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Biomass and nutrient distribution in aspen, pine, and spruce stands on the same soil type in Minnesota

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Vegetation and soils were sampled in adjacent 40-year-old stands of red pine (*Pinus resinosa* Ait.), jack pine (*Pinus banksiana* Lamb.), white spruce (*Picea glauca* (Moench.) Voss), and aspen (*Populus tremuloides* Michx., *P. grandidentata* Michx.) on a very fine sandy loam soil in north-central Minnesota. Total tree biomass was greatest for red pine followed by aspen, spruce, and jack pine. Nutrient weights (N, P, K, Ca, Mg) in the trees were greatest in aspen followed generally by spruce, red pine, and jack pine. Particularly large proportions of biomass and nutrients were found in aspen bark and spruce foliage and branches. Understory biomass contributed less than 1.2% of the total organic matter in the vegetation-soil complex but contributed up to 5.0% of the nutrients. Exchangeable Ca in the surface soil was much lower under aspen and spruce than under the pines. No significant soil differences between species were detected below 36 cm. Harvesting the entire aboveground portion of the tree would remove up to three times more nutrients from the site than would harvesting only the bole.

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Les auteurs ont échantillonné la végétation et les sols de peuplements adjacents de 40 ans de pin rouge (*Pinus resinosa* Ait.), de pin gris (*Pinus banksiana* Lamb.), d'épicéa (*Picea glauca* (Moench.) Voss), et de peuplier (*Populus tremuloides* Michx. et *P. grandidentata* Michx.) sur loam sableux très fin dans la partie nord-centrale du Minnesota. La biomasse totale des arbres était la plus élevée chez le pin rouge, suivi du peuplier, de l'épicéa et du pin gris. La masse d'éléments nutritifs (N, P, K, Ca, Mg) dans les arbres était la plus élevée chez le peuplier, suivi généralement de l'épicéa, du pin rouge et du pin gris. Des proportions particulièrement importantes de la biomasse et des éléments nutritifs ont été observées dans l'écorce du peuplier et les feuilles et les branches de l'épicéa. La biomasse de la sous-végétation contribuait moins de 1.2% de la matière organique totale dans le complexe sol-végétation, mais jusqu'à 5.0% des éléments nutritifs. Le calcium échangeable de la surface du sol était beaucoup plus faible sous le peuplier et l'épicéa que sous les pins. Aucune différence significative dans le sol au-delà de 36 cm ne fut décelée entre les espèces. La récolte de toute la partie aérienne des arbres enlèverait jusqu'à trois fois plus d'éléments nutritifs de la station que l'exploitation des seules tiges.

[Traduit par le journal]

Increasing wood and fiber yields are major goals of modern forestry. Yields can be increased by thinning, fertilizing, selecting genetically superior stock, matching the proper species to the site, and utilizing the entire tree. All of these practices may influence the site itself. Increasing the yield of a given species will increase the nutrient drain from the site, which may alter the site's productivity.

In order to quantify potential nutrient drain from timber harvesting we examined the biomass and nutrient distribution within four forest types on the same soil in Minnesota.

In this paper *total tree* refers to the entire tree including roots, and *aboveground tree* refers to that portion of the tree above a 15 cm stump.

Study Area

The study area is located in north-central Minnesota, U.S.A., on the Pike Bay Experimental Forest (47°20' N, 94°30' W). The climate is continental,

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TABLE 1. Stand characteristics

Stand	No. trees per hectare	Mean height, m	Mean dbh (outside bark), cm	Basal area, m ² /ha	Volume inside bark, m ³ /ha	Site index (50 years), m
Aspen						
Aspen	1334	20.3	18	34.7	286	22.9
Other species	1655	11.0	7	7.0	39	—
White spruce	2187	14.4	15	41.1	256	18.3
Red pine	1780	17.6	19	51.9	408	20.7
Jack pine	1580	18.4	17	35.1	263	21.3

meaning cold winters (mean January temperature -14°C), cool summers (mean July temperature 20°C), and 61 cm of precipitation (half falls during the growing season).

The soil has developed from calcareous glacial till and is classified as Warba very fine sandy loam (Typic Eutroboralf, Soil Survey Staff 1975); it is well drained and moderately acid (pH 5–6) above the C horizon. The soil occurs on a gently undulating till plain and is morphologically uniform for the entire study area. A generalized soil description follows.

