CHANGES IN NUTRIENT PROCUREMENT WITH AGE AND SITE PRODUCTIVITY IN JACK PINE FOREST

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ABSTRACT

The effect of age on forest nutrition was examined from sequential observations over 25 years in a natural *Pinus banksiana* Lamb. (jack pine) stand on glacio-fluvial soil in the boreal forest of northern Ontario, Canada. Comparisons of indicators of nutrition were made between this stand and other mature jack pine stands of lower site productivity in Ontario, New Brunswick, and Wisconsin. Greater phytomass and nutrient contents were associated with older stands of higher site productivity. Nutrient-use efficiency by jack pine varied with age and decreased with increasing site fertility. Jack pine net uptake of nitrogen and phosphorus increased from 16.5 and 2.6 kg/ha/year at SI 11.4, to 44.2 and 4.4 at SI 19.0. On less fertile, lower productivity sites, the proportion of the stand net uptake of nitrogen and phosphorus supplied by retranslocation did not increase. Retranslocation of nitrogen and phosphorus increased with increasing foliar phytomass and canopy nitrogen and phosphorus contents. There was a reduction in accumulation of phosphorus in the juvenile closed forest and potassium at the approach of maturity in the pine stand with the best nitrogen nutrition.

Keywords: nutrient-use efficiency; nitrogen; phosphorus; phytomass; site productivity; uptake; retranslocation, potassium; calcium; magnesium.

INTRODUCTION

Nutrient acquisition by forest stands varies with the demands of the vegetation and the ability of a site to supply nutrients. New growth is supported by nutrient uptake from the soil and by retranslocation of nutrient reserves from within the trees. Investigators of nutrition of coniferous forests have documented the importance of the cycle of nutrients between trees and soil in sustaining the production of long-lived forests (e.g., Rodin & Basilevich 1967; Cole 1981; Miller 1986). Age effects on patterns of nutrient accumulation and cycling have been published for temperate pine plantations (Ovington 1959; Switzer & Nelson 1972; Gholz *et al.* 1985) and natural boreal pine stands (Foster & Morrison 1976; MacLean & Wein 1977).

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Internal and external nutrient cycling by trees reduces the quantities of nutrients that must be supplied by the soil to the vegetation. In fact, these mechanisms may be critical to tree survival when nutrient supplies in soil are limiting or when the supply of nutrients from soil is temporarily interrupted. It has not been possible, however, to generalise on how the contributions of uptake and retranslocation change with stand age and site quality (Bockheim & Liede 1991). Our objective, therefore, was to determine the effect of age and site on nutrient uptake and retention by jack pine, a commercially important conifer in the Canadian boreal forest.

STUDY AREAS

Nutritional data collected from two jack pine sites in Ontario, Canada (Dupuis Township, Wells Township) were compared with that published for jack pine in New Brunswick, Canada (MacLean & Wein 1977) and Wisconsin, USA (Bockheim & Liede 1991). The stands (Table 1) were all even-aged pine that regenerated naturally after fire or clearing for grazing. Between ages 35 and 56, the stand basal area and dry matter at Wells increased from 27 to 35 m^2/ha and from 117 to 175 t/ha, respectively, and stocking decreased from 1952 to 1174 trees/ha. Between ages 45 and 68, the stand basal area and dry matter at Dupuis increased from 31 to 34 m^2/ha and 127 to 167 t/ha, respectively, and stocking decreased from 2926 to 1478 trees/ha. Phytomass and nutrient accumulation in these two forests were compared with that in 12 low-productivity jack pine stands representing an age sequence of 7 to 57 years (MacLean & Wein 1977). Soils were coarse-textured well-drained materials developed from glacial outwash.

TABLE 1–Mensurational data for the jack pine strands used in site productivity comparisons

Age	Site Index (m)	Diameter (cm)	Stocking (trees/ha)	Phyto-mass (t/ha)	Location	Reference
56*†	19.0	19.0	1174	175	Lat. 46°25´N, Long. 83°23´W	Foster *et al.* (1995)
55*‡	16.5	13.7	2174	154	Lat. 47°38´N, Long. 83°15´W	Foster *et al.* (1995)
51§	15.4	-	1625	68	Lat. 46°15´N, Long. 91°48´W	Bockheim & Leide (1991)
57*	11.4	10.9	2440	75	Lat. 47°30´N, Long. 65°20´W	MacLean & Wein (1977)

* = Fire origin
† = Wells Township
‡ = Dupuis Township
§ = Natural invaders after clearing for grazing.

