

Variation in mass and nutrient concentration of leaf litter across years and sites in a northern hardwood forest

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Abstract: Leaf litterfall represents an important nutrient flux in forests, but separating leaves by species and collecting fresh litter annually for nutrient analysis is time-consuming and expensive. To quantify the sources of variation in litterfall nutrient estimates and guide optimal allocation of research effort, we analyzed nutrient concentration (5 years) and mass (6 years) of leaf litter for nine tree species in 13 northern hardwood sites. Coefficients of variation (CVs) in nutrient concentration were higher across sites than over time within sites for most elements; phosphorus was especially variable across sites (56% CV). Thus, to estimate litterfall nutrient fluxes accurately in forests of this type, nutrient analyses should be site-specific as well as species-specific but may not need to be repeated annually (CVs over time averaged 17% for calcium, 21% for magnesium, 28% for potassium, and 32% for phosphorus concentration). Total leaf litterfall mass varied considerably from year to year, ranging from 234 to 370 g·m⁻² averaged over 13 sites. We recommend that litter collectors be elevated above the ground to avoid oversampling during extreme wind events. Use of species-specific allometric equations, or even basal area, to estimate the species composition of total litter mass may obviate the need to sort litter by species.

Résumé : La chute de litière de feuilles représente un flux important de nutriments dans les forêts mais la séparation des feuilles selon l'espèce et la collecte annuelle de litière fraîche pour analyser les nutriments coûtent cher et prennent beaucoup de temps. Afin de quantifier les sources de variation des estimations des nutriments présents dans la chute de litière et de favoriser une allocation optimale des efforts de recherche, nous avons analysé la concentration des nutriments (5 ans) et la masse de litière de feuilles (6 ans) pour neuf espèces d'arbres dans 13 stations de feuillus nordiques. Les coefficients de variation (CV) de la concentration des nutriments étaient plus élevés entre les stations qu'entre les années dans une même station pour la plupart des éléments; le phosphore était particulièrement variable d'une station à l'autre (CV = 56%). Par conséquent, pour estimer avec précision les flux de nutriments dans la chute de litière de ce type de forêt, l'analyse des nutriments devrait être spécifique à chaque station et à chaque espèce mais n'a pas besoin d'être répétée à chaque année (le CV entre les années atteignait en moyenne 17% pour la concentration de calcium, 21% pour le magnésium, 28% pour le potassium et 32% pour le phosphore). La masse totale de chute de litière de feuilles variait considérablement d'année en année, allant en moyenne pour les 13 stations de 234 à 370 g·m⁻². Nous recommandons que les collecteurs de litière soient surélevés par rapport au sol pour éviter de suréchantillonner lors d'épisodes de vents violents. L'utilisation d'équations allométriques propres à chaque espèce, ou même de la surface terrière, pour estimer la composition en espèce de la masse totale de litière peut éviter d'avoir à trier la litière selon l'espèce.

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Introduction

The mass and nutrient content of leaf production and turnover are important for estimating net primary productivity and nutrient cycling budgets in forested ecosystems (Whittaker et al. 1979; Clark et al. 2001). In addition, litterfall fluxes and nutrient concentrations can provide evidence for nutrient limitation and nutrient use efficiency (Vitousek 1982; Aerts 1997). Despite the importance of litterfall mass and nutrient data to ecosystem science and the intensity of effort allocated for obtaining such data, there are very few as-

essments of the temporal and spatial variability in the measurements, which could be used to optimize sampling schemes. There is some information on sampling methods targeted at the number (Finotti et al. 2003), size (McShane et al. 1983; Morrison 1991), and positioning (Hughes et al. 1987) of litterfall collectors and the allocation of sorting effort (Dellenbaugh et al. 2007). Variation across years has been reported (Hughes and Fahey 1994), especially for litterfall mass (Knutson 1997), including the response to drought (Newman et al. 2006). It is perhaps not surprising that in a

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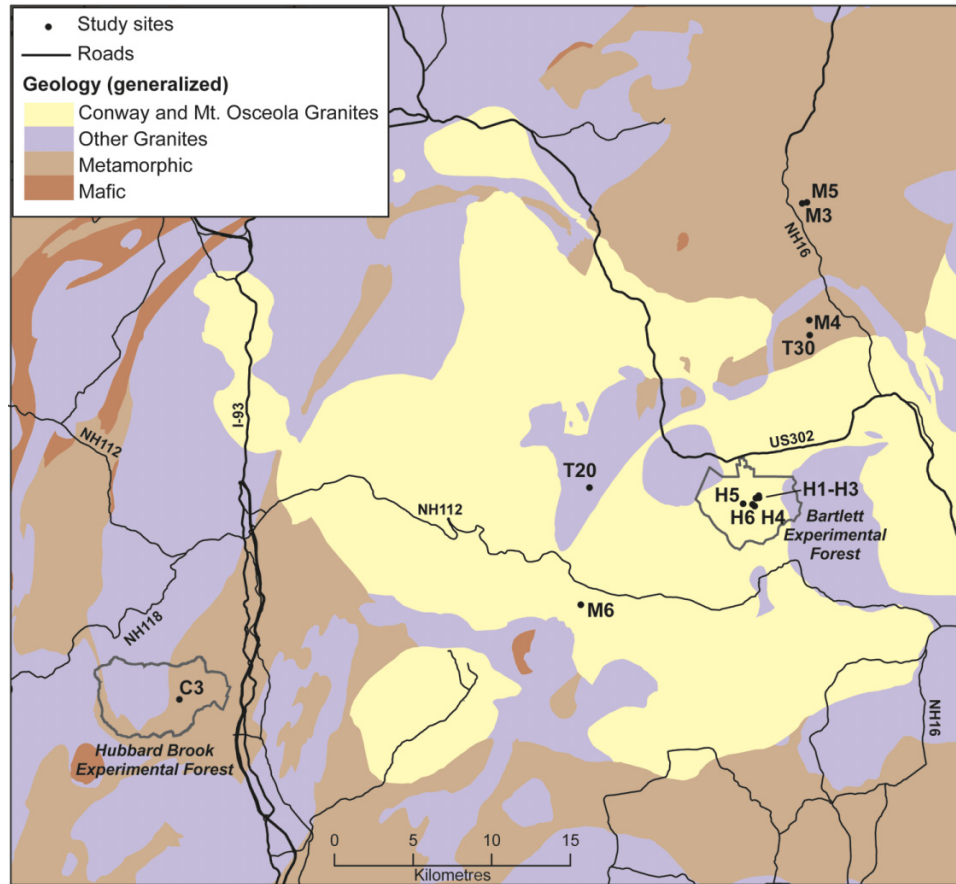
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Fig. 1. Locations of the 13 sites in the White Mountain National Forest showing generalized bedrock geology.



tropical rain forest, both litter mass and nutrient concentration reflect patterns in precipitation (Wood et al. 2005). However, there is no assessment, to our knowledge, of variation in litterfall mass and nutrient concentration across years and sites in temperate forests.

Constructing nutrient cycling budgets for forested ecosystems is time-consuming and expensive if every component must be measured on site. Some parameters, such as the allometric relationships describing tree biomass as a function of diameter, are sufficiently consistent that literature values can be applied to many sites (Jenkins et al. 2004; Fatemi et al. 2011). The mass of leaf litter, because it is constrained by tree allometry, might thus be expected to be predictable based on tree inventory data, although factors such as drought and defoliation could introduce interannual variation. Litterfall mass varied by only about 6% (coefficient of variation) over 5 years in a northern hardwood forest in New Hampshire (Rhoads et al. 2004) and by 10% over 18 years in a deciduous forest in northeast Iowa (Knutson 1997). In a mixed-mesophytic forest in eastern Kentucky, litterfall mass on mesic sites dropped by 50% the year after a severe drought, but not in xeric sites dominated by oak species (Newman et al. 2006). A study of multiple sites for multiple years would shed light on the consistency of litterfall mass over time within sites.

