NOTES

A plot-based method for rapid estimation of forest canopy chemistry

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Abstract: In this study we present a rapid method to scale the leaf-level chemistry of forest stands to the whole-canopy level. The method combines simple leaf-level measurements of mass and chemistry with a camera-based technique to estimate the fractional distribution of species' foliage area in a forest canopy. Results using this methodology for the estimation of whole-canopy N concentration (g/100 g) are presented and are shown to be comparable with those derived directly from litter fall collection. The ability to efficiently scale leaf-level traits to whole forest canopies enhances our ability to examine key relationships associated with these traits at various levels from the leaf to the forest stand and, with remote sensing technologies, to larger landscapes.

Résumé : Cette étude présente une méthode rapide pour transposer les caractéristiques chimiques de la feuille au niveau de l'ensemble du couvert dans les peuplements forestiers. La méthode combine la mesure de la masse et des caractéristiques chimiques au niveau d'une simple feuille avec une technique utilisant une caméra pour estimer la proportion du couvert forestier occupée par la surface foliaire de chaque espèce. Dans le cas de la concentration (g/100 g) globale de N dans le couvert forestier, les résultats obtenus par cette méthode sont comparables à ceux qui découlent directement du captage de litière. La possibilité de transposer efficacement les caractéristiques d'une feuille à l'ensemble du couvert forestier augmente notre capacité d'étudier les relations fondamentales associées à ces caractéristiques à diverses échelles, de la feuille jusqu'au peuplement et, à l'aide des techniques de télédétection, à des paysages plus vastes.

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Introduction

The chemical composition of forest canopies can provide useful indicators of a number of important ecosystem processes. A large and growing body of literature documents strong linkages among foliar chemistry, particularly N and lignin, and rates of decomposition, N cycling, and productivity (e.g., Aber and Mellilo 1982; Pastor et al. 1984; Yin 1992; Matson et al. 1994; Scott and Binkley 1997; Reich et al. 1999; Ollinger et al. 2001). Studies that have examined other nutrients such as P, Ca, and Mg have demonstrated correlations between foliar concentrations and soil concentrations, tree growth, crown condition, or physiological function (e.g., Cronan and Grigal 1995; Hallett et al. 1997; Reich and Schoettle 1998). Remote sensing studies employing emerging hyperspectral technologies demonstrate the capacity for accurate estimation of whole forest canopy nitrogen (N) and lignin concentration across broad spatial scales that can be linked, directly or through models, to forest ecosystem processes including growth and N cycling (Wessman et al. 1988; Martin and Aber 1997; Smith 2000; Ollinger et al. 2001).

Effective use of such relationships as indicators of ecological process or nutrient status requires efficient and accurate methods to measure foliar chemistry at the leaf level and similarly efficient and accurate methods to scale leaf-level chemistry to whole forest canopies. Near-infrared reflectance spectroscopy (NIRS) provides a rapid, accurate, and low-cost method for estimation of many leaf-level foliar constituents including concentration of N, lignin, and cellulose (McLellan et al. 1991; Bolster et al. 1996; Gillion et al. 1999) as well as elemental content of Al, Ca, Mn, and Mg (Hallett et al. 1997). In contrast, whole-canopy estimates are often both labor and time intensive to produce, because scaling requires knowledge of stand-level canopy leaf mass or area and the proportional contribution of each species to total leaf area and mass. Estimates are typically derived by collection of litter fall from fixed-area plots over one or more growing seasons to make direct measurement of canopy mass and area. Labor and time constraints typically limit such collections to small sample sizes. Alternative estimation techniques include those based on estimation of total or cumulative leaf area index (LAI) derived from light transmission measurements (e.g., Matson et al. 1994) and those based on optical quadrat sampling of forest canopies (e.g., Peterson et al. 1989).

Matson et al. (1994) combined estimates of total maxi-

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mum LAI, derived from light transmission measurements, with mean leaf-level chemistry and whole-canopy average leaf mass per area (LMA) to derive estimates of total canopy chemical content in seven forest stands (six coniferous and one deciduous). The light-transmission-based LAI estimation technique assumes that foliage is distributed randomly in a forest canopy. When foliage is clustered, as is characteristic of many forest types, this method underestimates total leaf area (Kucharik et al. 1999). Additionally, leaf-level chemistry and LMA can differ widely among species. Absent estimates of the proportional distribution of LAI by species, this technique is most appropriate in predominantly single-species or single-functional-type stands, where differences among species in leaf-level chemistry and LMA are minimized.

