

Canopy-scale relationships between foliar nitrogen and albedo are not observed in leaf reflectance and transmittance within temperate deciduous tree species

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Abstract: Strong positive correlations between the maximum rate of canopy photosynthesis, canopy-averaged foliar nitrogen concentration, and canopy albedo have been shown in previous studies. While leaf-level relationships between photosynthetic capacity and foliar nitrogen are well documented, it is not clear whether leaf-level relationships between solar-weighted reflectance and nitrogen underlie the canopy-scale patterns. Using an integrating sphere, we measured the reflectance and transmittance (350–2500 nm) of both individual leaves and multileaf stacks. Samples were collected from 12 broadleaf species at the Harvard Forest in central Massachusetts, USA. Across all species, foliar nitrogen (both mass-based nitrogen concentration and area-based nitrogen content) and leaf mass / area ratio were negatively, rather than positively, correlated with solar-weighted reflectance and transmittance in ultraviolet–visible and near-infrared wavelength bands (350–700 nm and 700–2500 nm, respectively). Leaf-level anatomy and biochemistry, therefore, do not appear to drive the canopy-level association between increasing foliar nitrogen content and increasing canopy albedo. This suggests that interactions between leaf optical properties and structural canopy-scale traits that correlate with nitrogen content (perhaps some combination of crown shape, leaf area index, leaf angular distribution, or other structural characteristics of the canopy), may instead underlie the previously observed relationship between nitrogen and canopy-level shortwave albedo.

Key words: albedo, leaf nitrogen, reflectance, photosynthesis, optical properties.

Résumé : Dans des études antérieures, l'on a démontré qu'il existe de fortes corrélations positives entre le taux maximum de photosynthèse dans la canopée, la teneur foliaire moyenne en azote dans la canopée et l'albédo de la canopée. Alors que les relations à l'échelle de la feuille entre la capacité photosynthétique et l'azote foliaire sont bien documentées, il n'est pas clair si les relations à l'échelle de la feuille entre la réflectance solaire pondérée et l'azote sous-tendent les patrons à l'échelle de la canopée. À l'aide d'une sphère d'intégration, les auteurs ont mesuré la réflectance et la transmittance (350 à 2500 nm) à la fois des feuilles individuelles et d'étages de feuilles superposées. Ils ont récolté les échantillons à partir de 12 espèces décidues sur la Forêt Harvard du Massachusetts central aux États-Unis. Sur l'ensemble des espèces, l'azote foliaire (à la fois la teneur en N basée sur la masse et la teneur en N basée sur la surface) le rapport masse/surface foliaire s'avère négativement plutôt que positivement corrélée avec la réflectance solaire pondérée et la transmittance dans les bandes de longueurs d'onde UV-visible et infrarouge rapproché (350–700 nm et 700–2500 nm, respectivement). Conséquemment, l'anatomie et la biochimie foliaires ne semblent pas responsables de l'association à l'échelle de la canopée entre l'augmentation de la teneur foliaire en azote et l'augmentation de l'albédo de la canopée. Ceci suggère que les interactions entre les propriétés optiques de la feuille et les caractères structuraux à l'échelle de la canopée corrélant avec la teneur en azote (peut être certaines combinaisons de la forme de la couronne, l'index de la surface foliaire, la distribution angulaire des feuilles, ou autres caractéristiques structurales de la canopée), pourraient plutôt sous-tendre la relation observée entre l'azote et l'albédo des ondes courtes à l'échelle de la canopée.

Mots-clés : albédo, azote foliaire, réflectance, photosynthèses, propriétés optiques.

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Introduction

At the ecosystem level, positive and statistically significant correlations have been documented among canopy nitrogen (N) content, maximum rates of canopy photosynthesis, and canopy albedo (Ollinger et al. 2008; see also Hollinger et al. 2010). These relationships link the carbon and N cycles to surface energy exchange, suggesting unexplored vegetation feedbacks to the climate system. The mechanisms underlying these relationships are unknown, but have been hypothesized to include leaf-level biochemical and anatomical properties, associated with higher photosynthetic capacity, that result in greater scattering of photons at near-infrared (NIR) wavelengths in high-N foliage (Ollinger et al. 2008; Hollinger et al. 2010).

