Foliar Nutrients in Sugar Maple Forests along a Regional Pollution–Climate Gradient

Andrew J. Burton,* Kurt S. Pregitzer, and Neil W. MacDonald

ABSTRACT

Stressing agents such as defoliation, adverse climatic conditions, and pollutant deposition have the potential to alter forest nutrition. Several recent instances of sugar maple (*Acer saccharum* Marsh.) decline and dieback have been associated with foliar nutrients deficiencies. This study assessed foliar nutrient status and cycling in five sugar maple dominated northern hardwood forests along a Great Lakes pollution–climatic gradient. Concentrations and contents in mid-July foliage and litterfall were determined at each site for N, P, S, Ca, Mg, K, Al, Fe, Mn, B, Zn, and Cu. Where differences existed among sites in foliar nutrient concentrations, they could be predicted primarily from soil properties. Two notable exceptions were foliar S, which was strongly related to SO_4 deposition, and foliar Al, which could be predicted by a combination of soil nutrient cation availability and SO_4 deposition. Nutrient content of mid-July foliage and litterfall increased from northwest to southeast along the gradient for N, S, Mg, Al, Fe, B, and Cu. This was the result of an increase in foliage and litterfall biomass, combined in some cases (S, Al, Fe, and B) with increasing foliar nutrient concentrations. Reproductive effort significantly affected total litter return of all nutrients and 43 to 62% of mid-July foliar N, P, K, and S were conserved through retranslocation prior to litterfall. Sugar maple foliar nutrient concentrations for the five sites revealed no obvious nutrient deficiencies or toxicities, and provide a regional baseline against which the effects of long-term pollutant deposition and other stresses can be assessed in the future.

INADEQUATE FOLIAR NUTRITION has been associated with several recent instances of sugar maple decline and dieback. Foliar K and P deficiencies were found in declining stands in the Quebec Appalachians (Bernier and Brazeau, 1988a,b; Pare and Bernier, 1989). Magnesium deficiency existed in sugar maple experiencing severe dieback in the Lower Laurentians of southeastern Quebec (Bernier and Brazeau, 1988c). Natural stresses including insect defoliation and adverse climatic conditions appear to be the primary causes of these deficiencies, but acidic deposition has been suggested as a contributing factor (Bernier et al., 1989). Potential mechanisms through which chronic acidic deposition might alter forest nutrient status include: (i) elevated leaching of cations from foliage (Tukey, 1980; Liechty et al., 1993); (ii) long-term soil cation depletion (Johnson et al., 1985; Johnson and Taylor, 1989; MacDonald et al., 1992); and (iii) mobilization of soil Al (Ulrich et al., 1980; Johnson and Taylor, 1989; Foster, 1989) leading to Al toxicity or impaired uptake of Mg and Ca (Thornton et al., 1986; Dewald et al., 1990).

The foliar nutrient status of northern hardwood stands has been documented for certain areas of the northeastern USA and southeastern Canada (Likens and Bormann, 1970; Gosz et al., 1972; Lea et al., 1979a,b, 1980; Leaf, 1973; McLaughlin et al., 1985; Morrison, 1985, 1990; Bernier and Brazeau, 1988a,b,c). Detailed information, however, is lacking for the Great Lakes states of the USA. This region experiences a pronounced gradient of pollutant deposition (Schwartz, 1989; MacDonald et al., 1991), and evidence suggests that deposition is influencing regional S cycling (Pregitzer et al., 1992; Ohmann and Grigal, 1990), soil properties (MacDonald et al., 1991, 1993; David et al., 1988), soil cation leaching (MacDonald et al., 1992), foliar cation leaching (Liechty et al., 1993; MacDonald et al., 1993), and plant tissue chemistry (Bockheim et al., 1989; Ohmann and Grigal, 1990). Other stresses, such as insect defoliation, unusual climatic conditions, and disease outbreaks, also have the potential to alter nutrient status of the region's northern hardwood forests (Bernier et al., 1989).

As part of a regional study, this work was undertaken to assess foliar nutrient status and cycling in sugar maple dominated northern hardwood forests of the Great Lakes states. Objectives of the study were to: (i) document current foliar nutrient levels for sugar maple across the region; (ii) compare foliar nutrient concentrations with published values for healthy stands and thresholds for deficiency and toxicity; (iii) determine if sugar maple foliar nutrient status can be predicted from soil, pollutant deposition, and climatic variables; and (iv) calculate nutrient contents in mid-July foliage, litterfall, and retranslocation for northern hardwood forests across the region.

The results of the study provide a regional baseline against which future evaluations of sugar maple nutrient status can be made and should prove useful to current efforts at modeling nutrient and C flow on a regional scale.

METHODS

Study Sites

Five study sites were established along a gradient of increasing pollutant (H, SO_4, and NO_3) deposition extending from northeastern Minnesota to central lower Michigan (Fig. 1). Site selection procedures (Burton et al., 1991b; Reed et al., 1988) identified stands along the gradient that were similar in terms of age, stand structure, physiography, soil classification, basal area, and species composition (Table 1). All sites are second-growth northern hardwoods, dominated by sugar maple, on sandy, well-drained Spodosols. The study sites span 4° of latitude and 6° of longitude, thus annual temperature covaries with pollution along the gradient (Table 1). Three 30 by 30 m measurement plots on which no destructive sampling was allowed were established at each site.

Pollutant Deposition

Site-specific estimates of wet deposition H, NO_3, SO_4, NH_4, Ca, Mg, and K fluxes were obtained from wet–dry collectors

A.J. Burton and K.S. Pregitzer, Dep. of Forestry, Michigan State Univ., E. Lansing, MI 48824–1222; and N.W. MacDonald, School of Natural Resources and Environment, Univ. of Michigan, Ann Arbor, MI 48109–1115. Received 30 Oct. 1992. *Corresponding author.

Published in Soil Sci. Soc. Am. J. 57:1619–1628 (1993).

Abbreviations: SLA, specific leaf area; NFW, net forest water; DC, direct current.

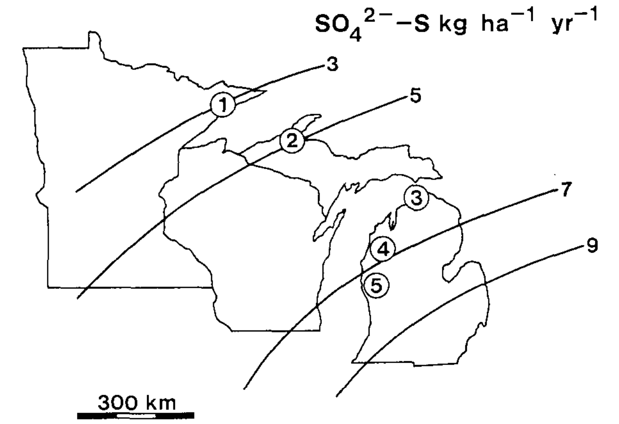

Fig. 1. Locations of the five study sites (circled) along the regional SO_4^{2-}–S deposition gradient. Wet SO_4^{2-}–S deposition was estimated from annual data summaries of the National Atmospheric Deposition Program (1985a,b, 1986, 1987).

(Aerochem Metrics, Bushnell, FL) and recording rain gauges (Belfort Instrument Co., Baltimore, MD) positioned in canopy openings near each site. Annual dry deposition fluxes were estimated by multiplying mean annual ambient concentrations for gases and particulates by published deposition velocities. Wet and dry deposition estimates for the sites were consistent with those made by others for the region and confirmed the existence of pronounced increases in pollutant deposition along the gradient (MacDonald et al., 1992). From Site 1 to Site 5, annual wet plus dry deposition increased from 0.15 to 0.68 kg ha^{-1} for H, from 4.10 to 9.71 kg ha^{-1} for SO_4–S, and from 2.82 to 7.63 kg ha^{-1} for NO_3–N. Annual wet plus dry deposition of (NO_3 + NH_4)–N increased from 5.64 kg ha^{-1} at Site 1 to 11.84 kg ha^{-1} at Site 5. Regional trends did not exist for the deposition of Ca, Mg, or K. Additional details on wet deposition monitoring and dry deposition estimation can be found in MacDonald et al. (1992).

Soil Characteristics

Soils at each site were sampled by horizon from three soil pits, one associated with each measurement plot, but located at least 5 m beyond the plot boundary (MacDonald et al., 1991). The forest floor was sampled in two layers (Oi and Oe + Oa) at five locations around each plot using 30.5 by 30.5 cm steel frame. Mineral soils and Oe + Oa material were analyzed for total N, total S, KCl-exchangeable Al, and NH_4Cl-exchangeable Ca, Mg, and K using standard methods as outlined by MacDonald et al. (1991). Total P of organic and mineral horizons was determined by automated colorimetry following H_2SO_4 digestion (Technicon Industrial Systems, 1977). Soils at the sites have similar classifications (Table 1), but significant differences in nutrient contents exist both among and within sites (Table 2).

