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Carbon dioxide fluxes over an ancient broadleaved deciduous woodland in southern England

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Abstract

We present results from a study of canopy-atmosphere fluxes of carbon dioxide from 2007 to 2009 above a site in Wytham Woods, an ancient temperate broadleaved deciduous forest in southern England. Gap-filled Net Ecosystem Exchange (NEE) data were partitioned into Gross Primary Productivity (GPP) and ecosystem respiration (R_e) and analysed on daily, monthly and annual timescales. Over the continuous 24 month study period annual GPP was estimated at $21.1 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ and R_e at $19.8 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$; Net Ecosystem Productivity (NEP) was $1.2 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$. These estimates are very consistent with independent bottom-up estimates derived from Net Primary Productivity (NPP) and flux chamber measurements in 2008 ($\text{GPP}=20.3\pm1.0 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$, $R_e=18.9\pm1.7 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$, biomass increment $\sim 1.4 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$). Interannual variability of seasonal NEP was predominantly driven by changes in ecosystem respiration, whereas GPP remained similar for equivalent months in different years. Although solar radiation was the largest influence on daytime CO_2 fluxes ($R^2=0.53$ for the summer months), interannual variation in R_e appeared to be driven by temperature. Our findings suggest that this ancient woodland site is currently a substantial sink for carbon, resulting from continued growth that is probably a legacy of past management practices abandoned over 40 years ago. Our GPP and R_e values are generally higher than other broadleaved temperate deciduous woodlands and may represent the influence of the UK's maritime climate, or the particular species composition of this site. The carbon sink value of Wytham Woods supports the protection and management of temperate deciduous woodlands (including those managed for conservation rather than silvicultural objectives) as a strategy to mitigate atmospheric carbon dioxide increases.

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1 Introduction

Forests are increasingly important in climate change debates, with studies estimating deforestation to account for approximately 12–15% of recent annual global carbon dioxide (CO₂) emissions (van der Werf et al., 2009). Sequestration of CO₂ from the atmosphere by the process of photosynthesis and the subsequent assimilation of carbon into above and below ground biomass partially offset anthropogenic emissions of CO₂ (Janssens et al., 2003). The global terrestrial carbon sink was $2.7 \pm 0.9 \text{ Pg C yr}^{-1}$ for the period 1990 to 2008 (Le Quéré et al., 2009) and tropical forests alone sequestered $1.09 \pm 0.29 \text{ Pg C yr}^{-1}$ over the period 2000 to 2005, equivalent to $12 \pm 3\%$ of total anthropogenic emissions (Malhi, 2010). Increasing global interest in the potential of terrestrial ecosystems such as forests to slow rises in CO₂ levels has led to a rise in research to quantify both terrestrial carbon stocks and factors influencing temporal and spatial variation in carbon uptake.

Eddy covariance provides a direct measurement of carbon dioxide fluxes between the atmosphere and forest vegetation and allows estimation of Net Ecosystem Exchange (NEE) of carbon dioxide over chosen timescales (Baldocchi et al., 1988). Flux equipment measures the covariance between fluctuations in vertical wind velocity (in the form of turbulence/eddies) and the mixing ratio of CO₂. In micrometeorological convention, negative flux values represent a net loss of CO₂ from the atmosphere to the vegetation and thus assimilation of carbon through photosynthesis. Positive values represent transfer of CO₂ to the atmosphere through both autotrophic and heterotrophic respiration. There is potential for eddy covariance to provide medium-scale (i.e. km²) estimates of CO₂ exchange between vegetation and the environment, resulting in the growth in flux sites since the 1990s. Now there are over 400 flux research sites worldwide and a global network of collaborating regions, FLUXNET, which assimilates information from research sites over a wide range of biomes (Baldocchi, 2008). By providing rapid continuous estimates of NEE over a given area, and thus vital information regarding how local environmental conditions can affect rates of carbon exchange

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(Urbanski et al., 2007), eddy covariance can both enhance and validate stock-based estimates of carbon budgets (Curtis et al., 2002).

