

Leaf Area and Foliar Biomass Relationships in Northern Hardwood Forests Located Along an 800 km Acid Deposition Gradient

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ABSTRACT. The canopies of northern hardwood forests dominated by sugar maple (*Acer saccharum* Marsh.) were examined at five locations spanning 800 km along an acid deposition and climatic gradient in the Great Lakes region. Leaf area index (LAI) calculated from litterfall ranged from 6.0 to 8.0 in 1988, from 4.9 to 7.9 in 1989, and from 5.3 to 7.8 in 1990. The data suggest that maximum LAI for the sites is between 7 and 8. Insect defoliation and the allocation of assimilates to reproductive parts in large seed years reduced LAI by up to 34%. Allometric equations for leaf area and foliar biomass were not significantly different among sites. They predicted higher LAI values than were estimated from litterfall and could not account for the influences of defoliation and seed production. Canopy transmittance was a viable alternative for estimating LAI. Extinction coefficients (K) of 0.49 to 0.65 were appropriate for solar elevations of 63° to 41°. Patterns of specific leaf area (SLA) were similar for the sites. Average sugar maple SLA increased from 147 $\text{cm}^2 \text{ g}^{-1}$ in the upper 5 m of the canopy to 389 $\text{cm}^2 \text{ g}^{-1}$ in the seedling layer. Litterfall SLA averaged 196 $\text{cm}^2 \text{ g}^{-1}$ for all species and 192 $\text{cm}^2 \text{ g}^{-1}$ for sugar maple. Similarity among the sites in allometric relationships, maximum LAI, canopy transmittance, and patterns of SLA suggests these characteristics were controlled primarily by the similar nutrient and moisture availability at the sites. A general increasing trend in litter production along the gradient could not be attributed to N deposition or length of growing season due to year to year variability resulting from insect defoliation and seed production. *FOR. SCI.* 37(4):1041-1059.

ADDITIONAL KEY WORDS. Leaf area index, specific leaf area, *Acer saccharum*, canopy transmittance, N deposition.

TREE LEAF AREA REGULATES MANY FOREST PROCESSES, including gas exchange (Watts et al. 1976), canopy light interception (Running et al. 1989), evapotranspiration (Grier and Running 1977), and photosynthesis (Beadle et al. 1985, Running et al. 1989). Consequently, leaf area is related to stand productivity (Waring 1983, Oren et al. 1987) and is a crucial component in studies of regional and global phenomenon such as acid rain and global warming (Running et al. 1989).

Foliar biomass is closely correlated with leaf area and is related to many of the same processes. Leaf area is generally a preferred measure because the ratio of leaf surface area to mass (specific leaf area, SLA) varies seasonally and changes from the upper to the lower canopy (Borghetti et al. 1986, Jurik 1986). Estimates

of foliar biomass, however, are required in carbon allocation studies for determining the construction and maintenance costs of foliage (Chung and Barnes 1977, Kinerson et al. 1977). Similarly, in studies of nutrient cycling and retranslocation at the stand level, foliar biomass estimates are needed to convert foliar nutrient concentrations to contents (Ostman and Weaver 1982).

A common method of estimating a tree's leaf area or foliar biomass is through the use of allometric equations (Borghetti et al. 1986, Ruark et al. 1987, Long and Smith 1988). Stand leaf area, which is commonly expressed in terms of leaf area index (LAI, surface area of leaves per unit ground area) has also been estimated using direct harvests (Jurik et al. 1985), litter traps (Madgwick and Olson 1974), and measurements of canopy transmittance (Pierce and Running 1988).

Foliar area and biomass may be sensitive to stressing agents such as acid deposition. Waring (1985) suggested that reductions in canopy leaf area should accompany the chronic stress induced by air pollution. Aber et al. (1989) theorized that an initial response of forests to chronic nitrogen deposition would be a gradual increase in foliar biomass which would be followed ultimately by a decrease in foliar biomass as forest decline occurred. Changes in growth efficiency (the ratio of stem biomass increment to leaf area, Waring et al. 1980) have been associated with environmental stress. Waring and Pitman (1985) found that susceptibility to insect attack in lodgepole pine (*Pinus contorta* Dougl.) increased as growth efficiency decreased. Oren et al. (1988) measured higher growth efficiency in healthy Norway spruce (*Picea abies* [L.] Karst.), than in nearby declining spruce having an acid deposition-induced imbalance of nitrogen and magnesium.

Accurate estimates of leaf area are required if changes in leaf area or growth efficiency resulting from acid deposition are to be detected. Year to year variation in leaf area (Miller 1986) and reductions in leaf area resulting from stochastic events (Grier 1988) must be accounted for before the effects of air pollution can be determined.

In this study the canopies of sugar maple-dominated northern hardwood forests were examined at five locations spanning 800 km along an acid deposition gradient in the Great Lakes region. Objectives were: (1) to examine year to year variability in canopy leaf area and foliage production; (2) to identify the nonpollution factors that contribute to the yearly variability in leaf area; (3) to compare three methods of estimating LAI (allometric relationships, litter weights and canopy transmittance) for accuracy and ease of use; and (4) to determine if any clear relationships existed between acid deposition and canopy characteristics such as LAI, SLA, canopy transmittance of solar radiation, and allometric relationships. The work was part of an integrated study of the ecological effects of acid deposition on northern hardwood forests across a regional deposition gradient.

MATERIALS AND METHODS

STUDY SITES

Five northern hardwood study sites were located across an acid deposition gradient extending from southern Michigan to northeastern Minnesota. A pronounced $\text{NO}_3\text{-N}$ deposition gradient exists across the region (Figure 1). Similar gradients occur for H^+ and $\text{SO}_4\text{-S}$.