At the leaf level, there is a well-established correlation between photosynthetic capacity and N content (Field and Mooney 1986), largely because most leaf N is incorporated in photosynthetic enzymes and pigments (Evans 1989; Smith et al. 1997). At the same time, there is a long history of relating foliage biochemical constituents and structure to the optical properties of the foliage, efforts that have resulted in models such as PROSPECT (Jacquemoud and Baret 1990; Jacquemoud et al. 2009). Prediction of foliar N and chlorophyll from leaf optical spectra has generally made use of spectral absorption features associated with protein- and pigment-bound N (Kokaly 2001; Sims and Gamon 2002; Blackburn 2006; Ferwerda and Skidmore 2007). This predictive capacity is stronger for dried than fresh tissue (Kokaly 2001) because of overlapping water absorption features in the NIR region. Furthermore, most studies have tried to use narrow waveband, rather than broadband, reflectances for this kind of analysis (Johnson 2001; Blackburn 2006; but see Broge and Mortensen 2002; Broge and Leblanc 2001). However, the idea that it is necessary or preferable to use high-resolution spectral data, or subtle spectral features, to predict leaf N is at odds with the canopy-level relationships demonstrated by Ollinger et al. (2008) and Hollinger et al. (2010).

The canopy albedo–N relationship is postulated to be mediated by photosynthetic capacity. Photosynthetic capacities are optimized through structural features that enhance cellular surface area for light and carbon dioxide absorption, including additional layers of photosynthetically active mesophyll cells and increased intercellular space (DeLucia et al. 1996; Vogelmann et al. 1996; Smith et al. 1997). Structural features of leaves associated with enhanced photosynthetic capacity have also been shown to be correlated with measured leaf optical properties of reflectance and transmittance (Lee et al. 1990; Ourcival et al. 1999; Carter and Knapp 2001). Slaton et al. (2001), for example, showed that increased leaf NIR bidirectional reflectance was associated with increases in the ratio of mesophyll cell surface area exposed per unit leaf area (A_{mes}/A) or the percent volume of mesophyll that is air space (%IAS).

In this study, we evaluated the hypothesis that it is the relationship between leaf-level structural features and light scattering that links N concentrations and broadband optical properties at the canopy scale. To test this hypothesis, we measured the reflectance and transmittance, at UV–visible (350–700 nm) and NIR (700–2500 nm) wavelengths, of

foliage from 12 broadleaf temperate deciduous forest species and related these values to foliage N concentration ($\text{g N} \cdot (100 \text{ g dry matter})^{-1}$; %N). We also determined leaf mass per unit leaf area ($\text{g dry matter}/\text{cm}^2$; LMA) and N content per unit leaf area ($\text{g N}/\text{cm}^2$) and investigated inter-relationships among leaf traits and optical properties for both individual leaves and for stacks of leaves up to 12 layers thick. Our objective with the stacks was to create an optically dense sample for the reflectance and transmittance measurements, thereby reducing the impact of covariation in leaf thickness and (or) tissue density as a possible confounding factor.

Methods

During the summer growing season, we collected foliage samples from 12 co-occurring deciduous tree and understory shrub species (Table 1) at the Harvard Forest (Petersham, Mass.). Vegetation at the site is dominated by transition hardwoods, most importantly red oak (*Quercus rubra* L.), which accounts for 36% of the basal area. Mean annual temperature at the site is 7.1 °C, and precipitation totals 1066 mm annually, distributed evenly throughout the year. Sampling was conducted across a range of growth conditions, including variable soil types, stand ages, and species composition.

