Nutrient export by leaching and whole-tree harvesting in a loblolly pine and mixed oak forest[1,2]

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Abstract

The combined effects of whole-tree harvesting (WTH) and soil leaching by both acid deposition and naturally-produced carbonic acid were evaluated in a mixed oak and a loblolly pine forest growing on similar soils in the Ridge and Valley province of eastern Tennessee. It was hypothesized that nutrient export via WTH would be greater in a mixed oak stand than in the loblolly pine stand because of greater nutrient concentrations in oak and hickory species than in pine. This hypothesis was true for N,P, and particularly Ca at the time of harvest, but not for K or Mg. When expressed on an annual basis, exports of N,P,K, and Mg were greater in the loblolly pine site and only Ca export was greater in the mixed oak site. It was also hypothesized that the large accumulation of Ca in the oak and hickory vegetation would cause lower exchangeable Ca^{2+} in soils, and, consequently, lower Ca^{2+} leaching in the mixed oak site than in the loblolly pine site. This hypothesis was supported by the data, which indicated 340–370% more exchangeable Ca and 100% more Ca^{2+} leaching in the loblolly pine site than in the mixed oak site.

Introduction

The effects of forest nutrient uptake upon soil change has been the subject of study for many decades. Some of the early work in the U.K. was initiated because of wide concern that afforestation with or site conversion to conifers would lead to soil deterioration through podzolization and associated soil acidification (Rennie, 1955). This concern stemmed from the long-held belief that certain tree species (primarily deciduous) are "soil improvers" because of their high rates of nutrient uptake and cycling. Stone (1975) disputes this supposition, arguing that it is based largely upon the coincidence of certain species and nutrient-rich soils rather than demonstrable cause-effect relationships (A notable exception being N-fixing species). Indeed, more recent assessments of the effects of whole-tree harvesting (WTH) indicate that deciduous species usually (but not always) have lower nutrient efficiencies (*e.g.*, the weight of biomass produced per unit of nutrient taken up) than coniferous species, an obvious consequence of differences in tissue nutrient concentration (Marion, 1979). Alban (1982) demonstrated what should have been obvious all along: rapid rates of uptake and recycling can lead to the depletion rather than the enrichment of soils. Specifically, he noted that Ca-accumulating aspen (*Populus tremuloides*) and white spruce (*Picea glauca*) stands had lower reserves of soil exchangeable Ca^{2+} than adjacent stands of non-Ca-accumulating red and jack pine (*Pinus resinosa* and *P. banksiana*) stands. He also noted that, as an apparent consequence of high rates of Ca cycling, Ca has been redistributed from subsoils to litter and surface soils in the aspen and white spruce stands, whereas subsoil Ca was greater than litter and surface soil Ca in the pine stands.

There are some interesting potential interactions between tree uptake and leaching which will profoundly affect the nutrient budgets of forest ecosystems subjected to both WTH and acid deposition. Cation exchange equations dictate that a decrease in the level of a given exchangeable cation in the soil will cause a relative decrease in the proportion of that cation and a relative increase in the proportions of other cations in soil solution. For instance, for Ca-Mg exchange, we have

$$\frac{XCa^{2+} \ [Mg^{2+}]}{XMg^{2+} \ [Ca^{2+}]} = Kgt \tag{1}$$

where [ ] denote soil solution concentrations (moles/L), X denotes the equivalent fraction on the exchange phase, (no units) and Kgt is the Gaines-Thomas (1953) selectivity coefficient (a constant). From equation 1) we see that if the ratio of XCa^{2+} / XMg^{2+} decreases (including the case where XCa^{2+} decreases and XM^{2+} remains constant), then the ratio $[Mg^{2+}]/[Ca^{2+}]$ must increase. Similarly, if the sum of exchangeable base cations decreases (*i.e.*, base saturation decreases), the ratio of the concentrations of total base cations to $H^+ + Al^{3+}$ decreases (*i.e.*, soil solutions become more acid). Thus, depletion of one or more base cations from subsoils by tree uptake will cause a reduction in the leaching of those base cations from the subsoil, whether the cations taken up are sequestered in tree biomass, forest floor, or upper soil horizons.

In this paper, we compare the combined effects of WTH, natural leaching, and acid deposition on the nutrient budgets of the upland mixed oak site previously described (Johnson *et al.*, 1982b) to those of a nearby loblolly pine (*Pinus taeda* L.) plantation growing on similar soils. Based upon the above discussions, we hypothesized that nutrient export by biomass would be lower in the pine than in the hardwood stand and that losses of Ca^{2+} by leaching would be lower in the mixed oak site because of Ca accumulation and conservation in trees.