O1	3–1.5 cm,	recognizable remains of foliage, twigs, cones, etc.
O2	1.5–0 cm,	well-decomposed organic remains
A21	0–5 cm,	dark gray very fine sandy loam, roots abundant
A22	5–36 cm,	gray-brown loamy very fine sand, roots common
A&B	36–61 cm,	mixed horizon that has characteristics of horizons above and below, very few roots
B2	61–70 cm,	dark brown clay loam with blocky structure
B3	70–104 cm,	brown loam
C	104–170+ cm,	olive brown loam, calcareous

The vegetation, if undisturbed, proceeds to maple (*Acer saccharum* Marsh.) – basswood (*Tilia americana* L.) (Kittredge 1934). Common shrubs and herbs presently include downy arrowwood (*Viburnum Rafinesquianum* Schult.), choke cherry (*Prunus virginiana* L.), hazel (*Corylus cornuta* Marsh., *C. americana* Walt.), dogwood (*Cornus rugosa* Lam., *C. stolonifera* Michx., *C. alternifolia* L.), false Solomon's seal (*Smilacina racemosa* (L.) Desf.), twisted stalk (*Streptopus roseus* Michx.), wild lily-of-the-valley (*Maianthemum canadense* Desf.), early-meadowrue (*Thalictrum dioicum* L.), large leaf aster (*Aster macrophyllus* L.), sedges (*Carex* sp.).

The area was harvested for white pine (*Pinus strobus* L.) before 1923, for aspen (*Populus tremuloides* Michx., *P. grandidentata* Michx.) and mixed hardwoods in 1929–1930, and for firewood in 1932–1933. In the spring of 1933 about 8 ha were cleared of remaining trees and 0.4-ha adjoining plantations were established with red pine (*Pinus resinosa* Ait.), jack pine (*Pinus banksiana* Lamb.), or white spruce (*Picea glauca* (Moench.) Voss). An unplanted control area developed through suckering into a fully stocked aspen stand. The conifer stock (mostly 2–O) was planted in scalped areas at spacings of 1×1.5 m and the conifer plantations were weeded as necessary for the first few years. The current study includes two 0.4-ha plantations each of red pine and white spruce and one 0.4-ha plantation each of aspen and jack pine. The conifer stands are nearly pure but the aspen stand contains a number of trees other than aspen (primarily *Acer saccharum*, *A. rubrum* L., and *Fraxinus pennsylvanica* Marsh.). However, these hardwoods are in the lower crown classes and thus their basal area and volume is small (Table 1). The site index values are about average for aspen and spruce in Minnesota and good for red and jack pine. Bole wood weights and volumes of these stands have been reported previously (Schlaegel 1975).

All four species are of the age and size at which a commercial bole harvesting operation for pulpwood would normally be undertaken. If red pine and white spruce are grown for saw logs, the stands are slightly past the age at which the first commercial thinnings might be begun.

Methods

Overstory

Overstory is defined here as all trees more than 3.8 cm diameter at breast height (dbh). Ten 80-m² plots were established in each of the 0.4-ha plots in the spring of 1973 after 40 years of growth. On each plot the dbh of every overstory tree was measured. Ten trees of each species were selected for destructive sampling (one tree per plot chosen randomly with the restriction that they represent the com-

TABLE 2. Organic matter (tonnes per hectare) and nutrients (kilograms per hectare) in overstory and understory vegetation and in soils (Standard errors^a in parentheses)

