

Long term variation of leaf abundance in a northern hardwood forest

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ARTICLE INFO

Keywords:

Disturbance
Drought
Hubbard Brook
Ice storm
Leaf area index

ABSTRACT

Leaf abundance of trees plays a dominant role in energy, water and nutrient flux of forest ecosystems, in defining the habitat structure of entrained biota and in mediating interspecific competition among tree species. We quantified leaf abundance of three dominant tree species (*Acer saccharum* Marsh.; *Fagus grandifolia* Ehrh.; *Betula alleghaniensis* Britt.) for 27 years in mature northern hardwood forest at the Hubbard Brook Experimental Forest, New Hampshire, USA using annual counts of leaves of each species collected in 117 litter traps (0.1 m², each). We hypothesized that variation in leaf abundance would reflect known disturbance events and canopy dieback episodes. No significant trend in leaf abundance of the three species over 27 years (1993–2019) was observed in seven reference stands despite known canopy dieback of sugar maple and American beech in these stands, indicating that 1) maple decline preceded our sampling interval and 2) expansion of beech understory compensated for canopy dieback caused by beech bark disease. Leaf abundance temporarily declined significantly in response to known disturbances (ice storm, 34 to 47%; late-spring frost, 13 to 16%). Increased leaf abundance, especially for sugar maple (30%), on a watershed where calcium addition restored acidified soils, was probably associated with increased soil pH, Ca availability and decreased Al. The temporal sequence of decline of paper birch at higher elevations following a severe drought in 2002 also was apparent. Leaf abundance based on leaf litterfall in deciduous forests provides a useful indicator of forest ecosystem function and forest health.

1. Introduction

Plant leaves play a dominant role in shaping the flow of energy, water and chemical elements on earth's surface. They also comprise the three-dimensional structure for the habitat of arboreal biota (e.g., birds, insects) and mediate inter-specific interactions among plant species. The abundance of foliage in the vegetation canopy varies spatially and temporally in relation to species composition, climate, environmental resource availability and the legacy of disturbance events (e.g., weather, fire) and biotic drivers (e.g., pathogens, herbivores) and such variation in leaf abundance in the vegetation canopy indicates patterns of energy flow and material flux in terrestrial ecosystems (Wright et al., 2004).

In the widely distributed deciduous forest biome of the north temperate zone, broadleaf mixed forests are typically dominated by several species of angiosperm trees. Leafless during the prolonged cold season, these forests usually support a closed canopy with relatively high leaf area index (LAI: 5 to 6; Bolstad et al., 2001); thus, the trees compete strongly for access to the light resource. Temporal variation in the

abundance of leaves of the various species accompanies forest succession following large-scale, catastrophic disturbance events (e.g., severe windstorms), but otherwise leaf abundance is relatively constant through time, although the species composition gradually changes with stand development (Oliver, 1980). However, less severe disturbance by weather events or biotic agents also can cause subtle temporal and spatial variation in leaf abundance, with possible consequences for productivity, hydrology, and nutrient cycling in these ecosystems. For example, the maximum leaf area index of boreal aspen (*Populus tremuloides* Michx.) stands ranged from 3.6 to 5.2 across ten years of measurement (Barr et al., 2004), with lower values linked to defoliation and drought in the previous year and subsequent exhaustion of carbohydrate reserves (Hogg, 1999). Functionally, this sort of variation is clearly indicative of the gross primary production of temperate deciduous forest ecosystems (Muraoka et al., 2010; Xie et al., 2014).

Detection of subtle variation in leaf abundance of different tree species in dense forest vegetation is challenging. Passive remote-sensing methods (e.g., NDVI; Carlson and Ripley, 1997) can be constrained by

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<https://doi.org/10.1016/j.ecolind.2022.108746>

Received 3 December 2021; Received in revised form 8 February 2022; Accepted 1 March 2022

Available online 4 March 2022

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the signal saturation of radiation reflection by the plant canopy (ca. LAI = 3; e.g., Wang et al., 2005). Moreover, although active sensors like Lidar (Riaño et al., 2004) provide the ability to detect variation in canopy structure and plant surface area at various spatial scales, these methods are not yet capable of distinguishing leaves from branches nor identifying leaves of different species in mixed species vegetation (Tang et al., 2014). One approach for estimating spatial variation in leaf abundance by species in woody vegetation relies on allometric relationships with more easily measured metrics, for example individual stem diameters (Whittaker and Woodwell, 1968) or crown area (Jones et al., 2015). However, canopy damage, dieback or defoliation are not reflected in immediate changes in stem diameter and allometric equations are typically developed only from representative, healthy trees. An alternative approach for quantifying leaf abundance patterns in deciduous forest vegetation is collection of leaf litterfall (Liu et al., 2015; Wang et al., 2019).

In the present study we quantified patterns in leaf abundance of the three dominant tree species in a mixed deciduous forest at the Hubbard Brook Experimental Forest (HBEF), NH, USA based on 27 years of leaf litter collections (Fahey and Cleavitt, 2021). The study area corresponds to a suite of experimental small watersheds where hydrologic and nutrient budgets have been quantified to indicate controls on the forest biogeochemical cycles (Likens, 2013). A detailed dimensional analysis of this forest, based on measurements from the mid-1960s (Whittaker et al., 1974) was used to quantify the leaf area, biomass and productivity of the forest watersheds at that time. Since then, the HBEF has experienced some modest successional changes, as well as various natural disturbances including, defoliation (Holmes et al., 1986), a severe ice storm (Ireland, 1998), a late-spring frost event (Hufkens et al., 2012), a microburst windstorm (Battles et al., 2017) and a late-summer drought (Mitchell et al., 2008). In addition, canopy declines of dominant species have occurred in recent decades; sugar maple (*Acer saccharum* Marsh.) has declined owing primarily to effects of acid deposition (Juice et al., 2006); American beech (*Fagus grandifolia* Ehrh.) has suffered from beech bark disease (Houston, 1994; Gavin and Peart, 1993; Cleavitt et al., 2021); and paper birch (*Betula papyrifera* Marsh.) has declined at the higher elevations (>700 m).

We asked the general question: How has the abundance of foliage of the three dominant species in this northern hardwood forest varied through time? We hypothesized leaf abundance would remain relatively constant from year to year except following disturbance events and species declines as noted above. In particular, previous reports of canopy damage by the severe ice storm in 1998 (Rhoads et al., 2002) indicated at least temporary declines in leaf abundance of the three canopy species, and a late-spring frost damaged foliage (Hufkens et al., 2012). We hoped that this detailed analysis of variation in leaf abundance would provide useful indicators of patterns and drivers of energy flow, habitat structure, hydrology and biogeochemistry in the intensively studied HBEF watershed-ecosystems, as well as a better general understanding of causes of variation in leaf abundance in temperate deciduous forests.

