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Global Net Primary Production: Combining Ecology and Remote Sensing

Christopher B. Field, James T. Randerson,* and Carolyn M. Malmström**

Terrestrial net primary production (NPP) is sensitive to a number of controls, including aspects of climate, topography, soils, plant and microbial characteristics, disturbance, and anthropogenic impacts. Yet, at least at the global scale, models based on very different types and numbers of parameters yield similar results. Part of the reason for this is that the major NPP controls influence each other, resulting, under current conditions, in broad correlations among controls. NPP models that include richer suites of controlling parameters should be more sensitive to conditions that disrupt the broad correlations, but the current paucity of global data limits the power of complex models. Improved data sets will facilitate applications of complex models, but many of the critical data are very difficult to produce, especially for applications dealing with the past or future. It may be possible to overcome some of the challenges of data availability through increased understanding and modeling of ecological processes that adjust plant physiology and architecture in relation to resources. The CASA (Carnegie, Stanford, Ames Approach) model introduced by Potter et al. (1993) and expanded here uses a combination of ecological principles, satellite data, and surface data to predict terrestrial NPP on a monthly time step. CASA calculates NPP as a product of absorbed photosynthetically active radiation, APAR, and an efficiency of radiation use, ε. The underlying postulate is that some of the limitations on NPP appear in each. CASA estimates annual terrestrial NPP to be 48 Pg and the maximum efficiency of PAR utilization (ε) to be 0.39 g C MJ^{-1} PAR. Spatial and temporal variation in APAR is more than fivefold greater than variation in ε.*

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GLOBAL NET PRIMARY PRODUCTION

Terrestrial net primary production (NPP), the time integral of the positive increments to plant biomass, is the central carbon-related variable summarizing the interface between plant and other processes. It describes both the removal of carbon from the atmosphere and the potential delivery of carbon to herbivores, decomposers, or humans interested in food or fiber.

At the global scale, terrestrial NPP is one of the most-modeled ecological parameters, with models that differ markedly in approach and complexity often yielding comparable estimates. Note that similarities at this scale reveal little about a model's ability to estimate local or regional NPP, NPP for subannual time increments, or NPP under conditions of changed climate or species distributions. Some models (e.g., Leith, 1975) calculate NPP as a function of climate only. Others assume that NPP is constant across each major biome and calculate a global total based on the distribution of the biomes (e.g., Whittaker and Likens, 1975; Atjay et al., 1979). Other global models supplement climate information with data on soils and nutrient availability (e.g., Schimel et al., 1994), while still others (e.g., Ruimy et al., 1994) base the calculation largely on the interception of solar radiation by vegetation.

In this article, we explore some of the reasons that global NPP can be modeled from several perspectives. We also discuss limitations of each approach and consider the challenge of testing and improving models at local and global scales.

Based on the evidence that general ecological principles structure the broad relationships among climate, resources, species characteristics, and NPP, we propose a simple approach to modeling global NPP. This approach combines ecological principles with satellite data to yield global estimates with reasonably high temporal and spatial resolution.

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WHAT IS NPP?

At the local scale, NPP can be defined and measured in terms of either biomass or CO_2 exchange, though measurements based on biomass data are by far the most common. As biomass, NPP is given by

$$\mathrm{NPP} = b_{t+1} - b_t + L_{t+1}, \quad (1)$$

where b_t and b_{t+1} are the plant biomass at the beginning and end of the measurement interval and L_{t+1} is the new litter produced during the interval. In addition to the shedding of leaves and branches, litter production should include root turnover and exudation as well as losses to herbivores. Depending on the ecosystem, either the biomass or litter terms may dominate, and it is possible to have a high NPP in ecosystems that are not accumulating live biomass. In terms of gas exchange, NPP can be defined as

$$\mathrm{NPP} = \mathrm{GPP} + R_a, \quad (2)$$

where GPP (gross primary production) is the carbon fixed during photosynthesis and R_a is autotrophic respiration. NPP is the sum of GPP and R_a when GPP and R_a have opposite signs.

NPP is the net flow of carbon from the atmosphere into plants and, at steady state, the net flow of carbon from plants to heterotrophs and storage pools in the soil. NPP is not the net exchange of carbon between the atmosphere and an ecosystem because this latter quantity, termed net ecosystem production or NEP, includes respiration by heterotrophs as well as net carbon fixation by plants (NPP).

Though simple in concept, NPP can be very difficult to measure accurately. Measurements based on biomass must confront the challenge of quantifying below ground processes, including root production and exudation (Sala et al., 1988). Measurements based on gas exchange are complicated by the fact that it is very difficult to measure either GPP or R_a in isolation. Gas exchange measurements at the leaf scale typically measure the sum of photosynthesis and leaf respiration, and canopy-scale gas-exchange techniques measure NEP. A gas-exchange measurement is always separated from NPP by at least a simple model. While gas-exchange techniques quantify processes related to NPP at scales up to tens or hundreds of square kilometers, few studies to date address the complete annual cycle. Ground-based NPP measurements are usually made at spatial scales in the range of less than one to a few hundred square meters. Even the most careful NPP estimates are not error free, and many of the reports in the literature are tentative or incomplete, often including only aboveground NPP.

FUNDAMENTAL CONTROLS ON NPP

NPP is sensitive to many controls, including climate, soils, plant characteristics, disturbance regime, and a number of other natural and anthropogenic factors. The important environmental variables include both resources and resource regulators. For this discussion, we define resources as required substances that are moved from the environment into or through plants as part of the growth process—nutrients, water, light, and CO_2. Resource regulators are factors that influence growth without being either required or taken from the environment—including temperature, physical characteristics of the soil, and pollutant gases. Anthropogenic effects potentially alter resources (e.g., through fertilization with nutrients or CO_2), resource regulators (e.g., through greenhouse warming or tropospheric ozone), disturbance regime (e.g., through fire suppression), and plant characteristics (e.g., as a result of clearing for agriculture).

The question of the number of NPP controls that needs to be included in a global model has no simple answer. Most of the uncertainties relate to two basic themes. First, the data base for evaluating NPP models is not adequate to support a comprehensive assessment. The data shortage relates to analyses at all spatial scales, but it is most acute at the global scale, where any model must operate over a broad range of climates, soils, and biome types. Weaknesses in the available data sets include both NPP values, especially on appropriate spatial scales and in conjunction with other necessary data, and global distributions of the driving variables. Global distributions of information on soils, biome type, and disturbance history are especially critical, and recent progress in developing approaches for obtaining some of these distributions (e.g., Running et al., 1994) should be a major contributor to future progress.

Second, mechanistic studies on the controls on NPP leave room for multiple explanations, especially at the global scale. Relatively few NPP studies have included experimental manipulations to support assessments of the independent effects of a range of potential controls. The ecosystem-scale manipulations that have been attempted have tended to focus on subsets of the potential NPP controllers (Mooney et al., 1991). The challenge of establishing the relative roles of a number of NPP controllers is increased by the fact that, at the global scale, many of the controllers tend to be strongly correlated. As a consequence, models based on different suites of variables may yield similar results. Models that assume these correlations, either implicitly or explicitly, may perform well over broad areas, but at the potential cost of decreased local accuracy and degraded performance under conditions that disrupt the correlations.