Stand	Overstory vegetation					Root + stump	Understory vegetation		Soil			Total ^b	
	Foliage	Branches	Bole bark	Bole wood	Herbs		Shrubs	Forest floor	Mineral soil				
									0-10 cm	10-36 cm			
Organic matter													
Aspen	3.6(0.3)	16.6(3.3)	27.6(2.8)	119(13)		38(6)	0.09(0.01)	3.1(1.2)		27(1.1)	35(1.6)	15(0.7)	285
Spruce	17.4(1.8)	34.6(5.1)	10.8(1.0)	88(8)		34(7)	0.02(0.01)	0.1(0.1)		33(0.9)	49(4.3)	22(0.8)	289
Red pine	13.8(0.9)	25.2(2.3)	13.4(0.7)	147(7)		44(1)	0.03(0.01)	4.4(1.1)		30(1.7)	58(5.9)	20(0.8)	356
Jack pine	5.5(0.9)	23.4(2.7)	12.4(1.0)	106(8)		28(2)	0.04(0.01)	2.9(1.0)		33(1.4)	48(2.0)	19(0.7)	278
Nitrogen													
Aspen	87(10)	82(15)	115(12)	84(9)		89(2)	1.8(0.20)	13(4.4)		667(32)	1313(47)	745(28)	3197
Spruce	153(15)	127(17)	43(5)	59(6)		67(15)	0.3(0.21)	1(0.6)		752(35)	1608(119)	934(25)	3744
Red pine	131(9)	60(5)	42(2)	113(6)		75(4)	0.5(0.07)	26(6.6)		538(38)	1894(126)	856(22)	3735
Jack pine	65(10)	76(8)	33(4)	85(7)		37(2)	0.8(0.15)	16(5.1)		689(29)	1502(60)	810(23)	3314
Phosphorus													
Aspen	9.0(0.6)	11.3(2.5)	16.4(1.8)	9.8(1.1)		20(2.0)	0.2(0.03)	1.4(0.4)		60(3.6)	26(2.7)	60(3.5)	214
Spruce	27.0(2.5)	17.2(1.9)	8.2(0.8)	5.0(0.7)		7(2.2)	0.1(0.03)	0.2(0.1)		61(4.1)	21(2.0)	47(5.2)	194
Red pine	18.7(1.3)	7.8(0.7)	6.4(0.5)	8.9(0.4)		8(0.5)	0.1(0.01)	3.6(1.0)		40(2.7)	24(2.8)	54(6.6)	172
Jack pine	7.7(1.2)	7.7(0.8)	4.7(0.5)	4.6(0.4)		5(0.1)	0.1(0.02)	1.8(0.5)		51(4.6)	24(1.3)	47(2.7)	154
Potassium													
Aspen	47(6)	42(8)	86(10)	112(14)		80(8)	2.4(0.29)	7.1(2.2)		78(4.3)	102(4)	192(8)	748
Spruce	86(10)	80(10)	31(4)	32(4)		25(9)	0.4(0.22)	0.5(0.3)		76(4.5)	104(6)	195(9)	630
Red pine	59(5)	32(3)	16(1)	68(4)		30(1)	0.7(0.17)	29.2(16)		62(3.1)	112(7)	191(22)	600
Jack pine	20(3)	25(3)	12(1)	40(4)		22(1)	0.9(0.20)	8.2(2.2)		68(7.6)	94(2)	187(9)	477
Calcium													
Aspen	37(8)	215(45)	435(39)	171(18)		216(59)	1.1(0.20)	22(5.7)		1081(58)	1195(103)	1448(77)	4821
Spruce	256(29)	217(34)	161(14)	85(7)		90(8)	0.2(0.13)	1(0.8)		1398(61)	1451(131)	1357(52)	5016
Red pine	42(4)	64(9)	70(6)	115(5)		44(5)	0.3(0.08)	44(12)		660(46)	2187(194)	1716(109)	4942
Jack pine	20(3)	51(6)	56(4)	72(6)		42(1)	0.4(0.07)	27(8.3)		770(95)	2080(114)	1722(74)	4840
Magnesium													
Aspen	6.0(0.6)	12.4(3.1)	20.5(2.4)	18.7(2.2)		18(3)	0.2(0.04)	4.1(3.0)		89(5)	91(5)	175(10)	435
Spruce	13.3(1.6)	13.4(1.6)	7.3(0.8)	6.3(0.7)		6(1)	0.1(0.04)	0.2(0.1)		77(5)	136(10)	202(13)	462
Red pine	14.4(0.7)	8.9(1.2)	8.3(0.6)	25.9(1.7)		14(1)	0.1(0.02)	4.2(1.3)		65(4)	138(8)	190(21)	469
Jack pine	5.6(0.8)	9.9(1.0)	5.7(0.6)	16.5(1.3)		8(1)	0.1(0.01)	2.2(0.7)		81(10)	134(4)	188(10)	451

^aThe standard error for soils, understory, roots and stump, and the average fall.

^aThe standard error for soils, understory, roots and stump, and the aspen foliage is the standard deviation divided by the square root of the number of samples. For the rest of the overstory components, the standard error is calculated using double sampling with regression techniques (see Methods). The standard error for the total is impossible to calculate because the magnitude of the covariance between components is unknown.

