Ph.D. DISSERTATION

MODELING PLANT-SOIL-ATMOSPHERE CARBON DIOXIDE EXCHANGE

USING OPTIMALITY PRINCIPLES

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ABSTRACT

The exchange of carbon dioxide (CO₂) between terrestrial ecosystems and the atmosphere plays a central role in the ecology of the biosphere and the climate system. A generalized model of plant-soil-atmosphere CO₂ exchange was described and evaluated using eddy covariance measurements of net ecosystem exchange of CO₂ (NEE) in arctic, boreal, temperate, and tropical landscapes. The model requires no calibration and is based on theories of plant resource optimization and plant-soil nutrient feedbacks and predicts canopy photosynthetic capacity (\( P_{\text{max}} \)), canopy photosynthesis (\( P_c \)), plant respiration (\( R_p \)), and soil heterotrophic respiration (\( R_H \)). The model can be applied globally using satellite-derived estimates of canopy light absorptance (\( f_{\text{APAR}} \)), incident radiation (PAR), and air temperature (\( T_{\text{air}} \)). It provides the means by which to relate satellite observations such as the Normalized Difference Vegetation Index (NDVI) to the physiological status of vegetation and carbon exchange.

A unique aspect of the model is its use of a recursive filter for calculating photosynthetic acclimation based on the integrated effect of environmental conditions. Good agreement was found between modeled and observed \( P_{\text{max}} \) (\( r^2=0.76 \)), the latter derived from light response curves fit to estimates of gross ecosystem exchange (GEE). Consistent with theories of resource optimization, \( P_{\text{max}} \) varied strongly with time-averaged absorbed PAR and temperature.

Modeled \( P_{\text{max}} \) combined with a 'big-leaf' canopy model explained 74 to 85% of the variability in GEE. The photo-acclimation model not only performed better than a traditional time-invariant model and as good or better than calibrated site-specific models, it did not require knowledge of vegetation type. The process of photo-acclimation appeared most important during periods of greatest transition in plant physiological status (e.g. spring and fall).

Agreement between modeled and observed NEE (\( r^2=0.66 \) to 0.81) was very similar to that for GEE, implying little additional error was introduced by predictions of \( R_p \) and \( R_H \). Despite excellent agreement between modeled and observed cumulative photosynthesis (\( r^2=0.98 \)) and ecosystem respiration (\( R_p+R_H \) ) (\( r^2=0.99 \)), the agreement for NEE was not as good (\( r^2=0.75 \)), due in part to NEE being the small difference between the two much larger fluxes of photosynthesis and ecosystem respiration.
INTRODUCTION

Quantifying the exchange of carbon dioxide (CO₂) between terrestrial ecosystems and the atmosphere is central to understanding the ecology of the biosphere and its influence on global biogeochemical cycles and the climate system. Photosynthetic fixation of CO₂ provides the energy that ultimately sustains the metabolism of all organisms and drives the exchange of materials and energy with the atmosphere (Mooney et al. 1987). This fixation combined with the release of CO₂ during respiration by plants and soil microbes drives seasonal changes in the concentration of atmospheric CO₂ (Keeling 1983). CO₂ is an important greenhouse gas which influences both the physics and chemistry of the atmosphere. Its current rise of about 1.8 ppmv per year (0.5%) may have profound effects on global climate (IPCC). This in turn may adversely affect ecosystems of considerable environmental and economic value (Costanza et al. 1997).

The increase in CO₂ during the last 150 years (Keeling 1986) from pre-industrial concentrations around 280 ppmv to its current level of about 360 ppmv is largely due to anthropogenic activities such as fossil fuel burning and deforestation (IPCC 1990). Spatial and temporal gradients in atmospheric CO₂ concentrations (Tans et al. 1990, Fan et al. 1998), \(^{13}\)C/\(^{12}\)C isotope ratios (Ciais et al. 1995), and \(\text{O}_2/\text{N}_2\) ratios (Bender et al. 1996, R. Keeling et al. 1996) suggest that terrestrial ecosystems at mid-latitudes of the Northern Hemisphere sequester much of this CO₂.

amplitude of the seasonal cycle of atmospheric CO₂ (Keeling 1983).

Atmospheric CO₂ monitoring and biomass inventories provide only indirect measures of net CO₂ flux from ecosystems and vegetation. Theoretical and logistical considerations limit the use of eddy covariance to select sites. These essentially “point measurements” may not be characteristic of entire biomes (Keller et al. 1996, Houghton 1997). Alternative methods such as satellite remote sensing are needed to better quantify the spatial and temporal patterns of ecosystem-atmosphere CO₂ exchange at regional to global scales.

Satellite remote sensing offers unequaled potential for synoptic monitoring of biosphere functioning with global coverage, near-continuous data acquisition, and consistent instrumentation (Hobbs and Mooney 1990, Matson and Ustin 1991). Satellite observations have proven useful for monitoring inter-annual vegetation activity (Myneni et al. 1998), the effects of land use change (Skole and Tucker 1993) and climate-biosphere interactions related to El Niño events (Myneni et al. 1996, Anyamba and Eastman 1996). Direct measurement, however, of net ecosystem CO₂ exchange is not possible with satellite sensors. Satellites have the potential of providing information on the fraction of incoming photosynthetically active radiation (PAR) absorbed by vegetation (FPAR) (Goward and Huemmrich 1992), incident radiation (PAR) (Eck and Dye 1991), surface temperature (Vazquez et al. 1997), near-surface (Prihodko and Goward 1997) and tropospheric air temperature (Spencer and Christy 1990), and atmospheric humidity (Ottle et al. 1997).

Remote sensing of ecosystem-atmosphere CO₂ exchange requires the use of models that relate these variables to rates of photosynthesis and respiration. The challenge remains to develop models that can provide estimates of land surface CO₂ exchange comparable to those obtained by ground-based eddy covariance (Baldocchi et al. 1996, Ruimy et al. 1996b). The principle limitation to meeting this challenge is the inability to remotely sense the physiological status of plants and soil microbes. Current models prescribe plant and soil characteristics from prior knowledge of the site in question or by applying generalized biome-specific values using vegetation maps.

A growing body of evidence suggest that parameter estimation may be greatly facilitated and
simplified by exploiting the fact that plants generally adapt and acclimate to their local environment to the extent that their physiological potential varies in parallel with the availability of resources (Figure 1). Such behavior is often well explained by optimality theory. Optimality theory is widely used in plant ecophysiology to generate and test hypotheses of plant form and function (Givnish 1986). As early as 1881, Greenhill employed optimality arguments to predict maximal tree height as a function of stem diameter with an analytical solution expressing the trade-off between height growth and stem stability. Observations have since confirmed Greenhill’s basic hypotheses (McMahon 1973) indicating the potential of optimality theory to describe the behavior of real plants.

More recently, optimality theory has been used to advance theories of water ($E$) and nitrogen ($N$) use in relation to leaf net CO$_2$ assimilation ($A$) (Cowan 1977, Cowan and Farquhar 1977, Field 1983, Field and Mooney 1986). Cowan (1977) predicted the optimal stomatal conductance ($g$) for a given rate of photosynthesis ($A$) occurs when the marginal water cost of carbon gain ($\partial E/\partial A$) is constant and transpirational water loss ($E$) is minimized. Although the absolute value of $\partial E/\partial A$ differs among plants, observations indicate that $\partial E/\partial A$ does in fact remain relatively constant (Givnish 1986b). Further, $A$ and $g$ generally vary in proportion to each other under unstressed conditions (e.g. Wong et al. 1979, Schulze and Hall 1982) consistent with the maintenance of constant $\partial E/\partial A$ through stomatal regulation.

Optimality arguments have been criticized as being “teleonomic” because they assume a purposeful behavior of a plant towards some goal (e.g. maximizing carbon gain) which is achieved through some unspecified mechanism (Monod 1972). However, the assumption of maximizing carbon gain is clearly valid because it bestows a competitive advantage for limited resources and increases selective fitness (Mooney and Gulmon 1979). Furthermore, optimality assumptions often provide practical solutions to complex problems, without which, a great deal more information would be required to develop “objective” models with fewer unsubstantiated $a$ priori arguments. Objective models such as transport-resistance models (e.g. Thornley 1972) have been developed but are difficult to parameterize such that simpler more “subjective” optimality models are often the best, if not only, model of choice.
Figure 1. Relationships among plant carbon gain ($\text{CO}_2$ uptake), environmental limitations (light and temperature), availability of resources (nitrogen and water), and satellite remote sensing that form the basis of the optimality arguments explored in this study.
Recent advances in understanding how photosynthetic capacity varies within leaves and canopies (Field 1983, Gutschick and Wiegel 1988, Farquhar 1989, Terashima and Hikosaka 1995) in relation to light availability has led to generalized theories of acclimation and resource optimization. Field (1983) predicted the optimal distribution of nitrogen among leaves that maximizes canopy photosynthesis occurs when the marginal increase in $A$ with respect to $N$ ($\partial A/\partial N$) is constant throughout the canopy. This implies that because light availability decreases exponentially with depth in a canopy so must potential rates of photosynthesis ($P_{\text{max}}$) and by extension, so must leaf nitrogen ($N$) ($P_{\text{max}} \propto \text{PAR}$). Observations support this hypothesis in that vertical profiles of photosynthetic capacity and nitrogen generally parallel vertical gradients of light availability (e.g. Field 1983, Hirose and Werger 1987, DeJong and Doyle 1985, Hollinger 1989, Ellsworth and Reich 1993). Sellers et al. (1992) demonstrated how such theories of light acclimation and nitrogen distribution can be exploited to greatly simplify the integration of canopy photosynthesis. Recent analyses suggest that these same principles can be further extended to the time-dependence of photosynthetic capacity and can be exploited to simplify the prediction of $P_{\text{max}}$ over the growing season (Takenaka 1989, Johnson et al. 1995, Haxeltine and Prentice 1996a).

Acclimation to the prevailing growth conditions allows plants to maintain optimal photosynthetic and resources use efficiency (Arnon 1982, Anderson et al. 1995). This strategy maximizes evolutionary fitness by ensuring optimal use of the environment and a competitive advantage for limited resources (Bloom et al. 1985). Field (1991) summarized these concepts on the economy of resource use and carbon gain first introduced by Mooney and Gulmon (1979) with the “functional convergence hypothesis”: biochemical capacity for $\text{CO}_2$ fixation should be curtailed whenever a limitation in the availability of any resource prevents the efficient exploitation of additional capacity. That is, plants predictably function with optimal efficiency in a given environment.

Other studies have shown that similar theories of acclimation and resource optimization applied at the level of the whole plant can be used to predict maximum rates of net primary productivity (NPP) and minimum rates of plant respiration ($R_p$) (Dewar 1996). Further, numerous studies indicate there are feedbacks between the nutrient status of plants and soils involving plant uptake, litterfall, and microbial decomposition and mineralization (Vitousek 1982, Reed 1990, Woodward and Smith 1994). Eventual
accommodation between these processes provides simplifying constraints to the estimation of rates of decomposition and soil respiration ($R_{hi}$).

These theories have the potential to greatly simplify parameter estimation in ecosystem models and may prove to be particularly useful when applied with remote sensing observations. The overall theme of this study is the application and evaluation of resource optimization constraints on the estimation of canopy photosynthetic capacity, gross photosynthesis, and respiration by plants and soil microbes within the framework of a generalized model of plant-soil-atmosphere CO$_2$ exchange.
CHAPTER I

A REVIEW OF REMOTE SENSING MODELS

Satellite Observations and Plant Productivity

Kumar and Monteith (1981) first noted that the cumulative net CO$_2$ uptake by a crop stand could be estimated from above canopy measurements of visible ($r_{VIS}$) and near-infrared ($r_{NIR}$) reflectance in the form of vegetation indices such as the normalized difference vegetation index:

$$NDVI = \frac{(r_{NIR} - r_{VIS})}{(r_{NIR} + r_{VIS})}$$ (1.1)


The underlying mechanism for these relationships is both biophysical and ecological in nature. In theory, NDVI varies between 0 and 1 for vegetated surfaces, with desert values near zero and those for tropical forests near one. Near-infrared reflectance is most sensitive to the amount of leaf area while visible reflectance is most sensitive to chlorophyll content (Gates 1965, Knipling 1970, Gausman and Allen 1973), therefore, vegetation indices can be used to gauge the relative amount of green photosynthetically active vegetation (Goward 1989). Both NDVI and FPAR integrate the effects of the
leaf quantity (LAI) and leaf quality (chlorophyll) (Allen and Richardson 1968, Goward et al. 1994) such that the relationship between the two is robust (Goward and Huemmrich 1992, Sellers 1985). On the other hand, relationships between NDVI and biomass, LAI, or canopy chlorophyll or nitrogen content are problematic (Plummer 1988, Wessman et al. 1988, Matson et al. 1994, Yoder and Waring 1994, Hall et al. 1995).

Sellers (1985) elaborated on the work of Monteith (1977) to show that for a range of canopy structures, photosynthetic capacity should be near-linearly related to NDVI because the response of both canopy photosynthesis and NDVI saturate with respect to LAI. This result provides a biophysical constraint on the observed correlation between NDVI and carbon gain and implies that NDVI should be near-linearly related to the change in photosynthesis \( P \) with respect to the change in incident photosynthetically active radiation (NDVI \( \propto \partial P / \partial \text{PAR} \)) (Sellers 1987). A bare soil surface will exhibit no “photosynthetic” sensitivity to a change in PAR while a fully vegetated surface will exhibit strong sensitivity (Verma et al. 1993). Verma et al. (1993) tested this hypothesis using canopy scale measurements of CO\(_2\) exchange and aircraft based measurements of canopy reflectance and found general agreement between the simple ratio (SR = \( r_{\text{NIR}} / r_{\text{VIS}} \)) and \( \partial P / \partial \text{PAR} \) for a tallgrass prairie (note SR = \([\text{NDVI}+1]/[1-\text{NDVI}]\)). This is consistent with the ecological interpretation that plant investment in light energy capture (i.e. NDVI) parallels changes in the capacity to utilize light for photosynthesis (i.e. \( \partial P / \partial \text{PAR} \)) (Field 1991).

Field (1991) argues that all plants face the similar challenge of maximizing carbon gain and resource use efficiency in their respective environments and that natural selection has favored individuals who regulate investment in leaf area, chlorophyll, and light energy capture in general, to levels that maximize net primary productivity. Accordingly, chronic stress typically causes parallel reductions in leaf area and carbon gain such that NDVI or FPAR generally integrate the effects of low nutrient availability and soil drought (e.g. Squire et al. 1986). The overall effect is conservative variation between the amount of radiation absorbed (APAR) and NPP (Field 1991). The intrinsic link between absorbed radiation and photosynthesis combined with the fact that NDVI can be obtained from satellite sensors underlies the use of NDVI as a general global index of plant carbon gain (Sellers 1985, Field et al. 1994).

The ratio of NPP to APAR also varies as a function of age and growth form (Penning de Vries 1972, Hunt 1994, Ruimy et al. 1996b, Goetz and Prince 1998a, 1998b). As plants age and accumulate dry matter, NPP generally decreases as maintenance respiratory costs increase (Hunt 1994). Further, different species and plant functional types generally have different respiratory costs owing to different allocation strategies among roots, shoots, and leaves (e.g. Ruimy et al. 1996b).

The sensitivity of the NPP/APAR ratio to these various conditions is consistent with the hypothesis that APAR is intrinsically related to potential gross photosynthesis (photosynthetic capacity) rather than actual photosynthesis or NPP (Sellers 1985; 1987, Field 1991, Prince 1991a, Ruimy et al. 1996b, Goetz and Prince 1998a). Accordingly, relationships between net ecosystem CO$_2$ exchange and APAR or NDVI are typically site specific and seasonally variable (Bartlett et al. 1990, Whiting et al. 1992, Cihlar et al. 1992, Whiting 1994, Ogunjemiyo et al. 1997). Bartlett et al. (1990) concluded that quantitative assessment of ecosystem-atmosphere CO$_2$ exchange using spectral reflectance requires knowledge on plant and soil responses to environmental factors which can reduce photosynthesis below its maximum unstressed rate and decouple photosynthesis from plant and soil respiration.
Remote Sensing Models

Photosynthesis and Primary Productivity. Numerous models have been developed that relate spectral reflectance to canopy photosynthesis ($P_c$), net primary productivity (NPP), and net ecosystem CO$_2$ exchange (NEE) under various environmental conditions. These models range in complexity from empirically based “Production Efficiency Models” (PEM) (Prince 1991a) to more detailed biochemically based models (e.g. Sellers et al. 1996). Both types of models are difficult to validate at regional to global scales. However, gas exchange measurements at the ecosystem level are becoming more common (Baldocchi et al. 1996). These datasets have proven useful for testing ecosystem models driven by remote sensing observations (Gao 1994, Waring et al. 1995, Ruimy et al. 1996b, Colello et al. 1998).


$$\text{NPP} = \varepsilon_n \sum \text{APAR} \cdot f_T f_D f_W \ldots \quad (1.2)$$

where $\varepsilon_n$ is the dry matter:radiation quotient ($\Delta \text{NPP}/\Delta \text{APAR}$), APAR is the absorbed photosynthetically active radiation, and $f_T$, $f_D$, and $f_W$ are multipliers (0<$f_x$<1) that account for the effects of various environmental factors such as air temperature, leaf-to-air vapor pressure difference, soil water, and so on. The dry matter:radiation quotient is equivalent to the so-called radiation use efficiency or light use efficiency (LUE) despite the fact that efficiencies range in value from 0 to 1. Recent applications have replaced $\varepsilon_n$ with $\varepsilon_g$, the dry-matter yield of APAR in gross primary production (GPP), because of significant variation in the ratio of respiration to gross production (Prince 1991a), although several recent analyses suggest that respiration is a conservative fraction (~0.5) of GPP (Ryan 1991, Gifford 1994, Waring et al. 1998).
One drawback to PEMs is that they operate at a daily or longer time step which precludes their use for evaluating diurnal variations in gas exchange or their incorporation into high temporal resolution general circulation models (GCM) (e.g. Sellers et al. 1996). An additional limitation to PEMs is that they must be calibrated for wide range of species or ecosystems representative of global vegetation. Numerous parameters for many ecosystems are unknown and must be arbitrarily prescribed.

Models based on the instantaneous response of photosynthesis to environmental conditions (Goward and Dye 1987, Running et al. 1989, Lüdeke et al. 1991, Hunt et al. 1996), including those based on the biochemistry of photosynthesis (Gao 1994, Warnant et al. 1994, Myneni et al. 1995, Sellers et al. 1996, Colello et al. 1998), represent carbon gain and respiration in a more physiologically realistic manner. Biochemically based models of photosynthesis (e.g. Farquhar et al. 1980, Collatz et al. 1991; 1992) theoretically apply to all plants with similar photosynthetic pathways (i.e. C_3 or C_4). In their simplest and most generalized form, models that couple stomatal conductance with photosynthesis (e.g. Collatz et al. 1991, 1992) require only a few critical parameters, such as the carboxylation capacity \( (V_{\text{cmax}}) \) of ribulose bisphosphate carboxylase-oxygenase (Rubisco), the quantum yield at limiting light levels \( (\alpha) \), and \( T_{\text{opt}} \), the temperature optimum for photosynthesis. Carboxylation capacity and the quantum yield define the initial slope and the light-saturated rate or asymptote of the photosynthetic light response curve. In simpler treatments, the carboxylation capacity may be represented by the light-saturated rate of photosynthesis, \( P_{\text{max}} \). Estimation of \( P_{\text{max}} \), \( \alpha \), and \( T_{\text{opt}} \), is recognized as the major constraint to the global application of process-based models of photosynthesis (Wullschleger 1993, Warnant et al. 1994, Hanan 1997, Dang et al. 1998, Colello et al. 1998).

**Respiration.** Respiration, both above and below ground is difficult to estimate with remote sensing models. Plant respiration is typically subsumed within the dry matter:radiation quotient \( (\varepsilon_a) \), estimated as a fraction of GPP (Goward and Dye 1987, Landsberg and Waring 1997), or modeled based on vegetation type (Ruimy et al. 1996a). Prince and Goward (1995) used an empirical relationship between biomass and maintenance respiration following Hunt (1994), where biomass was estimated from satellite-derived visible reflectance \( (r_{\text{VIS}}) \). As noted by Prince and Goward (1995), this approach requires further evaluation.
Soil heterotrophic respiration is similarly difficult to estimate given the inability to remotely sense soil conditions. Most models that predict net ecosystem CO$_2$ exchange (NEE) or its equivalent, net ecosystem productivity (NEP = NPP - $R_H$) estimate soil heterotrophic respiration using a standard “$Q_{10}$” type function (Fung et al. 1987, Ludeke et al. 1991, Knorr and Heimann 1995, Maisongrande et al. 1995):

$$R_H = R_{\text{ref}} Q_{10}^{(T - T_{\text{ref}})/10}$$

where $R_H$ is the respiration rate, $R_{\text{ref}}$ is the respiration rate at the reference temperature $T_{\text{ref}}$, $T$ is the ambient temperature, and $Q_{10}$ is the ratio of the rate at $T_{\text{ref}}$ to that at $T_{\text{ref}} \pm 10$ degrees (Jones 1983). Recognizing that $R_{\text{ref}}$ is site specific but lacking satellite-based methods for sensing soil conditions, $R_{\text{ref}}$ is typically estimated with the constraint that annual soil respiration equals annual NPP (NEP = 0). This assumption precludes the detection of carbon sequestration and is not consistent with recent findings indicating that many ecosystems act as net carbon sinks (e.g. Goulden et al. 1996, Grace et al. 1996, Greco and Baldocchi 1996, Hollinger et al. 1999) and others act as net carbon sources (e.g. Goulden et al. 1998, Lindroth et al. 1998). Models that do not assume annual zero net carbon exchange (e.g. Potter et al. 1993, Hunt et al. 1996) explicitly model soil respiration using simplified versions of the CENTURY model (Parton et al. 1987) or use functions calibrated to specific sites (Veroustraete et al. 1996, Gao 1994, Colello et al. 1998). Application of either approach requires parameters that cannot be remotely sensed such as the carbon and nitrogen content of the soil and litter as well as soil texture, temperature, and moisture.
CHAPTER II

SEASONALITY AND OPTIMALITY OF CANOPY PHOTOSYNTHETIC CAPACITY:
THEORY AND EVALUATION OF A GENERALIZED MODEL

Introduction

The exchange of carbon dioxide (CO$_2$) between terrestrial ecosystems and the atmosphere is central to the ecology of the biosphere and its influence on global biogeochemical cycles and the climate system. Photosynthetic fixation removes ~15% of the CO$_2$ in the atmosphere each year (Williams et al. 1997) and combined with the release of CO$_2$ during respiration by plants and soil microbes, photosynthesis drives seasonal changes in atmospheric CO$_2$ concentrations (Keeling 1983). However, seasonal and interannual variations in net terrestrial uptake (photosynthesis minus respiration) is uncertain and difficult to quantify.

Atmospheric CO$_2$ monitoring and biomass inventories provide only indirect measures of net CO$_2$ flux from ecosystems and vegetation while theoretical and logistical considerations limit the use of eddy covariance to select locations. Satellite remote sensing, on the other hand, offers unequaled potential for synoptic monitoring of biosphere functioning with global coverage, near-continuous data acquisition, and consistent instrumentation (Hobbs and Mooney 1990, Matson and Ustin 1991).

