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PREDICTING GROSS PRIMARY PRODUCTIVITY IN TERRESTRIAL ECOSYSTEMS

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Abstract. Our goal was to construct a simple, highly aggregated model, driven by easily available data sets, that accurately predicted terrestrial gross primary productivity (GPP; carboxylation plus oxygenation) in diverse environments and ecosystems. Our starting point was a fine-scale, multilayer model of half-hourly canopy processes that has been parametrized for Harvard Forest, Massachusetts. Over varied growing season conditions, this fine-scale model predicted hourly carbon and latent energy fluxes that were in good agreement with data from eddy covariance studies. Using an heuristic process, we derived a simple aggregated set of equations operating on cumulative or average values of the most sensitive driving variables (leaf area index, mean foliar N concentration, canopy height, average daily temperature and temperature range, atmospheric transmittance, latitude, day of year, atmospheric CO_2 concentration, and an index of soil moisture). We calibrated the aggregated model to provide estimates of GPP similar to those of the fine-scale model across a wide range of these driving variables. Our calibration across this broad range öf conditions captured 96% of fine-scale model behavior, but was computationally many orders of magnitude faster. We then tested the assumptions we had made in generating the aggregated model by applying it in different ecosystems. Using the same parameter values derived for Harvard Forest, the aggregated model made sound predictions of GPP for wet-sedge tundra in the Arctic under a variety of experimental manipulations, and also for a range of forest types across the OTTER (Oregon Transect Ecosystem Research) transect in Oregon, running from coastal Sitka spruce to high-plateau mountain juniper.

Key words: canopy model; carbon cycle; ecosystem models; gross primary productivity; Harvard Forest; leaf area index; model validation; OTTER project; Toolik Lake.

INTRODUCTION

Human impacts on the global carbon cycle, and the potential consequences of these on climate, are in debate (Schimel 1995). Gross primary production of terrestrial plants (the balance of photosynthetic CO_2 assimilation with photorespiratory CO_2 release) results in the assimilation of between 90 and 130 Tg C per year (Bolin and Fung 1992). Thus, ≈15% of the atmospheric pool of C is fixed annually by photosynthesis of terrestrial plants. Any changes in this rate of fixation, as a result of global environmental change, could have significant feedbacks on the rate of atmospheric CO_2 increase (Amthor 1995). Budgeting the global C cycle reveals a missing sink of ≈1.4 Tg C/yr (Schimel 1995), and inverse calculations suggest this sink may be located in the terrestrial biosphere (Tans et al. 1990, Enting and Mansbridge 1991, Denning et al. 1995). Several processes, including CO_2 fertilization of plant growth (Idso and Idso 1994), forest regrowth (Melillo et al. 1988, Kauppi et al. 1992, Dixon et al.

1994), N deposition (Peterson and Melillo 1985, Kauppi et al. 1992), and their interactions, may account for the budget imbalance.

The key controls on rates of photosynthetic C fixation at the leaf level are relatively well understood (Boardman 1977, Farquhar and Von Caemmerer 1982, Briggs 1989, Jones 1992). However, quantifying biological, climatic, and edaphic controls on C fixation and their inter-relationships has proved complex, for two reasons. Firstly, the diversity of experimental design, conditions, and measurements in photosynthesis investigations has often precluded direct comparison of results. Recently, Curtis (1996) has shown that meta-analysis can overcome these limitations to examine the relative (but not necessarily quantitative) importance of various factors affecting net CO_2 assimilation and photosynthetic acclimation under increased CO_2 concentration. Secondly, detailed modeling studies that have been undertaken for particular systems are generally not transferable to other data sets. Complex models designed for specific ecosystems and operating on numerous variables can successfully predict C fixation (Baldocchi 1992, Amthor et al. 1994, Williams et al. 1996). MBL/SPA (Marine Biological Laboratory/

Soil–Plant–Atmosphere), a fine-scale model of canopy processes developed for Harvard Forest, Massachusetts (Williams et al. 1996), operates at a 30-min time step, and incorporates 10 canopy layers. This spatial and temporal detail allows the model to correctly scale many of the nonlinear processes, such as diurnal variation in light attenuation through the canopy, and thus resolve the interaction between microclimate and physiology. However, the broader applicability of these models in alternate ecosystems is less certain, constrained by their demanding requirements for driving variables or validation data sets. This also makes them unsuitable for scaling across regions, given the paucity of regional ecological databases. The fine time scale of these models (in minutes) means that they are generally inappropriate for application to questions concerning ecosystem responses to global change (in years) (Luxmoore et al. 1991, Rastetter et al. 1992). Instead, we propose that mechanistic models, tested at their respective scales of operation, are most usefully employed to provide information to aid construction of models at successively coarser scales (Reynolds and Leadley 1992, Reynolds et al. 1996). This is a very different approach from the empirical techniques that are used to generate parametric models of regional net primary productivity, for example (Ruimy et al. 1994).

The scaling of photosynthetic responses to CO_2 from leaves to whole-ecosystem C storage using mechanistic models is critical to improving our understanding of the global C cycle (Schimel 1995). This is because ecosystem models, detailing C allocation and nutrient cycling (Parton et al. 1988, Rastetter et al. 1991), can incorporate the necessary feedbacks that may explain the acclimation responses to increased CO_2 concentration observed in experiments (Curtis 1996). A key component of any such ecosystem model will be an effectively scaled representation of gross canopy C fixation. The main requirements of this representation should be that it is derived from a more fine-scaled process-based model, that it operates at a daily/monthly time step, and that it gives predictions of whole-canopy responses with minimal data requirements.

Our goal in this paper is to describe the simplification and aggregation of an existing fine-scale model of canopy processes (Williams et al. 1996). The resulting aggregated model predicts daily values of gross C uptake given drivers collected at these scales (e.g., daily average temperature and temperature range, cumulative daily radiation, canopy leaf area). The aggregation procedure identified the relative importance of the key variables required to predict GPP, and determined their interrelationships. Having constructed the aggregated model, we tested its broader applicability through simulating GPP in alternate ecosystems, altering only driving variables according to relevant data, while leaving model parameters completely unchanged.