2. Methods

2.1. Study area

The Hubbard Brook Experimental Forest (HBEF) is located in north-central New Hampshire, USA (43° 56' N, 71° 45' W). The overstory vegetation is dominated by northern hardwoods: sugar maple, American beech, and yellow birch (*Betula alleghaniensis* Britt.), which together comprise 90% of the tree basal area (Van Doorn, et al., 2011; Table 1). At the highest elevations the hardwood forest is replaced by evergreen needleleaf forest of red spruce (*Picea rubens* Sarg.) and balsam fir (*Abies balsamea* (L.) Mill.); prior to its decline after year 2000, these forests were co-dominated by paper birch. Detailed descriptions of soils, hydrology, topography, and vegetation of the HBEF are presented in Bormann and Likens (2012). The climate is humid continental with short,

Table 1

Stand descriptions for northern hardwood litter collection sites at the Hubbard Brook Experimental Forest, New Hampshire. LAI is leaf area index calculated for 2019 collections with standard errors based on propagation of error from individual collections and area per leaf measurements (see text for detail).

Stand	Elevation (m)	LAI Mean (SE) (m ² m ⁻²)	Basal area		Relative dominance by basal area (%)	
			(m ² ha ⁻¹)	Sugar maple	Beech	Yellow birch
REF 1	520	5.8 (0.20)	39.4	40.9	34.6	24.5
REF 2	525	4.9 (0.29)	35.6	36.4	34.3	13.4
REF 3	580	5.4 (0.15)	32.3	46.3	20.2	33.5
REF 4	585	6.2 (0.20)	30.5	85.2	8.6	6.2
REF 5	725	5.9 (0.21)	29.4	52.5	9.8	26.1
REF 6	730	4.5 (0.21)	19.2	3.1	64.7	22.4
REF 7	830	5.9 (0.27)	17.1	15.5	72.4	7.8
CAL 1	520	6.7 (0.12)	28.8	60.9	13.7	14.8
CAL 2	600	5.2 (0.21)	24.5	46.3	45.3	5.7
CAL 3	710	5.2 (0.29)	23.2	16.4	29.6	32.7

cool summers and long, cold winters. Annual precipitation averages 140 cm; mean annual temperature is 5.5 °C; and daily temperatures average from −8.5 °C in January to 18.8 °C in July (Bailey, 2003). On the south-facing watersheds where the present work was conducted, soils are predominantly acidic Spodosols derived from base-poor glacial till.

2.2. Field sampling

The present study was conducted in 12 forest stands; eight mature forest stands were located adjacent to the biogeochemical reference watershed (WS6) where access is restricted to minimize inadvertent human disturbances (Fig. 1); hereafter these are designated REF stands. Four stands were in an adjacent calcium-treated watershed (CAL). Seven of the REF stand locations were chosen to span the range of elevation of the northern hardwood forest with two in the low elevation zone (525 m), two at mid-elevation (585 m) and three at high elevation (725–830 m). The composition and structure of these stands was measured in 2007 using belt transects that encompassed the array of litter traps (see below). The eighth stand was located in spruce-fir-birch forest at the highest elevation (790 m). The three CAL stands in the northern hardwood zone were situated to parallel the elevation zonation of the REF stands at low (520 m), mid (600 m) and high (710 m) elevation; note that the average composition of these forests was very similar prior to the calcium addition (Table S1). An additional CAL stand was located in the spruce-fir-birch forest near the top of WS1 (740 m).

Forest composition and structure varied among the seven northern hardwood REF stands (Table 1) as is typical for mature northern hardwood forests of the region (Bormann and Likens, 2012); the three dominant species were sugar maple, American beech and yellow birch, with a minor contribution from several other tree species (*Fraxinus americana* L., *Acer rubrum* L., *Acer pensylvanicum* L., red spruce). The additional reference stand in spruce-fir forest adjacent to the top of WS6 was dominated by balsam fir and red spruce.

In fall 1999, 4.6 Mg/ha of the calcium silicate mineral, wollastonite, was added to the CAL watershed. The measured dose of Ca (1.03 Mg/ha) was chosen to roughly replace Ca that was lost as a result of anthropogenic activity (acid deposition, logging) during the 20th century (Peters et al., 2004). All the trees (>10 cm DBH) in the calcium-treated

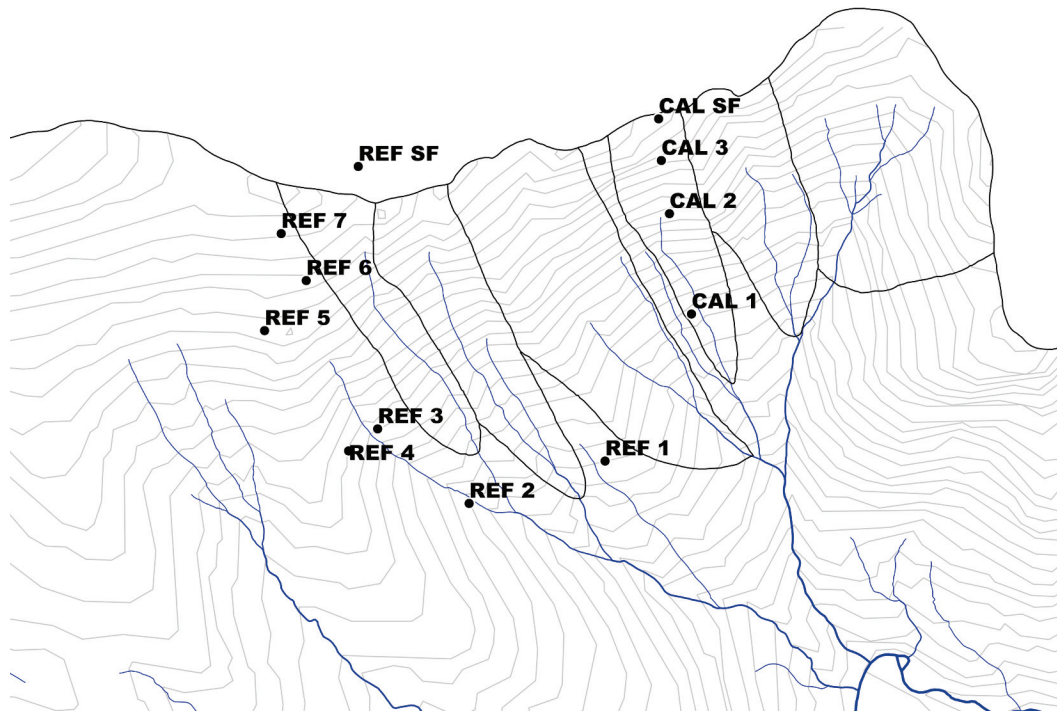


Fig. 1. Location of twelve forest stands in the Hubbard Brook Experimental Forest, New Hampshire, USA where litter traps were deployed to sample leaf abundance. REF = reference, CAL = calcium treated.

watershed have been periodically measured beginning in 1996.

