INTERRELATIONS AMONG SOIL NUTRIENT AVAILABILITY, N AND P CYCLING, AND N AND P USE EFFICIENCY IN FOUR HARDWOOD FOREST STANDS[1]

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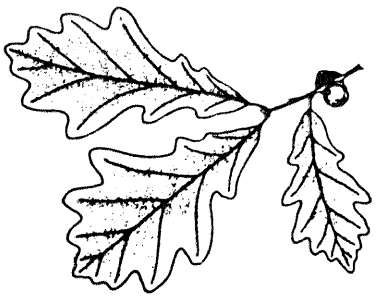

ABSTRACT.--One current projection for the longterm effects of acid deposition is a decrease in tree growth caused by progressive decreases in soil pH, and availability of N and P. To evaluate this, we have measured tree growth, and rates and pathways of N and P cycling in four hardwood forest stands along a gradient of soil fertility on the unglaciated Allegheny Plateau of Ohio. Along this gradient, mean soil pH varies from 3.7 to 5.2 while extractable phosphate and nitrate vary six- and three-fold respectively. Basal area, foliar mass and litterfall mass were similar among sites, while foliar and litterfall nutrient concentrations increased with increasing fertility. Nutrient mineralization and mass loss rates from litter correlated strongly with nitrogen and phosphorus content in litter while leaching of cations and P from the canopy by throughfall increased with increasing site fertility. Tree growth rates of four canopy tree species were similar among sites. Measures of nutrient use efficiency (resorption prior to litterfall, and growth efficiencies), generally increased with decreasing soil fertility. Therefore, as fertility decreased, N and P cycling rates decreased and efficiency of N and P use increased, at least over the pH/fertility ranges in these sites. Since growth rates did not vary greatly among sites in these four species, these data suggest that compensation strategies exist by which the effects of acid deposition on soil fertility can be mediated, at least to some threshold extent.

INTRODUCTION

Experimental analysis of the longterm effects of acid precipitation on forest ecosystems is exceedingly difficult for a variety of reasons including (1) the buffering of acids by canopy exchange, forest floor or soil interactions, (2) compensatory mechanisms within the ecosystem, (3) problems of scale involved in whole analyzing forest ecosystems, especially in complex terrain, and (4) problems associated with longterm, longitudinal ecosystem research. It is generally agreed, however, that one major longterm effect of acid deposition will be a decrease in soil nutrient availability, induced by increased leaching of cations, decreased surface soil pH, and decreased rates of litter mineralization and nitrification (Aber et al. 1982).

While a variety of studies have investigated the effect of fertilization (Miller et al. 1976) or acidification (Tveite 1980, Abrahamsen et al. 1980) on tree growth and nutrient turnover in conifer plantations, few parallel data exist for natural deciduous forest stands. In this paper I describe studies of four deciduous forest stands in a watershed in southeastern Ohio, which are similar in history, basal area, soil texture, and parent material, but which differ strongly in soil nutrient availability. It is hoped that by

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understanding how and why nutrient turnover and tree growth differ among these four stands, some insight into longterm acid deposition effects may be gained. Specifically, this paper will discuss (1) cycling of nitrogen and phosphorus via litterfall/decay and throughfall pathways, (2) responses of forest stands in terms of nutrient use efficiency, and (3) growth and nutrient use dynamics of selected major tree species.

STUDY AREA

Neotoma Valley is a 1.2 km. long, 73 ha, V-shaped watershed on the unglaciated Allegheny Plateau of southern Ohio, USA (Lat. 39° 35' N, Long. 82° 33' W). The climate of Neotoma is temperate, cool, continental with annual temperature maxima between 33 and 39 C, temperature minima between -20 and -29 C and annual precipitation of 100-105 cm (Wolfe et al. 1949). Parts of the valley were lumbered during the 1800's with the last select cutting occurring between 1900-1910 (Koch 1964). The four study sites are located in areas uncut since the mid-late 1800's.

Study sites have been established in the four major forest types found in the valley: Chestnut oak forest on the ridge-top, mixed oak forest on the southwest-facing slope, mixed mesophytic forest on the lower, northeast-facing slope, and transitional, red maple-tulip-chestnut oak forest on the mid-upper, northeast-facing slope (Table 1).

With the exception of the narrow floodplain in the valley bottom, which is covered by lacustrine deposits, the soils of the valley are all derived from the coarse grained, Mississippian-age sandstones and conglomerates which underlay the valley. The soils of the four study sites were all formed from the native bedrock (Wolfe et al. 1949, Riemenschneider 1964) and are all fine sandy loams, except those of the ridge-top which have slightly more silt and less very fine sand; all have <10% clay content (Riemenschneider 1964).

The three soil series mapped in these sites (Finney et al. 1962, Riemenschneider 1964) commonly intergrade on the slopes of these steep watersheds and are often mapped as a unit (Petro et al. 1967). Differences in horizon depth and development among these soils are related to slope position, aspect, vegetation (Finney et al. 1962; Petro et al. 1967), and litter redistribution patterns (Orndorff and Lang 1981, Boerner 1984a).

Differences in soil chemistry among sites were determined from twelve A-horizon (0-20 cm) samples per site taken in May and August 1983. Soil samples were extracted with 2N KCl (for nitrogen forms) and NH_4OAC (for cations and phosphate). Cation concentrations were determined by atomic absorption (Likens and Bormann 1970) while colorimetric methods were used for N and P analyses (phosphate:stannous chloride method, ammionium:phenate method, nitrate:ultraviolet method; A.P.H.A. 1976). Base saturation and cation exchange capacity were determined at the Ohio Agricultural Research and Development Center, Wooster, Ohio.

