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Response of total night-time respiration to differences in total daily photosynthesis for leaves in a *Quercus rubra* L. canopy: implications for modelling canopy CO_2 exchange

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Abstract

Measurements of photosynthesis and respiration were made on leaves in summer in a *Quercus rubra* L. canopy at approximately hourly intervals throughout 5 days and nights. Leaves were selected in the upper canopy in fully sunlit conditions (upper) and in the lower canopy (lower). In addition, leaves in the upper canopy were shaded (upper shaded) to decrease photosynthesis rates. The data were used to test the hypothesis that total night-time respiration is dependent on total photosynthesis during the previous day and that the response is mediated through changes in storage in carbohydrate pools. Measurements were made on clear sunny days with similar solar irradiance and air temperature, except for the last day when temperature, especially at night, was lower than that for the previous days. Maximum rates of photosynthesis in the upper leaves (18.7 $\mu mol\, m^{-2}\, s^{-1}$) were approximately four times higher than those in the lower leaves (4.3 $\mu mol\, m^{-2}\, s^{-1}$) and maximum photosynthesis rates in the upper shaded leaves (8.0 $\mu mol\, m^{-2}\, s^{-1}$) were about half those in the upper leaves. There was a strong linear relationship between total night-time respiration and total photosynthesis during the previous day when rates of respiration were normalized to a fixed temperature of 20 °C, removing the effects of temperature from this relationship. Measurements of specific leaf area, nitrogen and chlorophyll concentration and calculations of the maximum rate of carboxylation activity, V_{cmax}, were not significantly different between upper and upper shaded leaves 5 days after the shading treatment was started. There were small, but significant decreases in the rate of apparent maximum electron transport at saturating irradiance, J_{max} ($P > 0.05$), and light use efficiency, ε ($P < 0.05$), for upper shaded leaves compared with those for upper leaves. This suggests that the duration of shading in the experiment was sufficient to initiate changes in the electron transport, but not the carboxylation processes of photosynthesis. Support for the hypothesis was provided from analysis of soluble sugar and starch concentrations in leaves. Respiration rates in the upper shaded leaves were lower than those expected from a relationship between respiration and soluble sugar concentration for fully exposed upper and lower leaves. However, there was no similar difference in starch concentrations. This suggests that shading for the duration of several days did not affect sugar concentrations but reduced starch concentrations in leaves, leading to lower rates of respiration at night. A model

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was used to quantify the significance of the findings on estimated canopy CO_2 exchange for the full growing season. Introducing respiration as a function of total photosynthesis on the previous day resulted in a decrease in growing season night-time respiration by 23% compared with the value when respiration was held constant. This highlights the need for a process-based approach linking respiration to photosynthesis when modelling long-term carbon exchange in forest ecosystems.

Keywords: carbohydrate pools, carbon exchange, modelling, red oak, shading

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Introduction

Models incorporating the biophysical processes regulating the exchange of energy, water vapour and CO_2 between ecosystems and the atmosphere are required to quantify rates of exchange and identify the environmental variables limiting the exchange. There is considerable interest in applying models to provide estimates of the rates of CO_2 exchange at large spatial and temporal scales (Lloyd *et al.*, 1995; Sellers *et al.*, 1997) and to predict the impacts of elevated atmospheric CO_2 partial pressure and temperature (IPCC, 2001) on the global carbon balance.

Net CO_2 exchange is the small difference between the two large fluxes of photosynthesis and respiration, and variability in the carbon balance of forests has been accounted for largely by differences in ecosystem respiration (Valentini *et al.*, 2000). While the largest component of respiration for forest ecosystems is attributable to processes in the soil (Law *et al.*, 2001), night-time respiration from leaves is an important component of carbon balance and can account for 10–25% of daily photosynthesis, with the proportion increasing in older trees (Ryan *et al.*, 1994). Models based on biochemical processes of photosynthesis (Farquhar *et al.*, 1980) and the coupling of photosynthesis with stomatal conductance (Collatz *et al.*, 1991; Baldocchi & Harley, 1995; Leuning *et al.*, 1995; de Pury & Farquhar, 1997) have been used successfully to estimate rates of CO_2 exchange for canopies when compared with independent measurements using the eddy covariance technique (Dang *et al.*, 1998; Law *et al.*, 2000; Wilson *et al.*, 2001). There is, however, some concern about the reliability of direct measurements of ecosystem respiration at night at sites where wind speed is low or where air drainage is pronounced (Law *et al.*, 1999). This emphasizes the need for developing and testing models describing both photosynthesis and night-time respiration. There is general recognition that the mechanistic processes of respiration are poorly represented in models of net CO_2 exchange for canopies (Cannell & Thornley, 2000; Dewar, 2000; Tjoelker *et al.*, 2001). Respiration is often partitioned into 'growth' and 'maintenance' components and related to environmental variables, particularly temperature (Amthor, 2000), but the rate of respiration at a set base temperature for leaves is usually held constant (McMurtrie & Wang, 1983; Leuning *et al.*, 1995, Whitehead *et al.*, 2004) or allowed to vary seasonally in relation to measured, but unexplained, values (Wilson *et al.*, 2001).

Respiration is much more sensitive to temperature than photosynthesis (Amthor, 1989). However, contrary to the prediction from models based on short-term responses that the proportion of respiration to photosynthesis will increase with increasing temperature (Ryan *et al.*, 1994), Gifford (1995) showed that this ratio did not change with growing season temperature for a range of plants and provided evidence from the literature showing that the ratio is conservative (Gifford, 2003). Dewar *et al.* (1999) accounted for this by proposing a model linking the rate of respiration with photosynthesis through carbohydrate supply and demand. This model was able to incorporate acclimation responses to changes (time period days to weeks) in temperature (Dewar *et al.*, 1999) and variable light conditions (Dewar *et al.*, 1998), subsequently incorporating biochemical processes (Dewar, 2000).

Support for a relationship between night-time respiration and photosynthesis during the previous day, independent of temperature, is based on a number of studies with crop plants (Ludwig *et al.*, 1965, 1975; André *et al.*, 1982; Azcón-Bieto & Osmond, 1983; Amthor, 1989). Higher rates of dark respiration at night, resulting from high rates of photosynthesis on the previous day, have been attributed to the positive relationship between photosynthesis and carbohydrate concentrations in leaves. Higher concentrations of carbohydrates lead to increased energy available for respiration, but the mechanism is not entirely dependent on substrate supply and may also be driven by the demand for respiratory products (Amthor, 1989).