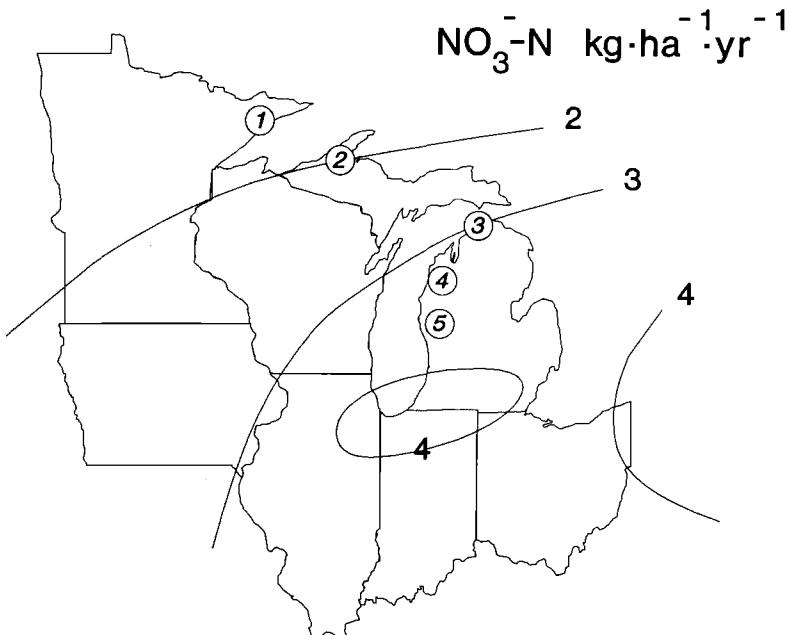


FIGURE 1. Locations of study sites (circled) in relation to a regional deposition gradient of $\text{NO}_3^- \cdot \text{N}$. Wet deposition data summarized from National Atmospheric Deposition Program records for 1980 thru 1984.

All sites were situated on sandy, well-drained soils in second-growth northern hardwood stands dominated by sugar maple (*Acer saccharum* Marsh.). Selection criteria ensured that sites were similar in age, basal area, species composition, soils, physiography and stand structure (Table 1) (Reed et al. 1988). The sandy, spodosol soils on which the sites were located are typical of a major portion of the 5.3 million ha of northern hardwoods in the Lake States. For example, the Kalkaska soil series (sandy, mixed, frigid, Typic Haplorthod) and Blue Lake soil series (sandy, mixed, frigid, Alfic Haplorthod), which are common on the study sites, occupy over 300,000 ha in a 20 county area of the northern lower peninsula of Michigan. The sites are fairly similar in mean yearly precipitation, although mean annual temperature and length of growing season do increase from north to south across the region (Table 1). The ecosystem studied is the most common type of northern hardwood forest occurring in Michigan (David Cleland, personal communication).

The overall area encompassed by each site was 5 to 6 ha. Within this area were three permanent 30 m by 30 m measurement plots on which no destructive sampling was permitted. Trees felled for the allometric portion of the study were located in the area bordering these permanent plots. Litter traps and light measurement points were located within the 30 × 30 m measurement plots.

ALLOMETRIC METHODS

Trees used in developing allometric equations for leaf area and foliar biomass were felled during July 1988. Eight sugar maple trees were sampled at each site—two

TABLE 1.
Selected site characteristics of five northern hardwood forests in the Great Lakes region.

	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'
Basal area ($m^2 \text{ ha}^{-1}$)	31 (0.8) ^a	32 (0.5)	30 (1.2)	30 (2.8)	30 (2.0)
Sugar maple basal area (%)	90 (7)	86 (7)	86 (8)	83 (5)	75 (13)
Canopy height (m)	20 (1)	24 (1)	27 (1)	28 (1)	24 (1)
Overshoot age (years)	78 (13)	79 (15)	73 (6)	74 (11)	78 (5)
Mean annual precipitation ^b (mm)	670	870	830	810	850
Mean annual temperature ^b (°C)	3.7	4.3	5.2	5.8	7.6
Growing degree days ^c (>5.6°C)	1319	1528	1736	1944	2083
Soil great group	Haplorthod/Fragiorthod	Haplorthod	Haplorthod	Haplorthod	Haplorthod

^a Mean \pm (standard deviation).

^b 30-year means for the nearest NOAA station (NOAA 1983).

^c Phillips and McCulloch 1972.

from each of four diameter classes: 5.0 to 9.9 cm; 10.0 to 19.9 cm; 20.0 to 29.9 cm; and 30 cm and larger. The two trees felled from each diameter class were randomly chosen from a preselected group of 10 trees per class located at each site. Diameter at breast height (dbh) was recorded for each tree felled.

A stem cross-section was taken from the base of the live crown of each tree (15 cm below the first major fork or branch) and returned to the lab for determination of sapwood area. Sapwood was distinguished by using a heat gun to dry moist stem sections (Keith 1977). The surface of the nonconducting heartwood dried faster, allowing it to be distinguished from the moister sapwood. Diameter inside bark and heartwood diameter were measured on the major and minor axes of each stem cross section. Total stem area and heartwood area were calculated using the geometric mean of their respective major and minor diameters. Sapwood area was determined by subtracting heartwood area from total stem area.

The canopy of each tree felled was divided into four zones for foliage sampling: Zone A—the top 5 m of the canopy facing north; Zone B—the top 5 m of the canopy facing south; Zone C—5 to 10 m beneath the top of the canopy; and Zone D—more than 10 m beneath the top of the canopy. Site canopy heights were estimated as the average height of dominant trees on the three plots at a site, measured with clinometers during fall 1987 (Table 1). Branch basal diameter (measured at 5 cm) and canopy zone were recorded for every branch on sampled trees. Four branches from each zone on each tree were then randomly selected for foliage sampling. All leaves from each of these branches were removed and counted, with 50 leaves from each zone on each tree returned on ice to the laboratory for determination of leaf area and weight. Leaf areas (one side) were determined using a Delta-T area meter. Leaf weights were measured after drying at 70°C for 48 hours. Values of SLA for each canopy zone were compared among sites using analysis of variance (ANOVA). Specific leaf area was also determined for samples of 100 leaves from seedlings (height < 0.5 m) and saplings (dbh < 5 cm, height > 0.5 m) at each site. These samples provided estimates of SLA at the lowest light levels existing at the sites.

