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HIGH SPECTRAL RESOLUTION REMOTE SENSING OF FOREST CANOPY LIGNIN, NITROGEN, AND ECOSYSTEM PROCESSES

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Abstract. Remote sensing of foliar chemistry has been recognized as an important element in producing large-scale, spatially explicit estimates of forest ecosystem function. This study was designed to determine whether data from NASA's Airborne Visible/Infrared Imaging Spectrometer (AVIRIS) could be used to determine forest canopy chemistry at a spatial resolution of 20 m, and if so, to use that information to drive an ecosystem productivity model. Foliage and leaf litter were sampled on 40 plots at Blackhawk Island, Wisconsin, and Harvard Forest, Massachusetts, to determine canopy-level nitrogen and lignin concentrations. At the time of the field sampling, AVIRIS data were acquired for both study areas. Calibration equations were developed, relating nitrogen and lignin to selected first-difference spectral bands ($R^2 = 0.87$ and 0.77, respectively). Calibration equations were evaluated on the basis of inter- and intrasite statistics. These equations were applied to all image pixels to make spatially explicit estimates of canopy nitrogen and lignin for both study sites. These estimates of nitrogen and lignin concentrations were then used with existing models to predict net ecosystem productivity at Harvard Forest and nitrogen mineralization rates at Blackhawk Island.

Key words: AVIRIS; canopy chemistry; ecosystem carbon balance; lignin; nitrogen; remote sensing; spectral resolution.

Introduction

Measurements of nutrient-cycling processes and photosynthesis are critical in assessing the exchange of greenhouse gases occurring between the soil, vegetation, and atmosphere (Mooney et al. 1987, Steudler et al. 1989, Wofsy et al. 1993). Traditionally, such measurements have been made by time-consuming field data collections that provide information on a very small scale. Remote sensing, used in combination with ecosystem models, offers one approach to estimating forest ecosystem function on a regional scale.

Foliar chemical composition is an important forest characteristic, in that it provides information about ecosystem processes and can be remotely sensed (Wessman et al. 1988, Aber and Federer 1992). Field studies have shown a close relationship between the chemical composition of foliage and litter decomposition rates, which affect nutrient cycling (Aber and Melillo 1982, Melillo et al. 1982, McClaugherty et al. 1985, Mc-Claugherty and Berg 1987). Foliar nitrogen is also closely related to the maximum photosynthetic rate (Field and Mooney 1986, Reich et al. 1992). Relationships between canopy chemistry and remotely sensed data have been investigated in a variety of forest ecosystems (Peterson et al. 1988, Wessman et al. 1988, Johnson and Peterson 1991, Johnson et al. 1994, Matson et al. 1994). In these studies, near infrared (NIR) spectral data (1100-2500 nm) have been correlated

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with field-measured foliar chemistry (i.e., nitrogen, lignin, starch). Data for these studies were acquired with the Airborne Imaging Spectrometer (AIS) and the Airborne Visible/Infrared Imaging Spectrometer (AVIR-IS). Although such studies have demonstrated the potential usefulness of remote sensing in estimating foliar chemistry, the use of these estimates to drive ecosystem models has been limited. The primary objectives of the research presented here were to determine relationships between AVIRIS spectral data and field-measured canopy chemical composition, and to use these relationships to derive spatial estimates of canopy chemistry as drivers for ecosystem models. Specifically, we use remotely sensed canopy nitrogen concentrations to drive a carbon balance model (PnET model; Aber and Federer 1992), and canopy lignin concentration to drive a a simple linear model of nitrogen mineralization (Wessman et al. 1988).

METHODS

Field study sites

The data used in this study were collected at the Harvard Forest, Massachusetts, and Blackhawk Island, Wisconsin. Twenty study plots were located at each site, chosen to cover a wide range of species composition and to cover the widest possible range of foliar chemistry.

The Harvard Forest (HF) is located in Petersham, Massachusetts (42°32′ N, 72°11′ W). The plots established at this site are located within an area $\approx 5 \times 10$ km and are distributed throughout both needle-leaved

and broad-leaved stands. These stands are composed of either mixed broad-leaved species: (primarily oak (Quercus rubra), and maple (Acer rubrum), or needle-leaved species: red pine (Pinus resinosa), white pine (P. strobus), Norway spruce (Abies balsamea), larch (Larix laricina), and Eastern hemlock (Tsuga canadensis)). The red pine, Norway spruce, and larch stands were planted, whereas the broad-leaved, white pine, and hemlock stands are naturally occurring. There has been a long history of research at this site, with many recent studies focusing on litter decomposition, nutrient cycling, carbon balance, and trace gas exchange (Aber et al. 1990, 1993, Bowden et al. 1991, Wofsy et al. 1993).

Blackhawk Island (BHI), located in south-central Wisconsin (43°40′ N, 89°45′ W) is a natural area containing a wide range of forest types, including primarily sugar maple (*Acer saccharum*), basswood (*Tilia americana*), black oak (*Quercus velutina*), red and white pine, and hemlock. Blackhawk Island has been the site of a number of studies providing data on soils, litter decomposition, nutrient cycling, net primary production, and remote sensing (Pastor et al. 1982, 1984, Wessman et al. 1988).

Field data collection

Field data collections were made to determine seasonal variations in foliar chemistry and to quantify the chemical composition of the plots used in the AVIRIS analysis.

Seasonal chemistry collection.—In order to determine the seasonal variation of foliar nitrogen and lignin in needle- and broad-leaved species, foliage was collected at ≈3-wk intervals during the 1989 and 1990 growing seasons (1989: 30 June, 19 July, 7 August, 1 September, and 8 October; 1990: 19 June, 10 July, 31 July, 27 August, 18 September, and 16 October). Foliage was collected from individual trees to assess the temporal variability in both foliar nitrogen and lignin. During each sampling, leaves were collected from three trees of each species. Each sample was a composite of leaves from three different heights within the canopy. The samples were analyzed for nitrogen and lignin concentration (percentage of dry mass) using the NIR method of McLellan et al. (1991).

