

**MODELING CARBON FLUXES, NET PRIMARY PRODUCTION
AND LIGHT UTILIZATION IN BOREAL FOREST STANDS**

by

Scott J. Goetz

ISBN: 0-9658564-5-3

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1997

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AND LIGHT UTILIZATION IN BOREAL FOREST STANDS**

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Scott J. Goetz

Dissertation submitted to the Faculty of the Graduate School
of The University of Maryland in partial fulfillment
of the requirements for the degree of
Doctor of Philosophy
1996

Advisory Committee:

Professor Stephen Prince (Chairman/Advisor)
Professor Samuel Goward
Professor John Townshend
Professor Irwin Forseth
Dr. Charles Walthall

ABSTRACT

Title of Dissertation: MODELING CARBON FLUXES, NET PRIMARY PRODUCTION, AND LIGHT UTILIZATION IN BOREAL FOREST STANDS

Scott J. Goetz, Doctor of Philosophy, 1996

Dissertation directed by: Dr. Stephen D. Prince, Professor
Department of Geography
University of Maryland

The use of satellite remote sensing for modeling net primary production (NPP) was evaluated in sixty boreal forest stands spanning a range of site conditions. The work included: (i) estimating annual phenological dynamics and photosynthetically active radiation (PAR) interception with remotely sensed spectral measurements, (ii) linking annually absorbed PAR (APAR) to measured NPP and quantifying variability in light use efficiency (ϵ_n), (iii) evaluating sources of variability in ϵ_n via mechanistic modeling of ecophysiology and associated carbon fluxes, particularly through analyses of respiratory carbon costs in relation to assimilation gains (the R:A ratio), (iv) assessing generalization of the results through an investigation of the evidence for evolutionary convergence in ϵ_n , the R:A ratio and assimilation per unit APAR (ϵ_g).

The analyses showed that observed variability in ϵ_n reflects a decoupling of PAR harvesting and utilization, primarily as a result of differences in the R:A ratio. Links between ϵ_n , the R:A ratio and standing above-ground biomass were related to differences the carbon (energy) costs associated with synthesis and maintenance of plant constituents, and longevity (i.e. the payback period on investment in carbon gain). Estimating the R:A ratio from above-ground biomass, in order to compensate for variability in ϵ_n , was found to be problematic owing primarily to covariation of R and A with the amount of respiring biomass (i.e. sapwood and foliage). The analyses also showed that the differences in carbon costs between functional types (plants with related life history traits) resulted in convergence on ϵ_g rather than ϵ_n . Variability in ϵ_g was, however, introduced by stomatal control at some stressed sites. These findings were supported by the remote sensing and simulation modeling results, and the synthesis of work related to evolutionary ecology.

The primary conclusions are that variability in light utilization in these boreal forest stands was determined largely by respiratory carbon costs, and that NPP models based on light harvesting require augmentation with terms that reflect PAR utilization. Possible methods to address these issues, and their implications for NPP modeling over large areas, are discussed.

DEDICATION

To Nadine for her patience and love,
my mother for her strength and character,
and to the memory of my father
for all he taught me.

ACKNOWLEDGMENTS

There are many people to whom I am indebted for the completion of this research. First and foremost, Steve Prince provided superb critical reviews of the dissertation and related publications, and encouraged me to pursue the evolutionary ecology that opened a great many avenues of higher learning. He fulfilled the role of mentor as well as any student could hope for. Support from Forrest Hall while I was employed at NASA allowed me to complete aspects of this research that might not otherwise have been possible. I learned much about remote sensing science under his tenure. Sam Goward, John Townshend, Irwin Forseth and Charlie Walthall all provided helpful comments on the dissertation. Jaime Nickeson and Fred Huemmerich assisted me with aspects of the phenology and canopy modeling, and helped me through the times when I thought I'd never complete a PhD and hold down a full-time job. Piers Sellers showed me that it was possible to do that and a whole lot more with a sense of humor. Finally, I am indebted to Frank Davis for introducing me to forest ecology and biodiversity research and for giving me the boost I needed after leaving UCSB.

TABLE OF CONTENTS

List of Tables.....	vi
List of Figures.....	vii
Chapter I. Introduction and Background	1
Approaches to Primary Production Modeling	2
Statistical and Climate Models	3
Gap Models	4
Ecophysiological Carbon Flux Models	4
Production Efficiency Models.....	6
PAR Harvesting	7
PAR Utilization	9
Hybrid Approaches	11
Modeling Boreal Forest Stand NPP.....	13
Hypotheses Tested	17
Study Area and Data.....	18
Chapter II. Remote Sensing of Net Primary Production in Boreal Forest Stands	25
Methodological Approach.....	25
Phenology.....	25
Fractional PAR Interception	27
Annual PAR Interception.....	28
Results.....	29
Phenological Dynamics	29
Fractional PAR Interception	30
Annual PAR Interception.....	34
Utilization of Annually Intercepted PAR.....	36
Comparison of PAR Utilization with Other Forest Stands.....	38
Within-Species Variability in PAR Utilization.....	40
Variation in Stand Composition and Physical Carbon Losses	41
Variation in Below-Ground Allocation	41
Variation in Available Resources	42
Variation in Respiration Demands.....	43
Regional NPP Estimation with Constant PAR Utilization.....	44
Summary of Remote Sensing Analyses	46
Chapter III. Modeling Carbon Fluxes in Boreal Forest Stands	48
Terrestrial Carbon Exchange (TCX) Model Description	48
Methodological Approach.....	52
Sensitivity Analysis.....	54
Parameterization	55
Stand Simulations.....	58
Simulation Results.....	59
Sensitivity Analysis.....	59
Comparison of Observed and Simulated NPP.....	63
Seasonal Patterns of Assimilation and Respiration	65
Sources of Variability in PAR Utilization.....	67
Variability of PAR Utilization in Relation to R:A Ratio	71
Variability of R:A Ratio in Relation to Biomass	77
Gross versus Net Carbon Yield of APAR.....	80
Summary of Simulation Analyses.....	82

