Chapter 15
Estimation of Forest Canopy Nitrogen Concentration

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Abstract The ability to detect patterns of carbon assimilation by vegetation is a key component of the North American Carbon Program. Because photosynthetic potential is strongly related to biochemical constituents such as nitrogen and chlorophyll concentrations in foliage, the ability to incorporate canopy chemistry into landscape- to regional-scale carbon cycling research represents an important contribution to NACP research goals. Here, we summarize the functional basis for using foliar N as a scalar of C uptake and recommend a practical, field-based approach for canopy N measurement that can be efficiently scaled using currently available remote sensing technology and ecosystem process modeling.

Keywords Forest productivity, light use efficiency, nitrogen, photosynthetic capacity, remote sensing, scaling

15.1 Introduction

The positive relationship between leaf nitrogen and photosynthetic capacity (e.g. Mooney and Gulmon 1979, Field and Mooney 1986, Reich et al. 1999) is one of the most robust results of modern ecophysiology and is at the core of a number of canopy productivity models (e.g. Aber et al. 1996). This relationship has as its

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basis the fact that foliar nitrogen is found primarily in cellular proteins and that the principal carboxylating enzyme, ribulose-bisphosphate carboxylase-oxygenase (Rubisco) makes up a majority of total leaf protein (Björkman 1968).

Additional evidence supporting canopy N concentration as a scalar for C uptake comes from both theoretical and empirical studies. An important theoretical breakthrough was made by Sellers et al. (1992) when they related canopy nitrogen distribution to the canopy light environment and then to productivity. Because nitrogen is generally a scarce resource that limits plant carbon gain, it has been argued that natural selection should favor individuals that allocate N in an efficient manner through the canopy (Field 1983, 1991, Hirose et al. 1987, Hollinger 1989). Sellers et al. (1992) extended these arguments using a biochemically based model of leaf photosynthesis, coupled to a radiative transfer model, to show that canopy C uptake is maximized when N is allocated optimally within a plant canopy in proportion to the availability of photosynthetically active radiation.

Field measurements in tree canopies suggest that these patterns are a robust and general result (e.g. Hollinger 1999, Dang et al. 1997, Bond et al. 1999, Meir et al. 2002, Green et al. 2003). An important consequence of this relationship is that if the leaf nitrogen level is known at the top of the canopy, given a canopy light transmission model, whole canopy photosynthesis can be readily calculated. According to Sellers et al. (1992), canopies should allocate N such that for a specific light regime operating over a period T,

$$U_1 \int_0^T A dt + U_2 \int_0^T \frac{A}{N} dt \tag{15.1}$$

is maximized for all L, where L is the cumulative leaf area index, A is photosynthesis, and U_1 and U_2 are cost-benefit weighting factors, largely determined by the local availability of nitrogen. The first term relates to maximizing photosynthesis and the second term to maximizing efficiency of N use. Importantly, Sellers et al. (1992) findings are only valid for the case where $U_1 >> U_2$ and do not hold in very low N availability environments. A consequence of this is that we would expect the N: NPP relationship to break down at low nutrient sites such as bogs.

The solution of Sellers et al. (1992) takes the form of:

$$A_N = A_{n0} \prod \tag{15.2}$$

where A_N is canopy photosynthesis produced by a certain amount of N, and A_{n0} and $\prod$ represent the separate effects of leaf biochemistry and canopy structure, respectively. A_{n0} can be thought of as a "single leaf" solution where the N at the top of the canopy sets maximum photosynthetic capacity and $\prod$ is a scaling factor to relate the "top" leaf performance to canopy performance. For a simple, exponential model of light attenuation,

$$\prod = \int_0^{LT} \overline{f(L)}\, dL = \left[\frac{1 - e^{-kLT}}{\bar{k}} \right] = \frac{\overline{FPAR}}{\bar{k}} \tag{15.3}$$

where k is the canopy light extinction coefficient and FPAR is the fraction of absorbed photosynthetically active radiation and the overbars denote a radiation-weighted mean value.

In other words, whole-canopy photosynthesis (GPP) is a simple function of leaf N at the top of the canopy and APAR. This result provides important simplifications and constraints for models of land surface CO_2 exchange. Data from several stand-level studies support these notions, having demonstrated significant positive relationships between mass-based foliar N concentrations and maximum net photosynthesis or A_{max} (Reich et al. 1995, 1999), and between aboveground net primary production (ANPP) and mass-based foliar N concentrations averaged over the entire canopy (Comeau and Kimmins 1985, Smith et al. 2002). A study by Green et al. (2003) highlighted the prominent role of N in explaining canopy light use efficiency across a broad array of C3 plants, providing additional evidence that the same factors responsible for the efficiency of leaf-level photosynthesis have strong potential to be directly scaled to whole plant canopies.

A promising extension of these results is the development of methods for quantifying canopy nitrogen concentrations that can substantially improve the accuracy of model-based production estimates derived using remote sensing (Ollinger and Smith 2005). Methods for estimating canopy N using high spectral resolution remote sensing have been in existence for some time (Matson et al. 1994, Zagloski et al. 1996, Martin and Aber 1997), and have been applied with a high degree of accuracy using high spectral resolution data from NASA's airborne imaging spectrometer, AVIRIS (Martin and Aber 1997, Smith et al. 2002, Asner and Vitousek 2005). A robust capacity for remote detection of canopy N from a space-based platform (Hyperion) has also recently been demonstrated within a number of forest biomes (Smith et al. 2003, Townsend et al. 2003, Coops et al. 2003, Martin et al. 2008). Regional- to continental-scale gradients in foliar N have been observed through analysis of field measurements and through combined field and hyperspectral remote sensing campaigns across multiple biomes (e.g. Yin 1992, Aber et al. 2003, McNeil 2006, Martin et al. in press). Methods for canopy N detection from broader-scale instruments such as MODIS are beginning to be developed (Potter et al. 2007, Ollinger et al. 2007).