Evidence from forest canopies shows that rates of photosynthesis and respiration for foliage adapted to fully illuminated conditions are higher than those for foliage adapted to shaded conditions (Brooks *et al.*, 1996) and that rates of photosynthesis and respiration

are broadly correlated for species growing across a wide range of conditions (Reich *et al*., 1998). These adaptive responses are positively correlated with foliage nitrogen concentration (Ryan, 1995; Niinemets & Tenhunen, 1997) resulting from the close association of nitrogen and the photosynthetic enzyme Rubisco (Evans, 1989). Rates of respiration and the response of respiration to temperature are known to vary with canopy position (Bolstad *et al*., 1999; Turnbull *et al*., 2003) and in relation to leaf nitrogen concentration (Griffin *et al*., 2001; Tissue *et al*., 2002). Seasonal changes in the rate of respiration, independent of temperature, were higher in early summer when new foliage was expanding than in winter in *Pinus ponderosa* (Law *et al*., 1999).

To improve models of net CO_2 exchange for forests, there is a need to determine the relationships between daily changes in respiration and photosynthesis in canopies associated with variable light and temperature conditions, rather than differences associated with long-term adaptation. Such an approach is also relevant for modelling the longer-term response of net CO_2 exchange to increasing night-time temperature (IPCC, 2001) and the fraction of diffuse radiation (Roderick *et al*., 2001) associated with global climate change. In this paper, we sought to reveal the relationship between photosynthesis and respiration at the leaf scale over a period of several days. This was achieved by making measurements of photosynthesis and respiration at hourly intervals throughout the period in the canopy of a mixed oak forest dominated by *Quercus rubra* during summer. Measurements were made on fully sunlit leaves in the upper canopy (upper), on leaves exposed to natural low irradiance in the lower canopy (lower) and on leaves in the upper canopy that were artificially shaded to reduce photosynthesis rates (upper shaded). Although we did not attempt to differentiate between maintenance and growth respiration, we hypothesized that the relationship between photosynthesis and growth respiration would be regulated by changes in pools of stored carbohydrates via processes driven by substrate supply or demand. Therefore, leaves exposed to lower irradiance (lower and upper shaded leaves) would have lower rates of photosynthesis during the day and thus lower rates of respiration during the following night in relation to reduced carbohydrate availability than leaves fully exposed in the upper canopy. We then used these data in a model to explore the significance of the findings for estimating seasonal net CO_2 exchange for the whole canopy. This was achieved by comparing an estimate of net CO_2 exchange for the canopy when respiration was calculated independently from photosynthesis, with an estimate when night-time respiration was dependent on total photosynthesis on the previous day.

Methods

Site description

Measurements were made in the canopies of two dominant *Q. rubra* L. trees growing in the Cascade Watershed at Black Rock Forest (New York, USA) (latitude 41.2°N, longitude 74.0°E, elevation ranging from 110 to 450 m above sea level) in midsummer. The soil at the site is a shallow, brown forest soil of medium texture over granite gneiss bedrock or glacial till parent material to a depth of approximately 250 mm (Olsson, 1981). The site comprises a mixed canopy of *Q. rubra*, *Q. prinus* and *Acer rubrum* trees with approximately 760 stems ha^{-1} and stem diameters ranging from 200 to 300 mm. Leaf area index during the measurement period was 5.8 $m^2\,m^{-2}$ and canopy height varied between 10 and 16 m above ground.

Measurements were made on mature, but not fully expanded leaves in summer (late June and early July) in 2000 and 2001. After measurements were made for 1 day during 2000, heavy and prolonged rain precluded completion of the experiment, so the same measurements were repeated during a continuous period of 10 days at the same time in 2001. During both these periods, the trees were well supplied with water and root-zone water content to a depth of 0.25 m ranged from 0.17 to 0.25 $m^3\,m^{-3}$.

Measurements of incident irradiance (400–700 nm), air temperature and relative humidity were made 2 m above the forest canopy at 5-s intervals and stored on a datalogger as hourly averages.

Measurements of photosynthesis and respiration

Measurements were made on four fully illuminated leaves at the top of the canopy (upper), four leaves at the bottom of the canopy (lower) and four leaves at the top of the canopy on branches covered by shade cloth at the start of the experiment (upper shaded) on two trees (eight replicate measurements in each treatment). The shade cloth reduced the irradiance reaching the leaves by 50%. For all leaves, rates of net photosynthesis, A, were measured at hourly intervals during daylight hours and rates of respiration, R, during the night were measured at 2-hourly intervals. Measurements were made continuously for 36 h in 2000, then repeated in 2001 over a period of 72 h, then continued for a further 36 h after a period of 5 days. Photosynthesis and respiration measurements were made using three portable photosynthesis systems (LI-6400, Li-Cor Inc., Lincoln, NE, USA) equipped with control modules to maintain the CO_2 partial pressure in the chamber at 36 Pa. The chambers were fitted with clear tops to allow

the leaves to be illuminated naturally and no attempt was made to control leaf temperature. Measurements were made by placing the chamber on the centre of the leaves and sampling an area of 600 mm^2. The irradiance incident on the leaf at the time of measurement was measured using a quantum sensor (LI-190, Li-Cor Inc.) placed parallel to the plane of the natural position of the leaf within the canopy. The rates of photosynthesis were calculated from the means of three measurements made generally within 2 min of placing the leaf in the chamber. At night, the rates of respiration were calculated from the means of six measurements made over 5 min. The total daily photosynthesis and night-time respiration were calculated by summing the hourly or 2-hourly values for the day and night periods, respectively.

Six days after the shading treatment was applied in 2001 and 1 day before the last set of continuous measurements were made, measurements of the response of photosynthesis, A, to intercellular CO_2 partial pressure, c_i, were made to determine values for the maximum rate of carboxylation, V_{cmax} and the apparent maximum rate of electron transport at saturating irradiance, J_{max}, following Farquhar *et al.* (1980). Eight leaves from each treatment were placed in the chamber fitted with an artificial light source (LI6400–02B, Li-Cor Inc.) and left to equilibrate for 15 min at a saturating CO_2 partial pressure of 150 Pa, saturating irradiance of 1200 $\mu mol\,m^{-2}\,s^{-1}$ and constant chamber temperature of 20 °C. The CO_2 partial pressure in the chamber was then reduced automatically in 14 steps down to 5 Pa using the CO_2 mixer on the instrument to generate the A/c_i curve. Values for V_{cmax} and J_{max} were estimated for each leaf by analysing the data from the A/c_i curves following the procedure described by Walcroft *et al.* (1997).

The response of photosynthesis, A, to irradiance, Q, for measurements made on leaves throughout the canopy on different days was best described by a rectangular hyperbola (Thornley & Johnson, 2000) as

$$A = \frac{\varepsilon Q A_{max}}{\varepsilon Q + A_{max}} - R, \qquad (1)$$

where A_{max} is the maximum rate of photosynthesis at saturating irradiance, ε is the initial slope of the curve known as the photosynthetic light use efficiency and R is respiration in the absence of light. The response of R to temperature was described using the modified Arrhenius function as adopted by Turnbull *et al.* (2003)

$$R = R_T e^{E_0/R_g(1/T - 1/T_a)}, \qquad (2)$$

where R_T is the rate of respiration at a base temperature, T (K), T_a is the leaf temperature (K), R_g is the gas constant (8.314 $J\,mol^{-1}\,K^{-1}$) and E_0 is a parameter related to the energy of activation. For the purposes of correcting rates of respiration to changes in temperature, it was assumed that leaf temperature and air temperature were the same at night.

