Scaling gross ecosystem production at Harvard Forest with remote sensing: a comparison of estimates from a constrained quantum-use efficiency model and eddy correlation

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ABSTRACT

Two independent methods of estimating gross ecosystem production (GEP) were compared over a period of 2 years at monthly integrals for a mixed forest of conifers and deciduous hardwoods at Harvard Forest in central Massachusetts. Continuous eddy flux measurements of net ecosystem exchange (NEE) provided one estimate of GEP by taking day to night temperature differences into account to estimate autotrophic and heterotrophic respiration. GEP was also estimated with a quantum efficiency model based on measurements of maximum quantum efficiency (Ωmax), seasonal variation in canopy phenotype and chlorophyll content, incident PAR, and the constraints of freezing temperatures and vapour pressure deficits on stomatal conductance. Quantum efficiency model estimates of GEP and those derived from eddy flux measurements compared well at monthly integrals over two consecutive years ($R^2 = 0.98$).

Remotely sensed data were acquired seasonally with an ultralight aircraft to provide a means of scaling the leaf area and leaf pigmentation changes that affected the light absorption of photosynthetically active radiation to larger areas. A linear correlation between chlorophyll concentrations in the upper canopy leaves of four hardwood species and their quantum efficiencies ($R^2 = 0.99$) suggested that seasonal changes in quantum efficiency for the entire canopy can be quantified with remotely sensed indices of chlorophyll. Analysis of video data collected from the ultralight aircraft indicated that the fraction of conifer cover varied from $< 7\%$ near the instrument tower to about $25\%$ for a larger sized area. At $25\%$ conifer cover, the quantum efficiency model predicted an increase in the estimate of annual GEP of $< 5\%$ because unfavourable environmental conditions limited conifer photosynthesis in much of the non-growing season when hardwoods lacked leaves.

Key-words: canopy chlorophyll content; canopy photosynthesis; CO2 eddy flux; modelling; NDVI; quantum-use efficiency; remote sensing.

INTRODUCTION

In most ecosystem models the general assumption is made that photosynthesis by an entire canopy is usually light-limited and, as a result, that the assimilation rate can be assumed to be near linearly related to the absorbed flux density of photosynthetically active radiation (Jarvis & Leveielsen 1983). This assumption has been widely accepted, variation in the efficiency by which PAR is absorbed under diffuse and direct-beam solar radiation at varying solar zenith angles being taken into account (Charles-Edwards 1982; Wang, McMurtrie & Landsberg 1992). If solar radiation data over periods of months or longer are integrated, the linearity of canopy photosynthetic response to absorbed photosynthetically active radiation increases as differences in the beam fraction and solar zenith angle of incident PAR are balanced out (Wang & Polglase 1995). To date, support for a simple canopy light-absorption model has been provided mainly from studies on homogeneous canopies of single-species composition (Baker, Hesketh & Duncan 1972; McCree 1984; Caldwell et al. 1986).

Natural vegetation is often a mixture of species or varies in structure, in contrast to a homogeneous monoculture of crops or tree plantations. It is desirable therefore to test how well the linear light absorption model applies to vegetation composed of a mixture of species. We had such an opportunity at the Harvard Forest which is situated in the temperate forest region of the northeastern USA. There, long-term studies of physiology and ecology have been combined with continuous eddy flux data since 1990 which provide measures of whole-system net ecosystem exchange (NEE) and gross ecosystem production (GEP) (Wofsy et al. 1993).

Calculations of net ecosystem production showed that Harvard Forest was accumulating 2–4 Mg C ha$^{-1}$ annually in biomass and soil organic matter (Wofsy et al. 1993), an

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interpretation that may apply to a wide range of temperate forests (Tans, Fung & Takahashi 1990). To date, few ecosystem models have been scaled regionally to evaluate these predictions. Most models are not dynamic, in the sense that vegetation boundaries, phenology, and weather conditions are assumed to be stable from year to year (Melillo et al. 1993; Potter et al. 1994).