Regression equations relating the number of leaves on a branch to branch basal diameter were developed for each zone at each site. Regressions took the form:

$$\ln Y = \ln a + b \ln X \quad (1)$$

Leaf number was the dependent variable (Y) and branch diameter the independent variable (X). Total leaf area (or biomass) for each sample tree was calculated by using the regression equations to estimate the number of leaves on each branch, multiplying each branch's leaf number by the average area (or weight) per leaf for the appropriate zone and tree, and summing for all branches on the tree. Regression estimates of branch leaf number were corrected for logarithmic bias using Sprugel's (1983) method.

Equations developed for predicting total tree leaf area (or biomass) included constant allometric ratio (CAR) equations in the form of Equation (1), and variable allometric ratio (VAR) equations (Ruark et al. 1987) in the form:

$$\ln Y = \ln a + b \ln X + c X \quad (2)$$

Regressions were estimated using dbh and sapwood area at the base of the live crown as the independent variable (X). Tree leaf area and foliar biomass were

each used as the dependent variable (Y). Slopes and intercepts of allometric equations were compared among sites using the method outlined by Zar (1984).

LEAF AREA INDEX

Leaf area indices for the five sites were calculated for 1988, 1989, and 1990 using allometric equations. The variable allometric (VAR) equation presented in this paper was used for sugar maple, which represented a majority of the LAI at each site. An equation for red maple (*Acer rubrum* L.) leaf area was developed using the methods outlined above for sugar maple, but using four trees per site for the three sites where it occurred (Witter et al. 1989). Relationships from the literature were used for oak (*Quercus* spp.) (Whittaker and Woodwell 1967); paper birch (*Betula papyrifera* Marsh.) (Jokela et al. 1980); American beech (*Fagus grandifolia* Ehrh.) (Whittaker et al. 1974); yellow birch (*Betula alleghaniensis* Britt.) (ibid.); and other hardwoods (ibid.). These other species represented from 9 to 14% of basal area at the sites. The equation for paper birch predicted foliar biomass, which was converted to leaf area using a SLA of $134 \text{ cm}^2 \text{ g}^{-1}$, which was measured on foliage samples collected in July 1988. Values for dbh used in the allometric equations for a given year were measured in November of the previous year at permanent marks on each tree. Leaf areas calculated for individual trees using the allometric equations were summed to estimate plot LAIs. Estimates of allometric LAI adjusted for insect defoliation were also made. Visible defoliation was estimated for each tree on the $30 \times 30 \text{ m}$ plots in late July of each year. Individual tree leaf areas from the allometric equations were then adjusted for defoliation using the estimates.

Eight 0.5 m^2 litter traps on each plot (24 per site) were used in determining LAI by the litterfall method. Material was collected from the traps on a monthly basis during the growing season and weekly in the fall, during the time of heaviest litter fall. Litter was sorted into leaves (by species), wood, and other material (primarily reproductive parts). Litter from one-half of one trap on each plot was returned in fresh condition to the lab where leaf area (one side) was measured, after which samples were dried and weighed so that SLA of the litter could be determined. All other litter was dried, sorted, and weighed. Litterfall LAIs were calculated by multiplying a species litter weight by its SLA and summing over all species at the site.

Canopy transmittance was used to determine LAI using a method similar to that outlined by Pierce and Running (1988). A "Sunfleck Ceptometer" (model SF-80, Decagon Devices, Incorporated) was used to measure photosynthetically active radiation (PAR, 400–700 nm) at 36 points within each plot (108 per site). Sampling points were located 5 m apart in a 25 m by 25 m square grid centered in each plot. At each sampling point eight measurements of PAR were made by holding the ceptometer horizontally and sampling a 360° circle in 45° increments. The average of the eight measurements was then stored in the ceptometer's memory. Measurements of total incoming PAR were made in openings near the sites before and after measuring each plot. Average canopy transmittance was converted to LAI using the Beer-Lambert Law:

$$\text{LAI} = -\ln(Q_t/Q_o)/K \quad (3)$$

where Q_t/Q_o is the ratio of PAR below the canopy to total incoming PAR, and K

is the light extinction coefficient. The Beer-Lambert Law assumes random foliage distribution in space (Jarvis and Leverenz 1983). A K value of 0.52 was used for initial calculations of LAI by the transmittance method. This value was found to be appropriate for use with the ceptometer when measuring LAI for conifer canopies (Pierce and Running 1988), and is within the range of K values presented for broadleaved canopies by Jarvis and Leverenz (1983). Canopy transmittance was measured near noon local solar time at sites 1, 3, and 4 on clear, cloudless days between September 10 and 19, 1989; and at all sites between July 24 and August 9, 1990. Additional readings at two lower solar angles were taken for sites 3 and 4 in 1989 so the effect of solar elevation on K could be examined.

RESULTS AND DISCUSSION

ALLOMETRIC RELATIONSHIPS

Regression slopes and intercepts for predicting leaf area and biomass were not significantly different among the five sites (Figure 2). This is not entirely unexpected considering the similarity of the sites in age, species composition, and soil characteristics. Confidence intervals for our equations were rather wide (Figure 2); thus it cannot be concluded that no important differences exist. However, it does appear that common equations can be applied to comparable sites located throughout the region. For red maple in the same geographical region as our study, Crow (1983) found that allometric equations for predicting foliar biomass did not differ among six stands with varying age and site index. In contrast, equations for predicting foliar area in lodgepole pine on southeastern Wyoming sites that differed greatly in precipitation and soil water storage capacity were only local in application (Long and Smith 1988). Caution should always be used in applying predictive equations to sites which differ from those used in developing the relationship.

Since the individual site equations were not significantly different, data from all sites were pooled and common regressions were estimated. The best predictor for both leaf area and foliar biomass was dbh (Table 2). Equations using a variable allometric ratio (VAR) performed better than those using a constant allometric ratio (CAR). This conclusion is based in part on a slight improvement in the coefficients of determination (Table 2); the partial F statistics for parameter c of the VAR equations suggest that it is important ($P < 0.10$ for both area and biomass). Geron and Ruark (1988) used dbh to estimate foliar biomass and found that VAR equations explained significant additional variation over CAR equations for three of six species studied. They attributed a declining allometric ratio (proportional growth rate of foliage to proportional growth rate of dbh) in aspen (*Populus tremuloides* Michx.) to self-pruning.