The total mass of leaf litterfall is relatively easy to measure, compared with sorting the collected litter by species,

which is very labor-intensive. Predictions of foliar mass by species through the use of stand inventory, using either basal area by species or the application of species-specific allometric equations, might provide a substitute for direct measurement of the species composition of litter, if not for the total mass.

The nutrient concentrations of plant tissues might be expected to show greater variation across sites than the total litter biomass because leaf area is fairly constant after canopy closure in these forests (Aber 1979). Some species are more sensitive than others to variation in soil nutrient availability. Sugar maple differed more than American beech, for example, in foliar K and Mn in contrasting sites in the Adirondacks, New York (Park and Yanai 2009). Sugar maple is also more responsive to Ca additions on acid soils than are other species (St.Clair et al. 2008).

We analyzed an extensive data set describing the mass and nutrient concentrations of leaf litter of nine northern hardwood species collected in six different years from 13 sites varying in stand age and site conditions. We assessed the variation across years and sites for total mass, mass by species, and nutrient concentration and content. From the point of view of simplifying future research efforts, we hoped to find that variation among years would be less than variation among sites and that the species composition of litterfall was consistent within sites and could be estimated based on stand inventory data.

Methods

Study sites

Leaf litterfall was studied in 13 sites in the northern hardwood forest type in the White Mountains of New Hampshire using a chronosequence established by Tony Federer in 1979 and 1980 (Federer 1984) (Fig. 1). The sites were similar in climate (humid continental), soils (Spodosols formed in granitoid glacial till), and elevation (Table 1). In this analysis, we treat them as 13 replicate sites in the northern hardwood forest type, with age among the sources of variation represented.

In 1993, these sites were relocated and permanently marked, with five measurement transects in each site, following, where possible, transects used earlier to sample the forest floor (Yanai et al. 1999, 2000). Transects were 50 m in length, except in one very small site where transects were only 33 m in length. In most sites, transects were located in areas of 0.25–0.50 ha.

Vegetation was surveyed in 1994–1995 and again in 2003 in each of the 13 sites. Species and diameter at breast height (DBH) of all trees >10 cm DBH were measured in each site. Species and DBH of stems 2–10 cm DBH were recorded in five subplots 2.5 m × 10 m (or 2.5 m × 5 m in the smaller site) per transect.

Litter collection

Fifteen litter baskets were deployed in each site, three on each of the five measurement transects, to assess the mass of leaf litter falling each year. These collectors consisted of plastic laundry baskets with a collecting area of 0.146 m², with the sides of the collectors having a height of approximately 0.35 m, placed on the forest floor and staked to the ground. Baskets were set out in August 1993 and were emptied at the end of the fall, after the bulk of the annual litterfall had fallen, and again in August each year until August 1997, to capture the full year of litterfall mass. In August 2003, similar baskets were set out; these had a collecting area of 0.23 m² and a height of 0.25 m. Litter was collected for 2 more years, using the same seasonal schedule, for a total of 6 years of observation over a period of 12 years.

Additional samples of leaf litter were collected for assessment of litter chemistry by species. We generally did not use the litter in the baskets for chemical analysis, as these samples were exposed to the weather for varying time periods. Instead, we collected fresh leaves falling on tarps during rain-free periods in 1994, 1995, 1996, and 2003. Up to three collections were made each fall and the samples were composited by species for analysis. In 2004, litter was collected frequently from the baskets that were used to collect litter for mass, and samples that fell during a rain-free period in October were used for chemical analysis.

We focused on the nine most important tree species in our sites, which together accounted for 96% of litterfall mass, on average. American beech (*Fagus grandifolia* Ehrh.) and sugar maple (*Acer saccharum* Marsh.) occurred in all sites and were sampled for chemistry in all sites. White birch (*Betula papyrifera* Marsh.), yellow birch (*Betula alleghaniensis* Britton), and red maple (*Acer rubrum* L.) occurred in all sites, but were not always sampled in sites where they were uncommon. Pin cherry (*Prunus pensylvanica* L. f.), white ash (*Fraxinus americana* L.), aspen (*Populus grandidentata*

Michx. and *Populus tremuloides* Michx.), and striped maple (*Acer pensylvanicum* L.) did not occur in all 13 sites, but they contributed significantly to the mass of some sites. The two aspen species were not distinguished in sorting leaves. Gray birch (*Betula populifolia* Marsh.) occurred infrequently and was included with white birch. In 2004, we separated fewer species for chemistry; some minor species that contributed <10% of the total mass in a given site were combined for chemical analysis.

Sample processing

Samples collected from litter baskets for analysis of mass and species composition were often wet when collected; to prevent decomposition, they were stored frozen until they could be processed. After thawing, they were sorted by species, oven dried at 60 °C, and weighed. Twigs, fruits, and other fine litter components were also weighed but are not included in the litterfall masses reported here.

Fresh litter samples collected by species for analysis of chemistry were also oven dried at 60 °C. Dried samples were ground to pass a 20-mesh screen, except for the samples from 2004, which were ground to a fine powder in a SPX CertiPrep 8000 Mixer/Mill (Metuchen, New Jersey). Samples from the 1990s (0.7 g) and 2003 (0.25 g) were ashed at 470 or 500 °C and digested in 6 N HNO₃. For samples from 2004, 0.1 g of each sample was digested in concentrated HNO₃ using high-pressure microwave digestion in reinforced XP-1500 Teflon vessels (MARS 5) (CEM Corporation, Matthews, North Carolina), evaporated to dryness, and redissolved in 5% HNO₃.

Digested solutions were analyzed for Ca, Mg, K, and P on an Atomic Absorption Spectrophotometer 4000 (Perkin-Elmer, Wellesley, Massachusetts) for samples from the 1990s. For samples from 2003 and 2004, digested solutions were analyzed using inductively coupled plasma optical emission spectrometry (ICP-OES) (PE-3300DV) (Perkin Elmer, Shelton, Connecticut, and Norwalk, Connecticut).

Nitrogen was analyzed on samples collected in 1996 and 2004 by total combustion on a LECO 2000 CN analyzer (LECO Corporation, St. Joseph, Michigan).

Estimation of species composition of litter

Leaf mass can be estimated based on stand inventory (tree diameter and species) using allometric analysis. We used equations relating foliar biomass to stem diameter developed by Hocker and Earley (1983) because they included most of the species that we studied. For pin cherry, we used the white birch equation, and for striped maple, we used the sugar maple equation.

Another set of equations (Whittaker et al. 1974; Siccama et al. 1994) was developed at the Hubbard Brook Experimental Forest, where one of our sites was located. These equations described some of the most important species in our study; for the remaining species, we used the substitutions common to biomass calculations at Hubbard Brook (Whittaker et al. 1974). Specifically, to predict white ash and northern red oak (*Quercus rubra* L.), we used the equation for American beech. To predict red maple, striped maple, American basswood (*Tilia americana* L.), and eastern hophornbeam (*Ostrya virginiana* (Mill.) K. Koch), we used the equation for sugar maple. To predict white birch, aspen, and pin cherry,

Table 1. Characteristics of the 13 northern hardwood sites used in this study.