Sites and methods

The mixed oak and loblolly pine sites are located within 1 km of each other on Chestnut ridge in the Ridge and Valley province of eastern Tennessee near Oak Ridge. The climate is humic mesothermal with a mean annual temperature of 14.3°C and mean annual precipitation of 151 cm, most of which falls as rain. Soils on both sites are deep (up to 30 m), highly weathered ultisols derived from dolomite. Fullerton series soils, cherty silt loam Typic Paleudults, are predominant on both sites. Bodine series soils (also Typic Paleudults, very similar to Fullerton soils, but occupying a lower slope position and containing a greater percent of coarse fragment in subsoils) also occur on the mixed oak site along with minor inclusions of Dewey and Dunmore series (both Typic Paleudults) in the lowest slope positions.

Vegetation in the mixed oak site consists primarily of chestnut oak (*Quercus prinus* L., accounting for over 50% of the biomass), with significant (> 5% of biomass) amounts of white oak (*Q. alba* L.), northern red oak (*Q. rubra* L.), black oak (*Q. velutina* Lam.), yellow-poplar (*Liriodendron tulipifera* L.), red maple (*Acer rubrum* L.) and hickories (*Carya tomentosa* Nutt. and *C. ovata* L.). Occasional shortleaf pine (*Pinus echinata* Mill.), sugar maple (*A. saccharum* Marsh.), sassafras (*Sassafras albidum* Nutt.), and dogwood (*Cornus florida*). Understory vegetation was virtually absent.

Vegetation in the loblolly pine site consisted primarily of loblolly pine (*Pinus taeda* L., > 90% of biomass) with an occasional dogwood, red maple, and yellow-poplar in the understory. Ground cover consisted primarily of Japanese honeysuckle (*Locinera japonica*) with patches of poison ivy (*Toxicondendron radiocans*).

At the mixed oak site, five small (0.25–0.54 ha) watersheds were laid out and total inventory of all trees > 10 cm dbh was conducted. Trees < 10 cm dbh were inventoried within 20 circular 0.0045 ha plots. Biomass was calculated from regression equations (Harris *et al.*, 1973). Each watershed was instrumented with 4 randomly-located throughfall, litterfall, and soil solution (ceramic cup tube type, Soil Moisture Corp., Santa Barbara, CA) collectors in the spring of 1979 (for a total of 8 replicates per treatment). Monthly collections were made prior to harvest in the autumn of 1980, when watersheds 1–4 were harvested for sawlogs (all material > 28 cm diameter inside bark). In watersheds 1 and 2, all above-stump material was skidded offsite to simulate WTH. Watershed 5 was left as a control. After harvest, collectors damaged during the har-

vesting operation were replaced and monthly coll-
ections continued until the spring of 1985 when the
project was terminated.

At the loblolly pine site, two 22 × 22 m subplots
were laid out in each treatment blocks (control,
thinning and WTH) and a total inventory of trees
was taken. Loblolly pine biomass was calculated
from the regression equations provided by Van
Lear *et al.* (1984), which were checked by sampling
5 trees from the study site. Hardwood understory
biomass was calculated from the equations
provided by Harris *et al.* (1973). Each plot was
instrumented with triplicate litterfall, throughfall,
and soil solution collectors each (for a total of 6
replicates per treatment) in the early spring of 1982.
Monthly collections were made prior to harvest in
the late spring of 1983. After harvest in the WTH
block, the site was bulldozed with a K-G blade,
raked, disked and replanted to loblolly pine.

Vegetation (32 trees including major species) lit-
terfall, and standing liter (sampled from randomly-
placed 0.25-m² dia rings) from both sites were
analyzed for N (Kjeldahl digestion), P, K, Ca, and
Mg. Both dry ashing and perchloric acid digestion
were used at different times and at different labs
(ORNL and A and L Labs, Memphis, TN, respec-
tively), for analyses of the latter nutrients, and
results were comparable (Johnson *et al.,* 1982b).
National bureau of standards orchard and pine
leaves were submitted with each vegetation analysis
set. Soils at both sites were sampled to a depth of
45 cm by 15-cm increments with a bucket auger and
analyzed for cation exchange capacity (CEC) and
exchangeable Ca^{2+}, Mg^2, K^+, Na^+, and Al^{3+} by
neutral salt method ($1 M NH_4Cl$ extraction for
exchangeable cations, followed by ethanol rinse
and $1 M KCl$ extraction for CEC), extractable P
(NH_4F/HCl; Olson and Dean, 1965) total C
(LECO furnace), total N (Kjeldahl digestion), total
P, K, Ca and Mg (nitric-perchloric acid digestion).