METHODS

Tree phytomass was determined as follows: firstly, equations relating foliage, fruit, live branch, dead branch, stem wood, stem bark, and total above-ground dry weight to diameter and age were prepared from trees on the two Ontario sites. The data set consisted of dry weights by components for 108 individual trees ranging in age from 30 to 100 years (though dominated by trees aged 50–70 years). These equations, solved for the required ages, were used in conjunction with stand tables derived from 1972, 1982, and 1993 measurements of four permanent sample plots in the Wells stand and 1970, 1975, 1980, 1985, and 1993 measurements of five permanent plots in the Dupuis stand to determine total phytomass by components at those ages. In 1993 the Wells and Dupuis stands were 56 and 68 years old, respectively.

Nutrient content was calculated by multiplying component weight by concentration as determined at different points in time. Intermediate values were interpolated from values measured in the early 1970s and either the late 1980s (Wells) or the early 1990s (Dupuis). Quality control was provided through the re-analysis of reference samples. Sequential measurements of tree nutrition and nutrient cycling, therefore, covered ages 30 to 56 at Wells and 45 to 68 at Dupuis. Adjacent 20- and 25-year-old understocked jack pine stands on the same soil, were included for age comparisons. Aboveground stand nutrient contents of these two forests were increased by adjustment to normal stocking.

Gross nutrient uptake by the trees was calculated in the following manner: $U = A - P + T + S + L$ where A, P, T, S, and L represent the amount of nutrient in annual accumulation in perennial organs, precipitation, throughfall, stemflow, and litterfall, respectively (Morrison & Foster 1974). Components of gross uptake were determined according to procedures described by Foster (1974). For the Wells forest, periodic mean accumulation was calculated between ages 1 and 35, 35 and 45, and 45 and 56; fluxes were based on 3-year averages at age 35, 45, and 56. The comparison of uptake between stands was based on fluxes measured in each stand and the average annual nutrient accumulation, from establishment to maturity, by the trees.

The net nutrient uptake by trees was defined as the sum of annual accumulation in perennial tissues and in current foliage production. Current foliage production was estimated by dividing foliar nutrients by the number of years the needles were retained. Retranslocation was the difference between net and gross nutrient uptake.

Nitrogen (N) in oven-dried (70°C) plant phytomass was determined using a Tecator 1030 Analyzer after semi-micro Kjeldahl digestion or by Hewlett-Packard 180B CNH Analyzer (Conversion to Kjeldahl × 1.1). Samples were analysed for phosphorus (P), potassium (K), calcium (Ca), and magnesium (Mg), after wet ashing with nitric-perchloric acids, by a Jarrell-Ash ICAP 1100 spectrometer, or by a Perkin-Elmer 290 flame/atomic absorption spectrophotometer.

Nutrient-use efficiency was calculated by dividing stand phytomass by stand nutrient content. Nutrient-use efficiency from litterfall (NUEL) was estimated by dividing annual litterfall phytomass by annual litterfall nitrogen. Nitrogen availability in soil was estimated from forest floor nitrogen reserves and the residence time for nitrogen in the forest floor.

RESULTS AND DISCUSSION

Age Effects

Nutrient acquisition

Rates of phytomass accumulation were similar between sites of different site index, but were sustained for a longer time in the more productive stands (Fig. 1). By maturity the most productive jack pine stand had an average rate of phytomass production of 3.1 t/ha/year and the least productive a rate of 1.3.