To make regional or global scale models more dynamic, there has been an effort to integrate satellite-derived data in a form useful for parametrizing and driving simplified ecosystem models. Current global satellite coverage can provide remotely sensed estimates of solar radiation, ambient air temperature, atmospheric humidity deficits and surface moisture conditions for areas of the order of 25–100 km² or larger (Dye & Goward 1993; Waring et al. 1993; Goward et al. 1994a; Prince & Goward 1995). In addition, spectral vegetation indices, calculated from the red (R) and near-infrared (NIR) portions of the spectrum, provide indicators of seasonal changes in the amount of green leaf cover (Kumar & Monteith 1982). Studies have shown that the normalized difference vegetation index (NDVI): (NIR-R)/(NIR + R)) is a linear to near-linear function of the fraction of photosynthetically active radiation (PAR) intercepted by many types of green vegetation (Asrar et al. 1984; Law & Waring 1994a,b; Goward et al. 1994a). Monthly integration of data is usually required to reduce errors to less than 5% in estimating solar radiation and to obtain cloud-free estimates of canopy properties and surface moisture conditions by remote sensing (Goward et al. 1994a). In combination, these remotely sensed variables are employed to provide time-integrated estimates of photosynthesis across landscapes for broadly similar types of vegetation, given knowledge of the apparent quantum efficiency of canopies and the extent to which environmental factors constrain stomatal conductance (Running et al. 1989; Sellers et al. 1992; Nemani, Pierce & Running 1993; Verma et al. 1993).

At Harvard Forest, all the requisite data required to drive the photosynthetic component of a whole-system model were available. A tower equipped with eddy-flux instrumentation provided an estimate of gross ecosystem production (GEP) that could be compared to independent estimates of GEP derived from a model based on measurements of maximum quantum efficiency (φₐ₅₃), seasonal variation in canopy leaf area index, leaf chlorophyll content, incident PAR, and restriction on CO₂ diffusion through stomata imposed by freezing temperatures, vapour pressure deficits and other environmental factors.

From an Oregon State University ultralight aircraft, video and spectroradiometer data were acquired seasonally to provide the necessary spatial resolution to characterize variation in conifer and deciduous hardwood cover and to document pigmentation and leaf area changes in the hardwood component of the canopy. With remotely sensed data obtained from the aircraft we gained an independent measure of phenology to compare with that obtained from ground observations. In this paper we compare predictions of monthly gross ecosystem production derived from the quantum efficiency model with those determined by eddy correlation and suggest how remotely sensed data can aid in scaling stand-level observations to larger areas.

**METHODS**

**Site description**

The study site was located in the Prospect Hill tract of Harvard Forest, north-central Massachusetts (42°54'N, 72°18'W; elevation 340 m). The forest, comprised of 50- to 70-year-old trees, regenerated following a hurricane in 1938 and has reached a height of 20–24 m and supports a leaf area index of between 3.5 and 4.0 during the growing season. At present, dominant species are red oak (Quercus rubra L.) and red maple (Acer rubrum L.), which together make up 80% of the total 30 m² ha⁻¹ of basal area. Some black birch (Betula lenta L.), white birch (Betula papyrifera Marsh.), yellow birch (Betula alleghaniensis Britton), black cherry (Prunus serotina Ehrh.), white pine (Pinus strobus L.), and hemlock (Tsuga canadensis L. Carr.) are also present, but together represent less than 20% of the total basal area and less than 10% of the 1300 stems ha⁻¹.

The climate is cool temperate (January mean weekly temperature -6°C, July mean 20°C), and humid, with precipitation distributed evenly throughout the year (annual mean 1100 mm). Summer drought rarely occurs. The terrain is moderately hilly, about 95% forested, with the nearest paved roads >1 km away and small towns >10 km away. Soils are mainly of the Gloucester series (fine loamy, mixed mesic Typic Dystrochrept) with a surface pH of 3.8 and a subsurface pH of 4.8 (Peterjohn et al. 1994).

**Meteorological data**

Meteorological sensors were installed at the top of a 30 m tower (Rohn 25G), 6–10 m above the top of the forest canopy (Wofsy et al. 1993). Data were logged on a computer situated in a climate-controlled shack 20 m from the base of the tower. Throughout the investigation, the system logged 60 min mean air temperature measured with an aspirated thermistor, relative humidity determined with an electrical-capacitance sensor, and horizontal photosynthetically active photon flux density obtained with a pair of silicon quantum sensors one above the canopy and the other below at a height of 8 m. The soil-surface temperature was also recorded using an array of potted thermistors. An integrated monthly measure of the fraction of light intercepted by the canopy (fIPAR) was subsequently calculated as 1 – the fraction of incident PAR that was transmitted through the canopy.

