly implicated. Tissue or cell structural characteristics which influence the access of microorganisms or microbial enzymes to potential substrates modify the role of substrate chemistry in controlling decomposition. Since different cell or tissue types often differ in chemical characteristics, correlation between structural and chemical controls on decomposition is to be expected. The general relationship observed between weight loss and lignin:N ratio (Figure 5-4) may have reflected structural differences which undoubtedly existed among the litters as well as chemical differences. It is likely that a specific functional relationship between litter chemistry and decomposition will be found only in groups of structurally similar litters such as the non-coniferous types used in this study or the data sets used by Melillo *et al.* (1982).

The decomposition rates calculated in this study are consistent with patterns of forest floor accumulations observed in the field. The forest floors associated with Pleurozium ground cover are generally thick and loose, comprising mainly a fermentation (F) layer of partially decomposed moss with intermixed needles. The humified layer below is thin or lacking. The thin forest floors observed in pine/lichen stands consist primarily of a loose F layer of slightly decomposed needles with little evidence of lichen litter accumulation probably because of its rapid rate of decomposition relative to production. Stands or locations with litter having intermediate decomposition rates (e.g. spruce/fir/Hylocomiumor beneath alder clumps) tend to have moderately thick, compact forest floors often with a dense F layer and distinct H horizon.

While examination of the decompositional characteristics of individual litters may elucidate basic decomposition processes, only a partial understanding of organic matter dynamics can be gained from these studies because, in the field, there is often an intimate mixing of different litter types and decomposition states. Further information on the interactions among litters during decomposition, such as the influence of rapidly decomposing Cladina, which increases in decomposition rate over time, on more slowly decomposing pine which slows in decomposition rate, is prerequisite to a complete understanding of forest floor dynamics. Spatial relationships among the particles within a forest floor, i.e. forest floor architecture, is undoubtedly of primary importance in such interactions. Microscopic examination and detailed chemical and biochemical analysis across forest floor profiles would provide valuable information on the physical and chemical changes which take place during the accumulation of surface organic matter in a forest environment and may elucidate functional differences between forest floor types.

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6. SOIL NITROGEN MINERALIZATION IN RELATION TO VEGETATION CHARACTERISTICS

6.1 Introduction

Growing understanding of the role of N in determining forest productivity has led to an increase in research relating to the impact of harvesting on loss of N from forest ecosystems (Vitousek 1981, Vitousek and Melillo 1979) and to the potential of fertilization to increase tree growth. Although such applied research has led to an improved understanding of N dynamics in forest ecosystems, full interpretation of results has often been difficult because controls on N cycling and availability in forest soils remain poorly understood (Binkley and Reid 1985). Basic information on the natural N fertility of stands differing in species composition, age or successional status, and on the degree to which the fertility of different sites can be manipulated, is required if the cost-effectiveness of silvicultural treatments is to be maximized.

Nitrogen mineralization and availability have been studied using numerous biological and chemical techniques, none of which have been universally adopted (Keeney 1980). Long-term aerobic incubation based on the method of Stanford and Smith (1972), however, has the following advantages: 1) it is directly dependent on natural biological mechanisms rather than chemical extractants; 2) the long incubation time reduces the influences of initial N mineralization, which may be affected by sample preparation, on the final results; and, 3) in addition to measurement of total N mineralization over time, it allows the calculation of theoretical mineralization parameters, namely: potentially mineralizable N (N_0) and mineralization rate constant (k).

The determination of N_0, as described for agricultural soils by Stanford and Smith (1972), assumes that N mineralization follows first-order kinetics such that the amount of N mineralized per unit time is proportional to the amount of mineralizable substrate present in the soil during that period. The equation describing this process is:

$$N_t = N_0(1-e^{-kt}) \qquad [1]$$

in which N_t is the accumulated mineralized N at time=t, N_0 is the potentially mineralizable N and k is the mineralization rate constant. The two unknown equation parameters (N_0, k) can be estimated using graphical techniques (Stanford and Smith 1972) or iterative non-linear regression procedures (Smith *et al.* 1980, Campbell *et al.* 1981).

The specific objectives of this research were: 1) to compare the N mineralization characteristics and the quantity and properties of total N in forest floors (LFH) and mineral soil of several upland coniferous forest stands; and 2) to interpret observed differences among stands and between soil horizons in terms of vegetation age and species composition and stand history.

Study Area

Soil samples were collected from eight stands located on a series of sand ridges with interspersed wetlands lying adjacent to the Athabasca River, 55 km southeast of the town of Slave Lake in central Alberta. The sands originated as fluvial deposits in post-glacial lakes (St. Onge 1972) and have been modified by aeolian processes. The area is within the Mixedwood Section of the Boreal Forest Region of Rowe(1972).

The upland vegetation of the area is a mosaic of open jackpine/lichen woodland, closed canopy jackpine or trembling aspen (Populus tremuloides (Michx.)) stands with lesser representation of white spruce/pine and white spruce/aspen stands. In this study, four stands (1, 2, 11, 12) represent different aged examples of the open woodland type dominated by jackpine with a shrub layer composed mainly of bearberry (Arctostaphylos uva-ursi (L.) Spreng.) and lingonberry (Vaccinium vitis-idaea (L.)). Green alder (Alnus crispa (Ait.) Pursh.) is present in stands 1, 2 and 12 but absent in stand 11. This species reaches its highest abundance among pine/lichen stands in stand 2. Ground cover is strongly dominated by lichens, particularly Cladina mitis (Sandst.) Hale & W. Culb. Small white spruce are occasionally observed in stands of this type.

Two stands (3 and 13) represent a closed canopy jackpine forest with a well-developed shrub canopy of green alder and a continuous feathermoss ground cover dominated by Pleurozium schreberi (Brid.) Mitt.. Scattered subdominant or suppressed white or black spruce (Picea mariana (Mill.) B.S.P.) occur in these stands.

Mixed pine/spruce forest is represented by stands 4 and 14. In stand 14 white spruce and jackpine form a codominant tree canopy along with scattered aspen. The shrub layer consists only of scattered low shrubs including Lonicera involucrata (Richards)Banks and Viburnum edule (Michx.) Raf. with a few young balsam fir(Abies balsamea (L.) Mill.). The feathermoss groundcover is almost continuous, being composed mainly of Hylocomium splendens (Hedw.) B.S.G. and Pleurozium schreberi. In stand 4 the tree canopy consists primarily of white and occasionally black spruce, with scattered aspen and paper birch (Betula papyrifera Marsh.). Balsam fir forms a well-developed subcanopy. As in stand 14, the shrub layer is insignificant while the ground cover of feathermoss is extensive. Stand characteristics are given in Table 6-1.

The soils of the area have developed from aeolian parent materials and are predominantly orthic and eluviated brunisols (stands 1, 2, 3, 11, 12, 13). In stands 4 and 14 the soils are classified as orthic and brunisolic gray luvisols (Canada Soil Survey Committee 1978).

Local topography in all stands is typical of aeolian landforms in the area with level to undulating ground surface, subdued relief (<2-3m) and gentle (<5%), complex slopes. Most stands exhibit no predominant slope direction although stand 3 is westerly and stand 4 northerly in aspect. Maximum distance between stands is 15 km over level terrain so that macro-climate differences among stands are negligible.

6.2 Methods

Soil cores (6 cm dia.) were taken at five randomly selected locations in each stand in October 1983. Each core was sectioned and undisturbed samples collected at the following depths: forest floor (LFH), 0-4 cm (Ah or Ahe) and 28-32 cm in three of the five locations

Table 6-1. Forest characteristics of the eight stands.

Stand	Forest Type	Age	Basal Area			
			Pine	Spruce	Aspen	Fir
		(yr.)	------------(m^2•ha^{-1})------------			
1	Pine/lichen	45	11.9			
2	Pine/lichen	65	20.3			
11	Pine/lichen	40	17.8			
12	Pine/lichen	85	27.9			
3	Pine/alder/feathermoss	85	33.3	0.9		
13	Pine/alder/feathermoss	65	30.1	1.8		
4	Spruce/pine/fir/feathermoss	140	3.5	28.7	2.1	4.2
14	Spruce/pine/feathermoss	80	17.4	18.3	4.1	

within each stand. The lowest depth corresponded to the Bm horizon in stands 1, 2, 11, 12, 13, to the Btj horizon in stand 3 and to the Bt horizon in stands 4 and 14. Core sections were placed directly into pre-weighed 6.5 cm diameter plastic suction funnels containing fiberglass filters and sealed in plastic bags for transport to the laboratory. Duplicate cores were taken immediately adjacent to the first core for measurement of moisture content to allow calculation of dry weight of the incubated samples and for measurement of pH.

Samples were not mixed with quartz sand as prescribed by Stanford and Smith (1972) because their sandy texture allowed rapid leaching even in undisturbed cores. In one Bt horizon sample, high in clay relative to the other samples, the rate of leaching was restricted on the last two leaching dates presumably because the filters in the suction funnel or soil pores had become clogged with fine material. Routine use of undisturbed cores would probably be unsuitable for soils containing more than 20% - 25% clay because of the extended time required for leaching.

The use of undisturbed cores was considered essential for the study of mineralization in LFH horizons and preferred for mineral horizons because the degree of decomposition of organic matter varies widely down a soil profile. Intact cores maintain the spatial separation between surface litter and humified material lower in the profile thereby eliminating the possibility that N mineralized from F or H layer material would, for example, be immobilized by undecomposed litter brought into close contact by mixing. Under such circumstances, N mineralization could be seriously underestimated.

In the laboratory, samples were leached to remove mineral N prior to the incubation. In this and subsequent leachings, three 100 mL aliquots of 0.01 M $CaCl_2$, followed by 100 mL of a N-free nutrient solution (Stanford and Smith 1972) were added to each sample and allowed to soak 3 minutes before removal with 60 kPa suction. Suction funnels were covered with thin polyethylene sheets perforated with several small holes to retard water loss. Samples were incubated in the dark at 30° C and leached at 2, 4, 7, 11, 15, 21, 29, and 37 weeks. Wet weight, measured after the inital leaching, was maintained by weekly additions of distilled water.

Leachates were analysed for ammonium and nitrate by autoanalyser (Technicon Industrial Methods 98-70W and 487-77A respectively). After incubation, samples were oven-dried and subsamples passed through a 10 mesh sieve prior to measurement of pH (deionized water:soil,LFH 10:1, mineral 2:1) or ground to pass a 100 mesh sieve prior to analysis for total N using Kjeldhal digestion (McKeague 1978) and autoanalyser techniques (Technicon Industrial Method 334-74 W/B+). Initial total N concentration was calculated as total N remaining in the sample plus that recovered in leachates.

The first-order mineralization model was fit to cumulative mineralization data for each sample using the NLIN procedure (secant method (DUD)) of the SAS statistical program package (SAS Institute Inc. 1982). This procedure estimates the derivatives of a non-linear equation which are then used to estimate equation parameters (N_0 and k in equation [1]) by iteration from initialized values. Coefficients of determination (r^2) were calculated from sums of squares provided by the program.

Equation parameters (N_0, k) were compared between stands using linear forms of the first-order equation [1] in which the parameter in question was represented by the slope of a line. Comparisons were made separately for each parameter with the other substituted into the linear equation to allow calculation of the slope. Values of N_0 were compared using:

$$N_t = N_0 - N_0(e^{kt}) \qquad [2]$$

in which (e^{kt}) is calculated to give X axis values. Values of k were compared using:

$$-\ln(1-N_t/N_0) = kt \qquad [3]$$

in which Y axis values were calculated as $-\ln(1-N_t/N_0)$. The slopes of these lines were compared using analysis of covariance procedures and the Newman-Keuls multiple comparison method described by Zar(1974). These tests, which consider each parameter separately, do not fully account for variablility in the data because error associated with the parameter used in the linear calculation is ignored. Therefore the significance of the inter-stand differences calculated using this method must be considered to be approximate. We are unaware of statistical techniques which would simultaneously compare two or more equation parameters and thus avoid this problem.

Data from this study were compared to those of Vitousek *et al.* (1982) by using N_0 and k values to calculate cumulative N mineralization expected over the 8 week incubation period used by these authors (t=8 in equation [1]). A value of $Q_{10} = 1.8$ (Stanford *et al.* 1973, Campbell *et al.* 1981) was applied to the k values prior to this calculation to correct for differences in incubation temperature (20°C vs 30°C in this study).

Comparisons among stands and horizons for data other than the first-order equation parameters used two-way analysis of variance and one-way analysis of variance followed by Duncan's multiple range test. Logarithmic transformations were required to ensure homogeneity of variance in data for total N and percent of N_0 mineralized. The Z test procedure described by Zar (1974) was employed in comparisons between correlation coefficients.

6.3 Results

Nitrogen Mineralization

The amount of N in the LFH horizons was not different from that in the A horizon but both exceeded that present in the B horizon (Table 6-2). Total N (N_T) concentration in LFH samples was generally lower (Table 6-2) and total N mineralized (N_M) by LFH samples during the 37 week incubation (Table 6-3) was significantly lower in the pine/lichen stands (1, 2, 11, 12) than in the other stands. In the A horizon, total N concentration in stand 11 was significantly lower than in other stands. Few significant differences between stands were observed in N mineralized by A horizon samples, although mineralization tended to be higher in stands containing a significant component of green alder (2, 3, 13). Although concentration of total N differed significantly among the B horizons, these differences were not reflected in mineralization. No consistent pattern was observed among stands in the percentage of total N mineralized (N_M/N_T) during incubation of either LFH or A horizons (Table 6-3). N_M/N_T was lower in B horizons of stands 4 and 14 than in those of other stands. N_M/N_T was inversely correlated ($r = -.868$ $P < .01$) and total N concentration and weight directly correlated

Table 6-2. Characteristics of the incubated samples. Clay contents are from other samples taken from equivalent horizons and depths from pits within each stand. Within horizons, means followed by the same letter do not differ significantly ($P > .05$). P/L: pine/lichen, P/A: pine/alder, S: spruce.

Stand	Type	Horizon	Total Nitrogen		Clay	Initial pH
			(%)	($g \cdot m^{-2}$)	(%)	
1	P/L	LFH	0.673b	35.5b	--	5.02bc
2	P/L		0.884bcd	28.6b	--	4.76b
11	P/L		0.352a	19.4b	--	4.79b
12	P/L		0.827bc	31.8b	--	4.70b
3	P/A		0.962bcd	43.3b	--	4.28a
13	P/A		1.170d	43.5b	--	5.28cd
4	S		1.124cd	81.1c	--	5.59d
14	S		1.106cd	46.7b	--	4.82bc
1	P/L	A	0.091ab	27.2a	2.2	5.33cde
2	P/L		0.116b	45.7b	2.2	5.17bcd
11	P/L		0.058a	26.2a	3.8	5.88e
12	P/L		0.089ab	38.1ab	5.4	5.59de
3	P/A		0.100b	37.7ab	3.8	4.62ab
13	P/A		0.124b	44.2b	6.8	5.14cd
4	S		0.126b	41.1ab	4.4	4.14a
14	S		0.112b	41.2ab	8.0	4.61abc
1	P/L	B	0.016ab	9.3a	4.0	5.25ab
2	P/L		0.017ab	9.3a	5.0	5.36bc
11	P/L		0.012a	9.1a	3.1	5.73d
12	P/L		0.017ab	10.0a	4.1	5.31b
3	P/A		0.020b	11.2a	6.6	5.13ab
13	P/A		0.027c	16.2b	4.6	5.16ab
4	S		0.050d	22.1c	12.5	4.95a
14	S		0.042d	23.6c	22.2	5.56cd

Table 6-3. Nitrogen mineralization characteristics including: N mineralized over the 37 week incubation (N_m), potentially mineralizable N (N_o), mineralization rate constant (k), number of samples fit by the first-order model (n) and ratios of parameters. N_T: total N. Within horizons, means followed by the same letter do not differ significantly (P>.05).

Stand	Type	Horizon	N_m ($g \cdot m^{-2}$)	N_o ($g \cdot g^{-1}$)	k ($week^{-1}$)	n	N_m/N_T (%)	N_m/N_o (%)	N_o/N_T (%)
1	P/L	LFH	2.86a	2440d	0.024cd	1	7.4a	56.7a	26.1ab
2	P/L		4.38a	4140a	0.035c	2	13.6abcd	92.4b	31.0ab
11	P/L		2.68a	1320g	0.019d	4	18.1bcd	46.3a	45.5b
12	P/L		4.27a	1600f	0.054b	5	13.2abcd	81.0b	16.3a
3	P/A		8.53b	2200d	0.068a	5	19.6cd	89.8b	21.8a
13	P/A		8.97b	2750c	0.060b	5	20.1d	88.1b	22.1a
4	S		10.22b	3790b	0.015d	4	12.8ab	41.4a	35.1b
14	S		7.41b	1910e	0.059b	5	15.8bcd	87.7b	18.0a
1	P/L	A	3.44a	170e	0.017e	2	13.1bc	44.6ns	26.9abc
2	P/L		4.36ab	539a	0.026a	4	9.5ab	54.4	33.2bc
11	P/L		2.47a	114f	0.026ab	4	9.6ab	59.9	17.9abc
12	P/L		3.80a	166e	0.023c	4	10.2ab	48.8	29.8abc
3	P/A		6.08b	340c	0.020c	4	15.7c	49.4	42.6c
13	P/A		4.55ab	481b	0.010g	3	10.3ab	26.3	41.5c
4	S		2.49a	150e	0.025b	5	6.2a	56.0	11.6a
14	S		2.97a	249d	0.014f	4	7.3a	38.9	18.6ab
1	P/L	B	0.60ns	27b	0.017d	3	6.4c	42.0ns	15.5
2	P/L		0.55	26b	0.024a	2	5.8c	49.2	35.8
11	P/L		0.57	14d	0.021b	3	6.4c	47.9	47.9
12	P/L		0.42	17c	0.017cd	2	4.2b	38.3	38.6
3	P/A		0.65	18c	0.016d	2	5.7c	44.7	44.7
13	P/A		0.74	39a	0.009e	3	4.5b	26.1	26.1
4	S		0.52	16c	0.019c	3	2.4a	40.6	40.6
14	S		0.36	---	------	0	1.5a	----	----

($r = .875$ $P < .01$ and $r = .748$ $P < .05$ respectively) with clay content in the B horizon(Table 6-2). These correlations were strongly influenced by the high clay contents in the B horizons of the spruce stands and may therefore reflect other differences between sites. Significant correlations were not observed between clay content and N characteristics in the A horizons.

Potentially Mineralizable Nitrogen

The first-order kinetic model successfully described cumulative N mineralization curves from 76 % of the incubated samples. The number of samples which could be described by the model differed among stands and horizons as shown in Table 6-3. The proportion of total variability explained by these regressions was high ($r^2 > .97$). With data from the remaining samples, the iterative procedure could not attain convergence on parameter estimates and this was taken to indicate that the first-order model was inappropriate for these data. The non-linear regression program did not appear to be sensitive to initialized values and, with data sets for which the model was appropriate, would converge on similar estimates of parameters from a wide range of initial values.

Cumulative mineralization curves of individual samples formed two distinctive patterns (Figure 6-1), which varied in overall slope, degree of curvature and duration of the initial lag in mineralization. Curve A is representative of samples with cumulative N mineralization fit by the first-order model while samples not fit by the model generally followed a pattern similar to curve B. In most of the latter cases, the first-order model could be fit to the data points after N mineralization began but values of N_0 and k calculated for these points were not directly comparable to those of other samples for which full data sets were used. Further research is required to determine whether the time lag in N mineralization reflects field conditions or is an artifact caused by sample disturbance or severing of plant roots.

Stands were compared with respect to N_0 and k from the first-order model although, in some cases, the general applicability of the estimates was low because only one or two replicates within a stand could be fit (n, Table 6-3). In particular, the value of N_0 in the

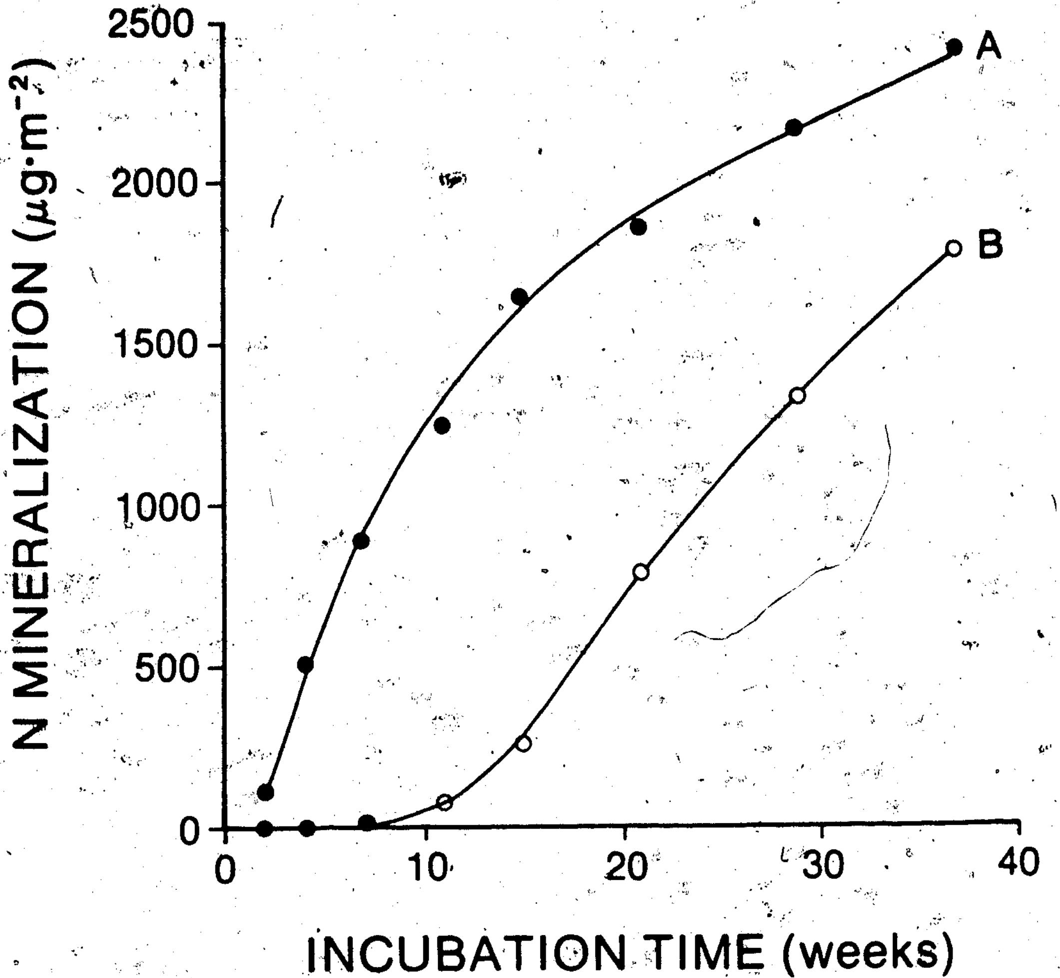

Figure 6-1. Cumulative N mineralization curves for two LFH samples from stand 2. Curve A could be fit by the first-order model while curve B could not.

LFH of stand 2 was strongly influenced by a single sample taken from beneath an old alder patch. Its contribution to the stand mean was exaggerated because three of the five samples could not be fit by the model. The value of numerous replicates, especially in stands with high spatial heterogeneity in N distribution such as 12, 1 and 2 was apparent.