Green leaf collections.—Green leaf samples were collected within 10 d of the AVIRIS overflights to determine the chemistry of each species on each plot (HF: 18–23 June 1992; BHI: 26–29 June 1992). On each plot, we identified all dominant overstory species and selected five trees of each species from which green leaves were collected (the total number of samples per plot ranged from five for the single-species plantation sites to 20 for the mixed broad-leaved sites). Leaves were collected by shooting small branches from the canopy with a shotgun. Each sample consisted of leaves composited from several heights in the canopy. For needle-leaved samples, no separation was made be-

tween needles of different ages. The samples were sealed in ziplock bags and weighed within several hours of collection. The samples were then oven-dried at 70°C for 48 h and reweighed. The fresh and dry sample masses were used to determine water content. After drying, the leaves were ground with a Wiley mill to pass through a 1-mm mesh screen.

Dried and ground leaves were analyzed for chemical composition. Cellulose and lignin were measured using a sequential extraction/digest method (TAPPI 1975, 1976, Effland 1977, McClaugherty et al. 1985, Newman et al. 1995). This method separates carbon compounds into nonpolar extractives (fats, waxes), polar extractives (starches, sugars, simple amino acids, and polyphenols), acid-digestible (cellulose), and acid-insoluble (lignin) fractions. The CHN combustion method (Perkin-Elmer 2400) was used to determine the carbon, nitrogen, and hydrogen content of each sample (Page et al. 1982). A subset of samples was also analyzed for nitrogen concentration using a modified Kjeldahl method. The CHN and Kjeldahl methods produced similar results (Newman et al. 1995).

Litterfall collection.—Litter collection data from September 1992 to August 1993 were used to determine the species composition of the canopy at each plot. Ten litter baskets were randomly placed in each plot on 1 September. The litter was collected from deciduous sites (broad-leaf and larch) through 15 December, when litterfall was complete. Litter from evergreen species was collected through 30 May of the following year to capture both fall and spring litterfall. Litter was collected at 2-3 wk intervals throughout this period, and these individual collections were composited into a single sample per litter basket prior to sorting. Litter was air-dried and sorted by species. All species were identified when possible, with leaf fragments and unidentifiable litter being classified as "no ID". This no ID category averaged <1% of the litter (by mass) in each basket. The litter was then oven-dried at 70°C for 48 h and weighed. Broad-leaf and larch litter mass values were used as measured; for all other litter types, mass values were multiplied by foliar retention time (1 yr of litterfall only represents a portion of the canopy biomass for evergreen species). Canopy-level nitrogen and lignin concentrations were calculated as mean concentration per species (green leaf collection) weighted by foliar mass per species (litter collection). Nitrogen and lignin measured by this method, for each litter basket, resulted in a coefficient of variation (standard deviation/mean) of cv < 5% for >75% of the plots. The cvs for the remaining plots were 5-8% (Tables 1 and 2).

Remote sensing data

AVIRIS data.—The Airborne Visible/Infrared Imaging Spectrometer (AVIRIS) was designed and built by NASA's Jet Propulsion Lab (JPL) to carry out high spectral resolution imaging of the Earth (Porter and

TABLE 1. Description of Harvard Forest plots. Dominant species are listed for each plot. Values for nitrogen, lignin, cellulose, and water are percentages of foliage dry mass as calculated from the green leaf and litter data for each plot. Each quantity is reported as the mean (with 1 sp in parentheses) for the 10 litter basket collections per plot.

Plot	Species	Nitrogen (%)	Lignin (%)	Cellulose (%)	Water (%)	Foliar biomass (kg·ha ⁻¹ ·yr ⁻¹)
1	Red oak, red maple	2.02 (0.02)	25.02 (0.34)	40.11 (0.40)	63.69 (0.21)	2510.75 (275.97)
2	Red maple, red oak	2.03 (0.04)	20.09 (0.82)	36.65 (1.26)	63.29 (0.80)	2347.77 (587.89)
3	Red oak, red maple	2.23 (0.12)	25.68 (0.43)	39.46 (0.69)	62.81 (1.41)	2355.48 (294.57)
4	Sugar maple, red maple	2.18 (0.17)	18.79 (0.75)	39.51 (2.58)	64.21 (1.76)	2675.50 (1009.23)
6	Larch	2.44 (0.06)	29.66 (1.19)	34.09 (0.24)	68.12 (0.81)	3158.42 (219.93)
7	Red pine, Norway spruce	1.25 (0.02)	26.75 (0.65)	38.92 (0.51)	51.28 (2.09)	2812.47 (5624.95)
8	Norway spruce	1.25 (0.01)	25.69 (0.02)	38.96 (0.03)	60.40 (0.03)	15897.70 (6609.41)
9	Hemlock	1.23 (0.11)	15.73 (0.71)	26.77 (1.30)	55.16 (1.17)	6457.05 (1591.17)
10	White pine, hemlock	1.41 (0.05)	22.91 (0.33)	36.25 (0.31)	55.16 (1.08)	3376.09 (363.21)
11	Red oak, red maple	2.23 (0.03)	23.53 (0.99)	39.21 (0.61)	64.69 (1.12)	2713.71 (210.64)
12	Norway spruce	1.36 (0.02)	23.69 (0.12)	41.79 (0.06)	58.62 (0.12)	17516.78 (3401.79)
13	Norway spruce	1.22 (0.01)	25.27 (0.13)	40.83 (0.19)	60.27 (0.02)	16286.02 (7212.80)
14	Red oak, red maple	2.04 (0.04)	23.35 (0.91)	35.74 (0.75)	61.62 (0.74)	2227.43 (936.66)
15	Red pine	1.06 (0.01)	26.17 (0.03)	39.07 (0.04)	55.26 (0.07)	9450.06 (1494.70)
16	Red oak, red maple	2.32 (0.03)	22.17 (0.88)	38.78 (1.22)	62.29 (0.58)	2771.21 (343.14)
17	Red pine	1.21 (0.07)	25.91 (0.15)	39.75 (0.13)	56.03 (0.46)	8635.10 (1230.03)
18	Red oak, red maple	2.33 (0.10)	20.92 (1.05)	39.72 (1.73)	63.57 (1.58)	1933.01 (231.28)
19	Red oak, red maple	1.94 (0.09)	23.32 (1.63)	35.08 (1.29)	59.04 (1.24)	2258.29 (277.78)
20	Red maple	1.86 (0.08)	19.20 (0.87)	33.03 (1.51)	57.97 (1.42)	2097.36 (580.24)
21	Red pine	1.04 (0.05)	25.53 (0.33)	38.19 (0.21)	54.42 (0.91)	9687.06 (1758.75)