Worldwide, climate (long-term mean patterns of temperature and precipitation) is a major driver of variation in NPP, making it a logical starting point for a discussion of the relationships among drivers. Some models use only climate parameters (e.g., Friedlingstein et al., 1992; Leith, 1975) and yield results that are

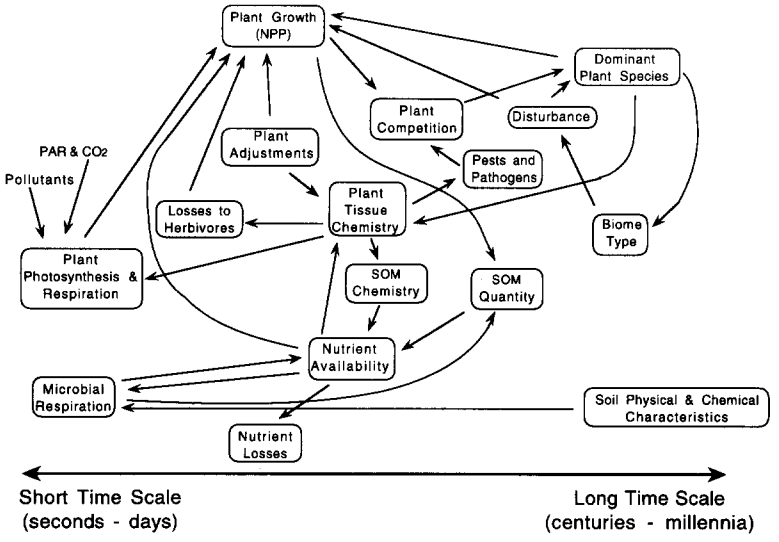

Figure 1. Schematic summary of the major controls on NPP, arranged with respect to the time scale over which changes in the process become important. Arrows indicate an effect of one parameter on another. Because temperature and moisture have direct effects on almost every parameter, they are not shown. With the large number of links, indirect effects are potentially important. Here, SOM refers to soil organic matter, PAR refers to photosynthetically active radiation, and Plant Adjustments refers to changes in both physiology and biomass allocation.

comparable in broad patterns but rarely in local details to those from more complex models. Does this imply that climate parameters are the dominant drivers of variation in global NPP? The answer to this question depends on time scale and the history of the site. Abundant evidence documents responses of NPP to experimental changes in nutrient availability, species composition, and management practice. Yet, over long time periods, soil nutrients and composition of the ecosystem adjust in response to climate. Over millennia, these adjustments often become complete enough to support the concept of a potential natural vegetation controlled by climate (Woodward, 1987).

The variables that regulate NPP are sensitive to climate through a number of mechanisms and on a number of time scales (Fig. 1). On short time scales, temperature, soil moisture, and atmospheric moisture affect the physiological processes that control plant photosynthesis and growth. Of course, other environmental variables, including the level of photosynthetically active radiation (PAR), the concentration of atmospheric carbon dioxide, and the levels of pollutant gases also influence photosynthesis and growth. Characteristics of plant species, the availability of nutrients in the soil, and the extent to which the plants on a site have adjusted to the ambient climate and nutrient availability establish constraints for these long-term effects.

In the short term, temperature and soil moisture regulate the metabolic activity of microbial decomposers, so that more nutrients are made available as conditions become more favorable for plant growth. Nutrient availability is, however, also sensitive to the amount, composition, and physical structure of the organic matter in the soil, to the loss of nutrients through gaseous emissions or leaching, and to the rates of nutrient uptake by soil microbes and plants, as well as to the depth, chemistry, and physical structure of the soil (Swift et al., 1979). Physical and chemical characteristics of the soil are sensitive to climate on a time scale of millennia, but they are also influenced by parent material and vegetation (Jenny, 1980). The power of climate in predicting soil characteristics may be magnified by predictable relationships between climate and vegetation type, but a climate-based model has no access to factors like nutrient inputs or loss of organic matter from management practices. In sum, climate should provide useful summary variables for a number of biogeochemical and physiological processes that regulate nutrient availability, but should give no access to anthropogenic or vegetation effects in cases where the vegetation is altered from the potential vegetation set by climate. Since some of the controls on nutrient availability develop over many centuries, climate-based predictions of NPP should be much less reliable for sites or conditions where the climate is changing rapidly.

Plant characteristics have a number of effects on NPP. Maximum growth potential varies widely among plant species, and plants of infertile habitats are genetically incapable of realizing high rates of biomass accumulation (Chapin, 1993). Plants also vary in their access to resources, especially those below ground. In water-limited habitats, presence of a deeply rooted woody species can increase NPP by enlarging the total pool of resources that can be utilized. Plant characteristics also regulate nutrient availability, both through effects on decomposability and through associations with microbes that fix atmospheric nitrogen. Plant characteristics affect disturbance regimes through effects on flammability (D'Antonio and Vitousek, 1992) and susceptibility to pests and pathogens.

The plant characteristics that affect NPP vary both within and among species. The tuning of plant characteristics to ambient conditions occurs through a combination of within-species acclimation or plastic adjustment,

responses of the relative abundance and genetic composition of species, and development of a species composition based on immigration and local extinction. Some of the critical questions about the general predictability of NPP concern the extent to which this tuning results in repeatable suites of species characteristics in similar habitats, a phenomenon called convergent evolution by Mooney and Dunn (1970) and functional convergence by Field (1991). Models based on climate alone, or on climate and resources assume, either explicitly or implicitly, that natural ecosystems tend toward combinations of species with functional properties that vary consistently with climate and resources. Models that specify biome types allow biome-specific functional properties that may or may not be predictable from climate and resources.

Disturbance can be an important controller of NPP, for several reasons. Some involve the role of disturbance in altering the natural species composition of an ecosystem. Others involve the role of disturbance in resetting natural ecosystem dynamics. In forest ecosystems, NPP is usually higher in young stands that are accumulating biomass than in mature stands near steady state. An increase in plant respiration due to the increased woody biomass probably accounts for some of the trend, though age-dependent changes in hydraulic architecture and photosynthetic capacity may be as or even more important (Ryan and Waring, 1992). Effects of disturbance history can be even more pronounced when the ecosystem dynamics after disturbance include changes in species composition. Early successional species often have higher rates of growth and photosynthesis than later successional species (Bazzaz, 1979). Even in grassland ecosystems, where above-ground biomass is relatively stable from year to year, time since fire can have large effects on NPP, resulting from the role of fire in increasing nutrient availability and light interception by living plants (Knapp et al., 1993).

Over large spatial scales, the distribution of disturbance types and age since disturbance may vary predictably with climate in most biome types. One example of this is fire frequency in chaparral, a mediterranean-climate shrubland in Southern California and nearby Baja California. Fire repeat frequencies are similar on the two sides of the U.S.–Mexico border, even though fires are suppressed in California but not in Baja California (Minnich, 1989). Under conditions of rapid climate change or human intervention, disturbance distributions could be substantially altered, perhaps altering NPP–climate relationships.

Events at higher trophic levels can also influence NPP. Herbivory by vertebrates or invertebrates leads to increased plant growth in some cases (McNaughton, 1976) but unchanged (Zellner et al., 1993) or decreased NPP in others (Pastor et al., 1993). Effects of animals on NPP result not only from direct effects of herbivory, but also from the role of animals in regulating plant community composition, through impacts on pollination, seed dispersal, and trampling. In biomes unaffected by anthropogenic perturbation or by climate change, the effects of animals on productivity might be subsumed in functions of climate and vegetation. But when anthropogenic impacts or climate changes become important, this tenuous approach becomes untenable.