Among LFH horizons, N_0 was highest in stands 2 and 4 and lowest in stand 11 with the remaining stands occupying a middle range of 1600-2800 ug g^{-1}. The N_0/N_T ratio was significantly higher in stands 11 and 4 than in other stands. During the 37 week incubation over 80% of N_0 was mineralized in most stands but this proportion was significantly lower (41% - 57%) in the old spruce stand (4) and young pine/lichen (1,11) stands. The mineralization rate constant was generally highest in those stands with a substantial component of green alder in the vegetation and was lowest in young pine/lichen (1 and 11) and old spruce stands (4). Variation in k values among stands was highest in the LFH horizon but, in general, k was higher in the LFH than in deeper horizons.

N_0 was significantly higher in the A horizon of stands with an extensive alder canopy (2, 13, 3) than in other stands, while stand 11 was lower. Few differences among stands in N_0/N_T were significant although this proportion was generally higher in stands 2, 3 and 13. N_M/N_0 in Ah samples did not differ significantly between stands. Values of k were highest in stands 2, 11 and 4 and lowest in stand 13 but no distinct pattern was apparent. Values of k in A horizons are more similar to those of the B horizon than the LFH implying that A horizon N is mainly in well-decomposed materials either because additions of fresh residues from roots are low or because such residues decompose rapidly in the mineral soil.

No pattern in N_0 values from B horizon samples was distinguished although stands with alder were generally higher than others. Values of k in B horizons were within a range similar to A horizons and also exhibited no pattern which could be related to general stand characteristics. The ratios of N_0/N_T and N_M/N_0 in the B horizon did not differ significantly among stands during the incubation.

Nitrification

Production of nitrate (NO_3^-) over the 37 week incubation differed substantially both between stands and between horizons within a stand (Table 6-4). NO_3^-/N_M in LFH samples was low (2% -23%) in most stands but significantly higher in stand 4. Nitrification in Ah samples from stands 3, 14, and 4 was significantly lower than in those from other stands while in samples from stands 11 and 12, it was significantly higher. Few differences in nitrate production among B samples were significant although stands 11 and 13 were higher and 3 and 4 were lower than other stands.

In most samples, the onset of nitrification was delayed by a period which differed among stands and horizons. In general, this time lag (Table 6-4) was shortest in B horizon samples and longest in LFH samples, many of which produced insignificant amounts of nitrate throughout the incubation. Among LFH horizons, those from the old spruce stand (4) had the shortest lag time while in the A horizons the lag was shortest in samples from the youngest pine/lichen stand (11). Stands 11, 1, 2 and 3 had the shortest lag times among the B horizons.

Over the 37 week incubation, the pH of most samples increased (mean change +0.3 pH units) with the magnitude of increase inversely correlated with inital pH ($r=-.811$ $P<.01$). Significant correlations were observed between initial pH of the incubated samples (Table 6-2) and NO_3^-/N_M over 37 weeks ($r=.621$ $P<.01$) and the duration of the time lag in nitrification ($r=-.563$ $P<.01$). The coefficient for the correlation between pH and nitrification was, however, significantly lower (z test, $P<.05$) when only the initial (0-2 week) incubation period was considered (NO_3/N_M vs initial pH, $r=.298$ $P<.01$). A functional relationship, if it existed, would have been expected to be most distinct in this initial period because the magnitude of changes in properties related to pH (e.g. organic matter), which may have occurred later in the incubation, would be minimal. The correlation between pH and nitrification in LFH and A horizon samples only, for the 0-2 week period, was not significant ($r=.177$ $P>.05$).

Table 6-4. Proportion of N mineralized over 37 weeks recovered as nitrate and lag time before nitrate represented 50% of the total N mineralized within an incubation period. Means followed by the same letter do not differ significantly ($P > .05$).

Stand	Type	LFH		A Horizon		B Horizon	
		NO_3^-/N_m (%)	Lag Time (weeks)	NO_3^-/N_m (%)	Lag Time (weeks)	NO_3^-/N_m (%)	Lag Time (weeks)
1	P/L	9.6a	37	19.1bc	27	46.3ab	6
2	P/L	4.6a	37	16.1abc	37	68.6ab	5
11	P/L	23.3a	34	81.8e	7	99.0b	0
12	P/L	11.3a	37	50.3d	30	57.8ab	19
3	P/A	2.2a	37	0.3a	32	20.8a	8
13	P/A	13.5a	37	33.5cd	37	88.3b	20
4	S	43.9b	23	2.2ab	37	30.4a	31
14	S	11.5a	37	0.5a	37	49.0ab	19

6.4 Discussion

Few studies have measured N mineralization in forest soil over a longterm incubation and there appear to be no data in the published literature which are directly comparable to those of this study with respect to methodology or ecosystem type. Burger and Pritchett (1984), working in Florida pine stands, examined the influence of post-harvest site preparation on N mineralization in mixed LFH and A horizon samples over an 18 week incubation. Values of N_0 in their soils (18-25 ug g^{-1}) were much lower than those from Alberta LFH or Ah horizons and represented a smaller proportion of total soil N (4-6%), although k values (0.053-0.061 $weeks^{-1}$) were similar. The low apparent values of N_0 in the Florida soils may have been the result of increased immobilization caused by mixing of forest floor and mineral horizons.

Vitousek *et al.* (1982) studied N mineralization and nitrification in soils at 17 sites, including 10 coniferous stands, in 6 states of the continental United States. An eight week aerobic incubation with a terminal extraction of mineral N was used. Values for mean total N mineralized during the incubation of coniferous forest floor samples were taken from their cumulative mineralization curves and fell within the 95% confidence interval of 82-554 ug g^{-1}. Predictions of N mineralization in LFH samples from the Alberta stands under equivalent conditions fell within a comparable confidence interval (263-563 ug g^{-1}). This suggests that properties of the soil which control N mineralization in soils of coniferous forests, do not differ greatly between regions. Consequently, studies of ecologically related stands within restricted geographical areas which provide detailed information about controls on N mineralization may then be applied to coniferous stands in general.

Estimates of N_0 in agricultural soils generally fall within a range of 50-400 ug g^{-1} (Stanford and Smith 1972, Herlihy 1979, Campbell *et al.* 1981), which is similar to the range of N_0 in A horizon samples in this study. Values of k in agricultural soils have been found to be relatively uniform among soils, commonly falling within the range of 0.054±.009 $weeks^{-1}$ at 35°C, originally determined by Stanford and Smith (1972) (Campbell *et. al.* 1981). If the assumed Q_{10} of 1.8 is applied to our data, confidence intervals for k at 35°C of 0.028±0.008

and 0.056±0.023 are obtained from A and LFH horizons respectively. Thus, N in surface mineral soils in the forest stands is biochemically less active than that in agricultural soils, probably because the mechanical mixing and incorporation of fresh plant residues caused by tillage is absent under undisturbed conditions. The similarity in k between LFH horizons and agricultural soil may indicate that N mineralization in agricultural soils is largely dependent on the decomposition of relatively recent plant or microbial residues such as those which form the bulk of forest floor materials. Nitrogen mineralization in the field has been calculated using the assumed value of $k=0.054$ week^{-1} and estimates of N_0 (Smith *et al.* 1977). Values of k measured in this study varied widely among sites and horizons indicating that the uniformity of k in tilled agricultural soils cannot be extended to forest soils.

On the basis of data collected in this study, the stands under consideration can be compared with respect to both quantity and biochemical nature (quality) of N involved in the mineralization process. Total N mineralized during the incubation and N_T provide information on quantitative differences between stands while N_0, k and the various ratios computed in Table 6-2, excluding those involving nitrate, describe the quality of N in different stands and horizons in terms of its relative activity in mineralization.

The results of this study indicate that N mineralization characteristics of LFH and A horizons vary with differences in vegetation species composition and, in the LFH only, with stand age. The effects of these two factors could not be fully evaluated individually through a full factorial experimental design because of the lack of appropriately aged stands of each forest type and restrictions imposed by research resources. Evidence for their independent influence can however be obtained by comparison within groups of equal aged stands (stands 2, 13 circa 65 years, stands 3, 12, 14 circa 85 years) or among different aged stands within the same forest type.

Stand Age

A general increase with age was observed in N_M, N_T concentration, k, and N_M/N_0 in pine/lichen forest floors. These data suggest that the quantity of N in LFH horizons is low in young stands and that this N is relatively inactive with respect to mineralization. This is to be expected because forest floors in young stands are composed mainly of fresh litter which has a high capacity to retain or immobilize N during decomposition (Berg and Staaf 1980). As stands age, progressive decomposition of litter leads to a dominance of N mineralization over immobilization processes and an increase in the relative mineralization activity of accumulated N.

Stand 4 is substantially older than any other stand and, as would be expected, has a significantly higher amount of total N accumulated in the forest floor. The proportion of this N which is potentially mineralizable is high relative to other stands but its relative mineralization activity, as reflected in k and N_M/N_0 is significantly lower. In contrast to stand 11, this low activity is not due to immobilization caused by accumulations of undecomposed litter but by accumulation of N in recalcitrant or inaccessible humified organic matter.

These observations suggest that as a stand ages and N accumulates in the forest floor, the quality of accumulated N initially increases in relative mineralization activity as decomposition of fresh litter progresses and then decreases as humification becomes an important process. The full age sequence (stands 11 to 4) discussed above involved a shift from pine/lichen to spruce/feathermoss forest. Fyles and McGill (submitted) have shown that Cladina lichen residues decomposed rapidly and appear not to accumulate resistant decomposition products while Pleurozium feathermoss decomposes slowly relative to other litter types from these stands. If a pine/lichen stand persists over time the hypothesized accumulation of humified materials may be delayed or retarded because the dominant litter types do not promote their formation. The early establishment of forest vegetation with feathermoss groundcover may, however, accelerate the transformation of organic N to resistant forms.

Vegetation Type

Pine/lichen LFH horizons mineralized substantially less N than those of other forest types, irrespective of age. This dichotomy in stand types was not consistently reflected in any of the parameters measured but appeared to relate to lower weights and concentrations of N and generally lower N_0 or k values in the pine/lichen stands relative to the other types. The presence of pine/lichen vegetation, however, did not appear to significantly influence the N mineralization characteristics of mineral horizons.

Differences between stands in which alder was abundant (3, 13) and other stands, were most prominent in the A horizon where they were observed consistently in N_M, N_0 and N_0/N_T. Total N in this horizon did not appear to be affected by the presence of alder indicating that this species has not increased the amount of N in the horizon but has caused a larger proportion of the N to be potentially mineralizable. The high value of N_0 in the A horizon of stand 2 is anomalous considering the low abundance of alder in this stand. Alder is common in the vicinity of stand 2 and patches within the stand appear to be well established relative to those in other pine/lichen stands. The similarity of the stand 2 A horizon with those of stands with more alder may indicate that this species was more abundant in stands which previously occupied the stand 2 site and that the observed mineralization properties relate more to historical conditions than to present vegetation.

Nitrogen characteristics in the LFH horizon of the young spruce stand (14) were very similar to those in the LFH of the pine/alder stand (3,13). This suggests that inputs, losses and internal transformations within the LFH horizons of both forest types have been similar during the life of these stands. Alder is absent in stand 14 and its surrounding area, implying that N accumulation in the LFH of this stand could not have depended on external N inputs through fixation by alder but must represent a redistribution of N from mineral horizons by cycling through litter from other species. Litter production in stands 3 and 14 did not differ significantly in 1983 (Fyles *et al.* in press) indicating that the potential for redistribution is similar in both stands. If alder had provided a major input of recently fixed N into the LFH of pine/alder stands in addition to redistribution inputs through non-alder litter, it is expected that some difference in N mineralization characteristics between ~~the~~ pine/alder and spruce stands would have been observed. The overall similarity in N characteristics between these stands leads to the conclusion that inputs from alder over the life of the pine/alder stands has been insignificant. The apparent influence of alder on N in the A horizon is probably the result of the historical presence of this species in previous stands. Nitrogen which has accumulated in the spruce stand has probably been conserved in that stand since its original fixation, possibly by alder growing on that site some time in the past. A smaller proportion of total N in the mineral soil in stand 14 is potentially mineralizable than in stands 3 and 13 suggesting that this spruce stand can maintain N mineralization characteristics in the LFH horizons similar to those in the pine/alder stands because of high levels of total N in the mineral soil.

Long Term N Accumulation

Campbell *et al.* (1967) measured mean residence times of various organic fractions in the plow layer of a cultivated grey-wooded forest soil in Saskatchewan and found residence times greater than 450 years for most organic C and 1200-1400 years for that associated with inorganic materials (Ca, Fe, clay). Organic matter in the B horizon below the plow layer (15 cm) probably has a higher mean residence time than that of the surface soil because of smaller inputs of recent residues and cooler average temperatures deep in the soil profile. O'Brien (1984) and O'Brien and Stout (1978) concluded that very old C is uniformly distributed down soil profiles, but that modern C decreases exponentially with increasing depth. Nitrogen is not subject to respiratory loss as is C and therefore must have a longer mean residence time than associated C. This is supported by the observation of Anderson *et al.* (1974) that the C/N ratio of clay-associated (non-extractable) humic acid was lower than that of extractable humic acid.

These observations suggest that N in B horizons examined in this study probably represents an accumulation possibly over thousands of years. The properties of B horizon N therefore reflect 'average' site conditions during a history of numerous generations of forest stands. Since the sites are similar in properties relating to climate and landform, the observed similarities in quality and quantity of B horizon N was to be expected.

The results suggest that the characteristics of N which control mineralization in LFH horizons are strongly influenced by conditions in the existing forest relating to stand age and species composition. Properties of N in A horizons may also be affected by existing vegetation but appear to be controlled to a greater degree by characteristics of previous stands occupying the same site. Nitrogen in B horizons does not appear to be influenced by current stand conditions and its characteristics reflect long-term processes of accumulation and transformation.

Nitrification

Nitrification in forest ecosystems has been discussed in the literature with respect to relationships between N transformations and plant succession (Reiners 1981) and to the impact of forest management on N cycling and loss from forest soils (Vitousek and Melillo 1979, Vitousek *et al.* 1979). Control of nitrification has been attributed to a variety of factors including organic and inorganic inhibitors, pH, nutrient limitations and restricted populations or activities of nitrifiers caused by low ammonium availability or competition with other organisms for N or C (see reviews in Christensen and MacAller 1985 and Olson and Reiners 1983).

Changes in pH were observed by Stanford and Smith (1972) but were considered to be of negligible consequence to total mineralization. Because nitrification has been reported to be pH sensitive (Alexander 1976), increases in the nitrification capacity of many samples over time could have been related to changes in pH brought about by leaching with neutral salt solutions.

The low proportion of total variability explained by the significant correlations between pH and NO_3^-/N_M ($r^2 = .09 - .39$) and the apparent dependence of significance on horizon differences suggest that the observed relationship between pH and nitrification was probably not direct but may have involved a common relationship to a third factor.

Controls on nitrification could not be attributed to low ammonium availability because individual samples commonly accumulated 100-350 ug g^{-1} of ammonium between leachings without significant nitrate production. Limitation of nitrifiers by deficiency in macronutrients is unlikely because a nutrient solution was added at each leaching date. Low initial populations of nitrifying bacteria may have limited nitrate production but even the slow growth rates associated with these organisms could not account for the long time-lags observed in many soils without some other limiting factor being active.

Many of the factors implicated in the control of nitrification are related, in a general way, to characteristics of vegetation or organic matter accumulated on or near the soil surface. The results of this study, in which nitrification was generally much more active in B horizons than in surface layers, are consistent with this observation. Vitousek *et al.* (1979) reported a similar trend for soils in the United States. Among A horizons in the present study, nitrification in samples with the highest organic enrichment was generally lower than in samples with lower organic matter. In this respect, A horizons high in organic matter generally behaved in a similar manner to their corresponding LFH horizons, while nitrification was almost complete in A horizons low in organic matter, as it was in B horizons. A relationship between organic matter and nitrate production is therefore suggested by these data.

Olson and Reiners (1983) and Baldwin *et al.* (1983) demonstrated that phenolic compounds were reponsible for inhibition of nitrification in a balsam fir forest soil. These compounds are gradually degraded in soil (Swain 1979, Haider *et al.* 1975) and their influence on nitrification would be expected to decrease over time if additions did not balance loss. This situation might occur during a long-term incubation because addition of such organics through fresh plant litter or root residues is eliminated. The commonly observed pattern of a time lag followed by an increase in nitrification are thus consistent with control of nitrification by decomposable organic compounds.

Destruction of vegetation by fire or harvesting eliminates organic matter additions to or removal of N from the soils, producing conditions in the field which are analogous to laboratory incubations. In these situations differences in nitrification among sites observed in the laboratory may be observed in the field. Soils of pine/lichen stands were more prone to nitrification. Therefore, under disturbed conditions, a greater proportion of N mineralized in pine/lichen stands would be expected to be nitrified and potentially lost than in other forest types. This prediction is contrary to the conclusion of Vitousek *et al.* (1982) that nitrate loss following disturbance is to be expected only in forest ecosystems with initial high N availability. Field studies using techniques similar to theirs will be required to determine the extent to which predictions based on the laboratory incubations in this study can be applied in the field.

It can be concluded from these data that soils from upland forest stands in central Alberta differ in their capacity to mineralize N as a result both of differences in the quantity of total or potentially mineralizable N, and differences in their first-order mineralization rates. Soils also differ in nitrification potential, possibly because of differences in the chemical properties of soil organic matter. Differences in these properties between surface horizons of the various stands relate mainly to characteristics of the existing vegetation including stand age and species composition. N mineralization characteristics of the mineral soil, however, appear to be more a function of stand history.

Controls on inherent soil properties which determine N mineralization capacity operate within three general time frames: the relatively short time frame of plant succession within which the influence of extant vegetation is expressed; an intermediate time frame required for the accumulation of N to present levels, its distribution throughout the soil profile and its transformation to the observed quality and; a long-term time frame required for the genesis of soil horizons with their associated depletion or enrichment in clay, metals and organic matter. The influence of each of these time frames on the development of N cycling varies with depth in the soil profile. There is little information available in the literature relating the N fertility of a forest stand to soil N properties which have developed within these time frames. Silvicultural procedures, such as prescribed burning or fertilization, influence site fertility primarily through manipulation of short-term controls on nutrient cycling. The effectiveness of these techniques in increasing site productivity is dependent upon the relative importance of the short- and longer-term processes in determining N availability in forest soils. Consequently, an understanding of controls on N cycling which act within different time frames is necessary if the success of management practices is to be predicted.

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7. CYCLING OF NITROGEN AND PHOSPHORUS

7.1 Introduction

The accumulation and properties of organic nutrients (C,N,P,S) in soil under uniform conditions of climate, parent material, and topography can be expected to be controlled primarily by the productivity and nutrient cycling characteristics of the vegetation which has historically occupied a site (Jenny 1980). Conversely, plant growth and nutrient allocation can be strongly influenced by soil nutrient availability (Chapin 1980). This feedback loop between soil nutrient status and cycling processes in plants, involving plant uptake, internal redistribution, litterfall, decomposition and mineralization, may impart stability to nutrient cycling patterns (Pastor *et al.* 1984). The general relationship between plant litter quality and site fertility, in which low nutrient litters are associated with infertile sites and high nutrient litters occur on fertile sites, discussed by Vitousek (1982), may relate to this type of feedback mechanism.

The examination of interrelationships between soil and vegetation requires study sites in which the vegetation has remained unchanged for sufficient time for the ecosystem to attain a steady-state condition, particularly with respect to organic nutrients in the soil profile. At steady-state and with continuous vegetation, soil characteristics can be expected to reflect nutrient cycling patterns of the dominant vegetation. This requirement is often difficult to satisfy because the time to steady-state is probably measured in hundreds of years, a period during which substantial successional change can occur in most ecosystems. Close interrelationships between vegetation and soils may be best expressed in climax communities, such as those studied by Pastor *et al.*(1984), although the period during which a stand has maintained a climax condition is difficult to establish. Long-lived forest stands of the Pacific coast, while not necessarily climax, often maintain a relatively constant species composition for hundreds of years (Franklin and Hemstrom 1981) which may be long enough to establish characteristic nutrient cycling patterns linking vegetation and soil.

In sand ridge ecosystems near Hondo in central Alberta, tree age-structure analysis and examination of soil profile development (Chapters 2 and 3) have suggested that stands regenerating after fire are similar in species composition to the pre-fire forest such that a given site may be occupied by similar stands over many fire cycles. In this situation the vegetation is not perpetual, as in a climax condition, but undergoes a cyclic sequence of short-lived post-fire communities and a longer-lived forest community which dominates the site through most of the stands' existence. Thus, the vegetation of an individual site has historically been dominated by a single forest community comprising relatively few species.

Nitrogen mineralization in forest floor and soil under different forest types has been studied in these sand ridge ecosystems (Chapter 6). N mineralization characteristics differ between pine/lichen, pine/alder and white spruce forest types and appear to reflect the influence of site history as well as present stand conditions. The purpose of this thesis is to report on studies examining interrelationships between soil properties, specifically organic C, N and P accumulation and N mineralization, and nutrient resorption during leaf senescence and nutrient transfer in litter. The specific objectives of the study were 1) to compare different forest types with respect to mass and concentration of C, N and organic and extractable P in LFH and mineral horizons and relate these properties to stand characteristics; 2) to examine foliage and litter N and P levels, nutrient resorption from foliage, and nutrient transfer from vegetation to soil in litterfall in relation to soil N mineralization and extractable P; and 3) to relate the observed nutrient cycling patterns to the stability of vegetation/soil associations over time.

7.2 Study Area

Eight study sites, representing three forest types, were located in an area of sand ridges with interspersed wetlands about 55 km southeast of the town of Slave Lake in central Alberta (55° 00'-10' N; 114° 00'-15' W). The sands originated as deltaic deposits in glacial meltwater lakes and have subsequently been modified by aeolian processes (St. Onge 1972).

Four stands (1,2,11,12), varying in age from 40 to 85 years, represented open jack pine/lichen woodland dominated by jack pine (Pinus banksianna Lamb) with a ground cover of prostrate evergreen shrubs and fruticose lichen, mainly Cladina mitis (Sandst.) Hale & W. Culb. Green alder (Alnus crispa(Ait.)Pursh) occurred in sporadic patches in three of the four stands of this forest type. Soils of these sites had a thin LFH, composed primarily of partially decomposed pine needles, over a weakly developed profile classified as an Orthic Dystric Brunisol.

Two stands, (3,13), aged 65 and 85 years, represented closed canopy jack pine forest with scattered, subdominant white spruce (Picea glauca (Moench)Voss) or black spruce (Picea mariana(Mill.)B.S.P.) and a well-developed shrub canopy of green alder. Feathermosses, predominantly Pleurozium schreberi(Brid.)Mitt., formed a continuous ground cover over a moderately thick, loose LFH of partially decomposed moss and needles. Soils of these stands were more strongly developed than those of the pine/lichen stands, with some evidence of eluviation of clay from the A horizon (Eluviated Dystric Brunisols).

Two stands (4 and 14) aged 80 and 140 years respectively, represented closed canopy white spruce forest with codominant jack pine and occasional aspen (Populus tremuloides(Michx.)) and paper birch (Betula papyrifera Marsh.). Balsam fir (Abies balsamea(C.)Mill.) formed a well-developed subcanopy in stand 4 but was represented only by scattered individuals in the low-shrub layer in stand 14. Shrub species were rather insignificant in this forest type. Feathermosses dominated by Hylocomium splendens(Hedw.)B.S.G. and Pleurozium shreberi formed a thick continuous ground cover. LFH horizons were generally thick and compact with a distinct humified layer lacking in those of other forest types. Soils were classified as Orthic and Brunisolic Gray Luvisols, and have well-developed eluvial A and illuvial B horizons.

Species composition and stand characteristics have been described in greater detail in Chapter 3. Differences in soil development among stands have been discussed in Chapter 2. All stands were located within an 8 km radius so that sites did not differ in macroclimate. The land surface varied throughout the study area with gentle, complex slopes typical of local aeolian landforms. Although stands varied in slope and aspect, there were no consistent differences among forest types.