Each sample consisted of 12 fully developed, undamaged leaves collected from the same branch of an individual tree or shrub. Samples were collected across a range of canopy heights and light environments, although most samples were from understory individuals, as logistical challenges precluded sampling from the upper canopy (we contend that this sampling should be adequate if the relationship between N and albedo holds generally at the leaf level). Following Richardson and Berlyn (2002), samples were collected in the morning, placed in Ziploc bags along with moistened paper towels, and kept cool until spectral measurements were made later the same day.

We used a portable spectrometer (ASD FieldSpec 3, Analytical Spectral Devices Inc., Boulder, Colo.) connected to a 5 cm (2 inch) three-port integrating sphere (SphereOptics, Concord, N.H.) and a 10 W hemispheric collimated light source with a regulated power supply set at 6 V to measure spectral reflectance and transmittance (350–2500 nm wavelengths). The sphere featured an 8° near-normal incidence port, meaning that reflectance measurements included both diffuse and specular components. The instrument was controlled via the manufacturer's RS3 software program (Analytical Spectral Devices Inc.). At approximately 10 min intervals, a white Spectralon reference standard was measured, and automatic optimization of the instrument's detector gain and offset was conducted by the software. Each recorded leaf spectrum was the average of 50+ individual scans. For reflectance measurements, we used the comparison method, which places both the sample and a reflectance reference on the sphere at the same time and switches the position of the sample and reference between two measurements (with both always on the sphere). Spectral reflectance was calculated as the ratio of the value with the sample in the beam to the value with the reference in the beam. Measurements were made first on individual leaves

Table 1. List of species sampled, with mean leaf mass per unit area (LMA) and percent nitrogen (%N) (standard errors are in parentheses).

Species name	Common name	No. of trees	LMA (g/cm ²)	%N
<i>Acer pensylvanicum</i> L.	Moose maple	3	0.267 (0.026)	2.487 (0.312)
<i>Acer rubrum</i> L.	Red maple	8	0.425 (0.025)	2.051 (0.051)
<i>Acer saccharum</i> Marsh.	Sugar maple	6	0.327 (0.020)	2.030 (0.058)
<i>Betula lenta</i> L.	Black birch	6	0.298 (0.020)	2.550 (0.106)
<i>Betula lutea</i> Michx. f.	Yellow birch	1	0.302 (0.016)	2.292 (0.068)
<i>Betula papyrifera</i> Marsh.	Paper birch	6	0.365 (0.036)	2.468 (0.174)
<i>Carya ovata</i> (Mill.) K. Koch	Shagbark hickory	5	0.274 (0.022)	2.650 (0.051)
<i>Fagus grandifolia</i> Ehrh.	Beech	7	0.296 (0.029)	2.228 (0.077)
<i>Prunus serotina</i> Ehrh.	Black cherry	3	0.346 (0.049)	2.743 (0.303)
<i>Quercus alba</i> L.	White oak	1	0.303	2.760
<i>Quercus rubra</i> L.	Red oak	9	0.427 (0.026)	2.669 (0.081)
<i>Quercus velutina</i> Lam.	Black oak	4	0.384 (0.023)	2.588 (0.114)
<i>Viburnum cassinoides</i> L.	Raisinbush	3	0.463 (0.018)	1.830 (0.050)

Note: With the exception of *Viburnum cassinoides* (an abundant understory shrub), all other species are common deciduous canopy trees.

and then for leaf stacks of increasing thickness (2, 3, 4, 6, 8, and 12 leaves).

Raw data were processed to reflectance spectra using the ViewSpecPro program (Analytical Spectral Devices Inc.). Individual wavelengths were then weighted by the solar spectrum energy (ASTM G173-03 Reference Spectra derived from SMARTS version 2.9.2; Gueymard 2004) to convert spectral reflectance values to a measure that approximates albedo measured using broadband radiometric instruments, with which incident and reflected radiation are measured in terms of energy fluxes (W/m²). Using the solar-weighted reflectance data, we calculated reflectance and transmittance separately for UV-visible and NIR wavebands and also for the entire measured spectrum. Thus, our weighted reflectance measures correspond more closely to broadband shortwave (350–2500 nm), UV-visible (350–700 nm), or NIR (700–2500 nm) albedo than to an arithmetic mean of the wavelength-specific spectral reflectances, making our measurements readily comparable to those of Ollinger et al. (2008).