Anthropogenic effects on NPP can be very large. Overgrazing, urbanization, water diversion, and some kinds of air pollution tend to decrease NPP, while irrigation, fertilization, and maintenance of rapidly growing commercial species and cultivars tend to increase NPP (Chameides et al., 1994). Locally, the establishment of nonnative plant species can favor increased NPP (Vitousek and Walker, 1989), but it can also lead to a stable conversion from forest or savanna to grassland (D'Antonio and Vitousek, 1992). Effects of global anthropogenic impacts like climate change, increased atmospheric CO_2, and increased nitrogen deposition are less clear, but are a major focus of a new generation of NPP models (e.g., Melillo et al., 1993).

APPROACHES TO INTEGRATING THE CONTROLS ON NPP

As might be expected from the number of potential controls on NPP, the interactions among the controls, and the diversity of objectives for which global NPP models have been developed, global NPP models differ dramatically in their emphasis on different controls. One important distinction among models is their relative emphasis on climate, resources, and ecosystem characteristics. A second is the relative role of three resources, light, water, and nutrients (Fig. 2). What explains the differences in emphasis? Some reflect the questions the models were designed to address; some reflect the dynamic nature of the data available on a global scale; and some reflect differences in researchers' experience or philosophy.

Models based solely on climate are attractive for their direct applicability to climate-change problems (e.g., Friedlingstein et al., 1992), though these models provide little or no insight into nonequilibrium phenomena. Models based on APAR only (e.g., Heimann and Keeling, 1989) are attractive for their direct connection with satellite data, but their power is limited by the difficulty of converting a satellite vegetation index into an estimate of the fraction of radiation absorbed (Begue, 1993) and by variability in the efficiency with absorbed radiation is converted into NPP (Running and Hunt, 1993; Ruimy et al., 1994). Models based solely on biome type (e.g., Whittaker and Likens, 1975; Fung et al., 1987) allow global calculations based on vegetation maps, but cannot account for NPP variation within biomes.

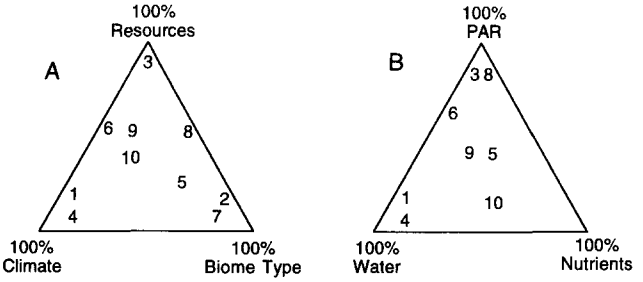

Figure 2. A rough positioning of ten global NPP models with respect to the relative importance of climate, ecosystem type, and resources (left triangle) and, for models in which resources are important, the relative imortance of water, nutrients, and PAR (right triangle). For panel A, climate includes temperature and precipitation, while resources includes light and nutrients. Panel B considers water a resource. The 10 models are: 1) Friedlingstein et al. (1992); 2) Fung et al. (1987); 3) Heimann and Keeling (1989); 4) Leith (1975); 5) Melillo et al. (1993); 6) Potter et al. (1993); 7) Whittaker and Likens (1975); 8) Ruimy et al. (1994); 9) Running and Hunt (1993); 10) Schimel et al. (1994).

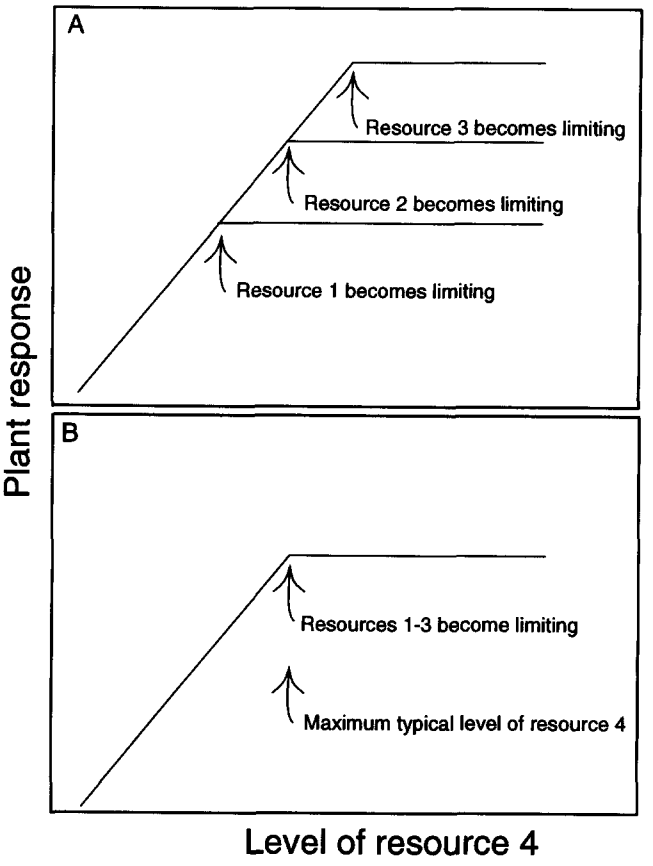

Figure 3. Schematic contrast between the conceptual model of NPP limitation by the most limiting resource (A) and NPP limitation predicted under the resource balance hypothesis (B). If a single resource is limiting, increasing supply of that resource allows NPP to increase, to the point where some other resource becomes limiting. If investments in resource acquisition are adjusted to make all resources limiting to NPP, then uptake addition of any single resource can stimulate NPP, but only after plant adjustments. Under the resource balance hypothesis, uptake of any resource can provide a useful index of NPP.

For models that attempt to capture the mechanistic basis of NPP, a number of approaches can be justified. Predictable relationships among photosynthesis, ecosystem type, and NPP (Mooney, 1972; Schulze and Chapin, 1987) motivate the view that photosynthesis is the primary driver of NPP. The roles of climate, ecosystem type, and resources can be evaluated in terms of effects on photosynthesis, biomass allocation, and respiration. With this conceptual model, factors that affect photosynthesis, especially PAR and CO_2 concentration, tend to be important.

Nutrient availability can also be considered the primary regulator of NPP. With this concept, factors like water availability, temperature, and species characteristics impact nutrient availability both directly and, along with effects of factors like CO_2 concentration, through effects on tissue decomposability. A third view, which might be called the resource balance perspective, postulates that ecological processes tend to adjust plant characteristics in response to ambient conditions in a way that tends to maximize growth. From this perspective, growth or NPP is basically an integrator of resource availability, with plant processes tending toward making all resources equally limiting (Bloom et al., 1985). Under some conditions, complete adjustment may not be possible, and NPP will be limited by the most limiting resource, with all others brought as close as possible to the point of limitation (Fig. 3). These conditions may include extreme resource imbalance, differences in the nature of limitation for different resources (Rastetter and Shaver, 1992), intrinsic limits to the potential for plant adjustment, and insufficient time for complete adjustment.