The VAR equations for sugar maple predicted lower leaf area and biomass than the CAR equations for both small (< 10 cm dbh) and large (> 30 cm dbh) trees (Figure 3). This is probably a realistic representation of what is occurring at the sites. During visual vigor rating of all measurement plot trees at each site, J.A. Witter (unpublished) found the small diameter trees to have the lowest vigor and highest mortality rates. These suppressed trees would have difficulty in obtaining resources (light, nutrients, water) and therefore might have lower average leaf

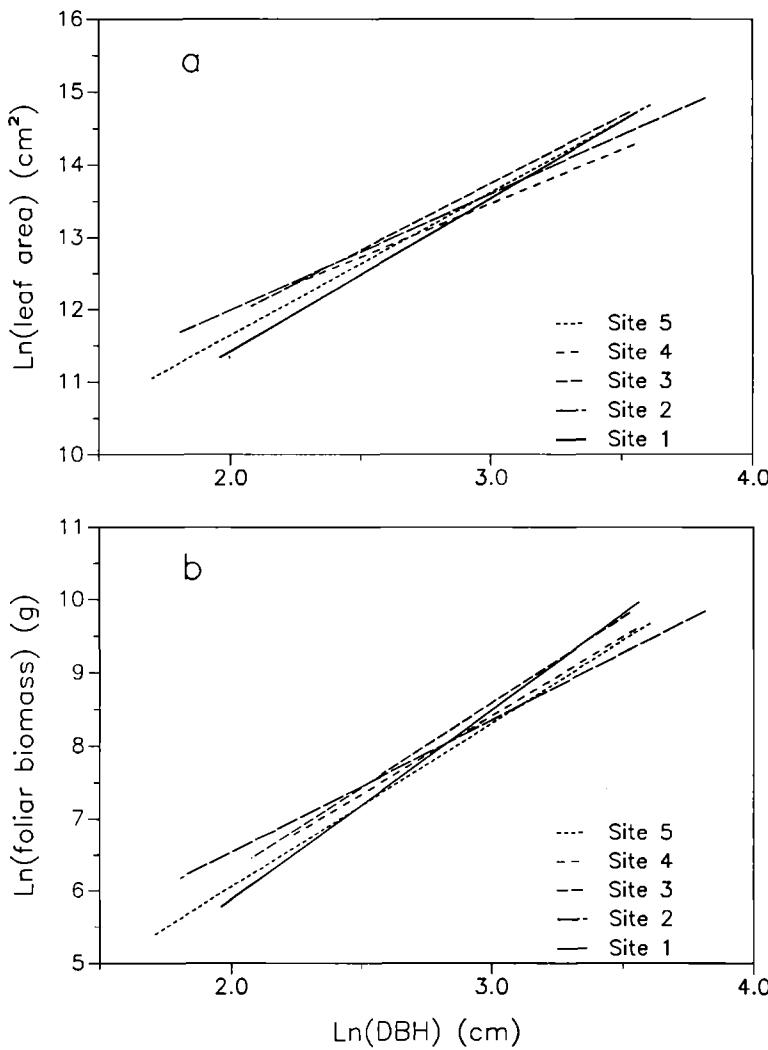


FIGURE 2. Individual site regressions (CAR) of leaf area (a) and foliar biomass (b) versus dbh.

area and biomass than the CAR equations predict. The large trees sampled (>30 cm dbh) included the oldest trees at the study sites. Leaf area and foliar biomass for trees in this diameter class were highly variable, suggesting that trees in the class varied greatly in relative health and vigor. Other studies have also found trees of large diameter to vary widely in foliar area (Marshall and Waring 1986). Although sugar maple is extremely shade-tolerant, self-pruning in these oldest trees has also likely contributed to the declining allometric ratio.

The CAR and VAR equations both predict greater leaf areas for a given diameter than does the equation of Whittaker et al. (1974), which was developed for sugar maple at Hubbard Brook, New Hampshire. The differences are less for large trees, which contain a majority of stand leaf area at our sites and at Hubbard Brook. For example, leaf areas calculated using the equation of Whittaker et al. were 36% lower than those predicted by the VAR equation for 10 cm dbh, but

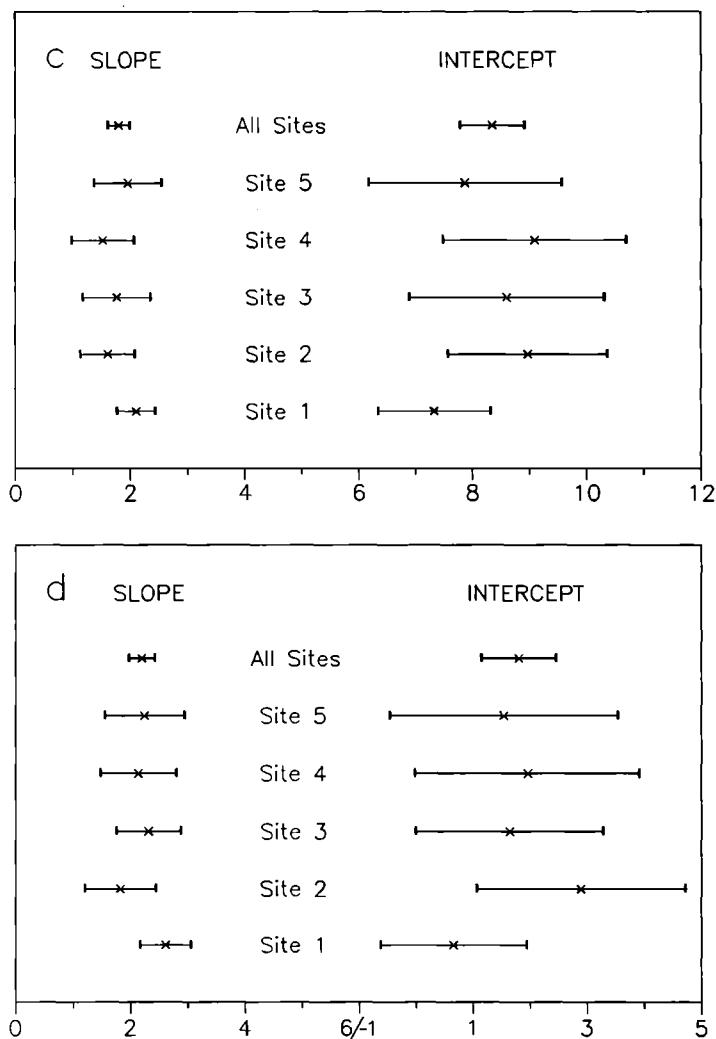


FIGURE 2 (cont.). 95% confidence intervals for slopes and intercepts of regressions (CAR) for leaf area (c) and foliar biomass (d).