7.3 Methods

Within each stand a staked plot, consisting of a 50m x 50m (stands 1-4) or 25m x 25m (stands 11-14) area divided into 5m x 5m quadrats, was laid out as a basis for randomizing all sampling. Each plot was equipped with 10, 0.5m x 0.5m wood and fiberglass screen litter traps to monitor litter over one (stands 11, 12, 14) or two (stands 1-4) annual cycles. Traps were installed in stand 13 in July 1983 so that litterfall in this stand was measured for ten months. Annual litter production in this stand was estimated by calculating the proportion of annual litterfall biomass, N and P produced in the other pine/alder stand (3) during the ten months monitored in stand 13 (72%) and increasing production values from stand 13 accordingly. Litter was dried at 65° C and sorted and weighed by components including foliage by species, male cones, and structural material including twigs, bark and associated lichen. Details of collection and sorting procedures are given in Chapter 4.

Sorted litter from each stand from all collection dates except October were bulked by component prior to nutrient analysis. Litter collected from each trap on the October sampling date was analysed separately to give an indication of within stand variability in nutrient concentrations. All samples were ground in a Wiley mill to pass a 20 mesh sieve followed by sulfuric acid/peroxide digestion (Thomas *et al.* 1967), and analysis for total N and NH_4^+ using standard autoanalyser techniques (Technicon Method #334-74W/B+). Samples collected during 1983-84 were analysed for total P using the same digest and autoanalyser method. Selected samples were analysed for total carbon using a LECO automatic C analyser (McKeague 1978).

Foliage was sampled from uppermid crown positions on 5-10 dominant trees of each canopy species in each stand four times in 1982 to determine the timing of peak foliar N and once during the peak period (August) in 1983. In stands containing alder (1, 2, 3, 12, 13), alder foliage was collected from several positions on each of ten alder bushes during the same sampling periods. Nutrient analysis of foliage was carried out using the methods described for litter.

Specific weight of alder foliage was measured on samples of 50 old and 50 young leaves (second and fifth leaves on a shoot respectively), collected from terminal shoots of 10 shrubs in each of stands 1-3 in August 1982. Leaves were pressed, air-dried and weighed and their areas determined using a Li-Cor 3100 leaf area meter. Samples of freshly fallen litter, collected from the ground during litterfall in September were treated similarly to allow calculation of mass loss prior to abscission. Specific weights of coniferous foliage or litter were not examined.

To examine the susceptibility of N and P to leaching loss during the senescence of foliage, samples of alder leaves and pine needles which had begun to change color were collected from two stands in September 1982. Foliage was soaked in distilled water (5-10g in 250 mL) with occasional stirring over one hour. Leachates were analysed for total N and P using the methods described for litter and compared with foliage nutrient concentrations to determine the proportion removed by leaching.

Soils in stands 1, 2, 3 and 4 were sampled to a depth of 40 cm using a 7.6 cm diameter coring tube. LFH horizons were collected from these cores in entirety to allow calculation of mass/area and 4 cm sections were removed in mineral soil horizons to allow calculation of bulk density. Two cores were taken at each of eight random locations in each stand and the mineral soils bulked within locations prior to analysis. Forest floor samples were analysed separately (16 per stand). Deep soil horizons were sampled from 3-4 pits dug to 1.5m in each site using several cores of known volume from each horizon. Soils in stands 11-14 were sampled similarly using pits at four locations. Forest floor and A horizon samples were collected as a composite of five 7.6 cm diameter cores from each location.

All soil samples were dried at 100°C and weighed to allow calculation of mass per area or bulk density. Subsamples were ground to pass a 100 mesh sieve for chemical analysis as follows: total N in forest floor samples using the method described for litter and in mineral soil horizons using a Kjeldahl digest (McKeague 1978) and the same autoanalyser procedure;

total C by LECO carbon analyser as indicated for litter; phosphorus in mineral soils using 0.03 M NH_4F + 0.025 M HCl (weak Bray) (McKeague 1978); organic P was estimated in a single bulked sample from each horizon in each stand by measuring the difference in 0.5 M H_2SO_4 extractable P between samples ignited at 550°C for 2 hr. and unignited samples (Olsen and Sommers 1982). Nitrogen mineralization in forest floors and soil was measured over a 37 week incubation as described in Chapter 6. Net mineralization to a depth of 40 cm was calculated from the data presented in Chapter 6 by multiplying the B horizon values by nine (4 cm sample depth) and summing with the A horizon and LFH values.

One-way analysis of variance (Zar 1974) followed by Duncan's multiple range tests (Chew 1976) were used for statistical comparisons among stands. Logarithmic transformation of data was generally required for weights and ratios of nutrients in soils and litter to ensure homogeneity of variance.

7.4 Results

Forest floor and soil characteristics

Concentrations of C in LFH horizons did not differ markedly between sites (Table 7-1) with only the youngest pine/lichen and old spruce stand differing significantly. Greater variation among stands was observed in N concentrations with pine/alder stands generally higher and pine/lichen stands lower than other forest types. Forest floor P concentrations were highest in the spruce stands but did not differ greatly among the other stands.

Weights of C, N and P in the LFH generally paralleled their concentrations (Table 7-1). The youngest pine/lichen stand (11) had significantly lower weights of all three elements than most other stands while weights of C, N and P in the LFH of the old spruce stand were higher than those of other stands. In general, pine/lichen stands had lower weights of N and P than other forest types. Weights of N in pine/alder forest floors tended to be high relative to other stands.

Similar C:N and C:P ratios were observed in all stands except stand 1. The high ratios in stand 1 probably relate to charcoal which was more commonly observed in the LFH of this

Table 7-1. Chemical characteristics of the forest floors in the 8 stands and the mean N:P ratio of litter produced during 1983 in each stand. **Within** each column, means followed by the same letter do not differ significantly (P .05). The significance of the difference between forest floor and litter N:P ratios determined by t test is indicated following the litter values: ns, not significantly different, * P .05, **P .01.

Stand	Forest Type	Concentration			Weight			C:N	C:P	N:P	Litter N:P
		C	N	P	C	N	P				
		(%)			(gm^{-2})						
1	Pine/lichen	34.8b	.537a	.046a	1600b	24.4b	2.10b	65.4b	762b	11.7ab	13.1**
2	Pine/lichen	30.7ab	.775b	.064bc	1180b	28.6b	2.44bc	41.1a	481a	11.7ab	13.9**
11	Pine/lichen	24.5a	.708ab	.061abc	481a	13.6a	1.20a	35.4a	400a	11.3ab	13.4*
12	Pine/lichen	26.8ab	.690ab	.050ab	992b	25.4b	1.85ab	39.0a	535b	13.7bc	12.8ns
3	Pine/alder/feathermoss	32.3ab	.970c	.064bc	1620b	48.6c	3.22c	33.4a	505a	15.1c	14.9ns
13	Pine/alder/feathermoss	31.3ab	1.053c	.058abc	1510b	51.2c	2.77bc	29.6a	547b	18.5d	14.9ns
4	Spruce/fir/feathermoss	33.0b	.853bc	.071c	3240c	83.6d	6.91d	38.8a	469a	12.1ab	7.9**
14	Spruce/pine/feathermoss	35.8b	.909bc	.088d	1260b	32.0bc	3.10bc	39.4a	408a	10.3a	9.0**

stand than in others. N:P ratios were generally higher in the pine/alder stands than in other forest types and did not differ significantly from the average N:P ratio of litterfall. Although LFH N:P ratios were similar in pine/lichen and spruce stands, they were significantly lower than litter fall ratios in pine/lichen stands and higher than litterfall ratios in the spruce stands.

Weights of C and N in a 50 cm soil profile were lower in pine/lichen stands than in other forest types with the exception of stand 13 (Table 7-2). Weight of organic P to 50 cm differed markedly between forest types being lowest in pine/lichen and highest in spruce stands. Extractable P was significantly lower in the soil of spruce stands than in those of other forest types. Although P extracted using the Bray method has been correlated with P uptake by certain crops growing in some soils, its validity as a measurement of P availability has not been demonstrated in forest systems in Alberta. This method extracts a proportion of readily soluble calcium and particularly iron and aluminum phosphates in acid soils (Olsen and Sommers 1982). The observed differences in extractable P between stands indicate that P in soils under spruce stands is contained in different chemical compounds than P in other soils but this may or may not indicate differences in P availability. Nitrogen mineralized in a 30 cm soil profile including the LFH was low in pine/lichen stands relative to other types and was highest in pine/alder stand soils.

Carbon and N in the mineral soil horizons were highly correlated ($r=0.952$ $P<.01$) but correlations between C and organic P, and N and organic P were not significant. In the LFH no correlations between elements were significant.

Nitrogen and phosphorus flux in litter

Transfer of N in litterfall was, in general, higher in 1983 than in 1982 in the three pine dominated stands (1,2,3)[illegible]t lower in the spruce stand (Table 7-3). Differences in N transfer among pine stands were much more pronounced in 1983 than in 1982 and reflected differences in litterfall biomass described in Chapter 4. The low litterfall in 1982 was associated with abnormally low precipitation in that year compared with abundant rainfall in

Table 7-2. Weights of C, N and extractable and organic P to 50cm depth and N mineralized during a 37 week laboratory incubation to 30cm depth (including forest floor) in the soil profile of each stand. Means followed by the same letter do not differ significantly ($P>.05$).

Stand	Forest Type	Total C	Total N	Organic P	Extractable P	Mineralized N
		gm^{-2}				
1	Pine/lichen	2440c	140bc	20.1	18.1a	10.5
2	Pine/lichen	2860bcd	162c	25.1	16.6a	12.6
11	Pine/lichen	834a	82a	28.2	17.9a	9.2
12	Pine/lichen	1714ab	108ab	25.5	15.8a	11.0
3	Pine/alder/feathermoss	3190cd	214d	30.3	15.9a	18.7
13	Pine/alder/feathermoss	2488bcd	159c	33.1	20.7a	18.7
4	Spruce/fir/feathermoss	3412d	216d	43.4	10.6b	16.4
14	Spruce/pine/feathermoss	3059cd	216d	41.4	8.2b	12.9

able 7-3. Annual transfer of N and P from vegetation to the forest floor in litter by litter component. Means followed by the same letter do not differ significantly (P>.05).

* Values for stand 13 are estimates based on 10 months litter collection.

	Stand	Pine	Spruce	Fir	Alder	Aspen	Total Foliage	Male Cones	Structural	Total
		------	------	------	------	------	(gm^{-2}) ------	------	------	------
1982-83	1	.513			.110		.623a	.026	.053	1.163ab
	2	.445			.195		.640a	.031	.130	0.804a
	3	.619	.016		.324		.960b	.102	.199	1.261b
	4	.059	.644	.155		.055	.913b	.272	.219	1.405b
1983-84	1	.524			.202		.727ab	.034	.068	0.829ab
	2	.645			.308		.953b	.071	.164	1.188bc
	11	.450					.450a	.025	.037	0.513a
	12	.764			.046		.809b	.056	.314	1.179bc
	3	1.031	.002		.559	.058	1.671c	.104	.743	2.519d
	13	1.040	.003		.656		1.724	.170	.359	2.253*
	4	.039	.507	.161		.118	.825b	.112	.433	1.328c
	14	.410	.374			.168	.951b	.043	.269	1.263bc
1983-84	1	.043			.013		.056ab	.002	.005	.063ab
	2	.050			.017		.067d	.005	.011	.083b
	11	.033					.033a	.002	.003	.038a
	12	.060			.002		.063b	.004	.026	.093b
	3	.077	.003		.032	.005	.118c	.007	.047	.168c
	13	.078	.003		.035		.116	.008	.027	.151*
	4	.004	.065	.016		.024	.109c	.010	.046	.164c
	14	.029	.047			.040	.118c	.003	.023	.141c

1983. In both years N transfer in the pine/alder stands was higher than in the other forest types. Phosphorus transfer in litter did not differ between the pine/alder and spruce stands but was significantly lower in pine/lichen stands.

Transfer of N and P in litter were closely related to basal area both on an individual species and a stand basis. Highly significant correlations were observed between N and P transfer in pine foliage and pine basal area ($r=0.951$ and 0.939 respectively, $p<0.01$) and between total litter P transfer and stand basal area ($r=0.891$ $P<.01$). The correlations of N transfer in total foliage litter and total litter with stand basal area were significant only when N transferred in alder foliage was subtracted ($r=0.871$ and $r=0.780$ respectively $P<.01$). Measurements of stand basal area included only canopy trees such that total basal area (including alder) was underestimated. Correlations of N transfer including alder may have been significant if alder basal area were included in the estimate.

Nitrogen transferred in foliage litter in both years was highly correlated with N mineralized in a 30 cm profile (1982, $r=0.960$ $P<.05$; 1983, $r=0.892$ $P<.01$). The correlation with 1983 data was improved by exclusion of stand 4 data from the data set ($r=0.992$ $P<.001$) (Figure 7-1). Nitrogen transferred in total litterfall in 1983 was also correlated with N mineralized ($r=0.940$ $P<.01$) as was P transferred in total and foliage litter ($r=0.900$ and 0.865 respectively $P<.01$).

Turnover times

The values of turnover time presented in Table 7-4 have been calculated using rates of elemental input to the forest floor and soil based on a single annual measurement in each stand. The calculation has ignored input from senescing root tissue which may be greater than that from aboveground litter. Therefore, the calculated values are considered to be approximate estimates only. Methods used in the collection of data and calculation of turnover were, however, consistent among stands and elements such that relative differences in turnover reflect differences in stand or elemental properties.

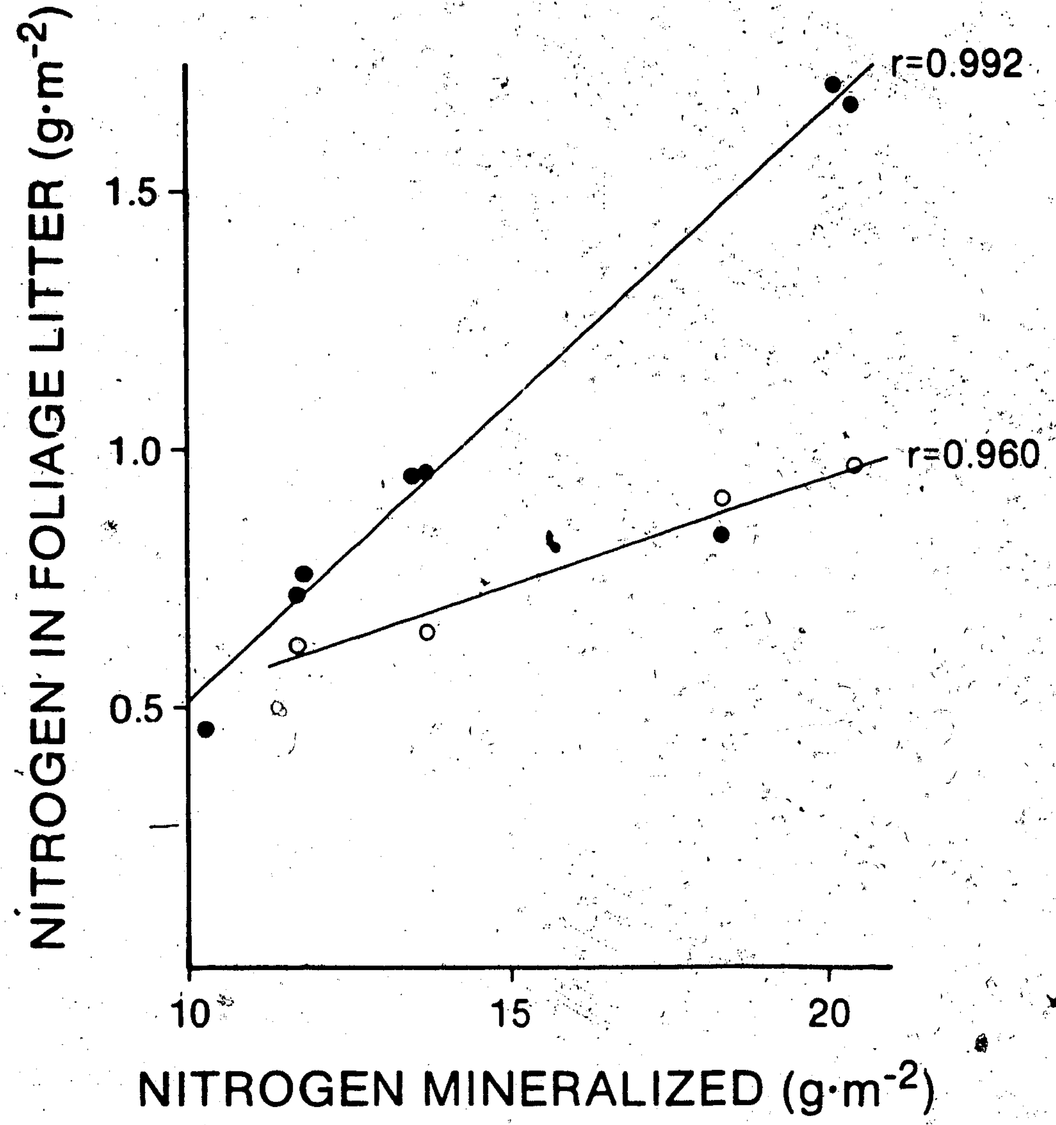

Figure 7-1. Nitrogen flux in foliage litter in 1982 (○) and 1983 (●) in relation to N mineralization in a 30 cm soil profile calculated from laboratory incubation data.

Table 7-4. Turnover times of C, N, and total or organic P in the forest floor and soil of the eight stands. All P in the forest floor was considered to be organic.

Stand	Forest Floor			Forest Floor and Mineral Soil		
	C	N	P	C	N	Org. P
	(yr)			(yr)		
1	23	31	35	58	200	360
2	13	26	31	45	160	330
11	6	29	34	16	190	770
12	8	24	22	23	116	300
3	9	20	20	28	105	200
13	9	23	19	24	94	240
4	29	65	44	60	227	300
14	10	26	22	33	197	370

Turnover times of C in the LFH were short relative to N and P with the exception of stands 1 and 4 in which turnover was considerably longer. Turnover times for N and P in the LFH fell within similar ranges of 19-35 years. Turnover of P was slower than that of N in the LFH of three of the four pine/lichen stands while it was faster than that of N in LFH of both spruce and the pine/alder stand.

In the soil profile to 50 cm, the C turnover varied among stands but in all sites was substantially shorter than that of N and P. Turnover times of N ranged from 160-230 years in most sites, with the exception of both pine/alder and the oldest pine/lichen stand in which it was about half of that in other stands. In most sites the turnover of organic P in a 50 cm profile ranged from 300-370 years. However, both pine/alder stands were below this range while the youngest pine/lichen stand (11) was substantially higher.

Dynamics of nutrient concentrations in foliage and litter

The concentrations of N in pine foliage in August (Table 7-5) differed significantly among stands and were highly correlated with N mineralized in a 30 cm profile ($r=0.876$ $P<.01$). Phosphorus concentration in pine foliage also varied among stands but differences did not consistently reflect forest types although both pine/alder stands had lower concentrations than the others. Foliar P concentrations were correlated with weight of organic P in the 50 cm profiles ($r=0.718$ $P<.05$) but not with extractable P ($r= -0.504$ $P>0.2$). The concentration of N in spruce foliage was highest in the pine/alder stand and lowest in the old spruce stand but foliar P concentrations did not differ among sites. Alder foliage did not differ in N concentration between stands in 1982 but was generally higher in the young pine/lichen stands than in other stands in 1983.

October pine and spruce litter had similar concentrations of N in all sites and in both years with values generally falling within the range of 0.3% - 0.4%. Phosphorus concentration in October litter also differed between stands but concentrations in spruce were about twice as high as in pine. Concentrations of N and P in alder litter were substantially higher than those in pine and spruce and variation among stands, particularly in N concentrations, was higher

Table 7-5. Concentration of N and P in August foliage and October litter and the proportion of each nutrient removed prior to abscission calculated as: (foliage - litter)/foliage. Within columns, means followed by the same letter do not differ significantly (P>.05).

Species	Year	Stand	Foliage		Litter		% Change	
			%N	%P	%N	%P	N	P
Jack Pine	1982	1	1.296ns		0.384		70.4	
		2	1.197		0.355		70.3	
		3	1.255		0.404		67.8	
		4	1.355		0.352		74.0	
	1983	1	1.112abc	0.124ab	0.348	0.021	68.7	83.1
		2	1.232cd	0.132ab	0.363	0.021	70.5	84.0
		11	1.015a	0.117a	0.301	0.021	70.3	82.1
		12	1.074ab	0.116a	0.364	0.028	66.1	77.6
		3	1.297d	0.149c	0.389	0.030	70.0	79.8
		13	1.234cd	0.135b	0.337	0.023	72.7	83.0
		4	1.222bcd	0.156c	0.337	0.043	69.1	72.5
		14	1.160abcd	0.139c	0.327	0.025	71.8	82.0
Spruce	1982	1						
		2						
		3	1.117		0.438		60.8	
		4	1.135		0.348		69.3	
	1983	1						
		2						
		11						
		12						
		3	1.177c	0.201ns	0.451	0.058	61.7	71.1
		13						
		4	0.880a	0.167	0.363	0.052	58.7	71.2
		14	1.038b	0.180	0.366	0.048	64.7	71.1
Alder	1982	1	2.155ns				37.7	
		2	2.582				36.5	
		3	2.530				32.0	
		4						
	1983	1	2.794c	0.203ns	1.849	0.106	33.8	47.7
		2	2.747bc	0.187	1.803	0.104	34.4	44.4
		11						
		12	2.623ab	0.188	1.882	0.104	28.2	44.8
		3	2.642abc	0.194	2.084	0.110	21.1	43.2
		13	2.582a	0.179	2.100	-	27.1	-
		4						
		14						

in alder than in other litters.

Change in nutrient concentration between young foliage and litter can be interpreted as the result of redistribution of nutrients as needles age on the tree and resorption prior to leaf abscission. Concentrations may, however, be influenced by changes in leaf mass caused by resorption of C and loss of nutrients by leaching as well as by nutrient resorption. Changes in specific weight of conifer needles were not measured but any changes in mass which may have occurred would be expected to be consistent among stands such that comparisons of resorption based on concentration are probably valid within a species and possibly between conifer species. The specific weight of October alder litter did not differ from that of August foliage (foliage, 7.07±0.18SE mg cm^{-2} vs litter, 6.71±0.17SE; t test, P>0.1). Leaching senescing foliage for one hour removed 0.33% ± 0.06SE of N and 1.18% ± 0.48SE of P from pine needles and 0.12% ± 0.03SE of N and 4.1% ± 0.59 SE of P from alder leaves.

Within each species percent change in nutrient concentration between foliage and litter was similar in all stands and in both years (Table 7-5). Nutrient concentrations were significantly lower in litter than in foliage in all cases but, because foliage and litter measurements were not directly paired, statistical comparison of the magnitude of change was not possible. It is unlikely, however, that differences between stands within a species are significant, with the possible exception of the change in P concentration in pine in stand 4 which was distinctly lower than comparable values in other stands. In all species, change in concentrations of P was higher than that of N and the magnitude of change of both N and P concentrations was consistently higher in pine than in spruce and higher in the conifers than in alder.