METHODS

The fine-scale model

The fine-scale, soil–plant–atmosphere canopy model (MBL/SPA; see Williams et al. 1996 for a full description) is a multilayer simulation of C_3-canopy processes parametrized for a temperate deciduous forest. The model employs some well-tested theoretical representations of ecophysiological processes, such as the Farquhar model of leaf-level photosynthesis (Farquhar and Von Caemmerer 1982), and the Penman-Monteith equation to determine leaf-level transpiration (Jones 1992). These two processes are linked by a unique model of stomatal conductance (g_s) that optimizes daily C gain per unit leaf N, within the limitations of canopy water storage and soil-to-canopy water transport. The model assumes that maximum carboxylation capacity (V_{cmax}) and maximum electron transport rate (J_{max}) are proportional to foliar N concentration (Harley et al. 1992).

The unique feature of this model lies in its treatment of stomatal opening, explicitly coupling water flows from soil to atmosphere with C fixation. The rate at which water can be supplied to the canopy is restricted by plant hydraulics (Tyree 1988) and soil water availability (Gollan et al. 1985, 1986). This rate ultimately limits transpiration because stomata will close at a threshold minimum leaf water potential to prevent xylem cavitation (Jones 1992). However, plant canopies also use water accumulated and stored during periods of low transpiration (e.g., at night). We argue that this stored water is used conservatively in the morning to delay the onset of stomatal closure in the early afternoon when atmospheric saturation deficits are high. By delaying stomatal closure, the canopy can maximize daily C assimilation. We assume that the photosynthetic apparatus is resistant to drought (Cornic et al. 1989, Epron and Dreyer 1993).

To ensure the efficient use of stored water in our model, stomatal conductance (g_s) in each canopy layer is adjusted until the incremental increase in net C assimilation (A) per incremental increase in g_s falls to a critical value of diminishing return. This adjustment of g_s is used until stored water in a layer is exhausted, at which point leaves must be irrigated by water transported from the soil (Meinzer and Grantz 1990). To avoid xylem cavitation, g_s is decreased until the transpiration rate from a canopy layer, as determined from the Penman-Monteith equation, equals the rate of water supply to that layer from the soil (Aston and Lawlor 1979). This stomatal closure, and the consequent decrease in C assimilation rate, is most pronounced in the upper canopy where atmospheric saturation deficits and plant hydraulic resistances can be high. As the canopy grows taller, hydraulic limitations on GPP will increase.

Fine-scale model predictions of both hourly CO_2 exchange rate ($r^2 = 0.86$) and latent energy ($r^2 = 0.87$)

TABLE 1. The maximum and minimum values of driving variables applied to the fine-scale model are listed. These define the bounds within which the aggregated model is calibrated.

Variable	Units	Minimum	Maximum
Leaf area index (LAI)	m^2/m^2	0.5	8.0
Foliar N concentration (N)	g/m^2 leaf area	1.0	4.0
Canopy height (H)	m	0.5	50.0
Average daily temperature (T)	°C	7.0	30.0
Daily temperature range [$(T_{max} - T_{min})/2$]	°C	1.0	12.0
Atmospheric transmittance	%	20.0	80.0
Day of year	day of year	173	365
Latitude	°N	0.0	70.0
Atmospheric CO_2 concentration (C_a)	μmol/mol	250.0	750.0
Leaf/soil water potential difference (Ψ_d)	MPa	−0.5	−4.0

are strongly correlated with independent whole-forest measurements made by the eddy covariance method during the summer of 1992 in Harvard Forest, Massachusetts (Wofsy et al. 1993, Goulden et al. 1996b, Williams et al. 1996). Our fine-scale model provides an explicit link between canopy structure, soil properties (including soil moisture), atmospheric conditions, and stomatal conductance. The submodels from which our fine-scale model is constructed (the Farquhar and Penman-Monteith models, Darcy's Law, a multi-layer model of radiation absorption) have been shown to be valid for a wide range of conditions. We therefore expect our model to have equally wide validity. However, both application and testing of our fine-scale model are hindered by the general unavailability of fine-scale data (eddy covariance measurements are relatively rare for natural ecosystems). We therefore developed an aggregated model, derived directly from the fine-scale model, but which operates with coarser scale data. This aggregated model was then tested for its general applicability.

The aggregated model

The coarse-scale aggregated model (MBL/CSA) was designed to predict daily gross primary productivity (GPP; in grams of carbon per square meter per day). The strategy to develop such a model was as follows:

1) Both fine- and coarse-scale models must be operated upon by the same set of driving variables; the nature and ranges of these drivers must be defined.

2) Develop procedures for relating coarse-scale daily driving variables (e.g., total daily irradiance) to the diurnal course of the half-hourly driving variables required by the fine-scale model (e.g., diurnal variations in irradiance).

3) For a comprehensive combination and broad range of the coarse-scale driving variables, generate half-hourly driver variables for a large number of days.

4) Use the fine-scale model to estimate daily, whole-canopy GPP for each of these days.

5) Develop aggregated equations relating these estimates of daily GPP to the coarse-scale driving variables.

The driving variables.—The aggregated model was designed to estimate daily CO_2 uptake across a wide range of coarse-scale driving variables. Selecting which driving variables to include in the model (Table 1) involved a two-stranded approach; the variables included had to have a demonstrated impact on stand-level photosynthesis, and they had to be relatively simple to obtain in the same temporal and spatial scales in which the aggregated model operates (i.e., daily, stand scale). Investigations with the fine-scale model parameterized for Harvard Forest, in conjunction with examination of the eddy flux data, showed that variations in leaf area index (LAI) and foliar N (during fall), temperature, atmospheric saturation deficit, irradiance, soil water potential, and time of year all had important impacts on GPP (Wofsy et al. 1993, Goulden et al. 1996a, b, Williams et al. 1996). Further, the literature demonstrates the importance of CO_2 concentration impacts (Curtis 1996), and recent research shows that increasing canopy height can reduce hydraulic conductivity, causing a corresponding reduction in photosynthesis (Yoder et al. 1994).

We selected LAI (0.5–8.0) and canopy height (0.5–70.0 m) to cover the wide range from sparse grassland or tundra to dense coniferous forest (Table 1). Values for the foliar N concentration (in grams of N per square meter leaf area) are derived to span the range of literature values (Reich et al. 1995). The atmospheric transmittance was varied between 20 and 80% to cover conditions from dense cloud cover to clear desert skies. Ambient CO_2 concentrations were selected to cover the range from pre-industrial (250 μmol/mol) to over double the present-day value (750 μmol/mol).