Measurements of carbohydrate, nitrogen and chlorophyll concentrations

On days when measurements of photosynthesis and respiration were made, three discs with a total area of 60 mm^2 were punched from adjacent leaves at sunset for carbohydrate analysis. The discs were placed immediately into vials, frozen in liquid nitrogen and stored at −70 °C until they were analysed colorimetrically for soluble sugars and starch concentrations using an ethanol extraction technique described by Griffin *et al.* (1999).

At the end of the experiment, three discs were punched from each leaf, placed immediately in vials and stored on ice for analysis of chlorophyll concentration. In the laboratory, the total chlorophyll concentration was determined by grinding the leaves with liquid nitrogen, extracting twice with 80% ($v\,v^{-1}$) ethanol, centrifuging for 1 min, filtering and measuring the absorbance of the supernatant at 646.6 and 663.6 nm (Porra *et al.*, 1989). The remainder of each leaf was removed and area and dry mass were measured to determine specific leaf area. The leaves were dried at 70 °C, weighed and then finely ground for analysis of total nitrogen concentration using a CNS analyser (Carlo Erba Na 1500, Milan, Italy). Carbohydrate, nitrogen and chlorophyll concentrations in leaves are expressed on a per unit leaf area basis.

Statistical analysis

Values of parameters in all equations were estimated by fitting the data to the appropriate functions using a nonlinear least squares routine (SigmaPlot 2001, SPSS Inc.). Statistical differences for properties and photosynthetic parameters between the three canopy treatments were examined using one-way ANOVA, with differences considered significant if probabilities, P, were less than 0.05. Treatment means were compared for significance using Tukey's test (Fowler & Cohen, 1990). Significance between parameters estimated from the nonlinear curve in Eqn (1) was tested using the student's t statistic.

Modelling canopy net photosynthesis and respiration

To determine the significance of the results from this paper on net CO_2 exchange, a model was used to

estimate annual photosynthesis and respiration for the canopy. The one-dimensional, multilayer model incorporating radiative transfer, energy balance, evaporation and photosynthesis (Leuning *et al*., 1995) and water balance (Whitehead *et al*., 2002), and values for parameters for the same mixed *Quercus* canopy have been described fully elsewhere (Whitehead *et al*., 2004), so only brief details will be provided here. The canopy is divided into 20 homogenous layers based on the vertical distribution of cumulative canopy leaf area index. Leaf energy balance and the coupling of photosynthesis with stomatal conductance (Leuning, 1995) are used to calculate photosynthesis for sunlit and shaded foliage in each layer (Leuning *et al*., 1995); total photosynthesis is estimated across layers within the canopy and daily values are obtained using Gaussian integration following Goudriaan & van Laar (1994).

Net carbon uptake on a daily basis is calculated from estimates of photosynthesis and respiration for leaves in the canopy. The rate of photosynthesis for leaves is the minimum of the rates of carboxylation and regeneration of RuBP (ribulose-1,5-bisphosphate) following Farquhar *et al*. (1980), described by the maximum rate of carboxylation, V_{cmax}, and the apparent maximum rate of electron transport, J_{max}. Values for these parameters were taken from measurements made on the upper and lower leaves (Table 1), values that were very close to those reported from more extensive measurements at the same site by Turnbull *et al*. (2000b). The temperature dependence of photosynthesis was incorporated following Bernacchi *et al*. (2001) using parameter values derived experimentally by Walcroft *et al*. (1997). Seasonal changes in V_{cmax} and J_{max} were adopted from a similar mixed *Quercus* canopy by Wilson *et al*. (2001). Respiration from leaves at night was based on data reported for the same site by Turnbull *et al*. (2003). For the simulation using a fixed rate of respiration, ('fixed respiration'), the base rate of respiration at 20 °C, R_{20}, was set at 2% of V_{cmax}, allowing changes with depth in the canopy to be incorporated. Alternatively, the value for R_{20} was set in proportion to the total photosynthesis on the previous day ('variable respiration') as determined from the results of this experiment (see Fig. 4 and Results). The response of respiration to temperature was given by Eqn (2), with values for E_0 for different positions in the canopy taken from Turnbull *et al*. (2003). Daily calculations of water balance (Whitehead *et al*. 2002) were used to define a coefficient to reduce photosynthesis and respiration when daily root-zone water storage fell below 50% of its maximum value.

The model was used to estimate daily values of photosynthesis and respiration for the *Quercus* canopy for the part of the year 2002 when leaves were present on the trees, using values for the parameters as described above and measurements of meteorological variables at the site.

Results

Weather conditions

Conditions remained clear and sunny on the 5 days when continuous measurements of photosynthesis and respiration were made throughout 24 h periods. Maximum incident irradiance (400–700 nm) at midday was 2230 μmol m^{-2} s^{-1} (Fig. 1). Day length was 16 h but net CO_2 exchange was positive for approximately 11 h for leaves throughout the canopy (Fig. 2). During daylight hours, the change in air temperature during the period was reasonably similar on each day, reaching a maximum of 26.9 °C, but minimum night temperature declined progressively during the measurement period in 2001, reaching the lowest value of 12.2 °C on the last day of measurements (Fig. 2). There was a corresponding decrease in air saturation deficit in the day and at night, with the maximum value of 19.8 mmol mol^{-1} occurring on the first day of measurement.

Table 1 Values of the maximum rate of carboxylation, V_{cmax}, the apparent maximum rate of electron transport, J_{max}, specific leaf area and nitrogen and chlorophyll concentrations in leaves at the end of the experiment in 2001

	Upper	Upper shaded	Lower	Significance
V_{cmax} (μmol m^2 s^{-1})	57.2 ± 2.3[a]	60.1 ± 3.6[a]	31.7 ± 1.6[b]	$P<0.001$
J_{max} (μmol quanta m^{-2} s^{-1})	116.2 ± 3.1[a]	92.7 ± 5.1[b]	55.7 ± 3.7[c]	$P<0.001$
Specific leaf area (m^2 kg^{-1})	8.2 ± 0.2[a]	8.8 ± 0.4[a]	15.4 ± 0.5[b]	$P<0.001$
Nitrogen concentration (mmol m^{-2})	206.0 ± 5.7[a]	183.6 ± 7.8[b]	94.2 ± 2.7[c]	$P<0.001$
Chlorophyll concentration (mmol m^{-2})	302.3 ± 24.5[a]	293.2 ± 15.7[a]	242.9 ± 13.4[a]	$P<0.05$

Values shown are means ± standard error for the eight leaves in each canopy position. Significance of the difference between the treatments from analysis of variance is indicated by the value of P and different letters within the rows indicate statistically different values at $P<0.05$.