Although satellite observations have proven useful for monitoring inter-annual vegetation activity (Myneni et al. 1998), the effects of land use change (Skole and Tucker 1993) and climate-biosphere interactions related to El Niño events (Myneni et al. 1996, Anyamba and Eastman 1996), direct measurement of net ecosystem CO$_2$ exchange is not possible. Recent advances have made it possible to derive estimates of many surface characteristics crucial to terrestrial ecosystem functioning including incident photosynthetically active radiation (PAR) (Eck and Dye 1991), the fraction of incoming PAR absorbed by vegetation (FPAR) (Goward and Huemmrich 1992), surface temperature (Vazquez et al. 1997), near-surface air temperature (Prihodko and Goward 1997), atmospheric humidity (Ottle et al. 1997), and functional vegetation type (Nemani et al. 1997).

The challenge remains to develop models that can relate these variables to estimates of net ecosystem CO$_2$ exchange comparable to those obtained by ground-based eddy covariance (Baldocchi et al. 1996, Ruimy et al. 1996b). With respect to photosynthesis, the principle limitation to meeting this challenge is the inability to remotely sense the physiological status of plants. Photosynthetic capacity ($P_{\text{max}}$) and its optimum temperature ($T_{\text{opt}}$) are typically prescribed in ecosystem models solely on the basis of ecosystem type. This approach not only relies on the accuracy of global ecosystem classifications, of which intercomparisons have revealed large discrepancies (Defries and Townsend 1994), but also assumes seasonally invariant physiological status despite the long recognized physiological plasticity of most plants (Larcher 1969, Bjorkman 1981, Pearcy and Sims 1994).


Temperature optima are thought to shift due to reduced enzyme activity at lower temperatures, the relative amount of various enzymes, each with a characteristic temperature optimum, and nitrogen partitioning between chlorophyll and ribulose bisphosphate carboxylase-oxygenase (Rubisco) (Hikosaka 1997). At the canopy scale, the variation in $P_{\text{max}}$ and $T_{\text{opt}}$ are less understood but crucial to the understanding and prediction of terrestrial photosynthesis.

A growing body of evidence indicates that parameter estimation may be greatly facilitated and simplified by exploiting the fact that plants generally adapt and acclimate to their local environment to the extent that their physiological potential varies in parallel with the availability of resources. Such behavior is often well explained by optimality theory. Field (1983) hypothesized that the optimal distribution of nitrogen among leaves is that which maximizes canopy photosynthesis and occurs when the marginal increase in $A$ with respect to $N$ is constant throughout the canopy ($\partial A / \partial N = \lambda$). This implies that because light availability decreases exponentially with depth in a canopy so must potential rates of both photosynthesis ($P_{\text{max}} \propto \text{PAR}$) and nitrogen ($N \propto \text{PAR}$).

Observations support this hypothesis in that vertical profiles of photosynthetic capacity and nitrogen generally parallel vertical gradients of light availability (e.g. Field 1983, Hirose and Werger 1987, DeJong and Doyle 1985, Hollinger 1989, Ellsworth and Reich 1993). Subsequent studies have employed theories of resource optimization to describe and predict the depth-distribution of nitrogen and

Based on these observations, Sellers et al. (1992) demonstrated that theories of acclimation can be exploited to simplify the integration of canopy photosynthesis. Recognizing that these same principles can be further extended to the time-dependence of photosynthetic capacity, Haxeltine and Prentice (1996) predicted seasonal patterns of canopy photosynthetic capacity that result from similar, albeit temporal, variations in light availability that occur throughout the growing season.

A drawback to optimality arguments is that they can be criticized as ‘teleonomic’ because they assume a purposeful behavior of a plant towards some goal (e.g. maximizing carbon gain) that is achieved through unspecified or unknown mechanisms (Monod 1972). For example, optimal photosynthetic capacity can be estimated as the value which provides maximum net assimilation ($P - R_d$) in a given light environment (Takenaka 1989, Johnson et al. 1995, Haxeltine and Prentice 1996a). Both leaf respiration (Merino et al. 1982) and photosynthetic capacity (Field and Mooney 1986) increase with leaf nitrogen, however respiration generally increases linearly while capacity increases non-linearly and eventually saturates. While maximizing carbon gain clearly bestows a competitive advantage for limited resources and increases selective fitness (Mooney and Gulmon 1979), assuming carbon gain is maximized without considering the limitations related to how it is maximized can only be approximately correct.

A better approach would be to include, in addition to the leaf respiration costs already considered, the costs of such factors as leaf construction and nutrient allocation (Mooney and Gulmon 1979, Hollinger 1996). Chen et al. (1993) proposed “coordination theory” as an alternative approach which indirectly addresses such costs associated with resource allocation. In contrast to simpler optimality models that are constrained by the condition of maximizing carbon gain without considering the “costs” associated with the underlying mechanisms (i.e. allocation), the coordination approach is constrained by a more mechanistic and less teleonomic criterion of maximizing resource use efficiency. Coordination theory is consistent with source-sink approaches inherent to more “objective” transport-resistance models.
Moreover, coordination theory greatly simplifies the estimation of photosynthetic capacity and holds promise for application with satellite data because the key variable is the absorbed irradiance or specifically, the absorbed photosynthetically-active radiation (APAR) -- the product of incident PAR and the fractional canopy light absorptance ($f_{\text{APAR}}$), both of which can be determined globally from satellite observations (e.g. Myneni 1997b, Prince et al. 1998).

Objectives

Coordination theory has been used to describe and predict the depth-distribution of nitrogen and photosynthetic capacity that results from spatial variation of light availability within a canopy (Chen et al. 1993), but it has not been used to explain or predict seasonal patterns of photosynthetic capacity at the canopy scale that result from temporal variations in light availability that occur throughout the growing season. The overall goals were to: (1) develop a simple generalized model suitable for application at canopy to global scales based on coordination theory and driven by light, temperature and $f_{\text{APAR}}$; (2) test the model at contrasting sites from a wide range of environments, and (3) evaluate the controls on canopy photosynthetic capacity as they relate to seasonality and theories of plant resource optimization. Observations of canopy photosynthetic capacity were derived from estimates of maximum gross ecosystem CO$_2$ exchange (GEE). Gross ecosystem CO$_2$ exchange was derived from eddy covariance measurements of net ecosystem CO$_2$ exchange (NEE) made in arctic, boreal, temperate, and tropical environments. A unique aspect of the model is its use of a recursive filter for calculating photosynthetic acclimation based on the integrated effect of environmental conditions. The sensitivity of modeled photosynthetic capacity to variation in the filter time constant was examined and site-specific time constants were inferred for each site by fitting the model predictions to the observations.

Datasets

The model was evaluated at ten sites covering a wide range of vegetation and climatological characteristics (Table 2.1). Ecosystems represented were arctic tundra, boreal forest, boreal wetland,
## Table 2.1. Site Characteristics

<table>
<thead>
<tr>
<th>Site</th>
<th>Description</th>
<th>Peak LAIe</th>
<th>MAT (°C)</th>
<th>Annual Rainfall (mm)</th>
<th>Year</th>
<th>Location</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Happy Valley</td>
<td>arctic tundra</td>
<td>1.0</td>
<td>-2.2</td>
<td>275</td>
<td>1994</td>
<td>Alaska, USA (69°09'N, 148°58'W)</td>
<td>Vourlitis and Oechel</td>
</tr>
<tr>
<td>NSA-OBS</td>
<td>boreal forest, (old black spruce)</td>
<td>2.7</td>
<td>-1.5</td>
<td>317</td>
<td>1996</td>
<td>Manitoba, Canada (55°54'N, 98°30'W)</td>
<td>Goulden et al. 1997</td>
</tr>
<tr>
<td>NSA-FEN</td>
<td>boreal fen</td>
<td>1.4</td>
<td>-1.6</td>
<td>317</td>
<td>1996</td>
<td>Manitoba, Canada (55°54'N, 98°24'W)</td>
<td>Lafleur et al. 1997</td>
</tr>
<tr>
<td>SSA-OBS</td>
<td>boreal forest, (old black spruce)</td>
<td>2.4</td>
<td>0.8</td>
<td>421</td>
<td>1996</td>
<td>Saskatchewan, Canada (53°54'N, 105°7'W)</td>
<td>Jarvis et al. 1997</td>
</tr>
<tr>
<td>Howland Forest</td>
<td>temperate coniferous forest</td>
<td>4.7</td>
<td>6.3</td>
<td>1040</td>
<td>1996</td>
<td>Maine, USA (45°15'N, 68°54'W)</td>
<td>Hollinger et al. 1999</td>
</tr>
<tr>
<td>Harvard Forest</td>
<td>temperate deciduous forest</td>
<td>3.4</td>
<td>7.6</td>
<td>1117</td>
<td>1992</td>
<td>Massachusetts, USA (42°32'N, 72°11'W)</td>
<td>Wofsy et al. 1993</td>
</tr>
<tr>
<td>Konza Prairie</td>
<td>temperate C₃/C₄ grassland</td>
<td>2.8</td>
<td>14.0</td>
<td>840</td>
<td>1987</td>
<td>Kansas, USA (39°03'N, 96°32'W)</td>
<td>Verma et al. 1992</td>
</tr>
<tr>
<td>Ponca City</td>
<td>temperate crop (winter wheat)</td>
<td>5.2</td>
<td>15.0</td>
<td>835</td>
<td>1997</td>
<td>Oklahoma, USA (36°46'N, 97°08'W)</td>
<td>Verma, unpublished??</td>
</tr>
<tr>
<td>ABRACOS</td>
<td>tropical rain forest</td>
<td>4.0</td>
<td>24.2</td>
<td>&gt;2000</td>
<td>1992</td>
<td>Rondonia, Brazil (10°5'S, 51°57'W)</td>
<td>Grace et al. 1996</td>
</tr>
</tbody>
</table>

Peak LAIe refers to the seasonal maximum effective LAI, the one-sided leaf area index (m² m⁻²) without adjustment for leaf clumping (see Chen et al. 1997).

MAT is the mean annual air temperature (°C).
temperate coniferous forest, temperate deciduous forest, temperate C\textsubscript{3}/C\textsubscript{4} grassland, temperate crop, tropical C\textsubscript{3}/C\textsubscript{4} savannah, and tropical forest (Figure 2.1). Net ecosystem exchange (NEE) of CO\textsubscript{2} was measured at each site by eddy covariance (Baldocchi et al. 1988) and gross ecosystem exchange (GEE) and maximum gross ecosystem exchange at saturating light and non-limiting temperature and moisture (GEE\textsubscript{max}) were estimated as described below. Meteorological variables and canopy leaf area index (LAI) and/or canopy light interceptance was also measured at each site. Light (PAR) absorbed by the green leaf area fraction of the canopy (f\textsubscript{APAR}) was determined from measurements of green leaf area index (LAI), light transmittance through the canopy, or above-canopy light reflectance, depending on the site (Table 2.2). Details are provided in the Appendix.

Gaps in field measurements invariably occur for various reasons including instrument malfunction, power failure, and system calibration (Wofsy et al. 1993). However, the present model requires a continuous time series of data to adequately characterize the running means. The three required variables for the model, incident PAR, air temperature (T\textsubscript{air}), and canopy light absorptance (f\textsubscript{APAR}), were filled using various techniques (Appendix). Briefly, gaps in T\textsubscript{air} were filled by simulating diel variations in temperature as a function of time, using daily minimum (T\textsubscript{min}) and maximum (T\textsubscript{max}) temperatures. For gaps on days without reliable measurements of T\textsubscript{min} and T\textsubscript{max}, their mean values from the nearest 10 days (5 prior and 5 after) were used. Gaps in incident PAR were filled by attenuating the top-of-the-atmosphere PAR flux density (I\textsubscript{toa}) by an atmospheric transmittance (β\textsubscript{a}) inferred from the diel temperature amplitude following Glassy and Running (1994).

**Observations of Canopy Photosynthetic Capacity and Optimum Temperature**

It is not possible to directly measure gross ecosystem exchange (GEE) nor the maximum exchange during optimal growth conditions (i.e. canopy photosynthetic capacity) using the eddy covariance technique. However, GEE is often derived from the sum of NEE and ecosystem respiration (R\textsubscript{eco}) estimated from nighttime NEE adjusted to daytime temperatures (Kim and Verma 1990, Verma et
Figure 2.1. Distribution of study sites with respect to mean annual temperature and precipitation.
Table 2.2. Methods used to derive $f_{\text{APAR}}$ at each site.

<table>
<thead>
<tr>
<th>Site</th>
<th>Description</th>
<th>Site Measurement</th>
<th>Steps taken to estimate $f_{\text{APAR}}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Happy Valley</td>
<td>arctic tundra</td>
<td>NDVI</td>
<td>NDVI→$f_{\text{APAR}}$</td>
</tr>
<tr>
<td>NSA-OBS</td>
<td>boreal forest</td>
<td>NDVI</td>
<td>NDVI→$f_{\text{APAR}}$</td>
</tr>
<tr>
<td>NSA-FEN</td>
<td>boreal fen</td>
<td>$r_{\text{VIS}}$ &amp; $r_{\text{SW}}$</td>
<td>$(r_{\text{VIS}}$ &amp; $r_{\text{SW}}$)→NDVI→$f_{\text{APAR}}$</td>
</tr>
<tr>
<td>SSA-OBS</td>
<td>boreal forest</td>
<td>LAI, e</td>
<td>LAI, $e$→$f_{\text{IPAR}}$→NDVI→$f_{\text{APAR}}$</td>
</tr>
<tr>
<td>Howland</td>
<td>temperate coniferous forest</td>
<td>NDVI</td>
<td>NDVI→$f_{\text{APAR}}$</td>
</tr>
<tr>
<td>Harvard Forest</td>
<td>temperate deciduous forest</td>
<td>$f_{\text{IPAR}}$ (subtracted 0.04 for PAR$_{\text{reflected}}$)</td>
<td>None (assumed $f_{\text{APAR}}$= $f_{\text{IPAR}}$)</td>
</tr>
<tr>
<td>Konza Prairie</td>
<td>temperate C$_3$/C$_4$ grassland</td>
<td>NDVI</td>
<td>NDVI→$f_{\text{APAR}}$</td>
</tr>
<tr>
<td>Ponca City</td>
<td>temperate crop, (winter wheat)</td>
<td>$r_{\text{VIS}}$ &amp; $r_{\text{SW}}$</td>
<td>$(r_{\text{VIS}}$ &amp; $r_{\text{SW}}$)→NDVI→$f_{\text{APAR}}$</td>
</tr>
<tr>
<td>HAPEX-Sahel</td>
<td>tropical C$_3$/C$_4$ savanna</td>
<td>$f_{\text{APAR}}$ (from Hanan et al. 1997)</td>
<td>None</td>
</tr>
<tr>
<td>ABRACOS</td>
<td>tropical rainforest</td>
<td>LAI, (assumed)</td>
<td>LAI, $e$→$f_{\text{IPAR}}$→NDVI→$f_{\text{APAR}}$</td>
</tr>
</tbody>
</table>

21

\[ \text{GEE} = \text{NEE} - \text{R}_{\text{eco}} \]  

where  

\[ \text{R}_{\text{eco}} = \text{NEE}_{\text{night}} \exp((T_{\text{air}} - T_{\text{night}})/10) \]  

and NEE_{night} and T_{night} are the average nighttime values of net ecosystem CO₂ exchange and air temperature, respectively, during the previous night. Consistent with studies of leaf level gas exchange, canopy photosynthetic capacity (GEE_{max}) is expressed as a positive value, in contrast to conventional micrometeorological notation. Eddy covariance measurements are not reliable during periods of low turbulent mixing between the atmosphere and the surface (Wofsy et al. 1993). Thus, fluxes of net ecosystem CO₂ exchange were not used when the friction velocity (u*) was below 0.15 m s⁻¹ (Wofsy et al. 1993) -- or, if u* was not available (e.g. NSA-FEN) -- when the windspeed (U) was less than 0.5 m s⁻¹ (Lafleur et al. 1997). At the tropical forest site (ABRACOS), fluxes were rejected if the absolute value of the storage flux exceeded 10 µmol m⁻² s⁻¹ following Grace et al. (1996).

\[ \text{GEE}_{\text{max}} \]  was inferred from GEE by fitting a rectangular hyperbola to the GEE estimates plotted as a function of incident PAR (I) (Ruimy et al. 1996):

\[ \text{GEE} = \frac{\text{GEE}_{\infty} I}{(K + I)} \]  

where K is the PAR level when GEE equals half GEE_{∞}, and re-evaluating the fitted light response model at a light level (I_{sat}) known to be saturating (Frolking et al. 1998):

\[ \text{GEE}_{\text{max}} = \frac{\text{GEE}_{\infty} I_{\text{sat}}}{(K + I_{\text{sat}})} \]  

As the goal was to examine canopy acclimation to variable light levels throughout the growing season, it would be inappropriate to presume the value of I_{sat}. Light saturation was simply taken as the maximum light level for each day the light response curve was fit. Thus, values of GEE_{max} derived in this fashion should represent a reasonable estimate of the maximum GEE achieved on any given day. Curves were fit at daily intervals to allow the distinction of days with clear skies and optimal growth conditions from those with stressful and/or cloudy conditions. GEE_{max} was determined only on those days when light
alone explained more than 90% of the variation in GEE ($r^2 > 0.9$), that is when other factors did not appear to have a confounding affect on the photosynthetic light response. Finally, afternoon fluxes consistently had a lower response than pre-noon fluxes. This response may be due in part to afternoon temperature and VPD effects on photosynthesis. Thus, only pre-noon fluxes were used for curve fitting. Inclusion of afternoon fluxes simply reduced the number of days with acceptable $r^2$ values.

This curve fitting approach was selected over other methods because it was simple, easy to apply, and easy to interpret the results. $GEE_{\text{max}}$ could have been inferred from the value of photosynthetic capacity used in a model of gross canopy photosynthesis calibrated to provide the best fit to the observations. However, any process that is not accurately represented in the model will affect the final estimate of photosynthetic capacity. Predictions may thus fit observations for the wrong reasons, leading to errors in tuned parameters (Mäkelä and Valentine, in press).

The optimum temperature for photosynthesis during the growing season at each site was determined from visual estimation of the time-averaged temperature corresponding to the seasonal maximum photosynthetic capacity ($GEE_{\text{max}}$) on a plot of $GEE_{\text{max}}$ versus temperature (not shown).

**Model Theory**

Coordination theory involves a balance between complementary processes, such as root and shoot activity or carbon and nitrogen supply, achieved through various means of coordination (e.g. allocation). Applied to photosynthesis, this theory implies that through time, leaves balance investment in $N$ between the ability for electron transport ($W_j$) and carboxylation ($W_c$) -- each of which potentially limits photosynthesis ($P = \min[W_j, W_c]$). Coordinated investment that results in co-limitation between $W_j$ and $W_c$ minimizes the overinvestment of resources in either rate.

If rates of electron transport and carboxylation are co-limiting, the supply of RuBP by electron transport exactly equals its demand by Rubisco such that the production of unusable RuBP is minimized. Resource allocation that balances limitation by electron transport and carboxylation also minimizes photoinhibition or damage due to the harvesting of excess unusable photons at saturating light levels.
(Anderson and Osmond 1987, Osmond 1994). The notion of co-limitation is consistent with the functional convergence hypothesis (Field 1991) in that leaves and or canopies will adjust to the mean growth conditions so that no one factor -- physiological (i.e. $W_j$, $W_c$) or environmental (light, temperature, water, nitrogen, CO$_2$) -- is more limiting than any another.

Observations of leaf level gas exchange are in general agreement with this functional convergence and coordination theory. Co-limitation between electron transport and carboxylation has been observed for many leaves (Evans 1989) and their respective capacities $U_{\text{max}}$ and $V_{\text{max}}$ are strongly correlated (Wullschleger 1993). Sun leaves have higher photosynthetic capacities than shade leaves (Boardman 1977, Bjorkman 1981), consistent with minimizing photoinhibition and maintaining co-limitation between electron transport and carboxylation at different levels of light availability. Additionally, both leaf nitrogen content and maximum stomatal conductance exhibit linear non-saturating relationships with photosynthetic capacity, reflecting regulated investment in nitrogen and the potential influx of CO$_2$ to useable levels (Cowan and Farquhar 1977, Ehleringer and Bjorkman 1977, Wong 1979, Field and Mooney 1986).

Functional convergence and coordination theory imply that since, on average, no one factor limits photosynthesis, the average conditions should be representative of the optimal conditions. That is, the average irradiance should equal the optimal irradiance ($\bar{I} = I_{\text{opt}}$) and the average temperature should equal the optimal temperature ($\bar{T} = T_{\text{opt}}$). It follows that as the average conditions change throughout a growing season, the biochemical capacity for photosynthesis and its temperature optimum will shift as well. Mathematically, co-limitation implies that $P_{\text{max}}$ is given by the point of intersection between the average rates of light limited ($\bar{W}_j = \bar{\alpha} \bar{I}$) and light saturated ($\bar{W}_c = P_{\text{max}}$) photosynthesis (Figure 2.2a).

**Model Equations**

Assuming canopy photosynthetic capacity ($P_{\text{cmax}}$) varies with light availability such that co-limitation is maintained between the light limited ($\alpha I$) and light saturated rates ($P_{\text{cmax}}$), $P_{\text{cmax}}$ may be
Figure 2.2. Model relationships between photosynthesis and light (a), relative photosynthesis and temperature (b), relative photosynthesis and VPD (c), quantum yield and temperature (d), and relative photosynthetic capacity and relative plant water status (e).
expressed as the product of the time-averaged quantum yield \( \bar{\alpha} \), \( \mu \text{mol} \mu \text{mol}^{-1} \) and the time-averaged PAR absorbed by the canopy \( \bar{I} \), \( \mu \text{mol} \text{m}^{-2} \text{s}^{-1} \):

\[
P_{\text{cmax}} = \bar{\alpha} \bar{I}
\]

(2.5)

In practice, Equation 2.5 can be applied using measurements of incident radiation (PAR), air temperature, and canopy light absorptance \( f_{\text{APAR}} \). In this study, PAR, air temperature, and \( f_{\text{APAR}} \) were determined at each site (Appendix). It should be noted that an analogous expression to Equation 2.5 could be derived for carboxylation capacity \( V_{\text{cmax}} \) using the biochemical model of Farquhar et al. (1980) as modified by Collatz et al. (1991, 1992) by setting \( \bar{W}_j = \bar{W}_c \):

\[
V_{\text{cmax},C3} = \bar{\alpha}_{C3} \bar{I} (\bar{\tau} + \bar{K}_m) / (\bar{\tau} + 2\bar{\Gamma})
\]

(2.6a)

\[
V_{\text{cmax},C4} = \bar{\alpha}_{C4} \bar{I}
\]

(2.6b)

where \( \bar{\alpha}_{C3} \), \( \bar{\alpha}_{C4} \), \( \bar{\tau} \), and \( \bar{\Gamma} \) are described below and \( \bar{K}_m \) is the effective half-saturation constant given by:

\[
\bar{K}_m = \bar{K}_i (1 + \bar{\Omega} / \bar{K}_o)
\]

(2.7)

where \( \bar{K}_i \) and \( \bar{K}_o \) are Michaelis-Menten constants and \( \bar{\Omega} \) is the time-averaged oxygen concentration in the leaf. To avoid potential difficulties associated with the inference of such parameter values from calibrated models, as discussed above, \( V_{\text{cmax}} \) was not estimated or examined. Rather, the remainder of this chapter deals with estimates of photosynthetic capacity \( \text{GEE}_{\text{max}} \), as derived from light response curves for gross ecosystem CO₂ exchange (GEE).