The soil moisture index (Ψ_d) is the difference between the canopy minimum leaf water potential (Ψ_{lmin}) and the soil water potential (Ψ_s). The more negative this value, the more water is available to the canopy. At Harvard Forest Ψ_{lmin} was determined from literature values (−2.5 MPa) and Ψ_s was set just below 0.0 MPa, reflecting a very moist soil and shallow water table (Bassow 1995, Williams et al. 1996). This gives a Ψ_d value of approximately −2.5 MPa; we set the range of this variable between −4.0 (reflecting a wet soil with drought-resistant vegetation) and −0.5 MPa (highly drought stressed).

Generating fine-scale drivers from coarse-scale drivers.—To link the fine-scale and aggregated models they must be run with equivalent driving variables. This means that the hourly inputs to the fine-scale model must be related to the daily values used in the aggregated model. Within a day LAI, canopy height, foliar N, soil moisture, and atmospheric CO_2 concentration do not differ significantly. However, we must account for the diurnal variation in radiation, temperature, and atmospheric saturation deficit (Running et al. 1987).

From latitude, time of year, and atmospheric transmittance, we defined the diurnal radiation climate using a standard sine function model (Gates 1980, McMurtrie 1993). We assumed that diurnal temperature variation was related to the radiation regime, so we modeled variation between the given daily maximum and minimum temperatures with a sine function. However, temperature tends to lag irradiance, so an extra parameter was required to determine the time at which temperature is at its maximum. We assumed that maximum temperatures occur after $\approx 77\%$ of the day-lit period has passed (a reasonable assumption based on Harvard Forest meteorological data). Diurnal changes in temperature were used to determine the course of atmospheric saturation deficit, on the assumption that the atmosphere was at dew point at the daily minimum temperature (Jones 1992).

These assumptions meant that, given site latitude and time of year, total daily irradiance, and maximum and minimum daily temperatures, we could construct diurnal (hour by hour) courses of irradiance, temperature, and atmospheric saturation deficit. Although highly simplified, these constructed time series allowed us to run the fine-scale model. Tests of the aggregated model would reveal whether or not these simplifications had introduced a significant bias.

Generating fine-scale predictions.—The ranges of the 10 coarse-scale driving variables define a hypervolume within which the aggregated model operates. To efficiently explore this hypervolume, we devised a factorial design within a Monte Carlo sampling scheme. The range for each variable was divided into two subranges (high and low), defining $1024 = 2^{10}$ subvolumes within the hypervolume. Within each of these subvolumes, we assumed a uniform distribution for all 10 variables. We used a Monte Carlo procedure to sample two sets of coarse-scale variables from each subvolume, for a total of 2048 sets of coarse-scale variables. These sets of coarse-scale variables were then used to generate fine-scale driver variables as described in the previous section and these were used in the fine-scale model to generate estimates of daily GPP.

Deriving the aggregated model

The aggregated model was designed to predict whole-canopy daily GPP given the coarse-scale driving variables. The number of driving variables included in this aggregated model was determined by our selection of the 10 drivers to which the fine-scale model was sensitive. The aggregated model uses a simple set of relationships designed to produce as close a fit as possible to estimates of daily GPP made with the fine-scale model. We judged the success of the alternate model structures using a root mean-square relative error (E) of the fine-scale vs. aggregated predictions. Parameters were estimated with PRAXIS, a conjugate gradient nonlinear parameter fitting routine (see *Acknowledgments*). The main advantage of PRAXIS is that it does not require information about derivatives of the aggregated model equations. It is also relatively fast, and is highly robust if a sine transformation is applied to the fitted parameters, ensuring that they stay within set bounds.

For development of the aggregated model, we excluded from the fitting those days where GPP was <1.0 g $C \cdot m^{-2} \cdot d^{-1}$, for two reasons. First, such days generally occur outside the regular growing season. Second, the relative errors of the fit for these days can be very large, though the absolute error is low. These high relative errors distort the statistics. After this exclusion, 1849 combinations of driving variables were retained for development of the aggregated model.

Aggregated model construction was an heuristic process in which coarse-scale equations were derived to fit daily GPP data estimated by the fine-scale model. This heuristic procedure involved posing a hypothesized simple structure, examining the residuals relative to the full set of driving variables, and using this information to make adjustments to the model structure. Our initial hypotheses were (1) plant photosynthetic capacity was linearly related to total foliar N; (2) metabolic and diffusive constraints were colimiting; and (3) incident radiation was hyperbolically related to GPP. The actual governing equations determined by the heuristic procedure are described below; they must be solved in sequential order 2,5,6,4,7,8,9 to give the final prediction (P_T) of daily gross primary productivity.

Central to the model, we included a strong linear relation between GPP and total canopy N (Harley et al. 1992), determined from foliar N concentration $(N;$ in grams per square meter *leaf area*) and leaf area index $(L;$ in square meters per square meter):

$$p_N = aNL \qquad (1)$$

where p_N is whole-canopy, N-limited photosynthetic capacity and a is a calibrated parameter. To incorporate the impacts of temperature on metabolic processes, we examined the nature of the temperature response from fine-scale model output operating between the ranges given in Table 1. We determined a revised form of Eq. 1 to mimic this model behavior as

$$p_N = a_1 NL \exp(a_2 T) \qquad (2)$$

where T is average daily temperature (°C, determined as the mean of maximum and minimum temperatures), and a_1 and a_2 are calibrated parameters. This simple

temperature function was adequate to describe the aggregated daily response even though the minute-by-minute response of the fine-scale model was far more complex (i.e., Arrhenius functions for the CO_2 compensation point and the half-saturation constants for CO_2 and O_2, and skewed bell-shaped curves for maximum carboxylation and electron transport rates).

In the fine-scale model C assimilation is colimited by metabolic and diffusive constraints. We used a highly simplified representation of this colimitation in the aggregated model. We assumed that photosynthetic capacity corrected for CO_2 limitation (P_C) was an asymptotic function of internal CO_2 concentration (C_i; in micromoles per mole), modified by the CO_2 compensation point (θ in micromoles per mole):

$$p_C = \frac{p_N(C_i - \theta)}{k + (C_i - \theta)} \qquad (3)$$

where k is a half-saturation constant (in micromoles per mole).