These three conceptual models predict that NPP should be set by one or more factors in the environment, relatively independent of the individual species on a site, except insofar as species differ in their capability to forage for resources (e.g., deeply rooted trees versus shallowly rooted herbs). Models with a heavy emphasis on ecosystem type (e.g., Whittaker and Likens, 1975) suggest that species characteristics play a fundamental role. Differences in the growth potential of dominant species from different ecosystems (Chapin, 1980; 1993; Schulze and Chapin, 1987) are consistent with this view but do not prove that species-based predictions are more robust than predictions based on climate or resources. The effects of species characteristics on NPP that are most difficult to predict from climate and resources are probably those related to disturbance and successional dynamics. To the extent that recovery from disturbance implies a succession of different NPPs on

a site of constant climate, those effects need to be modeled as consequences of species, time since disturbance, or some resource that changes through succession.

THE RESOURCE BALANCE PERSPECTIVE

The resource balance conceptual model makes an especially attractive starting point for a global NPP model, for several reasons. First, the resource balance approach is supported by an expanding body of empirical evidence (Chapin et al., 1987). Second, evidence for responses in the direction that tend to support the resource balance model is overwhelming (Bloom et al., 1985; Field et al., 1992). Third, the resource balance approach tends to integrate all of the NPP controllers in a relatively simple way. And fourth, the resource balance approach suggests straightforward ways to utilize remote sensing data in an NPP calculation (Field, 1991).

The resource balance perspective postulates that the combination of species sorting through ecological processes and plant acclimation through physiological, biochemical, and morphological processes should tend to make all resources equally limiting to growth (Bloom et al., 1985; Mooney and Gulmon, 1979). To the extent that this is true, it makes a very powerful prediction about the relationship between absorbed photosynthetically active radiation (APAR) and growth or NPP. If sorting by ecological processes and acclimation generally trims the capacity to harvest unnecessary resources in order to redirect harvesting potential to other resources, then plants should never invest in more light harvesting than they can utilize for growth. If this is the case, then APAR should be related to both the driving potential for photosynthesis and the availability of whatever resource limits growth. As long as investment in light harvesting is downregulated to match the availability of the resource that limits growth, it is not strictly necessary for all other resources to be equally limiting, though uneven limitation might have consequences for the efficiency with which the limiting resource(s) are used.

RESOURCE USE EFFICIENCY

In order to use any index of the availability or capture of a limiting resource as a basis for an NPP calculation, we need a conversion factor for relating uptake of that resource to NPP. That conversion factor can be a complex model that adjusts the ratio of resource captured to NPP in response to differences in the use of the resource among plant species or at different temperatures, or it can be as simple as a constant ratio. Among plants, the ratios of NPP to resources used, or resource use efficiencies, tend to be quite variable. Water use efficiency varies more than tenfold over all plants and by more than threefold among plants with the C_3 photosynthetic pathway (Larcher, 1980). Nutrient use efficiency is also variable. Nitrogen use efficiency, the most commonly measured index of nutrient use efficiency varies more than fivefold (Vitousek, 1982). Some of the initial studies on the efficiency of light utilization (ε) in NPP indicated that it might be quite constant across a range of plant types (Monteith, 1972), but broader surveys indicate more than fivefold variation (Prince, 1991; Ruimy et al., 1994; Running and Hunt, 1993; Russell et al., 1989).

LIGHT UTILIZATION AS A BASIS FOR NPP

Given the evidence that APAR can be estimated with remote sensing (Kumar and Monteith, 1981; Sellers, 1987; Begue, 1993), NPP models based on APAR are very attractive. They convert the essence of the resource balance hypothesis into a paradigm for a global NPP model.

Monteith (1972) pioneered the concept of calculating NPP as a product of APAR and ε and introduced the idea of including explicit effects of water, temperature, and nutrient stress. Variants on this production efficiency model have now been tested many times, using both satellite and surface sources for APAR [summarized by Prince et al. (1994)]. Prince (1991) developed a regional, satellite-based model without explicit stress effects, which were included in the APAR-based model of Runyon et al. (1993). These regional-scale efforts establish the basic feasibility of global-scale models but also highlight many of the challenges and limitations, some of which are discussed in the following sections of this article.

Heimann and Keeling (1989), who published the first global NPP model based on APAR, used a single value for ε and applied that single value to all biomes at all seasons. Ruimy et al. (1994), recognizing the evidence for variability in ε, used a range of ecosystem-specific values. They did not, however, consider the possibility of within biome or seasonal variation. The CASA model (Potter et al., 1993) is based on ε, but with a structure that allows ε to vary seasonally and within biomes, and without recourse to ecosystem-specific ε values.

Satellite-based APAR estimates as a source of information for NPP calculations have advantages and disadvantages. The primary advantages concern the ability of satellite data to capture spatial and temporal detail at the global scale. The temporal and spatial detail in remote sensing data are unparalleled. The measurements are integrated over the spatial scale of the model units and can be processed with highly controlled, consistent algorithms. Depending on the sensor and product, the coverage can be up to global with revisit frequencies up to several times per day.

The limitation on remote sensing data for simulations of climate change arises because a satellite vegetation index is measuring a parameter that is a product as well as a driver of plant growth (Demetriades-Shah et al., 1992). NPP models based on a vegetation index always involve some aspect of circularity. The models are based on the postulate that the vegetation index is related to the potential for future production. The vegetation index, however, is also a product of past production. Thus, an NPP model based on a vegetation index could drive the calculation with past NPP, other mechanistic drivers, or some combination of the two. For some applications, the relative role of each of these components may not be a major determinant of the accuracy of the estimate. For others, especially in settings where the typical correlations are disrupted, models that emphasize mechanistic drivers of NPP should be most successful.

A second aspect of the uncertainty about predicting the future and measuring the past with satellite data is that it is unclear how to modify a satellite-based model to allow a simulation for a treatment (e.g., altered climate, CO_2, nutrient deposition) for which satellite data are not available. If these treatments alter plant growth or allocation, they are very likely to alter the vegetation index. This sensitivity limits the use of current data. Approaches that combine the spatial and temporal information from satellite data with other models that predict responses to change offer the potential for effective mutualisms.

CASA OVERVIEW

The CASA (for Carnegie–Ames–Stanford Approach) model, introduced by Potter et al. (1993) and expanded here, is structured so that, for a given area, the amount of photosynthetically active radiation absorbed annually by green vegetation (APAR) multiplied by the efficiency by which that radiation is converted to plant biomass increment (ε) equals the net primary production (NPP). For each of 14,713 $1° \times 1°$ terrestrial grid cells, CASA calculates APAR as the product of solar surface irradiance (S) and the fraction of photosynthetically active radiation absorbed by green vegetation (FPAR), where FPAR is derived from AVHRR NDVI. CASA calculates ε for each grid cell as the product of a globally uniform maximum ε^*, determined using a calibration with field data, and scalars representing the availability of water (W) and the suitability of temperature (T_1, T_2). NPP for a location (x) and time (t) is represented as

$$\mathrm{NPP}(x,t) = \mathrm{APAR}(x,t) \cdot \varepsilon(x,t) \tag{3}$$

or as

$$\mathrm{NPP} = S(x,t) \cdot \mathrm{FPAR}(x,t) \cdot \varepsilon^* \cdot T_1(x,t) \cdot T_2(x,t) \cdot W(x,t)\,. \tag{4}$$

CASA PARAMETERS

APAR

APAR is calculated at each monthly time step as the product of PAR surface irradiance and FPAR. PAR surface irradiance is calculated as 1/2 the total solar surface irradiance from the data of Bishop and Rossow (1991). FPAR is a linear function of the Simple Ratio vegetation index derived from the $1° \times 1°$ FASIR-NDVI product of Los et al. (1994) and Sellers et al. (1994). To account for differences in canopy architecture and leaf clumping, the slope and maximum in the function relating FPAR to Simple Ratio are somewhat different for needleleaf trees, broadleaf trees, mixed needleleaf and broadleaf trees, and short vegetation (Sellers et al., 1994). This approach gives values of APAR that vary from about 3000 MJ yr^{-1} in tropical forests to less than 500 MJ yr^{-1} in deserts and polar regions (Fig. 4).