Nutrient fluxes in precipitation and throughfall
were collected by multiplying volume or weight
data by volume-weighted average annual con-
centrations. Nutrient fluxes in soil solution were
calculated by multiplying average annual soil solu-
tion concentrations by an independent estimate of
soil water flux based upon measured precipitation
input and calculated evapotranspiration
(Luxmoore, 1983). All values are expressed in stan-
dard international (S.I.) units unless otherwise in-

dicated. Thus, "mmol(c)", "kmol(c)", *etc.* refer to
moles of charge.

Results and discussion

*Nutrient distribution and export with whole-tree
harvesting*

As hypothesized, there were some major dif-
ferences in nutrient distribution between the mixed
oak and loblolly pine stands, especially with respect
to Ca. Although biomass values were similar (with-
in 10–15% of one another), the mixed oak sites
contained 100% more N, 50% more P, 50–100%
more K, and 360–640% more Ca than the loblolly
pine sites (Table 1). Only in the case of Mg were
tree nutrient contents similar (within 1–11% of one
another). Also as hypothesized, soil exchangeable
Ca^{2+} was 340–370% higher in the loblolly pine
than in the mixed oak sites (Table 1). It is interest-
ing to note that the sums of vegetation, forest floor,
and soil exchangeable Ca^{2+} in the mixed oak sites
(1965 Kg ha⁻¹ in control and 1780 Kg ha⁻¹ in
WTH site) were quite similar to those in the loblolly
pine sites (1443 kg ha⁻¹ in control and 1637 kg ha⁻¹
in WTH site) despite the large differences in Ca
distribution. The only other major soil difference
between the mixed oak and loblolly pine sites was
in extractable P, which was 400–800% higher in the
mixed oak site. Other minor but consistent differen-
ces in soils included organic matter (loblolly pine
approximately 20% higher), total P (mixed oak
approximately 30% higher), and total Mg (mixed
oak approximately 20% higher).

Despite the facts that (1) total biomass removals
were similar and (2) foliage was removed by WTH
in the loblolly pine but not in the mixed oak site
(the latter having been harvested after leaf-fall), N
and (especially) Ca export by WTH were greater in
the mixed oak site than in the loblolly pine site
(Table 1). Phosphorus, K, and Mg exports by
WTH were fairly similar in the two sites. As noted
previously (Johnson *et al.,* 1982b), Ca exports from
the mixed oak site were quite large relative to soil
reserves in the top 45 cm, equalling 300% of ex-
changeable Ca^{2+} and 25% of total soil Ca (Table
1). In contrast, Ca export by WTH equalled only
15% of exchangeable Ca^{2+} and 4% of total soil Ca
in the loblolly pine site.

Table 1. Biomass, nutrient contents, and removal (kg ha^{-1}) by whole-tree harvesting in the loblolly pine (LP) and mixed oak (MO) sites

Component	Biomass		N		P		K		Ca		Mg	
	LP	MO	LP	MO	LP	MO	LP	MO	LP	MO	LP	MO
Whole-tree harvested sites												
Vegetation												
Trees												
Foliage	3,600	3,900	39	60	3.3	4	19	50	9	40	3.5	6.0
Branch	18,00	35,300	27	85	3.7	7	19	35	43	200	7.8	10.2
Bole	123,200	133,800	111	240	11.3	16	69	90	116	910	31.9	28.1
Stump	11,600	14,700	10	30	0.9	2	6	10	11	100	2.4	3.1
Σ tree	156,600	187,700	187	415	19.2	29	113	185	179	1,250	45.6	47.4
Understory	3,080	5,900	9	10	0.8	0.6	7	8	17	41	2.0	2
Σ Aboveground	159,680	187,700	196	415	20.0	29	120	185	196	1,250	47.6	47.4
Forest floor	46,170	13,700	444	150	26.0	12	36	20	161	160	23	20
Soil												
Extractable					5	40	224	196	1,280	370	160	140
Total	93,700	77,500	3,050	3,160	790	1,000	23,200	23,000	5,130	4,860	6,300	7,350
Σ Ecosystem	299,500	278,900	3,690	3,725	836	1,041	23,356	23,205	5,487	6,270	6,371	7,417
Removed by WTH	159,680	165,530	196	315	20	22	120	120	196	1,090	47.6	41
(% of total)	(53)	(59)	(5)	(8)	(2)	(2)	(0.5)	(0.5)	(4)	(17)	(0.8)	(0.5)
Control sites												
Vegetation												
Trees												
Foliage	4,100	3,800	44	58	3.9	4.0	22	48	10	47	4.0	7.7
Branch	19,300	35,440	29	88	3.9	7	20	32	46	209	8.3	14.2
Bole	143,800	133,300	129	225	13.2	15.8	81	115	135	919	37.9	48.6
Stump	15,000	14,500	13	25	1.1	2.1	7	21	14	107	3.0	5.4
Σ tree	174,900	187,000	215	396	22.1	28.9	130	216	205	1,282	53.2	75.9
Understory	34.800	4,700	75	8	7	0.5	56	7	187	33	16	2
Σ Aboveground	209,700	191,700	290	404	29.1	29.4	186	223	392	1,315	69.2	77.9
Forest floor	22,860	26,700	247	224	15	17	25	57	121	400	16	51.2
Soil												
Extractable					8	35	243	430	930	250	140	65
total	93,700	77,100	3,500	3,790	960	1,250	25,400	24,600	5,800	3,630	6,040	7.300
Σ Ecosystem	326,260	276,340	4,037	4,440	1,004	1,300	25,611	25,057	6,313	5,345	6,125	7,427