Peterson et al. (1989) estimated total canopy nutrient content of mixed deciduous and coniferous forest stands in Wisconsin by weighting green-leaf chemical concentrations by the proportion of leaf area in each height class and multiplying weighted averages by total leaf mass from litter fall data. Proportion of leaf area by height was estimated using the camera-based optical quadrat method of MacArthur and Horn (1969) and Aber (1979*a*). Measurements were made with a tripod-mounted camera equipped with a telephoto lens calibrated to distance. As with light-transmission measurements, this technique assumes foliage is randomly distributed throughout a forest canopy and, as such, also underestimates total leaf area when foliage is clustered. However, as underestimation is constant at all canopy levels, relative leaf area profiles can be derived that accurately describe the proportion of leaf area by height through a canopy (Aber 1979*a*). Reliance on litter fall based measures of leaf mass, however, reduces sampling efficiency.

In this paper we present an alternative, more rapid method to scale leaf-level chemical content to canopy scales by combining the camera-based optical quadrat technique to estimate the fractional distribution of foliage area by species in a forest canopy with leaf-level measurements of LMA and chemistry derived from green-leaf sampling. A comparison of results using this methodology with an annual litter fall based approach for the estimation of whole-canopy N concentration (g/100 g) is presented.

Methods

Study area

The study was conducted on the Bartlett Experimental Forest (BEF) that lies within the White Mountain National Forest in north-central New Hampshire, U.S.A. Established in 1932 by the USDA Forest Service as an experimental and forest management demonstration area, the BEF is a 1052-ha tract of secondary successional deciduous and coniferous forest types: northern hardwood (e.g., sugar maple (*Acer saccharum* Marsh.), beech (*Fagus grandifolia* Ehrh.), yellow birch (*Betula alleghaniensis* Britt.), red spruce – balsam fir (*Picea rubens* Sarg. – *Abies balsamea* (L.) Mill.), eastern hemlock (*Tsuga candensis* (L.) Carrière), and red oak – white pine (*Quercus rubra* L. – *Pinus strobus* L.)). Soils are derived from granitic drift and tend to be coarse textured ranging from shallow weathered bedrock to outwash and compact sediments, to basal tills and washed ablational tills (Leak 1982). Elevations on the BEF range from 200 to 850 m. The climate of the southeastern White Mountains is characterized by a relatively short growing season (frost free period of about 120 days) and long, cold winters. Air temperatures at the BEF average –12° and 19°C in January and July, respectively (BEF, unpublished data). Precipitation is evenly distributed throughout the year and averages 120–140 cm, with about one-third in the form of snow.

The BEF has a long history of active forest manipulation that is reflected in a range of successional sequences, forest patch sizes, and structural distributions (Leak and Smith 1996). Forest manipulations that include clear-cutting, group- and individual-tree selection, and shelterwood cutting comprise 50% of the forest. Forest ages in manipulated stands range from more than 80 to less than 5 years old. The remaining half of the forest is unmanipulated. Age of this portion of the forest ranges upwards of 100 years and is characterized by natural forest disturbance regimes. In 1931, 500 one-tenth hectare (32 × 32 m) permanent plots, spaced about 200 by 100 m apart were established throughout the forest. For this study, 18 of these established permanent plots were selected for sampling of canopy composition and chemistry. Plots were chosen to represent a broad range in species composition and stand age (Table 1). Selected plots are part of a larger study directed at the application of hyperspectral remote sensing to analysis of canopy chemistry and ecosystem function at stand to landscape scales (Ollinger et al. 2001; Smith 2000).