Soil chemistry varied considerably more than texture. A-horizon pH, base saturation, and extractable levels of major nutrients all increased in the order: chestnut oak < mixed oak < mixed mesophytic < transitional, including a threefold range in extractable nitrate and sixfold ranges in phosphate and calcium availability (Table 3). Thus while texture and exchange capacity were similar among the study sites, pH, base saturation and nutrient availability all varied strongly and in a consistent pattern.

TABLE 1.--Species composition of four forest study sites in Neotoma Valley, Ohio. Importance percentages (IP) are the mean of relative density and relative basal area in six 10 X 10 m plots per site. Only species with IP greater than 10 in at least one study site are indicated; 47 tree species occur in the valley. Nomenclature follows Braun (1961).

	Sites			
Species	Chestnut Oak	Mixed Oak	Mixed Mesophytic	Transitional
Quercus prinus	66.5	23.4	2.7	24.9
Acer rubrum	28.0	23.1	3.9	17.7
Fagus grandifolia	1.3	8.2	17.5	9.5
Quercus coccinea	—	21.1	—	—
Quercus alba	—	11.4	16.1	8.8
Nyssa sylvatica	—	5.1	5.0	12.4
Prunus serotina	—	—	16.5	—
Liriodendron tulipifera	—	—	18.3	14.6
Quercus borealis	—	—	14.8	—
Slope (°)	<5°	15-25°	20-25°	25-35°
Aspect (°)	—	230°	50°	50°
Basal Area (m^2/ha) [Mean, (std. err.)]	36.4 (6.1)	32.4 (2.9)	33.4 (5.3)	30.5 (2.3)

TABLE 2.--Soil series, texture, profile characteristics, and classification of the four sites. Classifications are from Petro et al. (1967) while profile data are from three-five soil pits per site (Finney et al. 1962).

Site	Series and Texture	Classification	A-horizon depth (cm)	Depth to Bedrock (cm)
Chestnut Oak	Berk fine sandy loam-silt loam	Inceptisol: Typic Dystrochrept	30-40	60-100
Mixed Oak	DeKalb fine sandy loam	Inceptisol: Typic Dystrochrept	50-60	60-120
Mixed Mesophytic and Transitional	Neotoma fine sandy loam	Alfisol: Mollic Hapludalf	30-40	80-120

TABLE 3.--Selected A-horizon soil characteristics in four forest types in Neotoma Valley, Ohio. Extractable nutrient concentrations are in uEq/100g (except C.E.C.: mEq/100g). Values followed by the same lower case letter were not significantly different at p=.05. Base saturations were arc-sine transformed, and pH values converted to hydrogen ion concentrations, before analysis of variance, and Waller-Duncan K-ratio post-test.

Site	pH	Nitrate	Phosphate	Calcium	Magnesium	Potassium	Base Saturation (%)	Cation Exchange Capacity
Chestnut Oak	3.7 a	26.2a	87.2a	457.4a	144.0a	69.5a	3.0a	21.7a
Mixed Oak	4.0 a	33.3a	192.1a	831.7a	268.8ab	76.3a	7.8b	15.3b
Mixed Mesophytic	4.7 a	48.8b	361.6b	1114.4a	294.8ab	156.4ab	11.8b	13.0b
Transitional	5.2 b	80.9c	513.4b	2985.7b	481.3b	181.6b	35.6c	11.3b

LITTERFALL AND LITTER DECAY

The mass of leaf litterfall during 1982 varied from 332 $g/m^2/yr$ (Chestnut oak) to 496 $g/m^2/yr$ (Transitional) (Table 4). These values fall within the range for temperate deciduous forests of the region (Bray and Gorham 1964, Sharpe et al. 1980). Litterfall mass was significantly higher at the transitional site than at the other three sites (Table 4).

Over 90% of annual leaf litterfall occurred between 1 September and 15 December (Table 4). Rates of autumn leaf fall were similar in the two years except in the mixed oak stand where several treefalls occurred during April 1982. The removal of several large canopy trees from the immediate area of several littertraps resulted in a 20% decrease in harvested leaf litter in the mixed oak site during autumn 1982. While this change was statistically significant, it was well within established ranges of year-to-year variability in litterfall in deciduous forests (Bray and Gorham 1964).

While the total mass of leaf litterfall was not determined during autumn 1980, fresh litter was trapped that autumn for use in litterbags. Thus, nutrient concentrations in autumn leaf litter are available for three years. Nitrogen and phosphorus concentrations were consistent over the three years at each site, and varied directly with the availability of each in the soil (Fig. 1).

While the mass of leaf litterfall was not significantly different among the chestnut-oak, mixed oak and mixed mesophytic sites, the higher fertility site (mesophytic) had higher fluxes of all elements in leaf litterfall than the lower fertility sites. The transitional site, the most fertile site, had the highest rates of litter mass (Table 4) and nutrient (Table 5) transfer in leaf litter of the four sites. Thus, while litterfall mass differed relatively little among sites, litter nutrient concentrations, and therefore litterfall nutrient fluxes, differed markedly.

Mass loss and nutrient mineralization from leaf litter were measured by placing 3mm mesh, polyethylene litterbags with 20g of air-dried litter in each site on 15 November 1980 and 1981 and recovering them in groups of 3-5 monthly over the next 24 months. Mass loss rates fit single exponential functions closely, though year-to-year differences did exist (Table 6).

Regression of mass loss rates vs environmental factors (litter N and P content, litter and soil moisture, annual and summer evapotranspiration, annual and summer rainfall, lignin concentrations, soil N and P pool sizes) showed initial litter N concentration to be the single strongest correlate

TABLE 4.--Litterfall mass in $g/m^2/yr$ in four forest stands during 1981 and 1982. Means are based on collections from six $0.25m^2$ littertraps per site harvested biweekly. Standard errors are given in parentheses. Values followed by the same lower case letter were not significantly different at (p=.05).