Chapter IV. Analysis of Results in the Context of Functional Convergence	85
Resource Constraints and Adaptive Strategies	85
Allocation Strategies, Defenses Costs and Payback Intervals	86
Evidence for Optimization of Resource Allocation and Use Efficiency	90
Water.....	91
Nitrogen.....	91
Photosynthetically Active Radiation (PAR).....	92
Combined Resource Use Efficiencies.....	92
Links Between Optimization and Leaf Mass Per Unit Area.....	93
Optimized or Compromised Resource Use?	94
Links Between Maximization of Fitness and Carbon Gain.....	95
Implications of Functional Convergence for Modeling Net Primary Production	96
Summary of Functional Convergence Analyses	98
Synopsis and Conclusions	100
Appendix	103
References	106

LIST OF TABLES

<u>Number</u>		<u>Page</u>
1a.	Population characteristics of lowland black spruce stands.	21
1b.	Same as Table 1a but for aspen stands	22
2.	Landsat Multispectral Scanner (MSS) imagery.	23
3a.	Goodness-of-fit statistics on spruce stand phenology models and mid-season fractional canopy PAR interception	30
3b.	Same as Table 3a but for aspen stands	31
4a.	Annual PAR interception and utilization (ϵ_j) in spruce stands.	34
4b.	Same as Table 4a but for aspen stands	35
5.	Sequence of routines called in TCX model.....	49
6.	Input variables required and output variables simulated by the TCX model.	50
7.	Maintenance respiration coefficients and carbon allocation parameters.....	55
8.	Results of TCX sensitivity analysis with respect to total tree NPP.	60
9a.	Simulated annual PAR absorption and utilization (ϵ_j) in spruce stands.	69
9b.	Same as Table 9a but for aspen stands	70
10.	Goodness-of-fit statistics on regression relationships between various stand variables.....	73
11.	Summary statistics of variation in ϵ_n and ϵ_g	81

LIST OF FIGURES

<u>Number</u>		<u>Page</u>
1.	Superior National Forest study area in northeastern Minnesota.....	19
2.	Flow chart of the methodological approach used for the remote sensing portion of the analysis.....	26
3.	Greenness vegetation index response to growing degree days (phenology) fit with the temporal profile model.....	30
4.	Overstory <i>fipar</i> as a function of stand Greenness for a range of overstory LAI	33
5.	Canopy model simulations of overstory <i>fipar</i> as a function of stand Greenness.....	33
6.	Annually intercepted PAR versus measured mid-season LAI.....	36
7.	Annually intercepted PAR versus annual above-ground NPP.....	37
8.	A comparison of the ranges in reported values of the dry matter yield of intercepted or absorbed PAR.....	39
9.	Observed annual NPP compared to predicted values derived from estimated Σ IPAR and ε_i values.....	45
10.	Flow chart of the methodological approach used for the carbon flux modeling portion of the analysis.....	53
11.	Diffuse, direct and total daily PAR amounts (MJ) as a function of fractional cloud cover.....	54
12a.	Age dependence of aspen below-ground biomass amount.....	57
12b.	Same as Figure 12a but for aspen sapwood biomass.....	57
13a.	Variation in simulated total spruce production as a result of combined variations in LAI and foliage N content.....	61
13b.	Same as Figure 13a but for aspen stands.....	61
14.	Variation in simulated total tree production in relation to foliage N content, at constant LAI.....	62
15a.	Simulated AANPP for spruce simulations with measured stand variables.....	64
15b.	Same as Figure 15a but for aspen stands.....	64

LIST OF FIGURES

<u>Number</u>	<u>Page</u>
16a. Seasonal dynamics of daily assimilation and maintenance respiration for spruce stands.....	66
16b. Same as Figure 16a but for aspen stands.....	66
17. Simulated annually absorbed PAR and annual above-ground NPP.....	67
18. Comparison of simulated annual PAR absorption with different approaches.	68
19. Simulated variation in PAR utilization as a function of variability in the respiration : assimilation ratio.	72
20a. Simulated variation in PAR utilization and respiration : assimilation ratio, as a function of LAI.	74
20b. Same as Figure 20a but as a function of foliage N content.	74
21a. Simulated variation in PAR utilization and respiration : assimilation ratio for generalized spruce stands.	76
21b. Same as Figure 21a but for aspen stands.....	76
22a. Variation in the proportion of spruce assimilation not used in maintenance respiration, in relation to standing above-ground biomass.....	79
22b. Same as Figure 22a but for aspen stands.....	79
23. Annual assimilation versus annual APAR for all spruce and aspen simulations.	80
24. Average daily assimilation per unit APAR in spruce versus aspen stands.....	82
25. Generalized suites of life-history traits.....	87
26. Foliage construction costs.....	89

Chapter I. Introduction and Background

The forces that drive changes in global climate and the predicted extent of future climate change have been the focus of much research and debate (Hansen et al. 1981; Ramanathan 1988; Schneider 1989). The measured concentration of atmospheric "greenhouse gases," which trap longwave radiation emitted from the Earth's surface, have increased approximately 30% since the industrial revolution, primarily as a result of fossil fuel burning (Bacastow et al. 1985; Raynaud et al. 1993; Keeling et al. 1995). The increase has, in turn, been unambiguously linked to an observed increase in near-surface warming of the atmosphere (Thompson 1995).

The response of terrestrial vegetation to the most widely studied greenhouse gas, carbon dioxide (CO₂), introduces a possible negative feedback mechanism through which CO₂ "fertilization" and associated storage of sequestered carbon in vegetation and soils may mitigate further climate warming (LaMarche et al. 1984; Prentice 1986; Bazzaz et al. 1990; Körner and Arnone 1992). A combination of other studies, including use of simulation models and laboratory and field experiments, suggests that initial increases in vegetation carbon uptake under amplified CO₂ may quickly reach new equilibrium levels or return to previous levels owing to limitations in the availability of other resources (primarily trace nutrients) (Williams et al. 1986; Pastor and Post 1988; Kirschbaum et al. 1994; Jacoby and D'Arrigo 1995).