After the optical measurements were completed, we collected two circular punches (each 3 cm²) from each leaf in the stack. These were oven dried at 60 °C overnight and then weighed to determine dry (LMA (g dry matter/cm²)). From each stack, two punches were analyzed for N with a combustion C–N analyzer (Fisons Instruments, Beverly, Mass.). To monitor accuracy and ensure quality control, standard reference material was included every 10 samples. We express N data in terms of N concentration (%N; g N · (100 g dry matter)⁻¹) and N content per unit leaf area (g N/cm²).

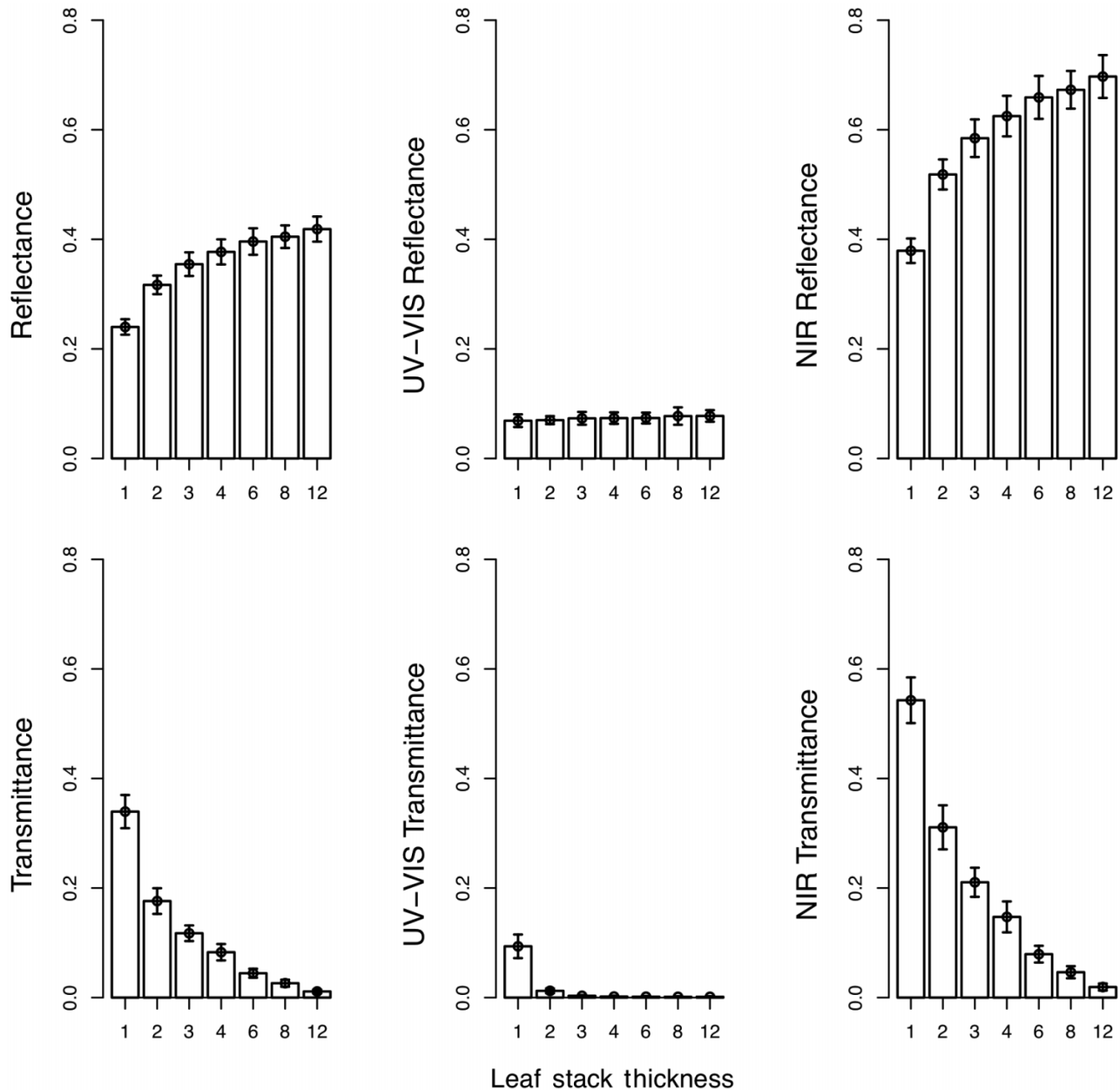
Results

The optical properties of leaf stacks varied according to the number of layers in the stack. As expected, total solar-weighted shortwave reflectance increased and total solar-weighted shortwave transmittance decreased with increasing stack thickness. UV-visible solar-weighted reflectance was relatively constant (≈ 0.08) with respect to stack thickness, while solar-weighted NIR reflectance increased from 0.38 for a single leaf to 0.70 for a stack of 12 leaves (Fig. 1). Changes in both reflectance and transmittance were minimal, as stack thickness was increased from 8 to 12 layers, particularly for UV-visible wavelengths.

We had hypothesized that there would be a positive correlation between leaf N and total shortwave reflectance, but our data do not support this. In fact, we found that there was surprisingly little variation in either visible or NIR waveband reflectance despite wide variation in oven-dry LMA, N concentration (%N, g · (100 g dry matter)⁻¹), and N content (g N/cm²) (Fig. 2). In the few instances where the pairwise correlations illustrated in Fig. 2 were statistically significant, the correlations were always negative. The slopes of the relationships between N concentration and total shortwave reflectance, transmittance, and absorbance did not change significantly with stack thickness ($P = 0.41, 0.97,$ and 0.73 respectively; see also the pairwise correlations illustrated in Fig. 2). Thus, these patterns were consistent for both individual leaves and for stacks of leaves up to 12 layers thick. We note the strong contrast between these results and the findings of Ollinger et al. (2008), in which a 1 unit increase in canopy %N (e.g., from 1% to 2%) was associated with a 0.05 unit increase in canopy albedo (from 0.10 to 0.15).