Litterfall Component	Site: Chestnut Oak	Mixed Oak	Mixed Mesophytic	Transitional
Full Year 1982	332 (19.3) a	365 (11.6) a	386 (18.8) a	496 (15.1) b
Autumn 1981	355	429	367	358
Autumn 1982	310	342	358	368
1981-1982 Difference	n.s.	p<.01	n.s.	n.s.

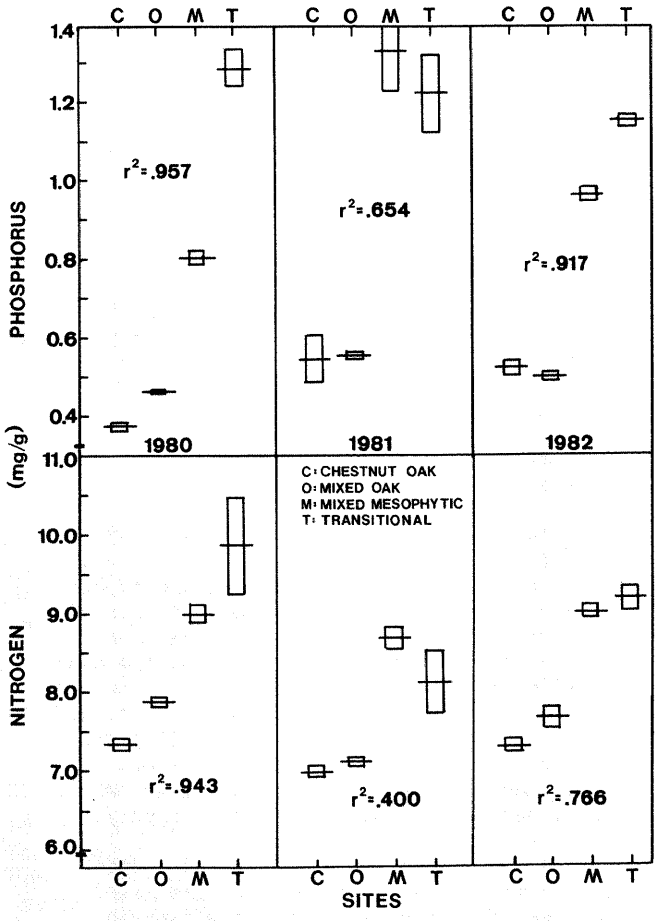

FIGURE 1.--Litter N and P concentrations in leaves from four forest stands. Means and standard errors are plotted and coefficients of determination (r^2) from regressions of litter concentrations on soil pool sizes given. Leaf nitrogen content was determined by Kjeldahl digestion (Bremner 1965) while phosphorus was determined by dry-ashing (Likens and Bormann 1970) followed by stannous chloride determination (A.P.H.A. 1976).

to decay rate (r^2=.799); only litter nitrogen and phosphorus (r^2=.396) were significant single factor correlates to relative decay rate.

The lack of strong correlations with lignin and evapotranspiration (c.f. Meentemeyer 1978) were likely due to relatively small ranges among sites for these variables (e.g. lignin ranged 16.1-20.7% of dry mass). Thus while microclimate and lignin may be the best predictors of decay rate on a broad scale, on this narrower landscape scale, initial litter N and P concentrations, which are dependant on the availability of these elements in the soil, correlated most strongly with decay rates.

Nitrogen was immobilized in litter during the first year of decay in all sites and during both initial years. Litterbags at the more fertile mixed mesophytic sites gained 7-20% nitrogen by mass, depending on site and year, while litterbags at the less fertile chestnut oak and mixed oak sites gained 18-29%. Thus, while litterbags at all sites immobilized nitrogen, proportional and absolute nitrogen immobilization were higher at the less fertile sites (Table 7). Net nitrogen mineralization began during the second year at the more fertile sites while the less fertile oak sites continued to immobilize N during the second year (Table 7).

TABLE 5.--Fluxes of nitrogen and phosphorus (kg/ha/yr) in leaf litterfall estimated as the product of leaf litterfall mass and mean nutrient concentration from collections made biweekly during 1982. Values followed by the same lower case letter were not significantly different at p = .05, following analysis of variance and Waller-Duncan K-ratio post-test. Standard errors of the means are given in parentheses.

Sites	Nitrogen	Phosphorus
Chestnut Oak	24.1 (1.6)a	1.9 (0.1)a
Mixed Oak	27.5 (1.2)a	1.7 (0.1)a
Mixed Mesophytic	33.6 (1.7)b	3.8 (0.2)b
Transitional	38.1 (1.1)b	5.8 (0.2)c

TABLE 6.--Proportion of mass remaining (% mass), relative decomposition rate (k), and coefficients of determination (r^2) from non-linear regression of mass losses from litterbags over one and two years. Standard errors of estimates are given in parentheses. Rates followed by the same lower case letter were not significantly different following pairwise t tests using the standard error of the slope estimate from the non-linear regressions.

Parameters:	Sites: Chestnut Oak	Mixed Oak	Mixed Mesophytic	Transitional
1980 Litter: One Year				
% mass	68.2 (2.9)	62.3 (4.6)	53.0 (1.7)	59.5 (5.6)
k	.403 a	.454 a	.595 b	.594 b
r^2	.877	.823	.907	.870
1981 Litter: One Year				
% mass	70.6 (2.1)	80.3 (7.5)	60.2 (3.8)	59.0 (2.0)
k	.332 a	.275 a	.507 b	.531 b
r^2	.750	.635	.815	.866
1980 Litter: Two Years				
% mass	63.9 (2.6)	57.7 (5.0)	40.8 (1.7)	49.4 (4.3)
k	.238 a	.290 a	.437 b	.442 b
r^2	.648	.707	.888	.753

TABLE 7.--Nutrient mineralization (immobilization) during litter decay in four Ohio forest stands. Fluxes ($mg/m^2/yr$) are the product of 1982 litterfall fluxes and the proportion of mass of each nutrient remaining at the end of one and two years of incubation in litterbags.