Litter fall was collected in each stand with a randomly located array of ten to fifteen litter baskets (0.1 m^2 , each); the tops of the baskets were raised to about 1.5 m height above ground to minimize error associated with animal disturbance and wind transport across the soil surface. Litter fall collection began in summer 1993 or 1994 in the seven REF stands and in 1998 in the CAL stands; it has continued to the present except for a brief interruption in three of the REF stands (2016–2017) owing to funding limitations. Accumulated litter was removed in May, late August and early November each year and returned to the laboratory where it was stored cold until processing. Here we report the data from the November collections which represent leaf abundances in late summer, normally comprising over 95% of leaves.

2.3. Sample processing and analysis

Litter samples were sorted into various components, including leaves (by species), fruits and seeds (by species), and other non-woody (e.g., bud scales), woody (e.g., twigs, small branches) and miscellaneous other components. Leaf samples were counted (by species). Representative subsamples of about 50 leaves for estimating average area per leaf were collected in 2019 for each plot and species. Area per leaf of intact leaves was measured by scanning photocopies of leaves, and LAI of each species in each stand was estimated as the product of mean area per leaf and leaf counts. For the present analysis we focus primarily on leaf count data for statistical inferences because these are the primary data whereas leaf area index is a derived value; thus, the basic data are number of leaves of each of the three dominant species in each litter collection basket in each year; basket locations were fixed. While we convert the leaf count data into leaf area to provide context and ease comparisons with other sites, the basic data of leaf counts eliminates the uncertainty associated with variation in mean area per leaf and thus allows us to more precisely examine temporal trends. The data used in this paper are from the dataset: Fine Litterfall Data at the Hubbard Brook Experimental Forest, 1992 – present (Fahey and Cleavitt, 2021). For

convenience, the data used in this manuscript are included as discrete files in Supplementary Tables. All of the code for these programs were written in R programming language (R Core Team, 2020) with version R-4.0.2 (64 bit) as indicated in the Supplement.

We conducted a full error analysis to quantify the magnitude of uncertainty associated with intra-stand variation among the collectors as well as the uncertainty for LAI estimates associated with variation in leaf size among the 50 leaves of each species sampled from each stand in 2019. We quantified stand-level variation in leaf abundance and in leaf size with the standard error (SE) of the mean (Tables S2 and S3). The uncertainty in LAI was estimated using Monte Carlo resampling. Specifically, we ran 1000 simulations where both leaf count and leaf area varied as a random function defined by their respective standard errors. Then for each simulation we calculated the LAI as the product of count and area. The variance in LAI was calculated as the standard deviation among the 1000 simulations of the mean (i.e., the standard error of the mean).

We evaluated long-term trends in leaf abundance for each of the three dominant species across the seven REF stands and three CAL stands. We considered stand-level summaries as the experimental unit and used mean annual leaf count (leaves m^{-2}) for each stand as the key indicator. We tested for temporal autocorrelation in leaf counts for each study area. Since we found no significant lag effects, we used Mann-Kendall tests to determine if there were trends in leaf abundance in REF and CAL. If there was evidence for a trend, we evaluated the form with three generalized mixed-effects models that define linear, quadratic, and saturating (i.e., Michaelis–Menten) functions. Specifically, we used the R-package “nlme” (Version 3.1–152) with leaf counts as the independent variable, year and year² (in the quadratic model) as the dependent variables and stand as the random variable. All variables were centered and standardized prior to analysis. We implemented an information theoretic approach to compare model performance (Burnham and Anderson, 2002). We calculated Akaike’s information criterion with an adjustment for small samples sizes (AIC_c) and ranked models based on the differences in AIC relative to the lowest AIC (ΔAIC). The

best model was evaluated for goodness of fit using a coefficient of determination (i.e., a pseudo- R^2) that calculates the conditional and marginal values for generalized mixed-effects models (Nakagawa et al., 2017, R-package “MuMIn”).

Three major disturbance events visited the HBEF during the period of study: an ice storm in January 1998 (Rhoads et al., 2002), a late-spring frost event in May 2010 (Hufkens et al., 2012) and a microburst wind-storm in 2013 (Battles et al., 2017). To evaluate the impact of these disturbances at the small watershed landscape scale (Likens, 2013), we quantified the inter-annual variations in the abundance of leaves in the REF stands by analyzing patterns in the annual residuals. For year = i :

$$\text{Residual}_i = \text{LeafCount}_i - \text{GrandMean} \quad (1)$$

where the leaf count (leaves m^{-2}) is the mean for all stands in year i and the grand mean is the mean for all years. We calculated residuals by species and for the total of all three species. We examined Pearson's correlations between these residuals of annual variation in leaf abundance for each species and several indices of climatic variation: spring leaf out date, growing season length, sum of degree days above 4°C and departures of weather from the long-term normal for hot and cold days; these variables were chosen on the basis of previous reports on inter-annual variation in tree growth and climate for northern hardwood forests (Kim and Siccama, 1987; Ouimette et al., 2018). In addition, we examined correlations with seed production for beech and sugar maple (Cleavitt and Fahey, 2017).

We evaluated temporal patterns in the abundance of paper birch leaves in four stands where it was abundant at the beginning of the study (see above) but where decline was observed following the ice storm in 1998 and a late-summer drought in 2002. However, there were significant lag effects (up to four years) in paper birch leaf abundance following the drought in these high elevation stands. Sieve bootstrapping (Bühlmann and Bühlmann, 1997) is a statistical approach that accounts for temporal autocorrelation by first fitting an autoregressive model and then resampling the data using the autoregressive model to preserve the serial dependence in the data while not requiring any assumptions about the distribution of the data. Noguchi et al. (2011) demonstrated the value of sieve bootstrapping for detecting trends in hydrological time series. We used sieve bootstrapping to test the hypothesis of a non-monotonic trend in paper birch leaf abundance. The test was implemented using function “notrend_test” from the R package “funtimes”.

To evaluate the robustness of comparisons of trends in leaf abundance and LAI by species between the REF and CAL stands, we generated 1000 Monte Carlo simulations with all sources of error included (see above). For both leaf counts and LAI in 2019, we generated stand-level estimates (by species and total) as a random function of the observed standard error in each stand (Tables S2 and S3). We then calculated the difference between the means for REF and CAL (CAL-REF). For these 1000 simulated differences, we tested if the mean was different than 0 using a t -test. We acknowledge that the study design was not ideal for attributing treatment effects because pre-treatment leaf abundance data were not available for CAL; however, given the close similarity between the REF and CAL forests before the treatment (Table S1), the responses observed are likely a result of the treatment.