Research employing the eddy covariance technique has been undertaken in temperate deciduous forests across the globe, providing useful information on carbon storage (Granier et al., 2000; Curtis et al., 2002; Knohl et al., 2003), partitioning of forest carbon fluxes (Misson et al., 2007), the impacts of climate change (Urbanski et al., 2007), weather anomalies and seasonal cycles (Saigusa et al., 2008). It has also clarified the impacts of stand age upon carbon sequestration (Wirth et al., 2002; Knohl et al., 2003; Paw et al., 2004; Amiro et al., 2006), with findings challenging the traditional ecological paradigm that mature forests no longer achieve manifest net sequestration of atmospheric CO₂ (Jarvis et al., 1989). However, there are still many questions regarding factors influencing carbon sequestration, and a requirement to provide accurate estimates to be utilised in terrestrial carbon cycle models and coupled vegetation-atmospheric models.

Here we present results from a two-year study of carbon dioxide fluxes above an ancient deciduous broadleaved woodland in southern England. We aim to quantify absolute magnitudes and temporal changes in Gross Primary Productivity (GPP), ecosystem respiration (R_e) and net ecosystem productivity (NEP) in order to explore the driving influences of local meteorology and generate estimates of carbon balance. A companion paper (Fenn et al., 2010) provides a detailed “bottom-up” analysis of the components of productivity and ecosystem respiration at this site; comparison of the two studies together provides independent testing of the consistency of our understanding of the carbon cycle at our study site. This work adds to the existing carbon dioxide flux literature by focussing on a woodland in a temperate maritime climate (most reported temperate sites have a more continental climate), and in particular an ancient woodland site where tree cover has never been removed, although substantial human management has taken place over many centuries.

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2 Methodology

2.1 Study site description

Contained within a loop of the River Thames, Wytham Woods (51°46' N 1°20' W; UK National Grid SP: 460 080) is a 400 ha predominantly broadleaved deciduous forest, 5 km northwest of Oxford in southern England (Fig. 1). The site rises to an altitude of 160 m at the top of Wytham Hill and is surrounded by agricultural land. The Woods mostly fall into the category of W8 *Fraxinus excelsior* – *Acer campestre* – *Mercurialis perennis* woodland, in the UK National Vegetation Classification (Rodwell, 1991), with the most common canopy trees species pedunculate oak (*Quercus robur*), ash (*Fraxinus excelsior*), sycamore (*Acer pseudoplatanus*) and beech (*Fagus sylvatica*), with some conifers in the more recent plantations, understory shrubs such as hazel (*Corylus avellana*), hawthorn (*Crataegus monogyna*) and blackthorn (*Prunus spinosa*), with ground flora including dog's mercury (*Mercurialis perennis*) and bluebell (*Endymion non-scripta*). Fuller descriptions are provided in Savill et al. (2010). The climate is typical of the English Midlands region, with average annual precipitation at Wytham around 730 mm between 1992 and 2009. Meteorological data recorded at Wytham between 1992 and 2009 shows the mean annual temperature to be 10.1 °C. The warmest month of the year, July, averaged temperatures of 16.7 °C whereas the coldest month, December, averaged 4.4 °C over this time period. The soils are well-drained at higher elevations and clay-rich and poorly drained at lower altitude.

Owned by Oxford University, Wytham Woods has hosted numerous ecological studies and since 1992 has been part of the UK Environmental Change Network (ECN). Areas of the forest have been broadly classified by Morecroft et al. (2008) into five categories based upon age and species composition (Table 1, Fig. 1), ranging from small areas of 20th century coniferous plantations to serve timber production to ancient semi-natural woodland. The forest immediately surrounding the flux tower is defined as disturbed ancient woodland (Fig. 1), and the canopy is dominated by sycamore, *Acer pseudoplatanus*, and ash, *Fraxinus excelsior*. Ancient woodland is defined in the

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UK as forest that has not been cleared since records began, ~1600 AD (Peterken, 1981), although they may have been intensively managed for timber extraction, grazing, coppicing or as a source of fuelwood. Ancient woodlands cover approximately 3% of England's land area, representing around one third of all woodland in England. Their benefits in terms of climate change mitigation; adaptation; biodiversity and; recreation are increasingly being recognised by policymakers in the UK (Defra, 2007; Read et al., 2009).

