Reprinted from

Eleventh International Symposium

Machine Processing of

Remotely Sensed Data

with special emphasis on

Quantifying Global Process: Models, Sensor Systems, and Analytical Methods

June 25 - 27, 1985

Proceedings

Purdue University
The Laboratory for Applications of Remote Sensing
West Lafayette, Indiana 47907 USA

MODELING THE CONTROLS OF FOREST PRODUCTIVITY USING CANOPY VARIABLES

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ABSTRACT

A framework is presentedby which a generalized, canopy-driven model of biogeochemical cycling in forest ecosystems may be produced. Recent research results demonstrating relationships between canopy characteristics and important ecosystem processes are used to support this approach. Most relationships hold across species groups and suggest that identification of species may not be crucial. Linking this type of model to remote sensing will depend on developing the capability to measure a few key morphological and chemical parameters of whole forest canopies by reflectance characteristics.

I. INTRODUCTION

The field biological sciences have lagged behind many of the physical sciences in identifying the key processes and central variables which control the systems they study. Field biological research has to some degree been a celebration of diversity rather than an elucidation of underlying principles and simplifying concepts. The last ten years, coinciding with the increasing interest in the ecosystem-level of study, has seen a reversal of emphasis.

The study of ecosystems is now reaching the point where generalized models of biogeochemical cycling in terrestrial ecosystems is a possibility. When developed, these models could prove a very important component of remote sensing research in Global Habitability and Global Biology. The link lies in the realization that important system state variables are displayed in the forest canopy. These include total leaf mass and area as well as total nitrogen, cellulose, starch, and lignin content. When we learn how to estimate these crucial canopy characteristics remotely, we should be able to make accurate estimates of rates of biomass production and biogeochemical cycling for any terrestrial ecosystem. A model using this approach is currently being developed by a team of researchers including the authors and David Peterson and Pamela Matson (Ames Research Center), Steve Running (University of Montana) and Peter Vitousek (Stanford University).

This brief report has three purposes: 1) to provide an introductory outline of the important processes which control the biogeochemistry of terrestrial ecosystems, 2) to present recent results indicating the generality across large species groups of relationships between forest canopy characteristics and the rates of these processes, and 3) to present some indications that measuring spectral reflectance will allow estimation of these forest canopy characteristics.

II. OUTLINE OF ECOSYSTEM PROCESSES

There is an emerging view that terrestrial ecosystem function is controlled by the efficiency with which growth-limiting resources (Eg. water, light, nutrients) are used to fix carbon from the atmosphere. Restrictions on biological production (net carbon fixation) are approached as the ratio of the relative availability of these resources, expressed as rates, to the relative demand by the species present. Variability in the ratio of availability to demand alters total production as well as the partitioning of carbon and nutrients to different morphological tissues (roots, leaves, wood) and to different biochemical compounds (cellulose, lignin, protein, starch). Partitioning largely determines both the residence time of the tissues before decay begins and the rate of decay and nutrient release following senescence.

This is summarized in figure 1. Nutrient and water availability cause (within climatic constraints including net radiation) the fixation of carbon and the transfer of carbon and nutrients to a range of products with different life expectancies (turnover rates) and chemical content. This combination determines the rate of the next serial transfer to a set of litter compartments whose own decay (turnover) rates for carbon and nutrients are determined by their initial chemical content. Mineralization (or turnover of nutrients in the litter compartments) completes the feedback to inputs. Atmospheric and rock weathering inputs add to this signal, but in most systems (except heavily polluted ones) critical nutrient cycles are relatively closed, with most nutrient uptake being regenerated from decomposing litter. There is also a longer term storage pool termed "humus" which can contain large amounts of nutrients and which decays very slowly or may be permanently (on a biological time scale) fixed in mineral colloids. Initial litter chemistry can also play an important role in determining how much of deposited material eventually becomes humus.