Note: There is no plot 5.

Enmark 1987, Vane and Goetz 1988). Flying at an altitude of 20 km on board an ER-2 aircraft, the spatial resolution of this instrument is \approx 20 m, with each scene covering a width of 614 pixels. A spatial image is collected by a cross-track scanning mechanism (perpendicular to the direction of travel) and the forward motion of the aircraft. AVIRIS measures 224 contiguous spectral bands for each picture element (pixel) ranging from 0.4 to 2.4 μ m, with a spectral resolution of 10 nm (Vane et al. 1988). AVIRIS data are received from JPL with radiometric corrections applied. These corrections convert raw AVIRIS digital numbers to radi-

ance values for each pixel (in units of μW·cm⁻²· nm⁻¹·sr⁻¹; Reimer et al. 1987). AVIRIS data were acquired for the Harvard Forest on 15 June 1992, and for Blackhawk Island on 21 June 1992.

Ancillary data collection.—Ground-based reflectance measurements of large, uniform calibration sites (sandpit and water) within the Blackhawk Island scene were made during a period of several days surrounding the flight dates. These data were collected with a GER Mark IV spectroradiometer and were used in a ground-based atmospheric correction (Clark et al. 1993).

Latitude and longitude of features in the Harvard

TABLE 2. Description of Blackhawk Island plots. Dominant species are listed for each plot. Values for nitrogen, lignin, cellulose, and water are percentages of foliage dry mass as calculated from the green leaf and litter data for each plot. Each quantity is reported as the mean (with 1 sp in parentheses) for the 10 litter basket collections per plot.

Plot	Species	Nitrogen (%)	Lignin (%)	Cellulose (%)	Water (%)	Foliar biomass (kg·ha ⁻¹ ·yr ⁻¹)
1	Sugar maple, basswood	2.32 (0.06)	19.35 (1.02)	41.58 (0.70)	60.56 (0.31)	2888.53 (391.61)
2	Basswood, sugar maple	2.61 (0.05)	20.11 (1.10)	44.18 (0.54)	61.26 (0.78)	3326.82 (412.34)
3	Sugar maple, red oak	2.35 (0.07)	20.59 (0.88)	41.91 (0.55)	61.40 (0.56)	3376.77 (628.57)
4	Sugar maple, red oak	2.49(0.08)	19.73 (0.68)	42.55 (0.50)	60.08 (0.36)	2900.90 (519.75)
5	Red oak, poplar	2.39 (0.17)	23.67 (1.24)	40.73 (2.76)	58.65 (1.52)	2789.96 (464.88)
6	White pine, white oak	2.37(0.13)	22.53 (1.49)	42.99 (1.59)	59.18 (0.87)	3443.26 (506.15)
7	Red oak, sugar maple	2.41(0.05)	21.40 (0.95)	42.25 (1.00)	59.65 (0.56)	3228.06 (378.34)
8	Red oak, sugar maple	2.50(0.16)	21.22 (1.10)	41.99 (1.86)	58.53 (1.57)	3182.75 (380.59)
9	Sugar maple, red oak	2.37 (0.10)	20.53 (1.28)	40.02 (0.85)	58.09 (0.50)	3165.93 (670.07)
10	White oak, red maple	2.48(0.10)	21.42 (1.13)	41.22 (2.34)	57.84 (1.31)	2899.03 (372.81)
11	Sugar maple, red oak	2.40(0.07)	20.33 (0.92)	43.06 (0.68)	59.73 (0.99)	3538.42 (681.30)
12	Red maple, red oak	2.37 (0.16)	22.84 (0.93)	40.02 (2.52)	56.95 (1.82)	3286.21 (563.87)
13	Red oak, white pine	2.29 (0.18)	25.73 (0.68)	43.71 (0.65)	56.43 (0.21)	3309.17 (525.23)
14	Red oak, red maple	2.18(0.08)	23.81 (0.60)	39.81 (1.13)	55.12 (0.52)	3275.84 (317.86)
15	Red oak, red maple	2.38 (0.06)	24.12 (0.65)	41.19 (1.08)	56.75 (0.52)	3219.29 (403.30)
16	Red oak, white oak	2.27 (0.06)	23.48 (1.01)	40.76 (0.61)	56.38 (0.29)	3082.47 (636.65)
17	White pine, red oak	1.89 (0.07)	25.68 (0.42)	37.85 (0.36)	55.63 (0.23)	3943.21 (734.41)
18	White pine, red maple	1.91 (0.04)	25.86 (0.28)	37.92 (0.23)	55.89 (0.11)	4020.00 (450.62)
19	Red pine, white pine	1.49 (0.09)	25.78 (0.35)	39.15 (0.12)	56.21 (0.25)	3374.69 (474.60)
20	Red pine, white pine	1.50 (0.07)	26.33 (0.52)	39.06 (0.33)	56.27 (0.31)	3477.68 (616.14)

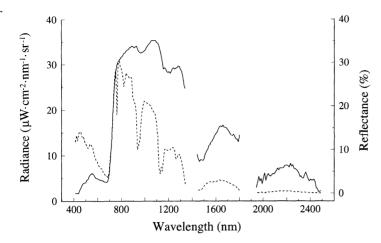


FIG. 1. AVIRIS radiance (- - -) and reflectance (----) spectra for a Blackhawk Island oak stand. Reflectance spectra are derived from radiance spectra using the ATREM atmospheric removal program.