We modeled diffusion of CO_2 from the atmosphere to the site of carboxylation as a function of daily canopy conductance (g_c) and the difference in CO_2 concentrations at these two locations. Thus, the rate of diffusion of CO_2 to the site of C fixation (p_D) was determined by

$$p_D = g_c(C_a - C_i) \qquad (4)$$

where C_a is ambient atmospheric CO_2 concentration and C_i is CO_2 concentration at the site of carboxylation (both in micromoles per mole). g_c cannot be directly scaled from leaf-level stomatal conductance (g_s), because it is not a purely physiological parameter (Raupach and Finnigan 1988). To discover the controls on g_c we relied on an analysis of the fine-scale model to help generate an empirical relationship. The fine-scale model showed that stomatal conductance (g_s) was highly responsive to atmospheric vapor pressure deficit, which itself was strongly related to temperature and temperature range. g_s was also affected by the availability of soil water for transpiration, and this was constrained by the soil-canopy water potential difference and the height of the canopy (Yoder et al. 1994, Williams et al. 1996). We determined that canopy conductance was related to temperature (b_1 and b_2 are temperature coefficients), temperature range (D_T), canopy height (H), and soil–canopy water potential difference (Ψ_d, MPa, the difference between minimum leaf water potential [Ψ_{lmin}] and soil water potential [Ψ_s]), so that

$$g_c = \frac{-\Psi_d e^{b_1 T}}{b_2 H + D_T}. \qquad (5)$$

We next assumed a steady state in which $p_C = p_D$. Rearrangement of this equality allowed the determination of C_i,

$$C_i = \frac{1}{2}\left[C_a + q - p \right.$$
$$\left. + \sqrt{(C_a + q - p)^2 - 4(C_a q - p\theta)} \right] \qquad (6)$$

where $q = \theta - k$, and $p = p_N/g_c$. This value of C_i was substituted into Eq. 4 to determine p_D.

The metabolic and diffusive constraints were modified by irradiance (I; in megajoules per square meter per day). We tried a relationship based on absorbed radiation, i.e., APAR $= I \cdot [1 - \exp(-k \cdot L)]$, but found that a simplified asymptotic relationship gave a significantly improved fit (average relative error $= 10.5$ vs. 29.5%). We determined the light limitation (p_I) as

$$p_I = \frac{E_0 I p_D}{E_0 I + p_D} \qquad (7)$$

where E_0 is a canopy-level quantum yield (in grams of carbon per megajoule per square meter per day). Based on the behavior of the fine-scale model, we calculated E_0 as a function of LAI (L),

$$E_0 = \frac{c_1 L^2}{c_2 + L^2}. \qquad (8)$$

Variation in latitude and in the day of year alters the incident daily radiation and day length, and thus has a considerable influence on carbon fixation. However, the model is already driven by incident daily radiation (I), and this takes account of much of the variability introduced by latitude and time of year, because the three are strongly covariant. We found that a simple correction factor based on day of year, and requiring two parameters, did improve the fit of the model. The final equation that specifies GPP on a particular day of the year (P_T) is

$$P_T = p_I(d_1 D_{ms} + d_2) \qquad (9)$$

where D_{ms} is the number of days from midsummer (i.e., the absolute value of $173 -$ day number, where 173 is 22 June, midsummer for the Northern Hemisphere), and d_1 and d_2 are calibrated parameters. This correction is applied because of the nonlinear response of photosynthesis to irradiance, which results in higher productivity on long days relative to short days with the same total daily radiation. Within the tropics D_{ms} should be set to 80 (i.e., the Spring equinox, where day length ≈ 12 h) to remove the effect of day length variation from the model.

To sum up, the final forms of the equations were initially based on our understanding of the underlying mechanisms (for instance, the colimitation of metabolism and diffusion). Empiricism was involved in fitting the various mechanistic components together, especially in the calculation of temperature responses and canopy conductance. As a measure of our success, using best-fit parameter estimates (Table 2), this 10-parameter model accounted for >96% of the variance in

TABLE 2. Calibrated values of the parameters for the aggregated GPP model.

Parameter	Symbol	Calibrated value
Nitrogen response		
Nitrogen-use efficiency (NUE) parameter	a_1	2.95
Temperature coefficient of NUE parameter	a_2	0.018
CO_2 response		
Canopy CO_2 compensation point	θ	32.6
Canopy CO_2 half-saturation point	k	576.7
Stomatal response		
Temperature coefficient of canopy conductance	b_1	−0.029
Temperature range constant of canopy conductance	b_2	0.315
LAI response		
Maximum canopy quantum yield	c_1	0.989
LAI-canopy quantum yield coefficient	c_2	0.873
Day length response		
Day length constant	d_1	−0.0018
Midsummer coefficient	d_2	1.81

the fine-scale model, with an average relative error of 10.5% (Fig. 1). This fit ensured that the aggregated model faithfully reproduced fine-scale model behavior within the specified bounds of driving variables. It does not, however, allow the aggregated model to extrapolate outside these bounds.

To evaluate the relative importance of the driving variables we refitted the aggregated model to the fine-scale data set, sequentially holding individual driving variables constant at their mean value (for simplicity, we used mean irradiance as a driver instead of varying latitude and atmospheric transmittance). We then examined how mean relative error varied as different drivers were held constant. The results (Table 3) showed that irradiance and LAI (which is linked to *total* canopy foliar N) were the most important drivers—mean relative error showed the largest increase when these drivers were held constant. The next most important were average foliar N concentration, ambient CO_2, and leaf/soil water potential difference. The least influential drivers were day of year, canopy height, temperature, and temperature range. The last three drivers are involved in the calculation of canopy conductance (Eq. 5). This analysis reveals that the most significant stomatal limitations on daily GPP generally occur because of soil drought rather than excessive atmospheric demand (i.e., high vapor pressure deficit). While the effects of some of drivers, like canopy height, are small, over decadal time scales the cumulative effect on ecosystem GPP could be significant in terms of impacts on ecosystem processes.