^bThe total does not include understory roots or tree roots less than 5 mm in diameter.

plete range of diameter classes). The sample tree was felled (15-cm stump), total height measured, and the stem sectioned into 1.2-m bolts that were weighed green in the field. Also all the limbs on each bolt were removed and weighed green. A 3-cm-thick disc and a randomly selected branch from each bolt were placed in plastic bags and transported to the laboratory the same day.

In the laboratory the bark was separated from the wood of each disc and the green weight of each component measured. The samples were then oven-dried at 100°C for 48 h and reweighed. The moisture content and bark:wood ratio were used to calculate the oven-dry weight of the bole bark and bole wood from the green weight of each bolt as measured in the field. Tree weights of bole wood and bole bark are the sum values calculated for each bolt.

The branch samples were weighed green in the laboratory, oven-dried at 70°C, defoliated by hand, and redried. The moisture content and foliage:branch ratio were used to calculate the oven-dry weight of foliage and branches from the field-measured green branch weight.

Based on the 10 sample trees per species, regression equations were developed to relate weight of nutrients or oven-dry biomass (by tree aboveground components) to tree diameter and height. The form of the equations was

$$[1] \quad \ln(\text{weight}) = a + b(\ln(D^2H))$$

where D is the tree diameter at breast height in centimetres, and H is estimated tree height (metres) calculated from a height-diameter equation developed from the 10 sample trees per species. There were 24 equations per species: four components (foliage, branches, bole bark, and bole wood), oven-dry weights, and five nutrients (N, P, K, Ca, and Mg). The equations were corrected for the ln-bias (Baskerville 1972) and generally had R^2 values greater than 0.90 and standard errors of the mean less than 10%. The equations were solved for every tree that had been measured for diameter and that had been estimated for height from the height-diameter equation. The average tree weight of nutrients or biomass (by tree component) was calculated and multiplied by the number of trees per hectare to obtain weights on an area basis.

The variance of these estimates takes into account the variances for the ln-ln equation, the height-diameter equation, and the number of trees per hectare. The square root of the variance gives the standard error (Table 2). The program for calculating the variance is a modified version³ of double sampling with regression (Cochran 1963).

For each species two additional trees of mean bole volume were felled in August 1974 and all roots greater than 5 mm were hand excavated. The entire root system (plus the 15 cm stump) was washed lightly with distilled water to remove soil particles, oven-dried (70°C), and weighed.

Because aspen foliage was not present when the 10 trees were sampled for aboveground biomass, all foliage of the two aspen root sample trees was removed by hand, oven-dried (70°C), and weighed. Although our aspen foliage sample is small, the foliage weights agree with literature values. We found aspen foliage to be 2.2% of the total aboveground tree weight, which is comparable with the values of 2.2, 1.6, and 2.4% reported for mature aspen in

Alberta, Ontario, and Wisconsin (Peterson *et al.* 1970; Pollard 1972; Zavitskovski 1971).

Understory

In early September 1972, ten 4-m² circular plots were systematically located in each forest type. All live vegetation less than 3.8 cm dbh was clipped at groundline and separated into the shrub layer (shrubs, vines, and hardwood seedlings and saplings) and the herbaceous layer. The shrub layer was weighed in the field, and a subsample of representative stems per plot was bagged for dry weight (70°C) and nutrient determinations in the laboratory. All herbaceous vegetation was bagged for these same determinations. The fresh and oven-dry shrub layer subsample weight ratio was used to determine plot dry weight from the plot fresh weight. The entire herbaceous layer sample was dried (70°C) and weighed. Roots of understory species were not sampled.

Soils

On each 0.4-ha area (two of red pine and white spruce, and one each of aspen and jack pine) twenty 930-cm² samples of the forest floor were collected and composited into five samples per plot. Directly beneath each forest floor sample location mineral soil samples were removed from the following depths: 0–10, 10–25, 25–36, and 36–61 cm. The mineral soil samples were also composited into five final samples for analysis per plot. In addition, two deep pits were dug under each species. In each pit the soil profile was described and horizon samples were collected to a depth of about 2 m.

Chemical Analysis

Samples of tree components, shrub and herb layers, and the forest floor were ground to pass a 20-mesh screen. Nitrogen in all samples was determined by the macro-Kjeldahl method (Bremner 1965). Tree components were dry ashed (500°C) and P, Ca, Mg, and K determined by emission spectroscopy. Understory plants and forest floor samples were dry ashed and analyzed for Ca, Mg, and K by atomic absorption and for P by the molybdophosphoric blue colorimetric method (Jackson 1958).