**Canopy Quantum Yield**

Canopy quantum yield is assumed to equal that of individual leaves and is determined differently for \( C_3 \) and \( C_4 \) plants (Figure 2.2d) due to their respective sensitivities to CO₂ concentration within the leaf \( c_i \) (Ehleringer and Bjorkman 1978):

\[
\bar{\alpha} = (f_{C3} \bar{\alpha}_{C3} + (1-f_{C3}) \bar{\alpha}_{C4})
\]

(2.8)
where \( f_{C3} \) is the C\(_3\) fraction. Assuming the time-averaged ratio of internal to atmospheric CO\(_2\) concentration (\( \frac{\bar{c}_i}{c_a} \)) is 0.7 for C\(_3\) plants, and the optimal leaf temperature equals the running mean daytime air temperature (\( \bar{T} \), see below), the time-averaged quantum yield may be expressed (Collatz et al. 1991, 1992):

\[
\bar{\alpha}_{C3} = 0.08 \left[ \frac{(\bar{c}_i - \Gamma)/(\bar{c}_i + 2\Gamma)}{f_{T_{opt}} f_W} \right] \tag{2.9a}
\]

\[
\bar{\alpha}_{C4} = 0.06 \left( f_{T_{opt}} f_W \right) \tag{2.9b}
\]

where \( f_{T_{opt}} \) and \( f_W \) are empirical temperature and moisture stress modifiers (see below) that account for non-CO\(_2\) related effects (e.g. Baker et al. 1988) that reduce the quantum yield below its unstressed value, \( \bar{c}_i \) is the time-averaged leaf internal CO\(_2\) mole fraction (mol mol\(^{-1}\)) equal to \( \frac{\bar{c}_i}{c_a} \bar{c}_a \), and \( \Gamma \) is the time-averaged CO\(_2\) compensation point (mol mol\(^{-1}\)):

\[
\Gamma = 0.5 \bar{O}_i / \left( \bar{S} \bar{P}_a \right) \tag{2.10}
\]

where \( \bar{O}_i \) is the average partial pressure of oxygen in the leaf (20900 Pa), \( \bar{P}_a \) is the average atmospheric pressure (Pa), and \( \bar{S} \) is the time-averaged specificity of Rubisco for CO\(_2\) relative to O\(_2\):

\[
\bar{S} = 2600 \cdot 0.57^{17.25/110} \tag{2.11}
\]

**Temperature and Moisture Modifiers**

Photosynthetic capacity generally increases with increasing temperature as a result of faster reaction rates at higher temperatures (Woodward and Smith 1994). As temperatures rise and fall throughout a growing season, the acclimating plant will thus exhibit a rise and fall of photosynthetic capacity (\( \bar{P}_{\text{max}} \)), concurrent with a rise and fall of the temperature optimum (e.g. Schulze et al. 1976). There is, however, a temperature beyond which any further increase causes lower rates of photosynthesis at saturating light levels (Woodward and Smith 1994). Optimality theory predicts this threshold temperature reflects genotypic adaptation, that is, optimal photosynthetic efficiency is achieved through adaptation to the local thermal climate. In contrast, seasonal shifts in the optimum temperature reflect...
acclimation or phenotypic plasticity in a given climate. Assuming genotypic adaptation to the local thermal climate, the threshold temperature ($T_{\text{opt}}$) was assumed equal to $T$ at the time of the seasonal maximum canopy light absorptance ($f_{\text{APAR}}$) (Potter et al. 1993). If $f_{\text{APAR}}$ does not vary (e.g. evergreen vegetation), $T_{\text{opt}}$ was set equal to the annual maximum $T$, assuming the greatest photosynthetic capacity that can occur does occur in a given location. The running mean daytime air temperature ($\bar{T}$) was calculated using Equation 13 (see below) and half-hourly (or hourly) air temperature ($^\circ C$) for periods when light levels were greater than zero (PAR>0). The photosynthetic temperature response ($f_{T_{\text{opt}}}$) thus determines the relative upper limit to photosynthetic capacity at a given temperature (Figure 2.2b):

$$f_{T_{\text{opt}}} = \frac{1.1814}{(1 + \exp(0.2[T_{\text{opt}} - 10 - T]))(1 + \exp(0.3[T - 10 - T_{\text{opt}}]))}$$

(2.12)

The form of this equation is taken from Potter et al. (1993). It was assumed that temperature effects on the quantum yield (Baker et al. 1988) parallels those on photosynthesis (Equation 2.9).

Photosynthetic capacity is reduced during times of low leaf water potential (Sharkey and Badger 1982, Von Caemmerer and Farquhar 1984, Sharkey and Seeman 1989) and it was assumed that such effects caused parallel reductions in quantum yield, consistent with known reductions in photochemical efficiency during drought stress (Bjorkman et al. 1984, Demmig-Adams et al. 1988, Werner et al. 1999). While neither soil water content nor plant moisture status were explicitly modeled, it was assumed that the relative change in LAI reflects long-term changes in plant water status and hence soil moisture (Grier and Running 1977, Squire et al. 1986). Short-term variation in plant water status (which occurs faster than variations in LAI) was inferred from the moisture status of the atmosphere (Figure 2.3). It was assumed that persistent atmospheric drought was consistent with low leaf water potential (Sellin 1999) which was consistent with persistent stomatal closure (Graham and Running 1984).

Atmospheric moisture status may be a reasonable indicator of plant moisture status due to feedback between stomatal conductance, transpiration, and leaf-to-air vapor pressure deficit (VPD). High VPD is consistent with low leaf water status because of VPD- and temperature-related inhibition of stomatal conductance. For example, high atmospheric VPD and high leaf temperatures induce low
Figure 2.3. Interrelationships among soil, plant, and atmospheric moisture status.

Assuming (1) plants maintain a balance between transpirational demand and soil moisture availability, then leaf area will decline with soil drought. Before this happens, plant water status will decrease as will atmospheric moisture, assuming (2) feedback and accommodation between transpiration and VPD.
stomatal conductance \((g)\), through VPD and temperature stress, leading to low rates of transpiration \((E\) where \(E=g\text{VPD}\)). For a given increase in VPD, there is a linear increase in transpiration while there is often an exponential decrease in stomatal conductance (Figure 2.2c):

\[
f_D = \frac{1}{1+\exp[1.3(\text{VPD}-3)]}
\]

where VPD (kPa) is the instantaneous (e.g. half-hourly or hourly) value. This relationship is based on measurements of stomatal conductance in tropical, temperate, and boreal ecosystems on crops, grasses, shrubs, and deciduous and evergreen trees (Aber & Federer 1992, Fan et al. 1995, Jarvis et al. 1976, Schulze and Hall 1982, Hollinger 1992, Hollinger et al. 1994, Kim and Verma 1991, Korner 1994, Leuning 1995, Monson and Grant 1989, Reich et al. 1990, Schulze et al. 1976, Smith and Goltz 1994, Whitehead et al. 1981). It is consistent with other relationships in the literature (e.g. Lohammer et al. 1980, Leuning 1995, Jacobs et al. 1996) with the exception that in Equation 10, there is little effect when VPD<1 kPa, (e.g. Korner 1994).

The calculation of relative plant water status \((f_W)\) from atmospheric moisture status requires consideration of the two following caveats. First, it is assumed that persistent stomatal closure occurs only when leaf water potential is very low, that is, leaf water potential should be related to time-averaged (rather than instantaneous) stomatal conductance. Second, feedback between plant moisture status, transpiration, and atmospheric moisture is likely to be realized only during midday hours (1000<\text{Hr}<1400) when physiological activity is near its daily peak and the canopy and atmospheric boundary layers are convective and well mixed (Monteith 1995). Given these constraints, relative plant water status \((f_W)\) was calculated as the running mean of midday relative stomatal conductance \((f_D)\):

\[
f_W = \overline{f_D}_{\text{midday}}
\]

Calculation of the running mean is described below.

**Time Constant for Acclimation**

Models of acclimation can be structured “objectively” (e.g. Thornley 1998) such that a change in
environmental conditions causes a physiologically realistic imbalance in one or more state conditions and eventually, a new steady state is reached. Alternatively, optimality models assume a new steady state is reached instantaneously, which is computationally simpler but physiologically unrealistic (Thornley 1991). The objective approach is realistic but impractical to apply at regional to global scales given the many parameters required. On the other hand, optimality assumptions may be unrealistic but suitable for global application. As a compromise, the optimality approach is used here with time-averaged environmental light and temperature conditions so as to minimize the influence of their short-term variations. One approach to averaging environmental factors suitable for this purpose is with recursive low pass filters of the form:

\[
X_i = \omega X_{i-1} + (1-\omega)X_i
\]  

(2.15)

where \(X\) is the filtered value of variable \(X\), \(X_{i-1}\) is the previous filtered value, \(X_i\) is the value of variable \(X\) at time \(i\), and \(\omega\) is the weighting factor which depends upon the time interval between measurements (\(\Delta t\)) and the time constant (\(\tau\)):

\[
\omega = \exp(-\Delta t/\tau)
\]  

(2.16)

Using the instantaneous-optimality approach with time-averaged variables should provide reasonable agreement with more accurate models of acclimation. As such, the problem reduces to determining the appropriate time constant for photosynthetic acclimation.

As noted by Cowan (1986), optimal photosynthetic acclimation could only be achieved if protein degradation and synthesis were so rapid that enzyme activities could vary precisely with external factors that affect light harvesting and carboxylation such as light, temperature, plant water status, humidity, and CO₂. Acclimation is more likely to occur over a period of a several days (Cowan 1986, Field 1991, Pearcy and Sims 1994, Thornley 1998). During this time materials and nutrients such as nitrogen can be reallocated in response to the prevailing growth conditions.

Canopy acclimation encompasses both leaf level changes in foliar biochemistry and anatomy and canopy level morphological changes in the amount of leaves and their orientation, inclination, and
distribution. The time constant discussed here primarily reflects changes in canopy physiology, as changes in canopy morphology were assumed to be captured by changes in canopy light absorptance ($f_{\text{APAR}}$) (Squire et al. 1986, Field 1991). The synthesis and reorganization of pigments, membranes and enzymes generally occur on the order of days while changes in leaf development and display occur over a period of days to weeks or longer (Pearcy 1994). The time scale for full acclimation ultimately depends on the rate of leaf turnover, which can be quite slow in some woody species (Kamaluddin and Grace 1992).

As a first approximation and in line with results from an ‘objective’ transport-resistance model initialized for a non-growing leaf on a non-growing plant (Thornley 1998), the time constant for acclimation was assumed to be five days. It should be noted that this value is also consistent with the typical residence time of weather fronts in many regions. Vegetation may have adapted to this natural periodicity by maintaining a common level of physiological plasticity.

**Results and Discussion**

Seasonal variation of the calculated 5-day running means of temperature ($\bar{T}$) and irradiance ($\bar{I}$) along with estimated $f_{\text{APAR}}$ for each site is shown in Figure 2.4. These variables were combined with predictions of relative photosynthetic capacity as a function of temperature ($f_{\text{Topt}}$) and predicted genotypic temperature optima (Figure 2.5) along with relative plant water status (Figure 2.6) to calculate canopy photosynthetic capacities at each site using Equations 2.5, 2.8, and 2.9 to 2.15 (Figure 2.7 and 2.8).

Predicted genotypic temperature optima show a strong relationship with observed values but with a relatively large offset (Figure 2.5). Much of this offset may stem from the difficulty in determining the observed temperature optima (visually estimated). With the exception of the winter wheat site, the boreal and temperate forest sites achieved peak photosynthetic capacity around 18-20°C, while the non-forest and tropical sites peak between 25-30°C. Unlike the non-forest sites, the predicted temperature optima for the forest sites consistently exceeded those observed by 3-5°C. This overestimation at the forest sites
Figure 2.4. Temporal variation of 5-day running means of temperature ($\bar{T}$) and irradiance ($\bar{I}$) and estimated canopy light absorptance ($f_{APAR}$).
Figure 2.4. Continued.
Figure 2.5. Relationship between predicted and observed genotypic temperature optima. Observed genotypic temperature optima were estimated as the time-averaged temperature ($\bar{T}$) concurrent with the seasonal peak gross ecosystem CO$_2$ exchange (GEE$_{\text{max}}$). Predicted optima ($T_{\text{opt}}$, see text) were derived from the time-averaged temperature concurrent with the seasonal peak light absorptance ($f_{\text{APAR}}$).

$y = 0.82x + 5.64$

$r^2 = 0.87$
Figure 2.6. Predicted relative plant water status ($f_w$) and observed pre-dawn leaf water potential (observations from Verma et al. 1992).
Figure 2.7. Temporal variation in predicted and observed canopy photosynthetic capacity by site.
Figure 2.7. Continued.
Figure 2.8. Relationship between predicted and observed canopy photosynthetic capacity.

$y = 0.97x + 2.54$

$r^2 = 0.76$
may have been in part due to the rough estimation of the timing of peak seasonal photosynthetic activity. At the evergreen sites (NSA-OBS, SSA-OBS, Howland), $f_{\text{APAR}}$ was assumed constant and thus provided no clear indication of seasonal peak leaf display. In contrast, at the non-forest sites, the seasonal peak in $f_{\text{APAR}}$ was relatively distinct (Figure 2.4), providing a clear indication of the timing of peak activity and better agreement between the predicted and observations peaks in photosynthetic capacity with respect to temperature (Figure 2.5).

The magnitude and seasonal variation in predicted plant water stress ($f_w$) was similar to the pattern of observed pre-dawn leaf water potential measured at the Konza Prairie site (Figure 2.6) with a few exceptions. The decrease in predicted plant water status near JD 165 did not coincide with a similar drop in observed pre-dawn leaf water potential. (The lack of measurements around JD 235 precludes a similar conclusion.) Additionally, around JD 210 both predictions and observations indicated a sharp decline in plant water status, but the predictions remained at low water status longer than the observations. Changes in pre-dawn leaf water potential appear to be less dynamic than time-averaged changes in atmospheric VPD. Despite these discrepancies, the overall agreement is encouraging, particularly considering the simplicity of the approach, and supports the notion that the time-averaged midday moisture status of the atmosphere may be a reasonable and useful index of vegetation moisture status.

The seasonal pattern and magnitude of the predicted canopy photosynthetic capacities were similar to those observed (Figure 2.7). Notable exceptions were found at the northern boreal forest (NSA-OBS) and boreal fen, and the winter wheat and tropical rainforest. Discrepancies at the northern old black spruce (NSA-OBS) site were likely due to the uncertainty and errors in $f_{\text{APAR}}$ estimates. Reported LAI, estimates ranged from 2.4 (Dang et al. 1997) to 2.7 (Chen et al. 1997) and NDVI ranged from 0.40 (K. Czajkowski, personal communication) to 0.70 (Dang et al. 1997). Overestimation at NSA-OBS and underestimation at NSA-FEN are not surprising given the potential errors in $f_{\text{APAR}}$. Using the lower range of $f_{\text{APAR}}$ at NSA-OBS (~0.4) provided excellent agreement between the predictions and observations (data not shown). The $f_{\text{APAR}}$ estimates for the boreal fen were questionable, given that they were derived from
reflected PAR and shortwave radiation (Appendix) and the relationship used to relate $f_{APAR}$ to NDVI (Equation A4) was derived for vascular plants. The non-vascular component of the fen may have a much different spectral response than vascular plants (Bubier et al. 1997).

Despite a clear overestimation of $f_{APAR}$ during the early period of canopy development prior to JD 50 at the winter wheat site (Figure 2.4) as compared to field measurements of LAI (S. Verma, unpublished, data not shown), estimates of canopy photosynthetic capacity (Figure 2.7) agreed well with observations. This is likely the result of large temperature constraints (low $f_{Topt}$) during this time period. In contrast, after JD 50, estimates of $f_{APAR}$ agree well with estimates derived from direct LAI measurements (data not shown), yet the model overestimates photosynthetic capacity during canopy senescence (Figure 2.7). Agreement was found after adjusting the temperature response function ($f_{Topt}$) so that relative photosynthetic capacity declined more sharply at temperatures above the genotypic optimum. This empirical a priori modification to the temperature response function was not used in the final model predictions. This result indicates that site-specific responses may deviate from the highly generalized function represented by Equation 2.13, although the latter may be adequate for global applications. It is not clear why the model overestimated capacities at the tropical forest site. Overall, the predicted photosynthetic capacities were close in both magnitude and seasonality with the observations, providing justification for the use of Equation 2.5.

The relationship between predicted and observed capacities is shown in Figure 2.8. Predicted photosynthetic capacity varied in a positive linear fashion with observed GEE$_{max}$. It should be noted that even if maximum rates of GEE can be derived from eddy covariance measurements of NEE, there is no way to know if the seasonal variation in maximum GEE is due to seasonal variation in stress (which reduces GEE below its potential maximum) or seasonal variation in the potential maximum itself. No attempt is made here to distinguish between these two conditions. Nevertheless, the overall agreement suggests that canopies acclimate to the prevailing light availability and regulate investment in photosynthetic capacity to levels in tune with multiple environmental constraints (e.g. light, temperature, and water).
Consistent with theories of resource optimization and photo-acclimation, canopy photosynthetic capacity exhibited a strong positive linear relationship with the time-averaged absorbed PAR, particularly when the latter was constrained during times of sub-optimal temperature and water status (Figure 2.9). Temperature and moisture constrained time-averaged absorbed PAR was calculated using site measurements of incident PAR and $f_{APAR}$ and temperature ($f_{Topt}$) and plant water status ($f_{W}$) constraints.

The solid line in Figure 2.9 is a linear regression forced through the origin, the slope of which equals the average quantum yield (mol CO$_2$ mol$^{-1}$ photon absorbed) across the sites. This value (0.051) is similar to maximal quantum yields exhibited by individual leaves (Ehleringer and Bjorkman 1978, Collatz et al. 1998). The strength of this relationship ($r^2=0.75$) supports the contention that the time-averaged radiation is a good general index of photosynthetic capacity. This result also implies that canopies maximize light utilization and regulate investment in photosynthetic capacity to levels in tune with light availability.

Temperature and moisture constraints account for a significant amount of the seasonal variability in canopy photosynthetic capacity. This undoubtedly stemmed from the fact much of the variability is not related to changes in $f_{APAR}$. Sites with evergreen vegetation and persistent leaf display absorb, but do not utilize absorbed radiation during winter periods. Similarly, vegetation in environments with occasional drought during the growing season (e.g. Konza Prairie) may maintain leaf area, albeit in reduced amounts, throughout drought periods. While canopies may be absorbing radiation during such periods, they may not be utilizing the absorbed radiation (Waring and Landsberg 1998). The application of temperature and moisture constraints on mean absorbed PAR ($\overline{APAR}$), accounted for an additional 29% of the variance in canopy photosynthetic capacity (Table 2.3). Daily maximum PAR (PAR$_{max}$) and mean incident PAR ($\overline{PAR}$) both accounted for a similar amount of the variability ($r^2=0.26$ and 0.29, respectively), while mean absorbed PAR ($\overline{APAR}$) accounted for an additional 17% over mean incident ($\overline{PAR}$). Constrained mean absorbed PAR ($\overline{APAR}_{f_{Topt}f_{W}}$) accounted for significantly more of the variability in GEE (29%) than any other measure.

Consistent with the previous studies showing increasing photosynthetic capacity with increasing
Figure 2.9. Relationship between observed photosynthetic capacity and time-averaged absorbed radiation. The latter was calculated as the product of canopy light absorptance ($f_{APAR}$) and the 5-day running mean of incident PAR ($\bar{I}$). This product was then constrained during times of sub-optimal temperature ($f_{Topt}$) and moisture ($f_W$).
Table 2.3. Proportion of variation in $GEE_{\text{max}}$ accounted for by different measures of light availability; maximum incident PAR ($\text{PAR}_{\text{max}}$), mean incident PAR ($\overline{\text{PAR}}$), mean absorbed PAR ($\overline{\text{APAR}}$), and mean absorbed PAR with moisture and temperature constraints ($\overline{\text{APAR}}_{W/\text{Topt}}$).

<table>
<thead>
<tr>
<th>Definition</th>
<th>$r^2$</th>
<th>Additional variance explained</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\text{PAR}_{\text{max}}$</td>
<td>0.26</td>
<td>---</td>
</tr>
<tr>
<td>$\overline{\text{PAR}}$</td>
<td>0.29</td>
<td>0.03</td>
</tr>
<tr>
<td>$\overline{\text{APAR}}$</td>
<td>0.46</td>
<td>0.17</td>
</tr>
<tr>
<td>$\overline{\text{APAR}}_{W/\text{Topt}}$</td>
<td>0.75</td>
<td>0.29</td>
</tr>
</tbody>
</table>
temperature at the leaf (Woodward and Smith 1994) and canopy scale (Hollinger et al. 1999), observed rates of canopy photosynthetic capacity (GEE$_{\text{max}}$) exhibited a strong positive exponential relationship with temperature (Figure 2.10). The strength of this relationship across a wide range of ecosystems from the arctic to the tropics underscores the important control by temperature on the seasonal variability of canopy photosynthetic capacity. While the data do not provide direct evidence for temperature acclimation, it is consistent with the hypothesis that plants acclimate to recent growth temperatures. The poor relationship between canopy photosynthetic capacity and temperature at the tropical sites (Figure 2.10) is likely due to the small temperature range observed during the measurement periods at these sites.

Model predictions of canopy photosynthetic capacity ($P_{\text{cmax}}$) for the coniferous forest site (Howland, 1997), calculated using half-hourly $T_{\text{air}}$ and PAR and a range of time constants (1, 5, 10, 20, 30, 60, and 120 days), is shown in Figure 2.11. For each run, the model was initialized using data from 1996. The model predictions appear relatively insensitive to changes in the time constant between 1 and 10 days. Lower values (1 day) were unrealistically sensitive to short-term variations in light and temperature while higher values (>10) introduced a large and unrealistic phase lag to the timing of the capacities. Given the relative insensitivity of the predictions to the time constant around 5 days and the unrealistic phase lag introduced at values greater than 10 days, the use of a 5-day time constant appeared reasonable.