RESULTS

Harvard Forest, Massachusetts

An eddy covariance system at Harvard Forest provided measurements of net ecosystem exchange (NEE)
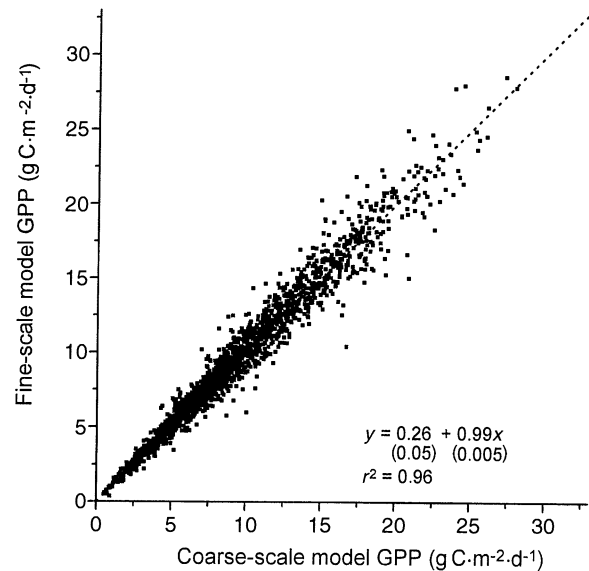

FIG. 1. Comparison of fine-scale model vs. aggregated model predictions of whole-canopy daily GPP (gross primary productivity) for 1849 different combinations of driving variables. The 1:1 line (– – –) is plotted on the figure. Numbers in parentheses below regression equations are standard errors of the corresponding coefficients.

$y = 0.26 + 0.99x$
(0.05) (0.005)
$r^2 = 0.96$

of CO_2; from the sum of NEE and leaf, stem, and soil respiration data (collected with chamber measurements), we were able to estimate GPP for 62 d in the late summer and fall of 1992 (Wofsy et al. 1993, Goulden et al. 1996b). From the same sources, we had available hourly meteorological data. Other ecosystem variables are listed in Table 4. Measurements by Bassow (1995) revealed that leaf N concentration declined significantly by October 1992. We therefore reduced foliar N concentration linearly from its growing season level

TABLE 3. The importance of individual driving variables in reducing average relative error (E) of aggregated model fit. Each driving variable was held constant in turn and a new best fit for the aggregated model determined; the new relative error and the increase compared to the full driving variable fit are given below.

Driving variable	E with variable held constant (%)	Increase in E (%)
Daily irradiance†	48.9	+38.4
LAI	48.1	+37.6
Average foliar [N]	19.2	+8.7
Ambient [CO_2]	17.5	+7.0
Leaf/soil water potential difference	16.1	+5.6
Canopy height	11.7	+1.2
Day of year	11.7	+1.2
Average temperature	11.3	+0.8
Temperature range	11.1	+0.6
Complete model	10.5	

† Irradiance is a function of latitude, day of year, and atmospheric transmittance; given the ranges of the latter from Table 1, daily irradiance varied between 0.2 and 35.0 $MJ \cdot m^{-2} \cdot d^{-1}$.

TABLE 4. Ecosystem variables at Harvard Forest, Massachusetts, 1992.

Variable	Value	Source
Location	42°32′ N, 72°11′ W	
Elevation (m)	340	
Canopy height (m)	24	
Canopy species	*Quercus rubra* L.	
	Acer rubrum L.	
Leaf area index (m^2/m^2)	3.5	Amthor (1994)
Average foliar N (g/m^2)	1.92	Aber et al. (1993)
Minimum leaf water potential (MPa)	−2.5	Bassow (1995)
Soil water potential (MPa)	≈0	
Atmospheric [CO_2] (μmol/mol)	355	

on day 250, to zero by day 300, by which time leaf abscission was complete.

These data were used to drive the aggregated model for comparison with measured GPP during late 1992 (Fig. 2). The model was in close agreement with the data ($r^2 = 0.91$), and successfully accounted for the impacts of changing temperature, humidity (related to temperature range), irradiance, and day length. After day 250, when temperatures started to decline (the first frost of the year occurred on day 275), the drop in foliar N concentration accounted for a sharp decline in GPP. The slight overestimation by the model after this date probably resulted from our oversimplified simulation of N retranslocation.

Toolik Lake, Alaska

Wet-sedge tundra is the second most widespread vegetation type in northern Alaska, and in the Arctic as a
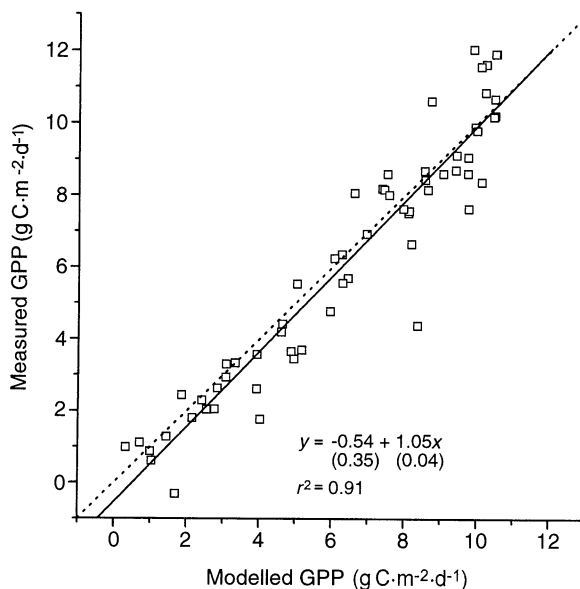

FIG. 2. Measured daily gross primary productivity at Harvard Forest, Massachusetts, during late summer 1992 (calculated from eddy flux and leaf, soil, and stem respiration measurements), plotted against predictions from the aggregated GPP model. The 1:1 line (– – –) and the regression line (———) are plotted on the figure. Numbers in parentheses below regression equations are standard errors of the corresponding coefficients.

whole accounts for a significant proportion of the storage and turnover of C (Oechel and Billings 1992). A series of manipulations undertaken over the past 7 yr has investigated ecosystem response to temperature, light and soil nutrients in the field (Chapin et al. 1995; L. C. Johnson et al., *unpublished manuscript*). Two wet-sedge tundra sites near Toolik Lake, Alaska (68°38′ N, 149°43′ W, elevation 760 m) were examined, one near the main inlet to the lake (the Inlet site), the other near the outlet (the Outlet site); the vegetation was dominated by rhizomatous sedges, mostly *Carex* and *Eriophorum* species. Experimental plots (5 × 10 m) were set up in August 1988. Our study focused on the greenhouse manipulation, the N × P fertilizer manipulation, and the control at each site.