The observations were interrupted by occasional extended gaps as a result of equipment failure, and by more frequent gaps associated with calibration, maintenance or data transfer. The meteorological data for 1991 were comparatively patchy, with 20% missing, while 10% were missing for 1992. In the current analysis we replaced miss-
ing meteorological data with the mean for that hour plus and minus 2 d.

**Eddy flux measurements**

Eddy-correlation measurements of net ecosystem CO₂ exchange were initiated at Harvard Forest in April 1990 on the same 30 m tower where meteorological instruments were installed. A three-axis sonic anemometer (Applied Technologie) and a closed-path infrared gas analyser (IRGA, LiCor 6262 or 6251) were used to sample simultaneously the vertical wind speed and the CO₂ mixing concentration at 30 m. The raw signals were digitized at 4 Hz and these data logged to disk for subsequent analysis. Air was drawn to the instrument shelter down a 50 m tube and through the IRGA at 6 to 8 dm³ min⁻¹, introducing a lag of several seconds which we adjusted for in the flux calculation (Wofsy et al. 1993; Fan et al. 1995). In computing the flux we accounted for the orientation of the streamlines by rotation to the plane where the mean vertical wind speed was zero (McMillen 1988).

A series of simulations, laboratory tests, and spectral analyses indicated a small underestimation of flux caused by the reliance on a closed path sensor for the CO₂ measurement (overall 90% response faster than 1 s). We corrected for this error by scaling the measured CO₂ flux by the ratio of the measured raw sensible heat flux to the sensible heat flux calculated after filtering the temperature signal to simulate an instrument with limited high-frequency response (Leuning & King 1992; Wofsy et al. 1993). This correction was generally small (<10%) because most flux is carried by eddies with a frequency of 0.1 to 0.002 Hz. Uncertainty associated with calibration was less than 10%. Additionally, we anticipate <10% underestimation of flux caused by finite sensor path length and spatial separation (Baldocchi & Meyers 1991; Lee & Black 1994). Data gaps occurred occasionally, particularly following lightning strikes. For these gaps we substituted values from hourly averages determined from the closest 3 d set of data.

Changes in atmospheric stability may cause shifts in the quantity of CO₂ stored in the air space below the sensor array, decoupling the flux through the eddy plane from biotic activity. We accounted for storage by monitoring the change in CO₂ in the air space beneath the sensor array, and decoupling the flux through the eddy plane from biotic activity. We accounted for storage by monitoring the change in CO₂ in the air space beneath the sensor array, with a second IRGA to sample sequentially inlets at 29, 24, 18, 12, 5, 3, 1 and 0.5 m. We then applied the rate of CO₂ storage change in combination with the eddy flux measurement to calculate net ecosystem exchange (NEE) (Wofsy et al. 1993).

In the convention of eddy-flux measurements, photosynthesis is a negative flux into the system and respiration is a positive flux out. Net ecosystem exchange measured during daylight hours includes gross photosynthesis (Pₚ) photosynthesis (Pₚ) respiration (Rₘ), maintenance respiration (Rₘ) and growth respiration (Rₚ) of autotrophic plants as well as all sources of heterotrophic respiration (Rₜ).

\[
\text{Day NEE} = Pₚ + Rₚ + Rₘ + Rₕ. 
\]

At night the photosynthetic terms, Pₚ and Rₚ, are absent. Night NEE = Rₘ + Rₕ = Rₜ.

where Rₜ is the total ecosystem respiration, Rₘ and Rₕ are largely controlled by temperature, allowing us to approximate Rₜ during daylight periods as a function of temperature. The relation between Night NEE during well mixed periods (Fan et al. 1995) and soil temperature (Tₛ) was

\[
\text{Day } Rₜ (\mu \text{mol m}^{-2} \text{s}^{-1}) = Tₛ (0.19) + 0.795. 
\]

Gross ecosystem production (GEP) is then calculated as

\[
\text{GEP} = \text{Day NEE} - \text{Day } Rₜ = Pₚ + Rₚ. 
\]

Day Rₜ is typically 20–30% of Day NEE. Consequently, large uncertainties in Day Rₜ have a relatively small effect on the accuracy of GEP.