Temperature and Water Scalars

The functions for the temperature and water scalars are simple attempts to capture as much as possible of the mechanistic basis of the effects of these factors on productivity. Some of the motivation is based on physiological studies and some is based on ecological studies, as discussed below. The functions are applied uniformly across the globe, with no distinction for biome types. Thus, the only effect of biome type in the CASA NPP calculation is the small effect on the function relating Simple Ratio to FPAR.

The water scalar is calculated on a monthly time step as a function of the ratio of estimated evapotranspiration (EET) to potential evapotranspiration (PET):

$$W(x,t) = 0.5 + \mathrm{EET}(x,t) / \mathrm{PET}(x,t)\,, \tag{5}$$

where PET is a function of temperature (from Leemans and Cramer, 1990) and latitude (Thornthwaite, 1948). EET includes both precipitation (from Leemans and Cramer, 1990) and evaporation from the soil profile. Because the rate of evaporation is controlled by the soil moisture from the previous time step, W includes a memory that buffers the transitions between dry and wet seasons. When EET exceeds PET, NPP is no longer restricted by soil moisture, and W equals 1. Each grid cell is assumed to be well drained, with the result that productivity in CASA is never limited by anaerobic conditions in supersaturated soils. CASA's soil moisture function is very similar to functions used in the biosphere models of Lüdeke et al. (1991) and Raich et al. (1991). The basic difference is that water limitation can drive NPP to 0 in the other models but limits NPP by a maximum of 50% in CASA. The less restrictive function in CASA reflects the evidence that water stress limits NDVI as well as ε (Garcia et al., 1988). Downregulation of NPP by the moisture scalar is most severe in desert ecosystems like the Sahara, the Gobi Desert, and

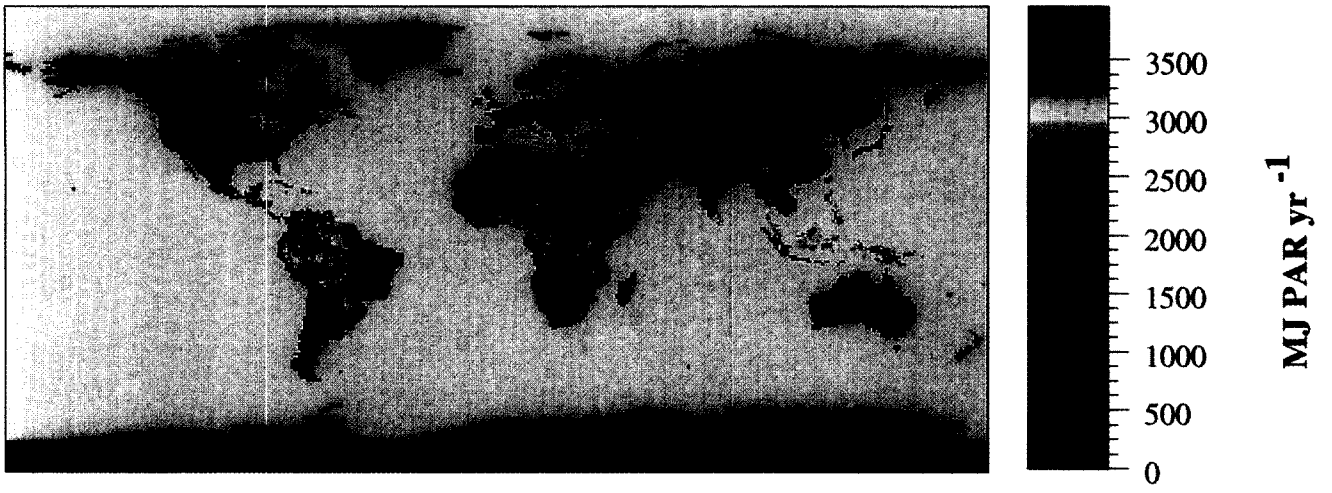

Figure 4. Annual sum of canopy APAR from the CASA NPP model, calculated at each time step as the product of FPAR and PAR insolation. FPAR is derived from AVHRR NDVI as described by Sellers et al. (1994). PAR was obtained from the total solar radiation data base of Bishop and Rossow (1991).

Tibetan plains in Asia, and in the southwestern United States (Fig. 5).

The two temperature scalars in CASA attempt to capture two aspects of the regulation of plant growth by temperature. One of the scalars, T_2, postulates that vegetation acclimates to the site-specific seasonal temperature trajectory. The other, T_1, sets limits to acclimation in extreme habitats.

The functional form of T_2 expresses the hypothesis that, at every site, growth acclimates to the temperature during the month of greatest NDVI. There is, however, no temperature acclimation during the year, and NPP is suppressed by temperatures warmer or cooler than that during the month of maximum NDVI. Though evidence for temperature acclimation of photosynthesis (Berry and Björkman, 1980) is abundant, the hypotheses behind T_1 and T_2 in CASA have not been explicitly tested.

T_2, calculated from Eq. (6), is plotted in Figure 2 of Potter et al. (1993):

$$T_2(x,t) = C \cdot 1 / \{1 + \exp[0.2 \cdot (T_{opt}(x) - 10 - T(x,t)]\} \cdot 1 / \{1 + \exp[0.3 \cdot (-T_{opt}(x) - 10 + T(x,t)]\}, \quad (6)$$

where C is a constant, T is the mean monthly temperature, and T_{opt} is the mean temperature during the month of maximum NDVI. The scalar equals 1 when $T = T_{opt}$, and falls to 0.5 at approximately 10°C above and 13°C below T_{opt}. T_2 has a large impact on NPP in sites that experience large seasonal swings in temperature. For ecosystems where temperature varies little, like some low-latitude deserts and tropical rainforests, T_2 has little effect.

T_2 is included in the CASA NPP equation because radiation use efficiency in highly seasonal ecosystems is likely to be reduced at the beginning and end of the growing season, for several reasons. Early in the season, radiation use efficiency may be reduced by the expense of initiating construction of leaves and fine roots (Amthor, 1989). Towards the end of the season, radiation use efficiency may be reduced by the costs of retranslocating leaf metabolites into other tissues (Chapin and Kedrowski, 1983). For boreal ecosystems, there is an observed lag between the time temperatures permit photosynthesis and the time the photosynthetic machinery becomes fully active (Linder and Flower-Ellis, 1992). For low-latitude deserts, T_2 reduces growth during months when temperatures greatly exceed those during the most favorable part of the growing season. T_2 falls more sharply at high than at low temperatures to reflect the exponential respiration costs associated with plants exposed to temperatures well above their normal operating range (Amthor, 1989).

