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DECOMPOSITION AND INTERNAL CYCLING MAKE IMPORTANT CONTRIBUTIONS TO NUTRIENT SUPPLY WITH AGE IN A JACK PINE STAND

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INTRODUCTION

Nutrient acquisition by forest stands varies with the demands of the vegetation and the ability of sites to supply nutrients. New growth is supported by nutrient uptake from the soil and by the translocation of nutrient reserves within the trees themselves. As a general rule, tree stands are assumed to accumulate less nutrients as they age, and to return more nutrients to the soil in the forms of litterfall and canopy wash. Nutrients returned to the soil may be reutilized by the trees or incorporated into organic layers. Immobilization of nutrients in the soil organic layers, however, may produce a slowdown in nutrient cycling between vegetation and soil in mature forests. Restricted nutrient cycling, therefore, may limit nitrogen (N) and possibly other nutrients in older boreal stands.

There are two approaches to estimating changes in nutrient supply. One examines changes in tree and soil nutrient pools as forests age. The other approach, which is less expensive, assesses changes in the annual transport of nutrients between trees and soil. This report summarizes results of the two approaches, and demonstrates how each provides insights into changes in jack pine (*Pinus banksiana* Lamb.) nutrient

supply with age. A more detailed account of changes in jack pine nutrient procurement with age and site class was described by Foster et al. (1994).

APPROACHES

Changes in Nutrient Pools with Age

This study utilizes growth and nutrient data collected over 25 years (1969–1993) from a fire-origin, boreal outlier jack pine stand with a Site Index 50 of 19 m. The study site is situated near Thessalon, Ontario (Lat. 46° 25'N, Long. 83° 23'W) and is representative of a Wendigo soil (coarse to medium outwash sand).

The diameter at breast height (DBH) of all trees and replicated samples of foliage, branches, stems, and soil were obtained from four 0.04-ha permanent sample plots. Stand contents of nitrogen (N), phosphorus (P), potassium (K), calcium (Ca), and magnesium (Mg) were calculated on a plot-by-plot basis using mean concentrations and tree component dry weights per area (Morrison 1973). Soil nutrient contents were determined as described in Foster and Morrison (1976). The humus layers and litterfall were sampled using forty 0.02-m plots and ten 0.25-m traps, respectively. Replicated precipitation and throughfall collectors were sampled at the beginning, middle, and end of the 25-year period.

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Annual Nutrient Fluxes

Annual nutrient fluxes were calculated as the product of water fluxes, estimated by the forest hydrology model ForHyM described by Arp and Yin (1992), and concentrations were determined bi-weekly. Nutrient-use efficiency is defined as the amount of dry matter produced per unit of nutrient retained by the stand. Adjacent 20- and 30-year-old jack pine stands on the same soil were included to examine changes in such efficiency with age.

RESULTS AND DISCUSSION

Stand Nutrient Accumulation

Forests in northern latitudes are generally characterized by low production and decomposition rates, and a significant accumulation of organic matter and nutrients within the forest floor. When the study stand was 35 years old, the mineral soil contained 98 t/ha of organic matter; 4 350 kg/ha of total N; 8 kg/ha of available P; and 96, 468, and 34 kg/ha of exchangeable K, Ca, and Mg, respectively. Half of the organic matter in this jack pine ecosystem was contained in the tree layer (Table 1). Almost one-third of the organic matter in the soil and substantial nutrients were contained in the forest floor. Forest floor nutrients can replenish a nutrient-depleted soil and sustain the growth of the maturing forest. For example, radial tree growth declined 30 percent over 8 years with annual removal of the forest floor in a 50-year-old jack pine stand (Weber et al. 1985).

Between the ages of 35 and 56 years, stand basal area and dry matter increased from 27 to 35 m²/ha and from 117 to 175 t/ha, respectively. Stocking decreased from 1 952 to 1 174 trees/ha. The stand increased its nutrient content by accumulating considerable dry matter in tree stems (Table 1). An increase in crown dry matter was accompanied by a large increase in crown nutrient contents.