There are sources of Ca deeper in the soil at both sites that could be tapped to provide forest Ca needs. Since vegetation Ca content was so high at the mixed oak site, some investigation of the magnitude of these sources has been made. It has been estimated that the top 150 cm of soil at the mixed oak site contains 600–700 kg ha^{-1} of exchangeable Ca^{2+} and 10,000 kg ha^{-1} of total Ca (Johnson *et al.*, 1982b); thus, WTH constitutes approximately 200% of exchangeable Ca^{2+} and 13% of total Ca when soil capital is defined in this way. The dolomite bedrock could provide a virtually inexhaustable source of Ca; however, trees would have to penetrate to as much as 30 m to reach it. Large accumulations of Ca in oaks and hickories growing on Ca-poor soil have been documented in Oklahoma (Johnson and Risser, 1974) and North Carolina (Henderson *et al.*, 1978), and thus it seems that Ca accumulations in these species (as well as in certain species of Picea. Populus, and Thuja; Alban, 1982) is a species-specific train rather than a luxury consumption from Ca-rich bedrock.

Nutrient export by leaching

As hypothesized, soil solution Ca^{2+} concentrations and, consequently, soil Ca^{2+} leaching were lower in the mixed oak site than in the loblolly pine site (Table 2 and 3). Soil solution from the mixed

Table 2. Weighted average annual concentrations in u mol(c)l^{-1}, in the loblolly pine (LP) and mixed oak (MO) control sites for April 1982–March 1985

	Precipitation		Throughfall		Soil solution	
	LP	MO	LP	MO	LP	MO
pH	4.3	4.3	43	4.6	5.4	4.9
H$^+$	48	51	51 ± 14	26 ± 8**	4 ± 4	11 ± 10
Ca^{2+}	22	36	73 ± 36	72 ± 25	207 ± 50	102 ± 23***
Mg^{2+}	4	8	24 ± 11	23 ± 9	63 ± 12	90 ± 27**
K$^+$	2	6	37 ± 21	45 ± 21	27 ± 18	25 ± 11
Na$^+$	4	5	6 ± 0.2	5 ± 0.2	23 ± 6	14 ± 4**
NH$_4^+$	5	9	11 ± 3	9 ± 2	2 ± 6	8 ± 17
SO$_4^{2-}$	61	64	113 ± 20	97 ± 19	251 ± 63	228 ± 56
HCO$_3^-$	<1	<1	20 ± 29	32 ± 14	86 ± 76	32 ± 36
NO$_3^-$	8	10	25 ± 6	20 ± 2	1 ± 2	0.2 ± 04
Cl$^-$	8	9	22 ± 7	17 ± 5	41 ± 22	30 ± 11
H$_2$PO$_4^-$	0.2	0.4	0.5 ± 0.3	0.7 ± 0.2	0.1 ± 0.2	0.1 ± 0.1
Σ Cations[a]	85	115	197 ± 47	179 ± 47	325 ± 56	249 ± 54
Σ Anions[a]	77	83	156 ± 19	166 ± 36	379 ± 92	290 ± 70

[a] Calculated as a weighted average total cation and total anion concentration from individual collections, not from the sum of the individual weighted average ion concentrations given in this table.

, * denote significant differences between the two sites at the 95 and 99% levels, respectively, using Student's t-test.

oak site also had significantly lower pH and HCO$_3^-$ concentrations than that from the loblolly pine site. These differences were consistent with the differences in soil exchangeable Ca^{2+} and base saturation at the 30–45 cm depth (Table 4), which corresponds to the depth at which lysimeters were placed (45 cm). The only other significant differences in soil solution concentration between the two sites were with respect to Mg^{2+} (mixed oak was higher) and Na$^+$ (mixed oak was lower). As noted in the Introduction, it follows from the Gaines-Thomas exchange equation that the ratio [Mg^{2+}]/[Ca^{2+}] should increase as the ratio XCa/XMg decreases (equation 1). The differences in Mg^{2+} concentration were consistent with this equation: the ratios of XCa^{2+}/XMg^{2+} (30–45 cm depths) were 4.6 and 1.6 in the loblolly pine and mixed oak soils respectively (Tabnle 4), and the ratios of [Mg^{2+}]/[Ca^{2+}] were 0.30 and 0.88, respectively (Table 2).