Litter fall collection

Eight litter baskets (0.23 m^2) were randomly located in each plot in late summer of 1996. Litter was collected every 2–3 weeks in the fall, once in the spring, and once at the end of the summer of 1997; these samples were composited into a single sample per litter basket prior to sorting. Litter from each basket was air-dried and sorted into leaf and non-leaf litter. Leaf litter was then oven-dried at 70°C for 48 h and weighed. Canopy foliar mass ($g \cdot m^{-2}$) was estimated by combining leaf litter fall data with estimates of leaf retention time. Because broad-leaved deciduous trees shed all of their leaves each year (leaf retention time = 1 year), foliar mass and foliar production are equivalent. For needle-leaved evergreens, foliar mass was calculated by multiplying annual litter fall mass by average leaf longevity (using values taken from the literature (Barnes and Wagner 1981)) to account for leaves retained for greater than one season. We recognize that the ratio of leaf production to litter fall in needle-leaved evergreen dominated forests is not always equivalent from year to year, and so measurements extrapolated from a single year's litter fall may underestimate or overestimate long-term mean leaf production (Gower et al. 1999).

Green-leaf collection

To determine growing season foliar chemistry, midsummer green-leaf samples were collected on each study plot over a 2-day period in August 1997. On each plot, all dominant and codominant species were identified and between two and seven trees per species were selected for green-leaf collection. Leaves were collected by shooting small branches from the canopy with a shotgun. Each sample consisted of leaves collected from several heights in the canopy. For needle-leaved species, no separation was made among needles of different ages. All samples were oven-dried at 70°C for 48 h and then ground with a Wiley mill to pass through a 1-mm mesh screen.

Additional leaf samples were collected from the upper canopies of each dominant or codominant species on each plot to make a determination of LMA for species found on the BEF. The samples were sealed in ziplock™ bags and transported to the laboratory. Leaf area of samples was determined by two methods. For deciduous species, disks of known area (2.035 cm^2) were taken from leaf samples by means of a sharpened metal punch. Five to seven disks per leaf were taken from three to five leaves per species per sample. For conifers, leaf area was determined by optical planimetry.

Table 1. Selected characteristics for 18 stands at the Bartlett Experimental Forest, New Hampshire.

Plot	Species composition[a]	Basal area ($m^2 \cdot ha^{-1}$)	Trees/ha	Stand age (years)[b]	Elevation (m)	Canopy %N[c]	
						Litter	Camera
7V	Red spruce	33.20	640	AA	603	1.13	1.00
7N	Red spruce	51.91	1571	AA	634	1.17	1.11
6N	Red spruce	39.88	1047	AA	658	1.22	1.17
10T	Red spruce, hemlock	52.20	1251	>120	530	1.17	1.05
30AE	Red spruce, white pine	43.30	1650	80–100	241	1.25	1.26
32O	Hemlock, red maple	65.56	1373	AA	293	1.38	1.30
34K	Hemlock, red maple	58.56	1699	AA	308	1.33	1.22
32AH	White pine, red maple	42.84	1245	60–80	219	1.56	1.64
32AF	White pine, hemlock	50.68	1304	100–120	235	1.37	1.35
25M	Sugar maple, white ash	37.90	830	100–120	296	2.04	2.08
24P	Sugar maple, beech, white ash	46.23	1344	80–100	296	2.01	2.02
9D	Sugar maple, beech	37.05	1146	AA	539	1.86	1.88
12H	Sugar maple, beech	38.48	1304	AA	542	2.13	2.15
38Q	Beech	43.94	1630	100–120	317	1.92	1.87
13J	Beech, red oak	41.88	790	AA	567	2.18	2.19
30Y	Red maple, beech	31.32	1250	60–80	268	1.74	1.76
36Z	Red maple, beech, paper birch	37.01	1591	60–80	247	1.74	1.85
30T	Paper birch, yellow birch, pin cherry	27.21	3359	25	290	2.20	2.30

[a] Species comprise >50% of total basal area of plot.

[b] Age is based on initial survey record of BEF (USDA Forest Service, Northeastern Research Station, unpublished data) or on time since last stand replacing silvicultural treatment. AA signifies all-aged, unmanaged stand.

[c] Nitrogen concentration (g/100 g) as estimated from green-leaf sampling and a litter fall collection method (litter) and a camera-based point-quadrat sampling method (camera), respectively.