Increases in nitrogen (Fig. 2), calcium, and magnesium (Fig. 3) contents with age generally paralled phytomass gains. In contrast, lower rates of accumulation were observed for phosphorus between ages 20 and 35 (Fig. 4) and potassium between ages 35 and 55 (Fig. 3) in the Wells (SI 19) pine stand. At ages 45 and 56, uptake and phosphorus retranslocation exceeded that in the 35-year-old stand (Table 2). We contend that the restricted rate of

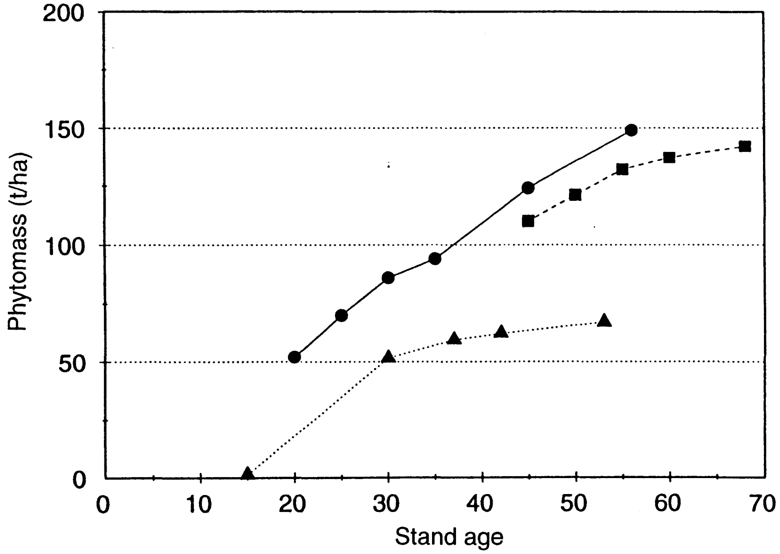

FIG. 1–Effect of age on dry matter contents in jack pine stands of site index 19.0 (●), 16.5 (■), and 11.4 (▲), the latter from MacLean & Wein (1977).

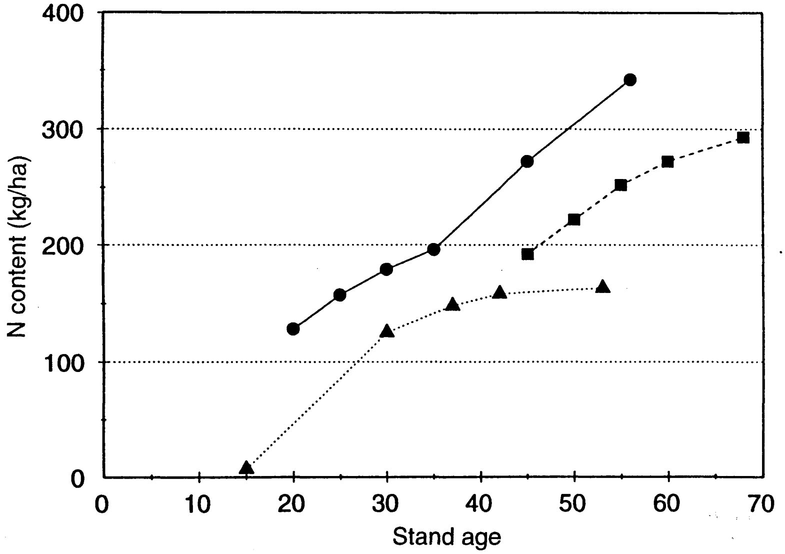

FIG. 2–Effect of age on nitrogen contents in jack pine stands of site index 19.0 (●), 16.5(■), and 11.4(▲), the latter from MacLean & Wein (1977).

accumulation of phosphorus between ages 20 and 35 was a result of the inability of the soil to supply phosphorus at the time when theoretically the greatest phosphorus demand by the stand should be observed (Miller 1981). The strongly acidic podsolised soil at Wells contains iron and aluminium hydrous oxides in the mineral soil that react with phosphorus, thereby reducing the availability of phosphorus to the trees.