**Vegetation measurements**

The basal area of tree species was determined by measuring tree diameters at breast height (1.37 m) in a 50 m x 50 m plot centred 100 m south of the eddy flux tower. Within the same area, leaf litter was collected in 35 0.122 m² traps to estimate the leaf area index (LAI) of deciduous hardwoods and the relative contribution of each species. Fewer than 10 white pine tree stems were present within the sampling area and were excluded from the analysis. Independent estimates of maximum and minimum LAI, which did include the conifers, were made in the same area using a LiCor LAI 2000 Plant Canopy Analyzer (Welles & Norman 1991). Phenological observations were provided by John O’Keefe at Harvard Forest, who recorded the dates of initial bud break, when leaves were at 75 and 95% of full expansion, when autumn colour was first observed, and when 10–25 and 98% of leaves had been shed. These data were available for all major tree species but we referenced whole-canopy phenology to only the two dominant species, red oak and red maple.

Apparent maximum quantum efficiency was determined in August when leaves were fully expanded on four hardwood species from samples of representative leaves growing near the top of the canopy. A Li-Cor 6200 gas exchange system (Lincoln, NE, USA) equipped with a 0.25 dm³ cuvette and a PAR sensor was used to obtain measurements of dark respiration, net photosynthesis and photon flux density. Neutral shade cloth incrementally reduced the light level incident on the leaf surface, allowing for repeated measurements of the same leaves at different light levels. Leaves were allowed to acclimate to the light levels for at least 5 to 8 min before instantaneous gas exchange measurements were taken. For red oak and red maple, measurements were made on 10 leaves located in the upper canopy and an additional 10 in the lower canopy strata (five leaves at both heights on two trees of each species). For other species, measurements were made on five leaves from each strata (one tree per species). Apparent maximum quantum efficiency and maximum
beneath the two types of vegetation is presented in Fig. 2. We emphasize that the regression equation for Fig. 2 was developed for green foliage only and is not appropriate for application during leaf senescence because of the influence of chlorophyll on red reflectance. These restricted clear-weather measurements were not appropriate for comparison with daily mean values of transmitted PAR acquired from sensors near the tower.

The maximum quantum efficiency determined in mid-summer varied nearly 2-fold, from a low value of 0.026 mol C mol⁻¹ photon for *Acer rubrum* to a high of 0.047 mol C mol⁻¹ photon for *Betula alleghaniensis* (Table 2). When weighted by the representative basal area, which was 50% *Quercus rubra* and 30% for *Acer rubrum*, the average quantum efficiency at mid-summer was 0.0298 mol C mol⁻¹ photon or 0.36 g C mol⁻¹ photon (*Q*ₘₐₓ). We observed on 10 October 1991 that the NDVI values acquired from the ultralight aircraft would suggest that a fully green canopy had been reduced in leaf area since July by ~50% (from Fig. 2: NDVI = 0.61 is equivalent to an *f*ᵢₚᵢₚₐᵢ value of 0.63, which corresponds to an LAI ~2.0). To account for seasonal differences in incident solar radiation, we calculated the ratio of the reflectance values recorded in the red (655–665 nm) and near-infrared (785–795 nm) bands against the total reflectance summed for all bands (400–900 nm). This normalizing procedure showed that reflectance in the red band increased from 3 to 6% between July and October, indicating a considerable reduction in chlorophyll absorption. Over the same period, near-infrared reflectance decreased by less than 30%, from 35 to 25–35% (R. W. McCreight, unpublished results). Phenological observations confirmed that only 10–25% of the leaves had fallen by 3 October 1991. The video image acquired on 10 October also confirmed that a dense canopy of hardwoods leaves was still present but in nearly full autumn colour (Fig. 3). We therefore interpreted the decrease in the hardwood NDVI in October (Table 1) to reflect mainly a reduction in chlorophyll absorption, which was confirmed by mid-September measurements that were nearly 50% below those measured in mid-August (Table 3).