Foliage and Litter Fall Sampling

Litterfall was collected at eight random locations on each plot (24 per site) using 0.5-m^2 wooden litter traps (Pregitzer et al., 1992). Litter collections were made from September through November in 1987 and during the entire year from 1988 through 1990. Traps were emptied weekly during the period of heavy litterfall in late September and early October, and monthly during snow-free periods of the remainder of the calendar year. Litter from one-half of each trap was sorted into foliage (by species), woody material, and reproductive parts. Sorted samples were composited for nutrient analyses by trap for sugar maple leaf litter and by plot for other litter components.

Live foliage samples were collected during mid-July of 1988, 1989, and 1990 from trees surrounding the measurement plots, but no closer than 10 m from plot borders. Mid-July was chosen for live foliage sampling as it is shortly after the period of most active shoot growth in these stands, a time when reserves of mobile elements are most likely to be depleted (Erdmann, et al., 1988). Others have recommended sampling northern hardwood foliage in August, which is generally considered to be the time of greatest elemental stability (Lea et al., 1979a;

Table 1. Locations, climatic conditions, and stand characteristics for the five northern hardwoods study sites.

	Site 1	Site 2	Site 3	Site 4	Site 5
Latitude (N)	47°41′	46°52′	45°33′	44°23′	43°40′
Longitude (W)	90°44′	88°53′	84°51′	85°50′	86°09′
Annual temperature†, °C	3.7	4.3	5.2	5.8	7.6
Precipitation, mm					
Mean annual†	670	870	830	810	850
Growing season‡	410	400	410	400	400
Basal area, m^2 ha^{-1}					
Total	31.4 (0.8)§	31.8 (0.4)	29.5 (1.2)	30.1 (2.8)	29.9 (1.9)
Acer saccharum Marsh.	28.0 (1.9)	27.5 (1.9)	25.4 (2.4)	24.9 (0.9)	22.5 (4.9)
Acer rubrum L.	0.2 (0.3)	1.4 (2.5)	0	2.4 (1.3)	4.1 (3.3)
Fagus grandifolia Ehrh.	0	0	0.9 (1.6)	0.1 (0.1)	0.5 (0.4)
Betula alleghaniensis Britton	0	2.3 (0.4)	0	0	0
Betula papyrifera Marshall	2.8 (2.3)	0	0	0	0
Fraxinus americana L.	0	0	2.4 (1.1)	0	0
Prunus serotina Ehrh.	0	0	0	1.5 (1.9)	2.1 (2.3)
Quercus rubra L.	0	0	0	1.3 (1.2)	0.7 (0.8)
Canopy height, m	20 (1)	24 (1)	27 (1)	28 (1)	24 (1)
Overstory age, yr	78 (13)	79 (15)	73 (6)	74 (11)	78 (5)
Soil Great Group	Haplorthod–Fragiorthod	Haplorthod	Haplorthod	Haplorthod	Haplorthod
Litter biomass¶, kg ha^{-1}					
Foliar litter	3132 (154)	3239 (41)	3609 (183)	3952 (234)	4078 (317)
Total litter	4275 (196)	4477 (94)	4846 (76)	5256 (137)	5396 (516)

† 30-yr mean temperature and precipitation are National Oceanic and Atmospheric Administration (1983) data for the nearest NOAA weather station.
‡ May through September.
§ Standard deviations (in parentheses) are for three plots per site for basal areas, for eight dominant and codominant trees per site for age, and for all dominant trees per site for height.
¶ Litter biomass values are the mean and standard deviation of average annual litterfall for three plots per site.

Morrison, 1985). Our results should be comparable to studies using August foliage sampling for most elements, as sugar maple foliar concentrations for N, P, K, Mg, Zn, and Al are relatively stable during July and August (Mitchell, 1936; Leaf, 1973; Lea et al., 1979a,b; Morrison, 1985). Concentrations of other elements in sugar maple foliage have been shown to increase (Ca, Fe, and Mn) or decrease (Cu) by approximately 15 to 20% (Leaf, 1973; Lea et al., 1979a,b) between July and August.

In 1988, trees were felled for detailed foliage sampling of sugar maple and the next most common species at each site, with minor species sampled using shotguns and pole pruners. Less intensive foliage sampling for all species was conducted in mid-July of 1989 and 1990 using shotguns and pole pruners. The diameters of sample trees encompassed the ranges existing at the sites. Samples were taken from the lower, middle, and upper portions of the canopy in 1988 and 1989. In 1990, labor constraints necessitated the restriction of sampling to the lower and middle crown as suggested by Morrison (1985). Upper crown concentrations in sugar maple are slightly lower than those found in the middle and lower crowns for Ca, K, Mg, Fe, and Zn (Morrison, 1985). Concentrations for these elements in 1990 were adjusted to compensate for this effect using relationships between canopy zones in 1988 and 1989. The adjustments had only a minor effect on 3-yr mean concentrations, reducing them by <3% in all cases. All mid-July foliage samples were stored at 4 °C until they could be returned to the laboratory for analysis.

The sampling procedures produced 24 sugar maple foliage samples per site in 1988, nine in 1989, and six in 1990. Samples from 1989 and 1990 were composites from at least four trees. A minimum of three composite samples from at least four trees was collected at each site for all non-sugar-maple species in 1988 and 1989. One-third of mid-July foliage samples from each site were taken from as close as possible to each plot, and all mid-July foliage samples contained 50 to 100 leaves. Additional details on foliage sampling can be found in Burton et al. (1991a).

Litterfall and July foliage samples were dried (70 °C for 48 h), ground to pass a 0.85-mm screen, and analyzed for N, P, S, Ca, Mg, K, Al, Fe, Mn, Zn, B, and Cu. Total Kjeldahl N and total P were determined colorimetrically following H_2SO_4 digestion (Technicon Industrial Systems, 1977). Calcium, Mg, K, Al, Fe, Mn, Zn, B, and Cu were determined by DC–Ar plasma atomic emission spectrometry following HNO_3–$HClO_4$ digestion. Total S was determined by automated turbidimetry following HNO_3–$HClO_4$ digestion (Wall et al., 1980). Mean recovery rates for nutrient analyses of National Institute of Standards and Technology standard reference materials (pine needles and citrus leaves) were: 98% for N and P, 95% for S, 101% for Ca, 100% for Mg, 96% for K, 98% for Al, 101% for Fe, 93% for Mn, 112% for Zn, and 94% for Cu. Petioles were included in both mid-July foliage and leaf litter samples.

Litterfall nutrient contents were calculated as the product of litter weights and nutrient concentrations for each litter component. Mid-July foliar nutrient contents were calculated as the product of summer foliage biomass and mid-July nutrient concentration for each species. Nutrient concentrations used for non-sugar-maple foliage in 1990 were individual species averages for 1988 and 1989. Mid-July foliage biomass was estimated by adjusting leaf litter weight for biomass lost between mid-July and leaf fall due to retranslocation of carbohydrates and nutrients. This was accomplished by multiplying leaf litter biomass by 1.14, the average ratio of leaf litter SLA to mid-July SLA for the five sites in 1988 (Burton et al., 1991a, Pregitzer et al., 1992). Our values of 1.14 is within the range reported for the ratio of leaf weights in mid-July and mid-October for sugar maple foliage (1.15, Morrison, 1991; 1.07 for shade leaves and 1.35 for sun leaves, Jurik, 1986; and 1.04 for midcrown foliage, Lea et al., 1979a). Foliage sampling in 1989 and 1990 was not detailed enough to allow SLA ratios to be estimated for individual years.

Allometric equations for determining mid-July foliar biomass are available for the sites, but we believe adjusted leaf litter weights are more accurate due to their ability to account for reductions in foliar biomass resulting from biotic and abiotic factors (Grier, 1988; Burton et al., 1991a). Since tree diameters at the sites changed little during the study period, allo-

Table 2. Soil nutrient contents and pH by horizon for the five study sites.