Ecosystem-level fluxes were measured using a LI-COR 6200 Portable Photosynthesis system (LI-COR, Lincoln, Nebraska, USA) attached to a custom-made clear Plexiglas cuvette (Vourlitis et al. 1993; L. C. Johnson et al., *unpublished manuscript*). The cuvette was placed directly over the tundra and into standing water to form a seal, to provide a measurement of net ecosystem production (NEP). Measurements were also made with the cuvette shaded, to determine ecosystem respiration (R_E). The difference between NEP and R_E determined gross ecosystem production (GEP). All CO_2 flux measurements were made at the exact locations from which biomass quadrats were later harvested in July and August 1994. Integrating the GEP and photosynthetic photon flux density (PPFD) readings taken over the course of 24 h provided daily measures of these quantities. A correction factor was required for the Inlet site GEP estimates, because these sites showed a significant moss cover, the carbon fixation of which is not accounted for by the model. To estimate vascular plant GEP, we assumed that the proportion of total GEP accounted for by vascular plants was in the same ratio as vascular aboveground N mass to total aboveground N mass (vascular plus moss), measurements of which were available. Table 5 shows the values of the driving variables at each of the sites and treatments that are required for driving the aggregated model.

A linear regression of aggregated model GPP against measured values showed a significant correspondence (Fig. 3; $r^2 = 0.76$; $P < 0.05$). The intercept (1.03 ±

TABLE 5. Ecosystem and environmental variables measured on given days in 1994 at the experimental manipulation sites at Toolik Lake.

Site	Treatment	LAI	Mean foliar N (g/m²)	Mean daily temperature (°C)	Daily range of temperature (±°C)	Total daily irradiance (MJ· m⁻²·d⁻¹)	Day of year
Inlet	Control	0.2	3.3	17.1	5.7	10.5	200
Inlet	Greenhouse	0.4	3.1	19.8	8.3	8.7	200
Inlet	N + P	0.9	4.0	16.7	5.8	11.7	200
Outlet	Control	0.3	3.5	11.3	4.9	13.9	204
Outlet	Greenhouse	0.9	2.7	12.2	4.9	7.5	204
Outlet	N + P	1.7	3.6	11.0	4.9	14.3	204

Notes: For all sites, ambient $[CO_2]$ = 355 μmol/mol, leaf–soil water potential difference = -2.5 MPa, and canopy height = 0.5 m.

0.79) did not differ significantly from zero ($P < 0.05$), nor did the slope of the regression differ significantly from 1.0 (0.71 ± 0.20). The model parameters applied to the tundra sites were identical to those used for Harvard Forest in every respect. The only alteration was in the driving variables—average temperature and range, irradiance, LAI, foliar N, canopy height and day of year. Ambient CO_2 and Ψ_d remained unchanged. The model was not refitted or modified in any other way. The largest deviation was for the control treatment at the Inlet site; this is not easily explained. The aggregated model regularly generated lower predictions than the fine-scale model; we hypothesize that this resulted because of the low LAI values of the sedge sites. During the fitting procedure, sensitivity tests showed that
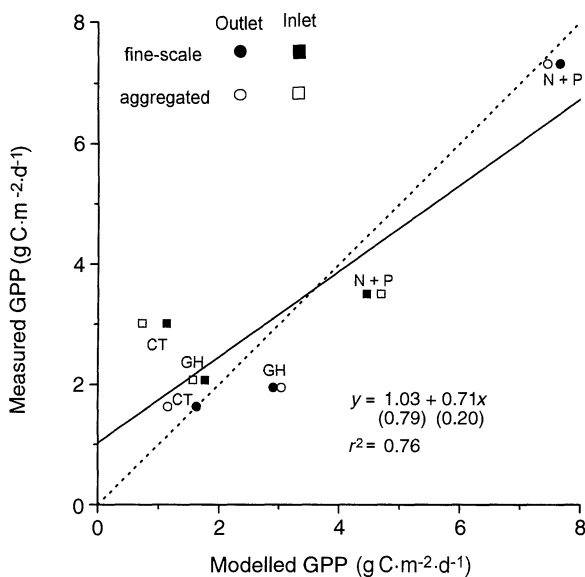

FIG. 3. Measured daily gross primary productivity at sites around Toolik Lake, Alaska, in 1994 plotted against aggregated and fine-scale model predictions. The 1:1 line (– – –) and the regression line (———) are plotted on the figure. CT are control sites, GH are greenhouse manipulation sites, and N+P are fertilized sites. Numbers in parentheses below regression equations are standard errors of the corresponding coefficients.

below an LAI of 2.0, the relative errors of fine-scale and aggregated model predictions tended to increase.

Unfortunately, the ranges of GPP in these data were not as wide as we wished for a rigorous test of the model. Also, because of the limited data set, the strength of the model fit in this test was dependent on the inclusion of the N+P outlet site—were this data point removed, the goodness of fit would be severely diminished. For this reason, we undertook a further independent test of the model.

The Oregon Transect

The Oregon Transect Ecosystem Research (OTTER) project (Peterson and Waring 1994) studied ecosystem function in a wide range of coniferous forest vegetation (Sites 1–6), and one deciduous site (Site 1A), arrayed along a 200-km transect at 44° N latitude (Table 6). Because of altitudinal and climate differences there is a wide range of productivity along this transect (Runyon et al. 1994). Meteorological stations at each of the sites (except site 6) provided year-round data on daily temperature and irradiance regimes. LAI was measured using a leaf area analyzer, a ceptometer, and the sapwood ratio method (Runyon et al. 1994). Foliage samples were collected and total N was measured colorimetrically (Matson et al. 1994). Seasonal variation in soil water potential was estimated from measurements of predawn leaf water potentials determined with a pressure bomb (Runyon et al. 1994). Only at sites 2, 5, and 6 did predawn water potentials reach critical levels that might constrain stomatal conductance (Runyon et al. 1994).