Site	Year cut	Latitude	Longitude	Elevation (m asl)	Aspect	Slope (%)	Year	Basal area (m ² ·ha ⁻¹)		
								<i>Fagus grandifolia</i>	<i>Acer saccharum</i>	<i>Betula papyrifera</i>
H6	1984	44°03'N	71°17'W	330	NNE	12	1994	0.7	0.4	1.6
							2003	2.2	0.7	4.7
M6	1979–1980	44°00'N	71°25'W	540	WNW	19	1994	1.2	1.5	1.2
							2003	2.3	1.3	5.0
M5	1976–1977	44°13'N	71°14'W	630	SSW	28	1994	2.6	6.1	4.1
							2003	3.6	8.5	6.4
C3	1971	43°56'N	71°44'W	520	S	21	1994	0.8	0.9	0.2
							2003	1.6	2.3	0.3
H5	1967	44°03'N	71°17'W	360	NNE	18	1994	3.9	3.4	5.8
							2003	6.4	3.3	6.9
T20	1958	44°04'N	71°25'W	540	ESE	14	1994	8.7	4.5	0.4
							2003	9.7	4.2	0.1
M4	1949–1950	44°09'N	71°14'W	460	NNE	9	1994	5.9	2.5	8.8
							2003	6.5	3.1	10.4
T30	1948	44°09'N	71°14'W	550	NNE	13	1994	6.8	7.1	4.2
							2003	7.6	9.4	3.2
H1	1939	44°03'N	71°17'W	320	Flat	2	1994	2.3	10.3	4.9
							2003	2.9	5.1	6.0
H4	1933–1935	44°03'N	71°17'W	350	NNE	18	1994	2.7	3.9	21.4
							2003	3.8	4.2	18.6
M3	1910	44°13'N	71°15'W	580	SSW	26	1994	12.3	3.0	2.7
							2003	10.7	3.5	2.8
H2	1875	44°03'N	71°17'W	320	Flat	5	1994	5.2	15.6	0.0
							2003	6.6	11.9	0.0

Note: More detailed site descriptions, including logging history, are given in Yanai et al. (2000).

we used the equation for yellow birch. The published equations combine the mass of twigs and foliage; the mass of twigs accounts for about 5% of both together, according to Whittaker et al. (1974), and we omitted this percentage from the predicted foliar mass.

We used the vegetation inventory described above to predict total leaf biomass from tree diameter and species for each of our sites. We made separate calculations based on the 1994–1995 inventory and the 2003 inventory and for the Whittaker and Hocker equations, for a total of four predictions for each of 13 sites. Using paired *t* tests, we compared the 1994–1995 foliar mass predicted by allometric equations with the average observed litterfall biomass measured from 1993 to 1995 for each species. Similarly, we compared the 2003 predictions with the average of litterfall biomass measured in 2003 and 2004. The number of stands in the *t* tests was at most 13, fewer for species that were not present in all of the stands.

In addition to comparing total mass, we wanted to evaluate the accuracy of the allometric equations at distributing litter mass by species. We used the data set from the 1990s for the comparison because it involved 3 years of observation. For each site, we used the proportion of total leaf mass represented by each species predicted by allometric equations to apportion the observed total litter mass to species. We also tested the use of basal area by species to distribute litter mass by species because calculating litter mass from allometry is computationally intensive. We compared the masses by species predicted by allometry or basal area with the ob-

served mass by species and reported the difference as a percentage of the total observed mass.

Statistical analysis

We used repeated-measures analysis of variance (ANOVA) to test for differences in total litterfall mass among sites, with the year of collection as the repeated measure. To compare total litterfall mass and nutrient content across years, we used sites as replicates ($n = 13$) in ANOVA. For each species and nutrient element, we compared litter nutrient concentrations across years using sites as replicates ($n = 13$). We compared means across years using Duncan's multiple range test.

Another approach that we took to describing the variation in litterfall mass and chemistry as a function of species, site, and year was to report coefficients of variation (CVs). The CV is the standard deviation as a percentage of the mean. Because it is unitless, it allows comparison of variation in variables that differ widely in magnitude, as is the case for the concentrations of different nutrients in litter and the mass of litter of different species. The CV can be compared for different numbers of observations because the standard deviation is a measure of the dispersion of the population, unlike the standard error.

To describe the magnitude of the temporal variation in total litterfall mass, we calculated the CV of litterfall mass across years using sites as replicates. To compare the variation in species contributions to mass across years, we computed CVs of mass of each species as a fraction of total mass over time for each of the 13 sites. We calculated the

<i>Betula alleghaniensis</i>	<i>Acer rubrum</i>	<i>Prunus pensylvanica</i>	<i>Fraxinus americana</i>	<i>Populus</i> spp.	<i>Acer pensylvanicum</i>	Other species	Total
1.8	0.01	5.1	0.5	0.03	0.2	0.08	10.5
3.8	0.2	6.4	0.5	0.3	0.3	0	18.9
6.7	0.3	8.1	0.01	0.1	1.4	2.0	22.2
3.7	0.7	9.4	0	0.0	2.9	2.6	27.9
1.1	0	4.6	0.8	0.9	1.8	0.8	22.8
1.4	0.3	3.5	0.9	1.4	0.6	1.0	27.5
7.0	0.01	14.9	0.1	0.3	1.3	0	25.4
9.0	0	13.8	0.3	0.4	2.3	0.09	30.1
2.2	0.07	6.3	1.6	1.4	0.8	0.4	25.8
2.0	0.3	2.1	1.9	1.9	0.3	0.4	25.5
6.7	2.9	0.8	0.1	1.7	0.8	3.1	29.6
7.7	4.0	0.4	0.2	1.6	0.0	1.2	29.1
4.5	1.6	0.05	3.3	1.4	0.8	4.1	33.0
4.1	1.7	0.07	3.9	0.6	0.3	2.5	33.2
4.1	0.1	0.0	4.7	3.2	0.4	0.2	30.6
2.6	0.6	0.0	5.6	2.2	0.3	0	31.5
0.0	10.9	0.0	2.2	2.7	0.0	0.4	33.7
0.1	16.6	0.0	2.7	3.3	0.0	0.02	36.8
0.9	1.1	0.0	0	7.2	0.9	0.1	38.2
2.0	0.6	0.0	0.4	8.1	0.08	0.04	37.8
5.5	5.9	0.0	0	0.3	0.3	1.9	31.9
8.7	4.8	0.0	0	0.3	0.5	2.8	34.1
1.8	0.2	0.0	9.7	0	0	1.4	33.9
1.3	4.8	0.0	9.6	0	0	2.7	36.8

mean CVs for all sites and also for only those sites in which the species under consideration contributed at least 10% of litter mass in all years.

To describe the magnitude of interannual variation in litter chemistry for each element and tree species, we calculated the CV across years ($n = 5$ years) using the average concentration across the sites. To describe the magnitude of variation in litter chemistry across sites, we used a parallel approach, calculating the CV across sites using the average concentration across years ($n = 13$ sites). As in the analysis of interannual variation in mass, we calculated CVs for each species and the average across all species.

To compare the interannual variation in litter chemistry with the intersite variation in litter chemistry, we used ANOVA, for each element, with species as replicates. We also compared the CVs across sites versus years using t tests comparing the average CVs by species, across five elements, and within each element, comparing CVs by species.