	Site 1	Site 2	Site 3	Site 4	Site 5
	kg ha^{-1}				
			Oe + Oa horizons		
Total N	913 (100)†	347 (108)	600 (206)	412 (136)	260 (34)
Total S	114 (11)	39 (18)	92 (23)	54 (23)	36 (6)
Total P	69 (9)	23 (6)	32 (10)	27 (7)	16 (4)
Exch. Ca	241 (16)	84 (19)	201 (47)	106 (58)	80 (9)
Exch. Mg	30 (2)	10 (3)	18 (5)	12 (5)	9 (3)
Exch. K	28 (5)	13 (3)	17 (4)	13 (3)	9 (1)
Exch. Al	0.7 (0.2)	0.4 (0.1)	0.5 (0.1)	0.5 (0.1)	0.3 (0.1)
			A + E horizons		
pH (H_2O)	4.2 (0.1)	4.9 (0.3)	5.0 (0.4)	4.5 (0.1)	4.7 (0.5)
Total N	830 (353)	536 (326)	838 (570)	1 125 (690)	1 408 (174)
Total S	114 (52)	61 (36)	112 (86)	104 (40)	155 (40)
Total P	98 (47)	98 (19)	91 (27)	191 (100)	156 (30)
Exch. Ca	181 (70)	198 (172)	439 (181)	166 (92)	262 (49)
Exch. Mg	25 (10)	24 (19)	38 (11)	27 (20)	32 (4)
Exch. K	64 (27)	38 (21)	27 (12)	48 (22)	33 (5)
Exch. Al	39 (15)	38 (14)	13 (6)	131 (44)	98 (34)
			B horizons to 75 cm		
pH (H_2O)	5.2 (0.4)	5.3 (0.2)	5.5 (0.2)	5.7 (0.5)	5.4 (0.2)
Total N	12 085 (6826)	4 020 (1905)	2 775 (220)	1 715 (490)	3 137 (214)
Total S	1 898 (861)	601 (225)	479 (43)	305 (110)	401 (69)
Total P	4 728 (1361)	1 947 (876)	932 (200)	1 340 (497)	999 (277)
Exch. Ca	2 883 (886)	1 526 (2260)	1 616 (1061)	422 (279)	478 (235)
Exch. Mg	377 (215)	425 (697)	352 (384)	42 (14)	49 (28)
Exch. K	376 (125)	167 (155)	99 (25)	84 (44)	68 (11)
Exch. Al	1 115 (496)	667 (453)	425 (141)	305 (77)	355 (152)

† Site vaues are the mean and standard deviation for three plots per site.

Table 3. Sugar maple foliar nutrient concentrations for the five sites and ranges reported in the literature†.

Element	Material	Site 1	Site 2	Site 3	Site 4	Site 5	Range in literature	References‡
N§, g kg^{-1}	July foliage	21.9 (0.9)	19.6(1.2)	20.1(0.8)	19.1(0.5)	19.7(1.0)	16.7–27.4	1–10
	Leaf litter	8.0(0.3)ab¶	7.1(0.5)b	8.4(0.3)a	8.5(0.3)a	7.7(0.8)ab	4.3–10.0	10,12–14
S§, g kg^{-1}	July foliage	1.69(0.03)bc	1.54(0.09)c	1.59(0.11)c	1.82(0.06)ab	1.90(0.06)a	1.90–2.20	7
	Leaf litter	0.94(0.03)cd	0.87(0.02)d	1.03(0.01)c	1.20(0.07)b	1.36(0.07)a	0.79–1.75	12,13
P, g kg^{-1}	July foliage	1.64(0.10)a	1.38(0.17)ab	1.18(0.14)b	1.54(0.10)a	1.19(0.03)b	0.57–2.20	1–10
	Leaf litter	0.52(0.11)b	0.51(0.07)b	0.49(0.05)b	0.81(0.07)a	0.38(0.02)b	0.30–1.50	10,12–14
Ca, g kg^{-1}	July foliage	12.3(1.1)	9.6(1.1)	12.5(2.4)	10.8(0.9)	11.5(0.8)	6.0–21.2	1–10
	Leaf litter	14.8(0.7)ab	13.7(0.8)b	17.7(1.3)a	13.8(1.3)b	14.7(1.4)ab	5.0–16.8	10,12–14
Mg, g kg^{-1}	July foliage	1.76(0.06)	1.59(0.24)	1.57(0.24)	1.49(0.07)	1.85(0.20)	0.9–4.4	1–10
	Leaf litter	1.63(0.11)	1.48(0.03)	1.63(0.13)	1.27(0.12)	1.56(0.29)	0.6–2.8	10,12–14
K, g kg^{-1}	July foliage	9.64(0.80)a	8.21(0.49)ab	7.91(1.02)ab	8.01(0.22)ab	7.17(0.75)b	5.2–11.4	1–10
	Leaf litter	3.92(0.54)	3.43(0.26)	3.24(0.08)	3.21(0.24)	3.23(0.52)	2.3–5.8	10,12–14
Al, mg kg^{-1}	July foliage	32.2(1.6)c	48.7(10.1)b	37.6(1.1)bc	45.1(1.0)b	66.2(2.5)a	23–60	1,6,9,11
	Leaf litter	54.8(2.8)c	82.4(10.3)b	62.1(1.0)bc	78.4(2.5)bc	108.4(18.4)a	—	—
Fe, mg kg^{-1}	July foliage	63.2(4.5)b	79.7(11.7)ab	64.4(8.2)ab	68.0(5.2)ab	82.6(2.0)a	51–119	1,2,4–7,9,11
	Leaf litter	80.8(5.0)bc	90.0(4.8)b	71.0(5.4)c	91.6(1.2)b	108.0(8.8)a	97–130	12,13
Mn, mg kg^{-1}	July foliage	789(207)c	1554(144)a	942(274)bc	1499(256)a	1393(103)ab	467–1740	1,2,4–7,9,11
	Leaf litter	1250(366)ab	1654(182)a	905(60)b	1566(262)a	1701(186)a	760–2999	12,13
B, mg kg^{-1}	July foliage	40.7(1.2)ab	29.5(3.5)b	43.1(5.4)a	44.9(6.7)a	48.8(4.6)a	26–81	1,6
	Leaf litter	43.0(1.6)b	25.9(2.9)c	43.4(2.2)b	49.1(0.8)a	54.1(1.5)a	—	—
Zn, mg kg^{-1}	July foliage	37.2(3.0)	30.7(4.3)	30.2(6.4)	34.2(7.8)	32.4(1.1)	28–72	1,2,4–7,9,11
	Leaf litter	37.5(5.5)	36.1(0.5)	35.1(4.6)	32.3(1.1)	31.9(1.4)	33–76	12,13
Cu, mg kg^{-1}	July foliage	5.46(1.16)	6.31(1.00)	5.29(0.93)	5.62(1.52)	4.29(0.98)	3–10	2,4–7,9,11
	Leaf litter	5.26(1.07)	5.95(0.26)	6.22(0.38)	6.06(0.33)	5.45(1.03)	7	12,13

† Plot concentrations averaged across all years were used to determine site means. Standard deviations (in parentheses) are for three plots per site. Mid-July concentrations are for 1988–1990, and leaf litter concentrations are for 1987–1990. Range reported in the literature is for sugar maple foliage from healthy, natural stands.

‡ Literature references on which ranges are based: 1 = Bernier and Brazeau, 1988a; 2 = Morrison, 1990; 3 = Mader and Thompson, 1969; 4 = Likens and Bormann, 1970; 5 = Pletscher, 1982; 6 = McLaughlin et al., 1985; 7 = Morrison, 1985; 8 = Lea et al., 1979a; 9 = Lea et al., 1980; 10 = Leaf, 1973; 11 = Lea et al., 1979b; 12 = Gosz et al., 1972; 13 = Morrison, 1991; 14 = Chandler 1941.

§ Nitrogen and S data are from Pregitzer et al. (1992).

¶ Row means without common letters differ significantly at $P < 0.05$ (Tukey's HSD test).

metric equations predicted essentially the same mid-July foliar biomass for all 3 yr at a given site. Such estimates clearly are in error, given measured reductions in leaf litter at the sites of up to 30% in years of heavy seed production and early-season defoliation (Pregitzer and Burton, 1991; Burton et al., 1991a).

Retranslocation estimates for Ca, Mg, K, and P were calculated as mid-July foliar nutrient content minus leaf litter nutrient content minus NFW occurring between mid-July and litterfall. Net forest water accounts for foliar nutrient leaching (or uptake) and was calculated as the difference between throughfall and wet deposition nutrient fluxes using the data of Liechty et al. (1993).

Statistical Analysis

Nutrient concentrations and contents in mid-July foliage and litterfall were compared among sites using analysis of variance. Our primary goal was to examine the sites for nutrient status and regional trends expressed over multiple years of record. Therefore, plot means averaged across all years of record were used to compare sites. Analysis of variance were performed on untransformed data unless transformation improved homogeneity of variance. Mean separation was performed using Tukey's Honestly Significant Difference test. Relationships between foliar nutrient concentrations and soil, deposition, and climatic variables were examined using correlation and regression analyses. Data for individual plots were used in these analyses (n = 15). Predictor variables selected in multiple regressions were independent, and all predictors were significant at $P \leq 0.10$.

The gradient approach used in this study does not involve the application of specific pollutant levels to homogeneous experimental units. Differences exist among sites in soil characteristics, and annual temperature covaries with pollutant deposition. The presence of parallel gradients is a complicating factor, but reflects real-world conditions, not an artifact of study design. A similar approach has been used in surveys of pollutant impacts in the Great Lakes region by David et al. (1988), Grigal and Ohmann (1989), and Bockheim et al. (1989). The regression approach that we used was designed to statistically account for the effects of soil properties on foliar nutrients and then determine if remaining variation is related to pollutant deposition in a way that is consistent with the hypothesized effects of acidic deposition.