To provide an indication of the actual time constants for photosynthetic acclimation of the different canopies, time constants were varied at each site until the sum of squared residuals between the predicted and observed capacities was minimized (Table 2.4). At the temperate sites, the tuned time constants were similar to the 5-day value used in the model. Tuned time constants were generally greater at the boreal and tropical sites. In the tropics the environment is so constant that the actual value used is likely to be of little consequence to the predictions. The time constant had to be increased by a factor of 12 at the tropical rainforest site to induce a 2.3 $\mu$mol m$^{-2}$ s$^{-1}$ difference in predicted capacity. Caution should be used when interpreting this result as the length of the time constant (58 days) is longer than the
measurement period (~50 days). Similarly, at the tropical savanna site, the fitted time constant is more

Figure 2.10. Relationship between observed canopy photosynthetic capacity and temperature. To facilitate comparison among sites, photosynthetic capacities (GEE$_{\text{max}}$) and time-averaged temperatures ($\overline{T}$) from each site were normalized to the seasonal maximum GEE$_{\text{max}}$ and to $\overline{T}$ concurrent with the seasonal maximum GEE$_{\text{max}}$, respectively.
Figure 2.11. Sensitivity of model predictions to variation in the time constant for acclimation. The numbers on each curve indicate the time constant (in days) used in the calculation.
Table 2.4. Tuned time constants for acclimation of canopy photosynthetic capacity to light and temperature. Tuning was done by minimizing the sum of squared differences between predicted and observed (GEE\textsubscript{max}) values over the full measurement period. ΔRMSE is the change in the root mean square error as a result of model tuning (RMSE\textsubscript{after} - RMSE\textsubscript{before}). The percentage change is given in parentheses. Note that the nominal value of the time constant is 5 days.

<table>
<thead>
<tr>
<th>Site</th>
<th>Tuned Time Constant (days)</th>
<th>RMSE (µmol m\textsuperscript{-2} s\textsuperscript{-1})</th>
</tr>
</thead>
<tbody>
<tr>
<td>Arctic Tundra</td>
<td>7</td>
<td>-0.01 (0.4 %)</td>
</tr>
<tr>
<td>Boreal Forest (NSA-OBS)</td>
<td>13</td>
<td>-4.70 (70%)</td>
</tr>
<tr>
<td>Boreal Fen</td>
<td>9</td>
<td>-0.09 (3%)</td>
</tr>
<tr>
<td>Boreal Forest (SSA-OBS)</td>
<td>3</td>
<td>-6.90 (62%)</td>
</tr>
<tr>
<td>Temperate Coniferous Forest</td>
<td>7</td>
<td>-0.13 (3%)</td>
</tr>
<tr>
<td>Temperate Deciduous Forest</td>
<td>4</td>
<td>-0.01 (0.1%)</td>
</tr>
<tr>
<td>Temperate C\textsubscript{3}/C\textsubscript{4} Grassland</td>
<td>8</td>
<td>-1.50 (3%)</td>
</tr>
<tr>
<td>Temperate Crop (Winter Wheat)</td>
<td>21</td>
<td>-0.39 (4%)</td>
</tr>
<tr>
<td>Tropical C\textsubscript{3}/C\textsubscript{4} Savanna</td>
<td>13</td>
<td>-0.04 (2%)</td>
</tr>
<tr>
<td>Tropical Rainforest</td>
<td>58</td>
<td>-2.30 (33%)</td>
</tr>
</tbody>
</table>
than double the nominal 5-day value. However, this greater time constant improves the model fit by less than 0.1 µmol m$^{-2}$ s$^{-1}$.

In contrast, the boreal forest northern old-black spruce site appeared much more sensitive to the time constant. For the identical increase (from 5 to 13 days), as the tropical savanna site, the predicted capacities changed by a much larger 4.7 µmol m$^{-2}$ s$^{-1}$ (a 70% decrease in error). Interestingly, the largest change as a result of allowing the time constant to change was observed at the southern old black spruce site. Decreasing the value from 5 to 2 decreased the RMSE by a relatively large 6.9 µmol m$^{-2}$ s$^{-1}$ or 62%. The reason for this is unclear and may be the result of other errors in the model or the data ($f_{\text{APAR}}$, for example).

These results are consistent with the constancy of tropical environments, more variable conditions (typical 5-day periodicity of weather fronts) in the temperate region, and a short growing season in the boreal zone characterized by a fast transition from winter to summer conditions (see Figure 2.4). In such an environment, maintenance of a high photosynthetic capacity (less physiological plasticity) would allow a plant to take advantage of favorable growth conditions as soon as they occur. Overall, however, it is difficult to separate the errors in $f_{\text{APAR}}$ (or in the predicted temperature response) from the errors in the time constant. Further, the tuning process had minimal effect on the model predictions for most sites (<4%), providing confidence in the 5-day time constant used in the model.

**Conclusions**

A generalized uncalibrated model of canopy photosynthetic capacity based on principles of resource optimization and driven by variables accessible via remote sensing ($f_{\text{APAR}}$, PAR, $T_{\text{air}}$) was described and evaluated in a wide range of ecosystems from arctic, boreal, temperate, and tropical environments. A unique aspect of the model is its use of a recursive filter for calculating photosynthetic acclimation based on the integrated effect of environmental conditions. This filtering method was found to be robust as the modeled photosynthetic capacity was relatively insensitive to value of the time
constant. A value of 5-days appears reasonable for most sites. Greater time constants provided better fits in the tropics and the boreal region, owing to constancy of environmental conditions in the tropics and potentially less physiological plasticity in the boreal region.

A strong positive linear relationship was found between modeled and observed canopy photosynthetic capacities and the predicted photosynthetic capacities were in close agreement with both the magnitude and seasonality of the observations. In addition, a strong linear relationship was found between modeled and observed genotypic temperature optima. Consistent with theories of resource optimization and photo-acclimation, canopy photosynthetic capacity exhibits a strong positive linear relationship with the temperature and moisture constrained time-averaged absorbed PAR. Temperature and moisture constraints accounted for a significant amount of the seasonal variability in canopy photosynthetic capacity as well. This undoubtedly stemmed from the fact much of the variability is not related to changes in $f_{\text{APAR}}$. Consistent with the previous studies showing increasing photosynthetic capacity with increasing temperature at the leaf and canopy scales, observed rates of canopy photosynthetic capacity exhibited a strong positive exponential relationship with temperature. The strength of this relationship underscores the importance of temperature to the seasonal variability of canopy photosynthetic capacity.

These results provide justification for the hypothesis that canopies acclimate to the prevailing light availability and regulate investment in photosynthetic capacity to levels in tune with multiple environmental constraints. Further, the model presented here provides the means by which to relate satellite NDVI to the physiological status of vegetation and provides justification for the use of NDVI as a global general index of potential carbon gain.
APPENDIX

Gaps in $T_{\text{air}}$ data were filled by simulating diel variations in temperature as a function of time, using measured $T_{\text{min}}$ and $T_{\text{max}}$ (Landsberg 1986):

\[
\text{Filled } T_{\text{air}} = 0.5(T_{\text{min}} + T_{\text{max}}) + 0.5(T_{\text{max}} - T_{\text{min}})\cos(2\pi(Hr - 12)/24) \tag{A1}
\]

For gaps on days without measurements of $T_{\text{min}}$ and $T_{\text{max}}$, their mean values from the nearest 10 days (5 prior and 5 after) were used. Gaps in incident PAR data were filled by attenuating the top-of-the-atmosphere PAR flux density ($I_{\text{toa}}$) by an atmospheric transmittance ($\beta_a$)

\[
\text{Filled PAR} = I_{\text{toa}} \beta_a \tag{A2}
\]

where atmospheric transmittance was estimated from the diel temperature amplitude ($\Delta T = T_{\text{max}} - T_{\text{min}}$) following Glassy and Running (1994):

\[
\beta_a = m(1 - \exp[-0.003 \Delta T^{2.4}]) \tag{A3}
\]

where $m$ was an empirical coefficient ($0 < m < 1$) used to provide the best fit (OLS) between measured and predicted PAR ($m$ was generally greater than 0.95 and $r^2$ values were generally 0.73, except for Harvard Forest where $m=0.68$ and $r^2=0.40$). Values of $I_{\text{toa}}$ were determined as described by Brock (1981), based on latitude and the position of the sun. This gap filling approach, while not as accurate as using measurements from nearby weather stations, was practical and provided reasonable and consistent results.

Light (PAR) absorbed by the green leaf area fraction of the canopy ($f_{\text{APAR}}$) was determined in various ways among the sites as summarized in Table 2.2. At the HAPEX-Sahel site, $f_{\text{APAR}}$ was determined by a combination of measurements and modeling (Hanan et al. 1997) and at the Harvard Forest site, $f_{\text{APAR}}$ was assumed to equal the fraction intercepted, assuming all leaves present in the canopy were green. For all the other sites, except NSA-FEN and the winter wheat site (see below), $f_{\text{APAR}}$ was derived from above-canopy estimates of NDVI using the following relationship (Figure A1):

\[
f_{\text{APAR}} = 1/(1 + \exp[6(0.64 - \text{NDVI})]) \tag{A4}
\]

($r^2=0.87$, $n=133$). Equation A4 was derived using measurements of light interceptance
Figure A1. Relationship between canopy light interceptance \( f_{IPAR} \) and NDVI (a) and canopy light absorptance \( f_{APAR} \) and NDVI (b). Canopy light interceptance refers to PAR interceptance by the entire canopy (green + nongreen components) whereas canopy light absorptance refers to PAR absorptance by the green leaf fraction.
the green leaf fraction. Senescence (in non-evergreen canopies). The canopies included annual grassland (Gamon et al. 1995), saltmarsh grassland (Bartlett et al. 1992), corn and cotton (Weigand et al. 1991), fallow shrub (Hanan et al. 1997), and evergreen and deciduous shrubs (Gamon et al. 1995). Reflected PAR (\(\text{PAR}_{\text{reflected}}\)) at the top of the canopy was assumed to be 4% if not otherwise cited.

NDVI was either measured at the site above the canopy from helicopter and corrected for atmospheric effects (Konza Prairie: Verma et al. 1993, NSA-OBS: Dang et al. 1997), from a boom extension (Howland: Ranson et al. 1994), or by a hand-held radiometer (Happy Valley: McMichael et al. 1999). At SSA-OBS and ABRACOS, NDVI was estimated from total (green + non-green) canopy interception \(f_{\text{IPAR}}\) which in turn was derived from effective LAI \(\text{LAI}_e\) measurements made with the LiCor LAI-2000 Plant Canopy Analyzer:

\[
f_{\text{IPAR}} = 1 - \exp(-k\text{LAI}_e)
\] (A5)

where \(k = 0.5\) (the light extinction coefficient) and \(\text{LAI}_e\) is the effective leaf area index defined as the one-sided LAI without adjustment for leaf clumping (Chen et al. 1997). NDVI was then estimated by inverting the relationship between total (green + non-green) interception \(f_{\text{IPAR}}\) and NDVI (Figure A1):

\[
\text{NDVI} = 0.56 - \ln\left[\frac{1}{f_{\text{IPAR}}} - 1\right]/7.3
\] (A6)

\((r^2=0.80, n=266)\). This relationship was determined using measurements of total PAR interception by green and non-green canopy fractions \((1-\text{PAR}_{\text{below}}/\text{PAR}_{\text{above}}-\text{PAR}_{\text{reflected}})\) made in number of canopies including grassland (Demetriades-Shah et al. 1992), fallow grass (Hanan et al. 1997), corn and cotton (Weigand et al. 1991), millet (Hanan et al. 1997), fallow shrub (Hanan et al. 1997), deciduous shrub (Law and Waring 1994), deciduous forest (Waring et al. 1994, Dang et al. 1997), evergreen shrub (Law and Waring 1994, Goward et al. 1994), and coniferous forest (Goward et al. 1994, Ranson et al. 1994, Waring et al. 1994, Dang et al. 1997).

At the NSA-FEN and Ponca City winter wheat sites, NDVI was estimated from measurements of PAR \(r_{\text{VIS}}\) and shortwave radiation \(r_{\text{SW}}\) reflected by the canopy. Near infrared reflectance \(r_{\text{NIR}}\) was determined by combining \(r_{\text{VIS}}\) and \(r_{\text{SW}}\): \(r_{\text{NIR}} = 2r_{\text{SW}} - r_{\text{VIS}}\). This assumes that half of the incident radiation is
in the visible wavelengths and the half is in near-infrared wavelengths such that \( r_{SW} \) is the average of \( r_{VIS} \) and \( r_{NIR} \). NDVI was then calculated as: \( \text{NDVI} = (r_{NIR} - r_{VIS})/(r_{NIR} + r_{VIS}) \) and \( f_{APAR} \) was then determined with Equation A4.

At each site, time-averaged midday \( f_{APAR} \) was determined by fitting (OLS) a 5th-order Fourier series to the instantaneous midday (1000<\( Hr <1400 \)) measurements of \( f_{APAR} \) following Sellers et al. (1995):

\[
f_{APAR} = \sum_{n}^{5} (a_{n} + a_{n}\cos[nt] + b_{n}\sin[nt])
\]

where \( a_{0}, a_{n}, \) and \( b_{n} \) are fitted coefficients and \( t \) is time in radians. The seasonal variation in \( f_{APAR} \), \( \bar{T} \), and \( \bar{T} \) is shown in Figure 2.4.
CHAPTER III

MODELING CARBON EXCHANGE IN TERRESTRIAL ECOSYSTEMS USING
LIGHT ABSORPTANCE AND OPTIMALITY THEORY

Introduction

The exchange of carbon dioxide (CO₂) between terrestrial ecosystems and the atmosphere plays a central role in the ecology of the biosphere and the climate system. CO₂ is an important greenhouse gas which influences both the physics and chemistry of the atmosphere. Thus, its current rise of about 1.8 ppmv per year (0.5%) may have profound effects on global climate (IPCC 1990). Roughly 15% of the atmospheric carbon pool is assimilated by plants each year (Williams et al. 1997). This fixation of CO₂ provides the energy that ultimately sustains the metabolism of all organisms and drives the exchange of materials and energy with the atmosphere (Mooney et al. 1987). A fraction of this fixed carbon is respired by plants and soil microorganisms back to atmosphere while the remainder is stored in plant biomass and soils. Quantifying the net balance between photosynthetic fixation and respiratory loss is critical to understanding how the climate system affects ecosystem processes which, in turn, feedback to regulate atmospheric CO₂ levels (Hollinger et al. 1999).

Studies based on atmospheric flask samples and transport models (Tans et al. 1990, Ciais et al. 1995, Keeling et al. 1996, Fan et al. 1998) provide only indirect measures of surface CO₂ exchange. Eddy covariance measurements, aside from theoretical and logistical constraints, provide only point measurements. Ecosystem models driven by remote sensing observations, on the other hand, offer the potential for synoptic monitoring of global ecosystem functioning (e.g. Sellers et al. 1996). However, aside from a few exceptions (e.g. Prince and Goward 1995), the application of ecosystem models with remote sensing data is limited by the paucity of regional ecological databases (Leuning et al. 1995, Williams et al. 1998). More importantly, satellite observations currently provide little information on the
physical or biological status of soils. Satellite-driven models thus have no consistent means of assessing carbon loss through soil heterotrophic respiration.

Most models that predict net ecosystem CO$_2$ exchange (NEE) or its equivalent, net ecosystem productivity (NEP = NPP - $R_H$) estimate soil heterotrophic respiration using standard temperature dependent functions (Fung et al. 1987, Ludeke et al. 1991, Knorr and Heimann 1995, Maisongrande et al. 1995). Such functions are typically parameterized with the constraint that annual soil respiration equals annual NPP ($\sum$NEP = 0). The few exceptions to this approach (Potter et al. 1993, Hunt et al. 1996) explicitly model soil respiration using simplified soil carbon cycle models (e.g. Parton et al. 1987) or use functions calibrated to specific sites (Veroustraete et al. 1996, Gao 1994, Colello et al. 1998). Application of either approach requires parameters that cannot be remotely sensed such as the carbon and nitrogen content of the soil and litter in addition to soil texture, temperature, and moisture.

Plant respiration is similarly difficult to predict. It is typically subsumed within the dry matter:radiation quotient ($\varepsilon_n$) (Prince 1991), estimated as a fraction of GPP (Goward and Dye 1987, Landsberg and Waring 1997), or modeled based on vegetation type (Ruimy et al. 1996a). A promising approach involves remotely sensing aboveground biomass and relating this to rates of maintenance respiration (e.g. Prince and Goward 1995).

Recent studies have shown that theories of resource optimization applied to plant canopies can provide suitable constraints to estimate canopy photosynthetic capacity (e.g. Johnson et al. 1995, Haxeltine and Prentice 1996). Such theories have a sound theoretical basis in that acclimation to the prevailing growth conditions allows plants to maintain optimal photosynthetic and resources use efficiency (Arnon 1982, Anderson et al. 1995). This strategy maximizes evolutionary fitness by ensuring optimal use of the environment and a competitive advantage when resources are limited (Bloom et al. 1985).

Estimates of canopy photosynthetic capacity, in turn, may be used to estimate the rate of whole plant respiration consistent with maximizing daily net primary productivity (e.g. Dewar 1996). Further,
numerous studies indicate the presence of feedbacks between the nutrient status of plants and soils involving plant uptake, litterfall, and subsequent microbial decomposition and mineralization (Vitousek 1982, Reed 1990, Woodward and Smith 1994). Eventual accommodation among these processes provides a link between canopy physiological status and soil metabolism. These interrelationships provide the framework for a potential link between remotely sensed variables, such as canopy light interceptance (FPAR), and ecosystem metabolism.

Utilizing theories of acclimation and resource optimization, a generalized model of plant-soil-atmosphere CO$_2$ exchange, OPTICAL (OPTimal CALibration), is described and evaluated using eddy covariance measurements of net ecosystem CO$_2$ exchange (NEE) at eight sites from boreal, temperate, and tropical environments. The model requires three variables, light, temperature, and canopy light absorptance. These variables are used in novel ways to constrain estimates of soil temperature and plant and soil moisture status. Canopy photosynthetic capacity is prescribed by assuming plants optimize both photosynthetic efficiency and carbon gain for a given level of light availability (Cowan 1986, Farquhar 1989, Takenaka 1989, Field 1991, Chen et al. 1993). Photosynthetic acclimation throughout the growing season is incorporated through a unique method of integrating the canopy response to recent changes in light and temperature. The importance of photo-acclimation was examined by running the model using both temporally dynamic and temporally static photosynthetic capacities. The generality of the model was also examined by comparison with simple statistical models calibrated at each site. Rates of whole plant respiration were estimated by solving for the optimal rate that maximized daily NPP and which was consistent with the prescribed rate of canopy photosynthetic capacity. Soil heterotrophic respiration was constrained using empirical relationships from the literature among leaf level photosynthetic capacity, litter decomposition, and soil organic carbon.
### Table 3.1. Site Characteristics

<table>
<thead>
<tr>
<th>Site</th>
<th>Description</th>
<th>Peak LAIe</th>
<th>MAT (°C)</th>
<th>Annual Rainfall (mm)</th>
<th>Year</th>
<th>Location</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>NSA-OBS</td>
<td>boreal forest, (old black spruce)</td>
<td>2.7</td>
<td>-1.5</td>
<td>317</td>
<td>1996</td>
<td>Manitoba, Canada (55°54'N, 98°30'W)</td>
<td>Goulden et al. 1997</td>
</tr>
<tr>
<td>NSA-FEN</td>
<td>boreal fen</td>
<td>1.4</td>
<td>-1.6</td>
<td>317</td>
<td>1996</td>
<td>Manitoba, Canada (55°54'N, 98°24'W)</td>
<td>Lafleur et al. 1997</td>
</tr>
<tr>
<td>SSA-OBS</td>
<td>boreal forest, (old black spruce)</td>
<td>2.4</td>
<td>0.8</td>
<td>421</td>
<td>1996</td>
<td>Saskatchewan, Canada (53°54'N, 105°7'W)</td>
<td>Jarvis et al. 1997</td>
</tr>
<tr>
<td>Howland Forest</td>
<td>temperate coniferous forest</td>
<td>4.7</td>
<td>6.3</td>
<td>1040</td>
<td>1996</td>
<td>Maine, USA (45°15'N, 68°54'W)</td>
<td>Hollinger et al. 1999</td>
</tr>
<tr>
<td>Harvard Forest</td>
<td>temperate deciduous forest</td>
<td>3.4</td>
<td>7.6</td>
<td>1117</td>
<td>1992</td>
<td>Massachusetts, USA (42°32'N, 72°11'W)</td>
<td>Wofsy et al. 1993</td>
</tr>
<tr>
<td>Konza Prairie</td>
<td>temperate C₃/C₄ grassland</td>
<td>2.8</td>
<td>14.0</td>
<td>840</td>
<td>1987</td>
<td>Kansas, USA (39°03'N, 96°32'W)</td>
<td>Verma et al. 1992</td>
</tr>
<tr>
<td>ABRACOS</td>
<td>tropical rain forest</td>
<td>4.0</td>
<td>24.2</td>
<td>&gt;2000</td>
<td>1992</td>
<td>Rondonia, Brazil (10°58'61°57'W)</td>
<td>Grace et al. 1996</td>
</tr>
</tbody>
</table>

Peak LAIe refers to the seasonal maximum effective LAI, the one-sided leaf area index (m² m⁻¹) without adjustment for leaf clumping (see Chen et al. 1997). MAT is the mean annual air temperature (°C).
Figure 3.1. Distribution of study sites with respect to mean annual temperature and precipitation.
Datasets and Methods

The model was applied in eight ecosystems (Table 3.1) from contrasting environments. These sites included two boreal forests, a sub-boreal coniferous forest, a temperate mixed deciduous forest, a temperate C$_3$/C$_4$ grassland, a tropical C$_3$/C$_4$ savannah, and a tropical forest (Figure 3.1). Seasonal variation in NEE for each site is shown in Figure 3.2. Measurements of incident photosynthetically active radiation (PAR) and air temperature ($T_{air}$) were made at each site. Measurements of canopy light absorptance ($f_{APAR}$) and methods for filling data gaps in light and temperature are described in Chapter II. Estimates of gross ecosystem CO$_2$ exchange (GEE) were derived from eddy covariance measurements of net ecosystem CO$_2$ exchange (NEE) for each site, as described in Chapter II.

Data at all sites except NSA-FEN was used only if the friction velocity ($u_l$) exceeded 0.15 m s$^{-1}$ and PAR>0 µmol m$^{-2}$ s$^{-1}$. At fen site, $u_l$ was not available so data was used only if the windspeed ($U$) exceeded 0.5 m s$^{-1}$. Further, at the ABRACOS site, all data for which the absolute value of the storage flux ($F_{storage}$) exceeded 10 µmol m$^{-2}$ s$^{-1}$ was not used (Grace et al. 1996). It should be noted that, in contrast to the typical micrometeorological sign convention, a positive CO$_2$ flux indicates uptake by the ecosystem.