Results and discussion

Total leaf litterfall mass

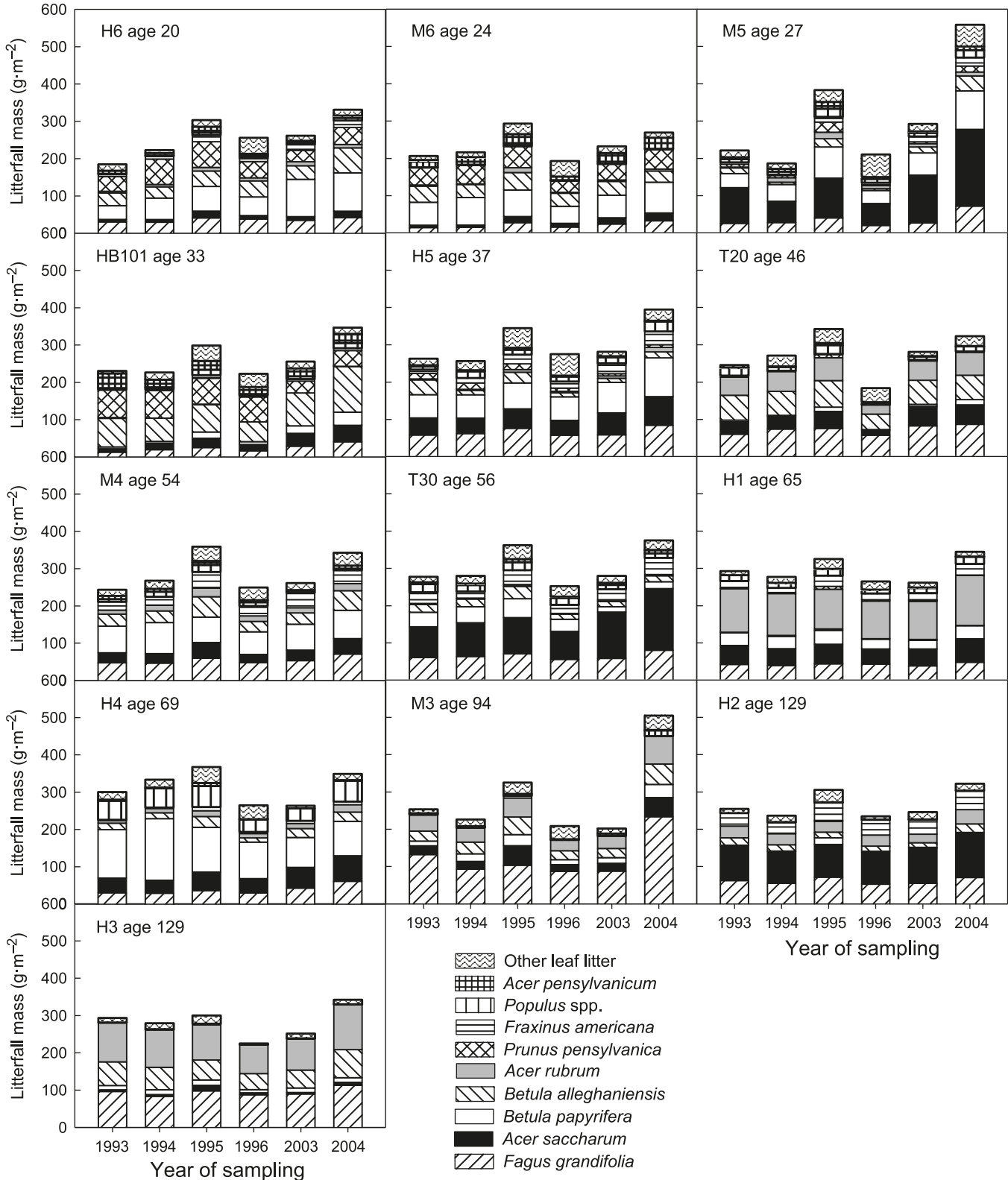
Total leaf litterfall mass varied significantly across our six measurement dates spanning 12 years (Fig. 2). Litter mass averaged across the 13 sites was the highest in 2004, at 370 $\text{g}\cdot\text{m}^{-2}$, which was 58% higher than in the lowest year 1996 (234 $\text{g}\cdot\text{m}^{-2}$). In 1995, litter mass was less than in 2004 but higher than in every other year. The mass of litter collected in 1993, 1994, and 1996 was statistically indistinguish-

able (averaging 246 $\text{g}\cdot\text{m}^{-2}$), while that in 2003 was significantly higher than that in 1996 but lower than that in 1995 and 2004. The CV for total litter mass across years was 21%, on average, across 13 sites.

The variation across sites in leaf litterfall mass was less than the variation across years. The CV for litter mass across sites was 13%, on average, across sampling dates. The site with the lowest litterfall mass (average of six annual measurements in a 12-year period) was a 24-year-old stand (M6), with 235 $\text{g}\cdot\text{m}^{-2}$, and the highest mass was 313 $\text{g}\cdot\text{m}^{-2}$ in a 70-year-old stand (H4), a difference of 33%. In general, litterfall mass was only 5% higher in older stands, averaging 289 $\text{g}\cdot\text{m}^{-2}$ in eight stands >45 years old, than in younger stands, which averaged 274 $\text{g}\cdot\text{m}^{-2}$ in five stands <45 years old ($P = 0.14$).

The high interannual variation that we found in leaf litterfall suggests that repeated sampling is important for accurate estimation of long-term fluxes. One possible source of interannual variation in litterfall mass is measurement error. In particular, if the litter collectors are low to the ground, litter is apt to blow into the baskets, and is less likely to be blown out, due to the smaller fetch (Morrison 1991). On 1 October 1995, there was an exceptionally windy storm event after a 5-day dry period. In 2004, there was a windy period from 10 to 14 October following a period of exceptionally dry weather. These two years stood out as having the highest litter mass in the record (Fig. 2). Note also that the highest masses that we ever recorded were in the two stands with the steepest slopes, M3 and M5 (Table 1), which could contribute to

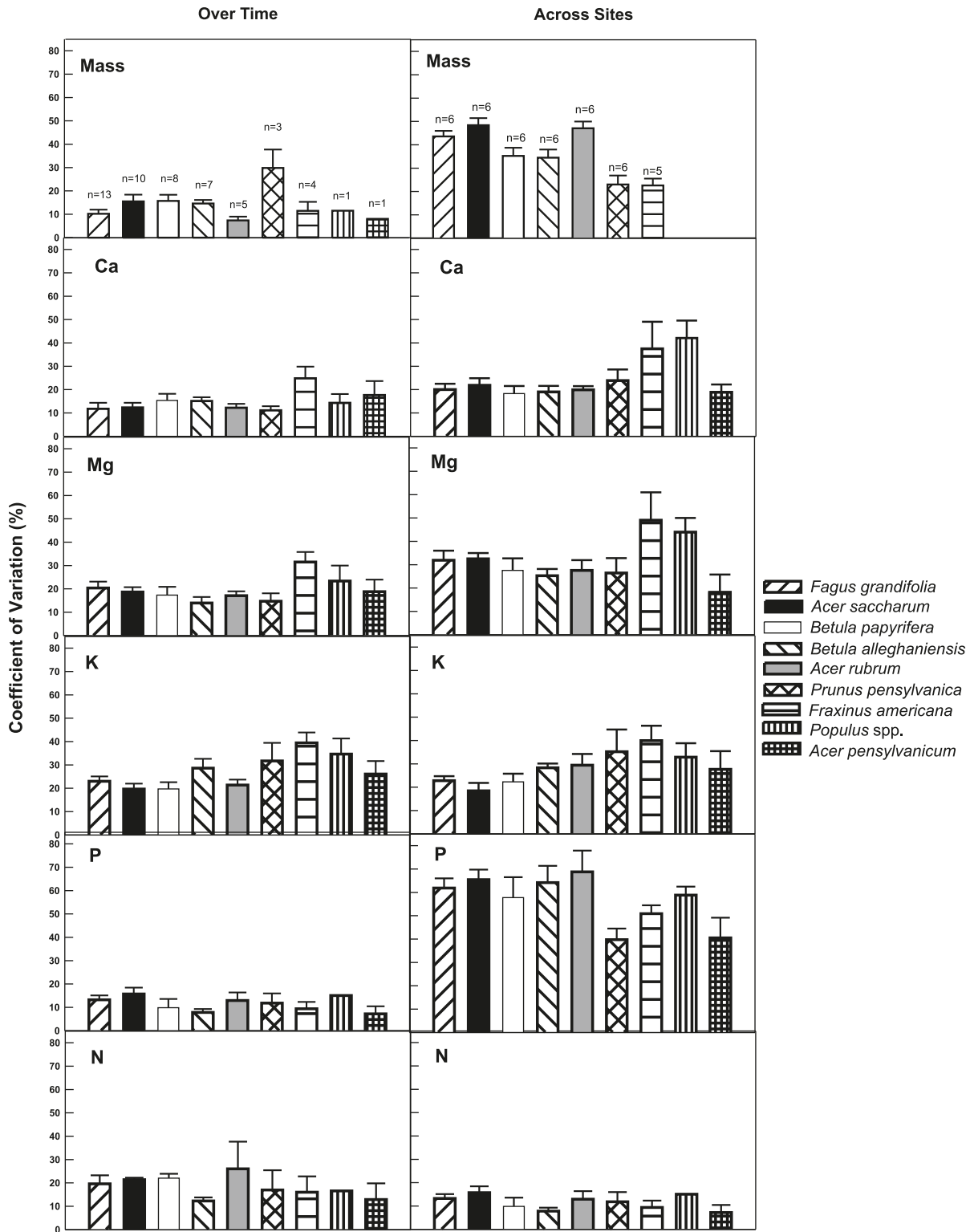
Fig. 2. Annual leaf litterfall biomass over six years of observation, stacked by species, for each of 13 sites of New Hampshire northern hardwoods. The sites are ordered from youngest to oldest in stand age, with the age in 2003 given after the site designation in each panel.



greater movement of litter that had already fallen. The design of litterfall collectors can help reduce spurious interannual variation (Hughes et al. 1987). Natural interannual variation,

such as that induced by drought (Le Dantec et al. 2000; Newman et al. 2006), can be estimated only by repeated sampling.