Measurements of GPP were not made at any of the sites, but many of the components of GPP were collected. We estimated annual GPP (in grams of carbon per square meter per year) from

$$GPP = NPP_A + NPP_B + R_{CA} + R_{CB} + R_{Msap} + R_{Mfol} + R_{Mroot} \qquad (10)$$

where NPP_A and NPP_B are aboveground and belowground net primary production, R_{CA} and R_{CB} are aboveground and belowground construction respiration, and R_{Msap}, R_{Mfol}, and R_{Mroots} are sapwood, foliage,

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TABLE 6. Ecosystem variables and annual environmental variables for the OTTER sites.

Site	Species	LAI	Mean foliar N (g/m²)	Mean annual temperature (°C)	Growing season† (day of year)	Annual total irradiance (MJ·m⁻²·y⁻¹)	Min. Ψ_s‡ (MPa)	Av. max. canopy ht. (m)
1	*Picea sitchensis, Tsuga heteropylla*	6.4	1.2	10.1	75–320	1934	−0.01	50
1A	*Almus rubra*	4.3	2.4	10.1	110–275	1934	−0.01	13
2	*Pseudotsuga menziesii*	5.3	1.8	11.2	75–280	2267	−1.7	40
3	*Tsuga heteropylla, Pseudotsuga menziesii*	8.6	1.7	10.6	75–305	2259	−0.01	30
4	*Tsuga mertensiana*	1.9	3.0	6.0	160–256	2088	−0.01	20
5	*Pinus ponderosa*	0.9	2.7	7.4	125–275	2735	−1.7	7
6	*Juniperus occidentalis*	0.4	5.8	9.1	125–275	2735	−2.5	10

† The period of maximum LAI occurs between these dates, defining the start and end of the growing season.

‡ Minimum soil water potential (Ψ_s) was estimated from measurements of minimum predawn leaf water potential (Runyon et al. 1994).

and fine roots maintenance respiration, respectively. NPP_A includes new foliage production and branch and stem growth; Runyon et al. (1994) provided estimates of these quantities. Belowground net primary production (NPP_B) was not measured directly; instead a relationship based on litterfall (Raich and Nadelhoffer 1989) was used to estimate total belowground allocation (i.e., net production plus growth and maintenance respiration; $NPP_B + R_{Mroot} + R_{CB}$). R_{CA} is estimated as 25% of NPP_A. Ryan et al. (1995) prepared estimates of sapwood maintenance respiration at Site 3 (western hemlock, Douglas-fir); the annual value is relatively small, ≈5% of estimated GPP. For the other sites we estimated R_{Msap} by assuming a similar ratio of R_{Msap} to NPP_A (≈18.5%). Foliage respiration (R_{Mfol}) was determined from total canopy N, daily temperature and temperature range, and relationships provided by Ryan (1991, 1995). In generating GPP estimates (Table 7), we had to make a number of assumptions. Our greatest uncertainty was associated with estimates of belowground allocation. Runyon et al. (1994) estimated litterfall from measurements of new growth on sampled branches, with a mass reduction of 15% for needles. Other studies (Nadelhoffer et al. 1995) have accounted

for abscission losses with a 10% reduction. This means that we may have underestimated belowground carbon allocation, and thus total estimated GPP.

Daily climate data from the site meteorological stations were used to run the unmodified aggregated model through the annual cycle. We assumed that on days where the temperature dropped below −2.0°C no C fixation occurred as a result of frost. LAI in the coniferous stands varied by ≈30% each year (Runyon et al. 1994). We hypothesized that LAI increased from its minimum value (70% of the measured maximum) once conditions were favorable (average daily temperatures exceeded 5°C), reaching the maximum value after 30 d. Once average temperatures fell below 5°C in the fall, LAI declined over the following 30 d to the minimum value. For the deciduous site, we used a similar procedure, varying LAI from 0 to its maximum value, but we estimated the start and end of the growing season based on a slightly more conservative average temperature threshold of 7°C. Seasonal measurements of area-based foliar N showed no or very few significant changes during the course of the year for all sites (Pierce et al. 1994), so we held foliar N concentrations constant throughout the simulations. Lassoie and Salo (1981) reported that for most coniferous species, predawn xylem pressure potentials of less than −1.5 MPa were associated with nearly complete stomatal closure. Thus, we set the minimum leaf water potential in the coniferous sites to −1.5 MPa. For the more drought-resistant *Juniperus occidentalis* we set Ψ_{lmin} to −2.5 MPa, and also for the deciduous *Alnus rubra*. Runyon et al. (1994) provided predawn xylem pressure potential data (a good proxy for soil water potential, Ψ_s) from May to October for sites 2, 5, and 6. We assumed an autumn recharge of soil water, and thus generated conjectural values for the remaining months. For each month we determined the value of Ψ_d, the maximum water potential difference, as the difference between Ψ_{lmin} and Ψ_s.

A comparison of GPP as estimated with the component method (Eq. 10) with that predicted by the ag-

TABLE 7. Calculation of annual gross primary productivity (GPP) using component analysis for the OTTER (Oregon Transect Ecosystem Research project) sites. All units are in g C·m⁻²·yr⁻¹.

Site	Above-ground NPP†	Above-ground R_c‡	Leaf R_m§	Sapwood R_m§	Below-ground C allocation	GPP
1	525	131	334	97	312	1400
1A	585	146	262	108	456	1558
2	580	145	453	107	380	1665
3	875	219	653	162	495	2404
4	255	64	278	47	236	879
5	75	19	88	13	168	364
6	45	11	84	8	154	302

† NPP = net primary productivity.
‡ R_c = construction respiration.
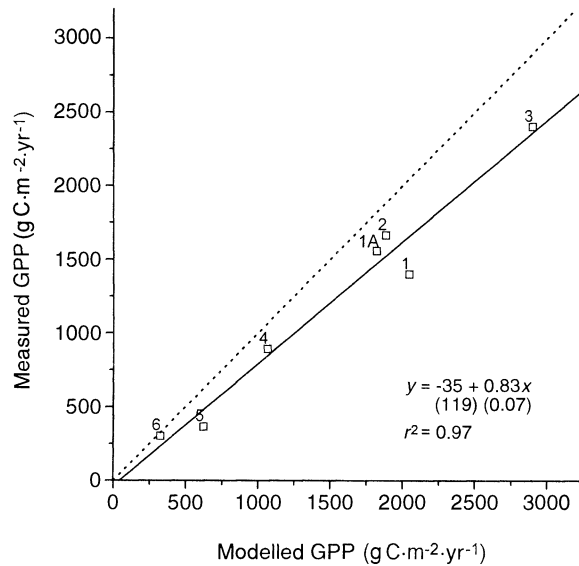§ R_m = maintenance respiration.