It is interesting to note the similarity between the concentrations and fluxes of most ions in throughfall at the two sites (Tables 2 and 3). The importance of throughfall relative to mid-summer foliage content and litterfall differed considerably between the two sites, however: throughfall fluxes of K$^+$, Ca^{2+}, and Mg^{2+} equalled 210, 90, and 108% of litterfall fluxes (respectively) in the loblolly pine site whereas throughfall K$^+$ and Ca^{2+} fluxes equalled only 58 and 15% of litterfall fluxes (respectively) in

the mixed oak site (litterfall Mg was not measured in this site). It is not possible to calculate foliar leaching accurately from these data, since neither dry deposition nor stemflow were measured, but it would appear that foliar leaching of K$^+$ and Mg^{2+} are major components of the total return of these elements to the forest floor in the loblolly pine site.

Sulfate was the dominant anion in all solutions from both the loblolly pine and mixed oak sites, WTH and control, suggesting that both soil and foliar leaching were dominated by atmospheric S inputs (Table 2). There were temporary increases in soil solution NO$_3^-$ concentration following WTH in both sites (Figure 1), but at no time did NO$_3^-$ become a dominant anion, nor did concentrations reach U.S. Environmental Protection Agency drinking water standards (714 umol.l^{-1}). Changes in the leaching rates of other major ions were much smaller than those for NO$_3^-$.

The lack of any apparent SO$_4^{2-}$ retention in the soils of these two sites is somewhat surprising in view of previous research on nearby Walker Branch Watershed (which is dominated by the same soil series; Johnson *et al.*, 1982a; Richter *et al.*, 1983). This may be due to differences in the depth of lysimeter placement (80–180 cm in the Walker Branch studies *vs* 45 cm in these studies), since SO$_4^{2-}$ adsorption does increase from shallower to deeper soil horizons (Johnson *et al.*, 1982a).

Table 3. Ion and element fluxes in the loblolly pine and mixed oak sites

	H_2O (cm)	Biomass (kg ha^{-1} or kg ha^{-1} yr^{-1})	Total N	Total P (kmol(c) ha^{-1} or kmol(c) ha^{-1} year^{-1})	K$^+$	Ca^{2+}	Mg^{2+}	H$^+$	SO$_4^{2-}$
Loblolly pine									
Bulk precipitation	133		0.50	0.005	0.03	0.28	0.05	0.73	0.81
Throughfall	117 ± 4		0.68 ± 0.03	0.03 ± 0.02	0.42 ± 0.10	0.85 ± 0.17	0.28 ± 0.05	0.60 ± 0.07	1.31 ± 0.08
Net throughfall			0.18	0.045	0.39	0.63	0.23		
Leaf litterfall		3600 ± 950	1.97 ± 0.39	0.06 ± 0.01	0.20 ± 0.07	0.94 ± 0.25	0.26 ± 0.12		
Foliage content[a]		8200	6.28	0.20	1.12	1.00	0.64		
Soil leaching	52[b]		0.12	0.006	0.14	1.08	0.33	0.01	1.31
Mixed oak									
Bulk precipitation	125		0.78	0.005	0.06	0.35	0.07	0.67	0.75
Throughfall	116 ± 2		0.84 ± 0.07	0.007	0.52 ± 0.12	0.84 ± 0.14	0.26 ± 0.05	0.30 ± 0.05	1.12 ± 0.10
Net throughfall			0.06	0.002	0.46	0.49	0.19		
Leaf litterfall		4300 ± 770	2.21 ± 0.36	0.06 ± 0.02	0.90 ± 0.19	4.40 ± 0.05	N.D		
Foliage content		5900	5.67	0.18	1.68	3.22	0.86		
Soil leaching	54[b]		0.19	0.004	0.14	0.55	0.49	0.04	1.23

[a] Midsummer values, obtained by multiplying estimates from Van Lear's *et al.* equations by the observed ratio of total foliage to new foliage (1.98) in trees harvested in August 1982.

[b] Calculated from precipitation inputs minus evapotranspiration estimates from Luxmoore (1983)

N.D. = Not determined.