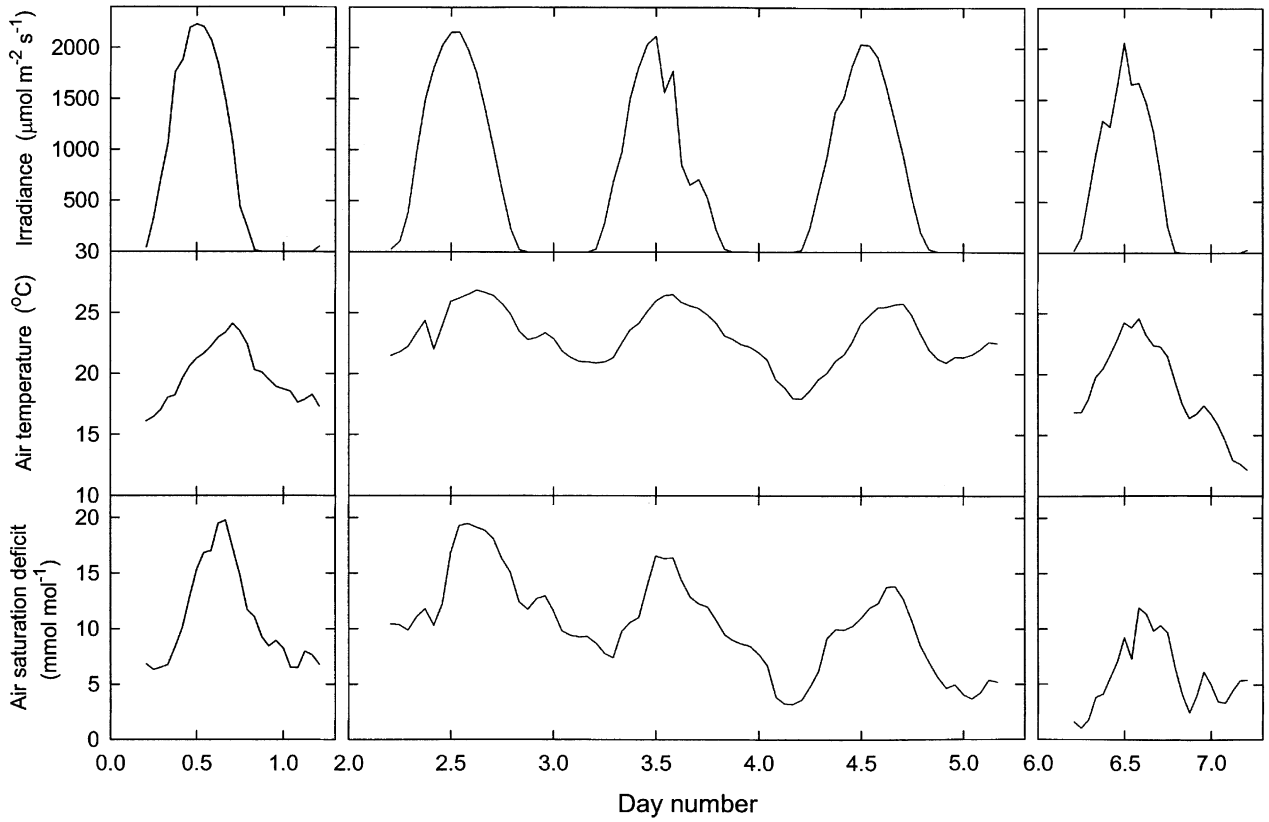


Fig. 1 Weather variables for 5 days when measurements were made. The data are separated for the three periods in June 2000 (left), late June 2001 (centre) with measurements continuing in early July 2001 after a period of 5 days (right). Values of incident irradiance shown are for photosynthetically active wavelengths (400–700 nm).

Rates of photosynthesis and respiration

Hourly average photosynthesis rates were highest for the upper, fully exposed leaves in the canopy, reaching a maximum rate of 18.7 $\mu mol\,m^{-2}\,s^{-1}$ on the second day of measurement (Fig. 2). Hourly average rates of respiration were also the highest in these leaves reaching a maximum (ignoring the negative sign shown for clarity in Fig. 2) of 2.7 $\mu mol\,m^{-2}\,s^{-1}$. The rates of photosynthesis in the upper shaded leaves were slightly less than half those of the upper leaves (maximum 8.0 $\mu mol\,m^{-2}\,s^{-1}$) and corresponding rates of respiration for upper shaded leaves were lower (maximum 23% less) than those for the upper leaves. The lowest rates of photosynthesis (maximum 4.3 $\mu mol\,m^{-2}\,s^{-1}$) and respiration (1.4 $\mu mol\,m^{-2}\,s^{-1}$) occurred in the lower leaves. The same differences occurred on the last day of measurements, 8 days after the shading treatment had been applied.

The response of hourly average photosynthesis to irradiance was described by the rectangular hyperbola provided by Eqn (1) for the upper, upper shaded and lower leaves in the canopy (Fig. 3). Maximum rates of photosynthesis at saturating irradiance, A_{max}, for the lower leaves were much less ($P<0.001$) than that for the upper leaves. A_{max} for the upper shaded leaves was not significantly different from that for the upper leaves but greater than that for the lower leaves ($P<0.05$). The value for light use efficiency, ε, was lower for upper shaded leaves than that for upper leaves ($P<0.05$). The value of ε for the lower leaves was higher and significantly different from values for the upper ($P<0.05$) and the upper shaded ($P<0.001$) leaves.