Fig. 3. Coefficients of variation in litterfall mass and nutrient concentration by species across sites (up to 13 sites averaged over n years) and over time (five collection years from 1994 to 2004 averaged over n sites). See Table 2 for the number of sites for each year and species (not all species appear in all sites and minor species were not collected in the later years).



Species composition of litterfall

The species composition of leaf litterfall differed dramatically across the sites in our study (Fig. 2). Some differences were associated with successional dynamics in northern hard-

woods; specifically, pin cherry and striped maple were most abundant in stands <40 years old (Table 1). Birches and aspen were present in stands of all age classes. Older stands were dominated by a variety of species, with the differences

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Fig. 4. Observed litterfall mass (average of 1994, 1995, and 1996) in 13 sites compared with foliar biomass estimated by allometric equations (Whittaker et al. 1974; Hocker and Earley 1983) using stand inventory data collected in 1994 and 1995.

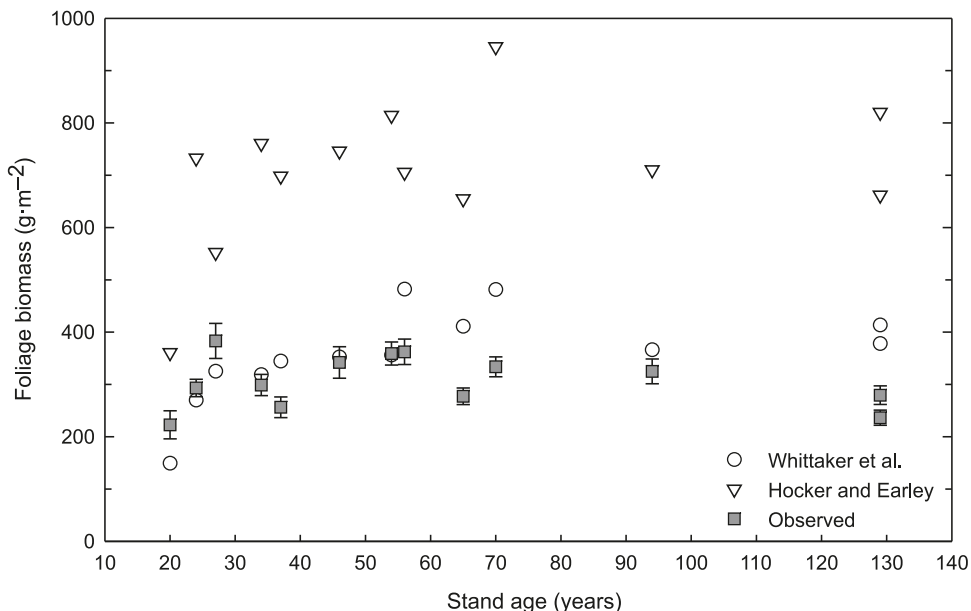
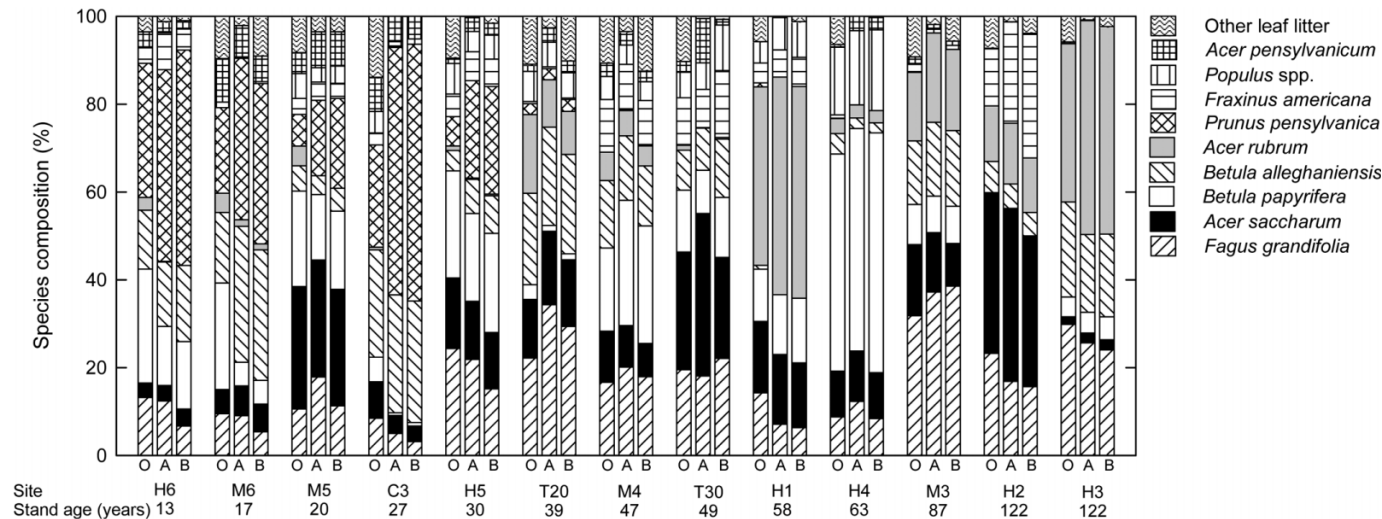


Fig. 5. Species composition of litter in the 13 sites based on the observed masses in the litter baskets (“O”) averaged for 1994, 1995, and 1996 and the predicted mass based on allometric equations (Whittaker et al. 1974) applied to stand inventory from 1994 to 1995 (“A”) or basal area (“B”). Age since clearcutting pertains to 1995.



not readily explained by age or location. For example, of the two oldest sites at Bartlett, H3 had red maple and H2 had sugar maple as the species accounting for the greatest fraction of basal area and leaf litterfall mass (Table 1; Fig. 2). Of the two sites at Bartlett 65–70 years old, H1 had red maple and H4 had white birch as the most dominant species (Table 1; Fig. 2). We described the variation in species composition across sites using the CV by species. We controlled for the annual variation in total mass by analyzing the proportion of the total mass contributed by each species.

Within sites, the species composition of leaf litter was relatively consistent over the time frame of our study (12 years) (Fig. 2). The average across 13 sites for the CV of this proportion across years was lowest for American beech (25%),

yellow birch (35%), and sugar maple (38%), which were three of the most dominant species (Fig. 2). The average CVs were very high for species that were present in small amounts in some sites: 69%–103% for striped maple and pin cherry and 73%–77% for white ash and aspen.