Fifty to 80 needles per sample were scanned using a high-resolution black and white optical scanner. Image processing software was used to determine needle perimeter based on change in digital number (DN) value across the projected perimeter of each needle. The DN counts below the perimeter threshold based on the scanner resolution (dots per centimetre) yield the projected leaf area.

All area-based measures were calculated for single-sided leaf area.

All leaf samples were dried at 70°C for 48 h and then weighed to the nearest 0.1 mg.

Leaf-level foliar chemistry determination

A visible near-infrared spectrophotometer (NIRSystems 6500 monochromator) was used to determine foliar nitrogen concentration of ovendried, ground, green leaf foliage samples according to the methods described by McLellan et al. (1991) and Bolster et al. (1996). This method uses partial least squares regression equations derived from a calibration data set in which both dried, ground leaf spectra and wet chemistry measurements were available for each sample. It has been demonstrated that the precision and accuracy of these estimates are as good or better than traditional wet chemistry methods (McLellan et al. 1991).

Canopy-level chemistry determination

As N concentration on a mass basis has been shown not to vary significantly in relation to vertical canopy gradients (Ellsworth and Reich 1993), plot-level whole canopy N concentration (g/100 g) can be simply calculated as the mean of foliar N concentrations (g/100 g) for individual species in each stand, weighted by fraction of canopy foliar mass per species.

Determination of canopy species fraction by mass was accomplished by two methods. For the first method, canopy species fraction by mass was calculated directly using litter fall data. For the second method, each species contribution to total canopy mass was determined by means of a camera-based point-quadrat sampling estimation of species' fraction of leaf area (MacArthur and Horn 1969; Aber 1979*a*, 1979*b*) combined with mean leaf-level LMA measurements.

The camera method uses a 35-mm camera with a 135-mm telephoto lens, calibrated to distance in metres, as the sampling device. The lens is used as a range finder and has a grid of 15 points marked on the focusing screen. In each sample plot the camera, mounted on a 1 m tall tripod, is directed upward towards the canopy and leveled. Species and height to lowest leaf covering each grid point is determined by focusing the lens and recording the calibrated distance. Fifteen grid point observations at nine sample points (plot center and each of the four cardinal and off cardinal directions at 15 m from plot center) were taken for a total of 135 observations per plot. Although not an accurate estimator of total leaf area, this method has been demonstrated to be a highly accurate means of determining the relative distribution or fraction of leaf area by height (Aber 1979*a*) and by species (Parker et al. 1989) in a forested canopy.

Using the equation of Aber (1979*a*) we calculated the LAI above a series of heights in the canopy (at 2 m increments from 2 to 38 m):

$$[1] \qquad \mathrm{LAI}_h = \ln\left(\frac{N_h}{S}\right)$$

where h is the canopy height above which LAI is calculated, LAI is the leaf area index above height h, N is the number of leaf intercepts above height h, and S is the total number of sky point intercepts.

From this calculation we determined the LAI within each of the 2-m vertical increments and the fraction of each species within each increment. The LAI attributed to each species was summed through the vertical profile and divided by the total canopy LAI to derive the fraction of total canopy LAI by species.

Fraction of species by leaf area was converted to fraction by weight by multiplying area fraction by measured mean LMA of

Table 2. Mean (with SD given in parentheses) nitrogen concentration (g/100 g) as estimated by near-infrared reflectance spectroscopy in foliage of common northeastern woody species found at the Bartlett Experimental Forest and as reported in the literature.