History of woodland management at Wytham is well documented (Savill et al., 2010) allowing ancient woodland to be divided into what we term “disturbed” and “undisturbed” classifications. Undisturbed ancient woodland has largely remained untouched since the abandonment of coppicing 40–100 years ago (Gibson, 1986). Areas of disturbed ancient woodland have also been managed as a “coppice-with-standards” in the past, with localised felling for commercial timber extraction and glade creation (to encourage invertebrate biodiversity) followed by localised planting and natural regeneration, leading to the development of a high forest structure. However, these areas have also remained largely unmanaged for the last 40 years (Morecroft et al., 2008) as the woods have increasingly been managed on a minimum intervention basis.

2.2 Instrumentation

Fluxes of energy (sensible heat and latent heat), momentum and CO₂ were measured at a height of 25 m using the eddy covariance technique (Baldocchi et al., 1988). Approximations of the flux footprint (or fetch) were generated using calculations adapted from a model by Schmid and Oke (1990) and are shown in Fig. B1. The flux tower (SP 457 089) fetch is estimated to vary with atmospheric stability from ~250 m in very unstable (daytime convective) conditions to over 2 km in very stable (calm night) conditions. Approximately 90% of fluxes are estimated to occur within 200 to 600 m of the tower, predominantly covering areas of disturbed ancient woodland to the southwest (with south-westerly prevailing winds). The flux equipment consists of a Solent R2 3-D sonic anemometer (Gill Instruments, UK) measuring wind vector components

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and a LiCOR 7500 open-path infrared gas analyser (IRGA: LiCOR Instruments, Nebraska, USA) measuring atmospheric CO₂ concentrations. The sonic anemometer was mounted to ensure complete exposure in all directions. The LiCOR sensor was placed close to the sonic anemometer stem in order to gain the most accurate measurements of wind characteristics and coupled CO₂ concentrations, but also slightly below and 0.1 m to the side of the anemometer's ultrasonic sensor in order to avoid creating flow disturbance. The IRGA sensor was angled slightly to allow surface moisture drainage and prevent direct solar radiation from possibly contaminating readings (Lloyd, 2006).

Measurements were made at 20 Hz, thus recording covariances every 0.05 s. Raw data outputs from the sonic anemometer and IRGA were recorded on a CR3000 Campbell Scientific Data Logger. Raw data was available from May 2007 to April 2009, on a continuous half-hourly basis with the exception of short-term periods of data loss. Figure 2 shows the view from the flux tower. Continuous hourly meteorological data were recorded from an Automatic Weather Station (Didcot Instruments, UK) at Wytham, approximately 840 m southeast of the tower location.

2.3 Flux calculations and corrections

2.3.1 Primary raw data processing

Binary files from 1 May 2007 to 30 April 2009 recorded by the data logger were initially processed using the software tool EdiRe (www.geos.ed.ac.uk/abs/research/micromet/EdiRe: developed by Edinburgh University). The standard averaging interval used by regional flux collaborations such as CarboEurope of 30 min was used and EdiRe was also run using 60 min intervals to explore the sensitivity of averaging interval on final CO₂ flux calculations. Block-averaging was used in the calculation of flux values within these intervals. Within EdiRe a number of calculations and standard corrections for open-path sensors were made following the extraction of raw signals within data

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files: the three wind velocity components (u , v and w); temperature; water vapour and; carbon dioxide.

Carbon dioxide flux (F_x) is essentially equal to the mean product of air density, vertical wind speed and the mixing ratio of CO_2 and was calculated as in Eq. (1):

$$F_x = \rho \bar{w} \bar{x} \quad (1)$$

Where ρ = the density of dry air, \bar{w} = the vertical wind speed and x = the mixing ratio of CO_2 . Standard corrections included those for air density effects using Webb-Pearson-Leuning (Webb et al., 1980) and vertical wind signal rotation to force the mean vertical velocity to zero. Some authors have argued that this approach is only appropriate for level, homogenous terrain. For undulating heterogeneous sites the planar fit method has been employed (Lee et al., 2004), which defines the rotation correction values using an ensemble of wind vectors. However, many studies have found the final flux values generated using “natural” and planar wind fit corrections to be similar (Knohl et al., 2003). Angle of attack corrections specific to Solent sonic anemometers were applied to extend the ability of the Solent to adequately measure wind vectors from outside default limits of ± 20 degrees from the horizontal. These corrections are now standard, but have resulted in large improvements on the accuracy of flux estimates (Nakai et al., 2006).