Multiple regression models were used to predict the visible and NIR components of solar-weighted reflectance, transmittance, and absorbance as functions of oven-dry LMA and N concentration (N content was not included because it equals %N × LMA), with separate regressions calculated for stacks of different thicknesses (Table 2). For UV-visible, NIR, and total shortwave reflectance, estimated coefficients for N concentration and LMA were consistently negative within leaf stacks of a given number of layers, from single leaves to 12-leaf stacks (Table 2). Thus, accounting for variation in LMA, solar-weighted reflectance decreased (rather than increased) with increasing leaf N concentration, although this relationship was not always statistically significant. LMA also exhibited negative correlations with reflectance variables in the multiple regression model for some leaf stack thicknesses, but in a univariate model showed some positive but statistically insignificant associations with shortwave reflectance and NIR reflectance. This highlights the importance of using similar statistical designs across studies to generalize the effects of leaf properties on reflectance. At the same time, for total shortwave leaf absorbance, estimated coefficients for N concentration and LMA were consistently positive (i.e., increasing N and increasing LMA were both correlated with

Fig. 1. Increases in solar-weighted shortwave, UV — visible (VIS), and near-infrared (NIR) reflectance (top panels) and decreases in transmittance (bottom panels) associated with changes in thickness of leaf stack (*x*-axis, in terms of number of leaf layers) largely reflect associated patterns within the NIR, rather than visible, spectrum. Error bars are standard errors. Data were pooled across all species.



increasing shortwave absorbance), although in many instances only the LMA coefficients were statistically significant (Table 2).