In general, because vegetation and the atmosphere are tightly coupled, as exemplified by established links between seasonal cycles of atmospheric CO₂ and vegetation activity (Tucker et al. 1986; D'Arrigo et al. 1987; Conway et al. 1994), there are likely to be significant changes in the productivity of terrestrial vegetation with further increases in atmospheric CO₂ concentration (Emanuel et al. 1985; Overpeck et al. 1991; Woodward et al. 1991). The greatest changes are predicted to occur in the forest ecosystems of the northern hemisphere, primarily the boreal forests (Pearman and Hyson 1981; Houghton 1987; Post et al. 1990). Recent work with isotope tracers in general circulation models also suggest that the largest net exchange of carbon between the terrestrial vegetation and the atmosphere occurs in the higher latitudes of the northern hemisphere (e.g., Tans et al. 1990; Ciais et al. 1995; Denning et al. 1995). This net ecosystem exchange of CO₂ is determined by net photosynthesis (the difference between CO₂ assimilation and autotrophic respiration) and soil (i.e., microbial or heterotrophic) respiration, the sum of which may dynamically alternate between a net source or sink (Sundquist 1993; Conway et al. 1994; Keeling et al. 1995). Net photosynthesis through time, or net primary production (NPP), is thus an integral component of the global carbon cycle and is important to monitor, particularly in high latitude forests.

As a result of its important role in global carbon dynamics, research designed to quantify terrestrial NPP has received a great deal of attention in recent years. Whereas a number of approaches to NPP estimation have been developed (reviewed in the next section) one of the most promising techniques utilizes satellite remote sensing to provide a means for monitoring vegetation light capture and utilization (Lurin et al. 1994; Prince et al. 1994). Related research has suggested that remote sensing of NPP can be simplified by taking advantage of the possibility that natural selection has resulted in a narrow range of light use efficiency (ϵ) among plant functional types (i.e., plants with a related suite of life history traits) (Field 1991). These developments in NPP evaluation and monitoring stimulated the work reported in this dissertation.

The objectives of the research reported herein were to test the use of satellite remote sensing techniques for inferring NPP and ϵ in boreal forest ecosystems, to examine sources of variability in the NPP and ϵ estimates with a mechanistic ecophysiological model, and to assess generalization of the results through arguments based in evolutionary ecology. A study site in the boreal forest of northeastern Minnesota was selected because it was well suited to addressing these objectives, particularly because it provided a wide range of vegetation productivity and biomass data, and great variability in site conditions, under similar climate. Moreover, it allowed the objectives to be addressed at a spatial scale that could be verified with surface measurements. The objectives were then tested with three hypotheses that are formalized following a review of background issues and recent advances related to the subject. Because of the interdisciplinary nature of the research, which includes components of physiological ecology, radiation physics, production biology and evolutionary ecology, a glossary of terms, definitions and their associated symbols and acronyms is provided as an appendix.

Approaches to Primary Production Modeling

Methods to model NPP over large areas range from simple correlation models to complex ecophysiological models that couple vegetation - atmosphere exchange of energy, mass and momentum. The methods of modeling NPP reviewed here include statistical extrapolation of point measurements, climate models, plant growth models, ecophysiological models, and models driven with satellite remote sensing measurements. While methods based on complex ecophysiological models have distinct advantages over statistical models, techniques using remotely sensed data are able to provide information on vegetation conditions, such as leaf area index and canopy light absorption, through time. The advantages and disadvantages of the different modeling approaches, alone and in combination, are examined. The implications of evolutionary factors that may limit the ranges of variables and introduce correlations that may simplify NPP modeling are also discussed. The review focuses primarily on production

modeling at the stand level, but methods to extend these to large-area primary production modeling are also discussed.

Statistical and Climate Models

Statistical relationships that associate measured stand NPP with land cover type classifications have been used to provide estimates of NPP at the global scale (Bazilevich et al. 1971; Whittaker and Likens 1973; Atjay et al. 1979; Brown and Lugo 1984). This method has many problems associated with the time and place-specific dependency of the measured values, ambiguities associated with the accuracy of land cover classifications, and errors associated with the use of very few points to represent large areas. For example, estimates of the magnitude of C storage in global vegetation have varied widely (420 - 830 Gt) depending on sampling methodology and ecosystem definitions (Moore et al. 1981; Houghton et al. 1983; Detwiler and Hall 1988). Such statistical models of NPP also offer little or no predictive or monitoring capability due to their strictly empirical nature. These methods are important to pursue in relation to potential simplification of complex mechanistic models and for interpretation of broad climate-vegetation patterns predicted by such models, but they can probably not be used to reliably estimate ecosystem productivity until a more adequate sampling network is in place.

Statistical relationships have also been used to relate climate to plant production (Lieth 1975; Rosenzweig 1968; Box 1978; Brown and Lugo 1982; Emanuel et al. 1985). This approach has been limited by the fact that it assumes homogeneous responses of vegetation to temperature and precipitation, and because it incorporates few plant physiological processes. Recently, Goward and Prince (1995) characterized several examples where climate and vegetation photosynthetic activity were poorly related, in a statistical sense, owing to lagged vegetation response to climate, disturbance frequency, and unique vegetation evolutionary adaptations (e.g., precipitation anticipation).

Statistical models of vegetation and climate associations have been largely supplanted by Soil-Vegetation-Atmosphere-Transfer (SVAT) models that incorporate feedback mechanisms between vegetation and the atmosphere by coupling plant physiological processes with climate models (e.g., Dickinson et al. 1986; Sellers et al. 1986). Such changes have been used, for example, to improve Global Circulation Models (GCMs; Sato et al. 1989; Dickinson 1995) and to predict the climatic effects of deforestation (Dickinson and Henderson-Sellers 1988; Shukla et al. 1990). The focus of this work has, however, generally been to improve climate models rather than to monitor terrestrial carbon dynamics or predict ecosystem response to changes in climate.