The key concept here is resource ratios. Species vary in the efficiency with which different resources are converted to fixed carbon as well as the ratio of resources required. For example, one species may require 100 g of water and .01 g of nitrogen to fix 1 g of carbon, another may require 150 g of water and .008 g of nitrogen. However, the species is not the fundamental unit. Broad generalizations on rates of function as related to leaf morphology and chemistry are beginning to emerge which apply for large species groups. Thus, species identification becomes much less critical. Rather, groups of organisms with significant differences in physiological mechanisms (Eg. C3 versus C4 photosynthesis nitrate versus ammonium uptake) become the "taxa" of interest.

Plants can alter their resource use and use-efficiency ratios by altering leaf chemistry, quantity and display. These should be visible as changes in spectral reflectance within narrow but detectable bounds for "normal" conditions, and ever wider ranges with increasing stress. Different types of stress (which is the physiological expression of imbalances in resource availability or the presence of toxins in the environment) should be visible as different spectral shifts. These shifts should be indicative of rates of biomass production, the partitioning of production to chemical form and tissue type and eventually to rate of decay of produced biomass. Together these processes largely control the internal biogeochemical cycles of forest ecosystems.

III. CANOPIES AND ECOSYSTEMS

This section will briefly describe selected recent research results which demonstrate relationships between canopy or leaf characteristics and rates of important ecosystem processes. It should be reemphasized that most of these relationships cross species boundaries and apply to larger species groups. They also demonstrate the ability of vegetative communities to alter ratios of resource use to fit different sets of environment conditions.

<u>Net photosynthesis at light saturation</u> - Mooney and coworkers (Eg. Mooney and Gulmon 1982) have hypothesized and demonstrated that maximum photo synthetic rate of individual leaves of C3 plants, regardless of species, is a direct function of nitrogen content per unit leaf weight. Individual plants can increase their maximum rate of net photosynthesis by a tighter "packing" of chloroplasts and carboxylating enzymes per unit leaf weight. Light is used more efficiently at a greater nitrogen cost.

<u>Water use efficiency/nitrogen use efficiency tradeoff</u> - An extension of the above work has tested the hypothesis that higher photosynthesis per unit leaf weight results in lower transpiration (water loss) per unit carbon fixed. Field et al (1983) have shown that higher nitrogen content per unit leaf weight does increase water use efficiency (gCO2 fixed per g water lost). Thus plasticity in leaf morphology can result in a range of water- and nitrogen-use efficiencies which match resource demand ratios with relative resource availability. Again, this spans species boundaries.

In forest ecosystems we have studied, three major species show weight/area and N/weight ratios in keeping with their ecological amplitudes. Oaks show high weight/area indicating increased water use efficiency. Maples have low weight/area and low N suggesting a shade-tolerant but water demanding physiology. Basswood has high N and low weight/area, suggesting a high requirement for both N and water.

<u>Structural characteristics - Sapwood area/leaf area/production</u> - Waring and coworkers (Waring et al. 1977, 1982, 1983) have shown a strong relationship

between the cross-sectional area of sapwood (water conducting tissue) in conifer trees and their leaf area. A comparison of current diameter increment versus sapwood area yields a measure of stem or whole stand vigor which has been related to tissue chemistry as well as susceptibility to insect attacks. The concept applies to conifer trees generally. Knowing tissue chemistry may thus allow a back calculation of rate of biomass production or likelihood of future mortality by insects and diseases.

Total canopy nitrogen and net primary production - Aber, Melillo and co-workers have shown a very strong relationship between nitrogen uptake in a wide range of forest ecosystems and net carbon fixation and allocation above ground (Aber et al. 1985; Lennon et al. 1985; Nadelhoffer et al. 1985; Pastor et al. 1984). An intermediate relationship exists between nitrogen mineralization and canopy green leaf N content and further between canopy N content and above ground production (Lennon et al. 1985). This latter relationship emphasizes the potential value of being able to estimate total canopy N.