The importance of photo-acclimation to the overall prediction of canopy photosynthesis throughout the growing season was examined by running the model using both temporally dynamic and temporally-static photosynthetic capacities. Time-invariant capacities and temperature optima were assigned to each site based on the values for the corresponding vegetation type in the SiB2 model (Sellers et al. 1996) as summarized in Table 3.4. As $V_{max0}$ represents the maximum carboxylation rate of a leaf at the top of the canopy, this value was scaled to a whole-canopy rate using Equation 3.18. Photosynthetic capacity ($P_{cmax}$) was derived from canopy $V_{max}$ ($V_{cmax}$) by inverting the biochemical model of photosynthesis (Collatz et al. 1991, 1992):

$$P_{cmax,C3} = \frac{V_{cmax}(c_i-\Gamma)/(c_i+K_c[1+O/K_o])}{(3.1)}$$

$$P_{cmax,C4} = V_{cmax} \quad (3.2)$$
Figure 3.2. Measured net ecosystem exchange (NEE).
where $c_i$ is the CO$_2$ concentration ($\mu$mol mol$^{-1}$) inside the leaf ($\sim$0.7$c_a$), $\Gamma$ is the CO$_2$ compensation point ($\mu$mol mol$^{-1}$), $O_i$ is O$_2$ concentration (20900 Pa) inside the leaf and $K_c$ and $K_o$ are Michaelis-Menten constants (Collatz et al. 1991, 1992):

$$K_c = (30)2.1(\frac{T}{25})^{10}$$

(3.3)

$$K_o = (30000)1.2(\frac{T}{25})^{10}$$

(3.4)

**Model Description**

The model is described in three parts as related to: (1) canopy photosynthetic capacity, canopy photosynthesis, (2) and net ecosystem productivity (Figure 3.3). The last section is further divided into sections describing soil heterotrophic respiration and plant respiration.

**Canopy Photosynthetic Capacity**


Further, it is well established that vertical profiles of photosynthetic capacity and nitrogen generally parallel vertical gradients of light availability (e.g. Field 1983, Hirose and Werger 1987, DeJong and Doyle 1985, Hollinger 1989, Ellsworth and Reich 1993). Theories of resource optimization have been used to describe and predict the depth-distribution of nitrogen and photosynthetic capacity that results from spatial variation in light availability within natural canopies (Field 1983, Hirose and Werger 1987,
Figure 3.3. Model flow and organization. The circles represent model inputs and the rectangles represent the end products of the three sub-models for canopy photosynthetic capacity (1), canopy photosynthesis (2), and net ecosystem productivity (3).

Theories of plant functional convergence (Field 1991) and coordination (Chen et al. 1993) applied to photosynthesis imply that leaves balance investment in $N$ between the ability for electron transport, $W_j$, and carboxylation $W_c$ in such a way that results in the co-limitation between $W_j$ and $W_c$. Such resource allocation minimizes photoinhibition or damage due to the harvesting of excess unusable photons at saturating light levels (Anderson and Osmond 1987, Osmond 1994) and ensures that no one factor, physiological (i.e., $W_j$, $W_c$) or environmental (light, temperature, water, nitrogen, $\text{CO}_2$) is more limiting than any another.

Observations of leaf level gas exchange are in general agreement with this theory. Co-limitation between $W_j$ and $W_c$ has been observed for many leaves (Evans 1989) and their respective capacities ($J_{\text{max}}$ and $V_{\text{cmax}}$) are strongly correlated (Wullschleger 1993). Sun leaves have higher photosynthetic capacities than shade leaves (Boardman 1977, Bjorkman 1981), consistent with minimizing photoinhibition and maintaining co-limitation between $W_j$ and $W_c$ at different levels of light availability. Both leaf nitrogen content and maximum stomatal conductance exhibit linear non-saturating relationships with photosynthetic capacity, reflecting regulated investment in nitrogen and the potential influx of $\text{CO}_2$ to useable levels (Cowan and Farquhar 1977, Ehleringer and Bjorkman 1977, Wong 1979, Field and Mooney 1986).

The overall result is that $P_{\text{max}}$ can be approximated by the point of intersection between the light limited ($P = \alpha \tilde{I}$) and light saturated ($P_{\text{max}}$) rates (Figure 3.4a). At the canopy scale this may be written:

$$P_{\text{cmax}} = \alpha \tilde{I} \quad (3.5)$$
Figure 3.4. Figure 2.2. Model relationships between photosynthesis and light (a), relative photosynthesis and temperature (b), relative photosynthesis and VPD (c), quantum yield and temperature (d), and relative photosynthetic capacity and relative plant water status (e).
Table 3.2. Canopy photosynthesis model equations and parameters.

<table>
<thead>
<tr>
<th>No.</th>
<th>Equation or Parameter</th>
<th>Definition</th>
</tr>
</thead>
<tbody>
<tr>
<td>(1)</td>
<td>( S = 2600(0.57(T-25)/10) )</td>
<td>specificity of Rubisco for CO(_2) relative to O(_2)</td>
</tr>
<tr>
<td>(2)</td>
<td>( \Gamma = O_i/(2SP) )</td>
<td>CO(_2) compensation point ((\mu)mol m(^{-2})s(^{-1}))</td>
</tr>
<tr>
<td>(3)</td>
<td>&quot; ( c_3 = 0.08(0.7c_i \Gamma/(0.7c_i+2\Gamma))f_w f_{rew} )</td>
<td>maximum ( c_3 ) quantum yield ((\mu)mol m(^{-1}))</td>
</tr>
<tr>
<td>(4)</td>
<td>&quot; ( c_4 = 0.06f_w f_{rew} )</td>
<td>maximum ( c_4 ) quantum yield ((\mu)mol m(^{-1}))</td>
</tr>
<tr>
<td>(5)</td>
<td>&quot; ( = (f_{c3})c_3 + (1-f_{c3})c_4 )</td>
<td>optimal quantum yield ((\mu)mol m(^{-1}))</td>
</tr>
<tr>
<td>(6)</td>
<td>( I = \text{PAR} f_{APAR} )</td>
<td>canopy absorbed PAR ((\mu)mol m(^{-2})s(^{-1}))</td>
</tr>
<tr>
<td>(7)</td>
<td>( P_{\text{can}}=\overline{I} )</td>
<td>canopy photosynthetic capacity ((\mu)mol m(^{-2})s(^{-1}))</td>
</tr>
<tr>
<td>(8)</td>
<td>( P_i=(1+P_{\text{can}}-1/(1+P_{\text{can}}))P_c )</td>
<td>canopy light response ((\mu)mol m(^{-2})s(^{-1}))</td>
</tr>
<tr>
<td>(9)</td>
<td>( P_c=\text{PAR} f_{T} f_{D} )</td>
<td>canopy photosynthesis ((\mu)mol m(^{-2})s(^{-1}))</td>
</tr>
<tr>
<td>(10)</td>
<td>( f_{rew} = 1.1814/(1+\exp[0.2(T_{rew}-10-T)])/(1+\exp[0.3(T_{rew}-10-T)]) )</td>
<td>temperature dependence of photosynthetic capacity</td>
</tr>
<tr>
<td>(11)</td>
<td>( f_c = 1.1814/(1+\exp[0.2(T_{rew}-10-T)])/(1+\exp[0.3(T_{rew}-10-T)]) )</td>
<td>temperature dependence of photosynthesis (-)</td>
</tr>
<tr>
<td>(12)</td>
<td>( f_{c}=1.1814/(1+\exp[1.3(VPD)]) )</td>
<td>VPD dependence of photosynthesis (-)</td>
</tr>
<tr>
<td>(13)</td>
<td>( f_{w}(\Gamma) f_{w}(1-\Gamma) f_{0} ) if ( Hr=1300 ) else ( f_{w}=f_{w} )</td>
<td>plant water stress function (-)</td>
</tr>
<tr>
<td>(14)</td>
<td>( I = (T) I_{i} + (1-T) I_{i} ) if ( I&gt;0 ) else ( I=I_{i} )</td>
<td>running mean incident PAR ((\mu)mol m(^{-2})s(^{-1}))</td>
</tr>
<tr>
<td>(15)</td>
<td>( T = (T) T_{i} + (1-T) T_{rew} ) if ( \text{PAR}&gt;0 ) else ( T=T_{rew} )</td>
<td>running mean daytime temperature (EC)</td>
</tr>
<tr>
<td>(16)</td>
<td>( T=\exp(-t) )</td>
<td>running mean weighting coefficient</td>
</tr>
</tbody>
</table>
where $P_{c_{\text{max}}}$ is the canopy photosynthetic capacity, $\bar{\alpha}$ is the canopy quantum yield and $\bar{I}$ is the time-averaged irradiance absorbed by the green fraction of the canopy (Table 3.2). This method provides the means to predict both the magnitude of photosynthetic capacity and its seasonal variation simply from the time-series of light, temperature, and $f_{\text{APAR}}$. This approach was previously applied and tested at the same sites used here (Chapter II).

**Canopy Photosynthesis**

Actual rates of canopy photosynthesis were calculated by reducing canopy photosynthetic capacity as a result of environmental constraints (Table 3.2):

$$P_c = P_c(I)f_Tf_D \tag{3.6}$$

where $P_c(I)$ is the unstressed rate of photosynthesis at a given irradiance (Table 3.2) and $f_T$ and $f_D$ are empirical constraints related to the effects of air temperature and moisture (Figure 3.4). Equation 3.6 is based on the 'big-leaf' concept (e.g. Sellers et al. 1992). If all leaves optimally acclimate then every leaf in a canopy should photosynthesize in concert and the transition from light-limitation to light-saturation will occur simultaneously among all leaves (Farquhar 1989, Field 1991, Terashima and Hikosaka 1995). Under these conditions, canopy photosynthesis can be modeled as the rate of an individual leaf but with the leaf area of an entire canopy.

Big-leaf assumptions are likely to breakdown given the instantaneous variations in sunlight that typically occur in a canopy as a result of diurnal changes in solar elevation and cloud cover, particularly with respect to gaps in the canopy (Terashima and Hikosaka 1995, DePury and Farquhar 1997). In addition to the fact that canopies are not evenly illuminated at instantaneous timescales, leaves may not fully acclimation to their local light environments. Under such conditions the non-linear nature of light response curves can invalidate big leaf approximations (Wang et al. 1998).

Multi-layer models are not subject to these potential problems but their complexity makes their application difficult. As noted by Raupach and Finnigan (1988), single-layer models are incorrect but useful, whereas multi-layer models are correct but often difficult to employ. As a compromise between
these two extremes, DePury and Farquhar (1998) and Wang et al. (1998) have extended the two-layer “sun-shade” model of Norman (1979) to include aspects of optimal nitrogen distribution (Field 1983) and coupling between stomatal conductance and photosynthesis (Ball 1988).

The principle variables in sun/shade models are fairly conservative such that they can be applied without considerable complexity beyond that of big-leaf models (DePury and Farquhar 1998). Assuming there is always an equal amount of leaf area exposed normal to sunlight (spherical leaf angle distribution), only a few key variables are required (Norman 1979). In more complex treatments (DePury and Farquhar 1998, Wang et al. 1998) several leaf and canopy optical properties must be specified including scattering, reflectance, and extinction coefficients to direct and diffuse PAR. These parameters are fairly conservative among most plants (Sellers et al. 1996) such that they should not impose significant constraints to the global application of sun/shade models.

Despite these recent advances, sun/shade models -- like big-leaf models-- still require an empirical curvature parameter describing the non-linear response of photosynthesis (or electron transport) to absorbed irradiance. Further, contrary to criticisms, many studies have found that big-leaf models are adequate for describing instantaneous ecosystem scale photosynthesis (Amthor et al. 1994, Lloyd et al. 1995, Hanan et al. 1998, Hollinger et al. 1999). Given the relative simplicity and proven success of big-leaf models, in addition to the inability to prescribe the canopy light response from first principles without detailed knowledge of foliar biochemistry (e.g. Kull and Kruijt et al. 1998), the big-leaf approach was used here.

**Canopy Quantum Yield.** Canopy quantum yield was assumed to equal that of individual leaves and was determined differently for C₃ and C₄ plants (Ehleringer and Bjorkman 1978, Collatz et al. 1998) (Figure 3.4d). Maximum canopy quantum yield was constrained as was photosynthetic capacity (Table 3.2). This assumes the efficiency of electron transport is inhibited similarly to carboxylation capacity (i.e. \( P_{\text{cmax}} \)).

**Temperature Effects.** The temperature to which the vegetation is adapted (\( T_{\text{opt}} \)) was assumed equal to the mean daytime air temperature, \( \bar{T} \), calculated as the 5-day running mean (Table 3.2) at the
time of the seasonal maximum light absorptance ($f_{\text{APAR}}$). For those sites where $f_{\text{APAR}}$ did not vary (e.g. sites with evergreen vegetation), it was assumed that the plants were adapted to their local thermal climate such that $T_{\text{opt}}$ was set equal to the annual maximum $\bar{T}$.

In this fashion, $T_{\text{opt}}$ represents a genotypic temperature optimum and characterizes a temperature response function ($f_{T_{\text{opt}}}$, see Table 3.2) which defines the upper limit to capacity for photosynthesis at a given temperature. The genotypic temperature optimum was distinguished from the phenotypic temperature optimum which changed with the mean daytime air temperature ($\bar{T}$). This temperature of acclimation due to phenotypic plasticity characterized a temperature response function ($f_{T}$, see Table 3.2) which defined the upper limit to actual photosynthesis at a given temperature. Thus, although a plant may be acclimated to the recent daytime air temperature ($\bar{T}$) and thus operating near its phenotypic optimum for most of the day, its capacity for photosynthesis may be relatively low if the phenotypic optimum was below or above the genotypic optimum ($T_{\text{opt}}$).

**Stomatal Limitations.** The response of photosynthesis to VPD-related effects ($f_{D}$, see Table 3.2), was described in Chapter II. Briefly, stomatal closure was induced above a VPD of 1 kPa with an exponential decline in stomatal conductance between 1 and 6 kPa (Figure 3.4c). This relative stomatal conductance function, $f_{D}$, was applied directly to photosynthesis because it was assumed that photosynthesis varied linearly with stomatal conductance. This assumption is strictly valid only during non-stressful conditions (Wong et al. 1979) but was employed because it is both simple and robust.

**Plant Water Stress.** The moisture status of the plant ($f_{W}$) was assumed to affect photosynthetic capacity directly (Figure 3.4e and Table 3.2) and was represented by the 5-day running mean of relative midday stomatal conductance:

$$f_{W} = f_{D,\text{midday}}$$

This assumes that persistent atmospheric drought occurs concurrently with persistent stomatal closure which only occurs when the plant is water stressed (Figure 3.5). This may be valid as long as there is feedback between transpiration and VPD. High VPD can induce low stomatal conductance ($g$) (Figure
Figure 3.5. Interrelationships among soil, plant, and atmospheric moisture status.

Assuming (1) plants maintain a balance between transpirational demand and soil moisture availability, then leaf area will decline with soil drought. Before this happens, plant water status will decrease as will atmospheric moisture, assuming (2) feedback and accommodation between transpiration and VPD.
3.4c), leading to low rates of transpiration ($E$ where $E=gVPD$). For a given increase in VPD, there is a linear increase in transpiration while there can be an exponential decrease in stomatal conductance (Figure 3.4c). Such accommodation between plant and atmospheric moisture is likely to occur only during midday hours when the canopy and atmospheric boundary layers are convective and well mixed (Monteith 1995). For further description of this parameterization, see Chapter II.

**Net Ecosystem Productivity**

Net ecosystem productivity (NEP) was calculated as the difference between CO$_2$ uptake by canopy gross photosynthesis ($P_c$) and CO$_2$ loss by plant ($R_p$) and soil heterotrophic respiration ($R_H$) (Figure 3.3):

$$\text{NEP} = P_c - R_p - R_H$$  \hspace{1cm} (3.8)

Canopy gross photosynthesis was described above and plant and soil respiration are described below. The calculation of soil temperature and moisture and their respective effects on soil respiration are described below as well. Equations related to prediction of net ecosystem productivity are summarized in Table 3.3.

**Plant Respiration.** Dewar (1996) extended the concept of photosynthetic nitrogen use efficiency (Field 1983) to the whole plant and proposed that for a given APAR, net primary productivity (NPP) has a maximum value with respect to plant nitrogen content. Nitrogen ($N$) is a strong determinant of both photosynthetic capacity (e.g. Field and Mooney 1986, Evans 1989) and maintenance respiration (Jones et al. 1978, Merino et al. 1982, McCree 1983, Waring et al. 1985, Irving and Silsbury 1987, Ryan 1991, Ryan 1995). The majority of plant nitrogen resides in proteins of which the replacement and repair accounts for approximately 60% of total maintenance respiration (Penning de Vries 1975).

As the nitrogen content of a canopy ($N_c$) increases, both the capacity for photosynthesis and the intrinsic rate of maintenance respiration increase. The optimum canopy nitrogen content is that which provides the maximum net carbon gain or net primary productivity (NPP), or the greatest difference between photosynthesis and respiration. In economic terms, the return on nitrogen investments theoretically diminishes for a leaf with increasing nitrogen invested (Field 1991) and there exists a point
Table 3.3. Net ecosystem productivity model equations and parameters.

<table>
<thead>
<tr>
<th>No.</th>
<th>Equation or Parameter</th>
<th>Definition</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>NEP = $P_c - R_p - R_H$</td>
<td>net ecosystem productivity ($\mu$mol m$^{-2}$ s$^{-1}$)</td>
</tr>
<tr>
<td>2</td>
<td>$R_T = 2^{7.2 T_{air}} T_{air} (1 + \exp(0.3(T_{air} - 10 - T_{air}))$</td>
<td>temperature dependence of maintenance respiration</td>
</tr>
<tr>
<td>3</td>
<td>$R_g = (1 - Y_g) \int_0^{t_{24}} (P_c - R_{m,inst}) dt$</td>
<td>daily growth respiration ($\mu$mol m$^{-2}$ d$^{-1}$)</td>
</tr>
<tr>
<td>4</td>
<td>$R_m = \int_0^{t_{24}} (0.34 P_{cmax} t / T^{0.24}) R_T f_W dt$</td>
<td>daily maintenance respiration ($\mu$mol m$^{-2}$ d$^{-1}$)</td>
</tr>
<tr>
<td>5</td>
<td>$R_{p,inst} \approx R_{p,inst} = (R_g + R_m) / t_{24}$</td>
<td>instantaneous maintenance respiration ($\mu$mol m$^{-2}$ s$^{-1}$)</td>
</tr>
<tr>
<td>6</td>
<td>$A_{max} = A_{cmax} (1 - t_{PAR}) / k_{PAR}$</td>
<td>maximum leaf assimilation rate ($\mu$mol m$^{-2}$ s$^{-1}$)</td>
</tr>
<tr>
<td>7</td>
<td>$A_{cmax} = P_{cmax} - (0.11 P_{cmax})^2 (T_{air} - T_{min}) / 10$</td>
<td>maximum canopy assimilation rate ($\mu$mol m$^{-2}$ s$^{-1}$)</td>
</tr>
<tr>
<td>8</td>
<td>$SOC = \ln(A_{max} / 50) / \ln(0.999927)$</td>
<td>soil organic carbon (g m$^{-2}$)</td>
</tr>
<tr>
<td>9</td>
<td>$L_{SO20} = (0.12775) 2.4^{20}$</td>
<td>soil carbon turnover time at 20°C (years)</td>
</tr>
<tr>
<td>10</td>
<td>$J_{L,0.1} = 12\exp(0.0954 A_{max})$</td>
<td>litter turnover time at 20°C (years)</td>
</tr>
<tr>
<td>11</td>
<td>$R_{0,20} = f_{c,0.00264} (0.55L_{L,20} + 0.55SOC/10^{20})$</td>
<td>soil heterotrophic respiration at 20°C ($\mu$mol m$^{-2}$ s$^{-1}$)</td>
</tr>
<tr>
<td>12</td>
<td>$A_{20} = R_{0,20} / \exp(-308.56[T_{air} + 46.02])$</td>
<td>Lloyd and Taylor coefficient</td>
</tr>
<tr>
<td>13</td>
<td>$R_{H,20} = f_{SW} f_{APAR} exp(308.56[T_{air} + 46.02]) / (1 + \exp(T_{air} - 40))$</td>
<td>soil heterotrophic respiration ($\mu$mol m$^{-2}$ s$^{-1}$)</td>
</tr>
<tr>
<td>14</td>
<td>$f_{SW} = f_{APAR}$</td>
<td>soil moisture stress function (-)</td>
</tr>
<tr>
<td>15</td>
<td>$f_{APAR} = f_{APAR}(f_{APAR, max}, f_{APAR, 0})$ if JD &lt; JD@ then $f_{APAR, max}$ else $f_{APAR} = 1$</td>
<td>normalized $f_{APAR}$ (-)</td>
</tr>
<tr>
<td>16</td>
<td>$T_{soil} = (T_{fsw} T_{max} + (1 - T_{fsw}) T_{max}) / T_{max}$ if $T_{air} &gt; 0$</td>
<td>time-averaged soil temperature (°C)</td>
</tr>
<tr>
<td>17</td>
<td>$T_{soil} = 0.1 (T_{fsw} / T_{max} + (1 - T_{fsw}) / T_{max})$ if $T_{air} &gt; 0$</td>
<td>time-averaged soil temperature (°C)</td>
</tr>
<tr>
<td>18</td>
<td>$T_{air} = T_{soil} + 0.5 (T_{max} - T_{min}) (1 - f_{fsw}) \cos(2\pi(t-1600)/2400)$</td>
<td>soil temperature (°C)</td>
</tr>
</tbody>
</table>
(optimal $N$) where further increase in $N$ will provide no further increase in net assimilation ($\partial A/\partial N=0$). This argument can be applied to canopy nitrogen ($N_c$) and whole plant NPP, that is, there exists a point (optimal $N_c$) where further increase in $N_c$ will provide no further increase in net carbon gain ($\partial \text{NPP}/\partial N_c=0$). The critical assumption here is that canopy nitrogen varies in proportion with whole plant nitrogen. This appears to be a reasonable assumption for most plants (Dewar 1996). An analogous argument can be made by replacing $N_c$ with canopy photosynthetic capacity ($P_{c\text{max}}$) because $N_c$ varies in proportion with $P_{c\text{max}}$. As such, optimal $P_{c\text{max}}$ is that which satisfies the constraint, $\partial \text{NPP}/\partial P_{c\text{max}}=0$.

Expressing instantaneous rates of both canopy gross photosynthesis ($P_c$) and maintenance respiration ($R_{m,\text{inst}}$) as functions of $P_{c\text{max}}$:

$$P_c = \frac{(\alpha I + P_{c\text{max}} - \{(\alpha I + P_{c\text{max}})^2 - 4\alpha I P_{c\text{max}}\theta\}^{0.5})}{(2\theta)} \quad (3.9)$$

$$R_{m,\text{inst}} = rP_{c\text{max}} \quad (3.10)$$

Where $\theta$ is an empirical curvature parameter (0.9), $I$ is the absorbed irradiance ($I = f_{\text{APAR}}$ PAR), and $r$ is the ratio of maintenance respiration to $P_{c\text{max}}$. Net primary productivity may be expressed:

$$\text{NPP} = Y_g (\int_0^{t_d} (\alpha I + P_{c\text{max}} - \{(\alpha I + P_{c\text{max}})^2 - 4\alpha I P_{c\text{max}}\theta\}^{0.5})/(2\theta) \, dt - \int_0^{t_d} rP_{c\text{max}} \, dt) \quad (3.11)$$

where $Y_g$ is the proportion of assimilate not lost as growth respiration and $t_d$ is daylength (s). Differentiation of the Equation 3.11 with respect to $P_{c\text{max}}$ and setting $\partial \text{NPP}/\partial P_{c\text{max}}=0$ (the optimality constraint) results in an expression with two unknowns, $P_{c\text{max}}$ and $r$. Thus, for every value of $P_{c\text{max}}$ there exists a unique value of $r$ which satisfies the condition $\partial \text{NPP}/\partial P_{c\text{max}}=0$. Given the complexity of differentiating Equation 3.11, numerical integration was performed with the constraint that NPP is maximized for a given $P_{c\text{max}}$ by allowing $r$ to vary. Assuming a sinusoidal variation in PAR over the course of a day with average irradiance equal to 71% of the maximum irradiance (Running and Coughlan 1988), the following relationship was found:

$$r = 0.34 \frac{t_d}{t_{24}} \quad (3.12)$$
where $t_{24}$ is the time in one day (86400s). Thus, for an average day with 12 hours of sunlight ($t_d=12$), the optimal instantaneous maintenance respiration rate is $0.17P_{\text{cmax}}$ or 17% of canopy photosynthetic capacity.