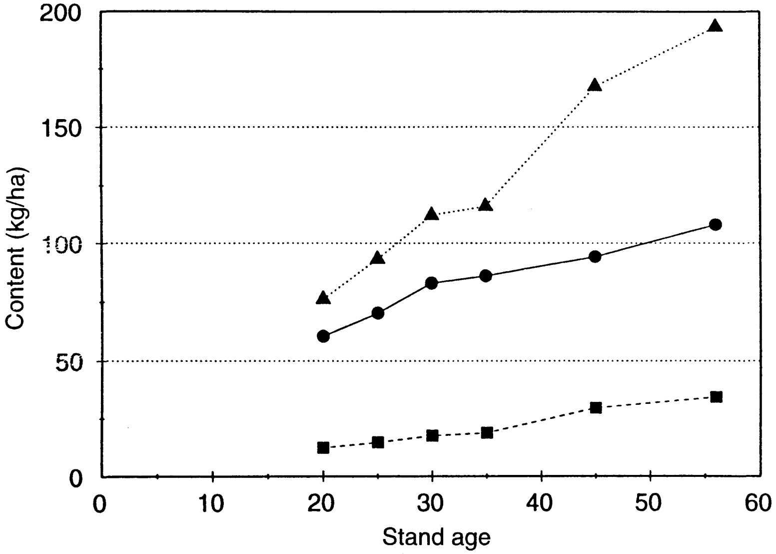

FIG. 3–Effect of age on potassium (●), calcium (■), and magnesium (▲), contents in Wells Township jack pine.

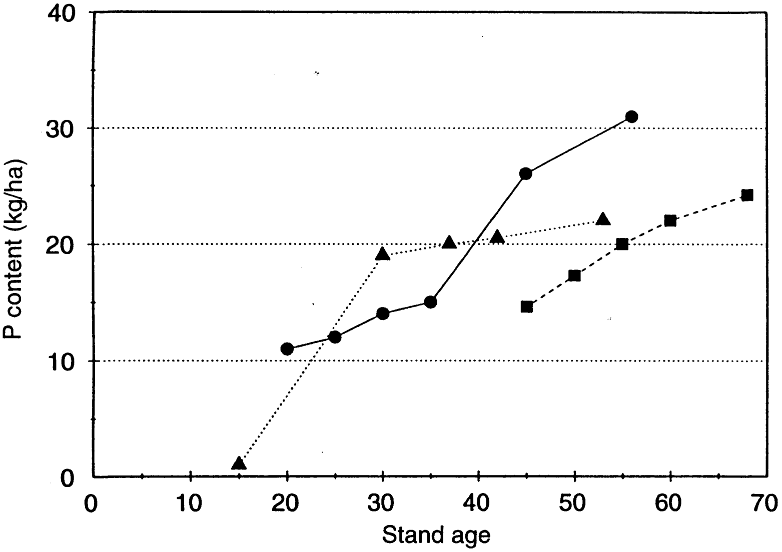

FIG. 4–Effect of age on phosphorus contents in jack pine stands of site index 19.0 (●), 16.5 (■), and 11.4 (▲), the latter from MacLean & Wein (1977).

TABLE 2–Age and site effects on annual nutrient acquisition (kg/ha) by Wells (SI 19.0) jack pine.

	Nitrogen			Phosphorus			Potassium			Calcium			Magnesium		
	GU*	NU†	RT‡	GU	NU	RT	GU	NU	RT	GU	NU	RT	GU	NU	RT
Age (years)															
35	26.6	30.7	4.1	1.0	2.7	1.7	14.4	8.3	–6.1	17.0	9.4	–7.6	2.5	1.8	–0.7
45	33.2	38.3	5.1	2.8	4.5	1.7	10.4	9.2	–1.2	24.6	13.0	–11.6	3.5	3.0	–0.5
56	27.0	44.3	17.3	1.6	4.2	2.6	10.1	11.4	1.3	14.7	11.4	–3.3	2.3	2.7	0.4
Site Index															
19.0	27.4	44.2	16.8	1.8	4.4	2.6	9.3	10.7	1.4	15.2	11.9	–3.3	2.4	2.8	0.4
16.5	16.5	26.9	10.4	1.2	3.3	1.1	6.0	9.0	3.0	10.6	10.2	–0.4	2.0	2.7	0.7
15.4	19.9	32.5	12.6	1.6	3.2	1.6	13.5	15.1	1.6	15.8	20.4	4.6	8.4	11.3	2.9
11.4	10.7	16.5	5.8	0.8	2.6	1.8	8.8	8.0	-0.8	5.6	3.7	–1.9	2.5	1.6	–0.9

* GU = Gross Uptake
† NU = Net Uptake
‡ RT = Retranslocation

The recovery of phosphorus accumulation rates in the semi-mature stand may be related to improved phosphorus availability in soil. After age 35 the demand for phosphorus by the stand was sustained (crown expansion continues) and phosphorus became more available in the forest floor, thus reducing dependence on the mineral soil for phosphorus supply. Paré & Bernier (1989) noted better phosphorus nutrition in maple-(*Acer* sp.)-dominated forests with relatively mineral-free mor humus layers than in those with mull layers (organic matter mixed with phosphorus-fixing soil minerals).