Site	Nitrogen	Phosphorus
1980 Litter: First Year		
Chestnut Oak	(593)	69
Mixed Oak	(495)	90
Mixed Mesophytic	(269)	276
Transitional	(282)	444
1980 Litter: Second Year		
Chestnut Oak	(161)	(227)
Mixed Oak	(74)	(176)
Mixed Mesophytic	441	(268)
Transitional	419	(350)
1980 Litter: Two Year Net		
Chestnut Oak	(754)	(139)
Mixed Oak	(569)	(85)
Mixed Mesophytic	172	8
Transitional	141	326

Litter phosphorus was mineralized rapidly at all sites during the first year, and immobilized during the second year (Table 7). Over a two year period, litter at the mixed mesophytic and transitional sites was a source of soluble N and P to the surface soil while litter at the less fertile mixed oak and chestnut oak sites was a sink for soluble N and P.

Thus, both the absolute mass and rate of cycling of N and P varied with soil nutrient availability. The lower the availability, the smaller the flux of N and P in litterfall and the longer the residence time in litter.

THROUGHFALL

Throughfall chemistry can affect cycling of N and P in two ways: (1) by moving nutrients from leaves and leaf surfaces to the forest floor and (2) by buffering acids in incident precipitation thus ameliorating potential hydrogen ion effects in the forest floor.

Throughfall was collected biweekly from six funnel collectors per site. The funnel tops were covered with polyethylene mesh to minimize contamination by large particles. Chloroform was added weekly to minimize algal and bacterial

TABLE 8.--Throughfall pH and element fluxes in four forest stands. Means are based on six collectors per site, samples collected and positions randomized biweekly. Rainfall flux means were based on three collectors. Data for cation fluxes in litterfall are from Boerner (1984a). Net canopy immobilization is indicated by negative values.

		(Growing Season (4/28 - 9/13))			FULL YEAR		
Site	pH[1,2]	H^+ Flux in Throughfall[2] (mEq/m^2)	Net H^+ Exchange[2] (mEq/m^2)	Net H^+ Exchange[2] (% of Ca ± Mg + K in leaf litterfall)	Net NH_4^+ Flux in Throughfall (mEq/m^2)	Net NO_3^- Flux in Throughfall (mEq/m^2)	Net PO_4^{3-} Flux in Throughfall (uEq/m^2)
Chestnut Oak	4.15	39.3	8.2	3.9	15.4	1.35	11.0
Mixed Oak	4.28	30.5	17.0	7.8	16.5	-0.80	-88.0
Mixed Mesophytic	4.52	17.5	30.0	9.3	21.0	-4.97	2741.0
Transitional	4.64	15.1	32.4	7.1	17.6	-3.79	4159.2
Rain	4.02	47.5	——	——	——	——	——

[1] Geometric Weighted Mean
[2] No Differences Existed Among Sites During Litterfall (9/13 - 11/15) or Leafless (11/15 - 4/28/83) Seasons.

growth. The positions of the collectors were changed to new, random positions after each sampling.

For purposes of comparison, the year was divided into three throughfall leaching seasons: the leafless season (15 November - 28 April), the growing season (29 April - 13 September) and the litterfall season (14 September - 14 November). No significant differences in throughfall volume among sites were recorded for any of the seasons, or for the entire year. In addition, pH and fluxes of N and P in throughfall among sites were similar during the litterfall and leafless seasons; during the growing season, however, significant differences in these fluxes were found (Table 8).

The geometric weighted mean pH of throughfall collected during the growing season increased with site fertility (Table 8). When pH was converted to hydrogen ion flux, and the buffering capacity of the canopy estimated as the difference between incident H^+ flux in rain and H^+ in throughfall (Net H^+ exchange), it was apparent that the canopies of the two more fertile sites exchanged 2-4 fold as much H^+ flux as did those of the nutrient poor sites.

Given that hydrogen ions are exchanged for calcium, magnesium and potassium ions (Cronan and Reiners 1983), the relative magnitude of the throughfall pathway can be evaluated by comparing net hydrogen exchange to total base cations in leaf litterfall. Among the three forest stands with similar leaf litterfall masses (chestnut oak, mixed oak, mixed mesophytic; Table 4), the relative magnitude of cation flux via throughfall ranged from 4-9% and increased with site fertility. Throughfall cation transfer was also relatively large at the transitional site (7%), but not as large as that of the mixed mesophytic site.

Total net inorganic nitrogen transfer in throughfall averaged about 16 mEq/m^2 and did not differ significantly among sites. This total masks, however, patterns of increasing ammonium leaching and nitrate immobilization with site fertility (Table 8). Phosphorus leaching was more than an order of magnitude higher at the two more fertile sites than the less fertile sites (Table 8). Therefore, fluxes of cations and phosphorus in throughfall, at least, follow the same general pattern as did transfers in litterfall and decomposition: increasing flux rate with increasing fertility.