only 5% lower at 40 cm dbh. The CAR and VAR equations for sugar maple foliar biomass predict values which are nearly identical to those produced by the equation of Pastor and Bockheim (1981) which was developed for an aspen-mixed hardwood ecosystem in northern Wisconsin. The soils at their study site were quite similar to those of this study.

Sapwood area at the base of the live crown did not predict sugar maple leaf area and biomass as well as dbh (Table 2). Many investigators have reported that sapwood area was a better predictor of leaf area than dbh in conifers (Kendall Snell and Brown 1978, Marshall and Waring 1986). This has been explained in terms of sapwood transport of water and nutrients to foliage. Still, several other studies have found dbh to be comparable to or better than sapwood area in predictive ability of conifer foliar area and biomass (Borghetti et al. 1986, Espinosa Bancalari et al. 1987). Differences in water-conducting ability in the sapwood of slow-

TABLE 2.
Parameter estimates of allometric equations for predicting sugar maple leaf area and foliar biomass.

Dependent variable	Independent variable	$\ln a$	b	c	F^a	R^2	E^b	CF^c
Area (cm^2)	dbh (CAR)	8.343	1.799			0.904	1.413	1.062
	dbh (VAR)	7.130	2.507	-0.040	0.057	0.913	1.396	1.057
	SABL C^d	11.082	0.791			0.848	1.547	1.100
Biomass (g)	dbh (CAR)	1.805	2.205			0.913	1.496	1.085
	dbh (VAR)	0.514	2.959	-0.042	0.083	0.920	1.480	1.080
	SABL C	5.125	0.981			0.877	1.613	1.121

Note: Constant allometric ratio (CAR): $\ln Y = \ln a + b \ln X$

Variable allometric ratio (VAR): $\ln Y = \ln a + b \ln X + c X$

^a Partial F statistic on parameter c of the VAR.

^b Estimate of relative error of regression, the antilog of the standard error of regression (Whittaker and Woodwell 1968).

^c Correction factor for bias of logarithmic equations (Sprugel 1983).

^d Sapwood area at the base of the live crown.

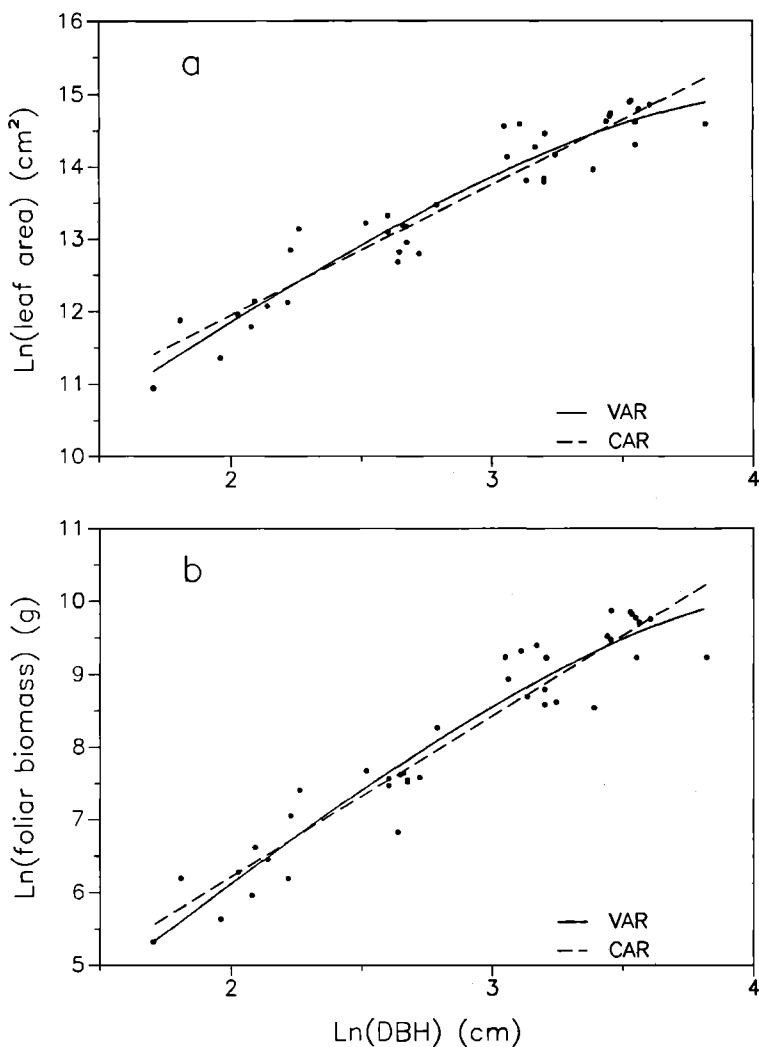


FIGURE 3. Comparison of CAR and VAR equations for predicting sugar maple leaf area (a) and foliar biomass (b) from dbh.

growing and fast-growing trees have been suggested as an explanation for the inability of sapwood area to consistently predict leaf area more accurately than dbh in studies of stands which differ in growth rate (Whitehead et al. 1984, Espinosa Bancalari et al. 1987). In sugar maple, the number of sapwood rings involved in water transport varies, and the effectiveness of older sapwood is often reduced by blocked vessels (Kramer 1983). This, along with difficulty in accurately delineating sapwood in the diffuse-porous sugar maple stem sections, certainly influenced the performance of sapwood area as a predictor. Were it possible to make accurate measurements of both sapwood permeability and the actual conducting area, better relationships may have been developed.