Table 1. Seasonal variation in the fraction of photosynthetically active radiation intercepted (*f*ᵢₚᵢₚᵢ) by a canopy of deciduous hardwoods and evergreen conifers is compared with the normalized difference vegetation index (NDVI) determined from measurements made at an altitude of 300 to 400 m with an airborne spectroradiometer. Standard errors (SE) are provided. Sample sizes varied as noted *

<table>
<thead>
<tr>
<th>Date</th>
<th>Type</th>
<th><em>f</em>ᵢₚᵢₚᵢ</th>
<th>SE</th>
<th>NDVI</th>
<th>SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>April</td>
<td>hardwoods</td>
<td>0.504</td>
<td>0.024</td>
<td>0.430</td>
<td>0.011</td>
</tr>
<tr>
<td>April</td>
<td>conifers</td>
<td>0.918</td>
<td>0.081</td>
<td>0.840</td>
<td>0.009</td>
</tr>
<tr>
<td>May</td>
<td>hardwoods</td>
<td>0.495</td>
<td>0.026</td>
<td>0.590</td>
<td>0.029</td>
</tr>
<tr>
<td>May</td>
<td>conifers</td>
<td>0.913</td>
<td>0.081</td>
<td>0.850</td>
<td>0.006</td>
</tr>
<tr>
<td>July</td>
<td>hardwoods</td>
<td>0.845</td>
<td>0.033</td>
<td>0.880</td>
<td>0.002</td>
</tr>
<tr>
<td>July</td>
<td>conifers</td>
<td>0.933</td>
<td>0.028</td>
<td>0.870</td>
<td>0.003</td>
</tr>
<tr>
<td>October</td>
<td>hardwoods</td>
<td>–</td>
<td>–</td>
<td>0.610</td>
<td>0.020</td>
</tr>
<tr>
<td>October</td>
<td>conifers</td>
<td>–</td>
<td>–</td>
<td>0.860</td>
<td>0.005</td>
</tr>
</tbody>
</table>


Table 2. Maximum quantum efficiency (Q<sub>max</sub>) in mol C mol<sup>-1</sup> photon, and in g C mol<sup>-1</sup> photon) measured on five sets of individual leaves from the tops of canopies, and the fraction of total site basal area (BA)

<table>
<thead>
<tr>
<th>Species</th>
<th>BA fraction</th>
<th>Q&lt;sub&gt;max&lt;/sub&gt; (mol C mol&lt;sup&gt;-1&lt;/sup&gt; photon)</th>
<th>Q&lt;sub&gt;max&lt;/sub&gt; (g C mol&lt;sup&gt;-1&lt;/sup&gt; photon)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Quercus rubra</td>
<td>0.50</td>
<td>0.0297</td>
<td>0.3564</td>
</tr>
<tr>
<td>Acer rubrum</td>
<td>0.30</td>
<td>0.0255</td>
<td>0.3060</td>
</tr>
<tr>
<td>Betula papyrifera</td>
<td>0.05</td>
<td>0.0548</td>
<td>0.0472</td>
</tr>
<tr>
<td>Betula alleghaniensis</td>
<td>0.05</td>
<td>0.0472</td>
<td>0.5664</td>
</tr>
<tr>
<td>Species-weighted mean</td>
<td></td>
<td>0.0298</td>
<td>0.3576</td>
</tr>
</tbody>
</table>

canopy leaves was linear with an R<sup>2</sup> of 0.99 (Fig. 4). These results suggest that seasonal estimates of NDVI or related reflectance indices may provide an integrated estimate of Q<sub>max</sub> for forests of mixed composition.

The constrained modelled quantum efficiency (Q<sub>e</sub>) for conifers shown in Fig. 5, remained above 0.3 g C mol<sup>-1</sup> photon from April to October in both 1991 and 1992. The VPD proved to be only a minor constraint, reducing monthly net photosynthesis by a maximum of 8% in May 1991 and 6% in June 1992. Freezing temperatures reached a maximum constraint of 82% for conifers in January 1991 and 86% in February 1992. The combined climatic constraints resulted in estimates of Q<sub>e</sub> for conifers which ranged from 0.07 g C mol<sup>-1</sup> photon in January to a maximum of 0.36 g C mol<sup>-1</sup> photon in September 1991, and from 0.05 g C mol<sup>-1</sup> photon in February to 0.36 g C mol<sup>-1</sup> photon in September 1992 (Fig. 5). The derived Q<sub>e</sub> values were the same for hardwoods when green leaves were on the trees as for conifers, because the same quantitative environmental constraints were applied.