The other temperature factor, T_1, sets limits on acclimation, reflecting the evidence that inherent biochemical constraints on photosynthesis act to reduce NPP at both very low and very high temperatures (Berry and Björkman, 1980). T_1 is a function of T_{opt}. It varies spatially but not temporally:

$$T_1(x) = 0.8 + 0.02 * T_{opt}(x) - 0.0005 * [T_{opt}(x)]^2. \quad (7)$$

For a T_{opt} of 0°C, T_1 equals 0.8. The scalar rises parabolically to 1.0 at 20°C and then falls to 0.8 at 40°C. Because virtually all terrestrial ecosystems have growing season temperatures between 0°C and 40°C, T_1 varies only between 0.8 and 1.

The combined annual effects of T_1 and T_2 on plant growth result in severe temperature limitations in deserts, while most boreal and broadleaf deciduous ecosystems across North America, Europe, and Asia experi-

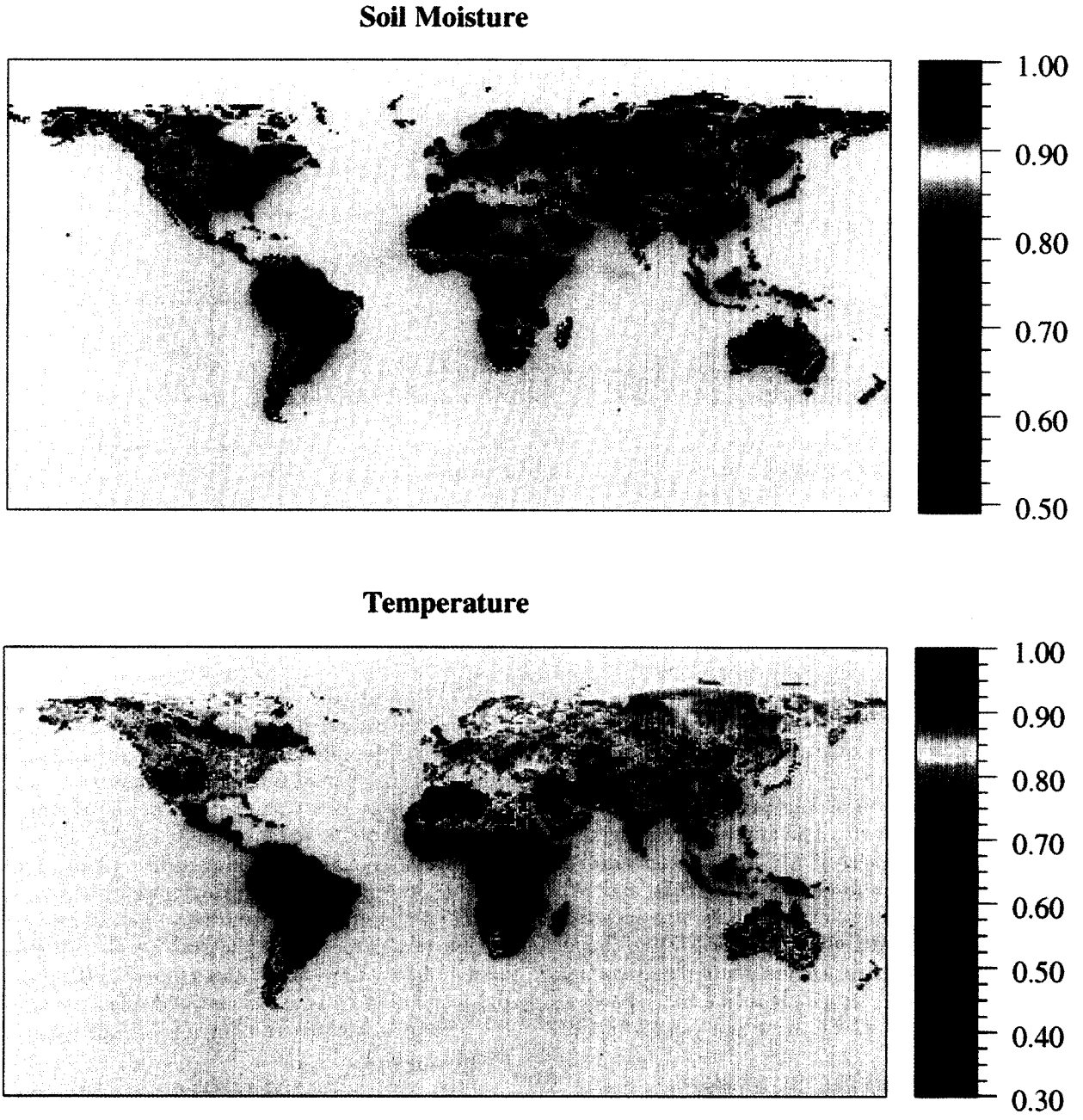

Figure 5. Upper) The annually integrated effect of the soil moisture scalar on NPP. A value of 1.0 represents no annual attenuation of NPP by the soil moisture scalar. A value of 0.5 represents a 50% decrease in potential NPP. Lower) the annually integrated effect of the two temperature scalars on NPP, interpreted the same way as in the upper panel.

ence only 10–30% reduction in growth due to the temperature scalars (Fig. 5).

In the current version of CASA, neither the temperature nor the moisture scalars are adjusted to account for differences between plants with the C_3 and C_4 photosynthesis pathways. While C_4 plants are not generally superior under extremely dry conditions, they often have higher temperature optima for photosynthesis and growth (Pearcy and Ehleringer, 1984). We are exploring ways to add this distinction to CASA.

CASA CALIBRATION

The CASA calibration involves three steps. First, the water and temperature scalars are calculated, for all pixels for an entire model year. Then, we select a suite of surface sites for which annual NPP is available. Finally, we run the model for the selected sites, adjusting a globally uniform ε^* to minimize the error over all the sites. The error minimization uses a modified least squares function [Eq. (9) of Potter et al. (1993)].

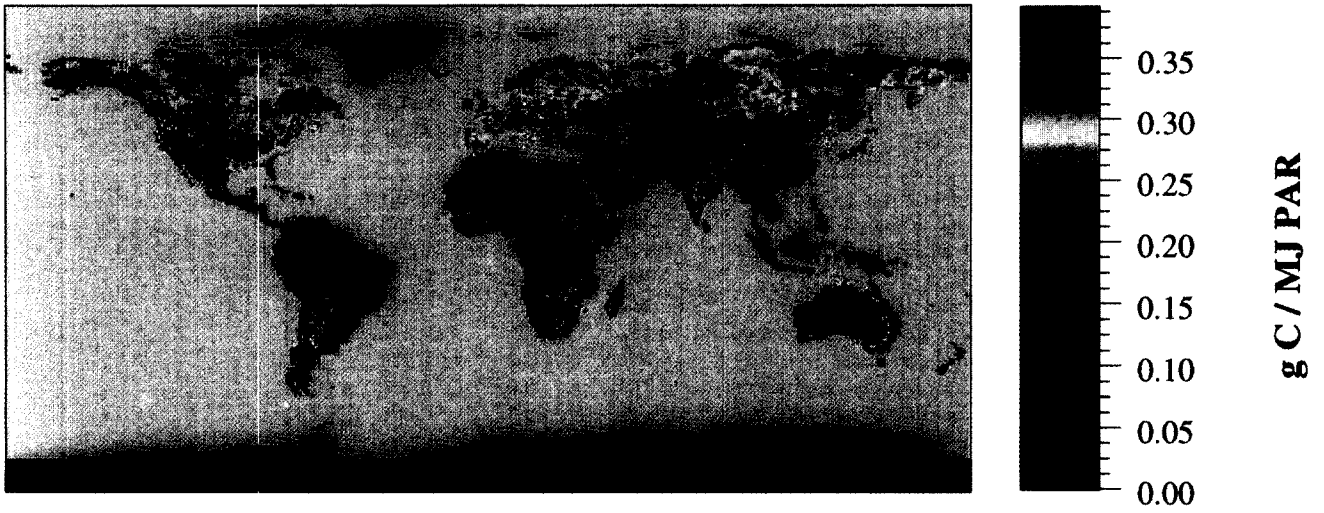

Figure 6. A global map of the CASA light use efficiencies averaged over months when $T > 0°C$.