RESULTS AND DISCUSSION

Foliar Nitrogen, Phosphorus, and Sulfur Concentrations

Foliar N concentrations for sugar maple leaf litter and mid-July foliage were near the midpoints of ranges reported in the literature (Table 3). Litterfall foliar S values were also within the range reported in the literature, but mid-July foliar S concentrations were lower than those reported by Morrison (1985) for Turkey Lakes Watershed in northern Ontario (Table 3). This may be a consequence of an annual wet plus dry S deposition rate at Turkey Lakes of 11.6 kg ha^{-1} during their study (Sirois and Vet, 1988), which exceeds the deposition levels for our five sites. Mid-July foliar S concentrations at our sites were well above the 0.7 g kg^{-1} reported by Erdmann et al. (1979) for the foliage of S-deficient sugar maple seedlings.

A detailed analysis of S and N cycling at the five gradient sites was presented by Pregitzer et al. (1992). They found a clear increase from northwest to southeast in foliar S concentrations and S/N molar ratios that was strongly related to SO_4 deposition. Foliar S concentra-

Table 4. Regression relationships for predicting foliar nutrient concentrations†.

Foliar nutrient	Regression relationship‡	R^2	P
	Mid-July sugar maple foliage		
N	No relationship		
S	1132 + 22.8(SO_4WTDRY) + 0.126(SB)	0.59	0.005
P	1170 + 0.101(POAB)	0.58	0.001
Ca	No relationship		
Mg	No relationship		
K	6375 + 112.8(KOe+Oa)	0.68	0.000
Al	46.9 − 0.099(CaOe+Oa) + 1.035 (SO_4WTDRY)	0.63	0.003
	Sugar maple leaf litter		
N	No relationship		
S	374 + 30.3(SO_4WTDRY) + 0.084(SB)	0.86	0.000
P	No relationship		
Ca	12370 + 6.554(CaOeOaAE)	0.38	0.015
Mg	No relationship		
K	3057 + 2.193(KB)	0.55	0.002
Al	82.7 − 0.174(CaOe+Oa) + 0.909 (SO_4WTDRY)	0.65	0.002

† Foliar nutrient concentrations are in mg kg^{-1}, soil nutrient contents in kg ha^{-1} and deposition estimates are in kg ha^{-1} yr^{-1}.
‡ Predictor variables (in parentheses) include: total S in the B horizon (SB); exchangeable K in the soil Oe+Oa (KOe+Oa) and B (KB) horizons; exchangeable Ca in the Oe+Oa horizon (CaOe+Oa); the sum of exchangeable Ca in the Oe+Oa and A+E horizons (CaOeOaAE); total wet plus dry SO_4 deposition (SO_4WTDRY); and the sum of total P in the Oe+Oa, A+E, and B horizons to 75 cm (POAB).

tions were not correlated with soil S, but soil S content did explain residual variability in foliar S not accounted for by SO_4 deposition (Table 4).

Annual temperature covaries with SO_4 deposition along the gradient and thus also is positively correlated with foliar S concentration. Warmer temperatures conceivably could increase S availability by increasing mineralization rates. Sulfur and N mineralization are tightly linked, however, and annual N mineralization rate does not increase from Site 1 to Site 5 along the gradient (Ouyang, 1990). In fact, N mineralization is several times greater at Site 1, presumably a consequence of the large soil organic matter and N pools at the site (Table 2, MacDonald et al., 1991). Given the lack of an increase in mineralization rate from Site 1 to Site 5, it is unlikely that the increase from north to south in foliar S concentrations and S/N ratios is a consequence of increasing annual temperature. Annual temperature also cannot explain the high sugar maple foliar S concentrations reported by Morrison (1985) for nearby Turkey Lakes Watershed, which received a higher annual rate of total S deposition than the five gradient sites (Sirois and Vet, 1988) but has lower mean annual temperature (Foster et al., 1992).

Phosphorus concentrations in sugar maple foliage (Table 3) showed no regional trends that might be related to acidic deposition or climate. Total P contents in the soil Oe + Oa and B horizons were positively correlated ($P \leq 0.01$) with sugar maple foliar P concentrations in mid-July but not in litterfall. Mid-July foliar P was within the range reported in the literature (Table 3) and exceeded the critical P concentration of 1.1 g kg^{-1} suggested by Bernier and Brazeau (1988a) for July sugar maple foliage. Foliar P concentrations at Sites 3 and 5, however, approach this threshold. Leaf litter P concentrations greatly exceeded those measured by Bernier and Brazeau (1988a) in leaf fall from individual P-deficient sugar maple trees (<0.2 g kg^{-1}), but at Sites 1, 2, 3, and 5 approached the range of 0.3 to 0.5 g kg^{-1} measured in freshly fallen leaf litter at five P-deficient sites in Quebec (Bernier and Brazeau, 1988c). Although P concentrations at several of the sites approached those reported by others for P-deficient locations, no visible evidence of P deficiency was noted from 1988 through 1991 during mid-July health assessment of all individual trees on the measurement plots (J.A. Witter, 1992, personal communication).

Calcium, Magnesium, and Potassium Concentrations

Concentrations of Ca, Mg, and K in sugar maple foliage were within the ranges commonly reported in the literature for both mid-July and litterfall (Table 3), suggesting these nutrients were in adequate supply. Foliar K concentrations were greater than those reported by Bernier and Brazeau (1988a,b) for K-deficient sugar maple foliage in July (<5.5 g kg^{-1}) and in fresh leaf litter (1.0 g kg^{-1}). Mid-July foliar Mg at all sites was well in excess of the 0.60 g kg^{-1} reported by Bernier and Brazeau (1988c) in Mg-deficient sugar maple in southeastern Quebec.

Foliar K concentrations decreased from northwest to southeast along the gradient (Table 3) and were correlated with annual temperature and deposition of H, SO_4, and NO_3 in both mid-July foliage ($P < 0.01$) and litterfall ($P < 0.05$). Significant correlations ($P \leq 0.01$) also existed, however, between foliar K concentrations and exchangeable K in the Oe + Oa and soil B horizons. Regression analysis indicates that the best predictors of sugar maple foliar K in mid-July and leaf litter are exchangeable K contents in soil horizons (Table 4).

There were no regional trends in foliar Ca or Mg concentrations that could be related to pollutant deposition or climate. Calcium concentrations tended to be greatest at Sites 3 and 1, which have the highest reserves of soil exchangeable Ca (Table 2). Calcium concentrations in sugar maple leaf litter were correlated with exchangeable Ca in the Oe + Oa horizon ($P < 0.05$) and the sum of exchangeable Ca in the Oe + Oa and A + E horizons ($P < 0.05$). Magnesium concentrations were not significantly different among sites (Table 3) and were not correlated with soil exchangeable Mg. Liechty et al. (1993) compared throughfall and incident precipitation at the five sites and reported increased leaching of foliar Ca and Mg at the higher deposition sites (3, 4, and 5). This increase in foliar leaching, however, does not appear to have significantly impacted foliar Ca and Mg concentrations.

Although acidic deposition does not appear to have affected current foliar nutrient cation concentrations, its influence on soil cation leaching could potentially lead to long-term problems. MacDonald et al. (1992) documented increased leaching of soil Ca and Mg at the higher deposition sites, and noted that Ca leaching losses exceeded maximum estimated weathering rates at Sites 3, 4, and 5. Sites 4 and 5 have relatively low nutrient cation reserves and thus may be susceptible to long-term effects of acidic deposition on nutrient cation availability. Foliar concentrations presented in Table 3 provide a reference against which such possibilities can be assessed in the future.

Foliar Aluminum Concentrations

Sugar maple foliar Al concentrations were lowest at Site 1 and highest at Site 5 for both mid-July foliage and leaf litter (Table 3). Sugar maple foliar Al in both mid-July and leaf litter was positively correlated with total (wet plus dry) deposition of H and SO_4 and with mean annual temperature ($P < 0.05$), but was negatively and more strongly correlated with indices of soil exchangeable nutrient cations including: Ca, Mg, K, and the sum of these nutrient cations in the Oe + Oa horizon ($P < 0.01$); nutrient cation saturation in the A horizon ($P < 0.01$); and Ca, K, and the sum of nutrient cations in the soil B horizon ($P < 0.05$). Foliar Al concentrations were not correlated with soil exchangeable Al, but were weakly correlated ($P < 0.10$) with exchangeable Al percentage (ratio of exchangeable Al to the sum of exchangeable Ca, Mg, K, and Al, based on $mol_c\ ha^{-1}$) in both the A + E and B horizons.