3. Results

Leaf abundance in the mature northern hardwood forest surrounding the biogeochemical reference watershed (REF) at the HBEF did not exhibit any significant long-term temporal trend (Fig. 2A, Mann-Kendall: $p = 0.2$). A summary of the long-term variability in leaf abundance by species is provided for the REF forest (Table S2).

Beech leaves were consistently the most abundant averaging 761 leaves m^{-2} ; yellow birch leaves were much less abundant (mean = 475 leaves m^{-2} , Fig. 2B) and sugar maple was intermediate. In the absence of

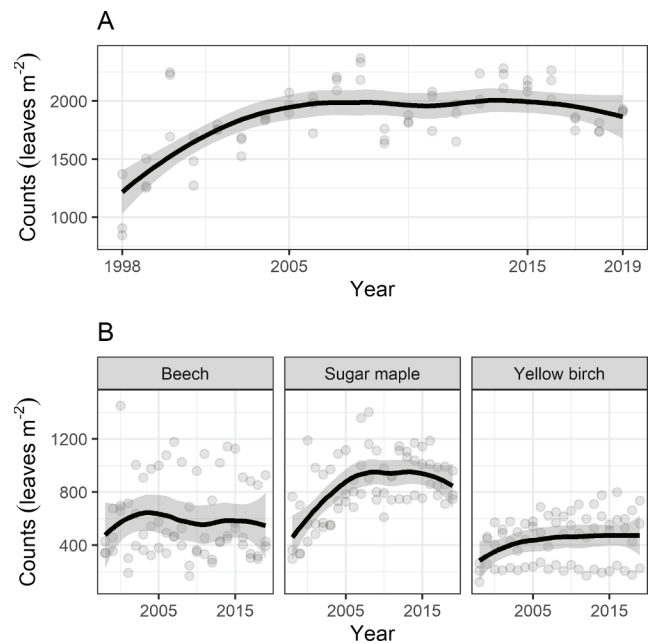


Fig. 2. Annual average leaf abundance for the three dominant tree species in the seven reference forest stands (REF) surrounding Watershed 6 at the HBEF from 1993 to 2019. A) Mean leaf abundance for the sum of all three species. The transparent points represent leaf abundance in the individual stands; the black curve denotes the trend in the data based on a locally weighted smoothing function; the gray band denotes the 95% confidence interval of the fitted curve; and the vertical, dotted line identifies the year of the ice storm in 1998. B) Leaf abundance trends reported by species. Graph details the same as described for Panel A.

known disturbances (see below), inter-annual fluctuations in leaf abundance were observed in the REF forest (Fig. 3). This inter-annual variation was similar among the seven stands except, of course, much higher variation in cases where a species was uncommon in a particular stand (e.g., sugar maple in stand 7; Table 1). Across the large landscape average inter-annual variation in leaf abundance ranged from coefficient of variation (CV) = 9.3% for sugar maple to 15.7% for yellow birch, with beech being intermediate (CV = 11.1%).

Stand level leaf abundance varied by stand and species (Table S3). Total leaf count variation as measured by standard error (SE) averaged 96 leaves m^{-2} with a CV of 5% (Table S4). Leaf counts of beech had the least collector-to-collector variability (CV = 10%); sugar maple (CV = 21%) and yellow birch (CV = 25%) were comparable. Variation in leaf size was remarkably consistent. The average CV across stands for leaf area ranged from 7% to 9% by species and by treatment (Table S3). On a stand-by-species basis, the variation in leaf count was larger than the variation in area per leaf (Table S4). The stand-level uncertainty in LAI estimates averaged 0.5 with SE ranging from 0.4 to 0.7 (Table S4). This variation represents an average CV of 10%. There were no major differences in LAI uncertainty among species or between REF and CAL stands (Table S4).

A significant time trend in leaf abundance was observed on the Ca-treated watershed, CAL (Fig. 4A, Mann-Kendall: $p = 0.04$). Based on subsequent modeling, the quadratic function ($\Delta\text{AIC} = -64.7$ compared to second best model) was clearly the most informative model. Overall leaf abundances increased from a minimum of 1,041 leaves m^{-2} in 1998 to a maximum of 2,294 leaves m^{-2} in 2008. Since this peak, there has been a slight decline with a post-2008 mean leaf count of 1,943 leaves m^{-2} (Fig. 4A). Both the increase in abundance and the temporal pattern were driven by sugar maple leaf abundance (Fig. 4B). Based on model comparisons for species-specific data, the quadratic function best described the trend in sugar maple leaf abundance with both the linear and quadratic terms significant ($p < 0.001$ in both cases). Yellow birch

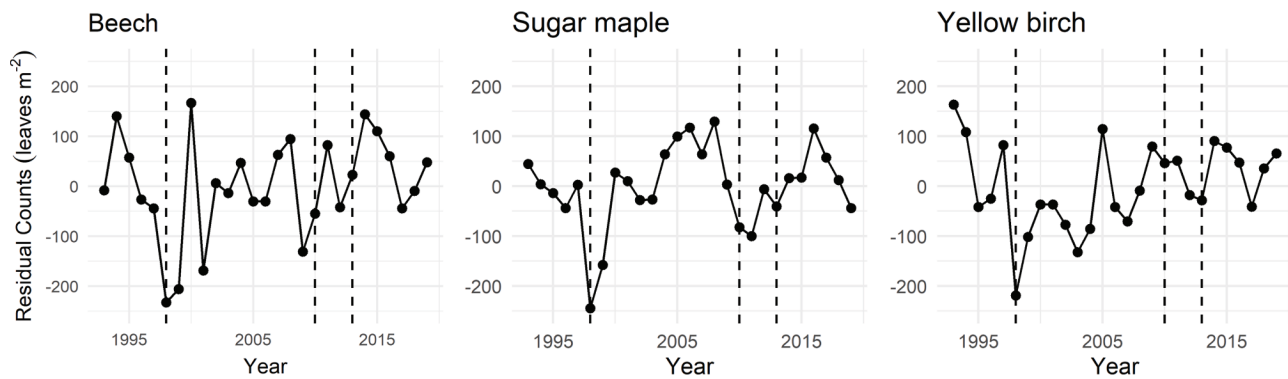


Fig. 3. Inter-annual variation in leaf abundance for the dominant tree species in the seven reference stands at the HBEF. The points are yearly residual leaf abundance as defined in Eq. (1). Vertical dashed lines indicate years of known disturbance events (ice storm – 1998).