The quantum-use efficiency model estimates of GEP by hardwoods and conifers within the 125 x 125 m area around the tower during 1991 ranged from 0.45 g m<sup>-2</sup> month<sup>-1</sup> in January to 351 g m<sup>-2</sup> month<sup>-1</sup> in June (Table 4). For 1992, the range was from 0.55 g m<sup>-2</sup> month<sup>-1</sup> in February to 304 g m<sup>-2</sup> month<sup>-1</sup> in July. The annual sums were 1476 g m<sup>-2</sup> in 1991 and 1305 g m<sup>-2</sup> in 1992. The hardwoods accounted for 1328 g m<sup>-2</sup> in 1991, and 1177 g m<sup>-2</sup> in 1992 (90% of total).

Comparison of monthly GEP calculated from the quantum-use efficiency model using the standard VPD constraints versus those calculated from the flux estimates of VPD constraints showed no significant difference between

Table 3. Seasonal changes in chlorophyll concentrations and specific leaf area (SLA) with standard deviations (SD) determined on 5–10 leaves collected from the top and lower canopy in August and September 1991

<table>
<thead>
<tr>
<th>Species</th>
<th>Strata</th>
<th>Chl (mg g&lt;sup&gt;-1&lt;/sup&gt;)</th>
<th>SD (mg g&lt;sup&gt;-1&lt;/sup&gt;)</th>
<th>SLA (mg cm&lt;sup&gt;-2&lt;/sup&gt;)</th>
<th>SD (mg cm&lt;sup&gt;-2&lt;/sup&gt;)</th>
<th>Chl (mg m&lt;sup&gt;2&lt;/sup&gt;)</th>
</tr>
</thead>
<tbody>
<tr>
<td>August</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>red oak</td>
<td>lower</td>
<td>6.88</td>
<td>1.80</td>
<td>5.46</td>
<td>0.96</td>
<td>376</td>
</tr>
<tr>
<td>red oak</td>
<td>upper</td>
<td>4.37</td>
<td>0.84</td>
<td>8.22</td>
<td>0.87</td>
<td>360</td>
</tr>
<tr>
<td>red maple</td>
<td>lower</td>
<td>7.24</td>
<td>1.11</td>
<td>5.05</td>
<td>0.60</td>
<td>366</td>
</tr>
<tr>
<td>red maple</td>
<td>upper</td>
<td>3.52</td>
<td>0.66</td>
<td>9.76</td>
<td>1.06</td>
<td>343</td>
</tr>
<tr>
<td>white birch</td>
<td>lower</td>
<td>6.34</td>
<td>0.43</td>
<td>5.67</td>
<td>0.49</td>
<td>360</td>
</tr>
<tr>
<td>white birch</td>
<td>upper</td>
<td>4.65</td>
<td>0.24</td>
<td>8.65</td>
<td>0.84</td>
<td>402</td>
</tr>
<tr>
<td>yellow birch</td>
<td>lower</td>
<td>9.15</td>
<td>0.48</td>
<td>4.10</td>
<td>0.37</td>
<td>375</td>
</tr>
<tr>
<td>yellow birch</td>
<td>upper</td>
<td>4.57</td>
<td>0.55</td>
<td>9.83</td>
<td>1.21</td>
<td>449</td>
</tr>
<tr>
<td>August Average</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>379 ± 33</td>
</tr>
</tbody>
</table>

| September  |        |                          |                        |                          |                        |                        |
| red oak    | lower  | 2.66                     | 1.65                   | 4.92                     | 0.72                   | 131                    |
| red oak    | upper  | 1.70                     | 0.64                   | 8.96                     | 0.79                   | 152                    |
| red maple  | lower  | 4.57                     | 0.64                   | 5.79                     | 1.44                   | 264                    |
| red maple  | upper  | 2.45                     | 0.56                   | 8.72                     | 1.37                   | 214                    |
| white birch| lower  | 3.31                     | 1.24                   | 6.94                     | 1.28                   | 230                    |
| white birch| upper  | 2.03                     | 0.50                   | 8.76                     | 0.85                   | 178                    |
| yellow birch| lower | 7.14                     | 0.71                   | 3.55                     | 0.25                   | 254                    |
| yellow birch| upper | 2.73                     | 1.13                   | 5.61                     | 0.53                   | 153                    |