NUTRIENT USE EFFICIENCY: FOREST STANDS

The nutrient mass necessary to support annual growth of foliage and wood comes from internal storage as well as from uptake from the soil system. Prior to litterfall, some of this nutrient mass is resorbed (=retranslocated), and some is leached from the leaves. Those nutrients not resorbed or leached from live leaves are added to the forest floor as litter. In such a system, nutrient use efficiency can be defined in several ways. One indication of a more efficient forest stand (or tree) is the ability to generate equivalent amounts of foliage and wood utilizing a smaller mass of nutrients. A second indicator of high nutrient use efficiency is a lower rate of leaching of essential nutrients from live foliage, thus minimizing uptake needs. Finally, a more nutrient efficient stand would resorb a larger mass and/or proportion of foliar nutrients prior to litterfall.

To determine to what degree nutrient use efficiency varied among the four study stands in Neotoma Valley, nutrient concentrations in foliage and litter were determined during the 1982 growing season for all species with relative basal area

TABLE 9.--Weighted average foliage and litter nutrient concentrations (mg/g dry mass) for four forest stands. Weighted averages are based on each species maximum foliar and litter nutrient concentrations, and the species contribution to stand basal area. Weighted estimates were made for three 0.1 ha plots within each stand, then averaged. Within a parameter, values followed by the same lower case letter were not significantly different at p = .05.

Parameter	Chestnut Oak	Mixed Oak	Mixed Mesophytic	Transitional
Maximum Foliar Nitrogen (mg/g)	19.8 a	19.5 a	20.3 b	20.3 b
Litter Nitrogen (mg/g)	7.0 a	7.1 a	8.9 b	9.8 c
Percent Resorption*	64.6 a	63.6 a	56.2 a	51.7 b
Maximum Foliar Phosphorus (mg/g)	1.59a	2.05b	2.06b	2.23c
Litter Phosphorus (mg/g)	0.65a	0.50b	1.22c	1.36c
Percent Resorption*	59.2 a	75.9 b	40.7 c	38.9 c

*calculated on a concentration basis

>5%. Weighted averages for each stand were calculated based on each species contribution to stand basal area.

Both maximum foliar nitrogen and phosphorus were significantly higher in the fertile sites than the infertile sites (Table 9). The inverse of maximum foliar concentration can be considered an estimate of the leaf mass produced per unit nutrient invested. This is an appropriate parameter of nutrient use efficiency, given the requirement that stand production rates do not differ. While the lack of wood, root and leaf production rates for all the species in these stands precluded robust estimates of production, it was clear that the stands on the less fertile sites, with lower foliar N and P concentrations, were generating equivalent leaf mass (Table 4) with a smaller nutrient investment than was the mixed mesophytic stand. What was unclear was whether those lower N leaves are capable of equivalent net production.

Litter N and P concentrations also paralleled site fertility (Table 9). Estimates of resorption made on a concentration basis show the two less fertile stands (Chestnut Oak and Mixed Oak) to have resorbed a significantly higher proportion of N and P prior to litterfall than did the most fertile sites (Transitional), though the differences between resorption rates were considerably larger for P than for N.

Estimating resorption on a concentration basis can, however, produce unreliable estimates since both the mass of nutrients and the mass of structural material in the leaf change with time. As a result, the concentration of N or P might decrease with time as structural carbohydrates are deposited in the leaf, even with no actual N or P resorption. To eliminate this potential error, resorption was determined on an absolute mass basis for the major species in each site (Fig. 2). Regression of resorption on nutrient mass in litterfall is a common indicator of nutrient availability (Vitousek 1982, 1984; Boerner 1984a), and showed a consistent decrease in P resorption with increasing P availability, but no significant difference in N resorption among sites. This difference between elements has also been discussed by Birk and Vitousek (1984).

NUTRIENT USE EFFICIENCY: SPECIES RESPONSES

Two mechanisms may be involved in any increase in nutrient use efficiency of forest stands along a gradient of decreasing soil fertility: (1) the replacement of nutrient inefficient, but fast-growing, species on rich soils with more nutrient efficient species on poor soils, and (2) an increase in nutrient use efficiency with decreasing fertility in species found throughout the gradient. While ample evidence exists for the former (Small 1972, Chapin and Kedrowski 1983), little information, especially for deciduous species, exists with which to evaluate the importance of the latter.

A comparison of resorption rates for species present in infertile or fertile Neotoma sites only showed species from the infertile stles resorbed significantly more P than did fertile site species (75.2% vs 52.3%, p<.05), though no differences existed for N resorption (61.3% vs 55.5%, p>.20). Thus, some of the differences in P use efficiency may be due to the replacement of nutrient-inefficient, fast-growing species on rich, moister sites with nutrient use efficient species on poor, drier sites.

To evaluate the degree to which species found on both fertile and infertile sites contribute to differences in N and P use efficiency, we measured several nutrient use parameters in populations of four species found in the mesophytic (fertile) and mixed oak (less fertile) sites: Quercus alba, Q. prinus, Acer rubrum and Fagus grandifolia.

In each site, three individuals of each of the four species were selected for monitoring. All were canopy individuals >50 yrs. of age, with a single main stem, and no obvious sign of damage. Neither mean age nor diameter of individuals of a species differed significantly between sites. Ages and radial increments were determined from