Gap Models

Forest succession or "gap" models offer an approach to evaluate terrestrial carbon dynamics that incorporates both plant ecology and climate variability. Such models have been developed almost exclusively for temperate forest ecosystems (Botkin et al. 1972; Shugart and West 1977; Pastor and Post 1985). Gap models consist of components that simulate disturbance, the soil regime (affected by soil physical properties), the solar regime (affected by cloudiness, latitude, and topography), and forest growth dynamics on an individual tree basis.

Although gap models incorporate plant physiological processes, they do so in a prescribed manner based on a database of life history characteristics. As such, gap models lack the ability to realistically incorporate the feedback mechanisms between the plant and the atmosphere, thus are limited in applications to different regions. Moreover, these models suffer from an inability to monitor changes in the landscape, except in a stochastic manner.

Despite these limitations, gap models are continuously being improved and recent efforts have focused on incorporating plant physiology in a more mechanistic manner (Friend et al. 1993) and in linking plant growth model components with soil process and radiative transfer models in a spatial framework (Levine et al. 1993).

Ecophysiological Carbon Flux Models

Unlike gap or climate models, ecophysiological C flux models are designed to incorporate plant ecophysiology (that is, the interrelationship between the plant's functioning and its environment) and biogeochemistry, rather than plant population characteristics or life-cycle dynamics. The strength of these models lies in simulating short-term plant physiological responses to moisture, temperature and nutrient limitations (stress), and the effect of these responses through stomatal conductance on mass fluxes (CO₂ exchange through photosynthesis and respiration) and energy fluxes (evapotranspiration, sensible and latent heat exchange).

Two examples of widely cited C flux models are reviewed here to characterize the advantages and disadvantages of this approach. The first, the Terrestrial Ecosystems Model (TEM; Raich et al. 1991) simulates C fluxes at the continental scale by calculating respiration carbon costs in conjunction with process-level relationships between photosynthesis, atmospheric CO₂ concentration, moisture availability, air temperature, nitrogen (N) availability and, to some extent, the seasonality of vegetation. This model predicts C and N fluxes and pool sizes at 0.5 x 0.5 degree cells on a monthly time step and includes coupling with an independent water balance model (Vorosmarty et al. 1989). The second, Biome-BGC (BioGeochemical Cycles; Running and Hunt 1993) was originally developed for conifer forests in the north-central United States (Forest-BGC; Running and Coughlan 1988; Running and Gower 1991). Biome-BGC was designed to be particularly sensitive to leaf area index (LAI) in order to incorporate LAI

estimates derived from satellite spectral measurements. LAI is used in calculations of canopy radiation interception, transpiration, respiration, photosynthesis, C allocation and litterfall.

In TEM, atmospheric CO₂ concentration and solar irradiance modify gross primary production (GPP) through modification of soil moisture, stomatal control of CO₂ assimilation, and air temperature effects on photosynthetic capacity (ρ_C). Nutrient uptake is based on C and N abundance and relative "root or shoot" allocation. Phenology is approximated as relative changes in photosynthetic capacity (0 to 1) based on the ratio of the current to the previous month's actual evapotranspiration (AET), and the previous month's ρ_C . Assimilate is lost through growth and maintenance respiration processes, and leaf litter. Below-ground allocation of NPP is divided into fine and large root production. Soil C is lost through mineralization, and N cycling is based on soil moisture and temperature. A geographic database of environmental variables (including soil, temperature, precipitation, solar irradiance and vegetation maps) is used to add a spatial component to the model. The model is then run with variables from calibration sites while adjusting rate constants to reach equilibrium and to match measured values of NPP.

TEM is based on an understanding of vegetation physiological responses to physical and biotic variables. Nevertheless, the model requires calibration for each ecosystem with empirical relationships developed from representative field data, and must be spatially extrapolated from these data as with the statistical models described earlier. This limitation is obvious in an application of the model to estimate NPP for South America using data from 12 sites, only 3 of which were actually located on the continent (Raich et al. 1991). In addition, the model is currently limited to five soil types and seven vegetation types, based on a somewhat outdated global vegetation map (Matthews 1983). Despite these limitations, the model represents a comprehensive development of C flux modeling for use over large regions, and has good potential to be better calibrated as additional data become available. It has been applied at regional scales and has demonstrated the importance of nutrient use efficiency in NPP modeling (McGuire et al. 1992; Melillo et al. 1993).

Biome-BGC treats the forest canopy as a homogenous three-dimensional leaf of depth proportional to LAI (i.e., a "big leaf"). As such, leaf-level measurements are treated as whole canopy average responses. The model has a dual (daily and yearly) timestep; daily calculations of hydrologic balance, canopy gas exchange and C assimilate partitioning to respiration and growth are passed along to the annual component of the model, which calculates above and below-ground C partitioning, litterfall, N cycling and decomposition processes. An example of the coupling of the daily and yearly timesteps of the model is the treatment of C assimilation and respiratory losses, which are accumulated daily, differenced to provide a daily measure of net photosynthesis, and passed along to the yearly part of the model for growth allocation.

Coarse resolution Biome-BGC results have been difficult to validate but components of the original Forest-BGC model have been validated at a local scale with field measurements. For example, in tests of Forest-BGC in a Montana conifer forest, simulated values of above-ground NPP were comparable to measured values for sites (Running and Coughlan 1988) and for individual trees (Korol et al. 1991). In tests of the model across a wide range of sites from Alaska to Florida, the response of annual photosynthesis to increasing LAI was quite variable between the different climates (Running and Nemani 1987). Variations in respiration estimates were large, and in some cases well outside the range of literature values, however, NPP estimates generally fell within the range of values reported in the literature for each of the test sites (with the exception of a boreal forest site in Alaska). This exception was attributed to inadequate model parameterization (i.e., higher soil N-content than would be found in such a site). Running et al. (1989) note that using LAI estimated from satellite imagery at 1 km nominal spatial resolution (with which the model is typically run) may result in significant errors being propagated through model calculations, particularly in heterogeneous landscapes. Despite these difficulties, Biome-BGC is a useful and widely applied model to simulate NPP over large areas, and it uses remote sensing data to provide a temporally and spatially specific state variable (LAI).