Mor humus layers in some jack pine forests have been shown to contain 40 to 50 kg P/ha (Foster & Morrison 1976; Alban *et al.* 1978). In closed-canopy jack pine forests, stand age appears to have little influence on decomposition and relase of nutrients from organic layers (Weber 1987; Foster *et al.* 1995). The re-establishment, under closed-canopy forest, of a steady state in nutrient turnover in the forest floor allows the trees access to organic phosphorus reserves, either directly by mycorrhizal fungi or indirectly after phosphorus mineralisation. At the Wells site, we estimated that the forest floor could supply 40–50% of the annual nitrogen uptake by semi-mature pine forest (Foster *et al.* 1995). Organic layers, therefore, represent an important continuous source of phosphorus and other nutrients to maturing pine forests.

Indices of jack pine nutrition

Estimated net nutrient uptake for the most productive pine forest examined (Wells) was 44 kg N/ha, 4 kg P/ha, 11 kg K/ha, 11 kg Ca/ha, and 3 kg Mg/ha annually (Table 2). Gross nutrient uptake was 27 kg N/ha, 2 kg P/ha, 9 kg K/ha, 15 kg Ca/ha, and 2 kg Mg/ha, annually. Uptake from the soil, therefore, supplied most of the potassium, calcium, and magnesium and a lot of the nitrogen and phosphorus to support current growth. Retranslocation of nitrogen and phosphorus, prior to needle mortality, made a significant contribution to net nutrient uptake.

Differences in the relative importance of litterfall, canopy leaching, and accumulation in perennial tissues to the estimate of gross nutrient uptake were observed for each nutrient. For nitrogen and phosphorus, litterfall accounted for 80%, accumulation for 16%, and canopy leaching for 4% of uptake. For calcium and magnesium, canopy leaching increased to 12–30% and litterfall decreased to 55–75%. For potassium, canopy leaching accounted for ~60% of uptake, litterfall 30%, and accumulation 10%. In closed-canopy jack pine forest, the relative contributions of the individual processes to the calculation of uptake were consistent across the range of age and site productivity examined.

Retranslocation of nitrogen and phosphorus, and the proportion of net nutrient uptake obtained from retranslocation, increased with stand age in the Wells forest. A similar observation of a progressive increase in retranslocation with Douglas-fir maturity has been reported by Turner (1981). Gross nutrient uptake in jack pine was greatest at age 45, except for potassium which declined beyond age 35, suggesting limitations in soil supply and/or efficient retranslocation. Less potassium was available in the foliage and potassium leaching from the canopy declined as the trees matured (Foster unpubl. data). As the Wells stand approached maturity, therefore, less potassium was accumulated in pine phytomass and potassium cycling between the vegetation and soil declined as a result of reductions in potassium leaching from the foliage and litterfall potassium concentrations.

Nutrient-use efficiency

Unless stated otherwise, nutrient-use efficiency was calculated by dividing stand phytomass by accumulated stand nutrient content. It represents the amount of phytomass produced per unit of nutrient retained by the stand. The highest nutrient-use efficiency was observed at age 35 for the Wells site. An exception was potassium-use efficiency, which increased with age (Table 3). In this productive pine forest, nutrient levels in the canopy and total stand phytomass (Fig. 2–4) did not decline before age 55 and hence nutrient-use efficiency ratios did not increase with age. In fact the ratios for nitrogen, phosphorus, calcium, and magnesium narrowed somewhat with maturity, suggesting enhanced nutrient retention with age. Once crown development stabilises, the relative proportion of most elements in the crown would decrease with age, and the relative proportion in the stems would increase. Stem components contain much lower nutrient concentrations than foliage and branches, hence nutrient-use efficiency theoretically should increase once full canopy development has been obtained. The widening potassium ratio between ages 20 and 56 indicates that potassium was being used more efficiently—presumably because the uptake of potassium was limited by decreasing potassium availability in the soil as the forest aged.