Mineral soil samples were air dried and passed through a 2-mm screen. The material greater than 2 mm was weighed and discarded. Mineral soil Ca, Mg, and K were extracted with 1 N NH₄OAc and determined by atomic absorption; P was extracted with 0.002 N H₂SO₄ and determined by the molybdophosphoric blue colorimetric method. Organic matter in the mineral soil is the total carbon (C) content (by induction furnace, Allison *et al.* 1965) multiplied by the conversion factor of 1.7 (Broadbent 1965). Organic matter in the forest floor is the total oven-dry weight minus the ash content.

Results

The trees contained two-thirds to three-fourths of the total measured organic matter (Fig. 1). The biomass in these stands is similar to that of comparable stands of *Pinus* and *Picea* in the temperate forest zone (Art and Marks 1971; Ovington 1962) and to aspen in Minnesota (Bray and Dudkiewicz 1963) and Wisconsin (Boyle and Ek 1972). Total tree biomass is greatest for red pine followed by

³Margaret Martin. Variances in some biomass studies utilizing double sampling. Manuscript in preparation.

FIG. 1. Organic matter distribution.

aspen, spruce, and jack pine. Bole wood and root biomass follow similar species trends (Table 2). Branch and foliage weights are greatest for spruce whereas bole bark weight is greater for aspen than for any other species. The understory contributes little to total biomass in these dense stands. Organic matter in the soil is lowest under aspen. Similar comparisons (but with different species) in England also showed spruce canopy biomass to be greater than other species, and showed that conifer stands generally have greater biomass than hardwoods of the same age (Ovington 1956).

In contrast to organic matter, which is concentrated in the living vegetation, the nutrients are concentrated in the soil (Fig. 2). Only 6–23% of the N, Ca, and Mg and only 21–50% of the P and K is found in the vegetation. The shrub and herb layers, because of their high nutrient concentrations, comprise a larger part of the nutrient pool than the organic matter pool. But even so the understory contains at most only a small percentage of each nutrient.

The species differed greatly in nutrient contents. Aspen contained the greatest amount of each nutrient and jack pine contained the least (Fig. 2). In spite of having the largest biomass per hectare, red pine generally had lower amounts of nutrients than either aspen or white spruce, which reflects the low nutrient concentration in red pine tissues. Not only does the total amount of nutrient differ between species but its distribution among components differs also. Spruce contains a higher proportion of

total tree nutrients in the branches and foliage than other species, whereas aspen contains a higher proportion in the bark. These trends are similar to those for biomass but accentuated because of the high nutrient concentrations found in aspen bark and spruce foliage and branches. Approximately half of the aboveground tree nutrients are in the bole; about half is in the wood and the other half in the bark. So only about a fourth of the nutrients in the aboveground tree are in the bole wood.

Soil organic matter and nutrients are concentrated in the forest floor and the surface 10 cm of mineral soil. Soil properties that differed significantly between the tree species were organic matter, N, and Ca. Differences were greatest in the forest floor and the 0–10 cm mineral soil layer, and decreased rapidly with depth. In the 25–36 cm layer few differences due to species were significant, and below 36 cm no significant differences occurred. This substantiates the assumption that the soils did not differ significantly when the forests were established.

Discussion

If these stands were harvested, more nutrients would be removed from the aspen and spruce sites than from the pines, and about twice as much of the nutrients would be removed if the entire aboveground tree were taken than if only the boles were removed (Table 2). The nutrients removed in such logging of the aspen stand would be about twice as great as reported from a Wisconsin aspen stand of similar age and biomass harvested commercially (diameter limit 12.7 cm) during leaf off time (Boyle and Ek 1972). Nutrient removal by aboveground tree harvesting of the jack pine, red pine, and white spruce stands would be somewhat greater than for jack pine in Ontario (Morrison 1973), red pine in New York (Jurgensen and Leaf 1965; Madgwick *et al.* 1970) or spruce–fir in Quebec (Weetman and Webber 1972), all of which are growing on poorer sites than those of this study.