To reveal the dependence of night-time respiration on photosynthesis during the previous day, it was necessary to remove the effects of temperature on respiration by scaling rates to a common temperature of 20 °C using Eqn (2). We applied the equation to our data using values for the parameters R_{10} and E_0 of 0.49 and 0.42 $\mu mol\,m^{-2}\,s^{-1}$ and 53.65 and 44.20 $kJ\,mol^{-1}$ for upper and lower leaves, respectively, adopted from a more detailed concurrent study of the characteristics of respiration in the same canopy (Turnbull *et al.*, 2003). There was a strong linear relationship between the averages of total night-time respiration at 20 °C and total photosynthesis during the previous day, with a

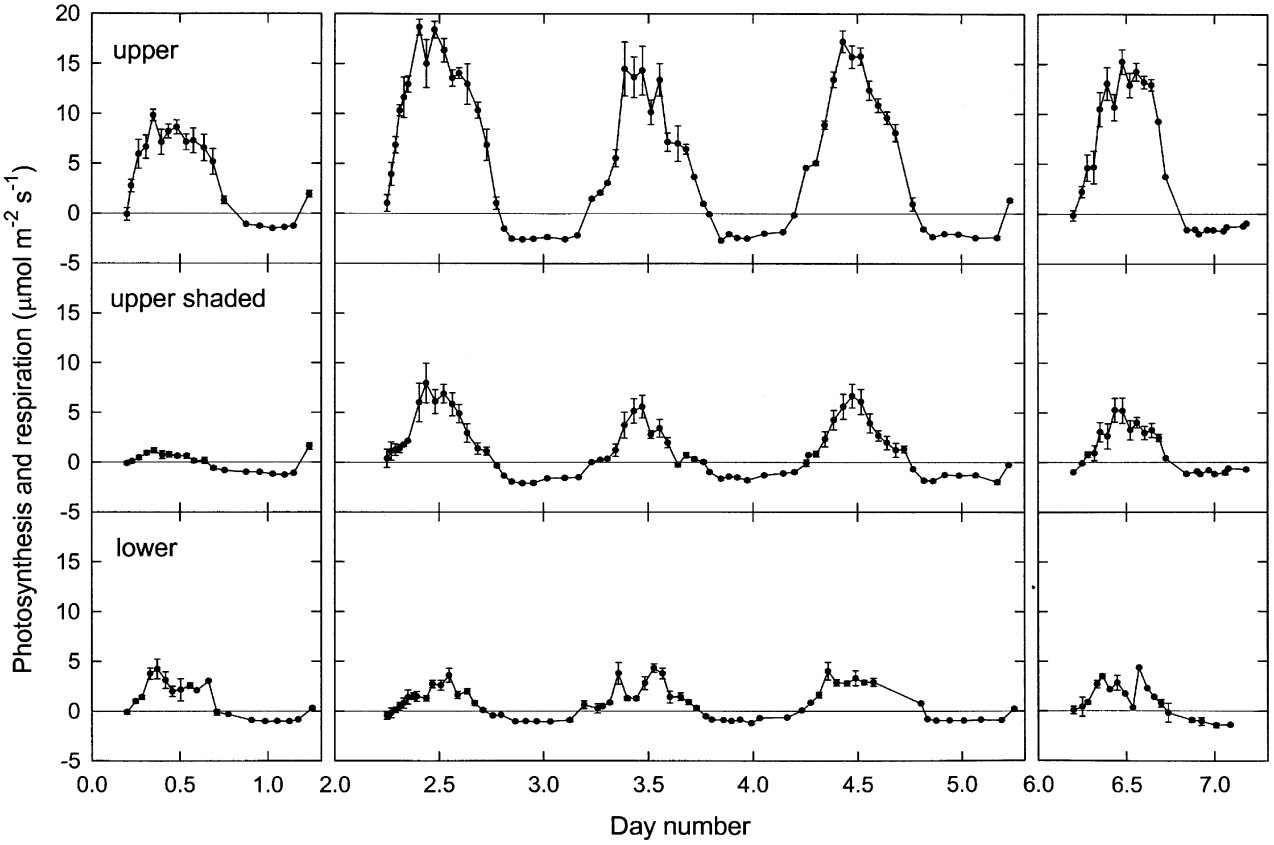


Fig. 2 Measurements of photosynthesis and respiration at approximately hourly intervals in the day and 2-hourly intervals at night for leaves in the upper, upper shaded and lower parts of the canopies during the 5 days. Separation of the data is the same as that shown in Fig. 1. Each point shows the mean ± 1 standard error of measurements made on eight leaves. For the purposes of clarity, rates of respiration in this figure are shown with a negative sign.

clear separation of data for the three treatments (Fig. 4). There was no significant difference in the relationship between data collected in the different years.

Estimates of photosynthetic parameters from analysis of the A/c_i curves showed that the average value of V_{cmax} was significantly lower ($P<0.05$) for leaves in the lower canopy compared with that for leaves in the upper canopy (Table 1). However, there was no significant difference in V_{cmax} between upper and upper shaded leaves. There was a small, but significant ($P<0.05$) decrease in J_{max} for upper shaded leaves compared with that for upper leaves, and J_{max} was much lower for leaves in the lower canopy.

Carbohydrate, nitrogen and chlorophyll concentrations

Soluble sugar and starch concentrations for leaves in the upper canopy were higher than those for lower canopy leaves when concentrations were expressed on a unit area basis (Fig. 5). There was a strong linear relationship between total respiration integrated through the night, R_t, and the soluble sugar concentration for leaves in the upper and lower canopy positions measured at dusk. When the same data for the upper shaded leaves were superimposed on the relationship, R_t was lower for given leaf soluble sugar concentrations. The relationship between R_t and starch concentration measured at dusk for leaves in the upper and lower canopy positions was also linear but more variable than that for soluble sugars. However, when data for leaves in the upper shaded treatment were superimposed, they were scattered around the line rather than lying below it.

Values for specific leaf area, S, measured at the end of the experiment were higher for leaves in the lower canopy compared with those in the upper canopy but there was no significant difference in S between upper and upper shaded leaves (Table 1). Leaf nitrogen concentrations per unit leaf area at the end of the experiment were highest in the upper leaves, significantly ($P<0.001$) lower in upper shaded leaves and much lower ($P<0.001$) in lower leaves. There were similar trends in chlorophyll concentration per unit

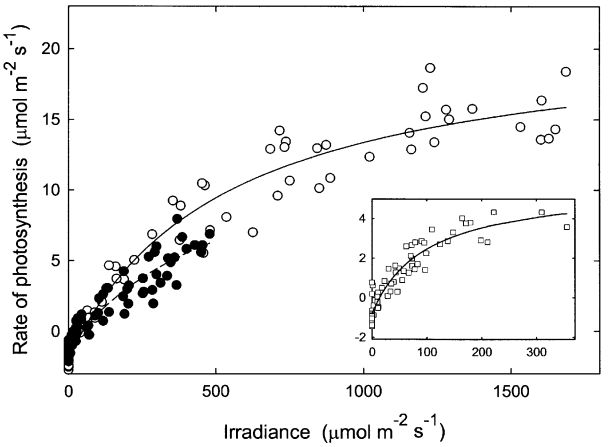


Fig. 3 Relationships between photosynthesis and incident irradiance (400–700 nm) for leaves in the upper (○), upper shaded (●) and lower (□) parts of the canopy. Measurements were made in June 2001 after the shade had been in place for 4 days. Each symbol shows average photosynthesis for the eight leaves in each canopy position. Curves given by Eqn (1) are fitted to the data with the values ± 1 standard error for the parameters for maximum photosynthesis rate at saturating irradiance, A_{max}, as 23.4 ± 1.1, 16.1 ± 3.7 and 6.5 ± 0.6 μmol $m^{-2} s^{-1}$ and photosynthetic light-use efficiency as 44.4 ± 4.2, 28.8 ± 4.3 and 66.2 ± 8.5 mmol CO_2 mol quanta^{-1}, for leaves in the upper, upper shaded and lower (expanded in inset) canopy, respectively.