SPECIFIC LEAF AREA

Patterns of SLA were similar among the five sites during July 1988. Values of SLA increased from an average of $147 \text{ cm}^2 \text{ g}^{-1}$ at the top of the canopy (zones A and

B) to an average of $284 \text{ cm}^2 \text{ g}^{-1}$ in the lower canopy (zone D), and $389 \text{ cm}^2 \text{ g}^{-1}$ for seedlings (Table 3). The values of SLA given for sugar maple shade and sun leaves by Jurik (1986) are essentially the same as those we found for seedlings/saplings and the upper canopy (zones A and B), respectively. There were no significant differences in SLA among the sites for zones A, B, and D. In zone C, the mean values for SLA at sites 3 and 4 were significantly lower than those for sites 2 and 5 (Table 3). These zone C differences evidently are a result of differences in the amount of foliage existing above that zone. At sites 3 and 4 a few very tall trees appear to have influenced the canopy height upon which sampling was based. The amount of foliage actually existing above the zone C sampling height was lower for these sites, allowing more light to reach the zone, resulting in lower SLA within the zone.

Average values of litterfall SLA across all sites in 1989 were $199 \text{ cm}^2 \text{ g}^{-1}$ for sugar maple and $193 \text{ cm}^2 \text{ g}^{-1}$ for all species combined; 1990 values for sugar maple and all species, respectively, were 194 and $189 \text{ cm}^2 \text{ g}^{-1}$. The values for SLA presented in Table 3 are similar to the values of 167 and $200 \text{ cm}^2 \text{ g}^{-1}$ used by Jurik et al. (1985) to estimate LAI for young successional hardwood stands in northern lower Michigan dominated by red maple, northern red oak (*Quercus rubra* L.), and bigtooth aspen (*Populus grandidentata* Michx.). The mean SLA values for litter from site 1 in 1989 and site 2 in 1990 were significantly higher than those for the other four sites. The reasons for this are not clear. Possible explanations include greater retranslocation at these sites, which are near the northern extreme of sugar maple's range, and altered allocation of assimilates to foliage following the prolific seed production at these two sites in 1989 (Table 4). The lower litterfall SLAs for site 3 in 1990 were a consequence of defoliation (Table 4). Preferential defoliation of less dense, interveinal portions of leaves resulted in significantly lower litterfall SLA (Table 3).

TABLE 3.
Specific leaf area means and (standard deviations) for the five sites.^a

	Site 1	Site 2	Site 3	Site 4	Site 5
Sugar maple foliage SLA ($\text{cm}^2 \text{ g}^{-1}$), July 1988					
Zone A (top 5 m, north facing)	134 (13)	161 (17)	131 (22)	131 (16)	162 (34)
Zone B (top 5 m, south facing)	132 (23)	172 (46)	147 (15)	136 (22)	162 (19)
Zone C (5–10 m below canopy top)	189 (41)ab	229 (49)a	170 (22)b	154 (25)b	229 (44)a
Zone D (>10 m below canopy top)	275 (34)	319 (63)	261 (45)	266 (66)	303 (30)
Saplings	346	438	365	372	356
Seedlings	377	427	380	398	366
Litterfall SLA ($\text{cm}^2 \text{ g}^{-1}$)					
Sugar maple, 1989	233 (17)a	185 (17)b	196 (3)b	188 (9)b	194 (9)b
All species, 1989	229 (16)a	178 (17)b	196 (6)b	174 (12)b	191 (8)b
Sugar maple, 1990	201 (14)b	222 (7)a	164 (7)c	190 (9)b	191 (7)b
All species, 1990	199 (14)ab	214 (5)a	165 (5)c	181 (6)b	188 (3)b

^a Values in the same row followed by a different letter are significantly different at the 0.05 level of significance (Fisher's LSD).

TABLE 4.

Levels of defoliation, foliar litter production, and production of reproductive parts for the five sites. Values are the mean (standard deviation) for three plots per site.

		Site 1	Site 2	Site 3	Site 4	Site 5
1988	Defoliation ^a (%)	30.1 (8.0)	0.1 (0.2)	0.2 (0.3)	5.7 (3.5)	0.4 (0.7)
	Foliar litter (kg ha ⁻¹)	3133 (73)	3823 (153)	4095 (236)	3418 (148)	3895 (385)
	Reproductive litter ^b (kg ha ⁻¹)	357 (55)	306 (62)	779 (36)	1202 (127)	785 (145)
1989	Defoliation (%)	2.4 (1.4)	0.7 (0.8)	0.7 (0.9)	6.7 (3.3)	0.1 (0.2)
	Foliar litter (kg ha ⁻¹)	2561 (250)	2754 (59)	3583 (212)	4068 (357)	4225 (412)
	Reproductive litter (kg ha ⁻¹)	1377 (73)	1617 (137)	1161 (302)	602 (158)	621 (115)
1990	Defoliation (%)	0.0 (0.0)	0.4 (0.4)	21.9 (1.9)	0.5 (0.6)	0.0 (0.0)
	Foliar litter (kg ha ⁻¹)	3703 (223)	3140 (118)	3148 (357)	4371 (434)	4115 (211)
	Reproductive litter (kg ha ⁻¹)	226 (77)	294 (61)	222 (23)	422 (255)	298 (56)

^a Based on average visible defoliation per tree in excess of background levels in late July.

^b Primarily seeds and flower parts.

The ratio of litterfall SLA to weighted mean July SLA averaged 1.14 across all sites. This value could be used to estimate summer foliar biomass from litterfall biomass for northern hardwood sites similar to those studied here.