2.3.2 Secondary data processing

Secondary corrections involved the removal of spurious data, often associated with non-stationary meteorological conditions, and the replacement of these values with more plausible estimates. Such corrections are very much a site-specific task and are far from trivial. Data removal of 30–40% of values over one year, which are then “gap-filled”, are common (Moffat et al., 2007; Baldocchi, 2008). These issues may be more acute in fragmented forest such as Wytham, with increased likelihood of advection events from non-forest land or fossil fuel combustion sources. One of

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the aims of this paper is to explore the sensitivity of final calculated fluxes to data processing procedure. The corrections undertaken are summarised as follows:

– Secondary CO₂ flux spike removal

Despite the low and high-pass filtering undertaken in EdiRe, spikes still occurred in the final CO₂ fluxes. We assume that the extreme spikes do not represent natural localised CO₂ flux phenomena, but rather non-localised advection events or other non-stationary phenomena. These spikes were removed using a two-tier approach.

Firstly, flux values were split into positive and negative groups. Positive values two or more times greater than the standard deviation of all positive values were removed. Negative values two or more times smaller than the standard deviation of all negative values were removed. This had the effect of removing extreme spikes in the dataset and 5% of the CO₂ flux values were deleted. The second stage allowed for more fine-tuned removal of erroneous values. Here, for each month of the year, positive half-hour values were removed that were greater than the average of all CO₂ flux values for that month plus the average standard deviation for that month ($x > \bar{x} + \sigma$) for that half hour period of the day. The opposite was conducted for negative values ($x < \bar{x} - \sigma$). This removed a further 9% of all CO₂ flux values. This method of spike detection is very similar to that proposed by Papale et al. (2006), and comparison of the two methods produced very similar results.

– LE and H flux spike removal

Erroneous values (spikes) of latent energy flux, LE (< -100 or $> 800 \text{ W m}^{-2}$) and sensible heat flux, H (< -150 or $> 500 \text{ W m}^{-2}$) were removed from the dataset. These may have resulted from strong advection or sensor interference, thus casting doubt over the reliability of associated CO₂ flux values, which were also omitted. Seven percent of flux data exceeded the above energy thresholds and were deleted. These

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thresholds represent a compromise between minimising data loss, whilst ensuring as complete an energy balance closure as possible. Variation in the minimum H threshold in particular had a large impact upon data loss. Energy balance closure is calculated by the following equation:

$$SEB = \frac{(LE + H + dS)}{R_n} \quad (2)$$

Here, SEB = Surface Energy Budget, R_n = net Radiation, dS = change in heat stored in the canopy and soil. Over a 24-h period $dS \sim 0$, hence a SEB of 1.0 over a 24-h period would suggest that the eddy covariance method was accounting for all energy fluxes. Although precipitation events are known to interfere with flux sensors (Lloyd, 2006), LE and H thresholds were implemented rather than targeting precipitation events per se in order to retain the NEE response during wet periods. Furthermore, spikes in the LE and H fluxes were likely to result from such interference from precipitation, and would thus be captured by the spike removal. No adjustments to the flux data were made to compensate for incomplete energy balance closure.

– Negative night-time fluxes

Initial analysis of processed data post-spike removal highlighted a negative bias to night-time (periods where solar radiation – R_g – was $< 20 \text{ W m}^{-2}$) values, with 28% of all night-time CO_2 fluxes less than zero. This suggests net assimilation of CO_2 by the forest vegetation at night, very unlikely in this ecosystem and therefore indicative of advection events, which are likely at this site under stable night-time conditions. Other authors have recorded such errors with open-path setups (Lloyd, 2006; Hirata et al., 2007) and it is unlikely that such erroneous fluxes were caused solely by instrument error or interference by precipitation, with only 25% of erroneous results removed by implementing LE and H thresholds for Wytham Woods data. Negative night-time CO_2 fluxes were removed in order to be replaced by values generated using the gap-filling

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algorithm (see below) and the subsequent results were compared to calculations where these negative values were retained.