Seasonal change in nutrient concentration in foliage and litter

The data relating to seasonal change in foliage nutrient concentration are somewhat meager because sampling was conducted to broadly identify the period of peak N concentration rather than to specifically monitor seasonal patterns. Some distinct seasonal trends are, however, apparent (Figure 7-2). Nitrogen concentrations were, in general, lowest

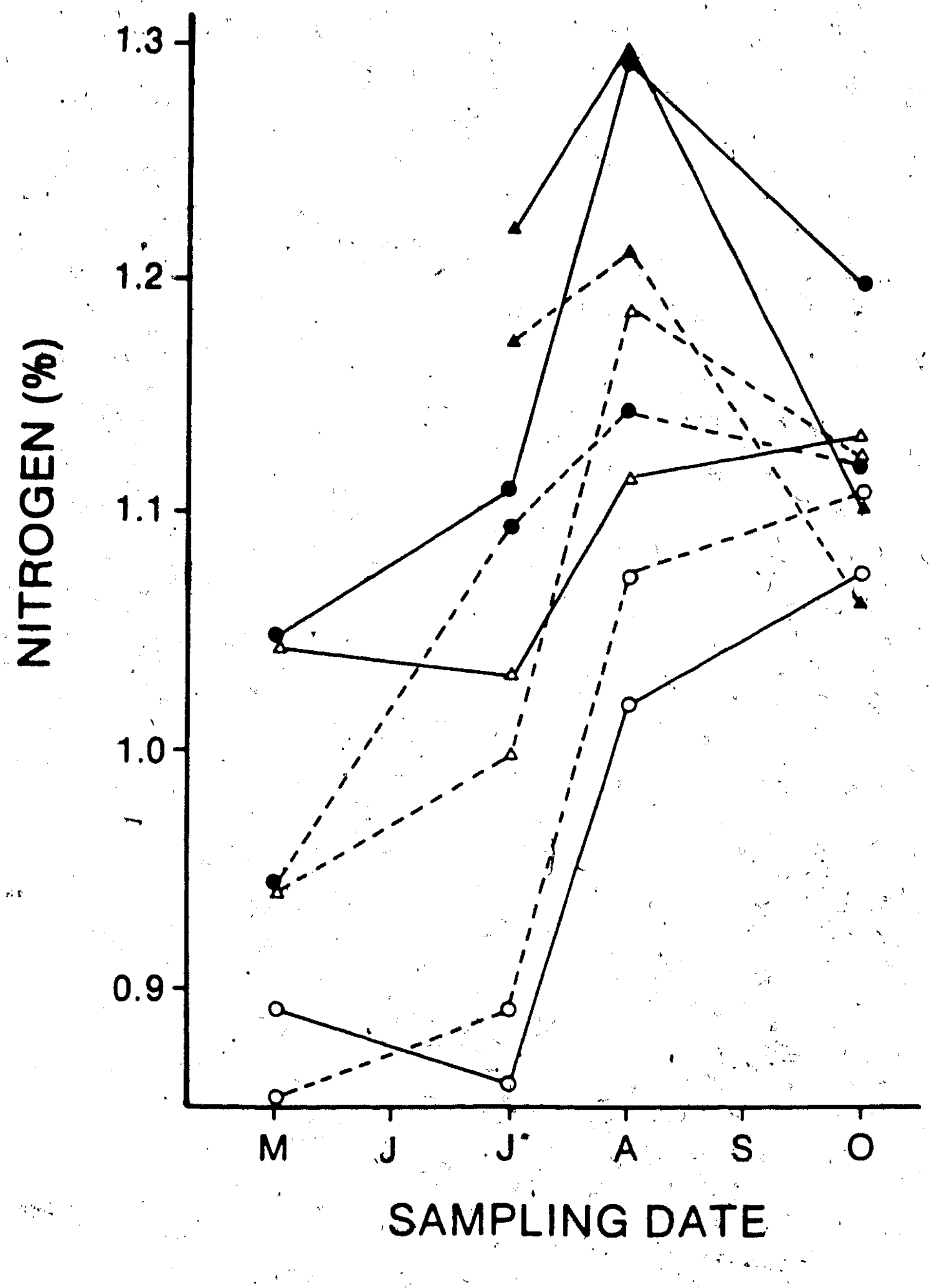

Figure 7-2. Nitrogen content of jack pine foliage from stands 1 (solid line) and 2 (dashed line) at four dates in 1982. Needle cohorts: 1982▲, 1981△, 1980●, 1979○.

in the spring prior to the flush of new growth and changed slightly during the June-July growth period. The pattern of change differed between needle age-classes with young needles increasing markedly in N concentration while older needls increased slightly or decreased during the same period. Nitrogen concentrations increased during August in all needle cohorts and then appeared to converge on similar values over the late summer and autumn.

Nutrient concentrations in foliage litter from all species in all stands followed a cyclical pattern over the year with concentrations rising from an autumn low to a peak in mid-summer and then declining again in the following autumn (Figures 7-3, 7-4). Patterns within species were similar but concentrations differed between stands at each date. Nitrogen concentrations in pine litter were consistently higher in stand 3 (pine/alder) than in other stands, were lower in stands 12 and 14 and much lower in stand 11. Phosphorus concentrations in pine litter were consistently higher in stand 4 than in other stands while stands 11 and 14 were lower. Cyclical patterns in N and P concentrations were observed in alder litter but standard errors, measured within stands in September litter, were so high that differences between dates were probably not statistically significant.

Nitrogen:phosphorus ratios of October pine needle litter were significantly higher than those of August foliage in all stands except 4 and 12 (Table 7-6). N:P ratios did not differ in alder foliage and litter and were not significantly or only slightly different in spruce.

7.5 Discussion

Accumulation of C, N and P in forest floors and soils

Forest stands in the Mixedwood Section (Rowe 1972) of western Canada are normally destroyed by fire at intervals ranging from 50 to 200 years (Heinselman 1981) and thus are short-lived relative to many other forests of the world. In the Hondo area stands or individual trees exeeding 100 years in age are uncommon. In these forests, the long-term supply of nutrients which drive or support ecosystem processes is dependent largely upon accumulated nutrients in the soil because nutrient pools maintained in the vegetation are subject to loss or are returned to the soil during fires. Differences in the accumulation of organic nutrients in

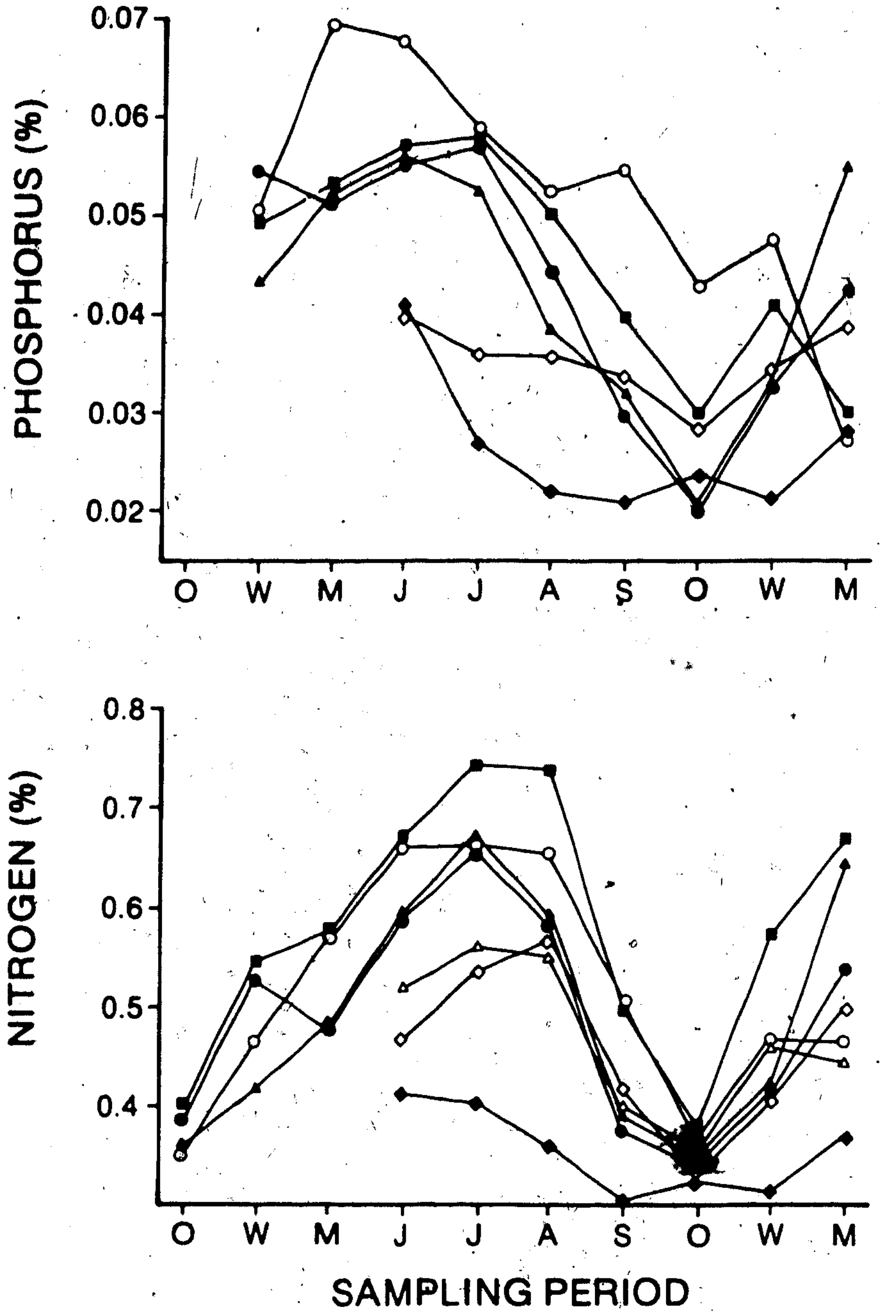

Figure 7-3. Nitrogen and phosphorus contents of jack pine foliage litter between October 1982 and May 1984. W=winter. Stands: 1●, 2▲, 3■, 4○, 11◆, 12△, 13□, 14◇.

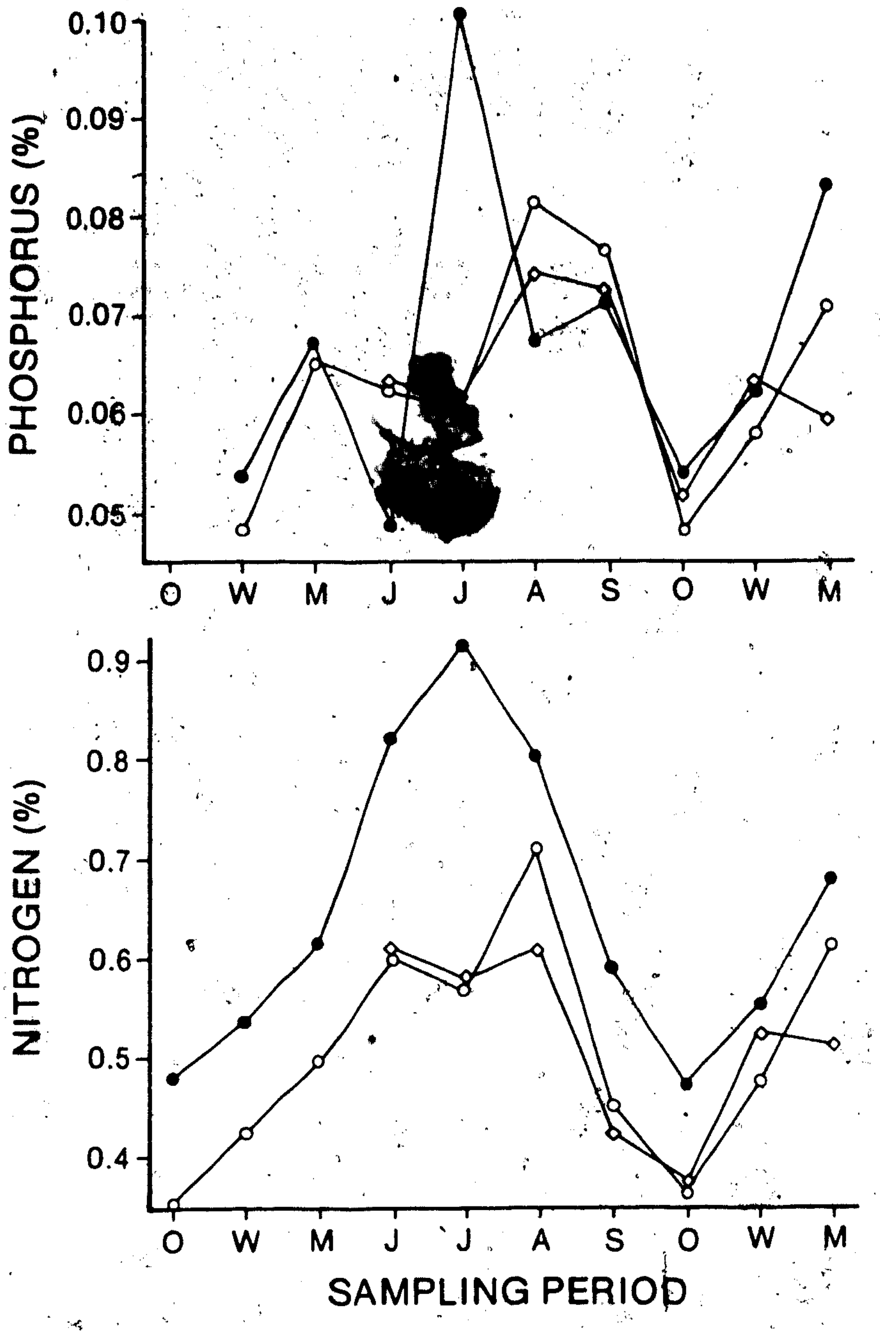

Figure 7-4. Nitrogen and phosphorus contents of spruce and fir foliage litter between October 1982 and May 1984. W=winter. Stand 4 spruce ○, stand 14 spruce ◇, stand 4 fir ●.

Table 7-6. N:P ratios of 1983 August foliage and October litter from pine, alder and spruce and the significance of the difference between them. ns: not significantly different, *: $P<.05$, **: $P<.01$.

	Pine			Alder			Spruce		
Stand	Foliage	Litter	Sign.	Foliage	Litter	Sign.	Foliage	Litter	Sign.
1	8.9	16.6	**	14.1	15.9	ns			
2	9.3	17.3	**	15.1	18.3	ns			
11	8.7	15.0	**						
12	9.5	13.0	ns						
3	8.8	13.0	**	13.1	16.2	ns			
13	9.5	14.7	**						
4	7.9	8.8	ns				5.4	7.6	*
14	8.3	16.4	**				5.9	5.8	ns

the soil among ecosystems can be expected to reflect fundamental and historical differences in ecosystem properties.

The accumulation and turnover rates differ among organic C, N and P because of differences in the mechanisms by which these elements are mineralized (McGill and Cole 1981). Carbon can be expected to cycle most rapidly through soil because it is subject to direct loss through microbial respiration. Organic N may be mineralized during microbial utilization of carbon-nitrogen compounds but may remain immobilized in microbial tissue or, will remain in soil in mineral form unless removed by plant uptake, leaching, ammonia volatilization or denitrification. The net turnover rate of N in the soil would, therefore, be expected to be slower than that of C. Organic P (P_0) is thought to be mineralized under conditions of P stress in microorganisms or plants because specific phosphatase enzymes must be synthesized to remove phosphate groups from organic molecules. The slow rate of turnover of P_0 in soil has led to its use as an indicator of soil development (Walker and Syers 1976). The close association of C and N mineralization and the independence of P from these elements is consistent with the high correlation between the C and N contents of the mineral soil and the lack of correlation of P_0 with these elements.

Differences in turnover time between C, N and P_0 observed in this study are consistent with their different turnover mechanisms. In both LFH and soil the turnover of C was substantially shorter than that of N or P. The turnover time of P in the LFH was similar to that of N but, in the mineral horizons was much longer. The degree to which accumulation of an organic nutrient in soil reflects historical conditions is dependent upon its rate of turnover. In this study the turnover times of C, N and P in the LFH horizon were shorter than stand age, suggesting that LFH characteristics primarily reflect conditions of the present stand. The turnover time of C in the 50 cm profile was also generally shorter than stand age implying that C concentration or weights are controlled by recent conditions. The longer turnover times of N and P_0 in the 50 cm profile suggest that concentrations and weights of these nutrients in the mineral soil can be expected to reflect historical differences between sites with P_0 reflecting a longer history than N. When interpreted in this context, the weights of N and P in mineral soil are consistent with observations of stand age structure and soil profile development (Chapters 2 and 3) which suggest that the present characteristics of these ecosystems relate to differences in vegetation history.

Mineral soil characteristics, while relatively uniform within forest types, vary between sites with respect to individual nutrients and may indicate similarities between stands which are not apparent in the existing vegetation. The weights of P_0 in the soil of the two pine/alder stands (3 and 13) are similar, which is consistent with the concept that the forest type occupying a given site has been constant historically. However, stand 13 has significantly less total soil N than stand 3 and is more similar to pine/lichen stands 1 and 2 in this respect. These data imply that stand 13 has been similar to stand 3 in the past but more recently may have had a lower abundance of alder and thus been more similar to the pine/lichen stands. Data presented in Chapter 6 suggested that alder may have been more abundant in stand 2 in the past, leading to the conclusion that alder abundance in these stands is somewhat dynamic. Stand 11 at present contains no alder, and the very low levels of N in the soil of this site suggests that this species may have been absent or in low abundance historically.

Relative demand for N and P

Differences in N:P ratios between litterfall and the LFH in each site may be interpreted with respect to the relative availabilities of N and P to plants and also provide information relevant to the understanding of organic nutrient dynamics in the soil. If N and P were mineralized from decomposing litter by the same mechanisms, and if demands for the two nutrients were equal, the ratio of N:P in the forest floor should equal that of the annual litter input. This was not the case in most stands examined. In three of the four pine/lichen stands the litter N:P ratio was significantly higher than that of the LFH indicating that N was being removed from the LFH more rapidly than P. In contrast, LFH N:P ratios were higher than those of incoming litter in the spruce stands indicating that P was being removed from the LFH horizons preferentially over N. Again, this is consistent with the turnover data in which the residence time of N was greater than that of P in these stands. Removal of N from a soil faster than P is to be expected because N is mineralized as a direct result of organic matter decomposition. Removal of P from soil faster than N would only be expected under conditions of P stress as indicated previously. This suggests that the demand for P relative to N in spruce stands is higher than that in pine stands. Further, roots, mycorrhizae or associated microorganisms in these stands must preferentially mobilize organic P, presumably through the synthesis of phosphatase enzymes in the forest floor. The hypothesized high demand for P by white spruce is consistent with high foliar P concentrations measured in this species relative to pine. Van Cleve and Noonan (1975) report turnover times of N in the forest floors of aspen stands in Alaska which were 3-4 times longer than those of P implying that aspen has a high demand for P. Aspen is more common in the Hondo spruce stands than on other sites and also may contribute to the rapid turnover of P in these LFH horizons.

The results also imply that pine/lichen stands may be limited by N availability, an observation which is consistent with low levels of N mineralization measured in pine/lichen stand soils. Severely N-limited systems could be expected to have a low demand for P and would be unlikely to invest energy to mobilize organic P. This is corroborated by data from stand 11. This is the stand most likely to be under acute N stress, it has the highest level of soil organic P among pine/lichen stands, and this P has a turnover time more than twice that in any other soil.

The two pine/alder stands and the oldest pine/lichen stand differ from the other sites in that the N:P ratios of litter and forest floor do not differ significantly. This implies that mineralization and uptake in these forest floors are somehow balanced. Alder maintains high foliar P levels and presumably has a high demand for this nutrient. It is possible that, in pine/alder stands, pine demand for N and alder demand for P preclude the accumulation of one nutrient over the other. It can be hypothesized that the overall rate of decomposition and N mineralization in pine/alder forest floors is increased by input of high-N alder litter and that high pine productivity and concommitant production of organic P is supported by high N availability. This would ensure continued abundance of LFH P which can be utilized by alder. In this connection, it is interesting that the turnover times of N and P in both the LFH and

50 cm profile are lower in the pine/alder stands than in the other forest types.

Controls on N and P transfer in litter

The nature of the controls on nutrient transfer in litter are suggested by the significant correlations of annual nutrient flux with basal area and soil N mineralization. The relationship between BA and nutrient flux undoubtedly stems from the relationship between BA and litterfall mass (Chapter 4) arising from the overall control of stand biomass on litter production. It is reasonable to expect that a species which accounts for a high proportion of stand biomass will make a larger contribution to litterfall nutrient flux than a species with small relative biomass. This generality is not, however, without exceptions. Old individuals, such as the jack pine in stand 4, may consitiute a large stem biomass but support a small foliage mass and contribute little to foliage litterfall; deciduous shrubs or trees, particularly alder, may have high foliar nutrient levels and litter productions relative to their total biomass. A corollary of the relationship between BA and nutrient flux is that factors controlling basal area will influence nutrient cycling. Stand BA increased with stand age ($r=.759$ $P<.05$) such that an increase in nutrient transfer in litter with increasing age would be expected. Comparison of basal area increments among forest types of similar age suggest that the rates of increase in BA and, by association, nutrient flux, differ among sites (BA increment (m^2yr^{-1}): stands 80-85 years; S3, 0.402; S12, 0.329; S4, 0.497; stands 65 years; S2, 0.312, S13, 0.490). A feedback mechanism appears to be in effect such that high site fertility tends to result in higher productivity and annual biomass increment, and larger amounts of nutrients cycled through litter which in turn maintains site fertility. While this feedback mechanism may explain the maintenance of nutrient cycling patterns in sites of differing fertility and productivity, it does not address the question of how different nutrient cycling patterns and rates originally became established in sites which are similar in edaphic and climatic conditions.

The correlations between N flux in litter and N mineralization (Figure 7-1) are consistent with the hypothesis that fertile sites cycle more nutrients than infertile sites. The estimate of N mineralized in a 30 cm soil profile is based on a laboratory incubation and must be interpreted as an index of the potential of a soil to mineralize N. It is expected that a soil with a high potential to mineralize N, as measured in the laboratory, would mineralize more N in the field than a soil with low mineralization potential under uniform field conditions. The correlation of mineralization estimates with N cycling and pine foliage N concentrations supports the validity of this assumption. The degree to which the N mineralization potential of a soil would be realized in the field, however, would be expected to vary with temperature and moisture such that differences in mineralization potentials among soils may not be fully expressed in very dry years.

Differences in N flux in foliage litter between stands were more distinct in 1983 when plant growth and mineralization would not have been restricted by moisture availability than in 1982 when moisture availability was more limiting. The magnitude of the difference between the two years in N flux in pine stands appeared to vary with N availability even though this difference was the result of changes in litter mass rather than nutrient concentration (Chapter 4). It is possible that retention of old needles in pine is dependent upon the amount of current growth such that needles will be abscissed if current year needle mass is high but will be retained if current growth is limited. In stands with low N availability, such as stand 1, current-year growth may be limited by N and not respond greatly to changes in moisture availability. Pines in these stands would be expected to abscise similar masses of needles in wet and dry years. In stands with higher N availability, such as stand 3, current year growth may be limited primarily by moisture such that growth and concomitant litter production is higher in wet years. Foliage litter N flux in the spruce stand did not differ between years even though N availability was high. The spruce and fir in this stand maintain their needles for 10 or more years with wide variation in needle retention between trees or branches within a tree. It is possible that these species have greater flexibility than pine in the biomass of needles maintained on a tree such that current-year growth does not replace but may be added to older needle cohorts.