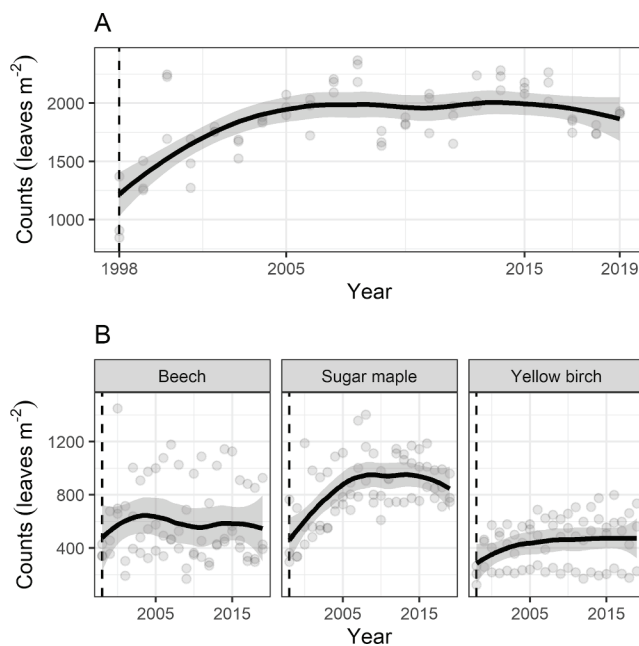


Fig. 4. Annual average leaf abundance for three dominant tree species in three forest stands in calcium-treated (CAL) Watershed 1 at the HBEF from 1998 to 2019. A) Mean leaf abundance for the sum of all three species. The transparent points represent leaf abundance in the individual stands; the black curve denotes the trend in the data based on a locally weighted smoothing function; the gray band denotes the 95% confidence interval of the fitted curve; and the vertical, dotted line identifies the year of the ice storm in 1998. B) Leaf abundance trends reported by species. Graph details the same as described for Panel A.

also followed an increasing quadratic trend ($p < 0.004$ in both cases), but the magnitude of the change was much less than sugar maple. Leaf counts for beech showed no trend over time (Fig. 4B).

Results from our Monte Carlo tests of species and treatment effects for the 2019 data were consistent with the conclusions drawn from our time series analyses. In terms of both leaf count and LAI, sugar maple leaf production increased after the calcium addition and beech leaf production declined (Fig. 4). Moreover, the magnitude of the response exceeded the propagated uncertainty in the metrics. For example, sugar maple leaf count increased on average by $261 \text{ leaves m}^{-2}$ and 0.9 LAI (Table S5) in the CAL stands. Standard errors based on propagated uncertainty for sugar maple leaf count averaged 85 leaves m^{-2} and 0.3 LAI (Table S3). For beech, leaf count decreased by $206 \text{ leaves m}^{-2}$ and 0.6 LAI in treated stands (Table S5); the comparable standard errors were 75 leaves m^{-2} and 0.3 LAI (Table S3). Thus, the treatment effects sizes were

more than double the estimates of uncertainty.

The impacts of three disturbance events on leaf counts in the REF stands varied. The effects of the ice storm of 1998 on leaf abundances of all three dominant species in subsequent years was obvious (Fig. 3). In the first growing season after the storm (1998) leaf abundance was reduced by 37.5% forest wide. The gradient spanned from a 46% decrease in yellow birch leaf counts to 31% for beech (Table 2). Damage was greatest in the upper elevation zones ($>600 \text{ m}$; 47% vs 34% decrease) reflecting higher ice loading, as previously reported (Rhoads et al., 2002). A limited recovery in leaf abundance of all three species was observed in the second summer after the ice storm. Surprisingly, in the third summer post-storm, a striking and significant “overshoot” in leaf abundance was observed for American beech, 22 % above the long-term mean for this species (Fig. 3, Table 2). Thereafter, leaf abundances of all three species returned to roughly normal, long-term values, although yellow birch leaf numbers remained slightly low through 2004.

The late-spring frost event of May 2010 mostly affected sugar maple, based on field observations at the HBEF (Hufkens et al., 2012). This event resulted in a two-year decline in sugar maple leaf abundance; that is, we detected a 13% decline in sugar maple leaf litterfall in 2010 (Table 2) that persisted for a second growing season (16% decline in 2011; Fig. 3).

The microburst windstorm that occurred on 2 June 2013 resulted in patchy canopy damage across a roughly 600 ha area of landscape on the south-facing slope of the HBEF, adjacent to our study area. Some limited evidence of this event was recorded in leaf abundance data for the high-elevation hardwood stands, but the response was not consistent across the stands and species. Severe effects of this disturbance event apparently were confined to discrete patches where over 75% canopy damage occurred. Although these areas were within 500 m of our stands (Battles et al., 2017), the areas exposed to damaging winds were relatively discrete.

No significant linear correlations as measured by the Pearson correlation coefficient were observed between interannual climatic variation and residuals of interannual variation in leaf abundance of the three species or all species together. Nor was seed production of beech and sugar maple significantly related to leaf abundance in the REF stands.

Table 2

Annual deviations in leaf abundance from the long-term mean (1998–2019) at the Hubbard Brook Experimental Forest. Results are from the seven stands measured in the reference forest. Delta values (Δ) are in percent.

Species	Δ 1998	Δ 1999	Δ 2000	Δ 2010	Δ 2013
Beech	−30.6	−27.1	22.0	−7.2	3.0
Sugar maple	−39.6	−25.5	4.4	−13.3	−6.6
Yellow birch	−45.9	−21.3	−7.7	9.6	−5.9
Total	−37.5	−25.1	8.5	−4.9	−2.5

A distinctive time trend in the abundance of paper birch leaves was observed in four high-elevation stands (740–830 m elevation; Table 1). Paper birch leaf abundance declined steadily from 1993 to 2006 (Fig. 5). By 2008 all paper birch trees had died in three of the stands; leaf abundance in the fourth stand was reduced by about 75% and persisted at roughly this level to the present.

The estimated LAI of the reference forest, calculated as the product of the average area per leaf of each species in each stand, varied between 5 and 6 across the seven stands in the absence of the known disturbances; this range matches values (5.5 to 6.2) for the same study site measured in the mid-1960s by Whittaker et al. (1974). The LAI of the forest in CAL increased gradually after the Ca treatment (Fig. 6) mostly reflecting the large increase in sugar maple leaf abundance (Fig. 4); this effect was previously detected based on visual observations of the tree crowns in REF vs CAL (Juice et al., 2006). We finally note that these estimates of LAI in REF and CAL are lower than those previously reported (Battles et al., 2014) because of a revision of average leaf size estimates (1998).