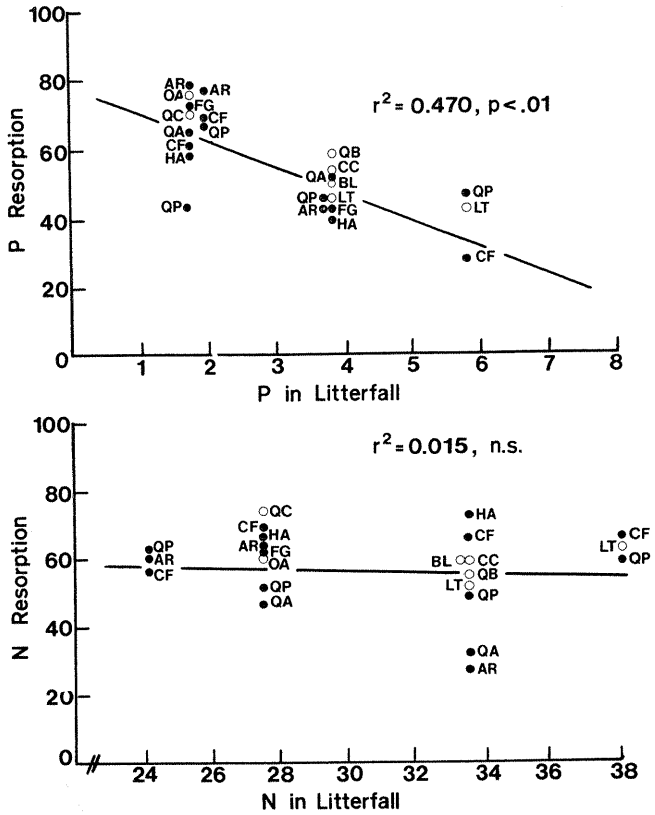

FIGURE 2.--Percent resorption of N and P on an absolute mass basis vs nutrient transfer (kg/ha/yr) in litterfall. Species found in both fertile and infertile sites are indicated by closed symbols while species found on fertile or infertile sites only are indicated by open symbols. Best fit lines and coefficients of determination from linear regression are given. Species codes are: AR = Acer rubrum, BL = Betula lenta, CC = Carpinus carolinianum, CF = Cornus florida, FG = Fagus grandifolia, HA = Hamamelis virginiana, LT = Liriodendron tulipifera, QA = Quercus alba, QB = Q. borealis, QC = Q. coccinea, QP = Q. prinus, OA = Oxydendrum arboreum.

duplicate cores taken from north and south sides at 1.35-1.40 m height during March 1984. Standing mass at the end of the 1983 growing season, and production of wood and leaves during that season, were determined using dimension regressions based on regression equations published by Tritton and Hornbeck (1982). Four estimates of radial increment were made for each tree: two based on the 1983 ring width of the north and south side cores, and two based on the mean radial increment for the five year period, 1979-1983. In general, five year mean increments differed from 1983 increments by <10%. Leaves were sampled every 2-3 weeks from the end of leaf expansion through the end of litterfall.

Foliar nitrogen and phosphorus concentrations generally decreased throughout the growing season in all species at both sites, on both mass and absolute bases. Maximum foliar nitrogen concentrations were higher at the more fertile mixed mesophytic site than the mixed oak site in Q. prinus, Q. alba, A. rubrum, though the differences observed among Q. alba trees were not significant (Table 10). As a result, significantly more dry leaf matter was produced per unit N invested by Q. prinus and A. rubrum when growing on the lower fertility soil (Table 10). Maximum foliar phosphorus content at the fertile site significantly exceeded that at the infertile site for both Quercus spp., so these two species produces more dry leaf matter per unit P invested on the nutrient-poor soil (Table 10). No significant differences in maximum foliar N and P levels between sites were observed in Fagus grandifolia (Table 10). Thus three of four species (Q. prinus, Q. alba, A. rubrum) had consistently higher foliar nitrogen and phosphorus concentrations, and lower leaf masses produced per unit N or P invested, when growing on the more fertile site. Fagus grandifolia showed no consistent intersite differences on foliar N or P.

Both the litter and foliar nutrient concentrations used in estimating proportional resorption were calculated on an absolute basis (mass/unit leaf area) to allow for differences in dry mass/unit leaf area caused by differential resorption or deposition of materials into the leaf prior to abscission (Ostman and Weaver 1982). Nitrogen resorption was 41-140% higher on the less fertile site, except for Q. prinus which resorbed similar proportions of N from leaves on the two sites (Table 11). Phosphorus resorption was 25-86% higher also in the mixed oak stand, again except for Q. prinus in which P resorption did not differ between sites (Table 11). Ostman and Weaver (1982) have also reported small differences in resorption by Q. prinus in sites of differing quality.

Because lower foliar N or P concentrations may result in lower photosynthetic rates (Chabot and Hicks 1982), and therefore less growth, relative growth rates were examined as well. Stem and branch production rates for the 1983 growing season were determined from winter 1984 standing mass, estimated from dbh, and winter 1983 standing mass, estimated from dbh-radial increment. Since growth rate generally decreases with increasing tree size, analysis of covariance was used to compare relative growth rates (g woo9d produced/kg wood present/yr) between sites, in relation to tree size.

For three of four species, relative growth rates were higher on the less fertile site (Table 12); Q. alba relative growth rates did not differ between sites. Even where differences were statistically significant, however, they were small in absolute magnitude: on the order of 7-25 g/kg/yr, or 1-3%, and based on only three trees per species per site. The important observation was that relative growth rates were not lower at the mixed oak site despite lower soil fertility and foliar nutrient levels, perhaps due to a somewhat deeper solum at the mixed oak site (Riememschneider 1964).

TABLE 12.--Relative growth rate (g wood produced/kg wood/yr), nitrogen growth efficiency (kg wood and leaves produced/g nitrogen lost in leaffall) and phosphorus growth effciency of four forest tree species are relatively fertile mesophytic and infertile oak sites. Significant differences following analysis of variance are indicated by *, ns = non significant. Standard errors of means are given in parentieses.