Controls on nutrient dynamics in foliage and litter

Growing tissues are considered to be nutrient sinks which draw on nutrients either from the soil or from older tissues (Hill 1980, Salisbury and Ross 1978). Nutrient demand or sink strength of growing tissue is high in early spring and decreases as new leaves mature later in the summer. Nitrogen availability in the soil is expected to be low in the early spring because of low soil temperatures but will increase as the soil warms if moisture is adequate. Consequently, older tissues are important nutrient sources in early spring. Mineralization of N is probably maximum in mid-August and diminishes thereafter as soils cool in the autumn. Phosphorus availability, which relates to both organic and mineral forms of P, follows a less predictable pattern and may depend, in part, on plant demand. Thus plant demand and nutrient availability vary independently resulting in seasonal variation in the demand placed on nutrient pools in older foliage which should be reflected in foliage and litter nutrient concentrations.

The pattern of change in foliage and litter nutrient concentrations and differences in this pattern among stands is generally consistent with predicted source/sink relationships controlled by plant growth and soil nutrient availability. Low N concentrations in foliage during the period of May-July are consistent with removal of N from mature foliage early in May to support the development of new needles prior to bud burst, at a time of low soil N availability. As the season progressed, both foliage and litter N concentrations increased as would be expected with decreasing nutrient demand by new needles and increasing supply. Differences between sites in the rate of increase and in peak N content of litter generally reflected soil N availability and suggested that resorption from needles prior to abscission was higher in less fertile sites. In pine litter P concentrations increased less than did N concentrations, and P content remained relatively high through the first half of the summer. In contrast, P concentrations in spruce litter remained relatively low from May until July and then rose rapidly to peak in August and September. These results corroborate previous suggestions that P stress was higher in spruce than in pine. High nutrient concentrations in associated fir litter suggests limited growth potential in the subcanopy position occupied by this species.

The concentrations of N and P in litter from all species declined markedly between August and October even though demand would be expected to be low during this period and nutrient availability would not have been restricted by low temperatures until well into September. These results suggest that nutrient resorption during autumn senescence is not controlled by source/sink relationships determined by the balance of growth demand and availability but is under the control of genetic, possibly hormonal, cues. This is consistent with observations of seasonal patterns of daily production which suggested that autumn litterfall was controlled by internal plant processes (Chapter 4). In addition, calculation of nutrient resorption from maximum foliage and minimum litter nutrient concentrations indicated that, although the proportion of nutrients resorbed prior to abscission differed among species, it was remarkably uniform within species, between sites which differed greatly in nutrient availability (Table 7-5). If autumn nutrient resorption was influenced by nutrient availability, differences among stands would have been expected to be much greater.

October litter N concentrations were uniform among stands, years, and pine and spruce indicating that the control on autumn N content may be universal in pine and spruce. Nitrogen remaining in needles at the minimum concentration may have been that associated with structural material. If this is true, autumn N resorption in pine and spruce represents total retrieval of N which can be enzymatically mobilized. The high N contents of October alder litter and their wide variability within and among sites suggest that controls on autumn resorption in this species are different from those active in conifers.

The results of this study relating to nutrient dynamics of foliage and litter indicated that feedback mechanisms linking the nutrient contents of litter falling on the LFH with soil nutrient availability via plant nutrient uptake and allocation, are active during the spring and early summer. The connection between soil nutrient availability and litter nutrient concentration does not, however, appear to be active during autumn senescence. In general, winter litter nutrient contents are similar to those in autumn suggesting that much of the litter collected during winter was abscissed in autumn but did not fall. Thus, litterfall nutrient concentrations appear to be independent of site fertility during the majority of the year, and the proportion of total litterfall in which nutrient concentrations are influenced by availability is low, probably less than 20 % (Chapter 4).

This research has shown that, although N and P concentrations in litter and foliage in early summer reflect soil nutrient availability, nutrient concentrations in a high proportion of litter are generally controlled by genetically determined processes characteristic of each species and independent of site fertility. The mass of N or P returned to the soil in litter produced by a given species in a stand is determined by these species-specific allocation patterns and the biomass of that species in the stand. Thus, stands may differ in their nutrient cycling characteristics because of differences in biomass or in species composition. One aspect of the feedback mechanism which ensures proportionality between nutrient cycling through plants and soil fertility undoubtedly relates directly to biomass accretion because sites with high nutrient availability support higher productivity and growth rates than less fertile sites. In addition, feedback control between soil fertility and species composition would exist if nutrient cycling patterns established by a species in one stand promoted the establishment and survival of that species or reduced the survival of other species in subsequent stands. A better understanding of the influence of soil fertility on growth and survival of individual species and on species interactions may be required before the stability in vegetation and nutrient cycles can be fully explained.

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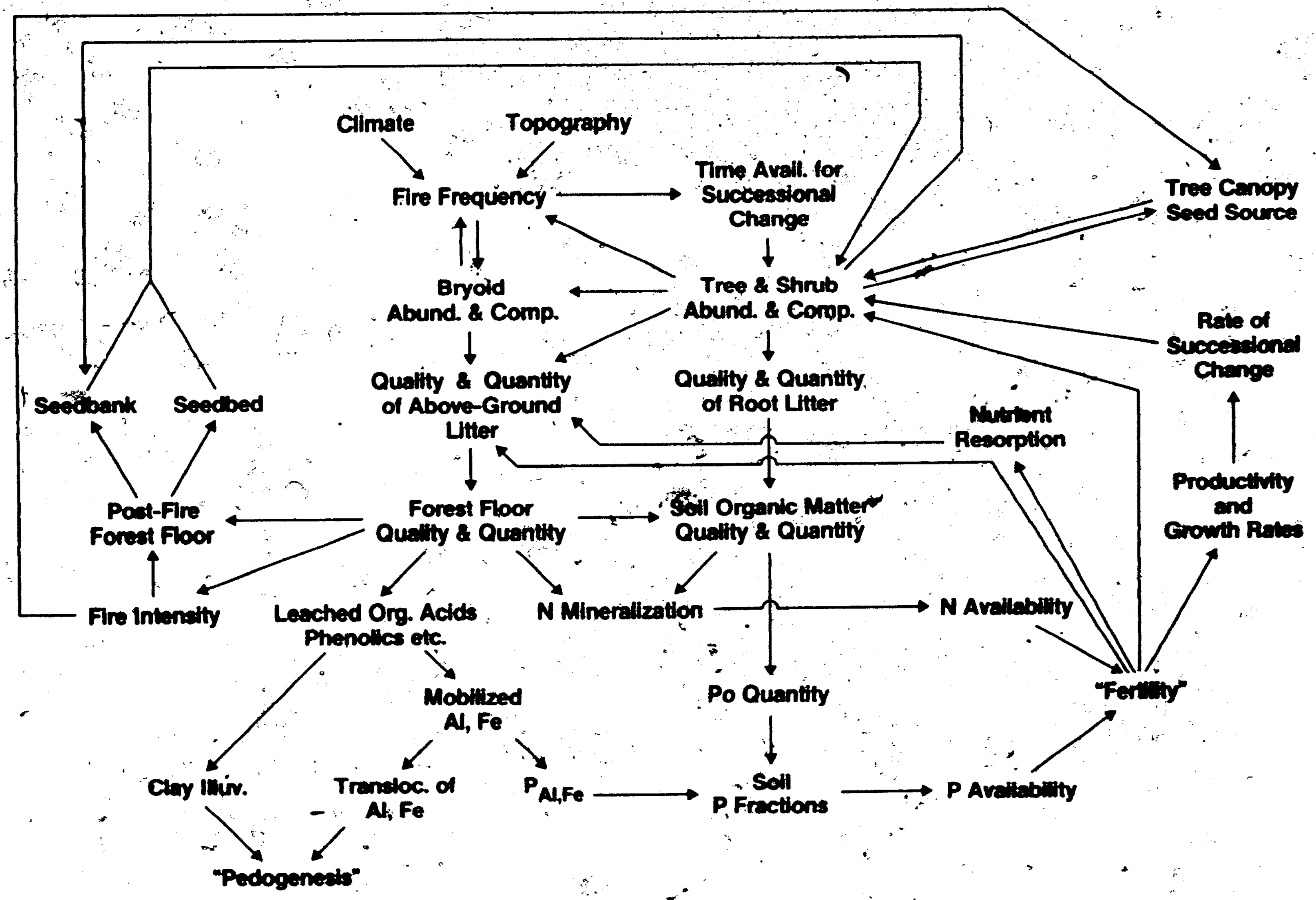
8. SYNTHESIS

The results of this research suggest that sand ridge ecosystems in the Hondo area have remained relatively stable with time and exhibit characteristic combinations of vegetation species composition, soil development and nutrient cycling patterns. In broad terms, ecosystems with pine/lichen vegetation have weakly developed soils with a small capital of N and P which support low levels of N and P cycling. In contrast, spruce-dominated systems have soils with greater profile development and a large nutrient capital which supports a high level of nutrient cycling. Pine/alder systems are intermediate between the other forest types in soil development and nutrient capital but appear to cycle nutrients more efficiently, resulting in higher levels of nutrient cycling than would be predicted from nutrient capital in relation to other systems.

During this research, a conceptual model was developed as a working hypothesis of controlling relationships among ecosystem properties and processes. The model was used to organize data collection and to identify parameters requiring measurement. Control mechanisms included in the model were demonstrated by, or inferred from, data collected in the Hondo stands or obtained from published reports of research in other areas.

The conceptual model, shown graphically in Figure 8-1, describes the Hondo ecosystems in terms of relationships among vegetation characteristics, fire frequency and intensity, forest floor properties and factors relating to soil profile development and soil fertility. Processes relating to the dynamics of soil water and to the influence of soil texture on various system components were not included specifically, although they cannot be considered insignificant. Relationships among system properties and processes result in a series of feedback loops which may explain the long-term ecosystem stability suggested by the results of this study. The processes described in the model can be broadly divided into three categories: 1) controls on the relative abundance of species within a stand; 2) controls on soil development; and 3) controls on site fertility. Within each of these categories, the mechanisms which may have resulted in the observed differences between ecosystems in the Hondo area are discussed in detail below.

Figure 8-1. Hypothetical conceptual model of processes active in the Hondo stands.


Climate
Topography
Fire Frequency
Time Avail. for Successional Change
Tree Canopy Seed Source
Bryoid Abund. & Comp.
Tree & Shrub Abund. & Comp.
Rate of Successional Change
Seedbank
Seedbed
Quality & Quantity of Above-Ground Litter
Quality & Quantity of Root Litter
Nutrient Resorption
Productivity and Growth Rates
Post-Fire Forest Floor
Forest Floor Quality & Quantity
Soil Organic Matter Quality & Quantity
Fire Intensity
Leached Org. Acids Phenolics etc.
N Mineralization
N Availability
Mobilized Al, Fe
Po Quantity
"Fertility"
Clay Illuv.
Transloc. of Al, Fe
$P_{Al,Fe}$
Soil P Fractions
P Availability
"Pedogenesis"

Controls on vegetation

Two basic questions regarding vegetation arose during this research: 1) why did different sites support different forest types? ; and 2) what mechanisms led to continued replacement of pre-fire stands by post-fire stands of similar species composition as has been suggested by Heinselman (1981) and the results of Chapters 2 and 4?

In Swedish boreal forests, sites which burn frequently, because of climatic, topographic or human influences, support pine/lichen woodland while sites protected from fire develop spruce/feathermoss forest (Tamm 1982). Although this relationship among forest types has not been demonstrated in Canadian boreal regions, Rowe (1971) has suggested that white spruce can become dominant only in areas with fire return intervals longer than its reproductive cycle of 40-60 years. In areas with more frequent fires, there is insufficient time for establishment, growth and sexual maturity of white spruce, and species with shorter reproductive cycles predominate.

Differences in fire frequency may explain differences in vegetation among the Hondo sites. Both spruce stands are located on sand ridges which are isolated from other upland sites by fen complexes and bog forest and would be unlikely to be burned by fires ignited in other areas. In contrast, the pine/lichen stands are located in extensive upland areas with few features that would restrict the spread of fire. The pine/alder stands are in an intermediate position located on the edge of a broad upland area.

Differences in soil texture among sites may also explain differences in forest vegetation. White spruce is more commonly observed growing on fine-textured soils than is jack pine and may have a requirement for, or an advantage on, soils with high clay contents. However, white spruce occurs extensively on sandy soils in northeastern Alberta (Raup 1946). The influence of soil texture on the geographic distribution of these species has not been examined in the literature so that conclusions must remain speculative.

Many boreal species appear to be adapted to frequent destruction by fire (Heinselman 1981) and possess modes of reproduction or regeneration which ensure their re-establishment in post-fire stands. This results in little change in species composition between generations of forest. The ability to sprout from below-ground organs is a[illegible]bute common to many boreal species including trembling aspen, green alder and [illegible]ow shrubs and herbs and allows immediate re-establishment after fire. Thus, the presence of these species in a stand is, in most cases, indicative of their presence in previous stands and probable presence in subsequent stands. Only a particularly hot ground fire will result in the elimination of clonally regenerative species. Jack pine has serotinous cones which open and shed seed only after being exposed to heat, ensuring timely input of seed to the post-fire stand and the continued presence of this species on a site. White spruce appears to have no specific adaptations for regeneration after fire although it frequently acts as a pioneer in post-fire stands (Chapter 3; Rowe 1971). This species is considered to be dependent on surviving trees within or on the periphery of a burned area as seed sources (Zasada and Gregory 1969). Preliminary evidence from the Hondo stands indicates that white spruce will germinate from seed-bank stored seed (Table 8-1), which may represent an alternative mode of entering post-fire stands as observed by Archibold (1979). Both sources of post-fire white spruce seed are strongly influenced by fire behavior. An extensive crown fire will reduce or eliminate potential seed trees surviving in an area which may result in reduced spruce seedling establishment particularly because seed dispersal in spruce is generally less than 100 m (Zasada and Gregory 1969). An intense ground fire will eliminate possible establishment from seed-bank sources.

Forest floor characteristics may play an important role in determining the relative abundance of jack pine and white spruce. Post-fire jack pine establishment is inhibited by organic accumulations deeper than 1 cm over the mineral soil (Chrosciewicz 1974) while white spruce is more tolerant of organic seed beds (Zasada and Gregory 1969). Forest floors in pine stands are generally loose and composed primarily of slightly decayed litter. This may be attributed to the inherently slow decomposition rates of pine needles and <u>Pleurozium</u> feathermoss (Chapter 5), and the rapid decomposition rate of <u>Cladina</u> lichen which reduce the accumulation of moderately decomposed and humified materials. In contrast, forest floors in spruce stands are commonly more compact and appear more decomposed than those of pine stands presumably because of the intermediate decomposition characteristics of spruce needle

Table 8-1. Density of seeds (mean(SE)) germinating from forest floor plus mineral soil to 4cm in four Hondo stands. Values are based on ten 7.6cm diameter cores taken from each stand and spread on peat moss provided with ample water in an outside cold-frame. Seeds germinated over a four-month period. Species nomenclature follows Moss (1983).

Forest type (stand)	Pine/lichen (1)	Pine/alder (3)	Spruce (14)	Spruce (4)
		seeds•m^{-2}		
Carex sp.	307(81)	66(33)	1425(680)	372(81)
Salix sp.	263(145)	153(88)	504(109)	110(48)
Betula papyrifera	44(44)	44(29)	153(72)	263(96)
Rubus idaeus	22(22)	66(33)	417(219)	88(66)
Dracocephalum parviflorum	88(35)	22(22)	0	0
Agrostis scabra	263(55)	44(29)	88(29)	0
Oryzopsis pungens	44(29)	0	0	0
Geranium bicknellii	0	44(29)	44(29)	110(59)
Viola renifolia	0	22(22)	44(29)	22(22)
Corydalis sp.	0	0	22(22)	0
Rumex acetosella	0	0	22(22)	0
Cornus canadensis	0	0	44(29)	0
Picea glauca	0	0	66(46)	66(23)
Total	1030(209)	504(127)	2830(780)	1030(179)

and Hylocomium litter (Chapter 5). Fine, loose fuels with high surface area:volume ratios and high porosity are generally more easily ignited and carry fire better than more compact fuels (Rundel 1981). Pine stand forest floors may, therefore, be more easily and completely destroyed by fire than spruce stand forest floors such that seed-beds produced by burning of pine stands may have little organic accumulation and be conducive to jack pine establishment. Seed beds in burned spruce stands would be expected to have higher residual organic accumulations which may inhibit the establishment of jack pine while promoting that of spruce. Resistance of spruce stand forest floors to burning would also increase the probability of regeneration of spruce and other species from seed-bank stored seed. Thomas and Wein (1985) found that jack pine establishment was reduced, while that of other boreal conifers was increased, by shading caused by herbaceous and shrub species on burned seed beds in New Brunswick. The higher density of seed of broad leaved species in spruce stand seed banks (Table 8-1) in conjunction with the higher probability that seedbank seed would survive fire in spruce stands, may further promote the replacement of spruce stands by spruce stands and pine stands by pine stands.

According to Tamm (1982), Swedish pine/lichen woodlands catch fire more readily than spruce/feathermoss forests. The mechanisms leading to differences in stand flammability have not been established but may relate to differences in forest floor characteristics as discussed above or to differences between species in canopy structure or volatile compounds in foliage (Rundel 1981). The combination of observations that pine stands burn more frequently than spruce stands and that frequently burned sites tend to be occupied by pine while rarely burned sites are occupied by spruce (Tamm 1982) implies inherent feedback mechanisms in these forest types which impart stability to vegetation patterns in a manner consistent with the results of this research.

Site fertility may also influence stand species composition although this control mechansism was not specifically examined in this research. Nutrient use efficiencies may differ among species such that their relative growth rates may vary with nutrient availability. For instance, spruce growing in pine/lichen stands may grow slowly relative to jack pine because of nutrient limitations, but may grow more rapidly relative to jack pine in more fertile pine/alder stands. Alder may be restricted in its establishment or growth in pine/lichen stands because of low organic P levels but be promoted by higher levels in pine/alder stands. These scenerios are speculative but such nutrient-mediated relationships among species may strongly influence vegetation patterns and should be examined.

Controls on soil horizon development

Evidence for vegetation control of soil development was obtained in this study through correlation of soil properties with forest type. It is generally accepted that factors relating to specific vegetation types or individual species play a role in mobilization and translocation of clay, iron and aluminum in soil profiles (Soil Survey Staff 1975). The participation of specific organic compounds, particularly polyphenols, in eluvial processes has been documented in the literature (Bloomfield 1957, Coulson *et al.* 1960). The occurrence of individual species has, in some locations, been linked to soil development (Fisher 1972, Crampton 1982) and extracts of specific litter types have been shown to cause reactions with soil constituents which may be involved in developmental processes (Ellis 1971). However, relationships between soil development and the chemical characteristics of litter or canopy drip of specific forest types within a landscape do not appear to have been examined. Preliminary data (Figure 8-2) collected in this study, suggest that the capacity of LFH horizon leachates to disperse clay differs between forest types. In particular, leachates from pine/lichen forest floors were significantly less effective in dispersing kaolinite than leachates from forest floors of other forest types. Forest floor leachates also differed in their capacity to disperse montmorillonite although the differences were not as marked as in kaolinite. Dispersion of clay is an important factor influencing clay eluviation from surface soil horizons (Soil Survey Staff 1975). These results imply that differences in eluviation among soils could be related to differences in the chemistry of forest floor leachates among forest types.

Controls on site fertility and nutrient cycling

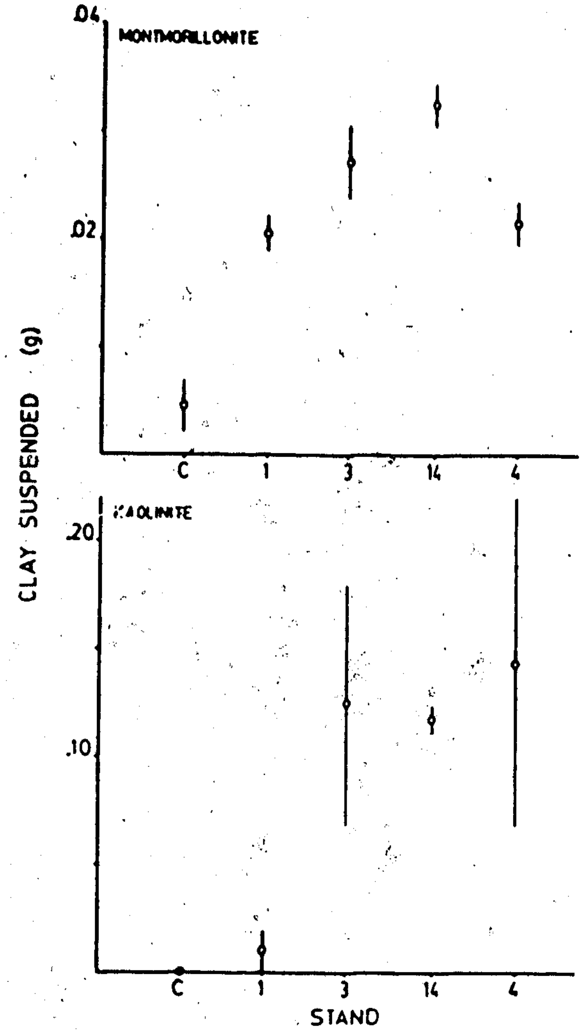


Figure 8-2. Clay suspended in 40 mL of solutions of leachates from LFH horizons of pine/lichen (1), pine/alder (3) and spruce (4,14) stands. Fifteen leachates per stand were prepared by filtering 125 mL deionized water through undisturbed LFH cores (6.7 cm diameter) which had been incubated moist in the laboratory for 10 days. Acidified clay (.500 g) was shaken in a centrifuge tube with 15 mL leachate + 25 mL deionized water, allowed to settle for 2 hours. Ten mL of supernatant was pipetted from 2 cm below the surface of the suspension and oven [illegible] to allow calculation of clay concentration. Method follows Durgin and Vogel[illegible]

Availability of N in the Hondo stands appeared to be closely related to characteristics of the vegetation. This effect was the result of differences in both quality and quantity of N in LFH and mineral soil horizons. Differences in N mineralization in LFH horizons between forest types primarily reflected differences in the amount of accumulated N rather than in N quality, indicating that controls on mineralization in these horizons related to the magnitude of N fluxes within a stand. In contrast, mineralization in A horizons was influenced to a greater extent by N quality implying that mineralization in these horizons was controlled by processes involved in decomposition and humification of above- and below-ground litter in addition to the magnitude of N fluxes. These observations indicate that vegetation influences soil N availability through its control of the amount of N cycled through litter, determined primarily by stand biomass, and through control of litter characteristics which modify decomposition processes, determined largely by stand species composition. Mineralization of N in pine/lichen stands was lower than in spruce stands mainly because of relatively low levels of N in the former rather than differences in N quality. In contrast, N availability was higher in pine/alder than in spruce stands, despite similar levels of N cycling in these forest types, because of higher mineralization rates related to the quality of N in soil of the pine/alder stands.

Estimation of phosphorus availability was dependent on indirect interpretations because the plant characteristics expected to relate to P availability, (foliar P content, litter P flux) did not reflect P recovered by chemical extraction. Soluble P in soil solution is derived by desorption and dissolution of various inorganic P compounds and by enzymatic cleavage of phosphate esters from organic compounds. Phosphorus availability would; therefore, be expected to be controlled by the relative abundance of the inorganic and organic forms. The results of this research suggest, however, that it may not be possible to measure available P in absolute terms because P availability may be controlled by plant demand in addition to soil chemistry. Turnover times of soil N and organic P and LFH N:P ratios indicated that spruce forests mobilized organic P preferentially to N while the opposite was true in pine/lichen woodland. Thus, the pool of P potentially available to the vegetation differed between these forest types with organic P playing a greater role in P cycling in spruce stands than in pine/lichen forest, possibly because the latter were more severely limited by N than by P. Differences in inorganic P fractions between soils under different forest types (Chapter 3), specifically low Fe-P and Al-P in spruce and low Ca-P in pine/alder stands, may be further evidence that sources of available P differ among plant species. Spruce stands may preferentially mobilize Fe-P and Al-P, possibly through calcium oxalate production by mycorrhizal fungi as suggested by Granstein *et al.* (1977), leading to the observed depletion of these phosphate compounds in soil. Mechanisms which might reduce Ca-P, relative to other inorganic forms of P, in soil under pine/alder stands are unknown and warrant further research.