Forest AVIRIS scene were determined with the use of a global positioning system (GPS). A Trimble Pathfinder Professional instrument was used to determine the coordinates of roads and study plots within the AVIRIS scene. Raw GPS data collected as latitude/ longitude were differentially corrected using base station data collected in Lexington, Massachusetts (≈80 km from Harvard Forest). Roads were located that could be identified in the AVIRIS scene for the purpose of geographic registration. Control points (primarily road intersections), distributed throughout the image and corresponding to GPS points, were used to generate a coordinate transformation matrix that enabled the mapping of latitude and longitude to image pixel locations. The root mean squared error of registration was ≈ 1 pixel. Average spectral values for 2×2 pixels centered on each plot location were then extracted from the AVIRIS image cube. Initial plot selection was such that the area surrounding each plot was of similar species composition, to minimize the errors due to pixel/ plot misregistration.

Global positioning data were not available for the Blackhawk Island study site. A digitized map of the island, including accurate locations of the study sites, was registered to the image to determine the pixel locations of the study sites. As with the Harvard Forest data, four pixels were averaged for each sample plot.

Atmospheric corrections.—Accurate transformations of AVIRIS radiance to reflectance at the canopy level must be made before any images acquired at different times can be compared. The accuracy of these corrections is crucial to the viability of remote sensing as an ecosystem-monitoring tool. Numerous atmospheric correction methods were evaluated for AVIRIS data in the context of NASA's Accelerated Canopy Chemistry Program (ACCP). Several of these methods have been applied to AVIRIS data from Blackhawk Island and Harvard Forest. A complete review and comparison of the atmospheric-correction algorithms used in the ACCP can be found in Clark et al. (1993, 1994).

Data from the 21 June 1992 Blackhawk Island scene were atmospherically corrected by Clark et al. (1993) using ground calibration data. This correction incorporated field reflectance spectra measured near Blackhawk Island at the time of the overflight. Using field, laboratory, and AVIRIS spectra measured at calibration sites, offsets and multipliers were derived to transform AVIRIS radiance to ground reflectance. For this study, both Harvard Forest and Blackhawk Island scenes were corrected at the Center for the Study of Earth from Space, University of Colorado, using the ATREM atmospheric-removal program of Gao et al. (1991, 1992). This method uses information within an AVIRIS radiance spectrum to estimate atmospheric water vapor for each pixel, which, in turn, is applied to a radiative transfer model to derive ground reflectance. In order to remove systematic errors in the data corrected by the ATREM model, a secondary correction, based on the difference between specific ground-calibrated Blackhawk Island pixels and the same ATREM-corrected pixels, was applied to all scenes (Clark et al. 1993; K. Heidebrecht, personal communication). Fig. 1 shows an AVIRIS radiance spectrum for a typical mixed broad-leaf pixel, and the same spectrum corrected to reflectance by this method.

DATA ANALYSIS

Seasonal variability in foliar chemistry

A one-way ANOVA was used to determine, for each species, whether or not foliar chemistry varied significantly throughout the growing season. If the ANOVA was significant at the $P \le 0.10$ level, paired t tests were made to determine the adjacent sampling periods between which significant differences occurred (Computing Resource Center 1992).

Correlating AVIRIS data with canopy chemistry data

Relationships between AVIRIS data and field-measured foliar chemical concentration were investigated with multiple linear regression analysis.

A first-difference transformation was used on AVIR-IS reflectance data as shown in Eq. 1:

$$R'(\lambda_i) = R(\lambda_{i+20 \text{ nm}}) - R(\lambda_{i-20 \text{ nm}}), \tag{1}$$

where $R(\lambda_i)$ is the mean reflectance value centered at λ_i for an average of three AVIRIS bands (\approx 30 nm). This first-order difference transformation results in a spectrum in which peaks and valleys correspond with inflection points in the reflectance spectra. This data treatment is similar to that used in laboratory nearinfrared calibrations in both dried and fresh leaves (McLellan et al. 1991, Martin and Aber 1995). The 40-nm gap between the center of the smoothed 30-nm segments provides a center point at which to report the value of the output difference spectra. The bands were selected from the full set of AVIRIS bands, with the exception of \pm 50 nm of the large water absorption features centered at 1450 and 1950 nm.

Regression equations in the form of Eq. 2 were developed using the first 2-4 bands selected by stepwise regression:

Concentration(%) =
$$b_0 + \sum_{i=1}^{n} b_i R'(\lambda_i)$$
, (2)

where $R'(\lambda_i)$ is the first-difference reflectance value centered at λ_i , and b_i is the regression-fitting coefficient for that term. To avoid overfitting, the number of terms used in the regression equation was set to a maximum of four. Resulting calibration equations were evaluated for overfitting, using the criteria of Hrushcka (1987).

Ecosystem modeling

The PnET model (Aber and Federer 1992), originally developed to predict carbon balance for a single plot, was modified for this exercise to make spatially explicit estimates of net ecosystem productivity. This generalized, lumped-parameter model of carbon and water balance (Aber and Federer 1992) has been validated against productivity data for 10 forested sites. A daily time-step version (Aber et al. 1996) has been used to improve basic photosynthesis and respiration algorithms and to validate predictions of whole-canopy carbon balance against daily, summed eddy-correlation measurements made at the Harvard Forest (Wofsy et al. 1993).