Production Efficiency Models

The use of remotely sensed data in NPP modeling compensates for some of the limitations inherent in ecophysiological models (e.g., spatial extent), but carries with it a new set of limitations and uncertainties. The link between satellite remote sensing data and NPP has been established through the relationship between spectral vegetation indices (SVIs) and the fraction of incident PAR intercepted (f_{ipar}) or absorbed (f_{apar}) by vegetation canopies (which will be referred to as f_{par} when a distinction is not necessary).

SVIs are derived from algebraic combinations of spectral measurements available from remote sensing. The physical basis for the observed correlation between SVIs and NPP lies in two linked but independent quantities: the relationship between light reflection and fractional PAR absorption by vegetation canopies (f_{par}), and the relationship between the amount of light absorbed and NPP (PAR utilization). In order to use remote sensing to estimate NPP it is not only necessary to characterize these two separate relationships, but also to quantify incident PAR fluxes, seasonal phenological dynamics, and the areal extent and composition of ecosystems. Each of these subjects has been the focus of a great deal of research in the past two decades.

Monteith (1972, 1977) suggested that seasonal crop production was largely determined by variability in intercepted PAR. Thus, Kumar and Monteith (1982) were able to use annually

integrated f_{par} and incident PAR ($\downarrow\text{PAR}$) to provide a measure of annual NPP. The product of f_{par} , derived from a given SVI, and $\downarrow\text{PAR}$ provides a measure of production (P) defined by Steven et al. (1983) as:

$$P = \varepsilon \bullet \sum_{t=1}^N (f_{\text{par}_t} \cdot \downarrow\text{PAR}_t) \quad (1)$$

where t is the time interval over a growing season (of length N), $\bullet (f_{\text{par}} \cdot \downarrow\text{PAR})$ is the seasonal sum of absorbed PAR, and ε is the net efficiency of conversion of PAR to biomass (PAR utilization efficiency, alternately referred to as biomass - energy quotient, light use efficiency, and dry matter yield of energy).

The seasonally integrated product of incident PAR and f_{par} results in an estimate of PAR absorption by the canopy (APAR), which is in turn related to productivity rates. Applications of this simple production efficiency model (PEM), assuming a constant value of ε , have provided moderate to strong correlation with surface measurements of NPP in crops (Asrar et al. 1985; Daughtry et al. 1992), semi-arid grasslands (Tucker et al. 1983; Prince and Tucker 1986; Prince 1991a), and even at continental (Goward et al. 1985) and global scales (Potter et al. 1993; Ruimy et al. 1994; Prince and Goward 1995).

Whereas these observations demonstrate a proportionality in annual PAR absorption and NPP, there are often large uncertainties in the estimates of NPP with remote sensing. Scatter in the relationships between SVI and f_{par} and between ΣIPAR and NPP exists, and can be attributed both to errors in the remote sensing of PAR absorption and the assumption of an invariant value of ε to describe PAR utilization.

PAR Harvesting

SVIs were first used to estimate f_{par} by Kumar and Monteith (1982) using Monsi and Saeki's formulation of the Bouguer-Ber law for exponential extinction of light in plant canopies:

$$f_{\text{par}} = \frac{I_{\text{par}}}{\downarrow\text{PAR}} = 1 - e^{-kL} \quad (2)$$

where I_{par} is the amount of $\downarrow\text{PAR}$ absorbed by the plant canopy, k is a coefficient describing the average projection of leaves in any direction, modified by a scattering coefficient based on canopy architecture, and L is the projected leaf area index (LAI). Asrar et al. (1984) and Sellers (1985, 1987) advanced this simple formulation using two-stream approximations of canopy radiative transfer, which, in turn, were later advanced to three-dimensional models that

incorporated additional canopy characteristics (e.g., spatial heterogeneity and clumping; Bégué 1991; Myneni et al. 1992a). Other techniques utilize geometric-optical approaches based on mixture modeling of spectral components (Strahler and Jupp 1991; Hall et al. 1995).

Regardless of the complexity of radiative transfer modeling approaches, estimation of f_{par} from SVIs is dependent on a number of factors, including view and solar geometry, leaf display, leaf optical properties, presence of non-photosynthetic elements in the canopy, the quality of irradiance (direct versus diffuse) and background reflectance. Canopy radiative transfer simulation studies of these effects, conducted by varying the soil background, time of reflectance observations (solar angles), leaf inclination angles, and photosynthetic behavior of individual leaves, show that the relationship between the SVIs and f_{par} exhibits various degrees of non-linearity, and that the non-linearity (or the differences between linear relationships) is driven mostly by background substrate properties (Choudhury 1987; Myneni et al. 1992b; Goel and Qin 1994; Roujean and Breon 1995). A combination of these effects can result in up to 30% errors in f_{par} for a given SVI (Goward and Huemmrich 1992).

It is important to quantify the degree of non-linearity in SVI- f_{par} relationships for consideration of scaling properties of the observations. Scaling of f_{par} is simplified if the same direct relationship can be used at various spatial resolutions, thereby allowing linkages between scales. Non-linearities become problematic because the results of non-linear processes vary with the scale at which they are observed. Correlation between terms may also introduce problems if they are not independent of the scale of observation. One of the primary concerns in SVI- f_{par} relationships is the degree to which non-linearity is introduced by non-photosynthetic material in the canopy, or heterogeneity in canopy cover. It has been demonstrated in a grassland ecosystem that the relationship between SVI and f_{par} becomes more linear when PAR absorption by the live (green) matter of the canopy alone is considered (Hall et al. 1992b). It has also been suggested that spatial heterogeneity in canopy cover has little effect on this scale invariance (Sellers et al. 1992). These results suggest that SVIs respond predominantly to the photosynthetically active components of the canopy, and in turn, that f_{par} estimates from SVIs scale linearly (at least in grassland cases).