Nitrogen mineralization and allocation/turnover/efficiency - Above ground production is only one component of total net primary production. However, both total production and its allocation are also related to the rate of N cycling (Nadelhoffer et al. 1985; Aber et al. 1985b). Other processes linked to the N cycle include the nitrogen content of leaf litter, an indicator of nutrient use efficiency (Vitousek 1982), and also rates of tissue turnover for both fine roots (Aber et al. 1985a) and leaves (Mooney and Gulmon 1982). An emerging pattern here is that higher nitrogen availability results in a faster N cycle, lower N use efficiency, shorter life span for physiologically active tissues and lower retranslocation of nitrogen from senescing tissues. Carbon partitioning (Eg. starch, cellulose, lignin) and total foliar N within canopies may go a long way toward predicting these rates in any given system, regardless of the species composition on a site.

Decomposition as a function of litter chemistry - Nitrogen concentration and carbon fraction contents of litter control decay rates in temperate

forests (Melillo et al. 1982). Lignin, a complex polyphenol, is especially significant in reducing decay rates while higher N content increases rates. Further studies have shown that nitrogen dynamics in decomposition are also predictable based on nitrogen and lignin contents (Aber and Melillo, 1982). Thus, if lignin and N content of foliage can be estimated by reflectance, a good prediction of the rate and nitrogen dynamics of decay can be made. This will allow an estimation of the rate of N mineralization (availability) in ecosystems.

Generalization to other resources - These studies have stressed interactions between carbon, nitrogen and water availability. They demonstrate that the metabolism of ecosystems is constrained within certain bounds and that measureable canopy variables are good indices to rates of function. This work is currently being extended by many researchers to include other potentially limiting resources through experiments with manipulated resource availability ratios. The field is young but the likelihood of further development of simple, generalized models of ecosystem biogeochemistry seems quite high.

IV. CANOPY REFLECTANCE

What is the likelihood that the key parameters of canopy chemistry (nitrogen, lignin, cellulose, starch, etc.) can be accurately measured by remote sensing? Several lines of evidence suggest that success is likely.

Nitrogen will be the easiest to estimate because of the strong correlation with chlorophyll content. For example, Tsay, et al. (1982) successfully predicted total N content of fresh loblolly pine needles using reflectance at 540 nm. Commercial devices have been developed which examine reflectance of dried, ground samples in the 2.0-2.4 um range (2 mm bandwidth) and which

estimate N content within the repeatability range of standard wet chemical methods (Hooten 1978; Rotolo 1979). These devices have become the accepted industrial standard for judging grain quality.

Specific methods for estimating carbon fractions (lignin, cellulose, starch) using commercial, laboratory near infrared reflectance devices have been presented but remain experimental. Corporate research publications list specific wavelength assignments for compounds of interest (table 1) but their value in quantitative analysis remains unverified.

At the other end of the spatial spectrum. Simple ratios expressing "greenness" in pixels at the thematic mapper scale correlate well with leaf area index and productivity for forest systems in Oregon (Spanner et al. 1984). At the scale of the AVHRR, Tucker et al. (1985) have been able to chart the seasonal course of photosynthetic activity for the entire globe using a similar "greenness" index. Shifts in reflectance spectra measured by Rock (1984) and Chang and Collins (1983) in response to stress suggest significant changes in leaf structure and content which may well relate to changes in carbon fractionation.

In summary, there are two converging areas of research which promise a successful application of remote sensing to measuring and modeling biogeochemical cycling rates in terrestrial ecosystems. One is the emergence of generalizable relationships between leaf and canopy characteristics and rates of important processes such as photosynthesis, net primary production and decomposition. The other is the rapidly advancing field of leaf and canopy chemical analysis by spectral reflectance in the visible and near infrared.

ACKNOWLEDGEMENTS

Support for this research has been provided by NASA-Ames Research Center under Interchange No. NCA2-1R865-401 and the College of Agricultural and Life Sciences, University of Wisconsin-Madison.

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