The impact of these nutrient removals on the productivity of the site can be known for certain only by measuring the growth of subsequent stands. Several cases have been reported where nutrient removal from forest land has reduced the growth of succeeding trees (Lutz and Chandler 1946). Past agricultural use of sandy soils in eastern North America resulted in poor growth of subsequently planted red pine, which could be corrected by K fertilization (Leaf *et al.* 1975; Wittwer *et al.* 1975). On infertile soils in Europe where a high percentage of the total nutrients are contained in the vegetation,

FIG. 2. Nutrient distribution in vegetation and soils.

the removal of this vegetation has resulted in reduced growth of subsequent forest stands (Rennie 1957), and similar declines are likely in many parts of Africa (Nye and Greenland 1960). In Australia

and New Zealand the second rotation of *Pinus radiata* (D. Don) has frequently produced lower yields than the first (Keeves 1966; Whyte 1973), and in some cases this has been shown to be due

TABLE 3. Nutrients in total aboveground tree as a percentage of the nutrients in the 0-36 cm soil layer^a

Element	Aspen	Spruce	Red pine	Jack pine
N	18	15	13	10
P	54	84	54	35
K	98	77	58	35
Ca	32	26	7	5
Mg	22	12	18	12

^aSoil P is extracted with dilute H₂SO₄; soil Ca, Mg, and K are extracted with NH₄OAc; and N represents total soil N by the Kjeldahl method.

to a nitrogen deficiency (Stone and Will 1965). In addition, the commonly increased growth response of trees to nutrient additions suggests that many sites are somewhat deficient in certain nutrients even before harvesting (Tennessee Valley Authority 1968). And the incidence of serious nutrient depletion can be expected to increase as more intensive forest management removes more nutrients through thinning, shorter rotations, and more complete tree utilization.

Two commonly used methods to estimate site alteration when long-term growth measurements are not known are (1) to relate present soil nutrient levels to nutrients removed, or (2) to compare forest nutrient uptake with the nutrient uptake of crops that need added nutrients to maintain yields.

The percentage of each mineral soil nutrient that would be removed in an aboveground tree harvest is shown in Table 3. The soil used in this calculation is the 0-36 cm depth; the mineral soil deeper than 36 cm is excluded because of the small number of roots below this depth. The amounts of nutrients in the soil are not absolute entities but can be altered with time. For example, soil N can be increased by fixation (Bartholomew and Clark 1965) and other nutrient levels can be changed if soil conditions such as pH are altered (Pearson and Adams 1967). Soil nutrient levels may also change if tree nutrient

uptake is greater than the replenishment ability of the soil (Heiberg *et al.* 1959). The data of Table 3 are still useful for comparing species and soils, however. The species differences are clear; jack pine removed the smallest percentage of nutrients and aspen the largest. Nutrient differences are also apparent; much larger percentages of P and K are removed than any other nutrient. This would indicate a potential for deficiencies of these nutrients, but that would depend on the rate of P and K released from less soluble forms in the soil. Our knowledge of nutrient solubilization rates in forest soils is limited, which makes it difficult to interpret the significance of nutrient removal from a site.

Average annual nutrient accumulation in the overstories are much lower, except for Ca, than the nutrient accumulations of agricultural crops or forest nurseries (Table 4). It should be noted that the high yields from agricultural crops can only be maintained by adding nutrients. Long-term studies have shown that if nutrients aren't added, the yield of wheat or corn stabilizes at 10-20 bushels per acre (1 bushel per acre = 36.37 dm³/0.405 ha) (Miller and Hudelson 1921; Russell 1961; University of Illinois 1960). If the wheat and corn uptake values in Table 4 are adjusted to correspond to a long-term, no-nutrient-addition system, we find that the aspen trees in the current study are taking up more Ca, about the same amount of K, about half as much N and Mg, and a quarter as much P as the agricultural crops. The most fertile soils are usually used for agriculture, which leaves the poorer ones for forests. A total or aboveground tree harvesting system drains the site of nutrients, particularly Ca. Rennie (1955) noted the large Ca uptake by European forest trees and found that on calluna soils of England, removal of soil Ca by *Pinus sylvestris* (L.) resulted in lessened subsequent tree growth.