2.3.3 Gap filling

The next processing step was to replace the deleted data with appropriate “gap-filled values”, an essential requirement for the calculation of complete carbon budgets. Several techniques have been developed to estimate flux values for missing data, based upon either interpolation from neighbouring values or more complex estimates such as derivations from non-linear regression models. However, biases associated with different gap-filling techniques are generally small (Papale et al., 2006; Moffat et al., 2007). In our study, missing data, spike removal and the application of LE and H thresholds resulted in the removal of 21% of CO₂ flux values (rising to 32.5% with the deletion of negative night-time values) from the final output file. In order to recreate a continuous flux dataset for the purposes of calculating carbon balances, deleted values were substituted with estimates using the standard gap-filling procedure employed by CarboEurope (<http://www.bgc-jena.mpg.de/bgc-mdi/html/eddyproc/index.html>; Reichstein et al., 2005). This Marginal Distribution Sampling (MDS) technique is effectively an enhancement of look-up tables whereby flux measurements are correlated to meteorological conditions and produced consistently accurate results when compared to other, more complex, techniques (Moffat et al., 2007). MDS accounts for temporal auto-correlation of fluxes, replacing missing data with the average value under similar meteorological conditions within a 7-day window. Where data gaps are large, the averaging window can be increased from the 7 days, but these data are assigned to a lower accuracy category. MDS requires flux data, in the form of CO₂, H and LE fluxes and the meteorological variables: solar radiation; relative humidity; air temperature; soil temperature and vapour pressure deficit.

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2.3.4 Friction velocity correction

Underestimation of eddy covariance fluxes can occur during calm night-time periods of low turbulence and stable atmospheric stratification if surface air containing respired CO₂ drains laterally from the study area, thus passing undetected by the IRGA. Data from these periods was corrected by implementing a standard friction velocity (u_*) correction (Goulden et al., 1996) to calculate night-time fluxes during well-mixed periods of moderate turbulence, which subsequently replaced data from calm periods where thermal stratification and drainage may have occurred. The method described by Reichstein et al. (2005) was used, with the gap-filled dataset split into six temperature categories of equal sample size and further subdivided into 20 classes of u_* values. The u_* threshold for each temperature class was calculated as the u_* class where the night-time flux reached $\geq 95\%$ of the average flux within the higher u_* classes. The final threshold was calculated as the median of the temperature classes and applied in 3 month subsets to account for seasonal variation. A default value of 0.4 m s^{-1} was used if no threshold could be calculated. This value corresponded well with manual estimates. Incorrect application of the u_* correction may occur if CO₂ respired on calm nights is not lost through advection but instead stored under the canopy and released as a pulse of CO₂ following daybreak (Moncrieff et al., 1996). Due to the open nature of the canopy at Wytham Woods and the uneven topography it was assumed that such “canopy storage” would not occur on a frequent basis, and there is very little evidence of morning “spikes” as stored CO₂ is flushed from the canopy.

2.3.5 Partitioning

Flux data were partitioned into Gross Primary Productivity (GPP) and respiration using the online CarboEurope partitioning tool (Reichstein et al., 2005) available at <http://www.bgc-jena.mpg.de/bgc-mdi/html/eddyproc/index.html>. For night-time values (where solar radiation $< 20 \text{ W m}^{-2}$), the Lloyd-Taylor regression model (Lloyd and Taylor, 1994) was used to estimate respiration rates from ecosystem soil temperature (in

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fact, the largest source of ecosystem respiration at this site is stem respiration (Fenn et al., 2010) and our implicit assumption is that stem near-surface temperature, which was not monitored, closely tracks soil surface temperature). The estimated value of respiration was then assigned to the central time point of the averaging interval (30 or 60 min) and linearly interpolated between time periods. GPP was subsequently calculated as the difference between NEE and respiration. As both negative GPP values, and non-zero GPP values at night, are impossible in the majority of plants, such values were interpreted as errors and forced to zero. Net Ecosystem Productivity (NEP) was calculated by subtracting respiration from this corrected GPP (in contrast to the measured NEE). Positive NEP values represent assimilation of CO₂ from the atmosphere through photosynthesis.