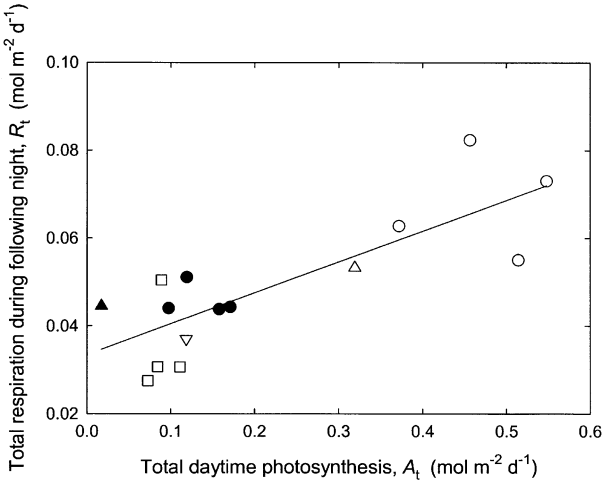


Fig. 4 Relationship between total daytime photosynthesis, A_t, and total respiration, R_t, during the following night for leaves in the three treatments. The symbols refer to leaves in the upper (△), upper shaded (▲) and lower (▽) parts of the canopy for measurements made in 2000 and upper (○), upper shaded (●) and lower (□) parts of the canopy in 2001. Each symbol shows average total photosynthesis and respiration for all leaves in each class on each day. The respiration data have been corrected to represent rates at a constant leaf temperature of 20°C to remove the effects of variation in temperature on different nights when measurements were made. The linear regression fitted through the data is described by $R_t = 0.074A_t + 0.030$, $r^2 = 0.75$.

leaf area but none of the differences were significant (Table 1).

Modelled estimates of canopy photosynthesis and respiration

Annual incident irradiance (400–700 nm) at the site in 2002 was 10.41 kmol m^{-2} (ground area), of which 47% was absorbed by the canopy. Estimated canopy net photosynthesis during the year when leaves were present from early May (day 93) to late October (day 302) from the model was 82.4 mol m^{-2} (ground area), with the seasonal pattern closely matching fluctuations in irradiance (Fig. 6). During this time, the limitation to photosynthesis from water deficits was negligible with root-zone water content falling to 45% of its maximum value for brief periods up to 4 days only in early May, mid-July and mid-September. Maximum daily photosynthesis occurred in early May (between days 134 and 154), then decreased during summer and especially during August and early September (days 220–260). This decline was due in part to decreasing leaf area index, but was attributable principally to lower values of the photosynthetic parameters V_{cmax} and J_{max} associated with leaf ageing used in the model following Wilson *et al.* (2001).

With the more conventional 'fixed respiration' approach assuming a fixed base rate of respiration for leaves at a given temperature, values of night-time respiration, R_t, were estimated in relation to temperature, using Eqn (2). The total night-time respiration for the canopy when leaves were present throughout the year was 28.4 mol m^{-2} (35% of net photosynthesis). Seasonal variability in R_t was small during most of the growing season, with maximum values occurring in early June (days 150–165, Fig. 6) and day-to-day variation attributable to differences in night-time temperature. To introduce the effects of photosynthesis on night-time respiration, the model was modified so that the base value of respiration at a temperature of 20 °C, R_{20}, was decreased as canopy photosynthesis on the previous day, A_t, fell below a maximum value, using the slope given by Fig. 4. This was achieved by normalizing values of A_t throughout the year to a maximum value of 0.84 mol m^{-2} day^{-1} that occurred in early June on day 159. The resulting values of R_{20} were then used to calculate R_t using Eqn (2), to introduce the effects of temperature with calculations identical to those used for the 'fixed respiration' approach. Values for R_t using the 'variable respiration' approach were lower than those from the 'fixed respiration' approach,

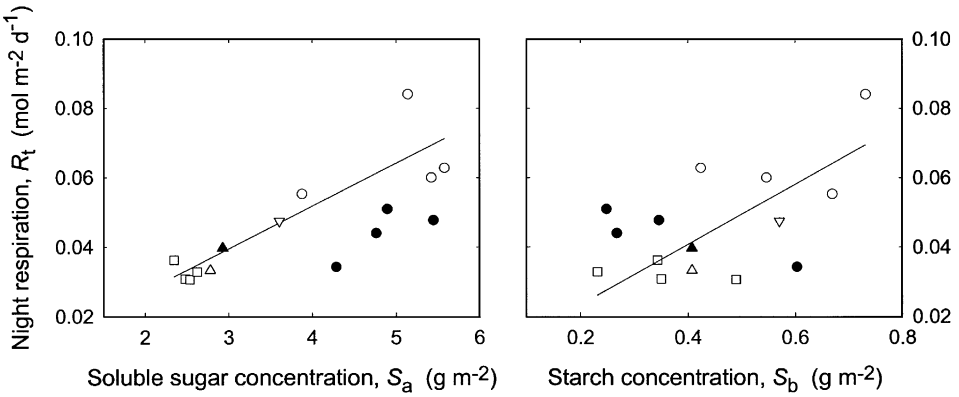


Fig. 5 Relationships between total night respiration, R_t, and soluble sugar, S_a, and starch, S_b concentrations in leaves in the canopy measured at dusk on the nights before respiration measurements were made. The symbols refer to the same treatment as those in Fig. 4. Data are averages for all leaves in each canopy position on each day. No corrections for differences in temperature have been made to the respiration data. The linear regressions shown are fitted to data for leaves in the upper and lower canopy positions only and are given by $R_t = 0.012S_a + 0.0019$, $r^2 = 0.87$ and $R_t = 0.0145S_b + 0.0062$, $r^2 = 0.52$.

especially during late summer (August and September) when irradiance and photosynthetic potential of the leaves were lower (Fig. 6). Total respiration for the growing season was 21.9 mol m^{-2}, 23% lower than the value using the 'fixed respiration' approach.