	Bartlett Forest		Bolster et. al. (1996)	
Species	*N*	Mean	*N*	Mean
Striped maple (*Acer pennsylvanicum* L.)	1	2.24	—	—
Red maple (*Acer rubrum* L.)	33	1.80 (0.29)	94	1.63 (0.31)
Sugar maple (*Acer saccharum* Marsh.)	37	1.82 (0.17)	30	2.08 (0.40)
Yellow birch (*Betula alleghaniensis* Britt.)	15	2.37 (0.26)	7	2.30 (0.19)
Paper birch (*Betula papyrifera* Marsh.)	22	2.26 (0.22)	30	1.95 (0.43)
American beech (*Fagus grandifolia* Ehrh.)	41	2.33 (0.28)	14	2.00 (0.46)
White ash (*Fraxinus americana* L.)	10	2.11 (0.15)	10	2.15 (0.26)
Trembling aspen (*Populus tremuloides* Michx.)	5	2.32 (0.22)	1	2.19
Pin cherry (*Prunus pennsylvanicum* L.)	10	2.93 (0.25)	—	—
Red oak (*Quercus rubra* L.)	13	2.34 (0.10)	94	2.39 (0.42)
Mountain ash (*Sorbus americana* Marsh.)	3	2.97 (0.28)	—	—
American basswood (*Tilia americana* L.)	1	2.80	—	—
Hobblebush (*Viburnum alnifolium* Marsh.)	1	2.00	—	—
Balsam fir (*Abies balsamea* (L.) Mill.)	13	1.56 (0.10)	3	1.19 (0.27)
Red spruce (*Picea rubens* Sarg.)	35	1.08 (0.16)	50	0.93 (0.09)
White pine (*Pinus strobus* L.)	10	1.57 (0.14)	40	1.54 (0.29)
Eastern hemlock (*Tsuga canadensis* (L.) Carrière)	30	1.19 (0.20)	46	1.08 (0.26)

Table 3. Leaf mass per area (LMA) ($g \cdot m^{-2}$) by species and site.

	New Hampshire				Wisconsin, Reich et al. (1999)	
Species	*N*	Bartlett Forest[a]	Massachusetts, Martin (1994)[a,b]	Michigan, Jurik (1986)	Obs. 1	Obs. 2
Striped maple	4	43.97 (10.49)				
Red maple	60	71.30 (11.88)	61.46 (18.30)	70–75	60.24	42.92
Sugar maple	56	62.58 (13.14)	51.83 (15.90)	60	75.19	84.75
Yellow birch	63	66.33 (15.22)				
Paper birch	53	74.40 (12.30)		100		
American beech	54	61.08 (13.88)	31.77 (11.40)	70		
White ash	18	61.32 (7.67)	42.71 (12.72)		75.76	72.76
Trembling aspen	3	65.61 (2.39)		65 (80)		
Pin cherry	8	53.25 (6.00)				
Red oak	6	79.46 (7.46)	76.82 (16.21)	85–110	76.34	74.07
Mountain ash	1	63.97				
American basswood	1	45.50				
Balsam fir	5	203.90 (32.52)				
Red spruce	10	304.67 (41.06)			285.71[c]	
Red pine	1	208.93			250.00	357.14
White pine	5	173.67 (21.07)			175.44	135.14
Eastern hemlock	8	169.87 (25.85)				

[a] Values reported are mean and standard deviation.
[b] Calculated from litter fall.
[c] This value is for white spruce (*Picea glauca* (Moench) Voss), a species that is very similar to red spruce.

each species and deriving a new fraction by weight for each species on sample plots.