TABLE 3–Age effects on nutrient-use efficiency in the Wells (SI 19.0) jack pine.

Age	N	P	K	Ca	Mg
20	394	4368	832	647	3744
30	475	5419	956	695	4278
35	478	6368	1090	807	5033
45	458	4700	1325	745	4236
56	434	4841	1376	770	4538

Site Effects

Nutrient acquisition

Jack pine above-ground phytomass production generally increased with increasing site productivity (Fig. 1). Differences between the most and least productive sites were observed from an early age (15 years) to maturity. The amounts of nutrients in above-ground tree components generally increased in proportion to phytomass production and, therefore, with site index (Fig. 1–4: potassium, calcium, and magnesium not shown). Limitations in phosphorus uptake were revealed in SI 19 and 16.5 pine stands, and so they accumulated less phosphorus than the SI 11.4 forest in juvenile closed forest. These limitations were covercome as the stand matured, restoring the expected relationship betwen phosphorus accumulation and site productivity in the mature pine forests.

Surprisingly, there was no difference in calcium accumulated in SI 19 and 16.5 pine stands over the limited period of observations (age 45 to 55). At maturity both exhibited a similar net uptake of calcium (Table 2). Major differences in the disposition of the calcium taken up, however, were detected between the two stands. The cycle of calcium between trees and soil (litterfall calcium, calcium uptake) was greater in the Wells (SI 19) forest, which carried a 40% greater foliar mass. The Dupuis forest on the other hand, accumulated more calcium but cycled less.

The higher calcium-use efficiency of the Wells forest (770 *v.* 724 at Dupuis) is a reflection of the lower exchangeable calcium supply in the soil to a depth of 100 cm (259 kg/ha) than at Dupuis (511 kg/ha) (Morrison & Foster 1987). The mature Dupuis pine forest, which could access more soil Ca, was able to incorporate considerably more Ca in its phytomass than the more productive Wells forest.

The Dupuis (SI 16.5) forest at age 45 responded to liming by increasing calcium uptake for a period of at least 17 years without any detectable effect on the total annual volume growth of the forest (Foster *et al.* 1988). Increasing phytomass production in the Dupuis forest by nitrogenous fertiliser application, however, resulted in a sharp increase in calcium-use efficiency (Table 4). The soil of the Dupuis site, in contrast to the soil of the Wells site, therefore, provided adequate calcium for the current level of tree growth; but its ability to supply additional calcium was limited.

TABLE 4–Nitrogenous fertiliser effects on nutrient-use efficiency in Dupuis (SI 16.5) jack pine.

Nutrient	Without fertiliser mean annual	Without fertiliser current	With fertiliser current
N	576	550	300
P	7572	7333	4100
K	759	660	820
Ca	691	846	3154
Mg	4268	3667	3154

Indices of jack pine nutrition

Jack pine net incorporation of nitrogen and phosphorus increased with increasing site productivity, whereas potassium, calcium, and magnesium retention was largely independent of site (Table 2). Gross uptake and retranslocation patterns followed similar trends. Retranslocation supplied more phosphorus than uptake; both were important for nitrogen; and uptake supplied most of the requirements for potassium, calcium, and magnesium at each of the sites.

We were unable to detect the differences in nitrogen availability in soil by examining nutrient concentrations in foliage and litter from the three pine sites (Tables 5, 6). It was not possible to detect the higher requirements for nitrogen of the more productive higher SI forests by assessing either foliar or litter nitrogen concentrations (Table 5). Significant year-to-year variations in dormant-season foliar concentrations have been detected in jack pine, even within succeeding years (Foster *et al.* 1995). These observations demonstrate some of the difficulties associated with using foliar analysis as a diagnostic tool.

Another common approach in fertility assessment is to examine nutrient ratios in foliage. For example, Reich & Schoettle (1988) determined that the efficiency of nitrogen use in

TABLE 5–Response of indices of jack pine nutrition to changes in nutrient availability

Site Index	N availability (kg/ha/year)	Foliar N (%)	Litter N (%)	Litter N (kg/ha/year)	NUE*
19.0	35	1.18	0.44	22.5	377
16.5	25	1.10	0.44	14.5	312
11.4	17	1.10	0.40	10.2	507

* NUE = Nitrogen-use efficiency

TABLE 6–Changes in nitrogen, phosphorus, and potassium retranslocation and soil nutrient contents with jack pine site characteristics.