2.4 CO₂ fluxes and weather data

Meteorological variables were associated with CO₂ NEE values for both hourly and half-hourly time averaging intervals by matching time and date for each period. As only hourly meteorological data were available, 30 min averages were estimated for (a) 0–30 min and (b) 30–60 min in each hour using the following equations:

$$V(a) = \frac{(3 V(x) + V(x-1))}{4} \quad (3)$$

$$V(b) = \frac{(3 V(x) + V(x + 1))}{4} \quad (4)$$

Here, V = the desired half-hourly meteorological variable value, x = the hour in which V resides. This weighting was applied because the mid-point of each half hour interval (e.g. 12:15) is 3/4 of the way between the mid-point of the adjacent hour (e.g. 11:30) and the mid-point of the current hour (e.g. 12:30). Hence such a weighted estimate is a better estimate of the half-hourly value. Precipitation, recorded as a total over each hourly period, was halved to produce totals for each half-hourly period. The meteorological variables were then correlated with pre gap-filled CO₂ fluxes for the relevant

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time period to produce R^2 (co-efficient of determination) values. Curves were fitted to monthly plots of daytime (where solar radiation $\geq 20 \text{ W m}^{-2}$) CO_2 flux versus solar radiation (as the main meteorological variable driving CO_2 fluxes), using a mixture of first to third degree polynomial equations that best described the relationship between these two variables for each month. Residuals calculated as the difference between observed daytime CO_2 fluxes and those predicted using polynomial equations for each month were then compared to other meteorological variables. Where appropriate, linear regression was used to test the significance of the aforementioned relationships. It should be noted that meteorological data was obtained from an open grassland rather site rather than the location of the flux tower. Summer soil temperatures in particular are likely to be lower within the forest than open grassland (Morecroft et al., 1998), although a depth of 300 mm was used to compare to flux data in order to minimise these differences. Daytime and night-time data were analysed at both half hourly and daily average intervals, for individual months and spring (March, April, May), summer (June, July, August), autumn (September, October, November) and winter (December, January, February).

3 Results and analysis

3.1 Meteorological data

Daily averages of key meteorological variables are shown in Fig. 3. Average annual precipitation over the study period was 902.4 mm – over 170 mm (or 24%) greater than the average for Wytham between 1992 and 2009. Temperatures were slightly below average, with a mean annual air temperature of 9.7°C . Winds were predominantly south westerly, coming from this direction for approximately 55% of the study period. Average daily air temperature in July was 16.0°C with a maximum hourly value of 26.7°C in 2008. December, January and February were the coldest months, with average daily air temperatures of 4.3°C , with minimum hourly air temperatures occasionally reaching

–5.0 °C. A surface energy budget ratio of 0.74 was calculated for 24 h periods over the study period. A review of studies using eddy covariance over forests suggests that a value of 0.7 to 0.8 is typical (Baldocchi, 2008). It is not yet fully understood why some energy fluxes are missing, although undetected low-frequency transport and advection is one likely possibility (Malhi et al., 2004).

3.2 Carbon dioxide flux sensitivity to processing procedures

Figure 4 shows the cumulative impact of secondary processing approaches upon 30 min interval NEE values for 2008. The daytime fluxes are predominantly negative, representing net assimilation of carbon into the forest ecosystem. The positive night-time (where solar radiation – R_g – $< 20 \text{ W m}^{-2}$) fluxes show net respiration – loss of carbon in the form of CO_2 from the forest to the atmosphere. With the exception of the original and spike-removed fluxes, the daytime fluxes show remarkable similarity between processing approaches, peaking at around $-12 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ in June. However, the use of different techniques and corrections when processing raw flux data can have a large impact upon NEE (Guan et al., 2006; Zhang et al., 2006). In our study, there is a marked difference between the night-time average hourly fluxes for secondary stage processing approaches. Although the resultant fluxes are higher than typical winter values for deciduous forest of $\sim 1 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ (Baldocchi and Valentini, 2004), the negative night-time CO_2 flux removal correction appears to most realistically represent winter night-time fluxes when compared to chamber measurements of combined autotrophic (predominantly stem and leaf) and heterotrophic (predominantly soil and litter) respiration (Fenn et al., 2010) in Fig. 4. Therefore, this correction was applied to calculate total carbon uptake. Although chamber measurements represent daytime CO_2 efflux, diurnal differences between day and night-time respiration are assumed to be small.

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3.3 Carbon fluxes at Wytham Woods

3.3.1 NEE fluxes

For the period 1 May 2007 to 30 April 2009 approximately 43% of the total half-hourly flux values were removed or missing (following u_* corrections) and thus required gap-filling. The largest periods of absent data were fortnights in May 2007 and July 2008 and the last week of April 2009. 91% of the gaps filled were classified as category A, the highest degree of estimation accuracy, whilst 8.5% and 0.5% were calculated as categories B and C respectively. Evaluation statistics for artificial gaps created by the gap-filling process show strong correlations when compared to measured data, providing confidence in the representativeness of the gap-filled fluxes.