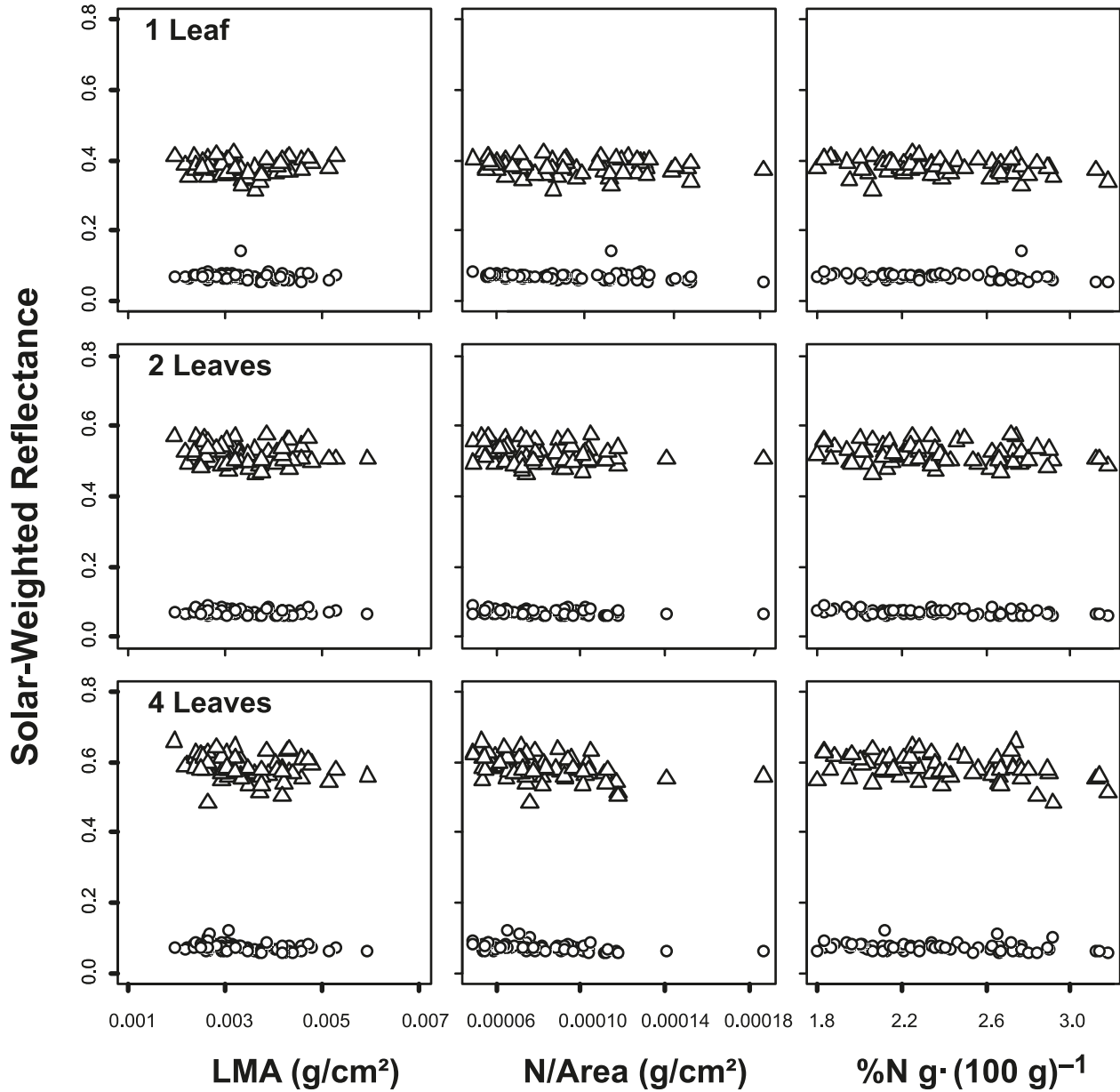
Discussion

The relationships between leaf optical properties and both leaf mass per unit area (LMA) and leaf N (%N) reported here (Table 2, Fig. 2) suggest that increases in LMA and %N are negatively, rather than positively, correlated with solar-spectrum-weighted reflectance in visible and NIR wavelengths and across the total shortwave spectrum. Therefore, the canopy-scale patterns observed by Ollinger et al. (2008) do not appear to result directly from coordination between N content and albedo at the leaf level. The present study utilized