Controls on nutrient cycling patterns related both to innate behaviors of individual species and to site fertility. Nutrient concentrations in foliage differed among species but remained relatively constant within a species across a range of fertility conditions. This suggests that the species examined were relatively inflexible with regard to nutrient concentration and responded to increased fertility by increasing biomass rather than nutrient content or that all systems had low fertility relative to demand. Similarly, although litter N concentration appeared to reflect N availability during the spring and early summer, the bulk of annual litterfall did not differ in N content across the fertility gradient. In addition, litter structure is unlikely to vary substantially with site fertility such that both chemical and structural characteristics of litter which influence decomposition processes are relatively fixed within a species, with little variation among sites. The significance of an individual species in controlling nutrient cycling patterns may differ among stands, but only as the result of differences in the biomass of that species on the different sites. Among stands of similar species composition, N flux in litter is expected to be higher on more fertile sites because of higher vegetation biomass and concomitant litter production rather than increased nutrient contents.

The uniformity in litter chemistry and structure within species across a range of site fertility suggests that the influence of an individual species on decomposition, and associated nutrient cycling processes controlled by these properties, also varies little among stands. Thus, for instance, pine needles would be expected to be inherently slow to decompose in both fertile and infertile environments although in fertile sites decomposition may be accelerated by nutrient released during the decomposition of other species such as alder. Consequently, the relative abundance of the species within a stand is one of the primary controls on decomposition and associated nutrient cycling processes. Controls on species abundance, which may relate to fire frequency or intensity, seed availability, or site fertility (Figure 8-1) therefore indirectly control nutrient cycling patterns and processes.

These results suggest that a major change in the species composition of a stand will result in a change in nutrient cycling patterns which, if persistent, will eventually be expressed in site fertility. If alder was removed from a pine/alder stand, LFH nutrient cycling processes would, over a period of time, become controlled by the decomposition characteristics of pine litter. If this new vegetation type were maintained through several generations of forest, the quality of N in the A horizon and, to a lesser degree, in the B horizon, would become more typical of that in pine/lichen stand soils; and the rate of N cycling through LFH and mineral horizons would decrease. The influence of such a change in cycling pattern on stand productivity is dependent upon the total amount of accumulated N. If total N is high, even a slow rate of mineralization will generate sufficient available N to support high stand productivity as appears to be the situation in the Hondo spruce stands. If total N in the sytem is low, however, decreased productivity would result.

8.1 Conclusion

The results of this research, as summarized in Figure 8-1, emphasize the highly integrated nature of ecosystem properties and processes, and suggest that research at the ecosystem level of abstraction must relate concepts drawn from several independent disciplines. This research considered aspects of plant population biology, vegetation science, fire science, soil chemistry and biochemistry and soil morphology and genesis. Many of these disciplines are not commonly examined within the context of a single study. One of the contributions of this research, therefore, has been the identification of links between processes in different disciplines which can be considered in future research. These links, as expressed in Figure 8-1, include:

1. Feedback control between vegetation and fire frequency.
2. Feedback control between vegetation and post-fire site conditions and propagule availability through controls on litter and forest floor conditions.
3. Feedback control between vegetation and site fertility through controls on litter characteristics, decomposition/mineralization in LFH and mineral soil horisons, soil phosphorus chemistry, and differential response of species to nutrient availability.
4. Control of vegetation on soil development through controls on litter and forest floor characteristics and decomposition processes.

Three general conclusions can be drawn from this research to summarize the specific conclusions of each chapter:

1. Forest types occupying individual sites in the Hondo area have remained relatively stable historically, with little change in species composition between generations of forest.
2. Nutrient cycling patterns are determined primarily by stand species composition such that long-term stability in vegetation has resulted in vegetation/nutrient cycling/site fertility/soil development characteristics specific to individual forest types.
3. These ecosystem characteristics appear to be stabilized over time by internal feedback mechanisms relating to interrelated controls between vegetation and soil.

Many areas requiring further investigation have been identified during the course of this research program as indicated in individual chapters. The majority of these areas relate in some way to characteristics of soil LFH and A horizons because these layers appear to integrate many ecosystem processes. LFH and A horizons warrant future research in many areas including:

1. Control of litterfall characteristics on LFH chemistry and architecture, including the interactions between litter types within the same horizon.
2. Interactions between LFH and A horizons.

3. Interrelationships between fire frequency and intensity and forest floor (LFH + bryoid layer) architecture and chemistry.
4. Control of LFH and A horizon characteristics on seedbank seed storage, post-fire seedbed conditions, and germination, establishment and growth of individual species.
5. Controls of LFH and A horizon properties on mineralization of N and P.
6. The influence of nutrient availability in LFH and A horizons on species interactions within a stand.

Aspects of several disciplines, including soil physics/hydrology, micrometeorology, and plant water relations, were not investigated directly but may be involved as controls in the Hondo ecosystems and should be investigated. In addition, this research has examined a small number of stands representing only three forest types and has not directly considered any of the aspen-dominated systems which cover most of the Mixedwood Section. In the sand ridge areas near Hondo, aspen stands exist close to most of the pine and spruce stand examined in this study and may represent a similar gradient in vegetation/soil/site fertility conditions. A parallel study of these stands, which examined relationships among aspen-dominated forest types in conjunction with the present data on coniferous forest would provide an understanding of ecosystem structure and function in forests occupying most upland sites in the Hondo area.

8.2 References

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APPENDICES

APPENDIX 1. Annual cumulative litterfall (g m^{-2}) in each trap in the Hondo and Alberta Oil Sands area stands. M: mean SD: standard deviation * missing value because of broken trap.

LITTER TYPE		STAND																	
	1-82	1-83	2-82	2-83	3-82	3-83	4-82	4-83	11	12	14	OS15	OS8	OS10	OS3	OS4	OS5N	OS4N	OS3N
PINE	55.1	*	73.2	113.6	89.2	204.8	0.0	0.0	95.6	*	97.9	*	38.3	82.8	*	75.0	*	62.1	*
	134.4	161.5	63.7	95.7	102.3	172.1	22.0	23.8	127.6	260.2	51.3	86.5	20.1	83.1	81.5	85.2	*	*	76.5
	129.6	158.4	56.2	73.5	107.7	185.0	2.0	2.6	139.2	61.9	112.8	52.6	*	*	108.2	51.1	*	*	49.8
	103.8	96.9	94.6	144.3	110.2	196.2	2.3	[illegible]	97.6	109.6	85.2	81.4	32.8	*	*	*	*	48.3	80.4
	61.0	70.5	151.0	186.2	119.2	184.4	1.4	0.4	[illegible]	186.2	118.5	54.8	29.4	*	73.0	*	*	*	*
	53.8	65.1	61.4	96.4	81.4	131.6	58.4	0.0	*	202.8	106.3	65.1	*	95.2	56.4	*	*	64.7	65.0
	115.4	127.0	87.0	122.0	86.0	189.1	0.4	0.4	*	159.2	118.3	*	41.1	*	*	*	58.2	*	42.6
	114.0	124.2	121.3	190.6	127.6	147.8	5.1	5.2	168.4	175.3	79.3	66.6	45.6	*	*	41.2	82.5	*	66.8
	75.0	92.3	139.4	189.4	115.7	156.7	24.7	26.1	186.3	186.2	77.1	*	*	59.8	110.9	122.9	*	*	79.7
	129.9	141.2	122.0	171.4	128.1	191.2	11.5	12.7	[illegible]	*	92.3	*	50.4	*	18.8	*	*	*	72.7
M	97.2	108.2	97.0	138.3	106.7	175.9	12.8	7.4	[illegible]	162.2	114.4	70.8	39.6	*	*	72.8	64.6	*	68.8
SD	36.6	43.8	38.3	53.0	31.4	39.8	25.5	10.6	[illegible]	67.2	33.6	15.4	20.2	*	*	38.3	19.3	*	24.0
SPRUCE	0.0	*	0.0	0.0	0.0	0.0	211.0	146.0	0.0	*	106.1	0.0	0.0	0.0	0.0	0.0	*	0.0	0.0
	0.0	0.0	0.0	0.0	5.9	46.8	88.9	55.9	0.0	0.0	49.0	0.0	0.0	0.0	0.0	0.0	*	0.0	0.0
	0.0	0.0	0.0	0.0	0.0	0.0	324.0	192.4	0.0	0.0	76.6	0.0	0.0	0.0	0.0	0.0	*	0.0	0.0
	0.0	0.0	0.0	0.0	0.0	0.0	169.6	*	0.0	0.0	60.6	0.0	0.0	0.0	0.0	0.0	*	0.0	0.0
	0.0	0.0	0.0	0.0	2.0	3.9	175.2	137.3	*	0.0	112.4	0.0	0.0	0.0	0.0	0.0	*	0.0	0.0
	0.0	0.0	0.0	0.0	27.3	27.1	134.6	86.8	*	0.0	45.8	0.0	0.0	0.0	0.0	0.0	*	0.0	0.0
	0.0	0.0	0.0	0.0	0.0	0.0	135.9	103.0	*	0.0	79.6	0.0	0.0	0.0	0.0	0.0	4.5	0.0	0.0
	0.0	0.0	0.0	0.0	0.0	0.0	97.3	90.2	0.0	0.0	127.4	0.0	0.0	0.0	0.0	0.0	10.1	0.0	0.0
	0.0	0.0	0.0	0.0	0.4	0.1	130.7	93.8	0.0	0.0	43.0	0.0	0.0	0.0	0.0	0.0	*	0.0	0.0
	0.0	0.0	0.0	0.0	0.0	0.1	79.0	57.7	0.0	*	87.0	0.0	0.0	0.0	0.0	0.0	*	0.0	0.0
M	0.0	0.0	0.0	0.0	3.6	4.8	154.4	109.7	0.0	0.0	75.0	0.0	0.0	0.0	0.0	0.0	18.0	0.0	0.0
SD	0.0	0.0	0.0	0.0	8.6	9.5	77.8	52.4	0.0	0.0	37.5	0.0	0.0	0.0	0.0	0.0	26.5	0.0	0.0

APPENDIX 1. (cont.) Annual cumulative litterfall(g m⁻²) in each trap in the Hondo and Alberta Oil Sands area stands. M: mean SD: standard deviation *: missing value because of broken trap.

LITTER TYPE	STAND																		
	1-82	1-83	2-82	2-83	3-82	3-83	4-82	4-83	11	12	14	OS15	OS8	OS10	OS3	OS4	OS5N	OS4N	OS3N
FIR	0.0	*	0.0	0.0	0.0	0.0	1.8	1.9	0.0	*	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	0.0	0.0	0.0	0.0	0.0	0.0	25.6	30.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	0.0	0.0	0.0	0.0	0.0	0.0	6.2	5.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	0.0	0.0	0.0	0.0	0.0	0.0	20.7	*	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	0.0	0.0	0.0	0.0	0.0	0.0	7.7	12.1	*	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	0.0	0.0	0.0	0.0	0.0	0.0	30.9	31.1	*	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	0.0	0.0	0.0	0.0	0.0	0.0	51.5	75.0	*	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	0.0	0.0	0.0	0.0	0.0	0.0	36.8	35.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	0.0	0.0	0.0	0.0	0.0	0.0	7.9	12.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	0.0	0.0	0.0	0.0	0.0	0.0	29.6	40.4	0.0	*	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
M	0.0	0.0	0.0	0.0	0.0	0.0	21.9	25.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
SD	0.0	0.0	0.0	0.0	0.0	0.0	19.7	24.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
ALDER	0.5	*	0.4	0.1	1.9	8.4	0.0	0.0	0.0	*	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	13.8	17.6	0.4	0.1	43.5	67.0	0.0	0.0	0.0	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	3.9	17.3	0.0	0.1	30.0	45.7	0.0	0.0	0.0	10.1	0.0	0.0	0.0	0.0	2.6	0.0	0.0	0.0	0.0
	37.1	28.0	7.6	18.6	31.4	35.3	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	18.8	43.8	5.4	5.0	6.3	6.5	0.0	0.0	*	0.0	0.0	0.0	0.0	6.7	0.0	0.0	0.0	0.0	0.0
	0.0	0.2	0.4	0.7	8.1	12.2	0.0	0.0	*	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	0.0	0.0	1.1	0.8	25.9	46.6	0.0	0.0	*	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	0.0	0.1	43.5	45.0	5.8	4.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	0.0	0.0	26.1	39.8	16.7	2.0	0.0	0.0	0.0	0.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	0.0	0.0	42.1	54.0	20.7	26.2	0.0	0.0	0.0	*	0.0	0.0	0.0	0.0	39.2	0.0	0.0	0.0	0.0
M	7.4	10.7	12.7	16.4	19.0	25.4	0.0	0.4	0.0	2.4	0.0	0.0	0.0	0.0	4.8	0.0	0.0	0.0	0.0
SD	12.9	16.4	18.5	23.2	15.2	27.0	0.0	1.0	0.0	3.9	0.0	0.0	0.0	0.0	12.3	0.0	0.0	0.0	0.0

APPENDIX 1. (cont.) Annual cumulative litterfall(g m⁻²) in each trap in the Hondo and Alberta Oil Sands area stands. M: mean, SD: standard deviation, •: missing value because of broken trap.

LITTER TYPE	STAND																	
	1-82	1-83	2-82	2-83	3-82	3-83	4-82	4-83	11	12	14	OS15	OS8	OS10	OS3	OS4	OS5N	OS4N	OS3N
ASPEN	0.0	•	0.0	0.0	0.0	0.0	37.5	39.6	0.0	•	34.8	0.0	0.0	0.0	0.0	0.0	•	0.0	0.0
	0.0	0.0	0.0	0.0	0.0	0.0	14.1	24.0	0.0	0.0	15.2	0.0	0.0	0.0	0.0	0.0	•	0.0	0.0
	0.0	0.0	0.0	0.0	0.0	0.0	1.7	6.7	0.0	0.0	25.0	0.0	0.0	0.0	0.0	0.0	•	0.0	0.0
	0.0	0.3	0.0	0.0	0.0	0.0	5.0	•	0.0	0.0	31.6	0.0	0.0	0.0	0.0	0.0	•	0.0	0.0
	0.0	1.0	0.0	0.7	0.0	0.0	17.4	17.5	•	0.0	26.3	0.0	0.0	0.0	0.0	0.0	•	0.0	0.0
	0.0	0.0	0.0	0.0	0.0	0.0	13.2	15.2	•	0.0	10.6	0.0	0.0	0.0	0.0	0.0	•	0.0	0.0
	0.0	0.0	0.0	0.5	0.0	0.0	7.5	11.4	•	0.0	18.5	0.0	0.0	0.0	[illegible]	0.0	0.0	0.0	0.0
	0.0	0.0	0.0	0.0	0.0	4.2	3.5	4.4	0.0	0.0	22.9	0.0	0.0	0.0	[illegible]	0.0	0.1	0.0	0.0
	0.0	0.0	0.0	0.0	0.0	21.2	0.2	3.4	0.0	0.0	38.4	0.0	0.0	0.0	0.0	0.0	•	0.0	0.0
	0.0	0.0	0.0	0.0	0.0	9.8	4.6	6.8	0.0	•	37.3	0.0	0.0	0.0	0.0	0.0	•	0.0	0.0
M	0.0	0.2	0.0	0.1	0.0	3.5	10.5	14.9	0.0	0.0	25.6	0.0	0.0	0.0	0.0	0.0	4.0	0.0	0.0
SD	0.0	0.5	0.0	0.3	0.0	7.2	12.0	13.4	0.0	0.1	12.6	0.0	0.0	0.0	0.0	0.0	8.0	0.0	0.0
TWIGS	0.3	•	2.0	11.6	11.9	85.3	30.7	76.8	6.6	•	135.6	•	4.2	25.3	•	23.0	•	31.0	•
AND	15.1	21.0	1.4	4.8	25.6	90.6	19.5	49.2	10.0	105.2	26.0	4.8	0.5	1.4	11.0	2.6	•	•	7.4
BARK	11.0	16.1	9.4	11.7	14.3	134.0	56.6	94.8	21.7	7.5	47.9	14.0	•	•	36.4	1.1	•	•	2.7
	0.6	15.3	3.3	45.2	12.0	120.6	64.4	•	1.1	22.1	48.3	11.2	0.7	•	•	•	•	19.9	7.2
	0.3	4.4	11.8	52.9	19.0	120.6	90.5	155.0	•	44.4	32.4	12.7	0.4	•	9.2	•	•	•	•
	0.4	6.2	0.7	3.6	32.2	177.0	19.2	40.8	•	50.1	35.2	7.8	•	12.7	1.5	•	•	15.3	17.2
	1.0	8.3	1.2	2.7	4.4	80.9	37.9	53.7	•	26.3	39.8	•	0.5	•	•	•	9.5	•	4.3
	3.6	8.0	3.8	35.0	9.1	45.4	11.0	38.1	22.3	57.0	52.9	9.1	0.8	•	•	9.3	24.7	•	4.8
	0.1	5.0	10.0	41.9	17.5	92.8	10.4	26.2	11.1	40.3	25.0	•	•	7.0	16.0	6.8	•	•	16.9
	3.0	13.1	6.8	62.4	12.0	238.3	55.7	54.0	7.9	•	34.4	•	0.7	•	29.4	•	•	•	36.4
M	3.5	9.9	5.0	27.2	15.8	118.5	39.6	67.3	9.8	44.2	45.7	[illegible]	1.0	•	•	7.5	22.9	•	15.0
SD	6.1	9.4	6.1	31.7	14.6	84.8	39.6	50.2	11.2	35.9	42.2	[illegible]	1.9	•	•	14.6	18.1	•	22.9

APPENDIX 1. (cont.) Annual cumulative litterfall(g m^{-2} y^{-1}) in each trap in the Hondo and Alberta Oil Sands area stands. M: mean SD: standard deviation •: missing value be[illegible] of broken trap.

LITTER TYPE	STAND																		
	1-82	1-83	2-82	2-83	3-82	3-83	4-82	4-83	11	12	14	OS15	OS8	OS10	OS3	OS4	OS5N	OS4N	OS3N
FEMALE CONES	2.8	•	4.4	6.0	9.6	11.4	10.6	10.4	1.6	•	9.6	•	1.2	3.6	•	0.2	[illegible]	0.7	•
	28.4	24.8	5.7	2.2	71.1	11.2	15.1	11.7	2.3	6.8	3.8	2.0	0.0	2.8	6.0	0.1	•	•	0.8
	19.7	4.7	5.6	3.8	29.2	11.8	21.5	10.9	2.0	2.0	5.5	1.0	•	•	4.1	1.7	•	•	0.2
	5.8	1.7	5.6	5.8	16.3	16.2	15.5	•	5.1	4.7	3.2	1.1	0.1	•	•	•	•	1.5	1.5
	7.0	4.0	12.6	7.6	13.0	13.3	10.5	6.3	•	6.1	2.8	1.0	0.1	•	6.0	•	•	•	•
	1.9	5.0	5.3	4.4	11.8	11.5	21.9	9.2	•	12.6	2.9	0.4	•	0.1	0.9	•	•	4.5	0.7
	3.1	3.5	10.5	2.5	12.2	14.3	5.6	7.4	•	6.3	6.1	•	0.4	•	•	•	2.5	•	1.2
	3.8	3.0	14.9	19.8	15.9	9.6	7.8	6.9	1.2	6.0	4.2	2.8	0.1	•	•	0.3	5.4	•	1.2
	7.0	0.9	14.8	12.2	13.1	11.6	59.4	7.7	2.8	7.9	3.0	•	•	2.7	14.6	1.1	•	•	2.8
	2.8	3.2	32.8	17.4	14.0	10.8	11.7	6.4	6.1	•	4.6	[illegible]	0.2	•	2.1	•	•	•	3.8
M	8.2	5.1	11.2	8.2	20.6	12.2	18.0	8.8	3.0	6.2	2.9	1.5	0.4	•	4.3	1.7	14.1	•	1.5
SD	12.4	7.7	9.4	6.9	22.6	3.1	22.2	3.7	1.9	3.8	3.5	1.1	0.6	•	5.1	2.3	26.6	•	1.3
TOTAL	58.8	•	79.9	131.3	112.6	309.8	291.6	274.6	103.8	•	384.0	•	43.7	111.8	•	98.1	•	93.8	•
	191.6	224.8	71.2	102.9	248.4	357.7	183.3	194.8	140.0	372.9	145.3	93.4	20.6	87.4	109.9	[illegible]	•	•	84.7
	164.1	196.4	71.2	89.1	181.2	376.6	412.0	313.1	162.8	81.6	267.9	[illegible]	•	•	139.8	[illegible]	•	•	52.8
	147.2	142.2	111.0	215.9	169.9	368.4	277.4	262.2	103.8	136.4	229.0	93.7	33.6	•	•	•	•	69.7	89.2
	87.1	123.8	180.8	253.0	159.4	328.6	302.7	328.7	•	236.8	292.5	68.4	29.9	•	95.0	•	•	•	•
	56.2	76.6	67.8	105.0	160.9	359.4	278.3	183.0	•	265.4	200.9	73.2	•	111.0	58.8	•	•	84.5	82.9
	119.6	138.8	99.8	139.3	128.4	331.2	238.8	250.9	•	192.2	262.3	•	42.0	•	•	•	71.0	•	48.1
	121.5	135.3	183.5	290.4	158.4	211.2	161.5	180.6	192.0	238.4	286.6	78.4	46.5	•	•	50.8	126.4	•	72.7
	82.1	98.2	190.3	306.4	163.4	284.5	233.2	169.9	200.2	235.0	1[illegible]6.6	•	•	69.4	141.5	130.7	•	•	99.4
	135.8	157.5	203.7	305.0	174.8	476.4	192.1	178.1	183.2	•	255.7	•	51.2	•	89.6	•	•	•	112.9
M	116.4	143.6	125.9	193.8	165.7	340.4	257.1	299.2	146.0	215.0	265.6	82.3	41.1	•	•	81.9	126.5	•	85.3
SD	54.0	45.6	61.8	104.7	58.0	68.5	132.7	119.2	50.5	111.1	129.5	25.5	21.9	•	•	46.6	64.2	•	44.7

APPENDIX 2. August foliage nutrient content by stand. • missing value.