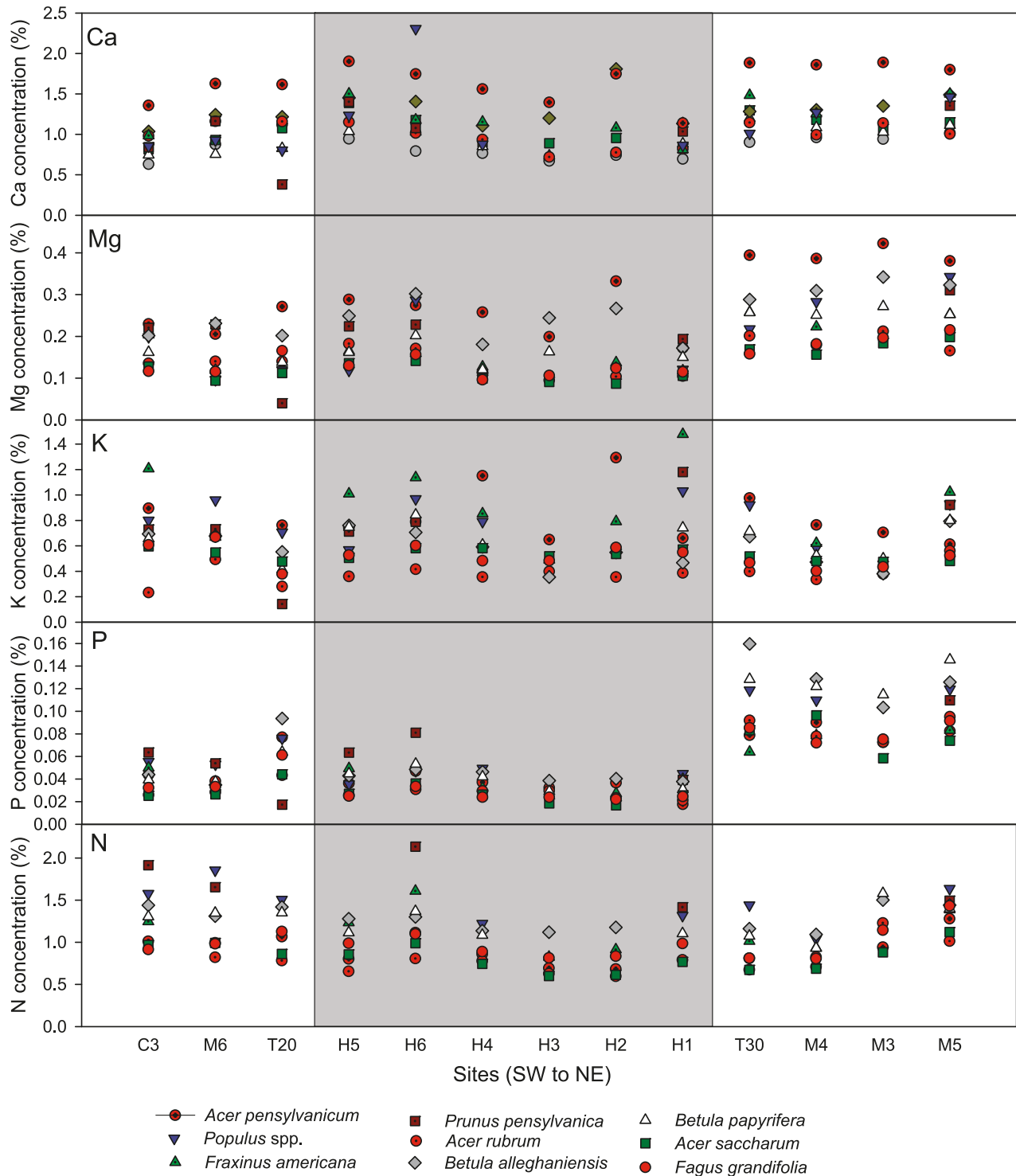
To reduce the effect of variation in small masses of relatively unimportant species, we repeated this analysis for only those sites in which the species in question contributed at least 10% of litter mass (Fig. 3). The average CV across these nine species for sites in which they were important was 14%. Pin cherry consistently contributed more than 10% of litter mass in only three sites (Fig. 2). It had the greatest variation in contribution to litter mass across years (30%), which reflects successional replacement of this short-lived species

Table 2. Nutrient concentrations of leaf litter of nine tree species over 5 years of collection.

Concentration (mg·g ⁻¹)	Year	<i>Fagus grandifolia</i>	<i>Acer saccharum</i>	<i>Betula papyrifera</i>	<i>Betula alleghaniensis</i>	<i>Acer rubrum</i>	<i>Prunus pensylvanica</i>	<i>Fraxinus americana</i>	<i>Populus</i> spp.	<i>Acer pensylvanicum</i>
Ca	1994	8.6ab (0.3)	11.2a (0.4)	10.1a (0.5)	13.1a (1.0)	8.5b (1.0)	11.4a (0.8)	13.0a (0.7)	11.3a (2.2)	17.8a (0.5)
	1995	8.0ab (0.5)	10.2a (0.6)	9.1a (0.5)	13.0a (0.6)	9.6ab (0.5)	10.8a (0.7)	12.2a (0.9)	12.7a (2.4)	14.6a (1.1)
	1996	8.8ab (0.4)	10.8a (0.5)	8.8a (0.6)	13.2a (0.6)	10.2ab(0.5)	10.7a (0.8)	13.0a (0.9)	10.8a (0.9)	17.9a (0.7)
	2003	7.4b (0.3)	8.2b (0.6)	9.4a (1.8)	10.5b (0.5)	9.5ab (0.9)	12.3a (1.6)	10.4a (2.1)	8.1a (1.3)	15.7a (1.7)
	2004	9.1a (0.7)	10.3a (0.7)	9.8a (0.8)	14.2a (0.5)	10.6a (0.5)	11.7a (1.9)	10.6a (2.9)	9.9a (na)	14.2a (1.9)
K	1994	6.1a (0.3)	5.5b (0.2)	7.2a (0.4)	6.7a (0.5)	4.0a (0.4)	8.7ab (1.1)	11.2a (1.5)	7.3a (0.8)	8.0ab (0.5)
	1995	5.0a (0.3)	5.1bc (0.2)	5.8ab (0.4)	5.9a (0.6)	3.8a (0.3)	9.6a (0.6)	11.1a (1.2)	9.3a (1.6)	8.3ab (1.0)
	1996	5.5a (0.4)	6.6a (0.3)	7.1a (0.6)	7.3a (0.7)	4.3a (0.2)	10.1a (0.7)	11.0a (1.1)	8.0a (0.7)	8.9a (0.6)
	2003	5.5a (0.4)	5.3bc (0.3)	6.1ab (0.6)	6.4a (0.7)	4.0a (0.6)	6.5bc (1.6)	7.2ab (1.0)	7.2a (1.1)	5.5ab (1.3)
	2004	4.0b (0.2)	4.7c (0.3)	5.6b (0.4)	4.1b (0.3)	3.9a (0.3)	3.9c (0.9)	3.5b (0.6)	6.4a (na)	5.0b (0.1)
Mg	1994	1.7a (0.1)	1.5a (0.1)	2.1a (0.2)	2.7a (0.2)	1.4ab (0.1)	2.4a (0.3)	2.2a (0.2)	2.6a (0.5)	3.2a (0.1)
	1995	1.5ab (0.1)	1.4a (0.1)	1.9a (0.1)	2.7a (0.1)	1.7a (0.2)	2.6a (0.2)	2.0ab (0.2)	2.0a (0.3)	2.9ab (0.3)
	1996	1.3b (0.1)	1.2ab (0.1)	1.7a (0.2)	2.7a (0.2)	1.5ab (0.1)	2.2a (0.1)	1.8ab (0.2)	1.8a (0.3)	2.9ab (0.2)
	2003	1.2b (0.1)	1.0b (0.1)	1.5a (0.2)	2.1b (0.2)	1.3b (0.1)	2.3a (0.3)	1.6ab (0.3)	1.1a (0.1)	2.6ab (0.3)
	2004	1.4ab (0.2)	1.2ab (0.1)	1.8a (0.2)	2.4ab (0.2)	1.5ab (0.1)	1.9a (0.4)	1.3b (0.5)	1.0a (na)	1.8b (0.0)
P	1994	0.50ab (0.09)	0.46a (0.09)	0.72a (0.13)	0.72a (0.13)	0.45a (0.07)	0.53b (0.06)	0.66a (0.11)	0.71a (0.18)	0.55a (0.07)
	1995	0.29b (0.05)	0.32a (0.07)	0.57a (0.12)	0.58a (0.10)	0.33a (0.07)	0.48b (0.09)	0.42ab (0.06)	0.50a (0.09)	0.41a (0.06)
	1996	0.55a (0.07)	0.53a (0.08)	0.79a (0.14)	0.91a (0.14)	0.56a (0.09)	0.98a (0.16)	0.66a (0.10)	0.93a (0.16)	0.65a (0.07)
	2003	0.55a (0.09)	0.43a (0.10)	0.85a (0.16)	1.00a (0.21)	0.47a (0.11)	0.75ab (0.08)	0.36b (0.05)	0.83a (0.18)	0.56a (0.13)
	2004	0.47ab (0.09)	0.39a (0.07)	0.68a (0.14)	0.70a (0.10)	0.51a (0.09)	0.73ab (0.16)	0.41ab (0.13)	0.43a (na)	0.48a (0.03)
N	1996	10.6 (0.5)	9.1 (0.5)	12.3 (0.8)	13.3 (0.4)	7.9 (0.3)	18.0 (2.0)	12.1 (1.0)	14.7 (0.9)	9.3 (0.5)
	2004	9.3 (0.6)	7.5 (0.5)	12.1 (0.8)	12.5 (0.5)	8.0 (1.0)	17.1 (0.7)	10.0 (0.5)	10.9 (na)	9.8 (0.4)
No. of samples	1994	13	13	12	13	11	6	9	7	13
	1995	13	13	11	12	11	6	9	9	13
	1996	13	13	12	12	12	6	9	9	12
	2003	12	11	8	12	11	5	8	8	5
	2004	13	13	12	13	13	6	4	1	2
N	1996	13	13	10	11	12	5	7	8	12
	2004	12	11	11	11	9	4	4	1	2