The diurnal and seasonal “pulse” of carbon fluxes in Wytham Woods for the study period is depicted in Fig. 5, which shows changes in gap-filled NEE (in $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) with time of day and year. The dark blue areas represent maximum CO_2 sequestration – occurring during the spring and summer months between daylight hours. Indeed, the impact of day length is illustrated by the changing width of the NEE “pulses”. Their ovoid shape also suggests rapid rise in NEE during the spring, followed by slower decline in the autumn. Net sequestration typically starts around 1 h after daybreak and net respiration 1 h prior to nightfall. The lowest CO_2 fluxes were observed in January, where net sequestration of carbon was rare even during maximum PAR. It is surprising that any net photosynthesis was detected during this period as the only photosynthetically active plants are evergreen trees and shrubs, some herbaceous species and bryophytes (mosses and a small number of liverworts). Evergreen trees and shrubs cover a very small proportion of the total woodland area. By March net sequestration occurred during daylight hours of 08.00 to 17.00 GMT. Half-hourly CO_2 assimilation rates peaked in June at around $20 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ between 11.00 and 14.00 GMT. The symmetrical shape of diurnal NEE suggests little evidence of factors limiting photosynthesis such as afternoon water stress (the summers of 2007

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and 2008 were atypically wet) or “pulses” of respiration following daybreak – indicating little canopy storage of CO₂ respired at night.

Graphs of latent heat of evaporation (LE) and sensible heat (H) fluxes over the study period are shown in Fig. B2. A slight net negative flux was found for H, with an average of -14.3 W m^{-2} over the study period. It is thought that any bias caused by instrument malfunction or interference was removed by introducing thresholds (see Sect. 2.3.2). Remaining bias may result from the topography of the site and the hillside position of the flux tower, resulting in cool air sinking away from the study site, daytime advection of warmer air from surrounding fields, and other advection-based complications. Other studies have also noted such a negative H bias (Clement, 2004). The average LE over the study period was 53.8 W m^{-2} , equal to an annual evapotranspiration rate of 690 mm. This represents 76% of precipitation over study period, but 95% of average long term precipitation, suggesting that Wytham Woods is likely to be water limited in late summer during normal years.

3.3.2 Partitioned fluxes

Figure 6 shows the daily 30 min average CO₂ flux estimates for Gross Primary Productivity (GPP), respiration and Net Ecosystem Productivity (NEP) from May 2007 to April 2009. The bold lines represent weekly averages for the partitioned values (GPP and R_e). Positive GPP and NEP values represent net sequestration by the forest ecosystem; negative values indicate a net loss of CO₂ to the atmosphere. Respiration values are always positive and represent net exchange of CO₂ from the ecosystem to the atmosphere. Half-hourly averaged GPP peaks at around $17 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ between mid-June to early July and falls to a minimum of around $1\text{--}1.5 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ in the winter months. Respiration fluctuates to a lesser extent than GPP on an annual scale, but more on a week-by-week basis. Increases in soil temperature in the summer months correlate well with increasing rates of respiration, as expected (Reichstein et

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al., 2005), with peaks in respiration corresponding with peaks in soil temperature. Respiration peaks occurring in late October/early November in both 2007 and 2008 do not appear to be driven by corresponding rises in soil temperature (Fig. 3). These peaks probably result from the decomposition of fresh leaf litter following peak litterfall and thus a rapid decline in leaf area index between mid October and mid November (Fenn, 2010). Respiration peaks in late December 2008 and January 2009 seem too late for leaf litter decay, and are possibly caused by periods of increased soil temperature and wind speeds between cold (sub-zero temperature) periods.