Changes in carbon allocation within a tree are reflected in a stand's nutrient-use efficiency. The highest nutrient-use efficiency was observed at the age of 35 years (Table 2), when the annual rate of biomass accumulation was greatest. An exception was K-use efficiency, which increased with age. The ratios for N, P, Ca, and Mg narrowed somewhat with

Table 2. Age effects on nutrient-use efficiency* in jack pine stands on a Wendigo soil.

Age (years)	Nutrient-use efficiency				
	N	P	K	C	Mg
20	394	4 368	832	647	3 744
30	475	5 419	956	695	4 278
35	478	6 368	1 090	807	5 033
45	458	4 700	1 325	745	4 236
56	434	4 841	1 376	770	4 538

* Nutrient-use efficiency is defined as the amount of dry matter produced per unit of nutrient retained by the stand.

maturity, suggesting an enhanced nutrient retention with age, presumably in response to crown expansion.

Nutrient-use efficiency should be highest in ecosystems that are nutrient deficient (Cole 1981). In general, N- and P-use efficiency in the study stand were below average for jack pine values, suggesting above average biological availability of these two nutrients in the Wendigo soil. The larger than average K-use efficiency in the older pine forest suggested low K availability in the Wendigo soil. In fact, the widening K ratio between the ages of 20 and 56 years indicates that K was being used more efficiently as the forest matured; presumably because the uptake of K was limited by decreasing availability in the soil.

Nutrient Cycling

The annual net uptake of N and K by the stand increased with age (Table 3), driven by the high demand for these nutrients by crown expansion. The net uptake of P, Ca, and Mg appears to peak at the age of 45 years and then decrease. After 35 years, there was a large pool of nutrients within the forest floor to meet tree nutrient demand (Table 1). In addition to these nutrients, the stand was able to obtain, after the age of 35 years, more N and P by nutrient translocation from foliage prior to abscission. For example, the trees obtained from retranslocation 4.1 kg N/ha per year at the age of 35 years and 17.3 kg N/ha per year at the age of 56 years. Resorption was positively related to the mass of N and P in the foliage of jack pine crowns (Foster et al. 1994). By the age of 56 years, the

Table 1. Organic matter (t/ha) and nutrient distribution (kg/ha) at the ages of 35 and 56 years in a jack pine stand growing on a Wendigo soil.

Component	Mass		N		P		K		Ca		Mg	
	35	56	35	56	35	56	35	56	35	56	35	56
Crown	23	32	125	241	11	24	42	73	48	77	8	19
Stem	70	117	71	101	4	7	44	35	68	116	10	15
Roots ¹	17	29	18	73	1	2	11	9	17	30	3	4
Total tree	110	178	214	415	16	33	97	117	133	223	21	38
Forest floor ²	4	48 ³	400	469 ³	2	10 ³	45	24 ³	114	85 ³	21	18 ³

¹ Includes stump.

² N = total; P = available Bray and Kurtz; K, Ca, Mg = Morgan's sodium acetate-acetic acid extractable.

³ Based on L and F mass at the age of 56 years; H mass at the age of 45 years; and L, F, and H nutrient concentrations at the age of 56 years.

Table 3. Age effects on annual net nutrient uptake (kg/ha per year) by jack pine forest growing on a Wendigo soil.

Age (years)	N	P	K	Ca	Mg
35	30.7	2.7	8.3	9.4	1.8
45	38.3	4.5	9.2	13.0	3.0
56	44.3	4.2	11.4	11.4	2.7

crowns also contained more K, and K retranslocation produced an increase in net K uptake. Uptake of K from the soil actually decreased as the stand matured (Foster et al. 1994).

Considerable quantities of nutrients were returned annually from trees to soil in the forms of litterfall (Table 4) and leafwash (Table 5). The mass and content of most nutrients in litterfall exhibited substantial year-to-year variation; however, this did not vary systematically with age (Table 4). However, the annual flux of K in litterfall and canopy leachings declined between the early 1970s and the early 1990s. This K decline supports the conclusion that soil K reserves are becoming exhausted.