Table 4. Selected chemical properties of soils from loblolly pine and mixed oak control sites

Horizon and depth (cm)	pH[a]	NH_4Cl CEC[b] (cmol(c) kg^{-1})	Sum[c] CEC	Ca^{2+}	K^+	Mg^{2+}	Na^+	Al^{3+}	NH_4Cl,[d] % BS	Sum[e] % BS
Loblolly pine site										
A(0–15)	4.0 ± 0.10	3.71 ± 1.24	1.76 ± 0.52	0.97 ± 0.46	0.20 ± 0.04	0.24 ± 0.09	0.05 ± 0.05	0.31 ± 0.20	39 ± 12	80 ± 18
B(15–30)	4.0 ± 0.04	7.04 ± 0.34	1.32 ± 0.34	0.55 ± 0.30	0.16 ± 0.04	0.15 ± 0.07	0.02 ± 0.01	0.45 ± 0.23	17 ± 13	64 ± 20
B(30–45)	4.0 ± 0.12	10.8 ± 4.71	1.92 ± 0.29	1.05 ± 0.36	0.17 ± 0.06	0.23 ± 0.06	0.02 ± 0.02	0.47 ± 0.54	18 ± 13	77 ± 26
Mixed oak site										
A(0–15)	4.6 ± 0.4***	5.5 ± 3.4	1.33 ± 0.37	0.41 ± 0.14**	0.26 ± 0.08	0.14 ± 0.03*	0.03 ± 0.01	0.38 ± 0.29	22 ± 8**	64 ± 7
B(15–30)	4.3 ± 0.1***	9.6 ± 5.3	0.64 ± 0.10***	0.16 ± 0.05***	0.19 ± 0.07	0.08 ± 0.01	0.02 ± 0.01	0.20 ± 0.06*	6 ± 6	68 ± 13
B(30–45)	4.1 ± 0.1	12.9 ± 1.8	2.10 ± 1.63	0.11 ± 0.06***	0.14 ± 0.06	0.07 ± 0.02***	0.02 ± 0.01	1.25 ± 0.56*	6 ± 8*	31 ± 19**

[a] In 0.01 M $CaCl_2$.
[b] 1 M NH_4Cl, followed by ethanol and KCl extraction.
[c] $Ca^{2+} + Mg^{2+} + K^+ + Na^+ + Al^{3+}$.
[d] Base saturation using NH_4Cl-CEC.
[e] Base saturation using SUM-CEC.
*, **, and *** denote significant differences between the two sites at the 90, 95, and 99% levels, respectively, using Student's t-test.
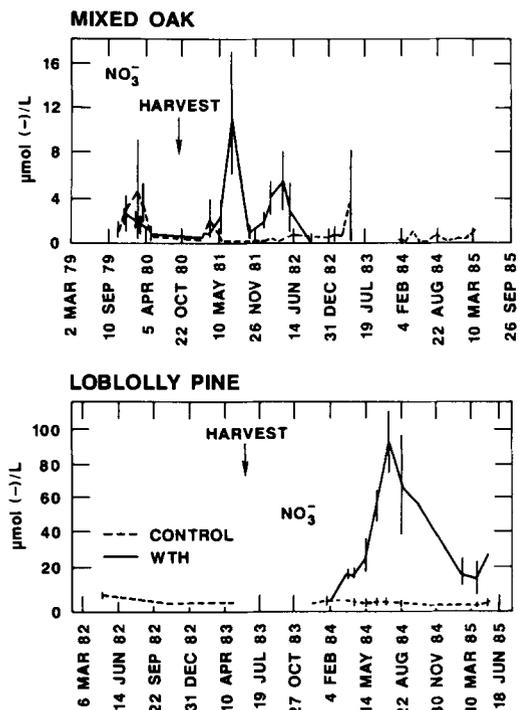
Fig. 1. Soil solution NO_3^- concentrations following whole-tree harvesting in the loblolly pine and mixed oak sites.

If we assume a natural background soil solution SO_4^{2-} level of approximately 50 umol(c).l^{-1} (*e.g.*, Johnson, 1981), then approximately 1.0 kmol(c)$^{-1}$ yr^{-1} of SO_4^{2-} leaching is designated as of anthropogenic origin in these two forest soils (Tables 2 and 3). This would imply that cation leaching in these soils has been increased by approximately 200–300% by acid deposition. This assumption does not take into account the possibility of "anion shift" in which the reduction in soil solution pH caused by the introduction of SO_4^{2-} (termed the "salt effect") causes a reduction in HCO_3^- concentration (Krug and Frink, 1983). To the extent that this anion shift has occurred, the above estimate of the increased leaching due to acid deposition is inflated. This effect is likely more pronounced in more acid mixed oak site soils where SO_4^{2-} increases were likely matched to a greater extent by H^+ than in the less acid loblolly pine soils. It should also be noted that, according to cation exchange relationships, the concentration of divalent cations will increase to a greater degree than concentrations of monovalent cations (Reuss and Johnson, 1986), and thus acid deposition has likely had a

greater influence upon the leaching of Ca^{2+} and Mg^{2+} than of K^+.