NITROGEN (%) 1982

PINE				SPRUCE	FIR	ALDER		
1	2	3	4	4	4	1	2	3
1.231	1.081	1.234	1.549	1.059	1.283	2.603	2.526	2.541
1.366	1.151	1.395	1.274	1.370	1.289	2.525	2.182	2.510
1.235	1.026	1.380	[illegible]	0.995	1.513	2.000	2.153	2.781
1.344	1.231	1.213	1.175	1.129	1.507	2.176	2.342	2.376
1.316	1.304	1.285	1.228	0.961	•	2.328	2.197	2.441
1.296	1.108	1.339	•	•	•	2.423	2.301	2.437
1.285	1.428	1.226	•	•	•	2.241	1.958	2.343
•	1.312	1.202	•	•	•	2.280	2.679	2.330
•	1.129	1.295	•	•	•	2.626	2.555	2.415
•	•	1.235	•	•	•	[illegible]	2.582	2.530

NITROGEN (%) 1983

PINE								SPRUCE			FIR	ALDER				
1	2	3	4	11	12	13	14	3	4	14	4	1	2	3	12	13
1.133	0.980	1.190	1.334	0.963	•	•	1.102	1.207	0.995	1.000	1.177	2.482	2.990	2.654	2.399	2.466
1.011	1.201	1.739	1.218	1.117	1.058	1.444	1.317	1.354	0.794	1.039	1.055	2.793	2.500	2.510	2.559	2.538
1.181	1.125	1.290	0.987	1.004	1.134	1.154	1.281	1.079	0.782	0.982	0.921	2.633	2.523	2.436	[illegible]	[illegible]
1.147	1.396	1.413	1.350	1.250	1.047	1.215	1.102	1.140	0.950	0.963	0.923	2.748	2.860	[illegible]	[illegible]	[illegible]
1.005	1.186	1.468	•	0.942	1.094	1.162	1.126	1.280	•	1.206	1.379	3.086	2.574	[illegible]	[illegible]	[illegible]
0.872	1.140	1.162	•	0.916	1.022	1.282	1.033	1.241	•	•	1.047	2.950	2.758	[illegible]	[illegible]	[illegible]
1.168	1.552	1.186	•	1.037	1.154	1.083	•	1.032	•	•	0.977	2.827	2.774	2.575	[illegible]	[illegible]
1.156	1.224	1.106	•	0.954	1.019	1.264	•	1.110	•	•	•	3.037	2.840	2.620	[illegible]	[illegible]
1.309	1.240	1.231	•	0.992	1.212	1.173	•	1.148	•	•	•	2.759	2.831	2.664	[illegible]	[illegible]
1.139	1.275	1.182	•	0.975	1.037	1.332	•	1.284	•	•	•	2.630	2.826	2.748	2.644	[illegible]
•	•	•	•	•	1.059	•	•	•	•	•	•	•	•	•	•	•

APPENDIX 2. (cont.) August foliage nutrient content. * missing value.

PHOSPHORUS (%) 1983

PINE								SPRUCE			FIR	ALDER				
1	2	3	4	11	12	13	14	3	4	14	4	1	2	3	12	13
0.111	0.114	0.125	0.189	0.120	0.131	*	0.135	0.215	0.183	0.152	0.209	0.233	0.214	0.205	0.175	0.186
0.109	0.123	0.197	0.133	0.130	0.134	0.161	0.160	0.222	1.350	0.168	0.145	0.228	0.167	0.217	0.186	0.189
0.117	0.123	0.128	0.123	0.090	0.101	0.140	0.143	0.177	0.204	0.169	0.111	0.178	0.138	0.135	0.177	0.216
0.120	0.147	0.164	0.181	0.141	0.123	0.123	0.136	0.203	0.149	0.194	0.215	0.170	0.252	0.234	0.185	0.202
0.116	0.131	0.165	*	0.112	0.104	0.127	0.135	0.226	*	0.218	0.118	0.218	0.192	0.227	0.182	0.194
0.112	0.128	0.122	*	0.103	0.109	0.144	0.126	0.201	*	*	0.136	0.229	0.170	0.172	0.247	0.129
0.133	0.155	0.154	*	0.126	0.106	0.135	*	0.201	*	*	*	0.207	0.180	0.185	0.168	0.105
0.146	0.129	0.124	*	0.110	0.126	0.119	*	0.176	*	*	*	0.180	0.172	0.186	0.226	0.157
0.141	0.129	0.148	*	0.120	0.130	0.134	*	0.187	*	*	*	0.178	0.171	0.186	0.161	0.176
0.131	0.137	0.160	*	0.123	0.088	0.133	*	0.203	*	*	*	0.205	0.217	0.192	0.178	0.175

APPENDIX 3. Pine foliage litter nutrient content by stand. • missing value.

	NITROGEN (%)								PHOSPHORUS (%)							
STAND	1	2	3	4	11	12	13	14	1	2	3	4	11	12	13	14
DATE																
5.83	0.526	0.417	0.545	0.459		•	•	•	0.054	0.044	0.049	0.051	•	•	•	•
6.83	0.502	0.522	0.600	0.597	•	•	•	•	0.051	0.052	[illegible]	0.070	•	•	•	•
7.83	0.591	0.595	0.666	0.665	0.415	0.516	0.570	0.469	0.055	0.055	[illegible]	0.069	0.041	0.055	0.05[illegible]	0.040
8.83	0.683	0.666	0.758	0.673	0.405	0.572	•	0.548	0.057	0.053	[illegible]	0.057	0.027	0.048	•	0.036
9.83	0.600	0.594	0.753	0.667	0.373	0.564	0.633	0.580	0.044	0.038	0.050	0.052	0.022	0.038	0.039	0.036
10.83	0.375	0.389	0.505	0.506	0.301	0.401	0.400	0.421	0.030	0.032	0.040	[illegible]	0.021	0.026	0.036	0.034
11.83	0.348	0.363	0.389	0.377	0.326	0.364	0.337	0.327	•	0.021	0.030	0.043	0.025	0.028	0.023	0.025
5.84	0.412	0.419	0.570	0.465	0.315	0.459	0.446	0.411	0.032	0.032	0.041	0.046	0.021	0.033	0.032	0.028
6.84	0.540	0.644	0.668	0.461	0.371	0.446	0.531	0.496	0.042	0.055	0.030	0.027	0.029	0.039	0.044	0.039

APPENDIX 3. (cont.) Foliage litter nutrient contents * missing value.

NITROGEN(%)

	SPRUCE				FIR			ALDER		
STAND	3	4	14	13	4	1	2	3	12	13
DATE										
5.83	0.573	0.423	*	*	0.534	*	1.978	2.0710	*	*
6.83	0.746	0.491	*	*	0.618	1.886	2.128	2.1040	[illegible]	*
7.83	0.716	0.605	0.611	*	0.824	1.667	1.973	*	*	*
8.83	*	0.567	0.568	*	0.928	*	*	2.5890	*	*
9.83	*	0.698	0.610	*	0.804	2.324	1.844	0.2355	*	2.124
10.83	*	0.447	0.424	*	0.591	1.849	1.803	2.0840	1.882	2.100
11.83	0.451	0.363	0.366	0.563	0.477	2.084	*	2.2450	1.981	*
5.84	0.528	0.478	0.529	0.566	0.553	2.673	2.203	2.2630	1.773	2.401
6.84	0.838	0.612	0.510	0.562	0.727	*	2.243	2.7410	0.522	*

PHOSPHORUS (%)

	SPRUCE				FIR			ALDER		
STAND	4	14	3	13	4	1	2	3	12	13
DATE										
5.83	0.048	*	0.060	*	0.053	*	0.075	0.117	*	*
6.83	0.065	*	0.101	*	0.067	0.085	0.096	0.093	*	*
7.83	0.062	0.063	0.072	*	0.048	0.055	0.080	*	*	*
8.83	0.061	0.061	*	*	0.105	*	*	0.139	*	*
9.83	0.081	0.074	*	*	0.067	0.115	0.122	0.146	*	*
10.83	0.076	0.072	*	*	0.072	0.124	0.104	0.130	0.106	0.118
11.83	0.048	0.052	0.058	0.053	0.054	0.106	*	0.110	0.104	*
5.84	0.058	0.063	0.058	0.050	0.063	0.120	0.106	0.130	0.107	0.120
6.84	0.071	0.059	0.111	0.052	0.078	*	0.093	0.142	*	0.114

APPENDIX 3. (cont.) Litter nutrient contents. * missing value.

STRUCTURAL MATERIAL

	NITROGEN (%)								PHOSPHORUS (%)							
STAND	1	2	3	4	11	12	13	14	1	2	3	4	11	12	13	14
DATE																
5.83	0.745	0.679	0.0920	0.549	*	*	*	*	0.068	0.042	0.049	0.048	*	*	*	*
6.83	0.848	0.617	0.7770	0.896	*	*	*	*	0.070	0.038	0.060	0.086	*	*	*	*
7.83	0.650	0.593	0.7740	0.443	0.476	0.692	0.350	0.703	0.045	0.043	0.047	0.045	0.037	0.058	0.072	0.066
8.83	0.672	0.468	0.5750	0.807	0.517	0.877	*	0.815	0.042	0.033	0.039	0.080	0.036	0.079	*	0.055
9.83	0.762	0.657	0.5600	0.791	0.470	0.636	0.784	0.488	0.048	0.047	0.038	0.088	0.031	0.061	0.083	0.039
10.83	0.457	0.700	0.5620	1.039	*	0.734	0.609	0.975	0.036	0.034	0.035	0.193	*	0.051	0.043	0.112
11.83	*	0.852	0.5800	0.954	*	1.158	0.601	0.510	*	0.058	0.072	0.113	*	0.135	0.046	0.063
5.84	0.654	0.691	0.6960	0.449	0.408	0.680	0.694	0.595	0.048	0.045	0.036	0.036	0.026	0.057	0.050	0.050
6.84	0.644	0.433	0.3620	0.465	0.394	0.610	0.604	0.364	0.046	0.037	0.027	0.040	0.027	*	0.045	0.028

FEMALE CONES

	NITROGEN (%)								PHOSPHORUS (%)							
STAND	1	2	3	4	11	12	13	14	1	2	3	4	11	12	13	14
DATE																
5.83	1.497	*	1.1840	1.510	*	*	*	*	0.104	*	0.087	0.151	*	*	*	*
6.83	1.429	1.394	0.1271	0.758	*	*	*	*	0.105	0.104	0.090	0.074	*	*	*	*
7.83	0.872	0.869	0.7430	1.068	0.756	0.773	0.812	0.803	0.057	0.061	0.053	0.099	0.051	0.054	0.054	0.065
8.83	0.890	0.861	0.8630	1.360	1.506	0.934	*	0.792	0.060	0.051	0.054	0.108	0.107	0.060	*	0.052
9.83	0.866	0.891	1.0790	1.529	0.882	0.952	*	1.149	0.054	0.054	0.068	0.117	0.049	0.063	*	0.099
10.83	0.176	*	1.1000	*	0.290	1.228	0.496	1.500	0.026	*	0.078	*	0.021	0.129	0.065	0.130
11.83	*	*	*	1.583	*	*	*	1.257	*	0.079	*	0.142	*	*	*	0.106
5.84	*	1.224	0.9950	1.608	*	1.083	1.156	1.269	*	0.182	0.061	0.130	*	0.069	0.078	0.095
6.84	1.295	1.557	1.4750	1.730	*	1.240	1.706	1.293	0.082	*	0.181	0.136	*	0.088	0.180	0.103

APPENDIX 4. Proportion of weight of litter remaining at five week intervals during the 35 week incubation.

PINE

WEEKS	1	2	3	4	5	6	7	8	9	10
	REPLICATE									
0	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
5	0.890	0.894	0.891	0.900	0.893	0.894	0.905	0.901	0.894	0.899
10	0.815	0.833	0.834	0.845	0.830	0.828	0.835	0.852	0.838	0.840
15	0.764	0.794	0.793	0.804	0.787	0.784	0.788	0.821	0.805	0.801
20	0.716	0.759	0.756	0.767	0.736	0.739	0.744	0.790	0.773	0.767
25	0.690	0.745	0.734	0.730	0.724	0.724	0.729	0.770	0.751	0.746
30	0.676	0.712	0.698	0.693	0.689	0.698	0.699	0.737	0.720	0.715
35	0.657	0.704	0.682	0.669	0.676	0.688	0.687	0.725	0.706	0.701

SPRUCE

0	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
5	0.926	0.940	0.895	0.934	0.935	0.925	0.925	0.916	0.931	0.933
10	0.894	0.896	0.761	0.900	0.895	0.888	0.883	0.867	0.902	0.900
15	0.862	0.857	0.649	0.879	0.860	0.850	0.847	0.830	0.864	0.866
20	0.820	0.815	0.611	0.850	0.830	0.821	0.802	0.791	0.823	0.836
25	0.816	0.803	0.600	0.831	0.817	0.802	0.795	0.785	0.809	0.823
30	0.797	0.778	0.586	0.803	0.792	0.773	0.773	0.768	0.788	0.801
35	0.784	0.766	0.584	0.791	0.785	0.762	0.766	0.760	0.778	0.791

CLADINA

0	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
5	0.969	0.982	0.978	0.983	0.981	0.919	0.920	0.928	0.904	0.927
10	0.925	0.934	0.925	0.936	0.936	0.884	0.888	0.895	0.867	0.888
15	0.884	0.880	0.882	0.898	0.897	0.841	0.845	0.872	0.804	0.861
20	0.822	0.776	0.813	0.840	0.817	0.814	0.821	0.769	0.766	0.838
25	0.780	0.692	0.770	0.806	0.741	0.791	0.800	0.720	0.739	0.813
30	0.727	0.612	0.726	0.764	0.674	0.769	0.780	0.701	0.719	0.788
35	0.674	0.543	0.680	0.725	0.631	0.769	0.780	0.701	0.719	0.788

APPENDIX.4. (cont.) Proportion of weight of litter remaining at
five week intervals during the 35 week incubation.

HYLOCOMIUM

WEEKS	REPLICATE 1	2	3	4	5	6	7	8	9	10
0	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
5	0.919	0.926	0.928	0.904	0.927	0.918	0.916	0.931	0.918	0.913
10	0.884	0.888	0.895	0.867	0.888	0.887	0.884	0.905	0.888	0.877
15	0.841	0.845	0.872	0.804	0.861	0.860	0.862	0.866	0.864	0.796
20	0.814	0.821	0.769	0.766	0.838	0.833	0.841	0.841	0.824	0.757
25	0.791	0.800	0.720	0.739	0.813	0.800	0.817	0.827	0.768	0.735
30	0.769	0.780	0.701	0.719	0.788	0.772	0.758	0.806	0.739	0.717
35	0.769	0.780	0.701	0.719	0.788	0.766	0.750	0.806	0.739	0.717

PLEUROZIUM

0	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
5	0.942	0.949	0.944	0.940	0.939	0.942	0.952	0.940	0.955	0.943
10	0.906	0.919	0.917	0.909	0.906	0.909	0.922	0.902	0.925	0.912
15	0.892	0.903	0.891	[illegible]	0.893	0.891	0.906	0.882	0.901	0.902
20	0.889	0.899	0.881	0.867	0.879	0.882	0.900	0.873	0.892	0.869
25	0.860	0.872	0.865	0.852	0.856	0.859	0.879	0.858	0.877	0.856
30	0.839	0.851	0.851	0.839	0.841	0.842	0.861	0.843	0.862	0.847
35	0.839	0.851	0.852	0.839	0.841	0.842	0.861	0.843	0.862	0.847

APPENDIX 4. (cont.) Proportion of weight of litter remaining at five week intervals during 35 week the incubation.

CUT PINE	REPLICATE				
WEEKS	1	2	3	4	5
0	1.000	1.000	1.000	1.000	1.000
5	0.882	0.915	0.920	0.911	0.873
10	0.747	0.868	0.862	0.860	0.767
15	0.635	0.821	0.808	0.811	0.648
20	0.581	0.773	0.765	0.769	0.603
25	0.580	0.765	0.751	0.755	0.587
30	0.566	0.742	0.726	0.728	0.567
35	0.562	0.734	0.714	0.717	0.563

FIR

0	1.000	1.000	1.000	1.000	1.000
5	0.899	0.904	0.920	0.906	0.908
10	0.849	0.858	0.880	0.856	0.869
15	0.805	0.820	0.836	0.813	0.829
20	0.772	0.782	0.794	0.777	0.797
25	0.749	0.772	0.776	0.760	0.781
30	0.715	0.750	0.746	0.734	0.753
35	0.693	0.739	0.717	0.720	0.741

ALDER

0	1.000	1.000	1.000	1.000	1.000
5	0.895	0.896	0.909	0.880	0.859
10	0.831	0.796	0.832	0.822	0.789
15	0.778	0.752	0.771	0.778	0.740
20	0.729	0.724	0.739	0.745	0.711
25	0.713	0.710	0.721	0.724	0.695
30	0.691	0.692	0.698	0.695	0.660
35	0.686	0.692	0.698	0.686	0.657

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APPENDIX 5. Weight (WT) and chemical characteristics of LFH horizons AF: ash free.

STAND	WT	AFWT	%C	%N	%P	WT C	WT N	WT P	C/N	C/P	N/P
1	2292	1213	31.5	0.610	0.051	721.98	13.98	1.17	51.64	617.65	11.96
1	2400	1392	31.7	0.567	0.050	760.80	13.61	1.20	55.91	634.00	11.34
1	5386	4216	43.5	0.423	0.037	2342.91	22.78	1.99	102.84	1175.68	11.43
1	8079	6490	42.2	0.650	0.050	3409.34	52.51	4.04	64.92	844.00	13.00
1	6415	4451	38.3	0.484	0.039	2456.94	31.05	2.50	79.13	982.05	12.41
1	10029	8442	47.3	0.401	0.033	4743.71	40.22	3.31	117.95	1433.33	12.15
1	10964	6337	32.2	0.371	0.037	3530.41	40.68	4.06	86.79	870.27	10.03
1	7294	2522	23.2	0.609	0.049	1692.21	44.42	3.57	38.09	473.42	12.43
1	5477	2569	25.2	0.589	0.053	1380.20	32.26	2.90	42.78	475.47	11.11
1	6700	4517	45.9	0.409	0.031	3075.30	27.40	2.08	112.22	1480.64	13.19
1	5878	4473	40.2	0.296	0.024	2362.96	17.40	1.41	135.81	1675.00	12.33
1	1930	1228	31.1	0.728	0.073	600.23	14.05	1.41	42.72	426.03	9.97
1	3825	1754	25.2	0.628	0.059	963.90	24.02	2.26	40.13	427.12	10.64
1	3302	2192	34.3	0.718	0.055	1132.58	23.71	1.82	47.77	623.64	13.05
1	1842	1140	30.7	0.571	0.054	565.48	10.52	0.99	53.76	568.52	10.57
2	2526	1995	38.4	0.815	0.071	969.98	20.59	1.79	47.12	540.84	11.48
2	3361	1272	19.5	0.373	0.045	655.39	12.54	1.51	52.28	433.33	8.29
2	2619	1447	29.0	0.602	0.053	759.51	15.77	1.39	48.17	547.17	11.36
2	3265	1973	32.5	1.081	0.068	1061.12	35.29	2.22	30.06	477.94	15.90
2	3212	2741	44.0	1.062	0.088	1413.28	34.11	2.83	41.43	500.00	12.07
2	5413	3421	35.0	1.039	0.075	1894.55	56.24	4.06	33.69	466.67	13.85
2	4104	1754	21.1	0.509	0.050	865.94	20.89	2.05	41.45	422.00	10.18
2	5355	3640	35.8	0.481	0.038	1917.09	25.76	2.03	74.43	842.10	12.66
2	5553	2346	24.5	0.593	0.054	1360.48	32.93	3.00	41.31	453.70	10.98
2	2610	2236	37.5	1.410	0.078	978.75	36.80	2.04	26.60	480.77	18.08
2	3221	1973	32.3	0.813	0.082	1040.38	26.19	2.64	39.73	393.90	9.91
2	8180	3947	26.3	0.600	0.064	2151.34	49.08	5.24	43.83	410.94	9.37
2	5362	2500	25.6	0.558	0.043	1372.67	29.92	2.31	45.88	595.35	12.98
2	3412	1864	29.0	0.922	0.074	989.48	31.46	2.52	31.45	391.89	12.46
2	4750	2960	31.9	0.754	0.072	1515.25	35.81	3.42	42.31	443.05	10.47

APPENDIX 5. (cont.) Weight (WT) and chemical characteristics of LFH horizons AF: ash free

STAND	WT	AF WT	% C	% N	% P	WT C	WT N	WT P	C/N	C/P	N/P
3	3576	2529.8	35.0	0.993	0.086	1251.60	35.51	3.08	35.25	406.98	11.55
3	5515	4038.5	38.6	1.457	0.085	2128.79	80.35	4.69	26.49	454.12	17.14
3	3586	2203.7	31.2	1.111	0.073	1118.83	39.84	2.62	28.08	427.40	15.22
3	6197	5282.3	46.2	0.670	0.037	2863.01	41.52	2.29	68.95	1248.65	18.11
3	11974	4657.4	19.5	0.618	0.037	2334.93	74.00	4.43	31.55	527.03	16.70
3	8467	3444.5	21.9	0.827	0.060	1854.27	70.02	5.08	26.48	365.00	13.78
3	2942	2396.3	42.4	1.132	0.066	1247.41	33.30	1.94	37.46	642.42	17.15
3	6414	3681.5	30.5	0.934	0.057	1956.27	59.91	3.66	32.65	535.09	16.39
3	6222	3092.8	24.9	0.836	0.067	1549.28	52.02	4.17	29.78	371.64	12.48
3	5478	3867.1	36.7	1.067	0.071	2010.43	58.45	3.89	34.40	516.90	15.03
3	6822	3685.0	27.9	1.107	0.067	1903.34	75.52	4.57	25.20	416.42	16.52
3	3844	2698.5	37.0	1.164	0.085	1422.28	44.74	3.27	31.79	435.29	13.69
3	2835	1775.7	32.5	0.908	0.061	921.37	25.74	1.73	35.79	532.79	14.89
3	6064	3544.7	29.5	0.942	0.067	1788.88	57.12	4.06	31.32	440.30	14.06
3	4139	2708.5	32.8	0.774	0.047	1357.59	32.04	1.95	42.38	697.87	16.47
3	4500	2690.7	30.6	0.914	0.064	1377.00	41.13	2.88	33.48	478.12	14.28
4	7400	4085.3	28.4	0.887	0.042	2101.60	65.64	3.11	32.02	676.19	21.12
4	7702	4811.2	31.9	0.951	0.069	2456.94	73.25	5.31	33.54	462.32	13.78
4	6989	5082.4	38.4	1.053	0.088	2683.77	73.59	6.15	36.47	436.36	11.97
4	10250	6366.4	32.1	0.922	0.072	3290.25	94.50	7.38	34.82	445.83	12.81
4	13303	8242.7	31.5	0.892	0.080	4190.44	118.66	10.64	35.31	393.75	11.15
4	12772	9097.8	36.7	0.842	0.070	4687.32	107.54	8.94	43.59	524.29	12.03
4	7667	5287.6	35.1	0.698	0.061	2691.12	53.52	4.68	50.29	575.41	11.44
4	10695	5805.8	29.3	0.851	0.081	3133.63	91.01	8.66	34.43	361.73	10.51
4	14016	5987.5	22.3	0.661	0.063	3125.57	92.65	8.83	33.74	353.97	10.49
4	14461	6866.6	25.2	0.742	0.072	3644.17	107.30	10.41	33.96	350.00	10.31
4	10059	5308.5	27.8	0.843	0.077	2796.40	84.80	7.75	32.98	361.04	10.95
4	10967	8309.4	39.9	1.074	0.096	4375.83	117.79	10.53	37.15	415.62	11.19
4	10643	5387.0	26.6	0.797	0.069	2831.04	84.82	7.34	33.37	385.51	11.55
4	4635	3259.3	37.3	1.069	0.087	1728.85	49.55	4.03	34.89	428.74	12.29
4	17550	14691.1	45.5	0.449	0.038	7985.25	78.80	6.67	101.34	1197.37	11.82
4	8899	7046.3	40.6	0.930	0.071	3612.99	82.76	6.32	43.66	571.83	13.10

APPENDIX 5. (cont.) Weight (WT) and chemical characteristics of LFH horizons AF: ash free.