Regression analysis suggests that observed foliar Al concentrations can be predicted by the combination of soil nutrient cation status and SO_4 deposition (Table 4). Sites 1 and 3, which have the highest exchangeable nutrient cation reserves (Table 2), had the lowest foliar Al concentrations. Of these two sites, Site 3, which receives a higher pollutant input, had slightly higher Al concentrations. Sites 2, 4, and 5 have lower nutrient cation reserves than Sites 1 and 3, and had higher levels of foliar Al. Site 5, which receives the greatest total pollutant deposition, had the highest foliar Al of these three sites. Chronic acidic inputs may have contributed to the low nutrient cations levels observed at Sites 4 and 5, but inherent soil properties (e.g., low clay content) appear to be the primary cause (MacDonald et al., 1991, 1992). Pollutant deposition can also affect Al availability by altering soil solution ionic strength (Reuss, 1983; Johnson and Taylor, 1989). Cation-exchange principles dictate that, as solution ionic strength increases, trivalent cations such as Al^{3+} increase in activity to the 3/2 power of divalent cations and to the third power of monovalent cations (Binkley et al., 1989; Reuss, 1983). This effect can occur without major changes in soil pH. Calcium saturation at Sites 2, 4, and 5 is within the range felt to be susceptible to such effects (Reuss, 1983), and MacDonald et al. (1992) have noted that the ionic strength of soil solutions at 15 cm increases from Site 1 to Site 5, evidently a consequence of acidic deposition. This increase in soil solution ionic strength should result in an increase in solution Al^{3+} across the gradient, and foliar Al in sugar maple seedlings has been shown to be positively correlated with solution monomeric Al in laboratory experiments (Thornton et al., 1986). Thus the positive relationship between acidic deposition and foliar Al along the gradient is consistent with the hypothesized effects of acidic deposition on soil solution Al.

When SO_4 deposition is replaced by mean annual temperature in the regressions for predicting foliar Al, predictive ability is essentially unchanged. Temperature could influence Al availability by impacting rates of soil chemical and biological processes, but measured soil variables probably account for variation in foliar Al related to both inherent soil properties and soil properties under climatic control. If this is the case, variability in foliar Al unexplained by soil variables would be attributable to SO_4 deposition rather than temperature effects.

Mid-July foliar Al at Site 5 exceeded the range of values observed in the literature (Table 3). Highest Al concentrations at Site 5 were observed in 1988 when the site mean was 75 mg kg^{-1} and concentrations in individual samples exceeded 90 mg kg^{-1}. Still, these concentrations do not appear to be cause for immediate concern as they are well below the foliar toxicity thresholds established by Thornton et al. (1986) for a 20% biomass reduction in sugar maple seedlings (137 mg kg^{-1} for newly expanded leaves and 338 mg kg^{-1} for older foliage). Symptoms of Al toxicity can include induced P deficiency in plant tops (Foy and Brown, 1964). High Al concentration and low P concentration at Site 5 are consistent with such a relationship and may indicate that the site is susceptible to Al-induced P deficiency if continually exposed to elevated acidic inputs.

As stated above, MacDonald et al. (1992) have measured increased leaching of soil Ca as deposition increases, which exceeds maximum estimated weathering rates at Sites 3, 4, and 5. Long-term acidic deposition at Sites 4 and 5, which have relatively low nutrient cation reserves, potentially could further deplete available Ca, increasing the ratio of exchangeable Al to exchangeable Ca. This conceivably could lead to higher solution Al concentrations, increased foliar Al levels, and possibly impaired Ca and Mg uptake (Thornton et al., 1986). Sites 1 and 3 have high soil nutrient cation reserves, and appear well buffered against the possible deleterious effects of long-term acidic deposition.

Boron, Copper, Iron, Manganese, and Zinc Concentrations

Mid-July foliar concentrations of B, Cu, Fe, Mn, and Zn were within the ranges reported in the literature for sugar maple foliage (Table 3). Boron concentrations are above the levels measured by Bernier and Brazeau (1988d) in B-deficient sugar maple regeneration (7–13 mg kg^{-1}) and mid-July overstory leaves (23 mg kg^{-1}). Specific threshold concentrations for deficiency and toxicity of Cu, Fe, Mn, and Zn in sugar maple foliage have not been determined, but the values measured at the five sites are above the critical values reported for foliage of trees and other plants (Leaf, 1973; Jones, 1972; Stone, 1968; Marschner, 1986; Chapman, 1966). Leaf litter concentrations of Zn, Fe, and Cu at some sites were below the range reported for sugar maple in the literature, but this is probably a consequence of the limited number of values reported for these elements. No geographic trends were apparent for sugar maple foliar Zn, Cu, and Mn concentrations in mid-July and litterfall or for B and Fe in mid-July (Table 3). Boron and Fe concentrations tended to increase from northwest to southeast in leaf litter. Foliar B concentrations were positively correlated with deposition of H, SO_4, and NO_3 in both mid-July ($P < 0.02$) and litterfall ($P < 0.01$), although a mechanism through which deposition might increase foliar B concentrations is not apparent.

As was the case for Al, sugar maple foliar Fe and Mn concentrations were negatively influenced by availability of nutrient cations in soil horizons. Mid-July foliar Mn and Fe were positively correlated ($P < 0.02$) with foliar Al, and were negatively correlated ($P < 0.03$) with exchangeable Ca in the Oe + Oa and A + E horizons and the sum of exchangeable Ca, Mg, and K in the Oe + Oa and A + E horizons. Mid-July foliar Mn concentrations were also positively correlated ($P < 0.01$) with nutrient cation saturation in the A horizon and negatively correlated ($P < 0.01$) with foliar Ca. Foliar Mn and Fe were not correlated with either pollutant deposition or annual temperature.

Nutrient Contents in Foliage and Litter

Nutrient contents in mid-July foliage and litterfall were influenced by both concentration and biomass. Foliar and litterfall biomass increase along the gradient from Site 1 to Site 5 (Table 1). This increase in biomass interacts with foliar nutrient concentrations to produce four general patterns of foliar nutrient content from northwest (Site 1) to southeast (Site 5) along the gradient (Table 5): (i) relatively constant concentration with foliar contents increasing as a result of increasing foliar biomass (N, Mg, and Cu); (ii) increasing concentration with increasing biomass to produce an enhanced increase in foliar nutrient content (S, Al, Fe, and B); (iii) decreasing concentration counteracting the biomass increase to produce relatively constant foliar nutrient contents (K and Zn); and (iv) differences in nutrient concentration great enough to mask the effect of differences in biomass, resulting in foliar nutrient contents that reflect foliar nu-

Table 5. Nutrient contents in July foliage and litterfall† from five northern hardwood forests.