Another consideration in SVI- f_{par} relationships is the degree to which an instantaneous measurement can be used to approximate diurnal variability in f_{par} with sun angle. Studies of f_{par} in several crop species suggest that accurate estimates of f_{par} from SVIs may require frequent measurements during the day, depending on canopy architecture and leaf display (Richardson and Wiegand 1989). Simulations of instantaneous measurements of f_{par} have, however, been shown to provide a stable and near-linear estimate of diurnal f_{par} when solar zenith angle is less than 60 degrees and sensor view angle is within 40 degrees of nadir (Goward

and Huemmrich 1992). Moreover, Daughtry et al. (1992) found an instantaneous measurement of f_{par} at solar noon was not significantly different from diurnally averaged values of f_{par} .

A related consideration is the degree to which the entire canopy system is represented in the instantaneous (SVI) estimate of f_{par} . Sellers et al. (1992) have demonstrated through canopy radiative transfer simulations that SVIs provide a measure of entire canopy photosynthetic capacity due to a concentration of the photosynthetic machinery of canopies (N, photosynthetic enzymes and chlorophyll) in more exposed (sunlit) leaves. This analysis is supported by observations in a lodgepole pine (*Pinus contorta*) canopy, where the sensitivity of f_{par} to solar zenith angle effects was found to vary widely between different canopy layers, but to remain relatively constant for the entire canopy system (Kimes et al. 1980).

In general, the studies reviewed here have shown that the relationship between f_{par} and a given SVI is best for a continuous canopy and becomes less reliable as the canopy becomes spatially discontinuous due to background or shadowing effects, or in the presence of a large proportion of non-photosynthetic elements. While some results suggest SVIs respond predominantly to photosynthetic elements of the canopy, and that this results in spatial scale invariance of the relationship between SVI and f_{par} , additional work is needed to quantify how SVIs are affected by non-photosynthetic PAR absorption in different canopies, particularly when this component is large.

PAR Utilization

The link between seasonal light absorption and NPP has become an important topic because of its implications for the applicability of remotely sensed APAR to the estimation of NPP. If the relationship between annual NPP and canopy light absorption is similar between different plant types in different biomes, then the task of NPP estimation with remotely sensed APAR is simplified. If, however, it varies widely, then representative values must be determined for each growth-form or biome on a case by case basis (Ruimy et al. 1994) or other techniques must be devised to characterize the observed variability.

In most remote sensing applications, ϵ has been assumed constant between vegetation types and through various growth stages because measured values, or even reasonable approximations, were unavailable. Various measures of NPP and light use by plants suggest, however, that ϵ ranges from about 0.3 to 3.7 g MJ⁻¹ among a wide range of plant species, crop varieties, and forest stands (Prince 1991b; Ruimy et al. 1994; Landsberg et al. 1996). Simulated values derived from an ecophysiological model of plant growth driven by meteorological data encompass a similar range of values (0.4 - 3.9 g MJ⁻¹) for a variety of ecosystems in North America (Running and Hunt 1993).

The range in observed values of annual ϵ is known to be affected by the radiation measure used, whether incident, intercepted or absorbed, and whether total radiation or PAR is considered. Although photosynthesis is a function of PAR absorption, it is typically easier to estimate interception through relatively straightforward measures of incident and transmitted radiation. Prince (1991b) has shown that interception and absorption are not significantly different when LAI is greater than 1.0. Other factors, including photosynthetic pathway, the measure of production used (above-ground, below-ground, or total NPP), and measurement error are involved. For example, the values of ϵ reported in the literature are rarely whole ecosystem values, which include below-ground production and may also incorporate understory and ground cover vegetation, herbivory, decomposition, and other carbon losses.

Known variations in ϵ also occur through the growing season as both environmental (soil moisture, vapor pressure deficit, leaf water potential) and biotic conditions (phenological stage) change. Similarly, annually averaged values of ϵ may vary on an inter-annual basis due to variations in climatic and edaphic conditions, particularly in species that maintain relatively invariant leaf area (i.e., non-deciduous conifers). The concept of a constant ϵ is thus open to question.

Modeling the effects of environmental stress on NPP has demonstrated that temperature, moisture, and nutrients can limit potential (unstressed) production. For example, physiological adjustments such as stomatal dependence on temperature and vapor pressure deficit have been shown to directly affect total assimilation in the short-term (Verma et al. 1986; Baldocchi et al. 1987). These observations make it important to quantify the influence of physiological adjustments on a daily basis and their net effect on annual production estimates. Several studies have shown that the range in ϵ can be greatly reduced by accounting for environmental physiology, respiration and other carbon losses (Potter et al. 1993; Runyon et al. 1994; Landsberg et al. 1996). The observed range in ϵ after accounting for these factors suggests it may not be necessary to establish unique values for different vegetation types to estimate NPP with remote sensing.

A hypothesis of functional convergence in resource utilization efficiencies has been proposed by Field (1991), in which it is suggested that there is an inherent stability in ϵ as a result of evolutionary tuning of APAR to environmental conditions. The hypothesis, which has been difficult to confirm owing to a paucity of comparable measurements at a variety of spatial scales, is discussed more thoroughly in following chapters. In the analysis of the results of the work reported in this dissertation, possible causes of variability in ϵ , both within and between species, are explored in the context of functional convergence.

Hybrid Approaches

A logical step to improve production modeling by ecophysiological models and production efficiency models would be to combine the two in a unified approach that minimizes the limitations of each. For example, Maas (1988) summarized the possible means by which spectral measurements can be incorporated into crop yield models. The methods include using remote sensing inputs to: (i) set the initial conditions of a growth model, (ii) update model state variables (e.g., LAI), (iii) adjust model parameters (e.g., canopy light extinction coefficient), (iv) provide frequent observations of the driving variables in model calculations (e.g., f_{par}). The appropriate methodology depends on the variables and parameters used in the model, as well as the temporal resolution of the spectral measurements.