Whether the removal of nutrients by harvesting

TABLE 4. Mean annual aboveground vegetation nutrient accumulation (in kilograms per hectare per year)

Species	Age	Site quality ^a	Element					Reference
			N	P	K	Ca	Mg	
Aspen	40	22.9	9.2	1.2	7.2	21.4	1.4	This study
White spruce	40	18.3	9.6	1.4	5.7	18.0	1.0	This study
Red pine	40	20.7	8.6	1.0	4.4	7.3	1.4	This study
Jack pine	40	21.3	6.5	0.6	2.4	5.0	0.9	This study
Aspen	47	22.9	4.4	0.5	2.3	9.4	0.9	Boyle and Ek 1972
Jack pine	30	18.3-19.8	6.5	0.5	3.2	4.2	0.7	Morrison 1973
Tree nursery	1-3	—	50.0	0.7	25.0	15.0	—	Stoeckeler and Arneman 1960
Wheat (grain)	1	40	50	11	13	1	6	Foth and Turk 1972
Corn (grain)	1	150	135	23	33	16	20	Foth and Turk 1972

^aSite quality is 50-year site index (metres) for trees and bushels per acre for crops.

TABLE 5. Forest ecosystem nutrient inputs by atmospheric deposition and outflows by leaching (in kilograms per hectare per year)

Element	Washington ^a		New Hampshire ^b		Minnesota ^c	
	Input	Outflow	Input	Outflow	Input	Outflow
N	1.1	0.6	7.8	3.0	6.3	2.2
P	—	—	0.1	0.02	0.49	0.26
K	0.8	1.0	0.8	2.4	3.9	3.3
Ca	2.8	4.5	3.0	12.2	4.8	6.5
Mg	—	—	0.8	3.4	1.3	1.9

^aCole *et al.* 1967.

^bLikens *et al.* 1970; Hobbie and Likens 1973.

^cTimmons *et al.* 1977; Verry and Timmons 1977.

will deplete the soil depends on whether these losses can be balanced by nutrient inputs in precipitation, mineral weathering, and N fixation. Nutrient inputs by precipitation in temperate regions vary (Weetman and Webber 1972), but are generally of the same magnitude as tree accumulation as shown in Table 4. However, the nutrients in the precipitation that falls outside of the growing season may be lost by leaching. In Washington (Cole *et al.* 1967), New Hampshire (Likens *et al.* 1970; Hobbie and Likens 1973), and Minnesota (Timmons *et al.* 1977; Verry and Timmons 1977) the nutrient input by precipitation and outflow below the rooting zone were measured in mature forest ecosystems (Table 5). More Ca and Mg left these systems by leaching than entered by precipitation, whereas the reverse was true for N and P (Table 5). The amount of N lost by denitrification is unknown. Potassium showed a net loss at two sites and a slight gain at one. Part of the leaching losses of the cations are contributed by weathering, which Johnson *et al.* (1968) have crudely estimated at 8, 8, and 4 kg/ha year⁻¹ for Ca, Mg, and K, respectively. According to long-term soil changes, basic cations are leached from the soil system in temperate zone areas (Simonson 1970). By contrast, the N content may increase markedly due to atmospheric fixation (Nutman 1965; Jensen 1965) and the percentage of P may increase because its rate of leaching is much lower than that of the other constituents.

Ca appears to be a key nutrient in forest ecosystems because of its large accumulation in comparison with many agricultural crops. Aspen and spruce have more Ca in their biomass and less in their surface soil than the pines (Table 2). The lower soil Ca levels under aspen and spruce have resulted in lower pH values under these species, which can affect reactions occurring in the soil and the avail-

ability of certain nutrients. The fact that forest crops take up large amounts of Ca in relation to agricultural crops suggests that micronutrients need to be examined to see if some of these might also be used in large amounts by forests. Our current knowledge of micronutrient uptake by forests and levels in forest soils is meager.

Our knowledge of fixation rates, weathering, and mineralization of organic matter in forest ecosystems as well as species nutritional needs is fragmentary, so definite conclusions about the effect of nutrient removal by timber harvesting cannot be made at this time. However, it is clear that the amount and distribution of nutrients that have accumulated in the four species studied are different and that these differences are significant. It is also clear that aboveground tree removal puts a 2- to 11-times greater drain on the site (depending on species and nutrient) than if only bole wood is removed. Since the amount of foliage, branches, and bark associated with a given amount of bole wood can be reduced by controlling spacing (Singer and Hutnik 1966; Stiehl 1966), it may be possible to reduce nutrient drains without sacrificing yields by the proper adjustment of spacing.

As forests are more intensively cropped for increased yields, nutritional deficiencies are likely to become more common. A great deal of work is needed to quantify the nutrient supplying potential of different sites; then either yields can be increased by fertilization or the yields can be adjusted to balance the natural potential of the site by species selection, degree of utilization, adjustment of rotation length, and other forest management alternatives.

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