Tree Species	Relative Growth Rate			Nitrogen Growth Efficiency			Phosphorus Growth Efficiency		
	Mixed Mesophytic		Mixed Oak	Mixed Mesophytic		Mixed Oak	Mixed Mesophytic		Mixed Oak
Q. prinus	14.6 (2.7)	*	22.1 (1.6)	123.7 (4.0)	*	149.0 (5.8)	1018.5 (75.2)	*	1616.4 (46.6)
Q. alba	21.9 (1.9)	ns	22.6 (2.7)	139.6 (10.0)	*	204.2 (5.7)	1080.0 (78.4)	*	1834.3 (94.2)
A. rubrum	17.9 (3.0)	*	33.3 (5.9)	179.6 (17.7)	*	267.7 (24.9)	1807.1 (176.0)	*	3173.5 (375.2)
F. grandifolia	10.6 (2.5)	*	23.2 (6.9)	138.6 (7.9)	*	155.6 (12.9)	1574.8 (84.9)	ns	1715.8 (77.3)

not been widely reported. Three general lines of research have been explored in an effort to predict longterm effects of acid deposition on forests: (1) laboratory microcosms, (2) field acidifications, and (3) mathematical modeling. Laboratory experiments using artificial acid precipitation have focused on tree seedlings, and have yielded conflicting results on seed germination, growth, foliar leaching and leaf damage. In general, direct effects only become significant at rain pH <3.0 (Wood and Bormann 1977; Lee and Weber 1979). Laboratory experiments involving leaching of intact soil profiles, either with or without plants, have demonstrated progressive leaching of calcium, potassium and other cations, and profile acidification, though once again, significant results are generally obtained only when rain pH <3.0 (Overrein 1972; Wood and Bormann 1977).

A common field approach has been the application of dilute H_2SO_4 directly to forest or plantation soils. In some cases, surface soils have decreased in pH and base saturation (Baath et al. 1980; Abrahamsen et al. 1976; Johnson and Cole 1976), though no consistent response in tree growth to such manipulations has been reported (Bormann and Wood 1977, Tveite 1980, Tveite and Abrahamsen 1980). Such results are difficult to generalize since (1) treatment solutions are applied directly to the forest floor and are thus not affected by canopy interactions, especially throughfall buffering (Cronan and Reiners 1983) and (2) the number of samples necessary to show significant soil effects is very large (Lloyd and McKee 1983).

The mathematical model of forest tree growth developed by Anderson et al. (1980) indicated that nitrogen dynamics in humus and soil were a fourfold more sensitive indicator of effects of altered soil chemistry than were tree rings. Aber et al. (1982) modeled the changes in relative abundance of northern hardwood forest tree species and marketable basal area using a model sensitive to changes in forest floor nitrogen dynamics and the differential tolerance of various tree species to changes in soil nitrogen availability. Increases of 10-20% and decreases of 10-50% in litter decomposition rates were evaluated as potential indicators of acid rain effects. Decreases would be expected if biota were sensitive to a drop in pH or an increase in sulfate; increases would be expected if nitrate additions decreased the C:N ratio of the litter. In the 10-20% range, increases on decomposition resulted in larger decreases in marketable basal area over 90 years than did similar decreases in decomposition rate (+10%:14% decrease vs -10%: 3% decrease; +20%: 23% decrease vs -20%: 7% decrease). A large decrease in decomposition rate (-50%) resulted in a large decrease in marketable yield (34%) (Aber et al. 1982).

Thus, while longterm changes on soil chemistry may occur as a result of acid precipitation, information currently available does not adequately demonstrate that either direct or indirect effects of acid precipitation alone decreases tree growth rates or marketable yield.

As an alternative to longterm, manipulative studies of forests subjected to acid deposition, this study compared neighboring stands of similar cutting history, parent material, soil texture and basal area, but different soil chemistry. Strong correlations existed among soil pH, extractable N and P pool sizes, foliar nutrient concentrations, nutrient transfers in litterfall and throughfall, and nutrient mineralization from leaf litter. In short, rates of N and P cycling were considerably lower, and turnover times higher, in the less fertile sites. This baseline information was used, then, to determine the effect that soil acidification might have on both tree nutrient dynamics (N and P) and growth rates (carbon dynamics).

TABLE 10.--Mean maximum foliar concentration (mg/g dry mass) and dry mass produced per unit nutrient investment (mg dry mass/mg N or P) in four deciduous tree species growing on relatively fertile and infertile sites. Standard errors of the concentration means are given in parentheses. Significant differences following analysis of variance are indicated by *.

Species	Nitrogen Concentration		Nitrogen Mass per Unit Invested	Phosphorus Concentration		Phosphorus Mass per Unit Invested
Quercus prinus						
Mixed Mesophytic	25.4(0.2)	*	39.4	1.98(0.06)	*	504.8
Mixed Oak	22.9(0.2)		43.7	1.76(0.04)		566.9
Quercus alba						
Mixed Mesophytic	23.7(0.5)		42.2	2.22(0.18)	*	450.5
Mixed Oak	22.4(0.8)		44.6	1.85(0.06)		539.4
Acer rubrum						
Mixed Mesophytic	17.7(0.6)	*	56.5	1.42(0.03)		702.7
Mixed Oak	13.8(0.4)		72.4	1.37(0.15)		727.8
Fagus grandifolia						
Mixed Mesophytic	22.7(0.5)		44.1	1.34(0.05)		749.1
Mixed Oak	23.2(0.6)		43.1	1.42(0.10)		702.7

TABLE 11.--Mean percent resorption of nitrogen and phosphorus from leaves of four tree species prior to litterfall. Significant differences among sites, as indicated by analysis of variance following arc-sine transformation, are shown by *.