Element	Material	Site 1	Site 2	Site 3	Site 4	Site 5
				kg ha^{-1}		
N‡	July foliage	79(4)bc§	74(3)c	85(4)bc	93(5)ab	99(8)a
	Leaf litter	28(1)b	27(2)b	34(2)ab	37(2)a	36(5)a
	Reproductive litter¶	17(0)a	18(2)a	17(3)a	17(3)a	11(1)b
	Total litter#	49(1)	48(4)	55(3)	57(4)	51(5)
S‡	July foliage	6.0(0.5)bc	5.6(0.2)c	6.8(0.3)b	7.8(0.4)a	8.2(0.4)a
	Leaf litter	3.1(0.1)c	3.0(0.1)c	4.2(0.3)b	4.4(0.2)b	5.0(0.2)a
	Reproductive litter	1.2(0.1)a	1.3(0.1)a	1.3(0.2)a	1.3(0.1)a	0.9(0.0)b
	Total litter	4.6(0.1)c	4.5(0.2)c	5.8(0.3)b	6.0(0.1)ab	6.4(0.3)a
P	July foliage	5.8(0.5)ab	5.1(0.3)b	4.8(0.2)b	6.5(0.5)a	5.5(0.4)ab
	Leaf litter	1.5(0.4)b	1.6(0.3)b	1.7(0.1)b	3.3(0.2)a	1.8(0.2)b
	Reproductive litter	1.3(0.2)a	1.5(0.3)a	1.1(0.3)ab	0.6(0.2)bc	0.5(0.1)c
	Total litter	3.2(0.6)b	3.4(0.5)b	3.5(0.3)b	4.9(0.1)a	3.0(0.3)b
Ca	July foliage	41(1)ab	34(3)b	47(6)a	43(3)ab	47(5)a
	Leaf litter	44(2)ab	42(4)b	58(7)a	48(6)ab	56(8)ab
	Reproductive litter	7(0)ab	8(1)a	8(2)a	7(1)ab	5(1)b
	Total litter	58(4)ab	56(5)b	74(6)a	61(5)ab	72(11)ab
Mg	July foliage	6.1(0.3)b	6.0(0.7)b	6.9(0.4)ab	6.9(0.6)b	8.8(1.2)a
	Leaf litter	4.9(0.7)ab	4.7(0.2)b	6.4(0.7)ab	5.1(0.5)ab	7.0(1.6)a
	Reproductive litter	1.0(0.1)a	1.1(0.1)a	1.1(0.2)a	0.9(0.1)ab	0.7(0.2)b
	Total litter	6.4(0.6)	6.1(0.3)	7.8(0.7)	6.3(0.4)	8.0(1.6)
K	July foliage	33(1)	30(2)	32(2)	35(3)	34(4)
	Leaf litter	12(2)	11(2)	13(1)	13(0)	14(3)
	Reproductive litter	4(1)ab	5(1)a	5(1)a	4(1)ab	3(1)b
	Total litter	18(3)	18(2)	19(1)	18(0)	18(2)
Al	July foliage	0.11(0.00)d	0.19(0.05)bc	0.15(0.01)c	0.20(0.02)b	0.29(0.01)a
	Leaf litter	0.18(0.01)c	0.28(0.02)b	0.21(0.02)bc	0.30(0.03)b	0.49(0.11)a
	Reproductive litter	0.06(0.00)ab	0.09(0.03)a	0.04(0.00)b	0.06(0.01)ab	0.06(0.01)ab
	Total litter	0.29(0.04)b	0.40(0.05)b	0.28(0.01)b	0.39(0.02)b	0.62(0.16)a
Fe	July foliage	0.22(0.00)c	0.31(0.06)ab	0.25(0.02)bc	0.29(0.01)ab	0.35(0.02)a
	Leaf litter	0.26(0.01)c	0.29(0.01)bc	0.26(0.03)c	0.33(0.02)b	0.45(0.04)a
	Reproductive litter	0.08(0.00)	0.10(0.03)	0.05(0.01)	0.07(0.02)	0.07(0.03)
	Total litter	0.39(0.11)bc	0.42(0.04)bc	0.34(0.03)c	0.44(0.02)b	0.59(0.05)a
Mn	July foliage	2.7(0.7)b	5.5(0.4)a	3.1(1.1)b	6.0(1.2)a	5.7(0.5)a
	Leaf litter	3.7(1.4)bc	5.1(0.6)ab	2.7(0.3)c	5.5(1.0)ab	6.3(0.8)a
	Reproductive litter	0.5(0.1)ab	0.8(0.2)a	0.4(0.0)b	0.6(0.2)ab	0.4(0.1)b
	Total litter	4.5(1.5)bc	6.2(0.8)ab	3.3(0.3)c	6.4(1.1)ab	7.1(0.6)a
B	July foliage	0.14(0.01)b	0.10(0.01)c	0.15(0.01)b	0.19(0.01)a	0.20(0.01)a
	Leaf litter	0.12(0.01)c	0.08(0.00)d	0.14(0.01)bc	0.16(0.01)ab	0.18(0.02)a
	Reproductive litter	0.02(0.00)	0.02(0.00)	0.02(0.00)	0.02(0.00)	0.01(0.00)
	Total litter	0.15(0.01)c	0.10(0.01)d	0.17(0.01)bc	0.19(0.01)ab	0.21(0.02)a
Zn	July foliage	0.15(0.04)	0.14(0.03)	0.11(0.02)	0.14(0.01)	0.17(0.05)
	Leaf litter	0.14(0.03)	0.14(0.01)	0.11(0.02)	0.13(0.01)	0.17(0.05)
	Reproductive litter	0.03(0.01)	0.04(0.01)	0.03(0.00)	0.03(0.00)	0.02(0.00)
	Total litter	0.21(0.04)	0.20(0.01)	0.15(0.01)	0.18(0.01)	0.22(0.06)
Cu	July foliage	0.018(0.005)	0.023(0.003)	0.022(0.004)	0.025(0.001)	0.022(0.002)
	Leaf litter	0.017(0.003)	0.019(0.001)	0.022(0.003)	0.023(0.002)	0.024(0.005)
	Reproductive litter	0.007(0.000)ab	0.009(0.000)a	0.008(0.001)a	0.008(0.001)a	0.005(0.001)b
	Total litter	0.026(0.003)	0.031(0.002)	0.034(0.002)	0.034(0.003)	0.032(0.004)

† Plot nutrient contents averaged across all years (1988–1990) were used to determine site means. Standard deviations (in parentheses) are for three plots per site.
‡ Nitrogen and S data are from Pregitzer et al. (1992).
§ Row means without common letters differ significantly at $P < 0.05$ (Tukey's HSD test).
¶ Reproductive litter contains minor amounts (<5%) of buds and bud scales.
# Woody litter accounts for the difference between total litter content and the sum of leaf and reproductive litter contents.

Table 6. Site retranslocation estimates for Ca, Mg, K, and P.

	Site 1	Site 2	Site 3	Site 4	Site 5
			kg ha^{-1}		
		Calcium			
Mid-July foliage	41.1	33.7	47.1	42.9	46.8
Leaf litter	43.5	42.2	58.4	48.4	56.2
Net forest water†	1.3	1.8	2.2	2.5	2.8
Retranslocation‡	−3.7	−10.3	−13.5	−8.0	−12.2
% retranslocation	−8.9	−30.5	−28.6	−18.7	−26.0
		Magnesium			
Mid-July foliage	6.1	6.0	6.9	6.9	8.8
Leaf litter	4.9	4.7	6.4	5.1	7.0
Net forest water	0.2	0.3	0.8	0.9	0.4
Retranslocation	0.9	1.1	−0.2	0.9	1.4
% retranslocation	15.3	18.1	−3.2	12.4	15.7
		Potassium			
Mid-July foliage	33.3	30.0	32.0	35.3	33.6
Leaf litter	12.3	11.1	12.5	12.6	13.6
Net forest water	6.0	4.6	6.4	6.9	4.3
Retranslocation	15.0	14.3	13.1	15.8	15.7
% retranslocation	44.9	47.7	40.9	44.7	46.6
		Phosphorus			
Mid-July foliage	5.8	5.1	4.8	6.5	5.5
Leaf litter	1.5	1.6	1.7	3.3	1.8
Net forest water	0.5	0.3	0.5	0.8	0.4
Retranslocation	3.8	3.1	2.6	2.5	3.3
% retranslocation	65.3	61.2	54.3	38.0	59.8

† Net forest water (NFW) is an estimate of foliar leaching losses occurring between the time of mid-July foliage sampling and leaf fall and was calculated as the difference in nutrient contents of throughfall and wet deposition during that period. Calcium, Mg and K in NFW were estimated using the data of Liechty et al. (1993). Data used to calculate P in NFW are from H.O. Liechty (1992, personal communication).
‡ Calculated as mid-July foliar content minus leaf litter content minus NFW content.

trient concentrations (P, Ca, and Mn). Nutrient contents in total litterfall follow the same patterns as leaf litter and mid-July foliage.

The increasing trend from Site 1 to Site 5 in foliar and litter biomass may be the result of increasing temperature and length of growing season, but also is consistent with the hypothesized effects of chronic N deposition (Pregitzer et al., 1992). Regardless of the cause, the trend is real and its effects should be addressed in attempts at modeling regional nutrient cycling and the effects of global change.

The rates for total litter return of N, S, P, Mg, K, Fe, Mn, and Cu for the five sites were within the range reported in the literature for other sugar maple forests (Morrison, 1985; Gosz et al., 1972). Return of Zn was lower than previously reported for sugar maple forests, while Ca return in litter at Sites 3 and 5 was higher than previously reported.

Reproductive parts and woody tissue contributed significantly to total nutrient return through litterfall, but the proportions varied greatly among nutrients. Averaged across all sites and years, reproductive parts accounted for large proportions of total litter content of P, N, K, Cu, and S (40, 31, 25, 24, and 22%, respectively); 14 to 17% of total litterfall Al, Fe, Mg, and Zn; and 10 to 11% of litter Ca, Mn, and B. Woody litterfall contributed 5 to 6% of total litterfall N, S, P, Mg, K, Mn, and B; and 10 to 12% of total litter return of Ca, Al, Fe, Zn, and Cu.

Nutrient return in reproductive litter varied greatly from year to year. For example, at Site 1 reproductive parts contributed 57% of litter N in 1989, but only 11% in 1990. Such variation could have significant impacts on stand-level nutrient requirements and productivity. Pregitzer and Burton (1991) noted that reproductive and foliar litter masses were negatively correlated for these sites, suggesting a direct trade-off between leaf biomass and reproductive biomass. Clearly, efforts at modeling the impacts of climate change and other stresses on northern hardwood ecosystems must account for the effects of reproductive effort. To do this, year-to-year variation in seed and flower production and the influence of stressing agents on reproductive effort will need to be assessed.

Retranslocation

Retranslocation, as defined here, primarily reflects net differences between foliar nutrient contents in mid-July and leaf litter. Calcium accumulated in foliage throughout the growing season at all sites, resulting in apparent negative values for retranslocation (Table 6). Such increases in foliar Ca during the growing season are commonly reported for sugar maple (Ryan and Bormann, 1982; Lea et al., 1979a; Mitchell, 1936). Calcium is relatively immobile in plants and accumulates due to its continual movement into foliage with the transpiration stream (Kramer and Kozlowski, 1979). Negative retranslocation for Ca reflects a net increase in foliar Ca between mid-July and leaf fall, but does not preclude the possibility that some Ca may be withdrawn prior to senescence.

Averaged across all sites, retranslocation of Mg, K, and P represented 15, 45, and 60% of mid-July foliar contents (Table 6). This compares with 62 and 43% retranslocation of N and S at the sites (Pregitzer et al., 1992). There were no regional trends in the proportions of Mg, K, and P retranslocated. Pregitzer et al. (1992) came to a similar conclusion regarding N retranslocation at these sites but found that a decreasing proportion of foliar S was retranslocated as S deposition increased. They concluded that increasing SO_4–S deposition resulted in a greater accumulation of excess foliar S, which was not retranslocated.