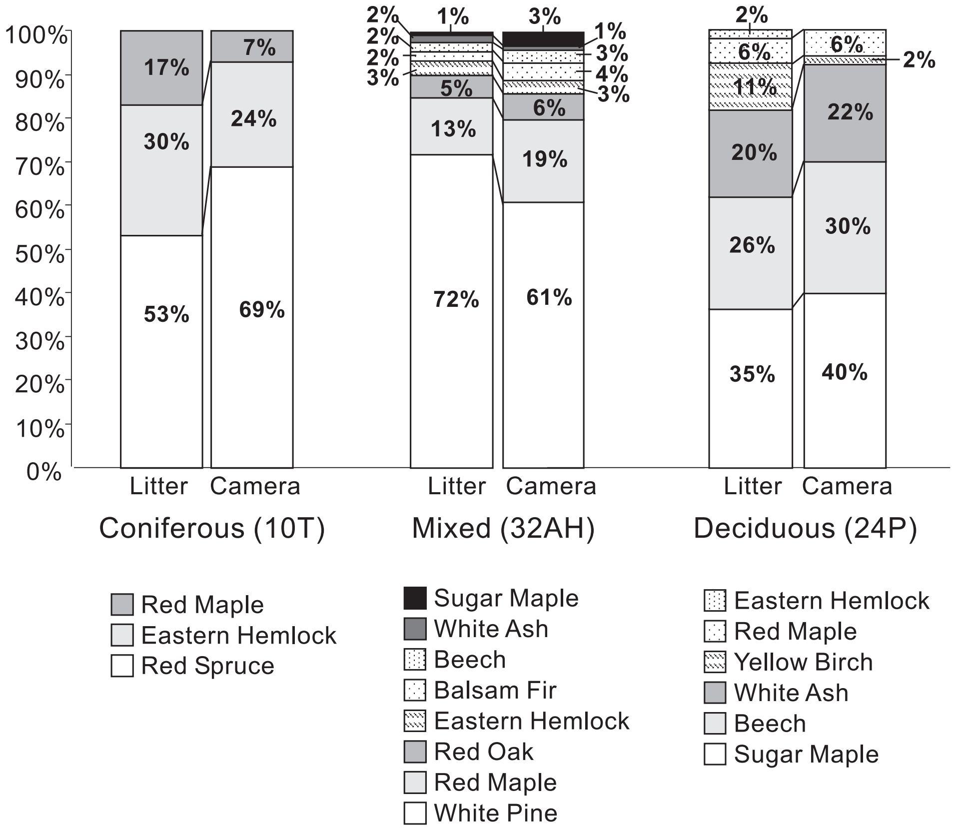
Statistical analysis

All statistical analysis was performed using SYSTAT 7.0 (SPSS, Inc. 1997). We used simple descriptive statistics to characterize mean and variance in the data set. We evaluated correlation between camera- and litter-basket-based estimates of whole canopy nitrogen content using reduced major axis (RMA) regression, a maximum-likelihood estimator when error structure is unknown and arises from both measurement error and natural variation (Leduc 1987).

Results and discussion

Mean species foliar nitrogen concentration (g/100 g) at the leaf-level ranged from 1.08 for red spruce to 2.97 for mountain ash, with nitrogen concentration for needle-leaved evergreen conifers ranging from 1.08 to 1.57 and for broad-leaved deciduous species from 1.80 to 2.97 (Table 1). Values for species mean nitrogen concentration in this study as estimated by NIR spectroscopy were consistent with those reported in an extensive NIR analysis of northern forest species chemistry by Bolster et al. (1996) (Table 2). Likewise, mean values of LMA for both deciduous and conifer-

Fig. 1. Comparison between litter fall (litter) and camera point (camera) based estimates of species' canopy fraction by weight (%) for a coniferous (10T), mixed conifer–hardwood (32AH), and deciduous (24P) sample stand.

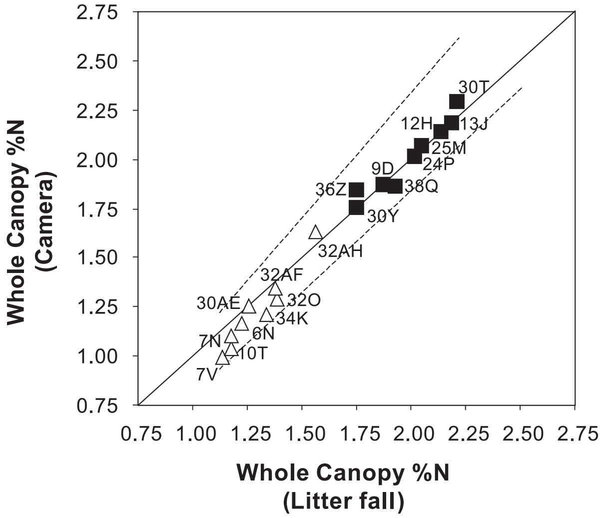


ous species from the BEF were similar to those reported in the literature for these species (Jurik 1986; Martin 1994; Reich et al. 1999) (Table 3).

Figure 1 presents a comparison of species canopy fraction by mass calculated by each method for three representative sample plots of differing canopy composition. Among methods, canopy species identified were nearly identical and fractional estimates were in reasonably close agreement. Comparison of whole canopy N concentrations derived using the camera point versus litter fall methods of calculating species fraction by mass demonstrated highly comparable prediction of mass-based nitrogen concentration among sample plots (Fig. 2). Litter fall collection-based estimates ranged from 1.13 for a red spruce dominated stand (7V) to 2.20 for an early successional stand dominated by paper birch (*Betula papyrifera* Marsh.), yellow birch, and pin cherry (*Prunus pennsylvanicum* L.) (30T). Estimates derived from the camera-based method range from 1.00 to 2.30.