Species	Nitrogen				Phosphorus			
Sites	Oak		Mesophytic	Oak/Mesophytic	Oak		Mesophytic	Oak/Mesophytic
Quercus prinus	50.3		48.1	1.05	43.7		45.2	0.97
Quercus alba	46.2	*	30.8	1.50	65.6	*	52.4	1.25
Acer rubrum	63.7	*	26.5	2.40	79.0	*	42.4	1.86
Fagus grandifolia	63.2	*	44.9	1.41	72.7	*	42.7	1.70

The nutrient growth efficiency of each tree was calculated as the ratio of wood and leaf mass produced to nitrogen or phosphorus mass lost in litterfall. Nitrogen growth efficiency was higher in trees from the infertile site than the fertile site for all four species (Table 12). The higher nitrogen growth efficiency of *Q. alba* was related, primarily, to lower litterfall nitrogen losses and higher resorption, while the differences between sites in *A. rubrum* and *F. grandifolia* were the result of both higher relative growth rate and lesser litterfall losses, the result of greater proportional resorption. Because nitrogen resorption in *Q. prinus* did not differ between sites, its higher nitrogen use efficiency at the mixed oak site was due to a higher relative growth rate at that site.

The differences in phosphorus growth efficiency among sites and species, and the relative contributions of relative growth rate and proportional resorption, paralleled those of nitrogen growth efficiency (Table 12). Relatively large tree-to-tree variation in *Fagus grandifolia* in both sites resulted in differences in phosphorus growth efficiency which approached, but did not achieve, statistical significance ($p=.07$).

DISCUSSION

While direct effects of acid precipitation and runoff on fish and other aquatic organisms has been repeatedly demonstrated, direct effects of acid deposition alone on forest ecosystems have

Studies of carbon balance and nutrient turnover in deciduous and evergreen plants have demonstrated a significant nutrient component in the evolution of these growth strategies (review by Chabot and Hicks 1982), and in the current geographic distribution of species with one strategy or the other. Evergreen plants, particularly those with sclerophyllous leaves, exhibit a larger gain in carbon per unit nitrogen or phosphorus absorbed. This is accomplished by combining long leaf lifespan, efficient resorption of nutrients prior to litterfall, and minimizing leaching losses (Monk 1966, Small 1972, Schlesinger and Chabot 1977).

Such studies demonstrate how species with such drastically different growth strategies as the evergreen and deciduous habits can persist in sites differing greatly in soil nutrient availability. They shed little light, however, on the importance of plant-soil nutrient dynamics in determining patterns of abundance of various deciduous tree species along more limited gradients of soil nutrient availability, despite data which suggest growth per unit nutrient uptake may be important in influencing the outcome of competitive interactions in such species (Racine 1971).

"Nutrient use efficiency" has been used as a convenient term describing the interactions among plant growth, plant tissue C:element rations, and soil nutrient availability. One indication of a more efficient plant is the production of equivalent amounts of foliage and wood utilizing a smaller mass of nutrients. A second indicator of higher nutrient use efficiency is a lower rate of leaching of essential nutrients from live foliage thus minimizing uptake needs. Finally, a more nutrient efficient plant or forest stand would resorb a larger mass and/or proportion of foliar nutrients prior to litterfall.

Several prior studies suggest that forest stands on infertile soils do demonstrate these patterns of higher nutrient use efficiency (Stachurski and Zimka 1975, Miller et al. 1976, Vitousek 1982, Boerner 1984b). Other studies compare one or more parameters of nutrient use efficiency among different species from nutrient-rich and nutrient-poor sites and generally conclude that nutrient use efficiency and nutrient availability vary inversely (e.g. Small 1972, Chapin and Kedrowski 1983). Fertilization experiments with conifer stands demonstrate decreases in nutrient use efficiency, but increases in growth rate, with increasing nitrogen availability (Miller et al. 1976, Turner 1977), though parallel studies with deciduous species are not available.

In this study, seven potential parameters of nutrient use efficiency between sites were assayed: Leaf production per unit N and P invested (=2), percent resorption of N and P (=2), relative growth rate (=1), and growth efficiency relative to nitrogen and phosphorus losses (=2). Individuals of Quercus alba and Quercus prinus growing in the less fertile soil of the mixed oak site, when compared to individuals growing on more fertile soil, both exhibited 5/7 indicators of higher efficiency. Mixed oak site Fagus grandifolia trees exhibited higher nutrient use efficiency in 4 of 7 cases while Acer rubrum was more efficient at the infertile site in 6 of 7 cases. In no instance was nutrient use efficiency significantly higher on the more fertile soil. Moreover, unlike coniferous trees (c.f. Miller et al. 1976), the increase in nutrient use efficiency in these four deciduous tree species occurred without a significant decrease in relative growth rate. Thus, within some limits, these deciduous trees may maintain productivity, despite decreasing soil nutrient availability, by increasing nutrient use efficiency. If, as currently projected, longterm acid deposition will result in decreasing soil nutrient availability (Abrahamsen 1980, Anderson et al. 1980), the limits of this physiological plasticity will be directly testable, though only over a lengthy period. One alternative is to analyze growth and nutrient dynamics of these species under even more nutrient-poor conditions, such as those of coastal plain sandy soils, though this then introduces further problems associated with comparison of distant, climatologically distinct sites. Another alternative is to experimentally manipulate the sites described here, either by acidifying or fertilizing, but this, once again substitutes a short-term, high-dosage regime for a long-term, chronic process.

Nonetheless, an appreciable portion of the higher nutrient use efficiency of deciduous forest stands on less fertile soils may be due to increased efficiency in persistent species. The ability to compensate, or adjust metabolically, under changing or stressful conditions has been shown to be an important component on the evergreen strategy (Mooney 1969, Chabot and Hicks 1982). This study suggests it is an important component in the strategy of some deciduous forest trees as well, and suggests that forests on soils moderately susceptible to acidification may be able to compensate, to some degree, for the affects of acid deposition on soil fertility.

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