Field (1995) generalized this by extending the consideration of hybrid models to a global scale. He suggested that remote sensing could be used in conjunction with ecophysiological models to improve terrestrial ecosystem NPP modeling through improvements in the estimation of: (i) ρ_c , f_{par} and LAI, (ii) ε and stomatal conductance, (iii) environmental variables required for determination of (i) and (ii).

The linkage of remote sensing and ecophysiology provides a spatially explicit method to monitor short-term variations in photosynthetic capacity through limitations imposed by the current environmental conditions. For example, remote sensing estimates of LAI used in applications of Biome-BGC, discussed earlier, are based on an approach that updates state variables. An alternative approach to merging ecophysiological modeling and remote sensing involved assigning representative C fluxes from an ecophysiological model to regional land cover classes mapped using spectral signatures from remote sensing (Bonan 1993a). The results of this exercise are important because they suggest that NPP can be estimated over large areas based solely on estimates of LAI, vegetation type and areal extent of the different vegetation types. Each of these components is amenable to estimation with remote sensing.

These studies emphasize the utility of a combination of ecosystem C flux simulations and remote sensing techniques for production modeling. Most integrations of C flux models and remote sensing has been one way, that is, remote sensing observations have been used to augment C flux models rather than vice versa. Simplified rules from C flux models may also be used to augment the remote sensing models. For example, if variability in plant growth, from whatever source, was incorporated into the ε term, remote sensing models could benefit without the full computational expense and complexity of C flux models. Landsberg (1986) and Prince (1991b) have suggested this approach can be accomplished by incorporating terms representing various components of plant physiology into an extended form of the model defined by Equation 1.

Using the formulations of Jarvis and Leverenz (1983) to explicitly consider plant respiratory components and the effect of multiple physiological stresses on an efficiency of net production (ϵ_n), Prince (1991b) proposed a revised model for use with remote sensing that has since been further extended (Prince and Goward 1995). A distinctive feature of the new production efficiency model (Glo-PEM; Equation 3) is the use of spatially comprehensive and high temporal frequency observations of both biological variables (e.g., APAR and biomass), and environmental variables (e.g., vapor pressure deficit and soil water status) to evaluate stomatal control.

The model consists of an energy harvesting component ($N_t S_t$) and an unstressed (potential) value of ϵ expressed in terms of gross production ($\epsilon_{(g),t}^*$). Environmental factors that reduce the conversion of APAR into plant material (σ) reduce the value of $\epsilon_{(g),t}^*$. Respiratory losses of carbon are represented by separate growth and maintenance respiration terms (Y_g , Y_m), and losses of biomass caused by death, grazing and decay are accounted for by d .

$$P_{(n)} = \sum_t \sigma_t \epsilon_{(g),t}^* (N_t S_t) Y_{g,t} Y_{m,t} d_t \quad (3)$$

where:

$$P(n) = \text{NPP (g m}^{-2}\text{)}$$

σ_t = a functional relationship accounting for the effect of environmental variables on the unstressed value of $\epsilon_{(g),t}^*$, owing to stomatal closure, temperature, etc.

(dimensionless)

$\epsilon_{(g),t}^*$ = potential, gross energy fixation per unit APAR (g MJ⁻¹)

$N(t)$ = proportion of incident PAR absorbed by canopy (dimensionless)

$S(t)$ = incident PAR (MJm⁻²)

Y_m = proportion of assimilate not used in maintenance respiration (R_m).

$$Y_m = \left(1 - \frac{R_m}{P_g}\right) \text{(dimensionless)} .$$

P_g = gross production (photosynthesis-photorespiration)

Y_g = efficiency of conversion of assimilate into biomass, including growth respiration R_g .

$$\text{Hence } Y_g = \left(1 - \frac{R_g}{Y_m P_g}\right) \text{(dimensionless)}$$

d = proportion of biomass lost in death, decay and grazing (dimensionless)

Note that the original use of ε (Monteith 1972) is equivalent to $\sigma_t \varepsilon_{(g)t}^* Y_{g,t} Y_{m,t} d_t$ and is now referred to as ε_n . The definition of ε in the form of a potential, or maximum gross rate of energy fixation ($\varepsilon_{(g)}^*$) is based on well-established physiological measurements of non-saturated, leaf-level quantum yields for C3 and C4 species (Collatz et al. 1991). The basis for this innovation was investigated as part of this research.

An important aspect of the extended PEM approach is that it requires only inputs that can potentially be derived from remote sensing measurements. Most of the variables needed to evaluate NPP are extracted from synergistic use of optical and thermal remotely sensed observations (Goward et al. 1994; Prince and Goward 1995).

Modeling Boreal Forest Stand NPP

Both gap and ecophysiological models have been applied to stand-level simulations of NPP and to examine the role of environmental constraints on productivity in boreal forest ecosystems (Pastor and Post 1988; Bonan 1990, 1991a, 1993b; Hunt and Running 1992b). Pastor and Post (1988) were concerned mostly with examining species composition and productivity changes under climate changes induced by a doubled atmospheric CO₂ environment. They found sites with soils of high water holding capacity experienced greater increases in productivity than sites with soils of low water retention. Changes in species composition were found to alter soil N availability, which in turn amplified the vegetation changes. As a result, there was a positive feedback between C and N cycles that was bounded by negative constraints of soil moisture availability and temperature.

Bonan (1990) compared forest growth model predictions with field measurements in different forest stands from Alaska to eastern Canada to examine the applicability of a gap model in different bioclimatic regions. Measures of 79 forest properties at the study sites, including above-ground tree biomass, basal area, density, litter fall, moss and lichen biomass, and forest floor variables (litter biomass, turnover, thickness, N-concentration, and N-mineralization) were compared with model simulations. Errors in the model estimates, defined as being outside the range of observed values, varied from 0 to 10% (for central Alaska forests) to 80% (for black spruce forests in Newfoundland). The majority of errors were associated with estimates of forest floor biomass, moss biomass and moss N.