Note: The number of sites represented by each mean varies from 1 to 13 depending on the number of sites in which each species was collected in a given year. Standard errors are shown in parentheses, unless the sample size was only 1 ("na"). Means within a species and nutrient element sharing letters do not differ significantly at $\alpha = 0.05$.

Fig. 6. Nutrient concentrations of litterfall by site ordered geographically from southwest to northeast. The sites at Bartlett (shaded) are quite close together (Fig. 1).

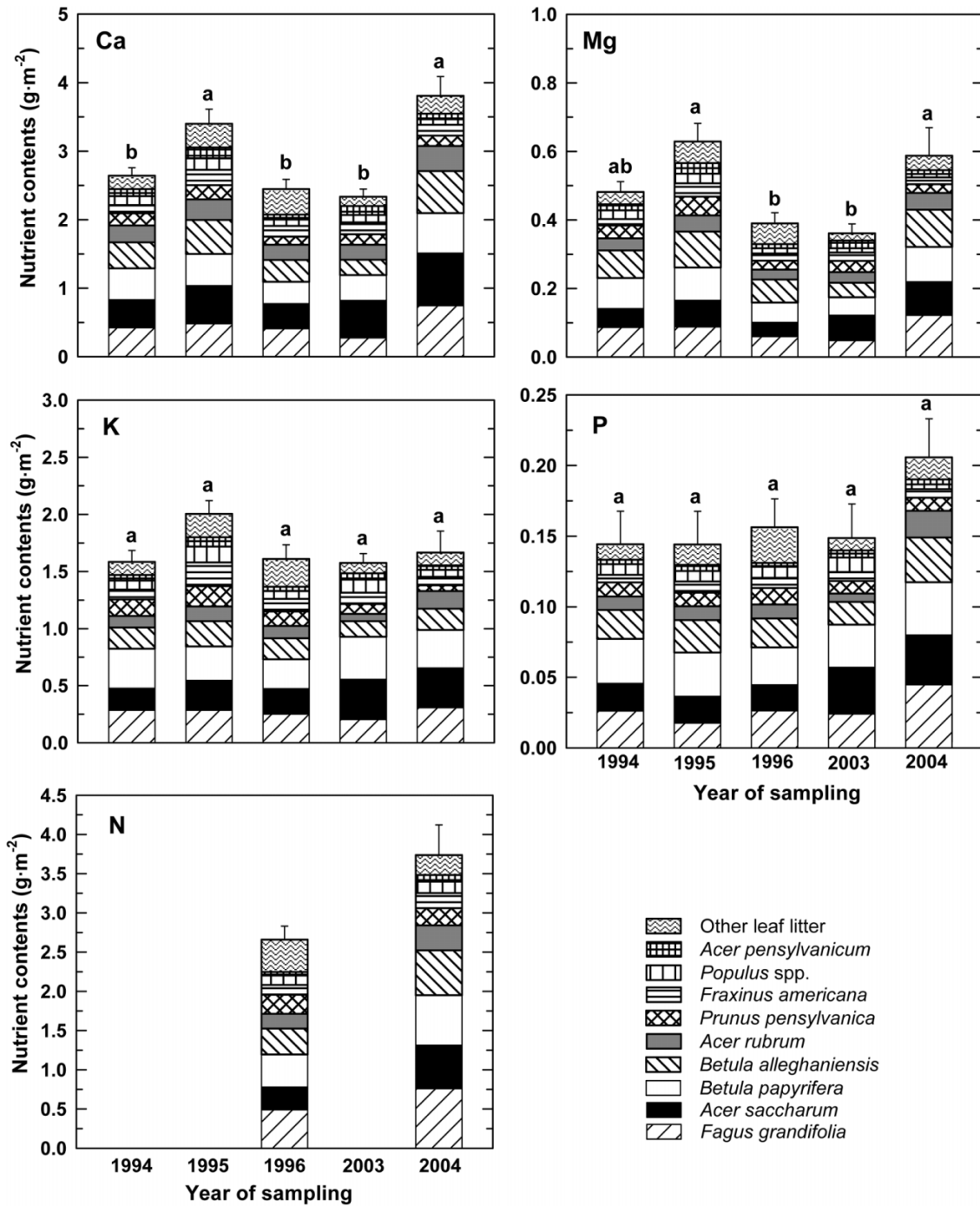


over our 12-year study. With the exception of pin cherry, species composition was fairly stable over time in these northern hardwood forests (Table 1).

We compared our measured leaf litterfall masses with foliar mass predicted by two different sets of allometric equations developed in New Hampshire for northern hardwoods. We had stand inventory data from both 1994–1995 and 2003. The allometric equations of Whittaker et al. (1974) ap-

plied to stand inventory in 1994–1995 overpredicted litterfall mass measured in 1994–1996 by 17%, on average (Fig. 4). The allometric equations by Hocker and Earley (1983) overpredicted litterfall mass by 131%. Hocker and Earley’s (1983) predictions for foliage are known to be high relative to Whittaker et al.’s (1974) and to recent measurements in young stands (Fatemi et al. 2011). Results were similar for the predictions based on 2003 inventory (not shown). About 10%

Fig. 7. Nutrient contents of litterfall for the five years in which nutrient concentrations were measured averaged across 13 sites. Years marked with different letters differed significantly in the nutrient content of litter at $\alpha = 0.05$.



mass loss might be expected between foliage and litter, due to herbivory, resorption, and leaching (Nadelhoffer et al. 1995). An additional mass loss probably occurs in the baskets before collection. Therefore, Whittaker et al.'s (1974) equations could be used to predict litter mass by species in the forests that we sampled with a correction for total mass loss of about 17%.

Total leaf litter mass is not difficult to assess, compared with the effort required to sort litter by species. We tested whether allometric equations could be used to apportion litter mass by species using tree inventory to predict leaf biomass

by species and comparing the predictions with the observed total mass (Fig. 5). We also tried a simpler approach to apportioning litter mass by species using basal area, which is more direct than using allometric equations. Using either approach, the overestimates in mass by species equal the underestimates because we used the observed total mass and distributed this total by species. Averaging across species and stands, the absolute value of the errors was 4.3% (reported relative to total mass) using Whittaker et al.'s (1974) equations (5.3% using Hocker and Earley's (1983), 4.2% using basal area). Pin cherry was overestimated by allometry by

12% (14% by basal area), on average ($P = 0.02$); the other species were not systematically in error. It is possible that the predicted masses are more accurate than our measurements from baskets at the end of the litterfall season, since pin cherry drops its leaves early and is readily decomposed.

We recommend using basal area or allometric equations to apportion the total measured litterfall mass to individual species when these estimates are needed for nutrient flux calculations. We do not recommend using allometric equations to estimate the total litterfall mass, because the allometric equations that we tested gave widely divergent predictions, and because interannual variation in litterfall mass over relatively short periods can be high.