The optimal instantaneous maintenance respiration rate, $R_{m,\text{inst}}$, was adjusted for the effects of temperature and plant water status. The temperature effect ($R_T$) was represented by an exponential function with a $Q_{10}$ of 2 and an upper temperature limit 10°C above the photosynthetic temperature optimum ($\bar{T}$):

$$R_T = 2^{[(T_{\text{air}} - \bar{T})/10](1+\exp[0.3(T_{\text{air}} - 10 - \bar{T})])}$$

(3.13)

In addition, it was assumed that respiration, along with all physiological activity, decreased during periods of water stress, the latter represented by $f_W$. In summary, instantaneous maintenance respiration ($R_{m,\text{inst}}$) was determined as:

$$R_{m,\text{inst}} = (0.34P_{\text{cmax}}t_d/t_{24})R_T f_W$$

(3.14)

Growth respiration ($R_g$) was estimated as a fraction $(1-Y_g)$ of the difference between daily total photosynthesis and maintenance respiration (Jarvis and Leverenz 1983):

$$R_g = (1-Y_g) \int_0^{t_{24}} (P_c - R_{m,\text{inst}}) \, dt$$

(3.15)

Thus, growth respiration could only be calculated at a daily time step ($R_g$ cannot be calculated correctly at using Equation 3.15 when $P_c$ is zero at night), although photosynthesis and maintenance respiration could be calculated at an instantaneous time step. In order to estimate an instantaneous rate of whole plant respiration ($R_{p,\text{inst}}$) consistent with the time interval of eddy covariance measurements, an average instantaneous rate ($\bar{R}_{p,\text{inst}}$) was determined by summing instantaneous $P_c$ and $R_{m,\text{inst}}$ over the whole day, solving for $R_g$ using Equation 3.15, and dividing by the time in one day:

$$R_{p,\text{inst}} \approx \bar{R}_{p,\text{inst}} = (R_g + R_m)/t_{24}$$

(3.16)

For lack of a better method, the instantaneous rate of whole plant respiration was thus held constant over the entire day with a new value calculated each day.
Soil Heterotrophic Respiration. Woodward and Smith (1994) provide evidence indicating that rates of plant nitrogen uptake are not only indicative of leaf photosynthetic capacity, but also reflect levels of soil nitrogen availability and soil fertility in general. As leaf level net assimilation capacity ($A_{\text{max}}$) decreases, plants increasingly rely on organic sources of nitrogen and soil organic carbon content generally increase. This is consistent with decreased nitrogen mineralization rates and increased soil carbon turnover times as a result of low microbial productivity in low productivity ecosystems (Vitousek 1982). If accommodation between plant and soil metabolism eventually occurs, $A_{\text{max}}$ should provide an indication of soil organic carbon (SOC) content (Woodward and Smith 1994):

$$SOC = \ln(A_{\text{max}}/50)/\ln(0.999927)$$  \hspace{1cm} (3.17)

where $A_{\text{max}}$ and $SOC$ have units of $\mu$mol CO$_2$ m$^{-2}$ s$^{-1}$ and gC m$^{-2}$, respectively. Assuming that Equation 3.17 is based on measurements of sunlit leaves near the top of the canopy, $A_{\text{max}}$ was estimated by assuming an optimal distribution of photosynthetic capacity with depth in a canopy (Sellers et al. 1992). That is, vertical gradients of $A_{\text{max}}$ parallel vertical gradients of light transmittance such that the whole canopy assimilation capacity $A_{\text{cmax}}$ can be related to the capacity of a sunlit leaf at the top of the canopy (Sellers et al. 1992):

$$A_{\text{max}} = A_{\text{cmax}}(1-\bar{\tau}_{\text{PAR}})/\bar{k}_{\text{PAR}}$$  \hspace{1cm} (3.18)

where $\bar{\tau}_{\text{PAR}}$ is the time-averaged whole canopy PAR transmittance (note $\bar{\tau}_{\text{PAR}} = 1-f_{\text{IPAR}}$) and $\bar{k}_{\text{PAR}}$ is the time-averaged PAR extinction coefficient (~0.5). Canopy net assimilation capacity, $A_{\text{cmax}}$, was calculated as:

$$A_{\text{cmax}} = P_{\text{cmax}} - (0.11P_{\text{cmax}})2^{(T_{\text{air}}-T)/10}$$  \hspace{1cm} (3.19)

where 0.11 is the fraction of photosynthetic capacity respired as dark respiration (Enriquez et al. 1996).

Based on results from the CENTURY model, Schimel et al. (1994) predicted small variations in the relative distribution of soil carbon among microbial, litter ($L$), and slow and active pools across a wide range of biomes types and mean annual temperatures and soil textures:

$$L=0.1 \text{SOC}$$  \hspace{1cm} (3.20)
Additionally, data presented by Woodward and Smith (1994) was used to relate leaf photosynthetic capacity to leaf litter turnover times (years) at a reference temperature of 20°C:

\[ \tau_{L,20} = 12 \exp(-0.095 A_{\text{max}}) \]  

(3.21)

It was assumed that total litter (leaf + root) has half the nitrogen concentration as leaf litter alone. Using data from Woodward and Smith (1994) relating leaf litter turnover times to C:N ratios indicates that doubling C:N has the effect of increasing turnover times by 66%.

Assuming a constant turnover time for SOC (\(\tau_{\text{SOC}}=0.12775\) years) at a reference temperature of 26°C and an exponential temperature dependence with a \(Q_{10}\) of 2.4 following Hunt et al. (1996), the turnover time (years) adjusted to 20°C was estimated as:

\[ \tau_{\text{SOC},20} = (0.12775) \cdot 2.4^{(20-26)/10} \]

(3.22)

Combining gives the rate of soil heterotrophic respiration (\(\mu\text{mol m}^{-2} s^{-1}\)) at 20°C:

\[ R_{H,20} = f_{c,\text{max}} 0.00264 (0.55 L \tau_{L,20}^{-1} + 0.55 \text{SOC} \tau_{\text{SOC},20}^{-1}) \]

(3.23)

where 0.00264 converts to \(\mu\text{mol m}^{-2} s^{-1}\), 0.55 is the proportion of decomposed C evolved as CO₂, and \(f_{c,\text{max}}\) is the seasonal maximum fractional vegetation cover (assumed equal to \(f_{\text{IPAR}}/0.962\), where 0.962 is the maximum \(f_{\text{IPAR}}\) value of the NDVI/f\(\text{IPAR}\) relationship described in the Appendix, Chapter II). Vegetation cover was included because unvegetated soil was assumed to have too little moisture and/or nutrients to support either plant growth or significant microbial activity. Under ambient conditions, \(R_H\) was adjusted for temperature and moisture effects assuming a temperature dependence described by Lloyd and Taylor (1996) and moisture limitations equal to plant moisture limitations (\(f_{SW}\), see below):

\[ R_H = f_{SW} A_{20} \exp(-308.56/[T_{\text{soil}}+46.02])/(1+\exp[T_{\text{soil}}-40]) \]

(3.24)

where \(f_{SW}\) is the soil moisture stress function (see below) and \(A_{20}\) is the Lloyd and Taylor (1996) coefficient:

\[ A_{20} = R_{H,20}/\exp(-308.56/[20+46.02]) \]

(3.25)

A schematic representation of the soil heterotrophic respiration calculation is shown in Figure 3.6.
Figure 3.6. Carbon and nitrogen interactions between plants and soil assumed in the simplified soil heterotrophic respiration model.
Soil Moisture. While neither soil water content nor plant moisture status was explicitly modeled, it was assumed that a relative change in the canopy leaf area index (LAI) reflected a long-term, time-averaged change in plant water status and hence soil moisture availability (Figure 3.5). Long-term changes in soil moisture availability were assumed related to the relative change in transpiring leaf area ($f_{\text{APAR}}$) assuming plants maintain a balance between transpirational demand and soil moisture availability. In addition, it was assumed that short-term changes in plant water status that occurred faster than changes in LAI could be inferred from the moisture status of the atmosphere (Equation 3.7 and see Chapter II). Thus, at any moment in time, soil moisture availability may be reflected by either changes in plant water status or by changes in $f_{\text{APAR}}$. The soil moisture stress function ($f_{SW}$) was thus calculated as the product of short-term ($f_{W}$) and long-term ($f_{\text{APAR}'}$) effects:

$$f_{SW} = f_{W} f_{\text{APAR}'}$$  \hspace{1cm} (3.26)

where $f_{\text{APAR}'}$ is the current $f_{\text{APAR}}$ value relative to its seasonal maximum:

$$f_{\text{APAR}'} = f_{\text{APAR}} / (f_{\text{APAR,max}} f_{\text{Topt}})$$  \hspace{1cm} (3.27)

Because it is unlikely that a plant will exhibit soil water stress prior to the seasonal peak leaf display, represented by $f_{\text{APAR,max}}$, $f_{\text{APAR}'}$ was set to unity before $f_{\text{APAR,max}}$ occurred. Finally, in order to deduce changes in soil moisture from changes in leaf area, the confounding effects of temperature must first be removed. Towards this end, $f_{\text{APAR}}$ was normalized to $f_{\text{Topt}}$ (Table 3.2) which represented temperature limitations above and below the genotypic temperature optimum ($T_{\text{opt}}$).

Soil Temperature. Soil temperature was assumed to track, on average, local air temperature. This implies that sites with persistently high air temperatures have high soil temperatures (and visa versa). Complicating the picture, the presence of a canopy covering the soil surface will shade and insulate the soil, effectively slowing the rise and fall of soil temperature and increasing its tendency towards the daily minimum air temperature ($T_{\text{min}}$), rather than the maximum. Conversely, in the absence of canopy cover the soil surface temperatures will rise with under direct sunlight and will tend towards the daily maximum air temperature ($T_{\text{max}}$). Soil moisture will have similar effects as canopy cover, slowing temperature
changes with a tendency towards the minimum air temperature as the soil approaches field capacity. Thus, the time-averaged soil temperature may be expressed as somewhere between the two extremes of the $T_{\text{min}}$ and $T_{\text{max}}$:

$$\overline{T_{\text{soil}}} = (f_{\text{fSW}})T_{\text{min}} + (1-f_{\text{fSW}})T_{\text{max}} \quad \text{if } T_{\text{air}}>0^\circ\text{C}$$

(3.28)

where $\overline{T_{\text{soil}}}$ is the daily average near-surface soil temperature ($^\circ\text{C}$), and $f_c$ is the fractional vegetation cover ($f_c=f_{\text{IPAR}}$ see above). Below $0^\circ\text{C}$, the situation is reversed because of the change in the sign convention, that is, soil temperature is assumed to track $T_{\text{max}}$ rather than $T_{\text{min}}$:

$$\overline{T_{\text{soil}}} = 0.1[(f_{\text{fSW}})T_{\text{max}} + (1-f_{\text{fSW}})T_{\text{min}}] \quad \text{if } T_{\text{air}}<0^\circ\text{C}$$

(3.29)

Initial results indicated that wintertime soil temperatures were not strongly influenced by changes in air temperature so $\overline{T_{\text{soil}}}$ was multiplied by 0.1. Presumably, this factor accounts for insulation by snow or ice which dampen temperature fluctuations. Diel variations in soil temperature, which can be large in the absence of vegetation cover and when soil moisture is low, was introduced by assuming the daily time course followed a cosine function:

$$T_{\text{soil}} = \overline{T_{\text{soil}}} + 0.5[(T_{\text{max}}-T_{\text{min}})(1-f_{\text{fSW}})\cos(2\pi[t-1600]/2400)]$$

(3.30)

where $t$ is the time (noon=1200).

**Results and Discussion**

Application and evaluation of the canopy photosynthetic capacity routine is presented and discussed in Chapter II.

**Canopy Photosynthesis**

**Diurnal Variation.** Diurnal variation in modeled and observed canopy photosynthesis, assumed here to be equivalent to gross ecosystem exchange (GEE), is shown in Figure 3.7 for three 1-week periods during early, middle, and late times of the measurement periods at each site. Overall, model predictions
Figure 3.7. Modeled (lines) and observed (symbols) gross ecosystem exchange of CO₂ (GEE) during early, middle and late periods of the measurement periods at each site.
agree well with the observations. However, the model overestimated on Julian Days (JD) 207 and 208 at the boreal northern old black spruce site (NSA-OBS) and underestimated on several days including JD 209 at the temperate coniferous forest, JDs 156, 203, 204, 206, and 210 at temperate deciduous forest, during most of the early period at the temperate grassland site, most of the late period at the tropical savanna, and JD 133 at the tropical rainforest. These discrepancies are indicative of problems with either $f_{\text{APAR}}$ estimation, temperature and PAR gap filling, the derivation of GEE from NEE or model parameterization (e.g. big-leaf approximation, temperature and VPD response functions, and estimates of $P_{\text{cmax}}$ or $T_{\text{opt}}$ etc.). Separation of these various effects is difficult. However, underestimations during the early period in the temperate grassland and during the late period at tropical savanna site are consistent with the underestimations of $P_{\text{cmax}}$ during these times (see Chapter II) implying errors in parameter estimation.

**Functional Responses.** Predicted and observed photosynthesis is plotted with respect to incident PAR in Figure 3.8. For each site, all the data from each 1-week period (early, middle, late) were pooled together. For all but northern boreal forest (NSA-OBS) and the tropical savanna, the big-leaf model appeared to provide good predictions of the canopy light response, as the residuals generally exhibited a weak relationship with incident PAR at most sites ($r^2<0.1, P>0.05$, data not shown). The discrepancies at the boreal forest and tropical savanna likely stem from errors at the $P_{\text{cmax}}$ level which, in turn, could result from errors in $f_{\text{APAR}}$.

Despite differences in canopy architecture, the identical parameterization of the big-leaf model at all sites provided reasonable predictions. For example, the coniferous canopy (Howland) has a relatively high total one-sided leaf area index (~6, Hollinger et al. 1999) with small needle-leaves that presumably scatter light to a greater extent than the more vertically-oriented leaves of the temperate C$_3$/C$_4$ grassland canopy (LAI~3), which allow greater light penetration deep in the canopy at high sun angles. However, consistent with the near-linear response of the grassland canopy, the model overestimated at low light levels and underestimated at high light levels. Knowledge of basic architectural characteristics as related to broad functional vegetation types (e.g. Nemani and Running 1997) may improve the estimation of
Figure 3.8 Predicted and observed photosynthetic light response. Only data from the early, middle, and late periods of the growing season (see Figure 3.4) are shown.
canopy light absorptance (e.g. Myneni et al. 1997) as well as the integration of whole canopy photosynthesis using sun/shade models with functional-group-specific radiation transfer coefficients.

Interestingly, the initial slope of the photosynthetic light response at the grassland was lower as compared to that of the coniferous forest (Figure 3.8). Yet, the maximum photosynthetic rates were higher at the grassland site. There may be trade-offs, related to either canopy architecture or physiology, such that the ability to achieve high photosynthetic rates at high light intensities correlates with lower photosynthetic efficiency at low light intensities. The lower initial slope at the C3/C4 grassland site may have also resulted from higher leaf temperatures which can effectively decrease C3 quantum efficiencies. This effect would not have been captured by the model because leaf temperatures were assumed equal to air temperatures.

Variation in canopy photosynthesis with respect to temperature and VPD appeared to be well predicted by the model based on the fact that the variation in residuals (observed GEE - predicted GEE) appeared to be independent of variations in these factors -- as indicated by low coefficients of determination for regressions between residuals and $T_{air}$ and VPD ($r^2<0.1$ for all sites, $P>0.05$, data not shown). Apparently, the unexplained variation in GEE was unrelated to variations in temperature and VPD and may have been due to inherent variability of the eddy covariance measurements. Models, calibrated or uncalibrated, across all levels of complexity, generally do not explain more than 80% of the variability in half-hourly eddy covariance measurements (e.g. Amthor et al. 1994, Goulden et al. 1997).

**Accuracy.** Consistent with the time series (Figure 3.7) and light response plots (Figure 3.8) there was good overall correspondence between the modeled and observed gross ecosystem exchange (Figure 3.9) for all sites. As expected from the over-predictions of canopy photosynthetic capacity found at the northern boreal forest site (NSA-OBS) (Figure 2.7), the slope of the relationship between modeled and observed GEE is greater than one. At all other sites, the slopes were less than one suggesting a systematic under-estimation of the highest fluxes. Among all sites, the model explained from 74 to 85% of the variability in gross ecosystem exchange.
Figure 3.9. Relationship between model predictions and field observations of gross ecosystem exchange of CO₂.
Table 3.4. Time-invariant parameter values (taken from SiB2, Sellers et al. 1996a) used for ‘without acclimation’ model predictions. $V_{\text{max}0}$ is the maximum Rubisco capacity of a sun leaf at the top of the canopy ($\mu$mol m$^{-2}$ s$^{-1}$). $T_{\text{low}}$ and $T_{\text{high}}$ are temperatures at which photosynthesis is at 50% of its maximum.

<table>
<thead>
<tr>
<th>Site</th>
<th>SiB2 Land Cover Type</th>
<th>$V_{\text{max}0}$</th>
<th>$T_{\text{low}}$</th>
<th>$T_{\text{high}}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Boreal Forest (NSA-OBS)</td>
<td>Needleleaf-evergreen trees</td>
<td>60</td>
<td>5</td>
<td>30</td>
</tr>
<tr>
<td>Boreal Fen</td>
<td>Dwarf trees and shrubs</td>
<td>60</td>
<td>5</td>
<td>30</td>
</tr>
<tr>
<td>Boreal Forest (SSA-OBS)</td>
<td>Needleleaf-evergreen trees</td>
<td>60</td>
<td>5</td>
<td>30</td>
</tr>
<tr>
<td>Temperate Coniferous Forest</td>
<td>Needleleaf-evergreen trees</td>
<td>60</td>
<td>5</td>
<td>30</td>
</tr>
<tr>
<td>Temperate Deciduous Forest</td>
<td>Broadleaf-deciduous trees</td>
<td>100</td>
<td>10</td>
<td>38</td>
</tr>
<tr>
<td>Temperate C$_3$/C$_4$ Grassland</td>
<td>C$_4$ grassland</td>
<td>30</td>
<td>15</td>
<td>40</td>
</tr>
<tr>
<td>Tropical C$_3$/C$_4$ Savanna</td>
<td>C4 groundcover &amp; tall vegetation</td>
<td>30</td>
<td>15</td>
<td>40</td>
</tr>
<tr>
<td>Tropical Rainforest</td>
<td>Broadleaf-evergreen trees</td>
<td>100</td>
<td>15</td>
<td>40</td>
</tr>
</tbody>
</table>
Table 3.5. Comparison of model predictions made with and without acclimation.

<table>
<thead>
<tr>
<th>Site</th>
<th>With Acclimation</th>
<th>Without Acclimation</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$m$</td>
<td>$b$</td>
</tr>
<tr>
<td>Boreal Forest (NSA-OBS)</td>
<td>1.08</td>
<td>0.43</td>
</tr>
<tr>
<td>Boreal Fen</td>
<td>0.69</td>
<td>0.42</td>
</tr>
<tr>
<td>Boreal Forest (SSA-OBS)</td>
<td>0.87</td>
<td>0.72</td>
</tr>
<tr>
<td>Temperate Coniferous Forest</td>
<td>0.83</td>
<td>0.73</td>
</tr>
<tr>
<td>Temperate Deciduous Forest</td>
<td>0.75</td>
<td>0.66</td>
</tr>
<tr>
<td>Temperate C3/C4 Grassland</td>
<td>0.79</td>
<td>2.97</td>
</tr>
<tr>
<td>Tropical C3/C4 Savanna</td>
<td>0.85</td>
<td>0.00</td>
</tr>
<tr>
<td>Tropical Rainforest</td>
<td>0.84</td>
<td>2.39</td>
</tr>
</tbody>
</table>

The cumulative error (tC ha$^{-1}$) is the sum of residuals ($\sum(O_i-P_i)$).
The percentage error ($100\times\sum(O_i-P_i)/\sum O_i$) is given in parentheses.
The variables $m$ and $b$ relate predicted values to those observed ($P<0.05$) such that Predicted=$m$Observed+$b$. 
Importance of Photoacclimation. Parameter values used in the model runs without photosynthetic acclimation are summarized in Table 3.4. The results of the model runs using these values as well as those produced with the acclimation routine are shown in Table 3.5. It should be noted that variation in the amount of leaf area though the growing season will cause the canopy capacity to vary, even though the leaf level rates remain constant. This may be considered a form of (morphological) acclimation if in fact plants regulate the amount of leaf area in tune with favorable growth conditions (Field 1991). Thus, the without-acclimation runs should be interpreted as being as close as possible to every thing else being equal except for variation in physiological status through time.

The performance of the model with and without acclimation as compared to the observed gross ecosystem exchange is summarized in Table 3.5. Overall, the model with acclimation provided better predictions, as indicated by higher $r^2$ values and smaller cumulative errors. Acclimation appeared to account for an additional 0 to 14% of the variability in gross ecosystem exchange. However, the slopes were generally closer to unity for the model without acclimation. Nevertheless, these differences were generally modest and, as such, may imply that photosynthetic acclimation is not crucial for accurate prediction of photosynthesis over the growing season. Further, the model runs without acclimation incorporate a certain degree of seasonal variation in canopy photosynthetic potential through variation in leaf area index ($f_{\text{APAR}}$). Changes in the amount of leaf area may thus be more important to the prediction of canopy photosynthesis than changes in physiological status of the leaves. However, visual inspection of the seasonal time course of predictions and observations (not shown) suggests that the model runs without acclimation did not accurately capture the timing of spring increases and fall declines in gross ecosystem exchange as well as the model with acclimation. Acclimation may provide the greatest benefit during the periods of greatest transition in physiological status, such as spring and fall or during onset and senescence.

The results also imply that canopy photosynthesis can be predicted equally well without any prior knowledge of vegetation type. At a minimum, all that is required is $f_{\text{APAR}}$, incident PAR, and air...
temperature. This provides support for the acclimation model and these three variables as being representative of the fundamental processes which control variation in photosynthesis throughout the growing season and among sites with contrasting vegetation and climate.

**Generality of the Model.** As noted by Aber et al. (1996) and Goulden et al. (1997), most of the variability in gross ecosystem exchange at a particular site can be explained by relatively simple models fit to the observations. Such models thus provide a benchmark against which the relative accuracy or generality of other more sophisticated models may be assessed. Parameter values and overall variance explained by fitting such simple models at each site is summarized in Table 3.6.