Bonan's work provides an example of the limitations of growth models calibrated with site-specific field measurements. It also identifies important limiting factors of production in boreal forest ecosystems, which in order of generally decreasing importance were: available N, depth of thaw (in permafrost areas), growing degree days (i.e., temperature), available light, and

soil moisture. The particular importance of nutrient availability to boreal forest production is supported by numerous stand-level ecological studies of black spruce (Mahendrappa and Salenius 1982; Van Cleve et al. 1983; Munson and Timmer 1990) and trembling aspen (Koerper and Richardson 1980; Van Cleve and Oliver 1982; Pastor and Bockheim 1984), including some in the boreal forests of northern Minnesota (Grigal and Arneman 1970; Nordin and Grigal 1976; Alban et al. 1978). It has also been suggested that boreal broadleaf species (short lived, fast growing) are more sensitive to nutrient limitations than boreal conifers (long lived, slow growing) owing to the life history adaptations of these different functional types (Bonan 1993a).

Simulations of C fluxes with the Biome-BGC model also provided reasonable ranges of NPP at a representative aspen and spruce stand in central Canada (Hunt and Running 1992b). The model was driven by climate data and parameterized for the two species with representative values of LAI, leaf N, respiration coefficients, and assimilate partitioning to different plant components. Incident photosynthetically active radiation (PAR) was calculated from solar geometry and daylength, reduced by an estimate of atmospheric transmission based on diurnal air temperature amplitude. Fractional canopy absorption of PAR was estimated from the Monsi-Saeki formulation of the Bouguer-Beer law and LAI (Equation 2), and seasonal PAR absorption was calculated as the sum of the daily product of incident PAR and fractional canopy PAR absorption (as described earlier). The authors reported estimates of gross production from 1204 to 2700 g m⁻² yr⁻¹ for spruce and 1308 to 3317 g m⁻² yr⁻¹ for aspen. Respiration losses are reported from 536 to 1047 g m⁻² yr⁻¹ for spruce and 1008 to 2004 g m⁻² yr⁻¹ for aspen. The resulting values of NPP range from 668 to 1653 g m⁻² yr⁻¹ for spruce and 300 to 1313 g m⁻² yr⁻¹ for aspen. Simulated PAR utilization efficiencies (ϵ) derived from NPP and seasonal absorbed PAR were 1.03 to 1.59 g MJ⁻¹ for spruce stands and 0.68 to 1.54 g MJ⁻¹ for aspen stands.

A significant finding from Hunt and Running's simulation was the large difference in respiration demand for spruce (39 to 44% of gross production) versus aspen (60 to 77% of gross production). This difference resulted in lower estimates of NPP in aspen than in spruce for equivalent gross production, which is inconsistent with field observations of NPP in these species (e.g., Viereck et al. 1983; Cannell et al. 1987; Woods et al. 1991). Spruce are typically less productive than aspen due to occupation of resource-poor environments, and the associated slow nutrient recycling that results from a combination of low soil temperature, and the high lignin and low N-content in spruce leaf litter (Van Cleve et al. 1983; Pastor et al. 1987). The Biome-BGC simulated ϵ values are affected by this discrepancy in NPP simulations between the two species.

Other stand-level C flux simulations in boreal forest have been made by Bonan (1991a) using an ecophysiological model with data from 23 intensively studied stands over a wide range of conditions in central Alaska. To avoid problems of calibrating and validating the model with

the same forest stands, the field data were not used to estimate required parameters for the model. Instead, the parameters that estimate photosynthesis and respiration were obtained from laboratory studies. The ranges of simulated values for photosynthetic capacity, root and microbial respiration, organic matter decomposition and tree net productivity were all found to be within the range of measured values, with the exception of net production at one low productivity black spruce stand (of the eight tested). Seasonal net ecosystem CO₂ fluxes were also calculated.

Bonan's (1991a) results showed a large drawdown of atmospheric CO₂ during the growing season, which corresponded to a two month lag in atmospheric CO₂ concentrations measured at Point Barrow, Alaska. A series of 200 Monte Carlo simulations, in which each of 27 model physiological variables were chosen at random, was used to examine the sensitivity of simulated CO₂ fluxes to variable error. Twelve variables defined the response of stomatal and mesophyll resistance to environmental factors, the remaining fifteen defined tree photosynthesis and respiration. The simulation results were narrowed down to those sets of variables that reproduced observed NPP, which resulted in only 4 sets (2% of those possible). The results of model simulations with these sets suggest that the forest stands were a net annual CO₂ sink. Moreover, NPP values of the forest stands were within the range of NPP values measured at all other boreal forest sites available at the time of publication (5 independent studies).

In addition to the stand-level results, Bonan (1993a) extended the model estimates of net canopy photosynthesis to estimate net ecosystem production for a 77 km² area using land cover maps derived from microwave imagery of the study area. This analysis demonstrated that knowledge of land cover type is an important variable in estimating C fluxes. Use of LAI without consideration of vegetation type led to large errors (40 - 70%) in estimates of net photosynthesis. Knowledge of species composition was shown to be relatively unimportant to C-exchange estimates, as long as a general vegetation type was considered (in this case evergreen conifer versus deciduous broadleaf). LAI and vegetation type alone accounted for 94% of the variability among forest stands in net photosynthesis. In addition, regionally averaged C fluxes were found to be sensitive to just three variables: LAI, vegetation type and area occupied by the vegetation types.

The results of this analysis suggest that LAI-driven ("big-leaf") models are likely to provide erroneous estimates of NPP unless a distinction between life forms is made, but they also demonstrate that NPP estimates at a stand-level can be extrapolated to larger areas using remotely sensed estimates of a few relatively simple variables (i.e., LAI, vegetation type and areal extent). In this way remote sensing can be used to augment ecophysiological models of NPP.