Camera-based estimates of whole-canopy foliar nitrogen concentration for conifer-dominated stands were on average 10% lower than those based on litter fall collection. Although conifer litter fall values were corrected for leaf longevity based on average values as taken from the literature, this correction is likely inadequate for accurate estimation of conifer canopy leaf mass. In conifer-dominated forests, needlefall in a year is not directly related to new growth as in deciduous-dominated forests but rather to the average lifespan of needles as well as to climate conditions over leaf lifespan (Chen et al. 1997). In this study, we believe that correction of needle-fall values by multiplication by literature-based species average needle longevity resulted in underestimation of conifer leaf mass and, hence, conifer leaf mass fraction. Underestimation of conifer leaf mass fraction re-

Fig. 2. Comparison between camera- and litter-fall-based estimation of whole canopy nitrogen concentration (RMA regression: y intercept = –0.225; slope = 1.131, 95% CI = 1.024–1.275). Open triangles represent stands dominated by needle-leaved evergreen species, solid squares are stands dominated by broadleaved deciduous species, the solid line represents the 1:1 relationship, broken lines are the upper and lower bounds of the 95% confidence interval of the slope estimate.



sulted in overestimation of the fraction of higher N content deciduous species, leading to higher overall estimates of whole canopy foliar N concentration. As camera- and litterfall-based estimates of foliar %N were in closer agreement for deciduous-dominated stands where canopy foliar mass and area were equivalent to those derived from litter fall, it may be that the camera-based method is the more accurate of the two approaches for estimation of the proportional distribution of leaf area for a variety of stand compositions.

All field data necessary for camera-based calculation of canopy-level nitrogen concentration can be obtained in about 1 h of field work on each sample plot, in contrast to the weeks or months required for litter fall collection. The rapidity of this method allows many more stands to be sampled during a given growing season than is often logistically possible using litter fall collection. This is particularly significant for remote sensing investigations as it is often the timing, spatial extent, and sample size of ground reference data collection that limits the calibration and validation of spectral data with field based measurements. The ability to scale leaf traits to whole forest canopies enhances our ability to examine key relationships associated with these traits (e.g., foliar N and productive potential) at various levels, from the leaf to the forest stand and, with remote sensing technologies, to larger landscapes.

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References

Aber, J.D. 1979*a*. A method for estimating foliage-height profiles in broad-leaved forests. J. Ecol. **67**: 35–40.

Aber, J.D. 1979*b*. Foliage-height profiles and succession in northern hardwood forests. Ecology, **60**: 18–23.

Aber, J.D., and Mellilo, J.M. 1982. Nitrogen immobilization in decaying hardwood leaf litter as a function of initial nitrogen and lignin content. Can. J. Bot. **60**: 2263–2269.

Barnes, B.V., and Wagner, W.H. 1981. Michigan trees: a guide to the trees of Michigan and the Great Lakes region. University of Michigan Press, Ann Arbor.

Bolster, K.L., Martin, M.E., and Aber, J.D. 1996. Determination of carbon fraction and nitrogen concentration in tree foliage by near infrared reflectance: a comparison of statistical methods. Can. J. For. Res. **26**: 590–600.

Chen, J.M., Rich, P.M., Gower, S.T., Norman, J.M, and Plummer, S. 1997. Leaf area index of boreal forests: theory, techniques, and measurements. J. Geophys. Res. **102**: 29 429 – 29 423.

Cronan, C.S., and Grigal, D.F. 1995. Use of calcium/aluminum ratios as indicators of stress in forest ecosystems. J. Environ. Qual. **24**: 209–226.

Ellsworth, D.S., and Reich, P.B. 1993. Canopy structure and vertical patterns of photosynthesis and related leaf traits in a deciduous forest. Oecologia, **96**: 169–178.

Gillion, D., Houssard, C., and Joffre, R. 1999. Using near infrared reflectance spectroscopy to predict carbon, nitrogen, and phosphorous content in heterogeneous plant material. Oecologia, **118**: 173–182.