The $r^2$ values of the simple calibrated models (Table 3.6) are very similar to those of the model without acclimation (Table 3.5). This is consistent with the fact that both models did not incorporate any form of acclimation. The OPTICAL model (with acclimation) accounted for up to 19% more of the variance in gross ecosystem exchange than the fitted site-specific models. Across all sites the OPTICAL model thus did nearly as well or better than the site-specific models, supporting the notion that the OPTICAL model is a good general model of canopy photosynthesis. Surprisingly, a “global” regression model, based solely on light and temperature, explained 62% of the variation in GEE across all sites. At each site, however, the $r^2$ values for the OPTICAL model exceeded those of the global regression model.

**Net Ecosystem Productivity**

**Soil Temperature.** Seasonal variation in predicted and observed soil temperature is shown in Figure 3.10. Overall, model predictions of the near-surface soil temperature agree reasonably well with the observations taken near 10 cm depth. The magnitude of the predicted soil temperatures also agree closely with observations at all sites except Harvard Forest where the model underestimates in early summer and is consistently low thereafter. This cause of this underestimation is not clear. It appears to be unrelated to concurrent changes in ambient or mean daytime air temperature or $f_{\text{APAR}}$.

The seasonality of soil temperature and much of its variability was accounted for by the model
Table 3.6. Fitted parameter values for site-specific statistical models.

<table>
<thead>
<tr>
<th>Site</th>
<th>GEE₄</th>
<th>K</th>
<th>T₉0</th>
<th>r²</th>
</tr>
</thead>
<tbody>
<tr>
<td>NSA-OBS</td>
<td>14.6</td>
<td>149</td>
<td>19.7</td>
<td>0.76</td>
</tr>
<tr>
<td>NSA-FEN</td>
<td>10.2</td>
<td>247</td>
<td>21.6</td>
<td>0.63</td>
</tr>
<tr>
<td>SSA-OBS</td>
<td>17.3</td>
<td>210</td>
<td>17.8</td>
<td>0.70</td>
</tr>
<tr>
<td>Howland</td>
<td>26.0</td>
<td>206</td>
<td>22.6</td>
<td>0.79</td>
</tr>
<tr>
<td>Harvard Forest</td>
<td>33.0</td>
<td>346</td>
<td>23.5</td>
<td>0.77</td>
</tr>
<tr>
<td>FIFE</td>
<td>&quot;=0.024 mol mol⁻¹, k=0.18 kPa⁻¹</td>
<td>25.0</td>
<td>0.69</td>
<td></td>
</tr>
<tr>
<td>HAPEX-Sahel</td>
<td>28.9</td>
<td>1502</td>
<td>25.7</td>
<td>0.82</td>
</tr>
<tr>
<td>ABRACOS</td>
<td>30.7</td>
<td>543</td>
<td>27.3</td>
<td>0.77</td>
</tr>
<tr>
<td>All Sites</td>
<td>19.6</td>
<td>253</td>
<td>22.5</td>
<td>0.62</td>
</tr>
</tbody>
</table>

GEE was modeled using a rectangular hyperbola constrained at low and high temperatures:

\[
GEE = \frac{GEE_4 I}{(K+I) C(T)}
\]

where \(I\) is incident PAR, \(GEE_4\) is the asymptote (µmol m⁻² s⁻¹), and \(K\) is the light level at half \(GEE_4\) (µmol m⁻² s⁻¹). The temperature modifier \(f(T)\) was calculated as:

\[
f(T) = \frac{1}{1+\exp(0.2[T_{opt}-10-T_{air}])}[1+\exp(0.3[T_{air}-10-T_{opt}])]
\]

where \(T_{opt}\) is the optimal temperature (EC). The temperate grassland site was best modeled with a linear light response and by adding a VPD response:

\[
GEE = \frac{"I C(T) C(VPD)}{1-k VPD}
\]

where " \(\) has units of mol mol⁻¹ and \(f(VPD)=1-kVDP\) with the constant \(k\) in units of kPa⁻¹. For all other sites, VPD generally explained only a small amount of the variation (<1%) in GEE and was not included.
Figure 3.10. Seasonal variation of modeled (line) and observed (symbols) midday soil temperature at 10 centimeter depth.
Figure 3.11. Seasonal variation of modeled soil moisture stress function (a value of 1 equals no stress) and observed soil moisture. The observations are represented by smooth curves fit to the data to facilitate comparison with the model predictions throughout the growing season.
(r²>0.8) except at the sites without complete annual temperature and $f_{\text{APAR}}$ measurements. For example, at the temperate grassland and the tropical savanna sites, only 40 and 26 percent, respectively, of the variation in soil temperature was accounted for by the model. This suggests that the model captures seasonal changes much better than short-term changes and points to the significance of cold periods to the overall r² values.

**Soil Moisture.** The predicted soil water stress function ($f_{SW}$) is shown for the temperate grassland and the tropical savanna sites in Figure 3.11. Also shown are the measurements of extractable soil moisture at these two sites. Seasonal changes in soil moisture appear strongly related to changes in $f_{SW}$, supporting the hypothesis that plant leaf area display, represented by $f_{\text{APAR}}$, and time-averaged midday stomatal conductance, represented by $f_{W}$, are related to soil moisture availability.

**Soil Heterotrophic Respiration.** Seasonal variation in predicted and observed soil heterotrophic respiration is shown in Figure 3.12. The observations were derived from simple temperature dependant models of total (root + microbial) soil respiration obtained from the literature (Table 3.7). These models were fit to either chamber or sub-canopy eddy covariance measurements with the exception of the tropical savanna site, where no measurements were made. At this site, a soil heterotrophic respiration model was calibrated concurrently with a plant respiration model to nighttime above-canopy eddy flux measurements.

Considerable debate exists over the accuracy of both chamber and sub-canopy eddy covariance measurements (Goulden et al. 1996, Lavigne et al. 1997). It is not clear which provides more reasonable measurements at each site thus both are presented when possible. Model predictions agree well with the sub-canopy eddy covariance observations at the temperate coniferous forest (Hollinger et al. 1999) and the temperate deciduous forest (Moore et al. 1996) but generally underestimate chamber measurements by a factor of two. Excluding the tropical savanna, the model captured the seasonality of soil heterotrophic respiration well (Figure 3.12).

**Diurnal Variation.** Diurnal variation in predicted and observed net ecosystem exchange (NEE) for three 1-week periods during early, middle, and late times of the measurement periods at each site is shown in Figure 3.13. Similar to the results for gross ecosystem exchange (Figure 3.7), model predictions...
Figure 3.12. Time series of predicted and observed midday soil heterotrophic respiration. Observations represent temperature dependent models fitted to either chamber or sub-canopy eddy covariance measurements (Table 3.6). Soil heterotrophic respiration was assumed to be 60% of the total CO$_2$ flux (roots + heterotrophs).
Table 3.7. Models used for observed soil heterotrophic respiration in Figure 3.11. Models were fit to measurements of total soil CO$_2$ efflux (roots + heterotrophs) as determined with chambers or by sub-canopy eddy covariance. Soil heterotrophic respiration ($R_H$) was assumed 60% of total soil CO$_2$ efflux (Schimel et al. 1994)

<table>
<thead>
<tr>
<th>Site</th>
<th>Model</th>
<th>Method</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Boreal Forest (NSA-OBS)</td>
<td>$R_H = 0.6 \times (0.6 \exp[0.119 \cdot T_{soil}])$</td>
<td>Chamber</td>
<td>Lavigne et al. 1997</td>
</tr>
</tbody>
</table>
| Boreal Forest (SSA-OBS)     | if 140<JD<195 then $R_H = 0.6(0.8+0.0218[JD-140])2.35^{(T_{soil}-15)/10}$
  if 195<JD<230 then $R_H = 0.6(2+0.0143[JD-195])2.35^{(T_{soil}-15)/10}$
  if 230<JD<270 then $R_H = 0.6(1.5+0.0175[JD-230])2.35^{(T_{soil}-15)/10}$
  if JD>270 then $R_H = 0.6(0.8)2.35^{(T_{soil}-15)/10}$ | Chamber    | Lavigne et al. 1997 |
| Temperate Coniferous Forest | $R_H = 0.6(3^{(T_{soil}-10)/10})$                                     | Eddy Covariance | Hollinger et al. 1999 |
| Temperate Deciduous Forest  | $R_H = 0.6(0.488 \exp[0.1372 \cdot T_{soil}])$
  $R_H = 0.6(2.31[0.0669 \cdot T_{soil}-0.4074])$ | Chamber    | Davidson et al. 1999 |
|                             |                                                                       | Eddy Covariance | Moore et al. 1996   |
| Temperate C$_3$/C$_4$ Grassland | $R_H = 0.6(0.135+0.054LAI) \cdot SW \cdot exp(0.069[T_{soil}-25])$ | Chamber    | Norman et al. 1987  |
| Tropical C$_3$/C$_4$ Savanna | $R_H = 0.6(1.194 \cdot f(T_{soil})f(SW))$
  $f(T_{soil})=exp(0.059[T_{soil}-20])/(1+exp[0.507(T_{soil}-35.8)])$
  $f(SW)=(SW-0.01)/(0.12-0.01)$ | Calibrated Model | Hanan et al. 1997   |
Figure 3.13. Modeled (lines) and measured (symbols) net ecosystem exchange of CO$_2$ (NEE) during early, middle, and late periods of the growing season.
of daytime net ecosystem exchange agree well with observations on most days. The overall patterns of modeled and observed NEE are very similar to the patterns for GEE (Figure 3.7) suggesting little additional error was introduced by the model predictions of plant and soil heterotrophic respiration. For example, the mid-season overestimation of NEE at the northern boreal forest during JDs 207 and 208 is not unlike the overestimation of GEE on these same days (Figure 3.7) which presumably stemmed from overestimation in canopy photosynthetic capacity (Figure 2.7). Similarly, the model underestimation of NEE during the early period at the temperate grassland site (Figure 3.13), was consistent with the underestimation of GEE during this time (Figure 3.7), which in turn was consistent with the underestimation in canopy photosynthetic capacity (Figure 2.7). This pattern is repeated for most of the other days at the other sites.

Across the wide range of sites represented, predicted and observed rates of nighttime net ecosystem exchange agree well except perhaps during the middle period at the temperate deciduous forest and during the middle and late periods at the tropical savanna. The overestimation of nighttime ecosystem respiration at the deciduous forest may be due to an overestimation of plant respiration. Given that nighttime ecosystem respiration is the sum of plant and soil heterotrophic respiration and model predictions of latter appear too low as compared to chamber measurements (Figure 3.12), an overestimation could only result from an overestimation in plant respiration. Similarly, the overestimation of nighttime ecosystem respiration at the savanna site during the middle and late periods (Figure 3.13) may also stem from an overestimation of plant respiration given that model predictions of soil heterotrophic respiration appear too low (Figure 3.12).

Accuracy and Generality. Consistent with the time series plots (Figure 3.13), there was good overall correspondence between the modeled and observed rates of net ecosystem exchange for all sites (Figure 3.14). The correspondence is also very similar to that shown in Figure 3.9 for gross ecosystem exchange. As expected from the over-predictions of canopy photosynthetic capacity found at the northern boreal forest site (Figure 2.7), the slope of the relationship between modeled and observed NEE is greater
Figure 3.14. Relationship between predicted and observed net ecosystem exchange of CO$_2$ (NEE).
Table 3.8. Relationships between predicted and observed NEE shown in Figure 3.13. The slope \((m)\) and intercept \((b)\) relate predicted NEE to observed NEE: Predicted = \(m\)Observed + \(b\). The slope of the relationship between predicted and observed GEE is provided for comparison. The statistical NEE model was identical to the GEE model (Table 3.6) with the exception that an ecosystem respiration constant was subtracted from GEE.

<table>
<thead>
<tr>
<th>Site</th>
<th>Statistical NEE</th>
<th>Modeled NEE</th>
<th>GEE</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>(r^2)</td>
<td>(r^2)</td>
<td>intercept</td>
</tr>
<tr>
<td>Boreal Forest (NSA-OBS)</td>
<td>0.71</td>
<td>0.72</td>
<td>0.33</td>
</tr>
<tr>
<td>Boreal Fen</td>
<td>0.62</td>
<td>0.70</td>
<td>0.01</td>
</tr>
<tr>
<td>Boreal Forest (SSA-OBS)</td>
<td>0.68</td>
<td>0.69</td>
<td>0.34</td>
</tr>
<tr>
<td>Temperate Coniferous Forest</td>
<td>0.70</td>
<td>0.73</td>
<td>0.12</td>
</tr>
<tr>
<td>Temperate Deciduous Forest</td>
<td>0.69</td>
<td>0.66</td>
<td>-0.22</td>
</tr>
<tr>
<td>Temperate C(_3)/C(_4) Grassland</td>
<td>0.74</td>
<td>0.81</td>
<td>1.27</td>
</tr>
<tr>
<td>Tropical C(_3)/C(_4) Savanna</td>
<td>0.81</td>
<td>0.80</td>
<td>-1.38</td>
</tr>
<tr>
<td>Tropical Rainforest</td>
<td>0.80</td>
<td>0.77</td>
<td>0.51</td>
</tr>
</tbody>
</table>
than one. At all other sites, the slopes were less than one and offsets were small, suggesting a systematic underestimation of the highest fluxes.

Across all sites, the model accounted for 66 to 81% of the variability in net ecosystem exchange. These results are summarized in Table 3.8 along with the $r^2$ values for simple models calibrated to measurements from each site. The $r^2$ values of the simple calibrated models are very similar to those of the OPTICAL model (Table 3.8). The fact that the model can provide predictions of net ecosystem exchange comparable to site-calibrated models supports the notion that the OPTICAL model is a good generalized model of net ecosystem exchange.

The slopes of the relationship between modeled and observed NEE are generally lower than the regression slopes relation modeled and observed GEE (Table 3.8). A NEE-slope closer to unity than a GEE-slope implies an improvement in model performance by the addition of plant and soil respiration predictions. Such an improvement could only occur as a result of compensating errors in the estimation of ecosystem respiration (plant + soil respiration). This only occurred at the tropical rainforest site and implies that ecosystem respiration was overestimated, counteracting an underestimation in gross ecosystem exchange (Table 3.8).

**Cumulative Carbon Exchange**

The time course of predicted and observed cumulative gross ecosystem exchange, net ecosystem exchange, and ecosystem respiration over the measurement period at each site is shown in Figure 3.15. In general, the agreement between the magnitude of the predictions and observations is very good, with notable discrepancies (e.g. temperate deciduous forest and tropical savanna) as previously discussed. At all sites, the model appears to track the temporal pattern of carbon exchange very well. In terms of both magnitude and seasonality, the best predictions are consistently for cumulative gross ecosystem exchange. Of the three component fluxes, gross ecosystem exchange involves the least number of assumptions and is the most directly related to $f_{APAR}$ (Field 1991). It should be noted that there are really only two component fluxes predicted by the model as net ecosystem exchange is simply predicted as the difference
Figure 3.15. Time course of predicted (dotted line) and observed (solid line) cumulative net ecosystem exchange (NEE), gross ecosystem exchange (GEE), and ecosystem respiration (Resp).
Figure 3.16. Relationship between cumulative predicted and observed gross photosynthesis (a), ecosystem respiration (b), and net CO$_2$ exchange (c).
between gross ecosystem exchange and ecosystem respiration and any error in ecosystem respiration translates directly into an error in net ecosystem exchange.

The final cumulative values at the end of the measurement period at each site (cumulative values do not necessarily equal annual totals) for each of the component fluxes are shown in Table 3.9 and plotted in Figure 3.16. Despite excellent agreement between model predictions of gross carbon fixation (Figure 3.16a) and ecosystem respiration (Figure 3.16b) across all sites ($r^2>0.98$, slopes=1, intercepts=0, $P>0.05$), the agreement for net carbon exchange is not as good. The regression slope between modeled and observed NEE was, however, not significantly different from one (Figure 3.16c). The modest errors in gross photosynthesis and ecosystem respiration are in fact large relative to the magnitude of net ecosystem exchange. As net ecosystem exchange is the small difference between two large fluxes (gross photosynthesis and ecosystem respiration), it is inherently difficult to predict. Nevertheless, across a range of sites, the OPTICAL model should thus provide reasonable estimates of gross and net ecosystem exchange.

The model predictions as shown in Figures 3.14 and 3.16 suggest good overall agreement with the observations, particularly with respect to $r^2$ values and regression statistics. However, as evident from Figure 3.15 and Table 3.9, regression analysis may mask important discrepancies relevant to carbon exchange. For example, the tropical savanna site has a slope of 0.80 (Figure 3.14) similar to that at the southern boreal forest (0.81), temperate coniferous forest (0.83), and temperate grassland (0.79) but has a much greater cumulative error -- 0.31 tons C ha$^{-1}$ or a 97% error, versus <10% error for the other sites. Although the magnitude of the fluxes at the savanna are relatively small and thus inherently more difficult to predict, regression analysis did not reveal the relatively large errors between model predictions and observations. On the other hand, cumulative totals can agree for the wrong reasons, as the cumulative totals could indicate exact agreement but the regression slope could be zero. Models which aim to accurately predict net ecosystem carbon exchange, should thus consider both the cumulative error in addition to regression statistics.

Inherent in the model is a link between ecosystem respiration and canopy photosynthetic
### Table 3.9. Summary of modeled and observed cumulative fluxes.

<table>
<thead>
<tr>
<th>Site</th>
<th>NEE (tons C ha⁻¹)</th>
<th>GEE (tons C ha⁻¹)</th>
<th>Resp (tons C ha⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Observed</td>
<td>Modeled</td>
<td>Observed</td>
</tr>
<tr>
<td>Boreal Forest (NSA-OBS)</td>
<td>0.81</td>
<td>1.31</td>
<td>4.84</td>
</tr>
<tr>
<td>Boreal Fen</td>
<td>0.86</td>
<td>0.48</td>
<td>2.78</td>
</tr>
<tr>
<td>Boreal Forest (SSA-OBS)</td>
<td>2.21</td>
<td>2.25</td>
<td>6.86</td>
</tr>
<tr>
<td>Temperate Coniferous Forest</td>
<td>2.21</td>
<td>1.87</td>
<td>6.69</td>
</tr>
<tr>
<td>Temperate Deciduous Forest</td>
<td>1.26</td>
<td>0.38</td>
<td>4.79</td>
</tr>
<tr>
<td>Temperate C₃/C₄ Grassland</td>
<td>0.86</td>
<td>0.80</td>
<td>1.49</td>
</tr>
<tr>
<td>Tropical C₃/C₄ Savanna</td>
<td>0.32</td>
<td>0.006</td>
<td>0.75</td>
</tr>
<tr>
<td>Tropical Rainforest</td>
<td>0.32</td>
<td>0.35</td>
<td>0.97</td>
</tr>
</tbody>
</table>
Figure 3.17. Relationship between ecosystem respiration and canopy photosynthesis.
capacity \( R_p \propto P_{\text{cmax}}, R_H \propto P_{\text{cmax}} \), the latter of which is, over time, intrinsically related to gross ecosystem exchange (Field 1991). There is thus an inherent connection in the model between gross ecosystem exchange and ecosystem respiration. This implies a connection not only between plant carbon assimilation and respiration but between plant productivity and soil microbial productivity (Raich and Schlesinger 1992). The data in Table 3.9 support such a relationship, albeit between ecosystem respiration and gross photosynthesis (Figure 3.17). Cumulative ecosystem respiration is, on average, 73% of cumulative gross primary productivity. Across sites, such a relationship may be valid but individual sites clearly do not lie on the 73% line (Figure 3.17). The observations presented in Figure 3.17 merely support the notion that ecosystem respiration generally covaries with gross primary productivity -- not that every site is accumulating carbon.

**Conclusion**

A generalized model of plant-soil-atmosphere CO2 exchange was described and evaluated using half-hourly and hourly eddy covariance measurements of ecosystem CO2 exchange in boreal, temperate, and tropical landscapes.

Canopy photosynthesis was calculated using a 'big-leaf' approach appeared to provide good predictions of canopy gross photosynthesis as there was good overall correspondence between the modeled and observed gross ecosystem exchange for all sites. Despite differences in canopy architecture, the identical parameterization of the big-leaf model at all sites provided reasonable predictions. Apparently, the unexplained variation in canopy gross photosynthesis was unrelated to variations in temperature and VPD and may have been due to inherent variability of the eddy covariance measurements. There appear, however, to be a systematic under-estimation of the highest fluxes. Among all sites, the model explained from 74 to 85% of the variability in gross ecosystem exchange.

The model with photosynthetic acclimation provided better predictions, as indicated by higher \( r^2 \) values and smaller cumulative errors than the model without acclimation. Acclimation appeared to account for an additional 0 to 14% of the variability in gross ecosystem exchange. These differences in
the model predictions, however, were generally modest and, as such, may imply that photosynthetic acclimation is not crucial for accurate prediction of photosynthesis over the growing season. However, visual inspection of the seasonal time course of predictions and observations suggests that the model runs without acclimation did not capture the timing of spring increases and fall declines in gross ecosystem exchange as well as the model with acclimation. Acclimation may provide the greatest benefit during the periods of greatest transition in physiological status, such as in the spring and fall during onset and senescence.

The results also imply that canopy photosynthesis can be predicted well without any prior knowledge of vegetation type. At a minimum, all that is required is $f_{\text{APAR}}$, incident PAR, and air temperature. This provides support for the acclimation model and the three driving variables as being representative of the fundamental processes which control variation in photosynthesis throughout the growing season and among sites with contrasting vegetation and climate. The model with acclimation accounted for up to 19% more of the variance in gross ecosystem exchange as compared to calibrated site-specific models. Across all sites the model thus did nearly as well or better than the site-specific models, supporting the notion that the acclimation model is a good general model of canopy photosynthesis.

Similar to the results for gross ecosystem exchange, model predictions of daytime net ecosystem exchange agree well with observations on most days. The overall patterns of modeled and observed net ecosystem exchange was very similar to the patterns for gross ecosystem exchange suggesting little additional error was introduced by the model predictions of plant and soil heterotrophic respiration. Predicted and observed rates of nighttime net ecosystem exchange agreed well and there was good overall correspondence between the modeled and observed rates of net ecosystem exchange, similar to that found for gross ecosystem exchange. At most sites, the regression slopes relating predictions to observations were less than one and offsets were small, suggesting a systematic underestimation of the highest fluxes. Across all sites, the model accounted for 66 to 81% of the variability in net ecosystem exchange. The $r^2$ values of calibrated site-specific models of net ecosystem exchange were very similar to those of the
OPTICAL model supporting the notion that the OPTICAL model is a good generalized model of net ecosystem exchange.

In general, the agreement between the predictions and observations of cumulative gross ecosystem exchange, net ecosystem exchange, and ecosystem respiration over the measurement period at each site was very good. At all sites, the model appears to track the temporal pattern of carbon exchange very well. In terms of both magnitude and seasonality, the best predictions are consistently for cumulative gross ecosystem exchange. Of the three component fluxes, gross ecosystem exchange involves the least number of assumptions and is the most directly related to \( f_{\text{APAR}} \). Despite excellent agreement between model predictions of gross carbon fixation and ecosystem respiration across all sites \( (r^2>0.98, \text{slopes}=1, \text{intercepts}=0, P>0.05) \), the agreement for net carbon exchange was not as good. The modest errors in gross photosynthesis and ecosystem respiration are in fact large relative to the magnitude of net ecosystem exchange. As net ecosystem exchange is the small difference between two large fluxes (gross photosynthesis and ecosystem respiration), it is inherently difficult to predict. Nevertheless, across a range of sites, the OPTICAL model should thus provide reasonable estimates of gross and net ecosystem exchange.