* P = 0.0002

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estimates. Monthly GEP estimates from the quantum-use efficiency model and from the flux residual approach were also similar throughout the year (Figure 6, Table 4). A linear regression of monthly GEP estimated using the two separate approaches showed a high correlation (Fig. 7; 1991 $R^2 = 0.97$; 1992 $R^2 = 0.99$). The slope was slightly, but significantly, different from unity in 1992 ($P = 0.01$), but not in 1991 ($P = 0.11$). The intercept was essentially zero in both years ($P = 0.52$ for both years).

When conifer cover was increased from 7% for the 125 $\times$ 125 m area to 25% representative of larger areas up to 1000 $\times$ 1000 m, the model predicted a maximum monthly increase in photosynthesis during the months of April and October of 14 to 18 g C m$^{-2}$ when hardwood trees were leafless (data not shown). At these times temperatures were still above freezing and PAR was well above the light compensation point for conifers (Fig. 1). Model estimates of annual GEP increased by only 4-5%, to 1525 g m$^{-2}$ year$^{-1}$ in 1991 and to 1369 g m$^{-2}$ year$^{-1}$ in 1992 by an increase in conifer cover from 7 to 25%.
The quantum-use efficiency model requires an accurate estimate of the apparent maximum quantum efficiency derived from cuvette gas-exchange measurements in the upper, most active canopy strata. We were fortunate to have tower access and to sample on days with high humidity so that VPD had little effect on stomata and thus $Q_{\text{max}}$. In more arid environments, cuvettes with environmental controls would be required to obtain maximum values of quantum efficiency. The weighting by species fraction of the total site basal area appears to be a reasonable approach to estimating the average $Q_{\text{max}}$. The oak and maple leaves collected in litter traps for both 1991 and 1992 represented 75–90% of the total leaf area collected whereas their basal area was 80% of the total (conifer basal area was ~10% but is not listed in Table 3).

In more open canopies, or canopies with lower quantum efficiencies, the assumption of linearity between light interception and photosynthetic activity may not be as valid as a curvilinear light-saturation model (McCree...
thesis in the preceding 1 to 24 h affected observed rates (M. L. Goulden, unpublished results).

In applying the quantum efficiency model, we assumed that common physiological thresholds apply to all species. We also ignored the possibility of delayed response to subfreezing or abnormally high temperatures (Leverenz & Öquist 1987; Bassow, McConnaughay & Bazzaz 1994). We recognize that species differ in the rates in which their stomata respond to light fluctuations, VPD and other environmental factors (Schulze et al. 1994). Because hourly data are integrated over monthly periods, however, errors in determining physiological thresholds are less critical than for models that predict in shorter time steps.

In this study, the major environmental constraint on canopy photosynthesis was IPAR. Subfreezing tempera-

1984; Hollinger et al. 1994). With a monthly resolution, it seems appropriate to treat the canopy as a single unit, particularly when \( f_{IPAR} \) values are acquired continuously and include overcast and clear sky conditions. Other studies have demonstrated that in moderately dense deciduous hardwood canopies, near-linear relations exist between light conditions and leaf mass \( m^{-2} \) foliage, nitrogen content \( m^{-2} \) of foliage, and photosynthetic capacity (Ellsworth & Reich 1993). Similar reports have also been published for evergreen hardwoods (Hollinger 1989) and for conifers (Oren et al. 1986), suggesting that estimates of quantum efficiency may be similar for leaves throughout closed canopies (Wang & Polglase 1995).

We were concerned that high photosynthetic rates on one day might cause accumulations of starch that would lead to photosynthetic inhibition on proceeding days (Luxmoore 1991). From inspection of data, however, we found little indication that previous high rates of photosyn-

Figure 6. Monthly integrated estimates of gross ecosystem production (GEP) made with the constrained quantum-use efficiency model agreed well with those derived from continuous flux measurements of \( CO_2 \) in both 1991 (a) and 1992 (b). - triangles, flux estimate; - squares, model estimate.