Note that the allometric equations predict a greater increase in foliar biomass from young to old stands than were observed in litterfall (Fig. 4). In young stands, the allometric equations predict less foliage than is measured because equations developed in mature stands describe small trees in subordinate canopy positions (Fatemi et al. 2011). Predicting litterfall fluxes based on allometric equations using the proportion of mass by species avoids this bias.

Interannual variation in litterfall chemistry

Most species had very consistent concentrations of Ca and Mg in leaf litter across our five collection dates spanning 12 years for 13 sites; K and P were more variable by year (Table 2). We calculated CVs across years for each species (Fig. 3): the mean CV was 17% for Ca, 21% for Mg, 28% for K, and 32% for P, averaging across all species. Nitrogen was measured in only two years; the mean CV across species in N concentration was 11%. We calculated the CVs for the other elements based on these two years and found that they were still high compared with N: 13% for Ca, 32% for K, 17% for Mg, and 21% for P. Similarly, a 4-year study of understory English oak (*Quercus robur* L.) found CVs of 18% for N but 36% for P (Covelo et al. 2008). In contrast, a study comparing sugar maple foliage for two years (one wet and one dry) found greater interannual variation in N than in Ca, Mg, K, or P (Horsley et al. 2000).

Calcium concentrations differed significantly across years in four of the species studied, namely American beech, sugar maple, yellow birch, and red maple, with 2003 having the lowest Ca concentrations (Table 2). CVs were relatively low for Ca concentrations in litterfall across years compared with other elements (Fig. 3).

Magnesium concentrations in leaf litter were highest in 1994 and 1995 and lowest in 2003 and 2004; these differences were significant in six of the nine species studied, namely the four species with significant Ca effects plus white ash and striped maple (Table 2).

Potassium varied more than the other base cations across years, as expected due to its greater mobility in plant tissue and high concentrations in throughfall (Hagen-Thorn et al. 2006). All of the species had the lowest K concentrations in 2004, and most had the second lowest in 2003 (Table 2).

For most species, P concentrations were highest in 1996 and lowest in 1995, but the differences across years were significant for only three species (Table 2).

Nitrogen concentrations were measured only in 1996 and 2004; in these two years, N concentrations were quite similar compared with the variations seen in other elements. Only for

sugar maple was the N concentration of litter significantly different between these two years (Table 2). The average CV across 11 sites was 17% for sugar maple. For some species, litter was analyzed for N from very few sites in both years (aspen, striped maple, white ash, and pin cherry) (Table 2). For species for which the two years could be compared in 9–12 sites, the average CVs were 8% for yellow birch, 10% for white birch, 13% for American beech, and 14% for red maple.

The high interannual variation in several nutrients for aspen and white ash was unexpected. These are minor species in our sites and the samples that we analyzed may be less representative than those describing the major species. European ash (*Fraxinus excelsior* L.) has been reported to be more susceptible to leaching of Ca, Mg, and P than *Betula*, *Quercus*, or *Tilia* species (Hagen-Thorn et al. 2006). White ash and aspen also senesce early, and their concentrations may have been changing rapidly during the time that we collected samples for analysis (Killingbeck et al. 1990).

Variation in litter chemistry across years could be due to natural variation in nutrient uptake. The timing and magnitude of nutrient mineralization vary with environmental conditions (Groffman et al. 2009); nutrient uptake rates, too, depend on soil moisture and temperature as well as nutrient availability in soils (Sverdrup et al. 1992). These effects would be difficult to isolate from the variation introduced by sampling, which includes uncertainty due to the timing of leaf collection relative to nutrient resorption and mass loss (Niinemets and Tamm 2005).

Variation among sites in litterfall chemistry

Nutrient concentrations differed significantly across sites within species (Fig. 6). The only exception was for K concentrations in sugar maple and aspen, which were indistinguishable across sites in ANOVA. The magnitude of this variation was greater than the variation across years (Fig. 3) based on a t test of CVs across the five elements ($P = 0.05$).

Within-element variation in nutrient concentrations measured across sites was greater than variation across years for Ca ($P = 0.01$), Mg ($P = 0.001$), and P ($P < 0.001$) based on a comparison of CVs by species. For individual species, intersite variation was significantly greater than interannual variation for Ca in yellow birch and pin cherry, for Mg in white birch and red maple, and for both Ca and Mg in sugar maple and aspen ($P < 0.05$). The sensitivity of sugar maple to site conditions is well known (St.Clair et al. 2008; Park and Yanai 2009; Lucash et al. 2012), but the sensitivities of white ash and aspen have not been previously documented. For K, the variation across years (27%) was similar to the variation among sites (28%) across all species ($P = 0.17$).

Phosphorus showed the greatest variability across sites, and all species were very sensitive to site variation ($P < 0.0001$) (Fig. 3), suggesting the importance of substrate differences in P supply. The primary mineral source of P in parent materials at these sites is apatite, which has been evaluated for four of the sites in this study (Nezat et al. 2008). Apatite in C horizons was 12 times higher at T30 than at M6 or H1, which is consistent with the differences in litter chemistry that we observed (Fig. 6). However, we observed lower P in litter at C3 than at T30 (Fig. 6), while ex-

tractions of C horizon material suggested that there was twice as much apatite present at C3 (Nezat et al. 2008).

Nitrogen variation across sites was much lower than other elements. There is less reason to expect N to vary with site, since the parent material is not a significant source of N, and atmospheric N deposition is probably similar across sites. We did not observe any patterns in the nutrient concentrations of leaf litter as a function of stand age.

Nutrient content

The nutrient content of Ca and Mg in litterfall in the five years in which concentrations were measured (Fig. 7) reflects the interannual pattern in litterfall mass, in that 1995 and 2004 were significantly higher in litterfall nutrient flux for these elements. Potassium and P flux showed no significant differences across years, in spite of the variation in litterfall mass. CVs across years ranged from 21% for K to 26% for Mg.

The variation in nutrient content of litterfall across sites was also high (data not shown). As in the case of nutrient concentrations by species, Ca showed the least variation in content across sites, with an average CV of 19%, and P showed the most (57%). Average CVs of K, Mg, and N were 25%, 30%, and 31%, respectively. This variation across sites in nutrient flux was less than the average variation across sites in nutrient concentration by species (Fig. 3) because the species with the greatest contribution to litterfall mass (Fig. 2) were not the most sensitive to site in nutrient concentration.

Recommendations for measuring litterfall mass and chemistry

Accurate estimation of long-term average litterfall nutrient fluxes requires measuring total litterfall mass. Allometric equations do not agree in their predictions of the long-term average in total mass and therefore cannot substitute for local measurements, unless they can be locally validated. Further, allometric equations will not predict interannual variations in litterfall mass, such as those associated with unusual weather events or other disturbances, that are not due to changes in stand structure. Interannual variation due to sampling bias could probably be reduced by elevating litter collectors above the ground; we observed high litter mass in two years with unusual wind events (very windy or very dry and somewhat windy).

Separating leaf litter collected for mass by species is very time-consuming. Since allometric equations, or even basal area, were good predictors of the proportional contribution of individual species to total litter mass, we suggest that they could be used to estimate the mass of each species as a fraction of the total measured mass, in the case of naturally senescing litter.

Collecting litter for nutrient analysis differs from collecting litter for mass, unless mass collections are very frequent; we collected fresh litter for nutrient analysis only during rain-free periods. It is probably less important to repeat annual measurements of litter chemistry than litter mass; we found most nutrient concentrations to be relatively consistent within site from year to year. Concentrations do vary across sites for the same species, so litter concentrations should be measured at each site.

In summary, the results of our study suggest that total mass should be measured, but shortcuts may be warranted in estimating species composition. If the uncertainty introduced by estimates of species composition is acceptable, then nutrient fluxes could be estimated from measured chemistry and measured total masses distributed to species based on basal area or allometric equations. In any setting, collecting preliminary information on sources of variation can help improve designs for data collection and analysis.

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