4. Discussion

We quantified leaf abundance of three dominant trees in a northern hardwood forest landscape as an indicator of forest health, energy flow and the hydrologic cycle in forest ecosystems. No long-term changes in leaf abundance of the three dominant tree species were observed between 1993 and 2019 in the mature forest adjacent to the reference research watershed (REF) at the Hubbard Brook Experimental Forest (Fig. 2). This forested landscape was heavily logged in the early 20th century; thus, the forest had already passed through successional stages during which shifts in canopy dominance are prominent (Oliver, 1980). For example, from 1996 to 1997 to 2016–2017 the structure and composition of the forest barely changed; total basal area decreased slightly from 25.8 to 24.6 m² ha⁻¹ and the basal area of sugar maple (9.7 vs 8.0 m² ha⁻¹), beech (9.0 vs 8.1 m² ha⁻¹) and yellow birch (5.3 vs 5.0 m² ha⁻¹) were stable (Cleavitt et al., 2021). The three dominant species are long lived (>200 years; Burns, 1990) so that stasis in canopy

dominance is not surprising. However, two of these dominant species have suffered canopy declines in recent decades: sugar maple owing primarily to soil base cation depletion (Sullivan et al., 2013) and beech to an introduced disease complex (beech bark disease (BBD); Cale et al., 2017). The fact that no decline in leaf abundance was observed for sugar maple suggests that canopy dieback of this acid rain sensitive species preceded the initiation of our sampling program (1993) and probably coincided with the most severe years of acid rain at the HBEF (ca. 1960–1980; Likens et al., 1996). In the case of American beech, although BBD was first observed at the HBEF in 1977 (Siccama et al., 2007) and increased canopy dieback and overstory mortality has occurred since the mid-1990s, vegetative sprouting and seed regeneration (Cleavitt et al., 2021) have apparently been sufficient to maintain leaf abundance throughout our sampling interval (Fig. 2).

4.1. Natural disturbances

A variety of natural disturbances commonly affects the canopy in the eastern deciduous forest biome (White, 1979), including defoliation by insects, occasional fires (Lorimer, 1977), windstorms of varying scale and intensity, as well as ice storms and other weather events. The effects of two disturbance events on leaf abundance of the three dominant tree species of the northern hardwood forest at the HBEF were evident from our long-term sampling of leaf litterfall: a severe ice-storm in January 1998 (Rhoads et al., 2002) and a late-spring frost event (May 2010; Hufkens et al., 2012).

In the 1998 ice storm at the HBEF, ice accretion, tree damage and LAI reduction increased with elevation, peaking at about 700 m. Tree damage was greatest for yellow birch (43% basal area damaged) and slightly lower for beech (34%) and sugar maple (33%) (Rhoads et al., 2002). These patterns were reflected in leaf abundance reductions which increased with elevation from 500 to 800 m and were greatest for yellow birch and similar for beech and sugar maple as indicated by deviations from long-term averages (Fig. 3). Little canopy recovery occurred during the second growing season after the ice storm both for the whole canopy and for each of the major species (Fig. 3). A highly distinctive recovery response was observed in year 3 for American beech, an apparent “overshoot” in leaf abundance; this response might be associated primarily with release of buds in the beech-dominated understory that was minimally damaged by the storm and received greatly increased light availability. For example, Weeks et al. (2009) noted that the mid-term (three to seven years) response of canopy vertical structure after the ice storm was associated primarily with understory beech. Presumably, the return to normal, pre-storm beech leaf abundance in year 4 (Fig. 3) reflected post-storm canopy closure and shading. Although ice storms may promote increased overstory mortality of beech from BBD (Cale et al., 2017), including in our study area (Cleavitt et al., 2021), any long-term effects of the ice storm on leaf abundance of the three dominant species were surprisingly minor (Fig. 2).

The effects of an unusual late-spring frost event on leaf dynamics and forest production at the HBEF and other regional forests were reported previously (Hufkens et al., 2012). Early spring 2010 was exceptionally warm, triggering early budbreak and leaf development, especially for sugar maple (17 days earlier than long-term average at the HBEF (USDA Forest Service, 2021) and less so for beech (11 days) and yellow birch (13 days). A severe late frost occurred on 11 May when a minimum temperature of −3 °C was recorded at the HBEF Headquarters (245 m elevation), −4 °C at station 6 (745 m elevation) and −5 °C at station 17 (895 m elevation). This frost event caused more severe leaf damage to sugar maple than beech or yellow birch (Hufkens et al., 2012), probably reflecting its opportunistic response to the early spring (Norby et al., 2003) in comparison to the more conservative beech and birch. Our observations indicated that sugar maple leaf abundance in the reference forest declined in 2010 in comparison with the previous nine years, a reduction that was comparable to the ice storm effect (Fig. 3); thus, re-leaving by sugar maple was limited. Moreover, this decrease persisted

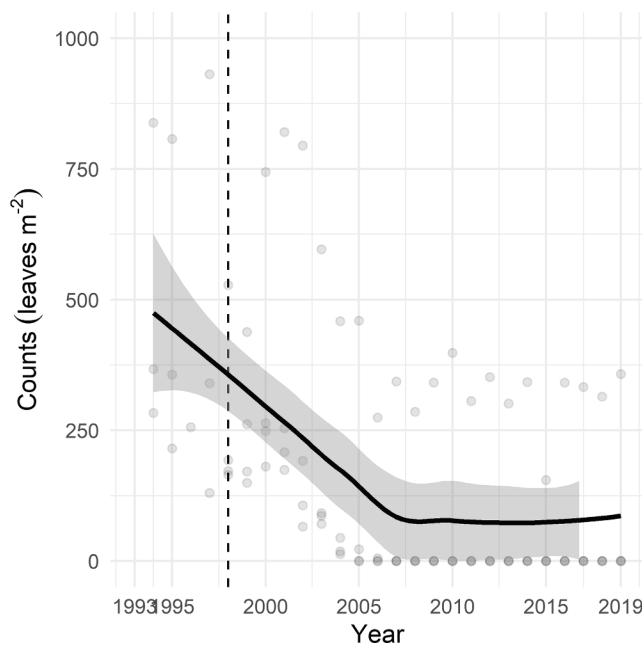


Fig. 5. Annual average leaf abundance of paper birch in four high elevation stands at the HBEF, NH where the species was abundant at the beginning of the study. The transparent points represent leaf abundance in the individual stands; the black line is the fit of the data based on a locally weighted smoothing function; the gray band denotes the 95% confidence interval of the fitted curve; and the vertical, dotted line identifies the year of the ice storm (1998).