Discussion

The positive linear relationship between the average total leaf night-time respiration, R_t, corrected to a base temperature of 20 °C and total photosynthesis during the previous day, A_t, suggests that the magnitude of R_t is related to the availability of resources resulting from A_t (Fig. 4). The range in A_t for leaves in the upper canopy varied from 0.30 to 0.55 mol m^{-2} with R_t as a proportion of A_t decreasing from 0.18 to 0.14 across this range. These values of the ratio of R_t to A_t are within the range for seven *Pinus* stands (0.09–0.25 with an average of 0.15) calculated by Ryan *et al.* (1994) for sites with mean annual temperatures between 3.6 °C and 21.6 °C. The ratio of R_t to A_t for leaves in the lower canopy and for upper shaded leaves was much higher at 0.40, showing that R_t as a proportion of A_t is higher at low daily values of A_t. These data for *Q. rubra* are consistent with the earlier findings of Ludwig *et al.* (1975) using tomato growing in steady-state conditions. Ludwig *et al.* (1975) further showed that the slope of the response of R_t to A_t was different when total daily photosynthesis was manipulated using ambient CO_2 partial pressure and shading treatments. André *et al.* (1982) showed that photosynthesis recovered rapidly within several days to the preshading level when shade was removed in maize plants but the return of dark respiration to preshading levels took longer. Taken together, these observations suggest that R_t is regulated by the quantity of carbohydrates accumulated during the previous day, rather than by photosynthesis *per se*.

Our data support the role of carbohydrates mediating the link between photosynthesis and respiration. Even after several days of the shading treatment, soluble sugar concentrations in the upper shaded leaves remained as high as those in the upper fully illuminated leaves, despite a reduction in R_t for the upper shaded leaves. On the other hand, reductions in R_t for upper shaded leaves compared with upper leaves were associated with reductions in starch concentration in upper shaded leaves (Fig. 5), suggesting that a depletion of starch in upper shaded leaves resulted in lower values of R_t. However, it is important that our results are not interpreted to preclude the regulation of respiration by processes other than substrate supply. Alternative 'demand-driven' regulation of the rate of respiration includes the energy-requiring processes of phloem loading and translocation (Amthor, 2000), demand for respiratory products (Amthor, 1989), enzyme capacity (Atkin & Tjoelker, 2003) and the activity of alternative biochemical pathways (Azcón-Bieto *et al.*, 1983; Amthor, 1994), likely related to phosphorus supply (Gonzàlez-Meler *et al.*, 2001). The mechanisms regulating R_t are complex and involve rates of import and export of carbohydrates and pools of carbon in carbohydrate and protein in leaves, but processes incorporating pool sizes and fluxes between pools have been described in models without the need to represent complex biochemical detail (Dewar *et al.*, 1998; Dewar, 2000; Thornley & Cannell, 2000). Such an approach is capable of explaining the acclimation of photosynthesis to irradiance during short-term daily

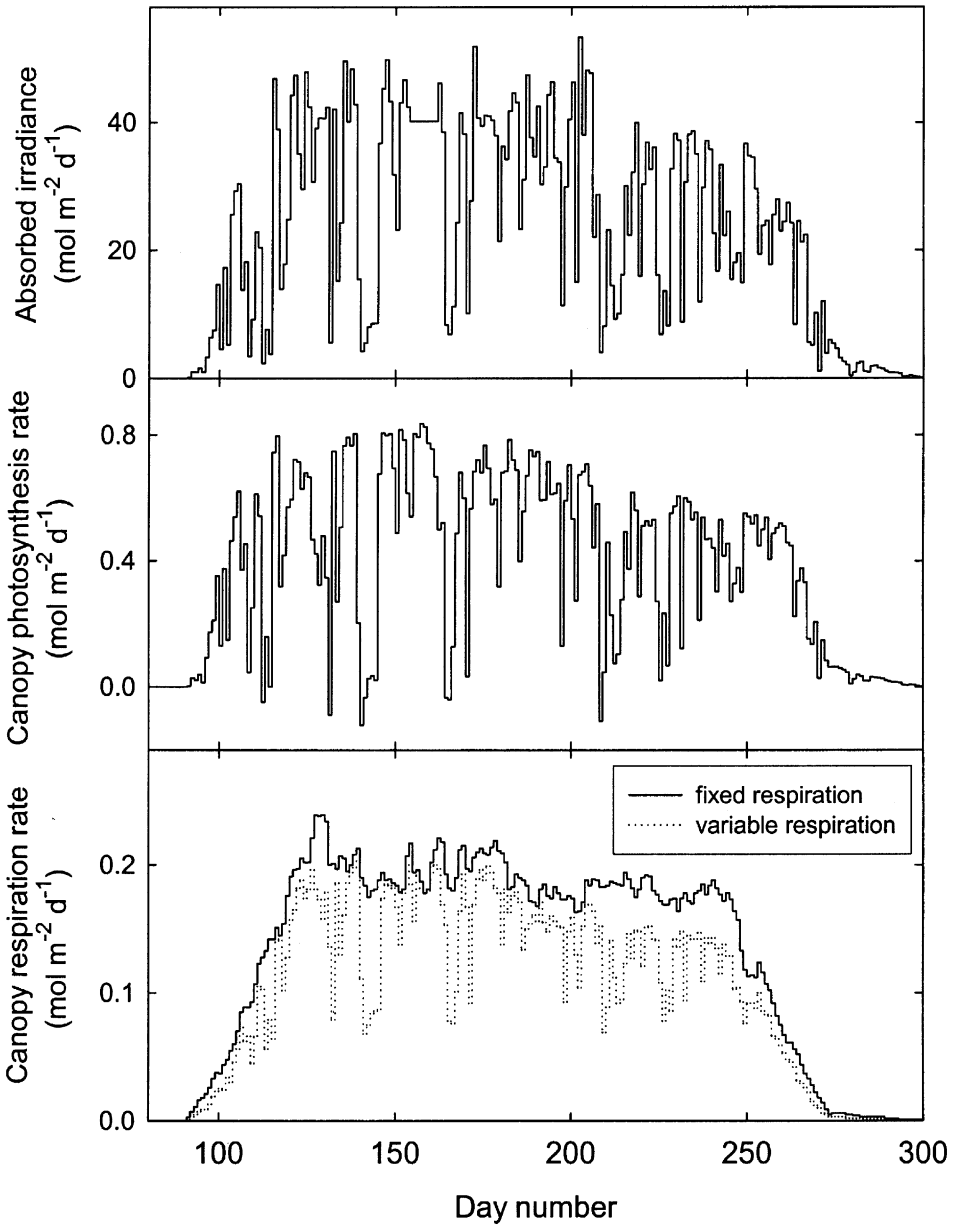


Fig. 6 Modelled absorbed irradiance (400–700 nm), photosynthesis and night-time respiration (per unit ground area) for the mixed *Quercus* canopy at the field site. Estimates are for each day for the period when leaves were present on the trees from early May (day 93) to late October (day 302). Respiration is shown using a simulation in which night-time respiration is dependent on temperature alone ('fixed respiration') and dependent on the amount of photosynthesis on the previous day and temperature ('variable respiration'). See the text for details of the model and the difference in the two approaches for estimating respiration.

changes and long-term seasonal changes (Dewar *et al.*, 1998) as well as acclimation of the ratio of R_t to A_t to changes in temperature (Dewar *et al.*, 1999). Application of the model described by Dewar *et al.* (1999) requires the estimation of dynamics in pool sizes and active and passive fluxes between pools related to carbohydrate and protein synthesis. The extension of our work to include such measurements in field conditions would provide valuable data for further development of models leading to improved seasonal estimates of net carbon exchange for canopies.