Improvements in the basic algorithms have been combined with new, monthly, time-step plant and soil respiration terms to produce PnET-II, an improved version of the full monthly carbon and water balance model (Aber et al. 1995b), which has been validated against water and carbon balance data for the Harvard Forest and Hubbard Brook ecosystems. A primary driver for this model is foliar nitrogen concentration, which is used to predict the maximum photosynthetic rate. Nitrogen concentration was also used to estimate broadand needle-leaved fractions of each pixel in the image. If N concentration >2.2%, the pixel was defined as all

broad-leaf and the model was run with a canopy N concentration equal to the AVIRIS measured value. If the N concentration was <1.28%, the pixel was defined as all needle-leaved and was run with red pine parameters (see Aber and Federer 1992). For pixels between 1.28 and 2.2% N, the model was run twice, once using red pine parameters, and once using broad-leaf parameters and 2.2% N. The final prediction of net ecosystem productivity for each mixed pixel was a weighted mean of the two model runs, with the weighting for broadand needle-leaf canopy fraction a function of AVIRIS-estimated N:

Hardwood fraction =
$$\frac{\%N - 1.28}{2.2 - 1.28}$$
,

and

Pine fraction = 1 - hardwood fraction.

At Blackhawk Island, nitrogen mineralization rates were predicted using a linear relationship between foliar lignin concentration and nitrogen mineralization rate reported by Wessman et al. (1988). Before using this existing model, we transformed our 1992 lignin data to the same scale as that used by Wessman et al. (1988). This correction is necessary because the chemical analysis for lignin varies between the two studies. The differences in lignin analysis occur in the ash content correction; in the data used by Wessman et al. (1988), the lignin analysis was calculated with the assumption that all ash in the initial sample was present in the lignin fraction. In the 1992 lignin analysis, lignin concentration was calculated with the assumption that ash was removed at each step in the extraction process in proportion to mass loss (Newman et al. 1995). We applied the linear relationship reported by Wessman et al. (1988) to the transformed 1992 canopy lignin values to predict nitrogen mineralization rates at Blackhawk Island.

RESULTS AND DISCUSSION

Seasonal leaf collections

Of the three needle-leaved species sampled, only Norway spruce showed significant variation in nitrogen concentration between the different seasonal sampling periods (Table 3). Red pine was the only needle-leaved species to show significant differences in foliar lignin concentration, with a decrease occurring midseason (Fig. 2b). In the red pine samples, needles of all ages were composited into a single sample, with ≈40% of the needles in the 1st-yr class. Lignin concentration drops with the expansion of new leaves, and then increases as these leaves begin to lignify later in the season (Rock et al. 1994). Although the same pattern of leaf expansion and lignification occurs in the 1st-yr needles of hemlock and Norway spruce, only 15-20% are 1st-yr needles, and their influence on sample chemistry is not as strong as in red pine.

TABLE 3. Results of one-way ANOVA for seasonal foliage collections.

			Nitrogen	Lignin		
Species	n	P	t test	P	t test	
Red pine	5	0.8229		0.0346	1:2*, 2:3*	
Hemlock	5	0.3562		0.1508	,	
Norway spruce	5	0.0362	2:3*, 3:4†	0.2454		
Red maple	5	0.0000	4:5*	0.1590		
Red oak	5	0.0086	4:5*	0.0024	1:2*	
White birch	5	0.0001	2:3†, 4:5*	0.0076	4:5*	
Grey birch	6	0.5551		0.0001	1:2*	
Hickory	6	0.0000	5:6*	0.0001	1:2†, 3:4†	
Poplar	6	0.0003	4:5†, 5:6*	0.7171	., .	
Sugar maple	6	0.0012	5:6*	0.0280	1:2*	
American beech	6	0.0002	5:6*	0.0003	1:2*, 2:3*	
Black birch	6	0.0000	1:2*, 2:3*, 4:5*, 5:6*	0.0140	1:2*	

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Notes: P represents the level at which significant differences occurred among the 5-6 collections per species; t test values report the adjacent sampling periods that differed significantly: *, P < 0.05; and †, P < 0.10 levels.

Eight of the nine broad-leaved species showed significant differences in nitrogen concentration between the last two sampling periods. This late-season decrease in foliar nitrogen concentration in broad-leaved species is due to the retranslocation of nitrogen from the foliage prior to leaf senescence (Fig. 2c). Lignin concentrations in broad-leaved species were significantly different between adjacent sampling periods for beech (Fagus grandifolia), gray birch (Betula populifolia), and hickory (Carya ovata) early in the growing season (Table 3).

These foliar chemistry data indicate that, for the species sampled, few significant differences occur in foliar nitrogen and lignin concentration between early July and mid-September. Therefore, samples collected during this period of the growing season could be used in conjunction with remote-sensing data acquired during the same time frame. However, during the early and late growing season, when foliar chemistry is rapidly changing (in some instances, within 3 wk), collections must occur within a short period surrounding the remote-sensing data acquisition.

Canopy-level chemistry

Plot-level data analysis at Blackhawk Island shows an east-west gradient in the concentration of several foliar constituents. This gradient is primarily due to changes in species distribution along an east-west soil and moisture gradient (Pastor et al. 1982). Nitrogen concentration (Fig. 3a) ranges from low (in the west) to high (in the east). Red and white pines on the west side of the island have a lower nitrogen concentration than the oaks and maples throughout the remainder of the island. Highest nitrogen concentrations occur in mixed stands of sugar maple/basswood near the east end of the island. In contrast, total nitrogen (Fig. 3b) varies less across the island, since multiple-year foliar retention in the low-nitrogen pines results in higher foliar biomass than for deciduous species, and a more even distribution of nitrogen content across the island.