LEAF AREA INDEX

Values of LAI (one-sided) calculated from litterfall ranged from 6.0 to 8.0 in 1988, from 4.9 to 7.9 in 1989, and from 5.3 to 7.8 in 1990 (Table 5). The data suggest that maximum LAI for these stands is between 7 and 8. Large seed years occurred at sites 1 and 2 in 1989 (Table 4), and this evidently reduced the allocation of assimilates to foliage, resulting in lower foliar biomass and leaf area for these two sites in 1989 (Tables 4 and 5). A similar effect occurred to a lesser degree for site 4 in 1988. Defoliation (Table 4) caused a reduction in litterfall LAI for site 3 in 1990 and also may have contributed to the lower LAI for site 4 in 1988 (Table 5). No consistent trends in LAI from north to south across the gradient which might be related to acid deposition or climate are evident. There appears to be a general increasing trend across the gradient in total litter production (foliage plus reproductive) over the 3-year record (Table 4). Such an increase is consistent with the predicted effects of chronic N deposition on forests (Aber et al. 1989). However, attribution of this trend to the effects of acid deposition or climate is prevented by the lack of a consistent pattern from year to year and the unknown residual effects of defoliation and seed production on litter production in subsequent years. In addition, the sites have not experienced the same levels of defoliation and seed production over the 3 years of record (Table 4).

TABLE 5.
Leaf area indices for the five sites. Values are the mean (standard deviation) for three plots per site.^a

Year	Method	Site 1	Site 2	Site 3	Site 4	Site 5
1988	Litterfall	7.4 (0.7)ab	6.9 (0.3)b	8.0 (0.3)a	6.0 (0.6)c	7.3 (0.3)ab
	Allometric (uncorrected) ^b	8.5 (0.4)	8.4 (0.9)	8.8 (0.6)	9.1 (0.7)	8.6 (0.3)
	Allometric (corrected) ^c	6.0 (0.5)b	8.4 (0.8)a	8.7 (0.6)a	8.4 (0.7)a	8.5 (0.3)a
1989	Litterfall	5.9 (1.0)bc	4.9 (0.3)c	7.0 (0.5)ab	7.1 (0.9)ab	7.9 (0.3)a
	Allometric (uncorrected)	8.6 (0.3)	8.4 (0.9)	8.8 (0.6)	9.2 (0.6)	8.6 (0.3)
	Allometric (corrected)	8.2 (0.2)	8.4 (0.8)	8.7 (0.7)	8.4 (0.6)	8.6 (0.4)
1990	PAR transmittance ^d	6.3 (0.2)b		8.3 (0.9)a	8.3 (0.7)a	
	Litterfall	7.3 (0.9)a	6.7 (0.2)a	5.3 (0.8)b	7.8 (0.5)a	7.7 (0.4)a
	Allometric (uncorrected)	8.7 (0.4)	8.5 (0.9)	8.8 (0.6)	9.2 (0.6)	8.6 (0.3)
	Allometric (corrected)	8.7 (0.4)a	8.5 (0.9)a	6.6 (0.4)b	9.1 (0.6)a	8.6 (0.3)a
	PAR transmittance ^d	7.2 (0.3)a	7.0 (0.2)a	4.8 (0.2)b	7.4 (0.7)a	7.1 (0.3)a
	PAR transmittance ^e	7.4 (0.3)a	7.4 (0.2)a	5.0 (0.2)b	7.7 (0.7)a	7.5 (0.3)a

^a Values in the same row followed by a different letter are significantly different at the 0.05 level of significance (Fisher's LSD).

^b Not corrected for defoliation.

^c Corrected for defoliation using visual estimates of defoliation made on an individual tree basis.

^d Calculated using $K = 0.52$.

^e Calculated using $K(\sin \theta) = 0.437$.

Values of LAI based on allometric equations were higher than those calculated from litterfall, ranging from 8.4 to 9.1 in 1988, from 8.4 to 9.2 in 1989, and from 8.5 to 9.2 in 1990 (Table 5). When visual estimates of defoliation were used to correct LAIs, estimates were still high, ranging from 6.0 to 8.7 in 1988, from 8.2 to 8.7 in 1989, and from 6.6 to 9.1 in 1990 (Table 5). This may indicate that the average health of trees at the sites was less than that of the sample trees. The ocular estimates of defoliation also did not adequately account for the defoliation occurring at sites 1 and 4 in 1988. Potential sources of error associated with the one-time visual defoliation estimates include biased estimates by field personnel, defoliation occurring after estimates were made in late July, and refoliation occurring after estimates were made. This last effect may account for the relatively high LAI at site 1 in 1988 (Table 5) despite the moderate defoliation that occurred at the site (Table 4). The equations, which are based on July 1988 conditions, also could not account for the effect on LAI of the large seed years which occurred at sites 1 and 2 in 1989. Allometric relationships are only applicable to sites with conditions similar to those existing at the time of sampling for equation development.

Leaf area indices for these mature northern hardwood stands are higher than those reported for most other deciduous canopies in the region. Jurik et al. (1985) measured LAIs of 1.4 to 3.6 for successional hardwoods in Michigan that were 12 to 30 years in age and 3 to 10 m in height. Crow (1978) reported LAIs of 4.9 to 5.5 for aspen-hardwood forests in northern Wisconsin. The stands he measured were 14.4 to 14.7 m in height and had basal areas of 17 to 18 $m^2 ha^{-1}$. The higher LAIs for our sites appear to be a consequence of dominance by shade-tolerant sugar maple combined with a higher degree of site occupation in the 75-year-old stands (basal areas of 30 to 32 $m^2 ha^{-1}$, height of 20 to 28 m). Better site quality at our sites also likely contributed to the higher LAIs. The LAIs we measured are similar to the range of 6.5 to 7.4 reported by Aber (1979) for New Hampshire northern hardwood stands of ages 40 to 57.

When transmittance of PAR is used to calculate LAI using an extinction coefficient (K) of 0.52 (Pierce and Running 1988), LAIs of 6.3 to 8.3 were predicted for 1989 (Table 5). These values are intermediate between those predicted using the litterfall method and the allometric method. The transmittance method was able to detect the lower LAI at site 1 caused by the prolific seed year in 1989 (Table 5). The method also was sensitive to the defoliation occurring at site 3 in 1990. The K value of 0.52 used in the calculation of LAI is based on coniferous stands and may not hold true for broad-leaved canopies. When the Beer-Lambert Law [Equation (3)] was solved for K using 1989 litterfall LAI values from Table 5, K for the sites ranged from 0.56 to 0.61 and averaged 0.59. Solar elevation (Θ) for these "solar noon" samplings ranged from 41° to 48°.