Two notable exceptions to the general levels of retranslocation (P at Site 4 and Mg at Site 3) appear to be related to differences in nutrient availability among sites. Higher P availability at Site 4, as evidenced by elevated foliar P concentrations (Table 3), probably caused the relatively low conservation of P at the site. Calcareous C horizons high in $CaCo_3$ and $MgCO_3$ at Site 3 result in soil solution Mg concentrations at 75 cm that are three to five times greater than at the other four sites (MacDonald et al., 1992). This could produce the observed net accumulation of foliar Mg from mid-July to litterfall at Site 3.

Estimates of P and Mg retranslocation for the five sites are in general agreement with reported values for northern hardwood stands of 64% P and 32% Mg by Morrison (1991) and 61% P and 4% Mg by Ryan and Bormann (1982). Our estimate of 45% K retranslocation is much higher than the 11% calculated by Ryan and Bormann (1982) but much lower than the 83% estimated by Morrison (1991). It should be noted that Morrison's estimate does not account for foliar leaching of K during the growing season, and therefore may overestimate K retranslocation.

Our retranslocation estimates do not take into account dry deposition or stemflow. The amounts of Ca and Mg in dry deposition for these sites and stemflow for northern hardwood stands (Shepard et al., 1989) are similar in magnitude, have opposite effects on calculated foliar leaching, and are small compared with site throughfall fluxes (<20%) and foliar nutrient contents (<8%). Therefore their effects on estimated foliar leaching and retranslocation of Ca and Mg were felt to be minor. Stemflow K, however, can represent a significant flux, up to 75% of that in wet deposition (Shepard et al., 1989). This could result in errors of up to 4 kg ha^{-1} in our estimates of foliar K leaching, reducing the average amount of K retranslocated from 45 to 33%.

Apparent retranslocation for Al, B, Cu, Fe, Mn, and Zn can be estimated from the difference in mid-July and leaf litter contents in Table 5. These estimates suggest that: (i) Al and Fe accumulate throughout the growing season, with the greatest accumulations occurring at Site 5; (ii) little (<10%) or no retranslocation occurs for Mn, Zn, and Cu; and (iii) about 15% of foliar B is retranslocated. These values may over- or underestimate actual retranslocation, depending on the effects of foliar leaching and canopy uptake.

CONCLUSIONS

Examination of foliar nutrient concentrations revealed no obvious nutrient deficiencies or toxicities at the five sites studied. Where differences existed among sites in nutrient concentrations, they could be predicted primarily from soil properties. Exceptions to this were foliar S, which was strongly related to SO_4 deposition, and foliar Al, which could be predicted by the combination of soil nutrient cation availability and SO_4 deposition. The increase in foliar Al at higher deposition sites is consistent with the hypothesized effects of acidic deposition on soil solution Al. Annual temperature covaries with SO_4 deposition along the gradient and could influence Al availability by impacting soil processes, but measured soil variables should account for such effects.

An increasing trend from northwest to southeast existed for mid-July foliage and litterfall contents of N, S, Mg, Al, Fe, B, and Cu. This was the result of an increase in the biomass of foliage and litterfall, combined in some cases (S, Al, Fe, and B) with increasing foliar nutrient concentrations. The trend should be accounted for when modeling regional nutrient cycling and the effects of global change on forest ecosystems. Reproductive effort and retranslocation also can significantly impact nutrient cycling in the region's northern hardwood forests, and should be considered in modeling efforts.

Northern hardwood forests at the five study sites currently appear healthy, exhibiting no signs of dieback, decline, or foliar nutrient deficiencies (J.A. Witter, 1992, personal communication). These forests and others in the Great Lakes region face a variety of stressing agents (e.g., chronic acidic deposition, climatic fluctuation, insect and disease outbreaks, and nutrient losses following harvest), all of which have the potential to alter forest health and nutrition. The results of this study provide a valuable baseline against which the nutritional status of the region's northern hardwood forests can be assessed in the future.

ACKNOWLEDGMENTS

This research was supported by funds provided by the Eastern Hardwoods Research Cooperative within the joint USEPA–USDA Forest Service Forest Response Program, the USDA Forest Service Northern Global Change Program, the Michigan Agricultural Experiment Station, the Michigan Department of Natural Resources, and the Michigan Energy and Resource Research Association. This paper has not been subject to peer review by these agencies and should not be construed to represent their policies. We extend our appreciation to Kathy Tschirhart, Charles Butler, Beth Jacqmain, Robert Vande Kopple, Hal Liechty, Jeff Lane, Margie Jaeger, Dan Oles, Noel Mullett, Sarah Hoffmann, and Lesley Loeffler for their help in sample collection and preparation.

REFERENCES

Bernier, B., and M. Brazeau. 1988a. Foliar nutrient status in relation to sugar maple dieback and decline in the Quebec Appalachians. Can. J. For. Res. 18:754–761.

Bernier, B., and M. Brazeau. 1988b. Nutrient deficiency symptoms associated with sugar maple dieback and decline in the Quebec Appalachians. Can. J. For. Res. 18:762–767.

Bernier, B., and M. Brazeau. 1988c. Magnesium deficiency symptoms associated with sugar maple dieback in a Lower Laurentians site in southeastern Quebec. Can. J. For. Res. 18:1265–1269.

Bernier, B., and M. Brazeau. 1988d. An occurrence of boron deficiency in the deciduous forest of the Quebec Appalachians and the St. Lawrence Lowlands. Can. J. For. Res. 18:1652–1655.

Bernier, B., D. Pare,and M. Brazeau. 1989. Natural stresses, nutrient imbalances and forest decline in southeastern Quebec. Water Air Soil Pollut. 48:239–250.

Binkley, D., C.T. Driscoll, H.L. Allen, P. Schoeneberger, and D. McAvoy. 1989. Acidic deposition and forest soils. Springer-Verlag, New York.

Bockheim, J.G., J.E. Leide, and L.E. Frelich. 1989. Red pine growth and chemical composition of foliage and forest floors across a precipitation–chemistry gradient in Wisconsin. Can. J. For. Res. 19:1543–1549.

Burton, A.J., K.S. Pregitzer, and D.D. Reed. 1991a. Leaf area and foliar biomass relationships in northern hardwood forests located along an 800 km acid deposition gradient. For. Sci. 37:1041–1059.

Burton, A.J., C.W. Ramm, D.D. Reed, and K.S. Pregitzer. 1991b. Use of multivariate methods in forest research site selection. Can. J. For. Res. 21:1573–1580.

Chandler, R.F., Jr. 1941. The amount and mineral nutrient content of freshly fallen leaf litter in the hardwood forests of central New York. J. Am. Soc. Agron. 33:859–871.

Chapman, H.D. 1966. Diagnostic criteria for plants and soils. Div. of Agric. Sci., Univ. of California, Berkeley.

David, M.B., D.F. Grigal, L.F. Ohmann, and G.Z. Gertner. 1988. Sulfur, carbon, and nitrogen relationships in forest soils across the northern Great Lakes as affected by atmospheric deposition and vegetation. Can. J. For . Res. 18:1386–1391.

Dewald, L.E., E.I. Sucoff, T. Ohno, and C.A. Buschena. 1990. Response of northern red oak (*Quercus rubra*) seedlings to soil solution aluminum. Can J. For. Res. 20:331–336.

Erdmann, G.G., T.R. Crow, and H.M. Rauscher. 1988. Foliar nutrient variation and sampling intensity for *Acer rubrum* trees. Can. J. For. Res. 18:134–139.

Erdmann, G.G., F.T. Metzger, and R.R. Oberg. 1979. Macronutrient deficiency symptoms in seedlings of four northern hardwoods. U.S. For. Serv. Gen. Tech. Rep.NC-53.

Foster, N.W. 1989. Acidic deposition: What is fact, what is speculation, what is needed? Water Air Soil Pollut. 48:299–306.

Foster, N.W., M.J. Mitchell, I.K. Morrison, and J.P. Shepard. 1992. Cycling of acid and base cations in deciduous stands of Huntington Forest, New York, and Turkey Lakes, Ontario. Can. J. for. Res. 22:167–174.

Foy, C.D., and J.C. Brown. 1964. Toxic factors in acid soils: II.

Differential aluminum tolerance of plant species. Soil Sci. Soc. Am. Proc. 28:27–32.

Gosz, J.R., G.E. Likens, and F.H. Bormann. 1972. Nutrient content of litter fall in the Hubbard Brook Forest. Oecologia 22:305–320.

Grier, C.C. 1988. Foliage loss due to snow, wind, and winter drying damage: Its effects on leaf biomass of some western conifers. Can. J. For. Res. 18:1097–1102.

Grigal, D.F., and L.F. Ohmann. 1989. Spatial patterns in elemental concentrations of the forest floor across the north central USA. J. Environ. Qual. 18:368–373.

Johnson, D.W., D.D. Richter, G.M. Lovett, and S.E. Lindberg. 1985. The effects of atmospheric deposition on potassium, calcium, and magnesium cycling in two deciduous forests. Can. J. For. Res. 15:773–782.