Carbon fraction concentrations vary across the is-

land, with lignin values ranging from a high of 26% (in the west) to a low of 19% (in the east) (Fig. 3c). Cellulose concentrations (Fig. 3d) are highly variable on each plot. However, the *total* concentration of insoluble carbon compounds (cellulose plus lignin; Fig. 3e) is relatively constant across the island, indicating a difference in the allocation patterns of carbon to structural molecules. Water fraction varies only slightly across the island (Fig. 3f), with concentrations slightly lower in the red and white pines, intermediate in oaks, and highest in sugar maples.

AVIRIS and field data correlations

The initial analysis of field and remote-sensing data was done for each site (Blackhawk Island and Harvard Forest) individually. In this analysis, the AVIRIS data from 20 plots at each site were correlated with the field data. The resulting equations were then used to predict canopy chemistry at the other site to test the generality of the relationships. A further analysis of the data combined all 40 plots from the two study sites.

Harvard Forest.—A two-term equation predicting nitrogen was developed between the AVIRIS first-difference reflectance data and field-measured nitrogen concentration at Harvard Forest (Table 4). The two bands used in this equation are centered at 750 and 2140 nm. Absorption in the 700-nm region of the spectrum is related to foliar chlorophyll concentration (Gates et al. 1965). Chlorophyll content in foliage is highly correlated with total protein and, hence, total nitrogen content (Field and Mooney 1986). Numerous studies have shown that the slope of both laboratory and remotely sensed spectra in this red-edge region is sensitive to chlorophyll concentration (Horler et al. 1988, Rock et al. 1988, Moss and Rock 1991, Curran and Kupiec 1995). Card et al. (1988) have also reported the use of this 750-nm band in protein calibration equations for leaf samples of mixed species. Absorption in the spectral region from 2110 to 2200 nm has also been attributed to N-H bonds in amino acids and proteins (Osborne and Fearn 1986).

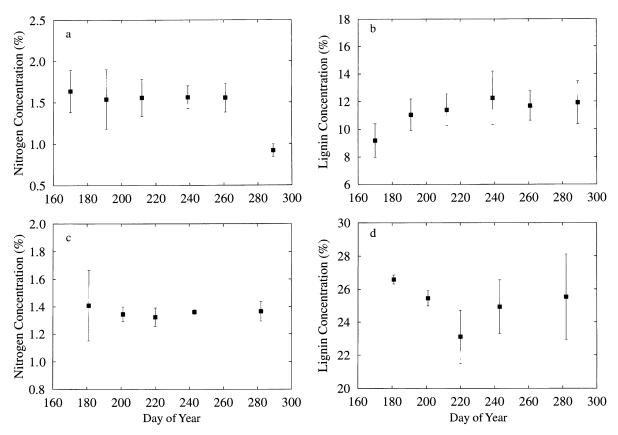


Fig. 2. Seasonal variation in foliar concentrations for sugar maple: (a) nitrogen, and (b) lignin; and for red pine: (c) nitrogen, and (d) lignin. Error bars depict ± 1 sp.

A four-term equation relating AVIRIS data to canopy lignin concentration used bands in the range of 1660-2280 nm (Table 4). Absorption in this region has been attributed to a number of different molecular bonds: 1620-1685 nm, C-H aromatic; 1740 nm, C-H and O-H; 1900 nm, O-H C-O combination; 2280 nm, C-H (Osborne and Fearn 1986, Murray and Williams 1987, Curran 1989). Validations of the calibration equations were assessed by an iterative cross-validation method in which each sample, in turn, was dropped from the calibration process and was predicted from the resulting equation (Mark and Workman 1991). These crossvalidation results show that the standard errors of cross validation for samples not included in the calibration are only slightly higher than the standard errors of calibration (Table 4).

Blackhawk Island.—The best relationship between AVIRIS data and field-measured canopy nitrogen at Blackhawk Island used first-difference reflectance bands at 950 and 2290 nm (Table 5). Absorption at 2294 nm has been attributed to a combination band of N-H and C=O in amino acid by Osborne and Fearn (1986). The lignin equation developed in this analysis used bands at 790 and 1700 nm. Osborne and Fearn (1986) assign absorption at 790 and 1685 nm to aro-

matic structures, which are found in abundance in lignin molecules.

Cross-site predictions.—The generality of the equations developed for Harvard Forest and Blackhawk Island was tested by making cross-site predictions (Table 6). All cross-site predictions produced poor results, indicating that the spectral and/or field information for each of the two study sites did not represent the other site. Several characteristics of these data may prevent this type of cross-site prediction from working. First, differences may be due, in part, to the fact that three of the four equations used in the cross-site predictions use AVIRIS bands in the spectral region with the lowest signal: noise (≥2000 nm). The atmospheric corrections on both scenes are fine-tuned by a secondary correction based on the conditions in the Blackhawk Island scene (Clark et al. 1994). These longer bands would be most sensitive to any noise in the AVIRIS spectra (which would vary from scene to scene) or to differences in atmospheric conditions between the two scenes. Second, the range in chemical composition of the plots sampled at Blackhawk Island is not as great as those sampled at Harvard Forest. We could not expect a calibration made with Blackhawk Island data to predict the chemistry of plots outside of the range of the calibration plot chem-