Combined effects of natural leaching, acid deposition, and whole-tree harvesting on nutrient budgets

To properly assess the combined effects of leaching and WTH on nutrient export, both factors must be expressed as fluxes with common units of time (Boyle *et al.*, 1973). In this context, WTH can be thought of as the average annual nutrient increment in biomass minus the amount of nutrient left on site as residue. In practical terms, it is simply nutrients removed by WTH in units of charge equivalents, kmol(c)ha^{-1}, divided by rotation age (years) to yield kmol(c)ha^{-1}yr^{-1}. Rotation age is well-known for the loblolly pine plantation (33 years old at the time of harvest), but subject to uncertainty in the uneven-aged mixed oak stand. The median age at harvest was 70 years, and that was taken as rotation age for this analysis. In constructing these nutrient budgets, we used nutrient pool and flux data from the control sites combined with estimates of potential WTH effects based upon the percent of total biomass and nutrient removals in the WTH sites.

When expressed on an average annual basis, it appears as if the rates of N, P, K, and Mg export by WTH in the loblolly pine site were greater than those in the mixed oak site (Figures 2 and 3). Thus, the hypothesis that nutrient export by WTH would be lower in the loblolly pine than in the mixed oak site appears to be false except in the case of Ca, and, consequently, the sum of base cations (Fig. 2). As noted above, the annualized estimates of nutrient export by WTH are very sensitive to assumptions about rotation age; however, the patterns described above would hold true for a wide range of rotation ages (45–180 years) and would therefore seem to be valid observations.

WTH appears to be the dominant factor in N and P export at both sites (Figure 3). The short-term increases in NO_3^- leaching following harvesting (Figure 1) are not accounted for in these figures, but the total N lost over these brief periods (< 0.01 kmol(c)ha^{-1}yr^{-1}) is insignificant relative to the N exports via leaching over a full rotation. In both cases, atmospheric N inputs approximately equalled net export due to leaching + WTH.
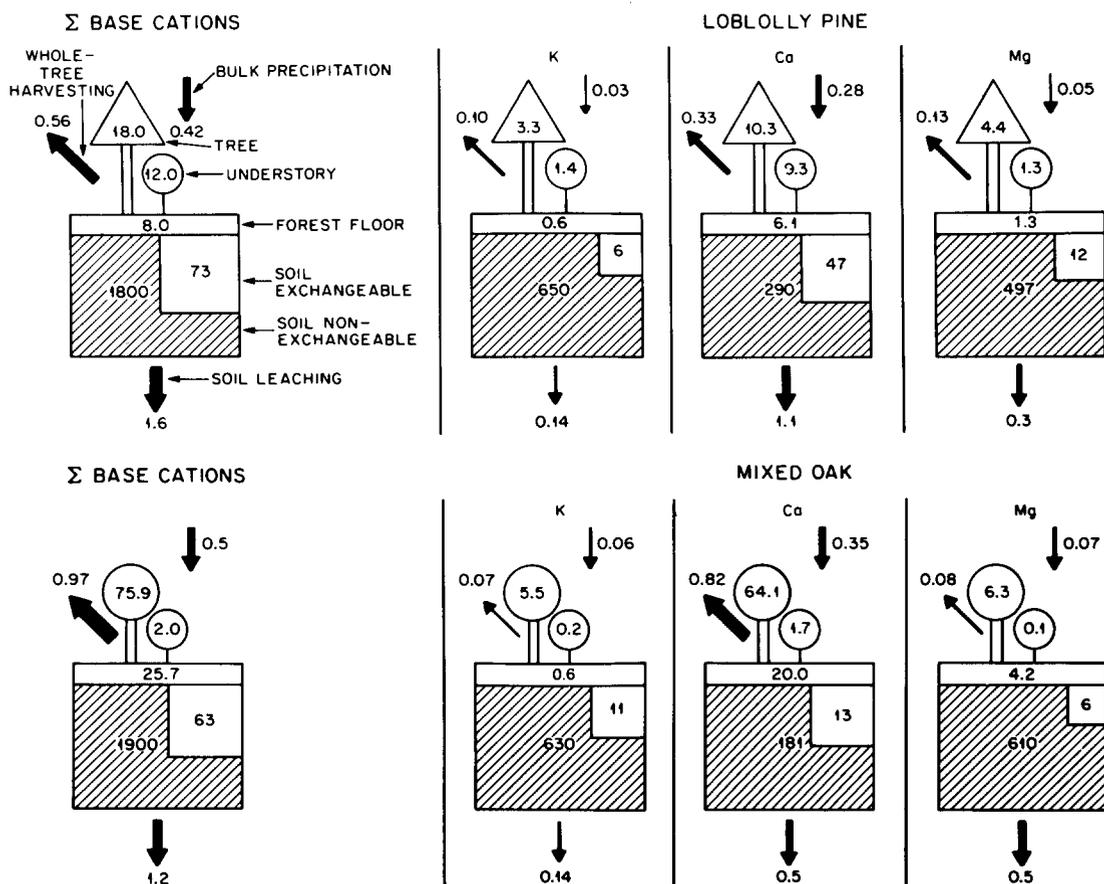
Fig. 2. Ecosystem contents $(kmol(c)ha^{-1})$ and bulk precipitation inputs and exports by leaching and whole-tree harvesting $(kmol(c)ha^{-1}year^{-1})$ of total base cations, K, Ca, and Mg in the loblolly pine and mixed oak sites.