Site Index	Soil N (kg/h)	N availability (kg/ha/year)	Wood production (kg/ha/year)	Retranslocation		
				N (kg/ha/year)	P (kg/ha/year)	K (kg/ha/year)
19.0	4350	35	2620	16.8	2.6	1.4
16.5	1950	25	1365	10.4	2.2	3.0
15.4	3800	31	890	12.6	1.6	1.6
11.4	1670	17	780	5.8	1.8	–0.8

photosynthesis by *Pinus strobus* L. (white pine) seedlings was positively correlated with needle P:N. They concluded that at P:N ratios <0.10–0.14 a relative lack of phosphorus can limit nitrogen use for photosynthesis. Jack pine P:N ratios for the Dupuis and Wells forests were generally 0.10 or lower (Table 7). Phosphorus limitation of nitrogen use for photosynthesis is suggested, although phosphorus addition to the Dupuis forest and other mature jack pine stands has rarely stimulated tree growth (Morrison & Foster 1990).

Differences in productivity were reflected in the amount of litter produced by each forest. Annual litterfall nitrogen contents increased with increasing site index at the three pine sites examined (Table 5). Litterfall nutrient content shows some promise as a method to assess site-to-site differences in tree nutrition. Other examples where litterfall nutrient contents have been successfully applied as a diagnostic tool can be found (e.g., Pastor *et al.* 1984).

We determined that retranslocation of nitrogen, phosphorus, and potassium occurred in all four mature jack pine stands examined (Table 2). Potassium retranslocation, however, was barely detectable in three stands but was prominent in the Dupuis forest. The potassium-use efficiency at Dupuis (759) was lower than the average jack pine value (1155) computed for 12 sites, and half that of the Wells forest (1376). Retranslocation of potassium was greatest in the pine stand with the greatest relative retention of potassium in phytomass and presumably a site with no limitation in potassium availability in soil. This contrasted with

TABLE 7–Changes in foliar P:N ratios and nitrogen-use efficiency with stand age in jack pine forests.

Wells: Site Index 19.0			Dupuis: Site Index 16.5		
Age	P:N ratio	NUEL*	Age	P:N ratio	NUEL*
31	0.059	–	47	–	160
33	–	149	48	0.068	139
34	0.099	158	49	–	139
42	0.102	–	50	–	161
46	–	160	53	–	145
47	–	146	60	0.103	–
48	–	165	66	0.101	160
49	–	147	67	–	165
54	0.085	–	68	0.098	139
55	–	145			
56	0.104	155			

*NUEL = Nitrogen-use efficiency = annual litterfall/litterfall N the Wells site with lower retranslocation and the highest potassium-use efficiency, suggesting low potassium availability in the soil.

Nitrogen availability in soil was determined to be approximately 1% of soil nitrogen contents (Table 6). Retranslocation of nitrogen increased with soil nitrogen content and the availability of nitrogen in the soil. Retranslocation of nitrogen and phosphorus was more closely correlated with soil nitrogen than site index or tree production (Table 6). Reabsorption of nitrogen and phosphorus (Table 8) increased with increasing foliar phytomass and canopy phosphorus contents. Others have found that, in other species, nitrogen retranslocation is not related (Staaf 1982), increases (Birk & Vitousek 1986), or decreases (Boerner 1984; Lennon *et al.* 1985) with increases in nitrogen availability.

TABLE 8–Changes in phosphorus and nitrogen re-absorption with jack pine site quality and foliage mass

Site Index	Foliage mass (kg/ha)	Foliage nutrient (kg/ha)	Retranslocation (kg/ha/year)	Retranslocation (canopy %)
Phosphorus				
19.0	9100	11.8	2.6	22
16.5	7032	9.4	2.2	22
15.4	6100	7.3	1.6	22
11.4	4295	7.2	1.8	25
Nitrogen				
19.0	9100	119	16.8	14
16.5	7032	91	10.4	11
15.4	6100	74	12.6	17
11.4	4295	56	5.8	10