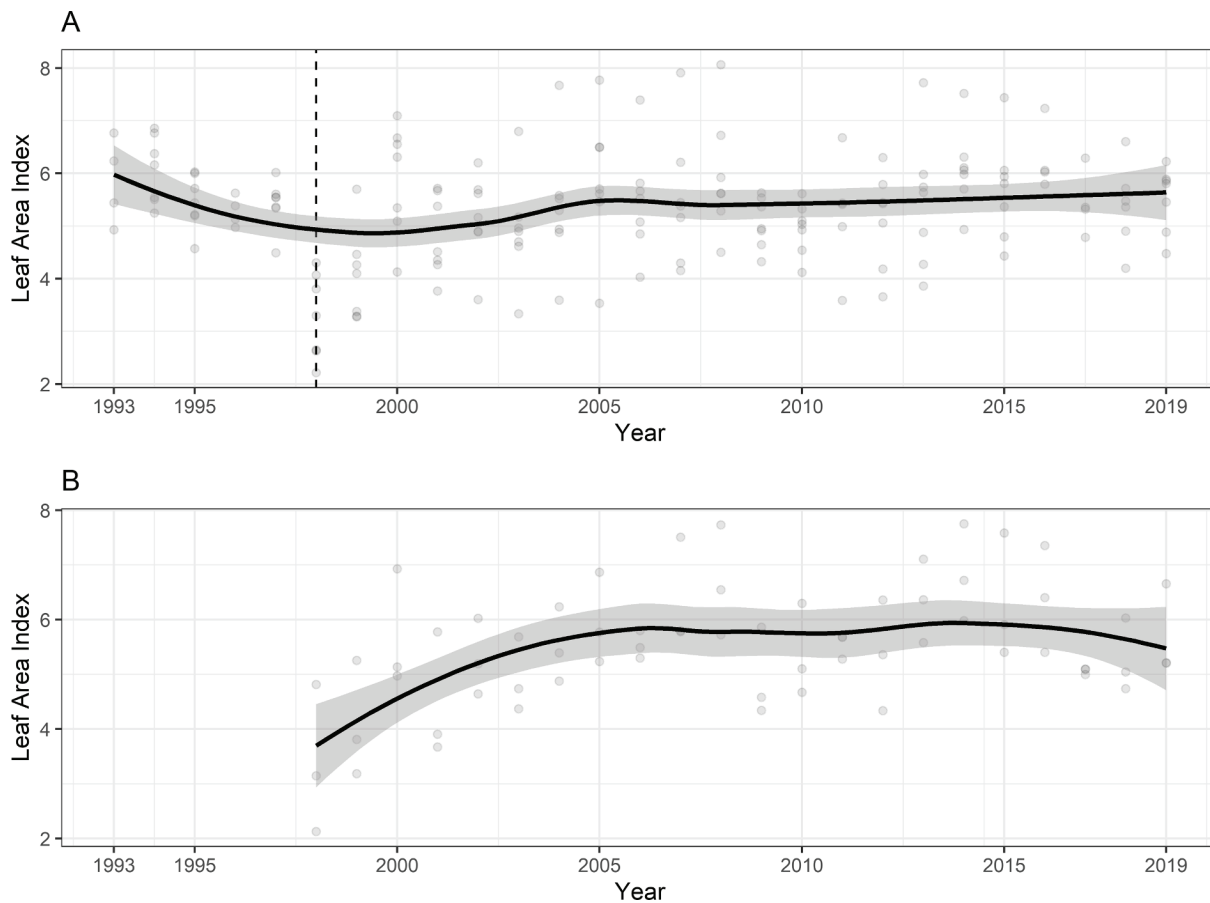


Fig. 6. Leaf area index for the two northern hardwood study areas at HBEF, NH. Leaf area index based on the product of leaf abundance ($\# \text{ leaves m}^{-2}$) and average area per leaf for all tree species. A) Leaf area index for the seven, reference forest stands. The transparent points represent leaf area index in the individual stands; the black curve denotes the trend in the data based on a locally weighted smoothing function; the gray band denotes the 95% confidence interval of the fitted curve; and the vertical, dotted line identifies the year of the ice storm in 1998. B) Leaf area index for the three forest stands in calcium-treated watershed. Graph details the same as described for Panel A.

into the next year, suggesting that the anomalously warm spring followed by the frost event damaged buds (Martin et al., 2010). Hufkens et al. (2012) estimated that a roughly 7% reduction in forest gross production resulted from this event, but our observations suggest that it could have been somewhat greater. Sampling of wood growth in tree rings from these plots would help to clarify functional implications of this event.

4.2. Watershed 1 calcium treatment

The changes in leaf abundance following calcium addition to the treated watershed (CAL) were striking (Fig. 4) and matched visual observations (Juice et al., 2006) and tree growth responses (Battles et al., 2014). Sugar maple leaf abundance increased by over 30% with most of the increase from year 3 to 8 following treatment (2003–2008, Fig. 4B). These results confirm the high sensitivity of this iconic northern hardwood species to soil Ca depletion; the Ca treatment at the HBEF raised soil base saturation from below to above the apparent threshold of 17% below which damage occurs (Sullivan et al., 2013) and greatly reduced exchangeable Al in surface soil horizons (Johnson et al., 2014).

We also detected a more subtle but significant increase in leaf abundance of yellow birch on CAL (Fig. 4). Although no growth response was observed for this regionally dominant species on CAL (Battles et al., 2014), Ouimet et al. (2017) observed significant increases in yellow birch stem growth in the second decade after liming of acidified northern hardwood soils in Canada. Leaf abundance of American beech did not respond significantly to the Ca treatment (Fig. 3). This species is

not sensitive to soil base cation depletion (Reid and Watmough, 2014). Although some experiments have noted possible suppressive effects of soil Ca addition on beech growth, probably caused by increased competition from rejuvenated sugar maple (Ouimet et al., 2017); such an effect on leaf abundance did not occur on CAL. Rather, the increased competitive performance of sugar maple in response to the Ca addition increased mortality of severely diseased beech trees (Cleavitt et al., 2021), but overall beech leaf abundance, including survivors and abundant regeneration, has been maintained. Finally, because both sugar maple and yellow birch leaf abundance increased, while beech did not change, total leaf abundance and total LAI increased on CAL. One consequence of this canopy response was increased net production both aboveground (Battles et al., 2014) and belowground (Fahey et al., 2016).

4.3. Inter-annual variation

In the absence of disturbance events leaf abundance was not expected to exhibit high inter-annual variation in this mesic climate. However, considerable chronic inter-annual variation was observed (Fig. 3); across the REF study area average LAI ranged across 27 years from 4.8 to 6.3. Other studies of inter-annual variation in leaf abundance in broadleaf deciduous forests have reported similar variation. For example, LAI in aspen forest in central Saskatchewan, Canada ranged from 3.6 to 5.2 across 10 years (Barr et al., 2004); from 5.1 to 5.9 in mixed *Quercus-Betula* forest in Japan across five years (Muraoka et al., 2010); and from 3.8 to 4.7 in *Quercus* forest in Ohio across seven years

(Xie et al., 2014). The causes of these chronic variations were not always clear, but depletion of C reserves associated with drought and defoliation have been proposed in some cases (Hogg, 1999; Le Dantec et al., 2000).