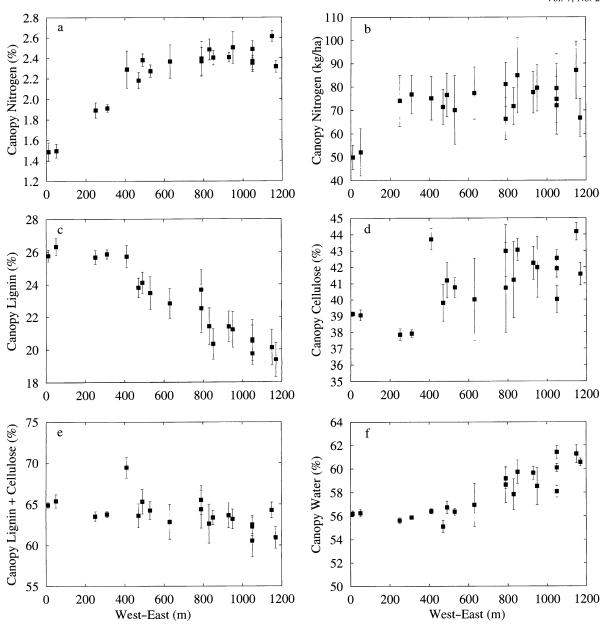


Fig. 3. Canopy chemistry gradients at Blackhawk Island along an east-west transect: (a) nitrogen concentration; (b) nitrogen content; (c) lignin concentration; (d) cellulose concentration; (e) lignin + cellulose concentration; and (f) water concentration. Error bars depict \pm 1 sp.

istry. For example, the plots with the lowest measured lignin concentration at Harvard Forest (values lower than those measured on Blackhawk Island) have the highest residuals when predicted with the equation developed at Blackhawk Island. The results of these cross-site predictions emphasize the importance of accurate atmospheric corrections in the comparison of scenes covering different areas, as well as different scenes of the same area. Additionally, calibration equations must be developed with field data covering the full range of conditions that will be encountered in scenes to which the equation will be applied. Ongoing efforts in the im-

provement of AVIRIS signal: noise and atmospheric-correction algorithms (Chrien et al. 1993, Green et al. 1993) should improve the success of this type of data analysis for future data sets.

Combined-site calibration.—Data from both Harvard Forest and Blackhawk Island (40 plots) were combined for the final lignin and nitrogen calibrations (Table 7, Fig. 4). Nitrogen was predicted with a two-term equation using both 783 and 1640-nm bands. Although some studies have reported the use of bands in the 700–750-nm range for nitrogen calibrations (Card et al. 1988, Curran and Kupiec 1995), Yoder and Pettigrew-

TABLE 4. AVIRIS calibration equations for Harvard Forest.

The best calibration equation relates first-difference AVIRIS reflectance to canopy chemistry using data from 20
plots at Harvard Forest.

Constit- uent	Coeffi- cient	Wavelength		SEC†	R^2	SECV‡
Nitrogen						
b_0	0.4568			0.19	0.87	0.23
b_1°	0.0009	λ_1	750			
b_2	-0.0016	λ_2	2140			
Lignin						
b_0	33.4107			1.99	0.70	2.38
$egin{array}{c} b_0 \ b_1 \ b_2 \ b_3 \end{array}$	0.1485	λ_1	1660			
b_2	0.0268	λ_2	1740			
b_3^-	-0.0005	λ_3	1900			
b_4	-0.0349	λ_4	2280			

Note: Refer to Eq. 2 for definitions of terms.

Crosby (1995) reported high correlations between nitrogen and first-difference absorbance at 780 nm in the laboratory spectra of fresh bigleaf maple leaves. The band centered at 1640 nm is a first overtone of a N-H absorption band (Murray and Williams 1987).

Absorption at 1660 nm is related to absorption overtones of unsaturated or phenolic carbon-carbon bonds, which are abundant in lignin molecules (Murray and Williams 1987). The three shorter wavelengths used in this equation correspond to a region of high absorbance observed in the laboratory spectra of lignin (Aber et al. 1995a).

The coefficients of determination for individual and combined sites were similar to those reported by Wessman et al. (1989) in an analysis of AIS data at Blackhawk Island.

These equations, based on calibration pixels within the images, were then applied to all pixels in the images, yielding spatial estimates of foliar nitrogen and lignin concentrations at the canopy level for Harvard Forest (Plate 1b, d) and Blackhawk Island (Plate 1a, c). In order to use this type of prediction on a large scale with repeat coverage, it will be necessary to de-

TABLE 5. AVIRIS calibration equations for Blackhawk Island. The best calibration equation relates first-difference AVIRIS reflectance to canopy chemistry using data from 20 plots at Blackhawk Island.

Constit- uent	Coeffi- cient	Wavelength		SEC†	R^2	SECV‡
Nitrogen						
b_0	0.8608			0.13	0.85	0.15
b_1	-0.0042	λ_1	950			
b_2	-0.0007	λ_2	2290			
Lignin						
b_0	31.65			0.78	0.90	0.85
b_1°	-0.0569	λ_1	790			
b_2	-0.0263	λ_2	1700			

[†] Standard error of calibration.

Table 6. AVIRIS cross-site predictions. Results are obtained when the calibration equation is developed with data from one site and is used to predict nitrogen and lignin at the other site.

Calibration	Constit-	Prediction site				
		Harvard Forest		Blackhawk Island		
site	uent	R^2	SEP†	R^2	SEP†	
Harvard Forest Harvard Forest	nitrogen lignin			0.83 0.27	0.27 3.87	
Blackhawk Island Blackhawk Island	nitrogen lignin	0.75 0.01	1.32 4.33			

[†] Standard error of the prediction.

velop calibration equations that will work on *multiple* scenes without the collection of field calibration data for each scene. This may be accomplished by extending the calibration data over a number of scenes covering the entire range of species and chemistry to be encountered in forthcoming data sets.

Modeling ecosystem processes with AVIRIS-derived canopy chemistry

AVIRIS-predicted nitrogen and lignin have been used as input data for two models of ecosystem processes.

Previous research at Blackhawk Island has demonstrated a very strong ($R^2 = 0.96$, n = 7, P < 0.001) relationship between canopy lignin concentration and annual net nitrogen mineralization, or nitrogen cycling (Wessman et al. 1988). This relationship has been used with remote-sensing data from a low-elevation, airborne platform to produce a verified map of nitrogen mineralization for Blackhawk Island (Wessman et al. 1988). Using 1992 AVIRIS-derived canopy lignin concentration as input to this model, we derived a map similar to that of Wessman et al. (1988), showing the spatial variability in nitrogen mineralization rates on Blackhawk Island. Predicted nitrogen mineralization rates show increasing rates from west to east across the island (Plate 1e). Predictions of absolute nitrogen mineralization values

TABLE 7. AVIRIS combined-site calibration. Equations were developed with data from all 40 Harvard Forest and Blackhawk Island plots.