15.2 Field Measurement

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. Field-based estimates of forest canopy chemistry are based on leaf-level measurements of mass and chemistry combined with estimates of the fractional distribution of species' leaf area in a forest canopy. The methods outlined below are largely drawn from Smith and Martin (2001) and Smith et al. (2002).

15.2.1 Green-Leaf Chemistry and Leaf Mass Per Unit Area (LMA)

On a per plot basis, two essential measurements are required: an estimate of the mean N concentration (mg/g) for each species on each plot combined with a mean value of leaf mass per area (g/cm^2, LMA) for each species.

A representative number of leaf samples are needed to derive a robust mean leaf-level N. In order to determine growing season foliar chemistry, mid-growing season green leaf samples should be collected on each study plot. On each plot, all canopy species should be identified and, depending on canopy composition, between two and seven trees per species selected for green leaf collection. Leaves can be quite efficiently collected in moderately tall canopies ($\leq$35 m) by shooting small branches from the canopy using shotguns (12 gauge, #3 or #4 steel shot). Each sample should consist of leaves collected from several places in the canopy. Leaf-level N can be determined by various methods including CHN analysis, laboratory spectroscopy (Bolster et al. 1996), or wet chemistry. Additional leaf samples should be collected from the upper canopy of each dominant or co-dominant species on each plot in order to make a determination of LMA for each species on a per plot basis (Chapter 14, Canopy Structure section on considerations for LMA sampling and measurement).

15.2.2 Scaling Leaf Level N to Whole Canopies

As N concentration on a mass basis does not vary significantly in relation to vertical canopy gradients (Ellsworth and Reich 1993, O'Neill et al. 2002), canopy-level nitrogen concentration (mg/g) on a per plot basis can be simply calculated as the sum of the mean of foliar N concentrations (mg/g) for individual species in each stand, weighted by fraction of canopy foliar mass per species.

Determination of canopy species fraction by mass can be accomplished variously. One method employs litterfall collection where canopy species fraction by mass is calculated directly from dried, sorted litterfall data. This method is most appropriate in deciduous stands where litterfall is equal to canopy production and complete leaf senescence occurs at the end of the growing season. In mixed or pure conifer stands this method is problematic and not recommended. Needle retention varies among species and from year to year based on climatic conditions and, absent a record of litter collection over multiple seasons, both total and species fraction of canopy mass will tend to be underestimated (see Chapter 14, Canopy Structure section).

The alternative and recommended method, validated against litterfall data from both deciduous and mixed stands, employs a camera-based point quadrat sampling technique to estimate species fraction of leaf area (Aber 1979a, b) and species LMA measurements (Smith and Martin 2001). A 35 mm camera with a 135 mm telephoto lens serves as the sampling device (Fig. 15.1).

The focal plane of the lens is calibrated to distance in meters to allow use as a range finder, and a grid of 15 points is marked on the camera's viewing screen (such

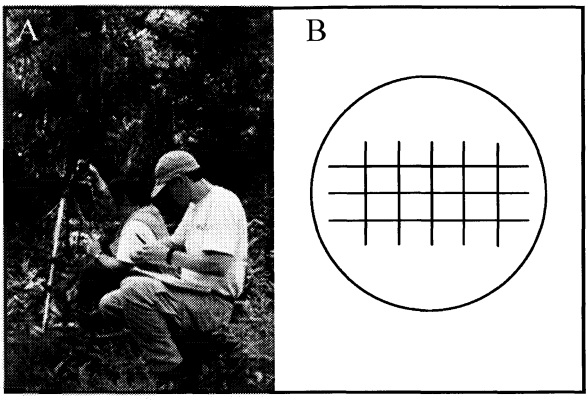

Fig. 15.1 Camera-based point quadrat sampling to estimate species' fraction of leaf area in a forest stand. A 35 mm camera is used as the sampling device (A). The focal plane of the lens, calibrated to distance, is used as a range finder and the camera's viewing screen is used as the sampling grid (B)

grids are commercially available). In each sample plot the camera, mounted on 1 m tall tripod, is directed upward towards the canopy and leveled. The species and height of the lowest leaf covering each grid point is determined by focusing the lens and recording the calibrated distance. In each sample plot, 15 grid-point observations are taken at nine sample points for a total of 135 observations per plot. Although not an accurate estimator of total leaf area, this method has been demonstrated to be an accurate means of determining the relative distribution or fraction of leaf area by height (MacArthur and Horn 1969, Aber 1979a, b) and by species (Parker et al. 1989) in a forested canopy.

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

$$LAI_h = \ln\left(\frac{N_h + S}{S}\right) \tag{15.4}$$

where:

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

From this calculation LAI is determined within each of the 2 m vertical increments and the fraction of each species within each increment. The LAI attributed to each species is 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 is converted to fraction by weight by multiplying area fraction by measured specific leaf weight of each species and deriving a new fraction by weight for each species on sample plots.

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