Inherent in the model is a link between ecosystem respiration and canopy photosynthetic capacity \( (R_p \propto P_{\text{cmax}}, \ R_H \propto P_{\text{cmax}}) \) the latter of which is, over time, intrinsically related to gross ecosystem exchange. The observations support such a relationship, albeit between ecosystem respiration and gross photosynthesis. Cumulative ecosystem respiration was, on average, 73% of cumulative gross primary productivity \( (r^2=0.98, P>0.05) \). Across sites, such a relationship may be valid but individual sites clearly do not all lie on the regression line. The observations merely support the notion that ecosystem respiration generally covaries with gross primary productivity -- not that every site was accumulating carbon.

The model, as described here, can be applied using satellite derived \( f_{\text{APAR}} \) (Myneni et al. 1997, Nemani and Running 1997), \( T_{\text{air}} \) (Prince et al. 1998), and incident PAR (Dye 1992). \( f_{\text{APAR}} \) can be derived from satellite NDVI using, for example, the approach of Myneni which requires knowledge of the functional vegetation type. The latter may be determined with the approach described by Nemani and
Running. This dependence on vegetation type does not nullify the advantage of the classification-independent OPTICAL model. Consistent with the OPTICAL model, the classification approach of Nemani and Running is based entirely on remote sensing observations. More importantly, the use of a vegetation classification for the estimation of parameters in a NDVI-driven $f_{\text{APAR}}$ model is justified because the parameters relating to canopy architecture do not change significantly over time. Further, the use of a vegetation classification to prescribe canopy optical characteristics does not preclude the use of a temporally dynamic model of plant and soil physiological characteristics which are known to vary significantly through time and between members of the same functional group.
### SYMBOLS AND ABBREVIATIONS

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Definition</th>
</tr>
</thead>
<tbody>
<tr>
<td>$A$</td>
<td>leaf net assimilation ($\mu$mol m$^{-2}$ s$^{-1}$)</td>
</tr>
<tr>
<td>$A_{\text{max}}$</td>
<td>maximum canopy net assimilation ($\mu$mol m$^{-2}$ s$^{-1}$)</td>
</tr>
<tr>
<td>$A_{\text{max}}$</td>
<td>maximum leaf net assimilation ($\mu$mol m$^{-2}$ s$^{-1}$)</td>
</tr>
<tr>
<td>$A_{20}$</td>
<td>Lloyd and Taylor coefficient</td>
</tr>
<tr>
<td>$a_0$</td>
<td>Fourier coefficient</td>
</tr>
<tr>
<td>$a_n$</td>
<td>Fourier coefficient</td>
</tr>
<tr>
<td>APAR</td>
<td>absorbed PAR ($\mu$mol m$^{-2}$ s$^{-1}$) (overbar denotes time-average)</td>
</tr>
<tr>
<td>$b_n$</td>
<td>Fourier coefficient</td>
</tr>
<tr>
<td>$c_a$</td>
<td>atmospheric CO$_2$ concentration ($\mu$mol mol$^{-1}$) (overbar denotes time-average)</td>
</tr>
<tr>
<td>$c_i$</td>
<td>CO$_2$ concentration in the leaf ($\mu$mol mol$^{-1}$) (overbar denotes time-average)</td>
</tr>
<tr>
<td>$c_i/c_a$</td>
<td>ratio of $c_i$ to $c_a$ (-) (overbar denotes time-average)</td>
</tr>
<tr>
<td>$E$</td>
<td>rate of transpiration (mol H$_2$O m$^{-2}$ s$^{-1}$)</td>
</tr>
<tr>
<td>$f_{\text{APAR}}$</td>
<td>fraction of incident PAR absorbed by the green fraction of the canopy (-)</td>
</tr>
<tr>
<td>$f_{\text{APAR}}'$</td>
<td>normalized $f_{\text{APAR}}$</td>
</tr>
<tr>
<td>$f_{\text{APAR,}\text{max}}$</td>
<td>annual maximum $f_{\text{APAR}}$</td>
</tr>
<tr>
<td>$f_{\text{IPAR}}$</td>
<td>fraction of incident PAR intercepted by the canopy (-)</td>
</tr>
<tr>
<td>$f_{\text{c,max}}$</td>
<td>maximum fractional vegetation cover (-)</td>
</tr>
<tr>
<td>$f_D$</td>
<td>relative stomatal conductance at ambient VPD (-)</td>
</tr>
<tr>
<td>$f_{\text{D,\text{midday}}}$</td>
<td>time-averaged relative stomatal conductance at midday VPD (-)</td>
</tr>
<tr>
<td>$f_{\text{IPAR}}$</td>
<td>fraction of incident PAR intercepted by the canopy (-)</td>
</tr>
<tr>
<td>$F_{\text{storage}}$</td>
<td>storage flux ($\mu$mol m$^{-2}$ s$^{-1}$)</td>
</tr>
<tr>
<td>$f_T$</td>
<td>relative photosynthesis at the ambient air temperature (-)</td>
</tr>
<tr>
<td>$f_{\text{opt}}$</td>
<td>relative photosynthetic capacity at the optimal temperature (-)</td>
</tr>
<tr>
<td>$f_S$</td>
<td>relative photosynthetic capacity at a given plant moisture status (-)</td>
</tr>
<tr>
<td>$f_{\text{SW}}$</td>
<td>soil water stress function (-)</td>
</tr>
<tr>
<td>$g$</td>
<td>stomatal conductance (mmol H$_2$O m$^{-2}$ s$^{-1}$)</td>
</tr>
<tr>
<td>GEE</td>
<td>gross ecosystem CO$_2$ exchange ($\mu$mol m$^{-2}$ s$^{-1}$)</td>
</tr>
<tr>
<td>GEE$_{\infty}$</td>
<td>Michaelis-Menten asymptote for maximum GEE ($\mu$mol m$^{-2}$ s$^{-1}$)</td>
</tr>
<tr>
<td>GEE$_{\text{max}}$</td>
<td>maximum gross ecosystem CO$_2$ exchange ($\mu$mol m$^{-2}$ s$^{-1}$)</td>
</tr>
<tr>
<td>GPP</td>
<td>gross primary productivity ($\mu$mol m$^{-2}$ s$^{-1}$)</td>
</tr>
<tr>
<td>$I$</td>
<td>incident PAR ($\mu$mol m$^{-2}$ s$^{-1}$) (overbar denotes time-average)</td>
</tr>
<tr>
<td>$I_{\text{opt}}$</td>
<td>optimal incident PAR ($\mu$mol m$^{-2}$ s$^{-1}$)</td>
</tr>
<tr>
<td>$I_{\text{sat}}$</td>
<td>saturating incident PAR ($\mu$mol m$^{-2}$ s$^{-1}$)</td>
</tr>
<tr>
<td>$I_{\text{toa}}$</td>
<td>incident PAR at the top of the atmosphere ($\mu$mol m$^{-2}$ s$^{-1}$)</td>
</tr>
<tr>
<td>JD</td>
<td>Julian Day (January 1 = JD 1)</td>
</tr>
<tr>
<td>$I_{\text{max}}$</td>
<td>electron transport capacity ($\mu$mol e$^{-}$ m$^{-2}$ s$^{-1}$)</td>
</tr>
<tr>
<td>$k$</td>
<td>PAR extinction coefficient (-)</td>
</tr>
<tr>
<td>$\bar{k}_{\text{PAR}}$</td>
<td>time-averaged PAR extinction coefficient (~0.5)</td>
</tr>
<tr>
<td>$K$</td>
<td>Michaelis-Menten half-saturation constant</td>
</tr>
<tr>
<td>$K_c$</td>
<td>Michaelis-Menten constant (overbar denotes time-average)</td>
</tr>
<tr>
<td>$K_m$</td>
<td>Michaelis-Menten constant (overbar denotes time-average)</td>
</tr>
<tr>
<td>$K_o$</td>
<td>Michaelis-Menten constant (overbar denotes time-average)</td>
</tr>
<tr>
<td>$L$</td>
<td>litter carbon (g m$^{-2}$)</td>
</tr>
<tr>
<td>LAI</td>
<td>total one-sided leaf area index (m$^2$ m$^{-2}$)</td>
</tr>
</tbody>
</table>
LAI_e  effective LAI, one-sided leaf area index without correction for clumping (m$^2$ m$^{-2}$)
m fitting parameter
N leaf nitrogen concentration (mg g$^{-1}$)
N_c canopy nitrogen concentration (mg g$^{-1}$)
NDVI Normalized Difference Vegetation Index (-)
NEE net ecosystem CO$_2$ exchange (µmol m$^{-2}$ s$^{-1}$)
NEE$_{night}$ nighttime net ecosystem CO$_2$ exchange (µmol m$^{-2}$ s$^{-1}$)
NEP net ecosystem productivity (µmol m$^{-2}$ s$^{-1}$)
NPP net primary productivity (µmol m$^{-2}$ s$^{-1}$)
O$_i$ oxygen concentration in the leaf (Pa) (overbar denotes time-average)
P rate of photosynthesis (µmol m$^{-2}$ s$^{-1}$)
P_a time-averaged atmospheric pressure (Pa) (overbar denotes time-average)
PAR photosynthetically active radiation (µmol m$^{-2}$ s$^{-1}$) (overbar denotes time-average)
PAR$_{above}$ PAR above the canopy (µmol m$^{-2}$ s$^{-1}$)
PAR$_{below}$ PAR below the canopy (µmol m$^{-2}$ s$^{-1}$)
PAR$_{max}$ daily maximum incident PAR above the canopy (µmol m$^{-2}$ s$^{-1}$)
PAR$_{reflected}$ PAR reflected by the canopy (µmol m$^{-2}$ s$^{-1}$)
P$_c$ canopy photosynthesis (µmol m$^{-2}$ s$^{-1}$)
P$_{c}(I)$ unstressed rate of photosynthesis at a given irradiance (µmol m$^{-2}$ s$^{-1}$)
P$_{cmax}$ canopy photosynthetic capacity (µmol m$^{-2}$ s$^{-1}$)
P$_{max}$ photosynthetic capacity (µmol m$^{-2}$ s$^{-1}$)
r ratio of maintenance respiration to $P_{cmax}$ (-)
$R_{eco}$ ecosystem respiration (µmol m$^{-2}$ s$^{-1}$)
$R_{g}$ growth respiration (µmol m$^{-2}$ d$^{-1}$)
$R_H$ soil heterotrophic respiration (µmol m$^{-2}$ s$^{-1}$)
$R_H,20$ soil heterotrophic respiration (µmol m$^{-2}$ s$^{-1}$) at a reference temperature of 20°C
$R_m$ maintenance respiration (µmol m$^{-2}$ d$^{-1}$)
$R_{m,inst}$ instantaneous plant maintenance respiration (µmol m$^{-2}$ s$^{-1}$)
$r_{NIR}$ near-infrared reflectance (-)
$R_p$ plant respiration (µmol m$^{-2}$ s$^{-1}$)
$R_p,inst$ instantaneous plant respiration (µmol m$^{-2}$ s$^{-1}$) (overbar denotes time-average)
$r_{SW}$ shortwave reflectance (-)
RuBP ribulose bisphosphate
Rubisco ribulose bisphosphate carboxylase-oxygenase
$R_T$ temperature dependence of maintenance respiration (-)
$r_{VIS}$ visible reflectance (-)
$S$ time-averaged specificity of Rubisco for CO$_2$ relative to O$_2$
SOC soil organic carbon (gC m$^{-2}$)
SR Simple Ratio
$t$ time (hours)
t$_{24}$ time in one day (86400 s)
$\overline{T}$ time-averaged air temperature (°C)
$T_{air}$ air temperature (°C)
t$_d$ daylength (s)
$T_{max}$ daily maximum air temperature (°C)
$T_{min}$ daily minimum air temperature (°C)
$T_{night}$ nighttime air temperature (°C)
$T_{opt}$ genotypic temperature optimum (°C)
$T_{soil}$ predicted near-surface soil temperature (°C) (overbar denotes time-average)
\( t_r \)  
  time in radians

\( U \)  
  wind speed (m s\(^{-1}\))

\( u_f \)  
  friction velocity (m s\(^{-1}\))

\( V_{\text{max}} \)  
  carboxylation capacity (\( \mu \text{mol m}^{-2} \text{s}^{-1} \))

\( V_{\text{cmax}} \)  
  canopy carboxylation capacity (\( \mu \text{mol m}^{-2} \text{s}^{-1} \))

\( V_{\text{max0}} \)  
  maximum carboxylation rate of a leaf the top of the canopy (\( \mu \text{mol m}^{-2} \text{s}^{-1} \))

\( \text{VPD} \)  
  saturation vapor pressure deficit (kPa)

\( W_c \)  
  rate of carboxylation (\( \mu \text{mol m}^{-2} \text{s}^{-1} \))

\( W_j \)  
  rate of electron transport (\( \mu \text{mol m}^{-2} \text{s}^{-1} \))

\( X \)  
  filtered value of variable X

\( X_i \)  
  previous filtered value of variable X

\( \overline{X_i} \)  
  \( X_i \) is the value of variable X at time \( i \)

\( Y_g \)  
  proportion of assimilate not lost as growth respiration (-)

\( \alpha \)  
  canopy quantum yield (mol mol\(^{-1}\)) (overbar denotes time-average)

\( \beta_a \)  
  atmospheric transmittance

\( \Delta t \)  
  time interval (days)

\( \Delta T \)  
  diel temperature amplitude (°C)

\( \epsilon_g \)  
  dry matter:radiation quotient for GPP (gC MJ\(^{-1}\))

\( \epsilon_a \)  
  dry matter:radiation quotient for NPP (gC MJ\(^{-1}\))

\( \tau \)  
  time constant (days)

\( \tau_{L,20} \)  
  leaf litter turnover times (years) at a reference temperature of 20°C

\( \tau_{SOC} \)  
  SOC turnover time (years) at a reference temperature of 26°C

\( \tau_{SOC,20} \)  
  SOC turnover time (years) at a reference temperature of 20°C

\( \overline{\tau_{PAR}} \)  
  time-averaged canopy PAR transmittance (-)

\( \Gamma \)  
  CO\(_2\) compensation point (mol mol\(^{-1}\)) (overbar denotes time-average)

\( \theta \)  
  curvature parameter (0.9)

\( \omega \)  
  weighting coefficient (-)
REFERENCES


Baldocchi, DD; Vogel, CA; Hall, B (1997): Seasonal variation of carbon dioxide exchange rates above and below a boreal jack pine forest. Agricultural and Forest Meteorology 83, 147-170.


Box, EO; Holben, BN; Kalb, V (1989): Accuracy of the AVHRR vegetation index as a predictor of biomass, primary productivity and net CO2 flux. Vegetatio 80, 71-89.


Ciais,P; Tans,PP; White,JWC; Trolier,M; Francey,RJ; Berry,JA; Randall,DR; Sellers,PJ;

Collatz,GJ; Ball,LT; Grivet,C; Berry,JA (1991): Physiological and environmental regulation of stomatal conductance, photosynthesis and transpiration: a model that includes a laminar boundary layer. Agricultural and Forest Meteorology 54, 107-136.


Costanza,R; d'Arge,R; de Groot,R; Farber,S; Grasso,M; Hannon,B; Limburg,K; Naeem,S; O'Neill,RV; Paruelo,J; Raskin,RG; Sutton,P; van den Belt,M (1997): The value of the world's ecosystem services and natural capital. Nature 387, 253-260.


Cowan,IR; Farquhar,GD (1977): Stomatal function in relation to leaf
Dang,QL; Margolis,HA; Sy,M; Coyea,MR; Collatz,GJ; Walthall,CL (1997): Profiles of photosynthetically active radiation, nitrogen and photosynthetic capacity in the boreal forest: Implications for scaling from leaf to canopy. J. Geophys. Res. 102(D24), 28,845-28,859.


De Jong,TM; Doyle,JF (1985): Seasonal relationships between leaf nitrogen content (photosynthetic capacity) and leaf canopy light exposure in peach (Prunus perspicata). Plant, Cell, and Environment 8, 701-706.


Dixon,RK; Brown,S; Houghton,RA; Solomon,AM; Trexler,MC; Winsiewski,J (1994): Carbon pools and flux of global forest ecosystems. Science 263, 185-190.


Ellsworth,DS; Reich,PB (1993): Canopy structure and vertical patterns of photosynthesis and related leaf traits in a deciduous forest. Oecologia 96, 169-178.


Fan, S-M; Goulden, ML; Munger, JW; Daube, BC; Bakwin, PS; Wofsy, SC; Amthor, JS; Fitzjararld, DR; Moore, KE; Moore, TR (1995): Environmental controls on the photosynthesis and respiration of a boreal lichen woodland: a growing season of whole-ecosystem exchange measurements by eddy correlation. Oecologia, .

Fan, S; Gloor, M; Mahlman, J; Pacala, S; Sarmiento, J; Takahashi, T; Tans, P (1998): A large terrestrial carbon sink in North America implied by atmospheric and oceanic carbon dioxide data and models. Science 282, 442-446.


Frolking, SE; Bubier, JL; Moore, TR; Ball, T; Bellisario, LM; Bhardwaj, A; Carroll, P; Crill, PM; Lafleur, PM; McCaughey, JM; Roulet, NT; Suyker, AE; Verma, SB; Waddington, JM; Whiting, GJ (1998): Relationship between ecosystem productivity and photosynthetically active radiation for northern peatlands. Global Biogeochem. Cycles 12(1), 115-126.


Goulden, ML; Wofsy, SC; Harden, JW; Trumbore, SE; Crill, PM; Gower, ST; Fries, T; Daube, BC; Fan, S-M; Sutton, DJ; Bazzaz, A; Munger, JW (1998): Sensitivity of boreal forest carbon balance to soil thaw. Science 279, 214-217.
Goulden, ML; Daube, BC; Fan, S-M; Sutton, DJ; Bazza, A; Munger, JW; Wofsy, SC (1997): Physiological responses of a black spruce forest to weather. J. Geophys. Res. 102 (D24), 28,987-28,996.

Goward, SN; Tucker, CJ; Dye, DG (1985): North American vegetation patterns observed with the NOAA-7 advanced very high resolution radiometer. Vegetatio 64, 3-14.


Grace, J; Malhi, Y; Lloyd, J; McIntyre, J; Miranda, A; Meir, P; Miranca, HS (1996): The use of eddy covariance to infer the net carbon dioxide uptake of Brazilian rain forest. Global Change Biology 2, 209-217.


Hollinger, DY; Kelliher, FM; Byers, JN; Hunt, JE; McSevery, TM; Weir, PL (1994): Carbon dioxide exchange between an undisturbed old growth temperate forest and the atmosphere. Ecology 75, 134-150.

Hollinger, DY; Kelliher, FM; Schulze, E-D; Bauer, G; Arneth, A; Byers, JN; Hunt, JE; McSevery, TM; Kobak, KI; Milukova, I; Sogatchev, A; Tatarinov, F; Varlargin, A; Ziegler, W; Vygodskaya, NN (1998): Forest-atmosphere carbon dioxide exchange in eastern Siberia. Agricultural and Forest Meteorology 90, 291-306.


Keller, M; Clark, DA; Clark, DB; Weitz, AM; Veldkamp, E (1996): If a tree falls in the forest... Science 273, 201.


Lloyd, J; Grace, J; Miranda, A.C; Meir, P; Wong, S.C; Miranda, H.S; Wright, I.R; Gash, J.H.C; McIntyre, J (1995): A simple calibrated model of Amazon rainforest productivity based on leaf biochemical properties. Plant, Cell, and Environment 18, 1129-1145.


Moore, KE; Fitjarald, DR; Sakai, RK; Goulden, ML; Munger, JW; Wofsy, SC (1996): Seasonal variation in radiative and turbulent exchange at a deciduous forest in central Massachusetts. J. Appl. Meteor. 35, 122-134.


Phillips, OL; Malhi, Y; Higuchi, N; Laurance, WF; Nunez, PV; Vasquez, M; Laurance, SG; Ferreira, LV; Stern, M; Brown, S; Grace, J (1998): Changes in the carbon balance of tropical forests: Evidence from long-term plots. Science 282, 439-442.


Prince, SD; Goetz, SJ; Dubayah, RO; Czajkowski, KP; Thawley, M (1998): Inference of surface and air temperature, atmospheric precipitable water and vapor pressure deficit using Advanced Very High-Resolution Radiometer satellite observations: Comparison with field observations. Journal of Hydrology 212-213, 230-249.


Reich, PB; Abrams, MD; Ellsworth, DS; Kruger, EL; Tabone, TJ (1990): Fire affects ecophysiology and community dynamics of central Wisconsin oak forest regeneration. Ecology 71, 2179-2190.


Schimel, DS; Braswell, BH; Holland, EA; McKeown, R; Ojima, DS; Painter, TH; Parton, WJ; Townsend, AR (1994): Climatic, edaphic, and biotic controls over carbon and turnover of carbon in soils. Global Biogeochem. Cycles 8, 279-293.


Strebel, DE; Landis, DR; Huemmrich, KF; Meeson, BW (1994): Collected data of the First ISLSCP Field Experiment, Volume 1: Surface observations and non-image data sets. Published on CD-ROM by NASA.


Wessman, CA; Aber, JD; Peterson, DL; Melillo, JM (1988): Remote sensing of canopy chemistry and nitrogen cycling in temperate forest ecosystems. Nature 335, 154-156.


Williams, M; Rastetter, EB; Fernandes, DN; Goulden, ML; Shaver, GR; Johnson, LC (1997): Predicting gross primary productivity in terrestrial ecosystems. Ecol. Appl. 7 (3), 882-894.

Williams, M; Malhi, Y; Nobre, AD; Rastetter, EB; Grace, J; Pereira, MGP (1998): Seasonal variation in net carbon exchange and evapotranspiration in a Brazilian rain forest: A modelling analysis. Plant, Cell, and Environment 21, 953-968.

Wofsy, SC; Goulden, ML; Munger, JW; Fan, SM; Bakwin, PS; et al. (1993): Net exchange of CO2 in a mid-latitude forest. Science 260, 1314-1317.


**Missing References**
Baker et al. 1988
Berry and Bjorkman 1982
Bjorkman et al. 1984
Davis et al. 1963
Demig-Adams et al. 1988
Garcia-Plazaolo et al. 1997
Graham and Running 1984
Grier and Running 1977
Hollinger et al. 1999
Jacobs et al. 1996
Lavigne et al. 1997
Lohammer et al. 1980
Norman 1979
McMichael et al. 1999
Raupach and Finnigan 1988
Reed, 1990
Sellers et al. 1995
Sellin 1999
Sharkey and Badger 1982
Tezara et al. 1998
Von Caemmerer and Farquhar 1984
Waring et al. 1994
Waring and Landsberg 1998
Werner et al. 1999