In the four mature jack pine stands, retranslocation of nitrogen and phosphorus was a relatively constant proportion (22–25% and 11–17%, respectively) of canopy nutrient contents (Table 8). Our results are in agreement with those of Prescott *et al.* (1989) who reported resorption was positively related to the mass of nitrogen and phosphorus in foliage of several boreal species. After fertiliser application, jack pine foliage exhibited an absolute increase in foliar resorption, but the proportion of nitrogen in the needles that was retranslocated increased only slightly (Foster unpubl. data). Further, when soil nitrogen supply was low, retranslocation did not contribute a much greater proportion of the total nitrogen available for plant production in jack pine, as it did in *Acer saccharum* Marsh (sugar maple) forest (Lennon *et al.* 1985).

Nutrient-use efficiency

The average nutrient-use efficiency of 12 jack pine forests across North America (*see* Foster *et al.* 1995) was computed to be nitrogen (577), phosphorus (6034), potassium (1155), calcium (709), and magnesium (3774). In general, nitrogen- and phosphorus-use efficiencies by the Wells forest (434, 4841, respectively) were below average jack pine values, suggesting above-average availability of these two nutrients in the soil of the Wells site. Magnesium-use efficiency was greater at Wells, as were potassium and calcium in the semi-mature or older forest.

Nutrient-use efficiency should be highest when ecosystems are nutrient deficient (Cole 1981). The higher nitrogen- and phosphorus-use efficiencies of the Dupuis stand suggest this pine forest is more nitrogen- and phosphorus-limited than the one at Wells, but not more limited than many pine stands. Increasing jack pine growth at the Dupuis site by addition of nitrogenous fertiliser significantly reduced nitrogen-use efficiency, as expected (Table 4). Phosphorus-use efficiency also declined considerably so that phosphorus uptake was favoured by nitrogen addition. Phosphorus availability in soil may have increased in response to increases of soil pH produced by urea dissolution in soil (Morrison & Foster 1977).

Nitrogen-use efficiency, calculated from litterfall parameters (NUEL), appeared to be independent of site productivity for the three sites examined (Table 7). There were no consistent year-to-year patterns in NUEL in either the Dupuis or the Wells forests (Table 7). Further, no overall differences in NUEL could be detected between the two forests. It was not possible, therefore, to detect measured differences in nitrogen accumulation by SI 19 and 16.5 forests by assessing nitrogen-use efficiency from litter properties. Our results provide little or no support for the use of litterfall / litterfall-nitrogen ratios, which has been advocated by others (e.g., Vitousek 1982), as an index of stand nutrient requirement. Decreases in NUEL with increases in nitrogen availability in soil have been reported elsewhere (Vitousek 1982; Birk & Vitousek 1986).

How does nutrient-use efficiency change in relation to site quality? An inverse correlation between productivity and nutrient-use efficiency may be demonstrated between sites where productivity is controlled by one nutrient. Our results indicate that between pine stands on different sites there are many differences in nutrient-use efficiency that do not correspond to differences in site productivity. Others have concluded that nitrogen-use efficiency is more characteristic of the species than the site (Prescott *et al.* 1989).

CONCLUSIONS

High rates of phytomass and nutrient accumulation, were sustained for a longer period in the more productive jack pine forests. Changes in nutrient-use efficiency with age suggested that nutrient accumulation increased somewhat, relative to phytomass production, in the semi-mature forest at Wells, with the exception of potassium. On this most productive, nitrogen-rich site, lower rates of accumulation of phosphorus in juvenile closed stands and potassium in the semi-mature forest were detected.

Jack pine phytomass production, nutrient accumulation, and net nutrient uptake increased with site productivity in the four stands examined. Estimated annual net nutrient uptake for the most productive pine forest was 44 kg N/ha, 4 kg P/ha, 11 kg K/ha, 11 kg Ca/ha, and 3 kg Mg/ha. Uptake from soil provided all the potassium, calcium, and magnesium and most of the nitrogen and phosphorus.

Retranslocation of nitrogen and phosphorus increased with increasing foliar phytomass and canopy nitrogen and phosphorus contents. In the mature pine forests retranslocation was a relatively constant proportion of canopy nutrient contents.

Litter nitrogen contents were a better indicator than foliage and litterfall nitrogen concentrations in detecting differences in nitrogen availability in soil between sites.

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