Johnson, D.W., and G.E. Taylor. 1989. Role of air pollution in forest decline in eastern North America. Water Air Soil Pollut. 48:21–43.

Jones, J.B. 1972. Plant tissue analysis for micronutrients. p. 319–346. *In* J.J. Mordvedt et al. (ed.) Micronutrients in agriculture — Zn Fe B Mo Cu Mn. SSSA, Madison, WI.

Jurik, T.W. 1986. Temporal and spatial patterns of specific leaf weight in successional northern hardwood tree species. Am. J. Bot. 73:1083–1092.

Kramer, P.J., and T.T. Kozlowski. 1979. Physiology of woody plants. Academic Press, New York.

Lea, R., W.C. Tierson, D.H. Bickelhaupt, and A.L. Leaf. 1979a. Stand treatment and sampling time of hardwood foliage. I. Macro-element analysis. Plant Soil 51:515–533.

Lea, R., W.C. Tierson, D.H. Bickelhaupt, and A.L. Leaf. 1979b. Stand treatment and sampling time of hardwood foliage. II. Micro-element analysis. Plant Soil 51:535–550.

Lea, R., W.C. Tierson, D.H. Bickelhaupt, and A.L. Leaf. 1980. Differential foliar responses of northern hardwoods to fertilization. Plant Soil 54:419–439.

Leaf, A.L. 1973. Plant analysis as an aid in fertilizing forests. p. 427–454. *In* L.M. Walsh and J.D. Beaton (ed.) Soil testing and plant analysis. (rev. ed.) SSSA, Madison, WI.

Liechty, H.O., G.D. Mroz, and D.D. Reed. 1993. Cation and anion fluxes in northern hardwood throughfall along an acidic deposition gradient. Can. J. For. Res. 23:457–467.

Likens, G.E., and F.H. Bormann. 1970. Chemical analyses of plant tissues from the Hubbard Brook ecosystem in New Hampshire. Yale Univ. School of For. Bull. 79.

MacDonald, N.W., A.J. Burton, M.F. Jurgensen, J.W. McLaughlin, and G.D. Mroz. 1991. Variation in forest soil properties along a Great Lakes air pollution gradient. Soil Sci. Soc. Am. J. 55:1709–1715.

MacDonald, N.W., A.J. Burton, H.O. Liechty, J.A. Witter, K.S. Pregitzer, G.D. Mroz, and D.D. Richter. 1992. Ion leaching in forest ecosystems along a Great Lakes air pollution gradient. J. Environ. Qual. 21:614–623.

MacDonald, N.W., J.A. Witter, A.J. Burton, K.S. Pregitzer, and D.D. Richter. 1993. Relationships among atmospheric deposition, throughfall, and soil properties in oak forest ecosystems. Can. J. For. Res. (in press).

Mader, D.L., and B.W. Thompson. 1969. Foliar and soil nutrients in relation to sugar maple decline. Soil Sci. Soc. Am. Proc. 33:794–800.

Marschner, H. 1986. Mineral nutrition of higher plants. Academic Press, London.

McLaughlin, D.L., S.N. Linzon, D.E. Dimma, and W.D. McIlveen. 1985. Sugar maple decline in Ontario. Ont. Ministry Environ. Rep. no. ARB-144–85-Phyto.

Mitchell, H.L. 1936. Trends in the nitrogen, phosphorus, potassium and calcium content of the levels of some forest trees during the growing season. Black Rock For. Pap. 1(6):30–44.

Morrison, I.K. 1985. Effects of crown position on foliar concentrations of 11 elements in *Acer saccharum* and *Betula alleghaniensis* trees on a till soil. Can. J. For. Res. 15:179–183.

Morrison, I.K. 1990. Organic matter and mineral distribution in an old-growth *Acer saccharum* forest near the northern limit of its range. Can. J. For. Res. 20:1332–1342.

Morrison, I.K. 1991. Addition of organic matter and elements to the forest floor of an old-growth *Acer saccharum* forest in the annual litter fall. Can. J. For. Res. 21:462–468.

National Atmospheric Deposition Program. 1985a. NADP annual data summary, precipitation chemistry of the United States, 1982. Nat. Resour. Ecol. Lab., Colorado State Univ., Fort Collins.

National Atmospheric Deposition Program. 1985b. NADP/NTN annual data summary, precipitation chemistry of the United States, 1983. Nat. Resour. Ecol. Lab., Colorado State Univ., Fort Collins.

National Atmospheric Deposition Program. 1986. NADP/NTN annual data summary, precipitation chemistry of the United States, 1984. Nat. Resour. Ecol. Lab., Colorado State Univ., Fort Collins.

National Atmospheric Deposition Program. 1987. NADP/NTN annual data summary, precipitation chemistry of the United States, 1985. Nat. Resour. Ecol. Lab., Colorado State Univ., Fort Collins.

National Oceanic and Atmospheric Administration. 1983. Climate normals for the U.S. (Base: 1951–1980) . Natl. Climatic Center, Environ. Data and Inf. Serv., Natl. Oceanic and Atmos. Admin., Gale Res. Co., Detroit.

Ohmann, L.F., and D.F. Grigal. 1990. Spatial and temporal patterns of sulfur and nitrogen in wood of trees across the north central United States. Can. J. For. Res. 20:508–513.

Ouyang, H. 1990. Effects of acid deposition on nitrogen mineralization in forest soils of the Great Lakes region. M.S. thesis. Michigan Technological Univ., Houghton.

Pare, D., and B. Bernier. 1989. Origin of the phosphorus deficiency observed in declining sugar maple stands in the Quebec Appalachians. Can. J. For. Res. 19:24–34.

Pletscher, D.H. 1982. White-tailed deer and nutrient cycling in the Hubbard Brook Experimental Forest, New Hampshire. Ph.D. diss. Yale Univ., New Haven, CT (Diss. Abstr. 83–10578).

Pregitzer, K.S., and A.J. Burton. 1991. Sugar maple seed production and nitrogen in litterfall. Can. J. For. Res. 21:1148–1153.

Pregitzer, K.S., A.J. Burton, G.D. Mroz, H.O. Liechty, and N.W. MacDonald. 1992. Foliar sulfur and nitrogen along an 800-km pollution gradient. Can. J. For. Res. 22:1761–1769.

Reed, D.D., G. Mroz, K. Pregitzer, and J. Witter. 1988. Site selection procedures in the Michigan gradient study. Ch. 2. *In* J.A. Witter (ed.) Effects of an air pollution gradient on northern hardwood forests in the northern Great Lakes region: 1988 Annu. Rep. Eastern Hardwoods Res. Cooperative. School of Natural Resources, Univ. of Michigan, Ann Arbor.

Reuss, J.O. 1983. Implications of the calcium–aluminum exchange system for the effect of acid precipitation on soils. J. Environ. Qual. 12:591–595.

Ryan, D.F., and F.H. Bormann. 1982. nutrient resorption in northern hardwood forests. BioScience 32:29–32.

Schwartz, S.E. 1989. Acid deposition: Unraveling a regional phenomenon. Science (Washington, DC) 243:753–763.

Shepard, J.P., M.J. Mitchell, T.J. Scott, Y.M. Zhang, and D.J. Raynal. 1989. Measurements of wet and dry deposition in a northern hardwood forest. Water Air Soil Pollut. 48:225–238.

Sirois, A., and R.J. Vet. 1988. Detailed analysis of sulphate and nitrate atmospheric deposition estimates at the Turkey Lakes Watershed. Can. J. Fish. Aquat. Sci. 45:14–25.

Stone, E.L. 1968. Microelement nutrition of forest trees: A review. p. 132–175. *In* Forest fertilization: theory and practice. Proc. Symp. TVA, USDA For. Serv., Univ. of Florida, Gainesville, FL. 18–21 Apr. 1967. TVA, Muscle Shoals, AL.

Technicon Industrial Systems. 1977. Individual/simultaneous determination of nitrogen and or phosphorous in BD acid digests. Technicon Industrial Method no. 334–74W/B. Technicon Ind. Syst., Tarrytown, NY.

Thornton, F.C., M. Schaedle, and D.J. Raynal. 1986. Effect of aluminum on the growth of sugar maple in solution culture. Can. J. For. Res. 16:892–896.

Tukey, H.B., Jr. 1980. Some effects in rain and mist on plants, with implications for acid precipitation. p. 141–150. *In* T.C. Hutchinson and M. Havas (ed.) Effects of acid precipitation on terrestrial ecosystems. Plenum Press, New York.

Ulrich, B., R. Mayer, and P.K. Khanna. 1980. Chemical changes due to acid precipitation in a loess-derived soil in central Europe. Soil Sci. 130:193–199.

Wall, L.L., C.W. Gehrke, and J. Suzuki. 1980. An automated turbidimetric method for total sulfur in plant tissue and sulfate sulfur in soils. Commun. Soil Sci. Plant Anal. 11:1087–1103.