Differences between predicted and observed NPP are scaled to the annual NPP of each site, so that a 10% error for a desert site carries the same weight as a 10% difference from a tropical rainforest site. Because the water and temperature scalars are calculated prior to fitting ε^*, the final value of ε^* represents the best estimate for a global maximum light use efficiency, in the absence of water or temperature constraints (other than those that appear in reduced FPAR). The product of the single value ε^* and the temporally and spatially varying correction terms for water and temperature yields the global fields of $\varepsilon(x, t)$ in Eq. (3). A global map of the average annual ε at each grid cell, for months when $T > 0°C$, is shown in Figure 6.

This approach for calculating $\varepsilon(x, t)$ contrasts with approaches employed by Heimann and Keeling (1989) and Ruimy et al. (1994). Heimann and Keeling (1989) used a single, uniform light use efficiency of 1.25 g C MJ^{-1} PAR. This value was based on a compilation of mostly crop studies reported by Monteith (1977). Ruimy et al. (1994) used different light use efficiencies for different ecosystems, basing their values on a more comprehensive review of the literature. These two approaches are similar in that light use efficiencies measured at the plot level are used to make regional and/or global predictions about NPP. In CASA, NPP data from a number of distributed sites are used to establish a value for ε^*. The following example illustrates the distinction between the two approaches. If the APAR fields in CASA were uniformly doubled, CASA's NPP fields would remain unchanged after recalibration, but ε would be halved. In the other two studies, a doubling of APAR would result in a doubling of NPP, because ε would remain unchanged.

This calibration procedure has at least two seriously problematic aspects. One, most of the available NPP data were not gathered in the year corresponding to the NDVI and solar radiation datasets. Addressing this problem and eliminating the possibility of errors due to year-to-year variation will require additional studies of ecosystem-scale NPP. Two, most of the NPP data were collected from small plots, typically less than 1 ha, but the calibration assumes that the measured NPP is characteristic of a $1° \times 1°$ pixel (often more than 10^6 ha). This vast scale mismatch could be a major source of error, especially if the NPP measurement sites represent a biased sample of their regions. Evaluating the calibration with higher resolution remote sensing data is a high priority.

CASA NPP AND ε

With the data sets and functions described above, the CASA value for ε^*, the maximum value of ε, is 0.389 g C MJ^{-1} PAR. Averaged by vegetation class from Dorman and Sellers (1989), values of ε vary from 0.354 g C MJ^{-1} PAR for broadleaf evergreen trees to 0.135 g C MJ^{-1} PAR for bare soil and desert (Table 1). If ε were equal to ε^* everywhere, global terrestrial NPP would be 57 pg C yr^{-1}. However, the water and temperature scalars act to reduce productivity by 16%, to 48 pg C yr^{-1} (Potter et al., 1993).

Constraints from Water and Temperature

Factors that constrain productivity, like limitations in resource availability, may reduce NPP by reducing APAR, ε, or both. Several studies of annuals suggest that if a limitation in resource availability occurs over a time period during which the vegetation has the capacity to respond by altering canopy characteristics, the response may be a change in FPAR such that ε remains relatively constant (Garcia et al., 1988; Russell

Table 1. Annual Mean FPAR and ϵ and Percentage Reduction of Annual Mean FPAR and ϵ from Maximum Values, for 12 SiB Vegetation Classes Defined by Dorman and Sellers (1989)[a]

Class	Vegetation Type	Annual FPAR	$\frac{(0.95 - FPAR)}{0.95}$	Annual Mean ϵ	$\frac{(0.389 - \epsilon)}{0.389}$
1	Broadleaf evergreen trees	0.780	0.18	0.354	0.09
2	Broadleaf deciduous trees	0.388	0.59	0.255	0.34
3	Broadleaf and needleleaf trees	0.411	0.57	0.283	0.27
4	Needleleaf evergreen trees	0.359	0.62	0.284	0.27
5	Needleleaf deciduous trees	0.269	0.72	0.280	0.28
6	Broadleaf trees with groundcover	0.480	0.49	0.302	0.22
7	Perennial grasslands	0.168	0.82	0.229	0.41
8	Broadleaf shrubs with grasslands	0.376	0.60	0.299	0.23
9	Broadleaf shrubs with bare soil	0.119	0.87	0.208	0.47
10	Tundra	0.160	0.83	0.269	0.31
11	Bare soil and desert	0.042	0.96	0.135	0.65
12	Cultivation	0.324	0.66	0.242	0.38

[a] Maximum FPAR is 0.95. Maximum ϵ is 0.389 g C MJ^{-1} PAR. Annual mean ϵ is based on the values of ϵ for all months where mean monthly temperature is > 0°C.

et al., 1989). When, however, a resource limitation or other factor perturbs the vegetation more quickly than the canopy can be adjusted, the response must be change in ε with relatively constant FPAR. In perennial systems, the degree of canopy plasticity and the relative costs of different strategies for balancing APAR and ε are likely to determine how vegetation adjusts to constraints and perturbations.

In CASA, both the annual mean and the seasonal variation in ε vary among biomes. For example, in boreal forests, below-freezing temperatures constrain photosynthesis but not radiation interception, so that APAR and growth become relatively uncoupled, and ε drops to near 0 under those conditions (Fig. 7). In contrast, in tropical evergreen forests photosynthesis is never limited by freezing temperatures, and ε remains high throughout the year. In deserts, ε is relatively constant over time, but the value is always low (Fig. 7).

In CASA, the mean annual FPAR for SiB vegetation classes ranges 19-fold, from 0.042 for areas of bare soil and desert to 0.780 for broadleaf evergreen forest (Table 1). In contrast, ε (for months when mean temperature > 0°C) varies only about threefold, from 0.135 g C MJ^{-1} PAR in areas of bare soil and desert to 0.354 g C MJ^{-1} PAR for broadleaf evergreen forest. FPAR varies fourfold between areas of broadleaf trees with ground cover and shrubs with bare soil, but ε varies only 1.5-fold. Similarly, there is almost a threefold difference in FPAR between mixed broadleaf/needleleaf forest and perennial grasslands, but just a 1.2-fold difference in ε.

The loading of the stress effects into FPAR also appears within vegetation types. In CASA, the maximum value of FPAR is 0.95, and the maximum of ε is ε^*, 0.389 g C MJ^{-1} PAR (Table 1). The mean FPAR for needleleaf evergreens is reduced 62% from the maximum, while ε (for months with temperatures greater than 0°C) is reduced only 27%. Mean FPAR for broadleaf deciduous forests is reduced by 59%, while ε is reduced just 34%.