STAND	WT	AFWT	% C	% N	% P	WT C	WT N	WT P	C/N	C/P	N/P
11	1135	771	34.9	0.734	0.058	396.11	8.33	0.66	47.55	601.72	12.66
11	2420	1072	23.6	1.099	0.090	571.12	26.60	2.18	21.47	262.22	12.21
11	2613	1050	20.2	0.492	0.047	527.83	12.86	1.23	41.06	429.79	10.47
11	2336	904	19.2	0.509	0.051	448.51	11.89	1.19	37.72	376.47	9.98
12	5590	3258	30.6	0.787	0.060	1710.54	43.99	3.35	38.88	510.00	13.12
12	3896	1948	24.2	0.593	0.047	942.83	23.10	1.83	40.81	514.89	12.62
12	2163	919	21.3	0.532	0.046	460.72	11.51	0.99	40.04	463.04	11.57
12	4201	2440	31.1	0.850	0.046	1306.51	35.71	1.93	36.59	676.09	18.48
13	4835	2818	33.1	1.079	0.047	1600.38	52.17	2.27	30.68	704.26	22.96
13	6124	3215	28.9	1.066	0.044	1769.84	65.28	2.69	27.11	656.82	24.23
13	5199	3218	32.8	1.125	0.075	1705.27	58.49	3.90	29.16	437.33	15.00
13	3670	2095	29.7	0.942	0.067	1089.99	34.57	2.46	31.53	443.28	14.06
14	4767	2888	32.1	0.772	0.071	1530.21	36.80	3.38	41.58	452.11	10.87
14	3771	2492	35.0	0.921	0.088	1319.85	34.73	3.32	38.00	397.73	10.47
14	2817	2052	37.7	1.002	0.100	1062.01	28.23	2.82	37.62	377.00	10.02
14	3118	2269	38.3	0.941	0.094	1194.19	29.34	2.93	40.70	407.45	10.01

APPENDIX 6. Supplementary soil nitrogen and phosphorus data. NO:non-occluded, O:occluded, Ex: acid ammonium fluoride extactable.

STAND	HOR	N	Ca-P	NO-P	O-P	Ex-P	Org-P
		(%)			(ug.g⁻¹)		
1	Ahe	0.090	0.0	64.9	197.2	20.7	39.7
	Bm1	0.030	47.8	73.5	306.5	31.8	41.7
	Bm2	0.008	162.9	70.9	103.4	17.1	11.1
	BC	•	235.7	0.0	66.5	5.0	0.0
	Ck	•	•	•	•	•	•
2	Ahe	0.086	0.0	0.0	173.4	17.7	47.6
	Bm1	0.040	38.5	0.0	368.5	38.0	31.5
	Bm2	0.012	145.0	0.0	117.3	15.4	33.6
	BC	•	240.1	66.0	64.5	6.3	14.6
	Ck	•	•	•	•	•	•
11	Ahe	0.041	0.0	0.0	187.4	32.5	39.3
	Bm1	0.013	40.2	51.9	149.8	40.3	32.9
	Bm2	0.009	98.3	55.0	65.8	17.2	45.4
	BC	0.006	184.9	0.0	0.0	14.8	29.8
	Ck	0.006	244.1	0.0	0.0	12.2	52.4
12	Ahe	0.089	0.0	0.0	142.3	27.0	58.7
	Bm1	0.016	58.7	74.2	126.0	33.4	32.5

APPENDIX 6. (con't) Supplementary soil nitrogen and phosphorus data.
NO:non-occluded, O:occluded, Ex: acid ammonium fluoride extactable.

STAND	HOR	N	Ca-P	NO-P	O-P	Ex-P	Org-P
		(%)		(ug.g^{-1})			
3	Ahe	0.115	0.0	0.0	[illegible]	14.0	61.0
	Bm	0.046	46.9	47.0	332.0	[illegible]	42.1
	Btj	0.016	74.6	51.2	178.6	17.6	45.8
	BC	*	111.0	53.9	142.7	13.0	40.8
	Ck	*	192.4	0.0	66.5	4.0	15.9
13	Ahe	0.140	0.0	0.0	235.1	50.1	113.9
	Bm	0.021	46.2	62.4	223.3	46.5	57.7
	Btj	0.011	109.5	71.2	55.4	8.7	31.8
	BC	0.011	182.5	0.0	0.0	6.8	21.4
	Ck	0.009	269.3	0.0	0.0	1.7	24.4
4	Ae1	0.079	0.0	0.0	174.5	19.6	54.6
	Bm	0.037	87.8	83.7	187.9	21.8	58.6
	Ae2	*	*	*	*	*	*
	Bt1	0.025	113.1	67.4	92.3	12.0	57.0
	Bt2	*	114.4	76.9	56.3	*	61.5
	BC	*	*	*	*	*	*
	Ck	*	221.0	0.0	0.0	1.7	46.8
14	Ae1	0.087	0.0	62.8	145.9	18.9	58.4
	Bm	0.035	63.6	105.1	247.9	20.9	61.9
	Ae2	*	66.4	91.5	81.8	*	56.6
	Bt1	0.027	89.2	92.5	56.1	7.9	71.6
	Bt2	0.018	148.7	63.1	0.0	6.1	46.3
	BC	0.017	241.7	55.0	0.0	6.8	33.0
	Ck	0.017	338.1	0.0	0.0	1.3	30.5

APPENDIX 7. Nitrogen mineralization data. NMIN: N mineralized over the 37 week incubation
NO3/NMIN: % of mineralized N measured as nitrate.

STAND.	NMIN g/m2			NMIN ug/g			NO3/NMIN %			TOTAL N ug/g			TOTAL N g/m2			NMIN/TOT N %		
	LFH	A	B	LFH	A	B	LFH	A	B	LFH	A	B	LFH	A	B	LFH	A	B
1	4.35	4.08	0.47	627	134	8.02	40.4	28.3	41.8	6637	1064	128.02	46.05	32.40	7.51	9.4	12.6	6.3
1	1.40	4.19	0.72	298	108	13.98	1.8	27.2	2.9	4038	988	213.98	18.97	38.33	11.03	7.4	10,9	6.5
1	0.60	2.90	0.60	162	70	9.47	1.8	0.7	94.1	6232	620	149.47	23.08	25.69	9.46	2.6	11.3	6.3
1	6.01	3.97	*	1340	165	*	2.6	18.6	*	9040	1115	*	40.54	26.83	1.00	14.8	14.8	*
1	1.95	2.07	*	218	135	*	1.3	20.8	*	7718	845	*	69.04	12.96	1.00	2.8	16.0	[illegible]
2	2.64	3.45	0.40	1018	74	6.92	0.7	17.7	100.0	6218	674	136,92	16.12	31.42	7.92	16.4	11.0	5.0
2	1.84	2.81	0.53	573	69	9.41	1.4	33.0	43.3	8043	999	169.41	25.83	40.68	9.55	7.1	6.9	5.5
2	7.19	5.49	0.72	1208	239	13.21	13.8	20.0	62.6	9258	3219	193.21	55.10	73.94	10.53	13.0	7.4	6.8
2	2.22	1.77	*	887	47	*	1.1	6.6	*	8727	877	*	21.84	33.03	1.00	10.2	[illegible]	*
2	8.03	8.27	*	2532	185	*	6.0	2.6	*	11982	1105	*	38.00	49.40	1.00	21.1	16.7	*
3	9.18	3.17	0.46	864	67	8.52	0.3	0.4	22.8	6754	557	158.52	71.80	26.33	8.57	12.8	12.0	5.4
3	7.40	9.10	0.57	1833	228	10.13	9.6	0.3	38.2	8513	1088	180.13	34.38	43.42	10.14	21.5	21.0	5.6
3	9.35	7.20	0.91	2234	206	15.48	0.4	0.2	1.4	12144	1156	255.48	50.81	40.38	15.02	18.4	17.8	6.1
3	5.65	6.86	*	1941	189	*	0.3	0.2	*	8801	1109	*	25.63	40.27	1.00	22.1	17.0	*
3	11.06	4.08	*	2791	134	*	0.2	0.4	*	11881	1254	*	47.09	38.18	1.00	23.5	10.7	*
4	10.85	2.10	0.41	736	158	7.57	48.0	0.8	5.7	9466	1638	407.57	139.55	21.77	22.04	7.8	9.6	1.9
4	10.95	1.46	0.49	1783	36	9.35	60.4	1.0	69.7	9983	746	379.35	61.31	30.25	19.92	17.9	4.8	2.5
4	7.94	1.58	0.66	1237	52	12.02	58.9	1.6	15.9	12087	1332	442.02	77.58	40.47	24.26	10.2	3.9	2.7
4	14.09	5.09	*	2067	122	*	30.2	5.8	*	13437	1542	*	91.59	64.33	1.00	15.4	7.9	*
4	7.26	2.23	*	1412	59	*	21.8	1.6	*	11222	1289	*	57.70	48.72	1.00	12.6	4.6	*

APPENDIX 7. (con't) Nitrogen mineralization data. NMIN: N mineralized over the 37 week incubation
NO3/NMIN: % of mineralized N measured as nitrate

STAND	NMIN g/m2			NMIN ug/g			NO3/NMIN %			TOTAL N ug/g			TOTAL N g/m2			NMIN/TOT N %		
	LFH	A	B	LFH	A	B	LFH	A	B	LFH	A	B	LFH	A	B	LFH	A	B
11	2.80	2.81	0.48	434	57	7.6	22.2	86.1	100.0	2444	557	107.6	15.77	27.46	6.80	17.8	10.2	7.1
11	2.75	1.74	0.35	425	33	6.4	26.6	80.9	98.0	1825	473	106.4	11.81	24.94	5.81	23.3	7.0	6.0
11	2.40	2.61	0.89	1150	70	9.1	7.7	85.3	99.0	7080	880	149.1	14.78	32.81	14.59	16.2	8.0	6.1
11	3.77	2.01	*	340	43	*	57.5	91.4	*	1540	473	*	17.08	22.11	1.00	22.[illegible]	9.1	*
11	1.68	3.20	*	523	83	*	2.3	65.1	*	4693	613	*	15.07	23.63	1.00	11.1	13.5	*
12	4.69	3.35	0.50	1507	101	8.5	11.4	70.7	100.0	10137	1121	178.5	31.55	37.18	10.50	14.9	9.0	4.8
12	6.16	4.16	0.38	2523	99	6.1	0.7	47.7	21.4	14153	879	166.1	34.55	36.94	10.[illegible]	17.8	11.3	3.7
12	2.91	2.48	0.38	499	52	7.4	15.8	63.3	52.1	7259	932	177.4	42.33	44.45	9.[illegible]	6.9	5.6	4.2
12	2.02	4.56	*	374	93	*	28.3	67.8	*	4084	783	*	22.06	38.39	1.00	9.2	11.9	*
12	5.57	4.46	*	1003	103	*	0.5	2.1	*	5723	773	*	31.78	33.47	1.00	17.5	13.3	*
13	8.79	4.60	0.76	2702	119	12.7	0.4	16.6	88.8	11482	1129	262.7	37.35	43.64	15.73	23.5	10.5	4.8
13	8.15	5.19	0.95	1388	132	15.5	20.0	46.4	86.1	9848	1422	315.5	57.82	55.91	19.35	14.1	9.3	4.9
13	12.18	4.94	0.52	3218	159	9.2	37.7	39.5	90.1	12888	1229	239.2	48.78	38.18	13.51	25.0	12.9	3.8
13	4.65	3.09	*	1800	91	*	5.9	44.6	*	11180	1091	*	28.88	37.05	1.00	16.1	8.3	*
13	11.09	4.92	*	2824	144	*	3.6	20.2	*	13084	1354	*	51.38	46.26	1.00	21.6	10.6	*
14	6.08	3.07	0.37	1668	104	6.8	1.7	0.4	72.9	12068	1084	396.8	43.99	32.00	21.64	13.8	9.6	1.7
14	9.21	2.52	0.39	1549	58	6.6	0.3	0.4	34.2	10819	908	466.6	64.33	39.45	27.66	14.3	6.4	1.4
14	5.78	1.95	0.31	1587	44	5.7	29.1	0.7	39.9	12107	744	395.7	44.09	32.97	21.53	13.1	5.9	1.4
14	7.17	2.20	*	1878	74	*	26.0	0.7	*	9218	1014	*	35.19	30.15	1.00	20.4	7.3	*
14	8.82	5.10	*	1933	181	*	0.3	0.4	*	11113	2531	*	50.71	71.32	1.00	17.4	7.2	*

APPENDIX B. Cumulative N mineralization (ug.g^{-1}) during the 37 week incubation. D.Wt.: sample dry weight.

STAND 1

WEEKS	2	4	7	11	15	21	29	37	D.Wt.
LFH1	62.50	98.21	100.51	180.10	242.86	367.09	466.07	627.04	19.6
A1	3.25	16.78	26.07	44.36	69.62	94.18	119.61	133.90	86.1
B1	0.09	0.58	0.64	2.99	4.48	5.58	6.68	8.02	163.9
LFH2	10.59	18.15	22.69	57.11	108.55	184.57	239.79	298.41	13.3
A2	0.18	6.46	10.87	29.88	48.76	69.05	89.88	107.71	109.9
B2	0.13	1.68	2.06	4.70	8.60	11.45	13.43	13.98	145.9
LFH3	1.42	6.16	6.16	36.97	72.51	121.33	160.19	162.08	10.6
A3	3.37	11.22	12.41	24.74	36.22	50.04	61.22	69.92	117.2
B3	0.50	1.17	1.56	2.85	4.67	7.38	8.83	9.47	179.0
LFH4	64.67	205.44	274.05	499.61	758.28	1001.58	1214.12	1339.90	12.7
A4	3.00	15.63	29.28	42.57	66.49	101.86	133.13	164.83	68.1
LFH5	1.38	9.50	20.59	47.70	86.30	135.19	175.97	218.72	25.3
A5	0.46	8.35	15.77	31.88	59.93	83.93	122.77	135.40	43.2

STAND 2

WEEKS	2	4	7	11	15	21	29	37	D.Wt.
LFH1	13.64	197.82	199.18	446.11	788.54	1170.53	1469.30	2036.83	7.3
A1	0.75	5.00	8.26	21.61	56.10	93.63	122.52	147.91	131.9
B1	0.86	1.79	4.99	6.53	8.25	10.28	12.50	13.86	162.3
LFH2	57.33	111.36	132.30	269.02	435.50	846.75	1063.95	1147.74	9.1
A2	11.45	21.60	28.98	48.85	69.93	95.96	125.37	138.04	115.3
B2	0.28	1.58	1.75	3.11	5.08	11.07	14.85	16.82	177.1
LFH3	114.15	505.35	815.10	1245.[illegible]	1633.77	1884.07	2175.98	2417.36	16.9
A3	17.09	74.85	155.55	204.68	291.39	386.88	444.17	478.36	64.9
B3	0.52	2.80	3.45	8.27	12.63	17.44	21.35	26.43	153.6
LFH4	1.41	14.14	15.56	80.62	254.60	794.91	1353.61	1775.10	7.7
A4	1.03	6.58	15.23	29.81	43.45	63.01	81.81	93.94	106.3
LFH5	600.89	1256.41	2150.50	2971.01	3366.78	3649.94	4127.09	5064.66	8.9
A5	15.64	49.07	104.23	186.09	242.28	307.47	342.95	369.66	126.5

APPENDIX 8. (cont.) Cumulative N mineralization (ug.g⁻¹ during the 37 week incubation. D.Wt.: sample dry weight.

STAND 3

WEEKS	2	4	7	11	15	21	29	37	D.Wt.
LFH1	50.98	140.45	263.48	438.47	572.51	683.86	794.71	864.45	30.4
A1	2.25	8.02	12.52	18.33	24.00	33.48	44.06	67.15	133.4
B1	0.09	2.86	2.90	3.13	3.19	5.53	7.07	8.52	152.0
LFH2	215.01	491.77	678.31	961.20	1196.35	1352.69	1549.31	1833.02	11.4
A2	8.49	32.39	56.69	85.08	113.29	137.80	166.59	228.98	112.3
B2	1.45	2.23	2.32	2.66	4.03	6.85	8.02	10.13	161.4
LFH3	257.04	504.35	791.41	1370.59	1560.83	1654.26	1915.11	2234.64	11.8
A3	12.66	36.22	54.51	86.07	108.82	139.57	170.47	206.13	98.7
B3	0.30	1.71	2.77	4.97	5.84	8.58	11.02	15.48	166.0
LFH4	199.29	500.06	713.33	891.97	984.32	1292.38	1610.16	1941.87	8.2
A4	13.54	38.63	54.33	77.16	99.12	121.37	147.43	189.78	102.5
LFH5	397.11	981.17	1610.30	2176.07	2421.02	2546.85	2655.72	2791.31	11.2
A5	2.09	10.64	20.01	44.97	61.72	80.28	99.65	134.21	85.9

STAND 4

WEEKS	2	4	7	11	15	21	29	37	D.Wt.
LFH1	46.56	97.45	140.06	225.52	283.12	447.67	601.42	736.32	9.2
A1	10.00	35.62	58.18	79.26	91.01	110.22	138.64	158.53	109.3
B1	0.36	1.05	1.15	2.37	3.65	5.10	6.45	7.57	168.8
LFH2	111.75	240.21	311.06	484.73	877.02	1327.48	[illegible]642.86	1783.70	16.6
A2	5.81	8.47	10.14	14.94	19.14	23.73	30.76	36.05	110.8
B2	0.60	1.38	1.69	2.53	3.89	5.68	7.60	9.36	174.6
LFH3	89.03	207.00	254.69	406.56	609.43	788.59	1069.73	1237.04	10.7
A3	4.26	9.00	9.76	17.13	22.92	31.98	40.16	52.20	87.7
B3	1.03	2.93	4.23	5.52	6.59	7.69	9.46	12.02	158.8
LFH4	204.20	463.16	592.63	832.38	934.61	1233.52	1734.82	2066.94	7.3
A4	7.66	17.46	30.50	51.08	67.57	82.05	102.72	122.53	95.7
LFH5	89.35	246.74	403.44	482.47	604.12	774.57	1034.36	1411.68	11.1
A5	2.85	6.74	11.89	19.62	28.46	37.92	50.28	59.13	96.7

APPENDIX 8. (cont.) Cumulative N mineralization (ug.g^{-1}) during the 37 week incubation. D.Wt.: sample dry weight.

STAND 11

WEEKS	2	4	7	11	15	21	29	37	D.Wt.
LFH1	4.67	13.73	13.74	27.20	122.25	269.78	359.34	434.61	18.2
A1	0.81	4.62	9.99	20.80	32.79	41.46	52.35	56.54	140.6
B1	0.50	1.25	1.84	3.13	4.25	5.14	6.79	7.57	178.9
LFH2	13.11	35.51	52.18	130.05	222.13	296.72	381.42	425.41	18.3
A2	0.03	0.87	2.15	6.14	9.62	18.51	29.24	33.07	149.3
B2	0.45	0.48	1.10	1.77	2.74	4.42	5.77	6.42	155.0
LFH3	61.12	165.53	211.37	397.28	631.58	861.63	1017.83	1150.25	5.9
A3	1.28	8.89	15.94	27.93	38.58	50.86	61.70	70.27	105.1
B3	0.87	1.80	2.48	3.56	5.25	6.97	8.43	9.13	171.4
LFH4	16.24	51.75	59.87	111.78	179.30	269.43	332.17	339.49	31.4
A4	0.37	4.73	8.57	16.42	21.34	30.47	37.00	42.71	133.1
LFH5	31.86	95.60	141.76	197.25	268.13	378.02	464.28	523.08	9.1
A5	5.36	17.00	23.92	39.18	50.09	64.67	75.07	82.81	109.2

STAND 12

WEEKS	2	4	7	11	15	21	29	37	D.Wt.
LFH1	66.48	194.89	355.68	713.64	1048.29	1181.82	1348.29	1507.39	8.8
A1	0.58	7.54	14.67	30.83	49.89	75.00	89.24	101.39	93.4
B1	0.45	1.08	1.56	3.37	4.93	6.70	7.91	8.48	166.3
LFH2	296.38	540.58	1024.64	1747.10	2136.96	2376.09	2519.56	2523.19	6.9
A2	4.28	12.56	19.96	31.26	42.73	61.43	81.76	98.91	119.0
B2	0.34	1.05	1.08	1.63	2.71	3.99	5.53	6.13	175.3
LFH3	47.57	116.36	200.30	233.33	293.03	343.94	427.27	499.09	16.5
A3	0.03	0.78	0.78	5.60	14.93	25.30	43.40	52.31	134.0
B3	0.07	0.83	0.84	0.98	2.52	4.55	6.08	7.45	143.0
LFH4	40.52	76.47	80.72	156.86	188.56	250.98	321.89	374.18	15.3
A4	1.40	8.51	19.40	39.33	57.22	71.59	84.84	92.71	139.2
LFH5	118.47	257.96	536.30	786.94	892.99	967.51	1003.50	1003.82	15.7
A5	7.67	27.80	35.72	48.19	61.07	77.48	91.38	103.40	121.9

APPENDIX B. (cont.) Cumulative N mineralization (ug.g⁻¹) during
the 37 week incubation. D.Wt.:sample dry weight.

STAND 43

WEEKS	2	4	7	11	15	21	29	37	D.Wt.
LFH1	372.28	686.96	1098.91	1526.63	1877.17	2228.26	2519.56	2702.17	9.2
A1	5.30	14.73	22.64	37.10	56.18	83.99	103.52	119.03	109.3
B1	0.74	2.07	2.43	3.55	5.57	7.35	9.69	12.74	168.8
LFH2	65.66	243.37	481.93	639.16	811.45	1016.87	1228.31	1388.55	16.6
A2	0.85	8.70	19.18	36.19	55.91	71.34	104.56	132.49	110.8
B2	0.51	2.23	3.47	6.04	7.36	10.31	13.14	15.46	174.6
LFH3	262.15	721.03	1124.77	1611.68	2017.29	2494.86	2918.22	3218.69	10.7
A3	5.01	15.05	26.62	50.51	78.33	111.29	141.73	159.24	87.7
B3	0.37	1.10	1.51	2.71	4.25	5.86	7.87	9.19	158.8
LFH4	226.03	482.19	573.97	862.33	1119.18	1292.46	1549.31	1800.00	7.3
A4	1.35	5.59	13.22	30.30	45.66	56.11	83.28	91.43	95.7
LFH5	369.37	867.12	1268.92	1557.66	1723.42	2104.05	2467.57	2824.32	11.1
A5	1.91	10.70	25.49	45.91	67.22	91.93	119.18	143.79	96.7

STAND 14

WEEKS	2	4	7	11	15	21	29	37	D.Wt.
LFH1	116.50	397.09	723.79	836.89	956.31	1164.56	1472.81	1668.93	10.3
A1	2.51	9.28	16.41	29.46	45.75	61.98	81.62	104.01	83.5
B1	0.06	0.16	0.26	0.69	1.47	2.29	3.99	6.77	162.9
LFH2	100.89	255.36	474.70	866.96	1037.80	1200.89	1401.49	1549.70	16.8
A2	1.71	6.89	11.62	21.13	28.34	37.93	48.29	58.12	122.6
B2	0.15	0.44	0.57	0.90	1.74	3.26	5.36	6.55	167.1
LFH3	414.08	580.58	585.44	643.69	676.21	891.75	1203.88	1587.86	10.3
A3	2.49	5.42	8.72	15.41	18.34	26.74	35.62	43.78	126.2
B3	0.16	0.54	1.45	1.78	2.23	3.10	4.23	5.75	154.9
LFH4	321.76	714.35	854.63	1018.52	1109.72	1325.00	1717.59	1878.24	10.7
A4	5.04	10.86	15.38	24.82	33.19	46.73	60.93	73.81	84.1
LFH5	166.67	358.53	699.6[illegible]	938.37	1212.40	1475.97	1749.61	1932.94	12.9
A5	11.76	28.99	47.11	[illegible].94	92.70	127.04	160.25	181.26	79.5