leaves from various light environments collected from a single forest site, whereas Ollinger et al. (2008) studied canopy-level spectral data collected from multiple forest types. We concede that it is possible that leaf-level albedo–N relationships might be restricted to upper-canopy foliage, but this seems unlikely. The patterns observed by Ollinger et al. (2008) could also potentially result from canopy-level structural differences among forest types (not just between, but also within, deciduous broadleaf and evergreen needleleaf species groups) that also happen to correlate with canopy N, perhaps because of broad geographic gradients in N availability and forest species composition.

Our results do not support our hypothesis of a leaf-level basis for canopy-scale relationships between %N and reflec-

Fig. 2. Relationships between visible (circular symbols) and near-infrared (triangular symbols) solar-weighted reflectances (*x*-axis) and leaf mass per unit area (LMA, g dry matter/cm²), foliar N content per unit area (g N/cm²), and foliar N concentration (%N, g N·(100 g dry matter)⁻¹), for stacks of 1, 2, and 4 leaves. (Stacks of 6, 8, and 12 leaves are omitted because they exhibit similar trends.) Data were pooled across all species.



tance driven by structural changes that would also be correlated with photosynthetic capacity. While higher leaf N content generally increases photosynthetic capacity (Field and Mooney 1986), and increased photosynthetic capacity is putatively coupled with structural or anatomical changes within the leaf (Smith et al. 1997), it appears that the associated structural changes, if they occur, do not necessarily result in measurable leaf-level reflectance increases. Although our observations are consistent with strategies that maximize photosynthetic capacity by increasing absorbance of visible (photosynthetically active) wavelengths, it is not clear from these data how other constraints to optimal leaf structure and function (such as reducing heat loading of foliage with high photosynthetic capacity by decreasing NIR absorbance)

might contribute to the observed canopy-scale correlation between N and albedo.

The ways in which radiation can be reflected, absorbed, and transmitted by the canopy is a function of the spectral and optical properties of individual leaves, as well as the factors that influence how leaves are oriented in space (including leaf area index (LAI), leaf angle and leaf orientation, crown shape and size, and clumping at scales from branches to crowns) in addition to the spectral characteristics of trunks and branches, visible soil, and leaf litter (Asner 1998). While our results suggest that the canopy-scale relationships observed by Ollinger et al. (2008) and Hollinger et al. (2010) likely reflect changes in properties at scales above the leaf level, there are few, if any, studies that have addressed how

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Table 2. Coefficients (standard errors in parentheses) from multiple regression models relating leaf optical properties (shortwave reflectance, UV–visible waveband reflectance, near-infrared (NIR) waveband reflectance, and shortwave absorbance) to leaf mass per unit area (LMA; g dry matter/cm²) and foliar N concentration (%N; g N·(100 g dry matter)⁻¹), for stacks of deciduous leaves 1, 2, 4, 8, and 12 leaves thick.