Constit- uent	Coeffi- cient	Wavelength		SEC†	R^2	SECV‡
Nitrogen						
b_0	0.5292			0.18	0.87	0.19
b_1°	0.0008	λ_1	783			
b_2	0.0035	λ_2	1641			
Lignin						
b_0	33.8706			1.43	0.77	1.64
b_1	0.1043	λ_1	627			
$egin{matrix} b_2^1 \ b_3 \end{matrix}$	0.0049	λ_2	755			
b_3	-0.0493	λ_3	822			
b_4	0.0519	λ_4	1661			

[†] Standard error of calibration.

[†] Standard error of calibration.

[‡] Standard error of cross-validation.

[‡] Standard error of cross-validation.

[‡] Standard error of cross-validation.

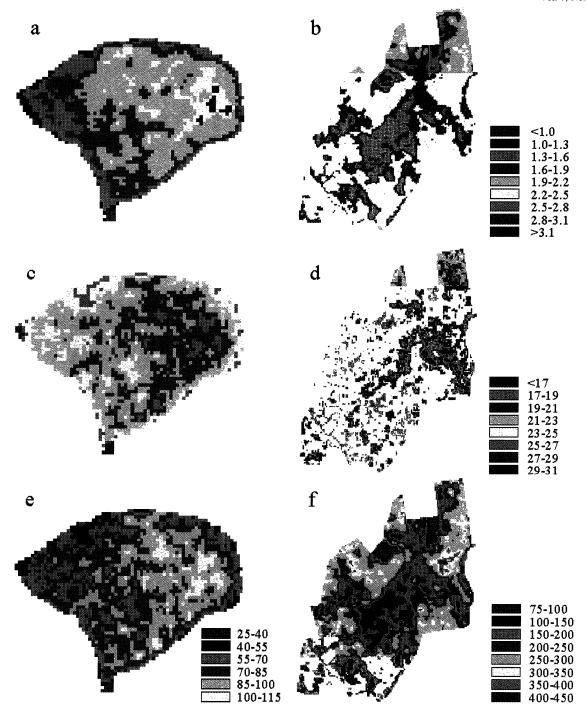
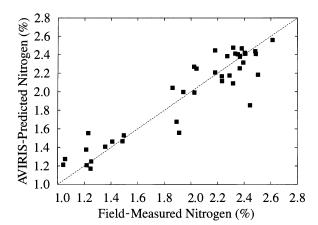


PLATE 1. AVIRIS-predicted foliar nitrogen and lignin concentrations (%), respectively, for Blackhawk Island (a, c) and Harvard Forest (b, d). The two bottom panels depict nitrogen mineralization (kg·ha·¹·yr¹) predicted from AVIRIS-derived lignin concentration for Blackhawk Island (e), and net ecosystem productivity (carbon, g·m⁻²·yr⁻¹) predicted with the PnET model using AVIRIS-derived lignin concentration for Harvard Forest (f).

cannot be compared, because of yearly variations in foliar chemistry and mineralization rates. However, the relative values across the east-west gradient, and the range of values, are similar in the AIS and AVIRIS data analyses. The PnET model, driven primarily by foliar nitrogen concentration, was applied to each Harvard Forest image pixel. Using AVIRIS-derived foliar nitrogen concentrations as input to the model, an estimate of net



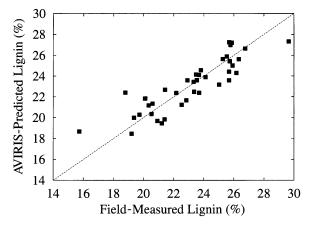


Fig. 4. AVIRIS-predicted vs. field-measured canopy concentrations of (a) nitrogen and (b) lignin, for 40 plots at Blackhawk Island and Harvard Forest.

ecosystem productivity was produced for the entire research site (Plate 1f). The resulting image shows net ecosystem productivity ranging from a low carbon level of 75 g·m⁻²·yr⁻¹ in needle-leaved stands to a high of 450 g C⋅m⁻²⋅yr⁻¹ in broad-leaved stands. These results demonstrate the potential for high spectral resolution remote sensing to increase both the accuracy of spatially averaged estimates of carbon and nitrogen cycling in temperate forest ecosystems, and to increase the spatial detail of those estimates. The accuracy of this model may be improved by increasing the detail of the species map used as input. Martin (1994) discusses the potential for deriving species identification from AVIRIS data. Improvements in the species input variable will allow for more variability in needleleaved stands due to differences in leaf area index and foliar retention time between needle-leaved species. At the present time, field measurements of carbon balance are being made at Harvard Forest with eddy correlation methods (Wofsy et al. 1993). These field measurements will provide important data for the validation of modeled ecosystem productivity derived from remotely sensed canopy chemistry.

CONCLUSIONS

Calibration equations relating AVIRIS spectral data to field-measured canopy chemistry can be used to make spatially explicit estimates of canopy nitrogen and lignin within entire AVIRIS scenes. These estimates have been made for both Harvard Forest, Massachusetts and Blackhawk Island, Wisconsin. The subsequent application of these canopy chemistry estimates in ecosystem models adds an important spatial dimension to estimates of forest ecosystem carbon balance and nutrient cycling. The further study of these data, and similar data sets, will be used to develop more generalized calibration equations addressing such issues as variability between scenes due to atmospheric conditions and forest species composition. Establishing a baseline of forest ecosystem function and monitoring changes that may occur in the future are crucial components in understanding the role of forests in global biogeochemical cycles.

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