Nutrient Accumulation in the Soil

Juvenile, fire-origin jack pine stands are dependent on mineral soil and unconsumed organic layers to sustain their growth. Until the trees reach crown closure, increasing quantities of nutrients are transferred to the soil by litter and canopy wash as the stand ages. The authors observed that by the age of 35 years the amount of nutrient in litterfall and crown wash was equivalent to a large part of the net nutrient uptake.

Table 4. Changes in annual organic matter and nutrient content (kg/ha) of jack pine litterfall with age.

Year	N	P	K	Ca	Mg	Mass
1969	24.0	0.8	4.6	15.4	1.6	3 582
1970	18.5	1.4	5.5	12.4	1.6	4 199
1971	19.0	1.4	4.4	12.1	2.1	3 405
1983	25.6	1.7	3.1	17.3	1.6	4 102
1984	31.7	2.2	4.5	22.8	2.3	4 628
1985	31.9	2.3	4.9	19.6	2.2	5 283
1986	18.0	1.3	2.7	12.1	1.5	2 648
1992	20.9	1.1	2.2	8.9	1.0	3 043
1993	24.9	1.3	2.6	11.9	1.9	3 856

Table 5. Changes in annual nutrient leaching (kg/ha) from a jack pine canopy with age.

Year	N	P	K	Ca	Mg
1970	-0.8	-	8.9	1.6	-
1971	-1.6	0.03	9.9	0.4	0.3
1984	-3.1	-0.02	3.7	0.7	0.4
1985	-1.2	0.05	6.3	1.9	0.8
1989	-0.8	0	5.0	1.4	0.6
1990	-1.1	0.01	5.4	1.1	0.8
1991	0.1	0.20	7.8	2.4	1.1
1992	-1.1	0.17	6.2	1.2	1.0

Further, by this age soil nutrient stores were augmented by substantial quantities of nutrients that accumulated as organic layers under the trees.

Between the ages of 35 and 56 years, the rate of N and P accumulation by the trees did not diminish. Sequential observations revealed that after 35 years there was a substantial increase in P availability in the forest floor (Table 1). Inputs of N to the forest floor exceeded outputs by only 3 kg/ha per year. The forest floor, therefore, represents an important source of N and P for older pine forests and for a new forest once the stand is harvested.

Between the ages of 35 and 56 years there was a decrease in K availability in the forest floor as ions were mobilized to meet the needs of the mature stand. A net release of 10 kg/ha per year of K from the forest floor was observed between 1989 and 1991. Therefore, the mature jack pine forest obtained K mainly from the forest floor, where reserves appeared to be diminishing as K accumulated in the trees.

Implications for Management

Nutrient accumulation rates vary with stand age and site quality. In the very productive jack pine stand examined, the rates of dry matter and nutrient accumulation, in both crowns and stems, did not diminish between the ages of 35 and 56 years. In contrast, jack pine stands of low productivity accumulated few nutrients beyond the age of 30 years (MacLean and Wein 1977). From midrotation to maturity, therefore, it is likely that nutrients from precipitation and weathering would be utilized to replenish available soil nutrients in jack pine forests of low productivity. In forests of higher productivity, these nutrient inputs would be utilized instead to sustain growth. In such productive forests, nutrients removed from the soil by the trees are less likely to be replaced during a managed pine rotation of 70 to 80 years.

Results of this study indicate that because more nutrients accumulate in productive pine forests, harvesting these stands will have a larger absolute impact on soil nutrient reserves. The differences in nutrient removals, between stands with high and low productivity, will be greater if the forests are full-tree logged. They will also increase with the length of the rotation.

Short rotations (40 to 50 years) and commercial thinnings are being considered within boreal Ontario because of wood shortages and skewed age-class distributions. The opportunity for serious nutrient depletion on jack pine sites will increase with the introduction of intensive forest management (complete tree utilization, thinnings, site preparation, and shorter rotations). For example, the potential removal of K from the study site would be 35 kg/ha by stem-only clear-cutting, 108 kg/ha by whole-tree logging, and 330 kg/ha by whole-tree with blade scarification (forest floor removal). Although N limitations to the growth of maturing jack pine forests are well established (Krause et al. 1982, Morrison and Foster 1990), K limitations may also develop at later stages of stand development on Wendigo and other similar soils.

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