Atmospheric P inputs fell short of compensating for P export via WTH, but soil total P reserves were very large, and if only a small fraction of this total P is made available, forest P needs will be adequate for several more rotations. Both sites showed net annual losses of all base cations by leaching alone, and leaching export exceeded WTH export for all but Ca in the mixed oak site (Fig 2). Given the assumptions on background natural SO_4^{2-} level described in the previous section, acid deposition was apparently the dominant single cause of total base cation export in the loblolly pine site (at 1 kmol(c) ha yr), nearly equalling the sum of natural leaching by carbonic acid $(0.6\,kmol-(c)ha^{-1}yr^{-1})$ and WTH $(0.56\,kmol(c)ha^{-1}yr^{-1})$ (Table 3 and figure 2). In the mixed oak site, acid deposition and WTH had about equal effects on total base cation export (about 1 kmol(c) ha^{-1} yr^{-1} each), and natural leaching by carbonic acid

$(0.3\,kmol(c)ha^{-1}yr^{-1}$; Table 3) is cautiously assessed as being the least important (noting the previously-mentioned caveat about the possibility of anion shift).

The contrast in Ca export by leaching *vs* WTH in the two forest types is consistent with the hypothesis that Ca accumulation in the mixed oak vegetation caused less Ca^{2+} leaching at that site (see Introduction). It is interesting to note, however, that while there were large differences in Ca export via leaching *vs* WTH between these two sites, the total exports by leaching + WTH were quite similar in magnitude (1.43 and 1.32 kmol(c) ha^{-1} yr^{-1}, respectively; Figure 2). It is also interesting to note that the net annual export of Ca by leaching + WTH in both sites constituted a greater percent of total ecosystem capital (0.5–0.7%) than that of any other nutrient (0.2% for N, 0.04–0.08% for P, 0.03–0.04% for K, and

LOBLOLLY PINE
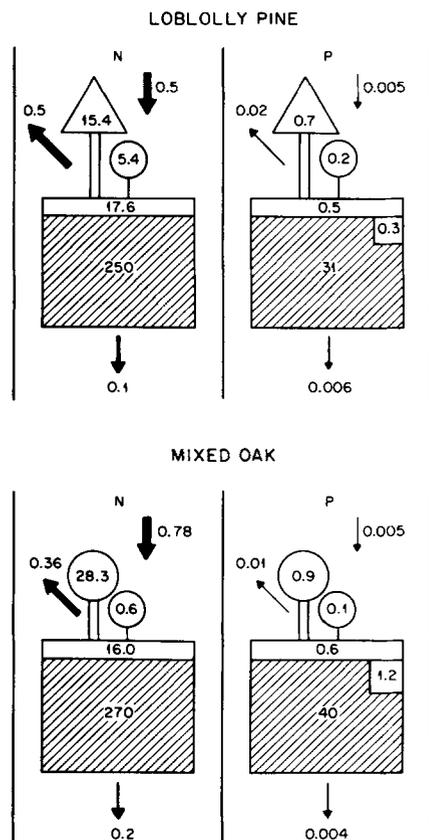
MIXED OAK

Fig. 3. Ecosystem contents (kmol ha^{-1}) and bulk precipitation inputs and exports by leaching and whole-tree harvesting (kmol ha^{-1}) of N and P in the loblolly pine and mixed oak site.

0.1% for Mg). However, N and P are probably more critical to the growth of subsequent forests on these sites than total ecosystem budgets would indicate: foliar N and P levels in the loblolly pine site (760 and 30 mmol kg^{-1}, respectively) were below critical levels for N and P deficiencies (830 and 35 mmol kg^{-1}, respectively; Wells, 1967; Lea and Ballard, 1982). Deciduous forests of this region are typically N deficient (Farmer *et al.*, 1970).

Acknowledgements

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