



Seasonal variability of multiple leaf traits captured by leaf spectroscopy at two temperate deciduous forests



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ABSTRACT

Understanding the temporal patterns of leaf traits is critical in determining the seasonality and magnitude of terrestrial carbon, water, and energy fluxes. However, we lack robust and efficient ways to monitor the temporal dynamics of leaf traits. Here we assessed the potential of leaf spectroscopy to predict and monitor leaf traits across their entire life cycle at different forest sites and light environments (sunlit vs. shaded) using a weekly sampled dataset across the entire growing season at two temperate deciduous forests. The dataset includes field measured leaf-level directional-hemispherical reflectance/transmittance together with seven important leaf traits [total chlorophyll (chlorophyll *a* and *b*), carotenoids, mass-based nitrogen concentration (N_{mass}), mass-based carbon concentration (C_{mass}), and leaf mass per area (LMA)]. All leaf traits varied significantly throughout the growing season, and displayed trait-specific temporal patterns. We used a Partial Least Square Regression (PLSR) modeling approach to estimate leaf traits from spectra, and found that PLSR was able to capture the variability across time, sites, and light environments of all leaf traits investigated ($R^2 = 0.6\text{--}0.8$ for temporal variability; $R^2 = 0.3\text{--}0.7$ for cross-site variability; $R^2 = 0.4\text{--}0.8$ for variability from light environments). We also tested alternative field sampling designs and found that for most leaf traits, biweekly leaf sampling throughout the growing season enabled accurate characterization of the seasonal patterns. Compared with the estimation of foliar pigments, the performance of N_{mass} , C_{mass} and LMA PLSR models improved more significantly with sampling frequency. Our results demonstrate that leaf spectra-trait relationships vary with time, and thus tracking the seasonality of leaf traits requires statistical models calibrated with data sampled throughout the growing season. Our results have broad implications for future research that use vegetation spectra to infer leaf traits at different growing stages.

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1. Introduction

Leaf traits are important indicators of plant physiology and critical components in numerous ecological processes (Kattge et al., 2011; Wright et al., 2004). For example, leaf chlorophyll concentration represents the light harvesting potential and is an indicator of photosynthetic activity (Niinemets, 2007; Laisk et al. 2009), while accessory pigments such as carotenoids protect leaves from damage when exposed to excessive sunlight (Demmig-Adams & Adams, 2000). Leaf mass per area (LMA) describes plants' investment to leaves in terms of carbon and nutrients to optimize sunlight interception (Poorter, Niinemets, Poorter,

Wright, & Villar, 2009). Carbon is one of the major elements in cellulose and lignin, which are used to build the cell walls of various leaf tissues (Kokaly, Asner, Ollinger, Martin, & Wessman, 2009). Nitrogen is the key element in both carbon fixation enzyme RuBisCO and chlorophyll (Evans, 1989a, 1989b), and thus plays an important role in modeling leaf and canopy photosynthesis (Bonan, Oleson, Fisher, Lasslop, & Reichstein, 2012). The aforementioned leaf traits, as well as the corresponding spectral properties, strongly depend on leaf developmental stages and light environments (Yang, Tang, & Mustard, 2014; Lewandowska & Jarvis, 1977; Poorter et al., 2009; Wilson, Baldocchi, & Hanson, 2000; Wu et al., 2016a). Thus, capturing the spatial and temporal variations of these leaf traits is important for understanding terrestrial ecosystem functioning (Schimel et al., 2015).

Despite the importance and increasing interests in the temporal and spatial variability of these (and many other) leaf traits, the capacity to monitor these traits over seasons has not progressed accordingly. Wet

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chemical analysis of these leaf traits is considered to be the standard method, yet the destructive and time-consuming protocols do not allow for rapid and repeated sampling of some traits. On the other hand, field spectroscopy can augment traditional approaches, and allows for repeated sampling of the same leaves and thus tracking time-sensitive changes such as frost damage (Asner & Martin, 2008; Couture, Serbin, & Townsend, 2013; Serbin, Singh, McNeil, Kingdon, & Townsend, 2014). Although spectroscopic approaches are promising, many previous efforts have only focused on mature sunlit leaves (e.g., Asner & Vitousek, 2005; Ustin, Roberts, Gamon, Asner, & Green, 2004; Wicklein et al., 2012; but see Sims and Gamon (2002)) and have not explored the ability of leaf spectral properties to track the continuous and developmental changes of leaf traits throughout the growing season. The temporal dimension of the spectra-trait relationship has mostly focused on leaf chlorophyll concentration (Belanger, Miller, & Boyer, 1995; Dillen, de Beeck, Hufkens, Buonanduci, & Phillips, 2012; Shen, Chen, Zhu, & Tang, 2009; Zhang et al., 2007), while it is largely unknown for other important leaf traits like nitrogen, carbon, and LMA. Moreover, the availability of high temporal resolution (~weekly) datasets on important leaf traits and spectra is limited. These data would be very useful for assessing the utility of leaf spectral properties (i.e. reflectance) for estimating the temporal variability of leaf traits, as well as scaling to broader regions and informing process modeling activities.

Leaf traits not only change with time, but also with the light environments, such as moving from sun-lit to shaded light conditions and the commensurate changes in microclimate which also affect leaf traits (Ellsworth & Reich, 1993; Niinemets, 2007; Wu et al., 2016b), as a consequence of underlying fundamental evolutionary and eco-physiological constraints (Terashima, Miyazawa, & Hanba, 2001). For example, shaded leaves display lower chlorophyll *a* to *b* ratio and higher LMA compared with sunlit leaves (Niinemets, 2007). This variation in the vertical domain can be as much as the trait variation across space (Serbin et al., 2014). As such, it is important to not only explore trait variation across sites but also as in the vertical canopy light gradients to better capture ecosystem responses to global change.