Figure 7. Seasonal course of the CASA radiation use efficiency for several ecosystem classes. Month 1 corresponds to January; Month 12 corresponds to December. Evergreen broadleaf forests (SiB Biome 1; denoted by squares, solid line) have the highest radiation use efficiencies with minimal seasonal variation. Deserts (SiB Class 11; triangles, short dashed line) have radiation use efficiencies that are approximately half of the evergreen broadleaf forests. Deciduous and needleleaf trees (SiB Classes 2, 3, and 4; crosses, dashed lines) have radiation use efficiencies with a distinct seasonality, symmetric around the month of July. Needleleaf deciduous trees (SiB Class 5; circles, dotted line) show a much sharper transition between conditions.

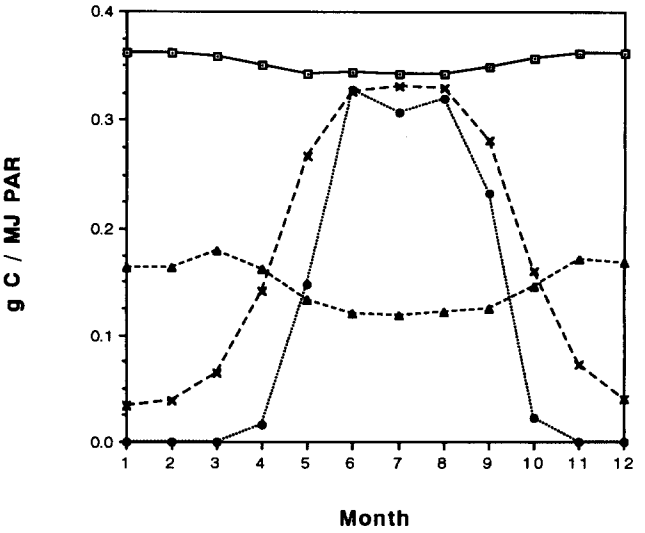

Table 2. A Comparison of Light Use Efficiencies from Several Sources[a]

Vegetation Type	*Matthews Class*	*Ruimy et al.*	*CASA*	Miami NPP / GCM APAR
Equatorial, tropical moist forests	1,2,3	0.310	0.340	0.409
Tropical, subtropical dry forests	5,6,7,9,12,13, 15,17,19	0.185	0.290	0.547
Mediterranean evergreen forests				
Temperate, deciduous forests	4,11,16	0.505	0.305	0.450
Temperate, subpolar, coniferous forests	8,14,18,20,21	0.785	0.272	0.428
Temperate grasslands	26,27,28,29	0.630	0.277	0.497
Deserts	30	0.630	0.160	0.763
Tundra, bog	22	0.630	0.263	0.590
Cultivation	32	1.035		

[a] Units: g C MJ^{-1} PAR. The Ruimy et al. estimates are the mean of literature values cited in Appendix 1 of Ruimy et al. (1994). The CASA and Miami NPP/GCM APAR estimates are described in the text. The two model estimates are averaged over vegetation classes from Matthews (1983).

A RANGE OF ε

How do CASA's estimates of light use efficiencies compare with other values? Table 2 shows mean light use efficiencies for ten vegetation types from Ruimy et al. (1994), CASA, and by the ratio of Miami model NPP (Lieth, 1975) to APAR from a GCM (Randall et al., 1994). The CASA values are annual efficiencies, averaged over the corresponding Matthews (1983) vegetation types and weighted by monthly NPP. The Miami / GCM calculation is included to provide, as much as possible, an independent assessment of the CASA estimates. The Miami model calculates NPP based on regressions of temperature and precipitation against observed NPP (Leith, 1975). The GCM APAR fields are based on the product of monthly integrals of PAR and FPAR. While the FPAR fields are the same as those used in CASA, the other two quantities used to calculate the light use efficiency are from independent sources. The Miami / GCM light use efficiencies also provide a potential upper bound to the light use efficiencies in Table 1 because the numerator is NPP for potential vegetation. The APAR denominator is attenuated by the effects of bare soil, water and rock surfaces, and land use modifications.

For moist tropical rainforests, all three estimates are similar (0.3–0.4 g C MJ^{-1} PAR) with the Miami / GCM value the highest. This ecosystem covers a significant fraction of the Earth's terrestrial surface and accounts for approximately 37% of the total terrestrial NPP. The CASA light use efficiencies are higher in this ecosystem than anywhere else because temperature and soil moisture conditions are optimal or nearly optimal. The three estimates for this ecosystem are in the range of 1 / 3 to 1 / 4 of efficiencies typically observed for crop canopies (Russell et al., 1989).

CASA light use efficiencies drop when moving towards high latitudes and low NPP ecosystems, while the other two estimates increase. For temperate, subpolar, and coniferous forests, Ruimy et al. (1994) report the highest light use efficiency for natural ecosystems (0.785 g C MJ^{-1} PAR) whereas CASA values are reduced by approximately 18% to 0.277 g C MJ^{-1} PAR. The low values for ε from CASA in temperate and high latitudes reflect the fact that water and temperature stress always reduce ε, pushing the maximum ε into the least-stressed region, the tropical rain forests. Including an effect of nutrient availability on tropical NPP (Vitousek and Sanford, 1986) might help increase temperate and high-latitude ε. Accounting for large-scale patterns of day length, solar elevation, and the relative proportions of direct and diffuse PAR could also help. More complete and higher quality calibration data is a critical step in understanding and addressing this problem.

Table 2 does not show ε for cultivated areas for CASA or Miami / GCM. While maps of cultivation are available at a global scale, the absence of a mechanism in CASA or the Miami model to account for the typical import of water and nutrients in agricultural systems makes it difficult to compare efficiencies. Both models predict light use efficiencies that should be consistent with the ambient climate at each cell, not conditions created by irrigation and / or fertilization. In contrast with the Miami model, CASA should detect some changes in NPP resulting from cultivation because of the model sensitivity to FPAR.

CONCLUDING REMARKS

NPP models driven by satellite data have many advantages over models driven only by climate and/or resources both for detecting global change and for yielding temporally and spatially resolved fields of NPP. The biological basis of the links between the inputs and the outputs for a model like CASA are not completely understood, but the same remark probably applies to all global NPP models. It is not yet clear how to incorporate satellite data into studies of past or future climate, but neither is it clear that approaches that do not incorporate satellite data capture all of the functionally important processes. In the future, models of past or future situations might benefit from using a satellite-based model like CASA to specify spatial and temporal patterns inaccessible to approaches that do not use satellite data.

The functional convergence hypothesis provides a useful ecological starting point for the CASA approach, but its general applicability has not been proven. To the extent that the functional convergence principle fails to predict global patterns, satellite-based NPP models may require specific ε for each vegetation class and for many combinations of resources.

Global NPP models are limited by the paucity of global data. Yet, the objectives for these models increasingly emphasize responses of NPP to altered climate, land use, or atmospheric composition, and these changes are likely to disrupt the broad correlations among controls that account for the generally good performance of simple models. Improvements in global data are a critical foundation for accurate NPP estimates for a wide array of global change scenarios. But it is also important to develop models based on the broad range of ecosystem responses to climate, resources, and disturbance. Some of these ecosystem responses may be individualistic and unpredictable, but many are highly consistent. Understanding the consistent responses is a key to defensible simplification.

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