We can only speculate on the possible causes of chronic inter-annual variation in leaf abundance at our site since none of our climatic indices were significantly correlated with this variation, and seed masting of sugar maple and beech was not correlated with leaf abundance. One likely cause of inter-annual variation was sampling error; although the position of the collectors was fixed, the direction of leaf fall certainly varies with weather during the fall (e.g., wind direction). Another possible cause of inter-annual variation in leaf abundance could be weather-related canopy damage. For example, undocumented weather events, including hailstorms, smaller windstorms, and heavy winter snow (Gosz et al., 1972) could contribute to inter-annual variation in leaf abundance.

4.4. Paper birch decline

The temporal sequence of decline of paper birch was clearly indicated by our collections of leaf litterfall (Fig. 5). This species was dominant in four stands at the highest elevations in the HBEF (Fig. 1). Following gradual recovery from damage by the ice storm from 1999 to 2002, paper birch leaf abundance declined sharply from 2002 to 2006 and thereafter remained roughly constant through the duration of the study (Fig. 5). One likely contributor to this canopy decline of paper birch was a severe late-summer drought in 2002 (Mitchell et al., 2008). During late August 2002 paper birch foliage in the study area exhibited desiccation damage, turning brown and shriveling (T. Fahey, personal observation), possibly associated with the xylem cavitation. In the following summer, although widespread mortality was not observed, the trees produced much less foliage (Fig. 5). By 2006 widespread mortality ensued; for example, between 2001 and 2006 tree inventories on REF and CAL indicated that the number of living paper birch trees (>10 cm DBH) declined by 90%. This pulse of mortality of paper birch following the 2002 drought was not confined to the HBEF; the first author observed similar mortality in 2006 in subalpine forests along the Appalachian Trail from central Vermont to western Maine.

Paper birch is known to be sensitive to severe drought (Aubin et al., 2018), exhibiting limited stomatal control and evidence of xylem cavitation at low soil water content (Sullivan et al., 2021). Decline of paper birch following drought in northern Michigan was attributed to irruption of damaging bronze birch borer facilitated by tree water stress (Jones et al., 1993); however, this insect pest was not observed in our study area.

An additional contributor to the decline of paper birch at the HBEF could be cohort senescence. Paper birch is a relatively short-lived tree (Burns, 1990), and the populations in our study area established primarily after clearcut logging in the early 20th century; thus, the trees in our study area were probably approaching maximum age (ca. 100 years; Graber et al., 1973) and indeed the trend of decreasing leaf abundance preceded the ice storm event. Finally, our paper birch populations included both *B. papyrifera* as well as the recently recognized species, mountain paper birch (*B. cordifolia* Regel.) that was previously considered a variety and was not distinguished in our leaf abundance measurements. All the surviving paper birch stems in the REF spruce-fir stand (Fig. 5) are mountain paper birch (N. Cleavitt, unpublished), and this species is also known to be potentially longer lived (Graber et al., 1973).

4.5. Implications

Our estimates of leaf abundance and LAI have been used to evaluate causes of annual deviations in actual evapotranspiration (AET) for REF and CAL (Green et al., 2013; Green et al., 2021). In particular, a transient, two-year increase in AET from CAL following the Ca addition was

not fully accounted for by increased LAI and the causal mechanism remains unclear (Green et al., 2013). Similarly, although a slight trend of increasing LAI between 2010 and 2018 was observed for REF (Fig. 6), this driver was not sufficient to explain an apparent 30% increase in AET for REF over this time interval (Green et al., 2021).

Variation in leaf abundance influences gross and net primary productivity, and the observations from the present study illustrate this influence. First, the 38 % reduction in leaf abundance in the REF stands resulting from the 1998 ice storm was reflected in a marked decline in wood growth during this interval (Battles et al., 2014). However, the exact contribution of reduced leaf abundance is uncertain; for example, wood production apparently remained about 30% below the long-term average even after leaf abundance recovered (2001–2006 vs 2006–2011) which Battles et al. (2014) tentatively attributed to the cost of structural repairs from ice damage. The increased leaf abundance on CAL also appeared to contribute to greater wood production. In particular, from 2006 to 2011, when LAI averaged 7 % higher on CAL (5.79) than REF (5.38, Fig. 6), wood production was 8% greater on CAL than REF (Battles et al., 2014).

The implications of chronic variations in leaf abundance of the three dominant species in the northern hardwood forest (Fig. 3) on forest productivity are unknown and worth further investigation. In general, LAI of the reference forest varies between five and six from year to year. Whether this one LAI unit difference translates to significant NPP variation is uncertain. Notably, at these high LAI levels most additional leaf surfaces are deeply shaded and may contribute little to the forest net C fixation (Zhao et al., 2021).

The observation of chronic inter-annual variation in leaf abundance of these tree species also has implication for the development and application of allometric approaches for estimating leaf biomass in deciduous forests. The standard approach is to harvest “representative” trees of different sizes and to quantify relationships between DBH and various biomass components (Whittaker et al., 1974; Jenkins et al., 2003). Our observations suggest that the year of sampling can significantly affect these relationships.

We acknowledge two methodological caveats that could contribute to our estimates of inter-annual variation of leaf abundance. First, these estimates are based on leaf counts representing the fall leaf abscission period, only; thus, any leaves that fell earlier in the growing season were not included. In a typical year a small number of leaves can be damaged and fall as a result of a variety of causes (e.g., hailstorms, herbivory). Replacement of some of these leaves sometimes occurs, and it can be difficult to properly account for this effect. Our measurements represent the late summer abundance of foliage. Second, leaf counts of American beech slightly underestimate total leaf abundance because some understory leaves typically persist into winter before falling and this effect probably varies from year to year.

In sum, monitoring litterfall provided indications of long-term trends in leaf abundance of the dominant tree species in a mixed deciduous forest as well as subtle responses of these species to disturbances and to mitigation of soil acidification. Continuation of this sampling program should be useful for demonstrating responses of this forest ecosystem to human-accelerated environmental changes.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

Cindy Wood was critical in maintaining the high quality of the litterfall data from 1993–2013.

This work is a contribution of the Hubbard Brook Ecosystem Study. Hubbard Brook is part of the LTER network, which is supported by the

US National Science Foundation. Hubbard Brook Experimental Forest is operated and maintained by the US Department of Agriculture, Forest Service, Northern Research Station.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2022.108746>.

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