Three categories of methods to estimate leaf traits from leaf spectral properties (i.e., reflectance and transmittance) are spectral vegetation indices (SVIs), statistical inversion methods exploiting the full wavelength (400–2500 nm), and leaf radiative transfer models like PROSPECT (Jacquemoud & Baret, 1990), which are limited to only a few leaf traits (do not include carbon and nitrogen) and thus are not the focus of this study. SVIs are typically calculated using the reflectance from two or three wavelengths (Huete et al., 2002; Richardson, Duigan, & Berlyn, 2002; Sims & Gamon, 2002). With proper calibration across a diverse range of vegetation types, SVIs can yield relatively robust models (Féret et al., 2011). Statistical methods such as Partial Least Square Regression (PLSR) modeling have become more popular in recent decades with the availability of high spectral resolution observations and increasing computational power (Asner & Martin, 2008; Couture et al., 2013; Wold, Sjöström, & Eriksson, 2001). Although both being widely used, these methods have not been thoroughly assessed, especially with respect to the robustness of PLSR models across time and different light environments (but see Serbin et al., 2014).

Here our primary goal was to assess the ability of leaf optical properties to track temporal variability of a suite of leaf traits across sites and different light environments. To explore this we collected a dataset of ~weekly-sampled leaf traits [including total chlorophyll (and chlorophyll *a* and *b*), carotenoids, mass-based nitrogen concentration (N_{mass}), mass-based carbon concentration (C_{mass}), and LMA] along with in situ directional-hemispherical reflectance/transmittance during the growing season at two temperate deciduous forests. We first present the temporal variations of leaf traits and spectra, and then highlight the ability of leaf spectra to track temporal variability of leaf traits. We investigate the robustness of the PLSR across season, sites, and light environments. We further explore the optimal field sampling strategy. We conclude by discussing the broad implications of our study.

2. Study area and methods

2.1. Study sites

Our field sampling was conducted in two temperate deciduous forests located in the northeastern United States. The first site, on the island of Martha's Vineyard (MV, 41.362N, 70.578W), is a white oak (*Quercus alba*) dominated forest with a stand age of 80–115 years after natural recovery from abandoned cropland and pasture (Foster, Hall, Barry, Clayden, & Parshall, 2002). Mean annual temperature is 10 °C, and annual precipitation is about 1200 mm from 1981 to 2010 (Yang et al., 2014). The second site, in Harvard Forest (HF, 42.538N, 72.171W), has two dominating deciduous tree species: red oak (*Quercus rubra*) and red maple (*Acer rubrum*), with a few scattered yellow birch (*Betula alleghaniensis*). The forest age is 70–100 years. The annual mean temperature is about 7.5 °C (Wofsy et al., 1993), and the annual precipitation is 1200 mm. Remote sensing studies suggested that the start of season in Martha's Vineyard was about 10–20 days later than that of HF (Fisher & Mustard, 2007; Yang, Mustard, Tang, & Xu, 2012).

2.2. Measurements of leaf spectral properties and traits

We conducted two field campaigns to collect leaf traits at the sites in Martha's Vineyard and Harvard Forest, respectively. In 2011, weekly (biweekly in August) sampling of leaves throughout the growing season (June–November) was conducted at the Martha's Vineyard site on three white oak trees. For each sampling period, we cut two fully sunlit branches (each having ~6 leaves) and one shaded branch using a tree pruner. The spectral properties of the leaves were immediately measured (see below). Then the leaves were placed in a plastic bag containing a moist paper towel, and all the samples were kept in a cooler filled with ice until being transferred back to the lab for further measurements. In 2012, the same weekly (biweekly from mid-July to late August) measurements in Harvard Forest were made on five individuals (two red oaks, two red maples and one yellow birch) from May to October. For each tree, two sunlit and one shaded branch were collected each time.

Directional-hemispherical leaf reflectance and transmittance were measured immediately after the sampling using a spectroradiometer (ASD FS-3, ASD Inc. Boulder, CO, USA; spectral range: 300–2500 nm, spectral resolution: 3 nm@700 nm, 10 nm@1400/2100 nm) and an integrating sphere (ASD Inc.). The intensity of light source in the integrating sphere decreases sharply beyond 2200 nm, with the signal in 2200–2500 nm being noisy (ASD Inc., personal communications), and thus is excluded from the spectral-leaf traits analysis below.

The measured leaf traits include total chlorophyll concentration (including chlorophyll *a* and chlorophyll *b*, $\mu\text{g}/\text{cm}^2$), carotenoids ($\mu\text{g}/\text{cm}^2$), leaf mass per area (LMA, g/m^2), nitrogen concentration by mass (N_{mass} , %), and carbon concentration by mass (C_{mass} , %). Each branch was divided into two subsets. One subset was used to measure pigment concentrations. To measure the chlorophyll and carotenoids concentration, three leaf discs (~0.28 cm^2 each) were taken from each leaf using a hole puncher, and then ground in a mortar with 100% acetone solution and MgO (Asner, Martin, Ford, Metcalfe, & Liddell, 2009). After an 8-minute centrifugation, the absorbance of the supernatant was measured using a spectrophotometer (Shimadzu UV-1201, Kyoto, Japan). Chlorophyll *a*, *b* and carotenoids concentrations were calculated using the readings from 470, 520, 645, 662 and 710 nm (Lichtenthaler & Buschmann, 2001). The other subset (3 leaves) was scanned using a digital scanner (EPSON V300, EPSON, Long Beach, CA, USA), and oven-dried (65 °C) for at least 48 h for quantification of leaf dry mass. LMA was calculated based on the following equations:

$$LMA = W_{\text{dry}}/A_{\text{leaf}}$$

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