	Shortwave reflectance		UV–visible reflectance		NIR reflectance		Absorbance	
	Coefficient	P value	Coefficient	P value	Coefficient	P value	Coefficient	P value
1 leaf								
Intercept	0.28 (0.01)	<0.0001	0.083 (0.013)	<0.0001	0.42 (0.02)	<0.001	0.31 (0.03)	<0.0001
LMA	-0.6 (1.9)	0.75	-1.9 (1.9)	0.35	0.6 (3.1)	0.84	16.9 (4.5)	<0.001
%N	-0.016 (0.005)	<0.01	-0.002 (0.005)	0.61	-0.020 (0.008)	0.01	0.021 (0.011)	0.05
R ²	0.12		0.01		0.09		0.18	
2 leaves								
Intercept	0.36 (0.02)	<0.0001	0.097 (0.009)	<0.0001	0.57 (0.03)	<0.0001	0.42 (0.02)	<0.0001
LMA	-3.2 (2.3)	0.17	-2.1 (1.4)	0.14	-3.9 (4.0)	0.34	17.8 (3.6)	<0.001
%N	-0.012 (0.006)	0.03	-0.008 (0.003)	0.02	-0.016 (0.009)	<0.01	0.012 (0.009)	0.15
R ²	0.06		0.08		0.06		0.26	
4 leaves								
Intercept	0.44 (0.02)	<0.0001	0.093 (0.011)	<0.0001	0.73 (0.03)	<0.0001	0.44 (0.02)	<0.0001
LMA	-7.1 (2.9)	0.02	-3.3 (1.7)	0.05	-12.3 (5.2)	0.02	13.9 (3.2)	<0.001
%N	-0.016 (0.007)	0.02	-0.003 (0.004)	0.46	-0.025 (0.012)	0.05	0.022 (0.008)	<0.001
R ²	0.14		0.06		0.14		0.26	
8 leaves								
Intercept	0.46 (0.02)	<0.0001	0.105 (0.015)	<0.0001	0.74 (0.03)	<0.0001	0.50 (0.02)	<0.0001
LMA	-8.7 (2.7)	0.01	-2.7 (2.3)	0.28	-11.5 (5.0)	0.023	11.7 (2.8)	<0.001
%N	-0.011 (0.007)	0.12	-0.008 (0.006)	0.16	-0.010 (0.012)	0.36	0.013 (0.007)	0.07
R ²	0.13		0.05		0.04		0.20	
12 leaves								
Intercept	0.51 (0.02)	<0.0001	0.104 (0.011)	<0.0001	0.84 (0.04)	<0.0001	0.47 (0.02)	<0.0001
LMA	-16.0 (2.6)	<0.0001	-3.2 (2.4)	0.074	-26.3 (4.9)	<0.0001	16.7 (2.5)	<0.0001
%N	-0.018 (0.007)	0.011	-0.007 (0.004)	0.080	-0.020 (0.012)	0.072	0.020 (0.007)	0.01
R ²	0.33		0.09		0.29		0.35	

Note: Data were pooled across all species. Results for stacks of 3 and 6 leaves followed similar patterns and are not shown.

foliar N concentration might correlate with canopy structural properties that could give rise to the observed albedo–N relationship. In theory, variation in LAI and leaf angle controls how strongly reflectance trends are manifested in the canopy, with increases in LAI and leaf angle increasing and decreasing, respectively, the leaf surface area available for scattering overhead light (Baret et al. 1994; Asner 1998). Previous studies suggest that LAI both affects canopy albedo and responds to foliar N content and soil N availability (Aerts and de Caluwe 1994; Pierce et al. 1994). However, high LAI values saturate the relationship between LAI and canopy albedo and are often characteristic of low-N evergreen species (Hollinger et al. 2010), making LAI an unlikely mediator of the canopy N and albedo relationship, a suggestion that is supported by the lack of evidence for an LAI–albedo relationship found by Ollinger et al. (2008). Reductions in LAI and increases in leaf angle also increase the relative contribution of branch, bark, litter, and soil material to site-level albedo, which may themselves exhibit currently unknown relationships between N content and optical properties (see Asner et al. 2000). Understanding canopy-scale relationships between N and albedo therefore most likely requires a better understanding of how leaf orientation, angle, and clustering along branches is either affected by N content directly or how these factors vary in relation to other factors that also correlate with N.

Thus, although there is robust evidence for a canopy-scale relationship between albedo and N, the mechanism underlying this pattern remains unknown and open to debate (see

also Fisher 2009; Ollinger et al. 2009). Understanding albedo–N relationships could potentially be leveraged to improve current-generation land surface models and remote sensing algorithms. In addition, identification of the mechanism involved could enhance the predictive capability of future climate models by extrapolating albedo responses to changes in N availability.

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