The value of K varies with Θ . This is largely attributable to the greater distance light must travel through the canopy to reach the ground at lower values of Θ . The distance is inversely proportional to $\sin \Theta$. The value of the quantity $K(\sin \Theta)$ is nearly identical for all seven Θ at which measurements of percent transmittance were made in 1989 (mean = 0.437, std. dev. = 0.019) (Figure 4). This relationship predicts K values of 0.49 to 0.51 for the Θ existing at the time of the 1990 sampling (63° to 61°). LAIs predicted using these K values are nearly identical to those predicted by the litterfall method for 1990. When the Beer-Lambert Law was solved for K using 1990 litterfall LAI values, the value of the quantity $K(\sin$

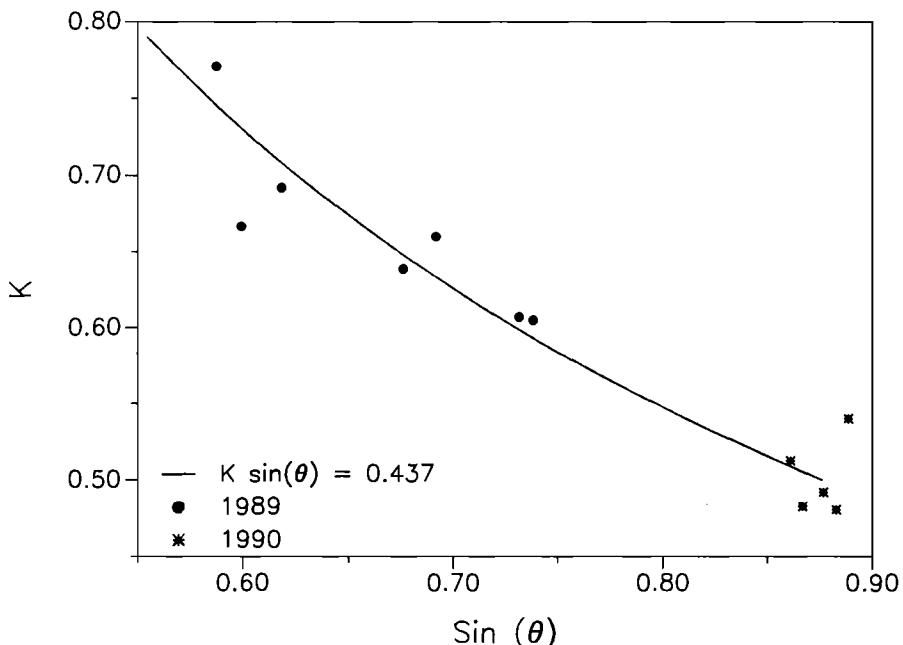


FIGURE 4. Relationship between solar elevation (Θ) and calculated extinction coefficients (K).

Θ) is virtually the same as in 1989 (mean = 0.438, std. dev. = 0.025) (Figure 4).

The stands utilized nearly all the available light. Percent transmittance of PAR was nearly identical in undefoliated stands in 1990, ranging from 2.3 to 2.7%. In contrast, Pierce and Running (1988) found transmitted PAR to be 7 to 10% of total PAR for coniferous stands in Montana with LAIs of 1.7 to 5.3.

CONCLUSIONS

Year to year variability of up to 34% was measured for northern hardwood LAI in this study. Deviations of LAI below the maximum range of 7 to 8 were attributed to allocation of assimilates to reproductive tissues in large seed years and to defoliation. Canopy transmittance, maximum LAI, allometric relationships, and patterns of SLA were remarkably similar among the five sites. These canopy characteristics were evidently controlled primarily by the similar soil characteristics and moisture availability at the sites and were not greatly influenced by differences along the 800 km gradient in length of growing season or levels of acid deposition.

The litterfall and canopy transmittance methods provided better estimates of LAI for the stands than did the allometric equations. These methods were better able to account for deviations in LAI caused by defoliation and prolific seed production. The litterfall method, in fact, allowed for direct measurement of the latter effect. The allometric method could not account for these effects. The litterfall method, although accurate, is labor intensive and can provide an estimate of LAI only after the growing season is over, whereas the availability of portable radi-

ometers, such as the ceptometer, allows for rapid measurement of LAI throughout the growing season using canopy transmittance. The average time needed to sample all plots at one of our sites was only one hour. This is of great importance to researchers needing timely estimates of LAI. For example, it may be possible to immediately measure the effects of insect defoliation or wind damage using this method. However, further quantification of extinction coefficients for various canopy types and solar elevations is needed for the method to be of widespread value.

The effects of events such as insect defoliation and prolific seed production on leaf area and biomass has important implications with regard to detecting the effects of environmental stresses such as acid deposition on forests. The changes in leaf area resulting from acid deposition may be quite small when compared to the 20 to 30% reduction in leaf area measured during heavy seed years. Statistically verifiable effects of pollution on leaf area or growth efficiency may be lost in the "noise" created by the vagaries of nature. Instead of asking programmatic questions like "Has there been a significant change in forest leaf area due to acid deposition?," perhaps we should have asked "Can we measure an $x\%$ decline in leaf area or growth efficiency due to acid deposition, given the inherent variability in life history events, weather, and insect/disease problems?" Our results certainly point out the fact that mature, second-growth northern hardwoods exhibit considerable year to year variability in stand leaf area. They also argue for ecosystem-scale, long-term studies of forest health and productivity. The reduction in stand leaf area due to seed production would not be apparent in chamber studies on young trees and might confound even the most rigorous experimental field study conducted over a short period of time. Multiple years of record and careful measurements of factors such as defoliation, seed production, drought, and wind and ice damage are necessary at a minimum if low-level initial effects of environmental stress on leaf area and growth efficiency are to be detected in the field.

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