FIG. 4. For seven sites in the OTTER project, (Oregon, 1991) measured annual gross primary productivity is plotted against estimates of the aggregated model. Each site is identified by its code number (see Table 6 for details). The 1:1 line (– – –) and the regression line (———) are plotted on the figure. Numbers in parentheses below regression equations are standard errors of the corresponding coefficients.

gregated model (Eqs. 2–9) showed a strong correspondence (Fig. 4; $r^2 = 0.97$). The simple representation of soil water stress within the aggregated model seemed to effectively capture impacts on stressed sites (2, 5, and 6). The aggregated model tended to consistently predict higher GPP than the component analysis. This may have been due to a consistent underestimation of belowground C allocation in the component analysis, and the failure to include allocation to flowers, fruiting, and isoprene emissions.

While the model does incorporate the impact of tall canopies on reduced hydraulic conductance and thus GPP, site 1 still showed a relatively larger difference between measurement and prediction. This was an old-growth forest with large stems over 300 yr old; these trees may have greater maintenance respiration (from a high sapwood volume) and reduced carboxylation capacity (from an aging hydraulic system that further limits stomatal opening in the upper canopy). Incorporating these two factors might bring the two estimates into better agreement.

DISCUSSION

We have presented an aggregation protocol that should be applicable to a wide variety of process-based models. The protocol is as follows: (1) define the ranges of driving variables of interest for the aggregation; (2) use the fine-scale process model to extrapolate across this range of conditions; (3) sum or average the predictions from this extrapolation to the desired spatial and temporal scale; and (4) use these data to develop

aggregated coarse-scale relationships among the summed or averaged drivers and predictions in the same way that empirical data would be used to develop a phenomenological model. With this protocol, extrapolations are only made with the process-based, fine-scale model. Confidence in the predictions of the aggregated model are therefore derived directly from the underlying process-based model.

By comparing the requirements of the fine-scale and aggregated models we can gain insight into the process of scaling from leaves to the whole canopy, and from minutes to whole days. The fine-scale model includes detail on vertical distributions of foliar N, leaf area, temperature, wind speed, and humidity. The fine-scale model predicts significant differences in water stress, and thus C fixation, with height in the canopy. However, the aggregated model operates as a "big-leaf" and is effectively able to dispense with this detail. The fine-scale model takes account of hourly variation in long-wave, near infra-red, and photosynthetically active radiation. The aggregated model operates effectively with only integrated daily total short-wave radiation. The fine-scale model simulates multiple hydraulic pathways from soil to atmosphere, and balances atmospheric demand for water with the rate of supply from the soil, through varying stomatal opening. The aggregated model employs a single relationship that combines the impacts of atmospheric saturation deficit with soil water limitation.

Some variables required in the fine-scale model are completely discarded for the aggregated version. In generating the set of fine-scale model predictions with which to derive the aggregated model, we held wind speed constant at 2.0 m/s. Although measured wind speed varied day to day at Harvard Forest, both models made excellent predictions of GPP for this site, and also for the Alaskan and Oregon ecosystems, with a constant wind speed applied (directly to the fine-scale model, indirectly within the calibration of the aggregated model). We can conclude that wind speed and associated variations in leaf boundary layer conductance do not have a significant impact on daily GPP, and so these data are not required in any regional scaling project.

The fine-scale model is constrained by several biological variables that are hard to determine accurately, among others, fine-root length and dimensions, canopy capacitance, stem hydraulic conductance, species-specific parameter values for the Farquhar and Von Caemmerer photosynthesis model (1982), and mesophyll conductance. The aggregated model has dispensed with this detail to a great degree. We can hypothesize that variables have been discarded for either of two reasons: (1) The variable covaries strongly with another variable—only one of the two is required, or (2) GPP is not sensitive to variation in the parameter, so it can be discarded.

As an example of the first case, we would expect

GPP to be highly sensitive to variations in the photosynthetic parameters, which vary greatly between species (Wullschleger 1993). However, the aggregation procedure has managed to effectively capture the essential relationship between foliar N concentration and metabolic limits on photosynthesis. The model can be driven with foliar N data, and the more complex facets of metabolic C fixation and their associated variables can be ignored. This is demonstrated by the applicability of the model to ecosystems with very different species composition.

In the second case, there are indications that the sensitivity of the fine-scale model to some variables is relatively small. For example, we would expect coniferous forests to have markedly different hydraulic characteristics from the deciduous forests for which the model was calibrated. However, the soundness of the simulations along the Oregon transect indicate that this variability is not important, since the predictions are good with unchanged hydraulic constraints (i.e., the Harvard Forest calibration).

We undertook an analysis of the relative importance of individual drivers in reducing the errors of the fit of the aggregated to fine-scale model (Table 3). The analysis revealed the relative importance of the driving variables in determining GPP across a broad range of vegetation properties and climatic and edaphic conditions. Based on this analysis we would expect the global distribution of GPP to be most strongly affected by the distributions of irradiance and LAI (thus absorbed radiation appears to be the dominant factor). The impacts of temperature and humidity (related to temperature range) were substantially less than we expected—soil water availability was a stronger constraint on GPP than constraints connected with vapor pressure deficit.

We have shown that a complex, fine-scale canopy model can be very effectively simplified while still retaining its essential behavior. The aggregated model has been calibrated to operate under a very wide range of driving variables, including measures of ecosystem structure, meteorology, latitude, and season. We have also demonstrated that the most important driving variables are LAI and irradiance; soil moisture stress, foliar [N], and ambient $[CO_2]$ are secondarily important. We tested the robustness of this calibration against daily data collected under ecosystem manipulations in Alaskan wet-sedge tundra, and against annual data along a vegetation transect in Oregon. In both cases the aggregated model, unmodified from its Harvard Forest calibration, fitted the data well. We can be confident that we have included the key driving variables in our aggregated model necessary to make predictions of ecosystem GPP over a wide range of sites and conditions. With its relatively modest data requirements, many of which can be gathered from satellite and standard meteorological observations, the aggregated model should provide an effective tool for developing regional estimates of C uptake, and should be easily incorporated into regional models of C cycling.

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