Other studies have shown that photosynthetic capacity is related to the amount of respiration during the previous night. Turnbull *et al.* (2002a) showed experimentally with *Populus deltoides* trees growing in controlled conditions that increased night-time respiration

resulting from elevated night-time temperature led to increased photosynthesis on the following day. Maximum rates of photosynthesis increased by up to 64% when day and night-time temperatures were increased by 6 °C and 10 °C, respectively. The difference in photosynthesis was associated with increases in V_{cmax} and J_{max} and attributed to a 'sink' (or demand)-driven response to the reduction in leaf carbohydrate concentrations resulting from enhanced respiration at higher temperatures (Turnbull *et al.*, 2002a). Any response of photosynthesis to respiration during the previous dark period in our data was too small to detect because the effects of differences in night-time temperature on respiration were very small. However, it is likely that the coupling of photosynthesis and respiration operates in both directions and involves several mechanisms.

Apart from the effects on leaf carbohydrate concentration, it is likely that shading resulted in changes in photosynthetic processes associated with both carboxylation and electron transport. Specific leaf area was much higher and photosynthesis rates (Fig. 2), nitrogen concentration and V_{cmax} much lower (Table 1) for leaves in the lower canopy than for those in the upper canopy. Strong relationships between photosynthesis and leaf nitrogen concentration in this (Turnbull *et al.*, 2002b) and other forest canopies (Ellsworth & Reich, 1993) are well documented. The close association of nitrogen allocation with the distribution of intercepted radiation and photosynthesis capacity is interpreted, using optimization theory, as leading to maximum carbon gain (Field, 1983; Sands, 1995). However, the lack of confirmation of this hypothesis (Livingston *et al.*, 1998; Porté & Loustau, 1998) is unlikely to result in a significant effect on canopy photosynthesis in conditions when nitrogen supply is adequate for photosynthesis (Leuning *et al.*, 1995; Warren & Adams, 2001). At the end of our experiment, 6 days after the shading treatment started, leaf nitrogen concentration was slightly, but significantly, lower in the upper shaded leaves than in the upper leaves, but there was no equivalent significant difference in chlorophyll concentration (Table 1). However, the difference in nitrogen concentration did not result in lower values of V_{cmax} in the upper shaded leaves compared with the upper leaves (Table 1). There was, however, a decrease in J_{max} in the upper shaded leaves (Table 1) such that the ratio of J_{max} to V_{cmax} decreased from 2.0 for the upper leaves to 1.5 in the upper shaded leaves. These results suggest that the effects of shading for 6 days had already initiated changes in the allocation of nitrogen for photosynthetic processes. Such changes are likely to be similar to those that occur seasonally during photosynthetic acclimation of leaves to changes in irradiance (Dewar *et al.*, 1998) and leaf age as the canopy develops, both of which are important in the processes of acclimation to low irradiance (Niinemets & Tenhunen, 1997). However, it is likely that the effects of changes in the allocation of nitrogen during our experiment were small because maximum rates of carboxylation, as indicated by V_{cmax}, were not significantly different between upper and upper shaded leaves. Further, there was only a small effect of shading on light-use efficiency from the initial slope of the response of photosynthesis to irradiance (Fig. 3). This is consistent with results comparing photosynthesis in shaded and nonshaded leaves (Björkman, 1981) and with the processes of seasonal acclimation of leaves to shading. Brooks *et al.* (1996) showed that shading fully expanded leaves grown in full sunlight resulted in a decrease in light-saturated photosynthesis to rates similar to those for shaded leaves, with no change in light-use efficiency. In our data, the more pronounced effect of shading on A_{max} during the experiment compared with that on V_{cmax} or J_{max} immediately after the experiment could possibly be attributed to reactivation of Rubisco in the light during the A/c_i measurements. Short-term changes in photosynthesis in fully illuminated leaves could also be attributed to increases in stomatal conductance following hydraulic adjustments when a large proportion of the foliage in a tree crown is shaded (Whitehead *et al.*, 1996). However, no differences in stomatal conductance between upper and upper shaded leaves were detected in our study (data not shown) because the proportion of leaves shaded was negligibly small.

The paradigm of maintenance and growth respiration has been the basis for interpreting and modelling the processes regulating respiration for 30 years, as described in recent reviews by Amthor (2000) and Gifford (2003). Our measurements were made on mature, but not yet fully expanded leaves, so our data comprise unknown proportions of respiration from both maintenance and growth processes. Measurements made after seasonal leaf growth has ceased are used frequently to estimate maintenance respiration when it is assumed that growth respiration is zero (Ryan, 1995), although this assumption ignores respiration associated with active processes such as translocation (Amthor, 2000). Nonetheless, our results lend support to the paradigm since they can be explained by a change in the proportion of total respiration that is linearly related to photosynthetic activity (growth respiration), while the remainder (maintenance respiration) is dependent on repair processes proportional to the mass of leaf tissue. Also, our results provide additional evidence, at the leaf scale, that the ratio of respiration to photosynthesis for whole plants is

conservative (Gifford, 2003). For further progress, two priorities were identified by Amthor (2000) as the need to develop methods to measure growth respiration independently and to quantify the proportion of maintenance respiration supported by photosynthesis under a range of growing conditions.

Returning to the need to quantify the significance of the results from this study on annual net CO_2 exchange for the canopy, the results from our model suggest that estimates of net CO_2 exchange for forest canopies may be substantially different when respiration is linked with photosynthesis, rather than allowing the two processes to be independent. Our estimates include the effects of seasonal changes in photosynthetic parameters following Wilson *et al.* (2001), but we note with caution that the model does not include potential seasonal acclimation of respiration to temperature. Such effects are likely to be important (Atkin *et al.*, 2000), and their inclusion in future analyses will further increase confidence in estimates of net CO_2 exchange using models. Thus, our analysis highlights the potential, rather than the actual, effects of modelling night-time respiration in relation to fluctuations in daily photosynthesis and temperature rather than temperature alone.

In conclusion, net carbon exchange in ecosystems is highly sensitive to the effects of night-time temperature on respiration (Houghton *et al.*, 1998), and the effects of irradiance and the degree of cloudiness on photosynthesis (Roderick *et al.*, 2001; Gu *et al.*, 2003). Further investigation of the interactive effects of temperature and fluctuating irradiance on the relationship between respiration and photosynthesis in field conditions will improve modelling capabilities to predict the effects of changing climate on the long-term carbon balance of forest ecosystems.

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