Gower, S.T., Kucharik, C.J., and Norman, J.M. 1999. Direct and indirect estimation of leaf area index, f_{APAR}, and net primary production of terrestrial ecosystems. Remote Sens. Environ. **70**(1): 29–51.

Hallett, R.A., Hornbeck, J.W., and Martin, M.E. 1997. Predicting elements in white pine and red oak foliage with visible-near infrared reflectance spectroscopy. J. Near Infrared Spectrosc. **5**: 77–82.

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

Kucharik, C.J, Norman, J.M., and Gower, S.T. 1999. Characterization of radiation regimes in nonrandom forest canopies: theory, measurements, and a simplified modeling approach. Tree Physiol. **19**: 695–706.

Leak, W.B. 1982. Habitat mapping and interpretation in New England. USDA For. Serv. Res. Pap. NE-496.

Leak, W.B., and Smith, M.L. 1996. Sixty years of management and natural disturbance in a New England forested landscape. For. Ecol. Manage. **81**: 63–73.

Leduc, D.J. 1987. A comparative analysis of the reduced major axis technique of fitting lines to bivariate data. Can. J. For. Res. **17**: 654–659.

MacArthur, R.H., and Horn, H.S. 1969. Foliage profile by vertical measurements. Ecology, **50**: 802–804.

Martin, M.E. 1994. Measurements of foliar chemistry using laboratory and airborne high spectral resolution visible and infrared data. Ph.D. thesis, University of New Hampshire, Durham.

Martin, M.E., and Aber, J.D. 1997. High spectral resolution remote sensing of forest canopy lignin, nitrogen, and ecosystem processes. Ecol. Appl. **7**: 431–443.

Matson, P.A., Johnson, L., Billow, C., Miller, J., and Pu, R. 1994. Seasonal patterns and remote spectral estimation of canopy chemistry across the Oregon transect. Ecol. Appl. **4**: 280–298.

McLellan, T.M., Martin, M.E., Aber, J.D., Melillo, J.M., Nadelhoffer, K.J., and Dewey, B. 1991. Comparison of wet chemistry and near infrared reflectance measurements of carbon-fraction and nitrogen concentration of forest foliage. Can. J. For. Res. **21**: 1689–1693.

Ollinger, S.V., Smith, M.L., Martin, M.E., Hallett, R.A., and Aber, J.D. 2001. Regional variation in foliar chemistry and soil nitrogen status among forests of diverse history and composition. Ecology In press.

Parker, G.G., O'Neill, J.P., and Higman, D. 1989. Vertical profile and canopy organization in a mixed deciduous forest. Vegetatio, **85**: 1–11.

Pastor, J., Aber, J.D., McClaugherty, C.A., and Mellilo, J. 1984. Aboveground production and N and P cycling along a nitrogen mineralization gradient on Blackhawk Island, Wisconsin. Ecology, **65**: 256–268.

Reich, P.B., and Schoettle, A.W. 1998. Role of phosphorous and nitrogen in photosynthesis and whole plant carbon gain and nutrient use efficiency in eastern white pine. Oecologia, **77**: 25–33.

Reich, P.B., Ellsworth, D.S., Walters, M.B., Vose, J.M., Gresham, C., Volin, J.C., and Bowman, W.D. 1999. Generality of leaf trait relationships: a test across six biomes. Ecology, **80**: 1955–1969.

Scott, N.A., and Binkley, D. 1997. Foliage litter quality and annual net N mineralization: comparison across North American forest sites. Oecologia, **111**: 151–159.

Smith, M.L. 2000. Landscape-scale prediction of forest productivity by hyperspectral remote sensing of canopy nitrogen. Ph.D. thesis, University of New Hampshire, Durham.

SPSS, Inc. 1997. SYSTAT, version 7.0 ed. SPSS, Inc., Chicago, Ill.

Wessman, C.A., Aber, J.D., Peterson, D.L., and Mellilo, J.M. 1988. Remote sensing of canopy chemistry and nitrogen cycling in temperate forest ecosystems. Nature (London), **333**: 154–156.

Yin, X. 1992. Empirical relationships between temperature and nitrogen availability across North American forests. Can. J. For. Res. **22**: 707–712.