Figure 7. The regression of monthly integrated estimates of gross ecosystem production (GEP) made by the constrained quantum-use efficiency model was linearly related to monthly integrated values obtained from ecosystem flux measurements at the tower in both (a) 1991 (\( y = -7.365 + 1.112x; R^2 = 0.97 \)) and (b) 1992 (\( y = -3.775 + 1.09x; R^2 = 0.99 \)).
tures had a significant effect only on the conifers during mid-winter at the time deciduous trees were leafless. Vapour pressure deficits were not extreme during the summer and therefore had little effect on $Q_c$. VPD and subfreezing temperatures restrict photosynthesis by 50–75% in shrub and evergreen forest vegetation in temperate regions such as the Pacific Northwest of the USA (Runyon et al. 1994; Law & Waring 1994a) and to a somewhat lesser extent on the South Island of New Zealand (Hollinger et al. 1994).

Good agreement between the constrained quantum-use efficiency estimates of GEP and those determined from two years of eddy flux measurements further supports the value of integrating at monthly time steps. It is not reasonable to expect model predictions to agree well with hourly or daily measurements of photosynthesis because varying quantities of direct and diffuse radiation influence photosynthetic efficiency differently. Diffuse light casts less shadow and therefore penetrates more efficiently through canopies. As a result, photosynthetic rates may not decrease as much as expected (Sheehy & Chapas 1976; Hollinger et al. 1994; Fan et al. 1995). Our approach may have partly solved this problem by obtaining $f_{\text{PAR}}$ values under a range of cloud conditions each month and by integrating model estimates of photosynthesis at monthly intervals.

We recognized that flux measurements taken from a single stationary tower may not represent gas exchange from a large forest (Hollinger et al. 1994). When conifers are clumped in their distribution, the wind direction may have a major influence on their contribution to area-wide fluxes. Similarly, restricted area sampling of $f_{\text{PAR}}$ measurements can bias estimates of photosynthesis if the sampling is not representative of the larger area. Both of these problems can be solved in part by measuring fluxes and remotely sensing canopy properties from aircraft (Dejardins et al. 1982; Spanner et al. 1994).

Scaling of the quantum-use efficiency model to larger areas may be accomplished through satellite or airborne estimates of $f_{\text{PAR}}$ and $Q_{\text{max}}$. Satellite estimates of $f_{\text{PAR}}$ require atmospheric correction, in particular for visible wavelengths. Low-altitude airborne sensors provide an advantage by acquiring reflectance data with little atmosphere between the ground and the sensor. Data acquired from aircraft can also validate atmospheric corrections modelled for satellite data (Goward et al. 1994a). In regions where snow cover is likely, NDVI estimates would be misrepresentative of canopy properties. We recommend obtaining minimum estimates of $f_{\text{PAR}}$ for the year by concentrating observations on clear days in the spring or autumn when deciduous trees are not in leaf to minimize effects of snow cover. Where evergreens dominate, seasonal variation in leaf area is often less than 30% (Spanner et al. 1994).

The potential exists for scaling the quantum-use efficiency model to biomes and the globe, as suggested by Running & Hunt (1993). A physiological model (BIOME-BGC) is available to estimate $Q_c$ from climatic data and certain biome-specific assumptions about nitrogen, carbon, and water movement through the system (Running et al. 1994). Meteorological data are also necessary as driving variables in this approach, and have been successfully estimated across mountainous topography where temporary weather stations were installed for validation (Glassy & Running 1994). An alternative would be to apply the simplified constraints of freezing temperature, drought, and high VPD to $Q_{\text{max}}$, using remote sensing to estimate the meteorological variables as well as $f_{\text{PAR}}$ and incident PAR (Goward et al. 1994a; Prince & Goward 1995).

We recommend that monthly resolution models of net photosynthesis and other ecosystem properties should be tested where continuous flux measurements are being made throughout the year. Harvard Forest is one of the first sites to attempt these long-term measurements (Wofsy et al. 1993). To scale predictions to larger areas, remote sensing of red and near-infrared reflectance, coupled with video analysis to resolve variation in deciduous and evergreen cover, showed promise as a viable approach at Harvard Forest.

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