The ecosystem was a net source of CO_2 (negative NEP) from the start of January to mid-April and from mid-October to the end of December, averaging around $-2 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$. In early April NEP becomes positive (net carbon uptake) as rates of photosynthesis become greater than respiration rates. The onset of net carbon uptake around 20 April (in 2008) coincides with the time of year when daily average soil temperature equals the mean annual air temperature of 9.7°C , reinforcing similar findings in other temperate forests (Baldocchi et al., 2005). The increases in GPP or NEP appear to occur in three distinct stages (Fig. 6). In stage 1 GPP rises slowly until the start of May, probably a result of expansion of ground flora and early leafing trees. This is followed by a rapid rise during May (stage 2) as much of the forest canopy has come into leaf and started photosynthesising. The final rise to a mid-summer peak (3) could result from late developing trees such as oak reaching full photosynthetic capacity by mid-June, which has been measured at Wytham (Morecroft et al., 2003), as well as a function of increasing sun elevation and day length. GPP reaches a maximum of $17.7 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ in mid-June, corresponding to a peak NEP of $8.8 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$. The rapid decline in GPP at the start of October corresponds with senescence (leaf aging) and abscission (leaf-fall). Day-to-day fluctuations in GPP or NEP following leaf emergence during the spring and summer months are likely to reflect changes in weather conditions. One definition of the forest growing season (ignoring ground flora activity) would be from the start of the rapid rise in GPP (canopy leaf-out) around 1 April to the flattening of the GPP curve by 1 November. This period

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is 214 days. The net carbon uptake period (the period between the first and last days with positive NEP) is 151 days.

Approximately 55% of the measured total carbon uptake recorded between May 2007 and April 2009 originated from areas to the southwest of the flux tower, with an average half hourly NEE of $-2.4 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ (Fig. B3). However, the greatest carbon sequestration rates (NEE of $-4.5 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) occurred in areas to the north/northwest of the flux tower (undisturbed ancient forest and 20th century plantations). The large seasonal variation in CO_2 sequestration rates detected from different wind directions may reflect the mixed composition of tree and undercanopy species in Wytham Woods and thus changes in seasonal photosynthetic activity between species.

3.3.3 Total carbon uptake and interannual variability

Over the period 1 May 2007 to 30 April 2009 we estimate cumulative NEP to be $1.2 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$. GPP is estimated at $21.1 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ and R_e $19.8 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$. GPP, R_e and NEP were all highest in the summer, with net respiration occurring in the autumn and winter.

Figure 7 plots the partitioned fluxes for each month of the study period, to allow comparison of interannual differences. GPP shows very little variation in its seasonal cycle, with 2008 showing slightly higher spring uptake and slightly greater autumn decline than 2007. Higher spring temperatures ($+1.5^\circ\text{C}$ in 2008) may have encouraged earlier growth of the deciduous canopy (Morecroft et al., 2003). Ecosystem respiration showed greater interannual variability, particularly in the autumn and winter months (September–January), but also in mid-summer (July). In most of these periods 2007 ecosystem respiration rates were substantially higher than 2008 rates. Periods of higher respiration (between years) appear to correspond to periods of higher temperature, reinforced by our findings in Section 3.3.4. According to Fenn et al. (2010) interannual variation in soil temperature at this Wytham site can explain up to 50% of

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interannual variance in CO₂ soil efflux, and soil moisture a further 18% of the residual variance. On this basis it is likely that greater losses of carbon to the atmosphere observed in October to December 2007 compared to 2008 are the result of higher rates of root and microbial respiration due to higher air temperatures (+1 °C), and increased soil moisture in the litter and soil layers suggested by heavier rainfall for these months in 2007. As soil and litter respiration account for only a small component of ecosystem respiration at the site (22% and 11% respectively; Fenn et al., 2010), the differences in ecosystem respiration between years also suggest changes in stem and leaf respiration rates between years, probably also linked to temperature variation.

As a consequence of lower ecosystem respiration rates in 2008, greater net sequestration occurred in 2008 compared to 2007, with smaller net losses of carbon to the atmosphere in the late autumn and early winter months (Fig. 7). Hence variation in ecosystem respiration appears to be the stronger driver of interannual variation of net carbon uptake, at least over the two-year study period, reinforcing findings that ecosystem respiration rates drive net ecosystem carbon exchange in European forests (Valentini et al., 2000). Longer term studies have shown convincing interannual variability in the balance between GPP and R_e (Ciais et al., 2005; Urbanski et al., 2007; Delpierre et al., 2009).

In 2008, the only complete year during the study, we found Wytham Woods to be a substantial sink of carbon of 265.2 g C m⁻² or approximately 2.7 Mg C ha⁻¹. We explored the sensitivity of this result to averaging period, by comparing 30 min averaging intervals to carbon sequestration estimated using hourly intervals. Using 60 min intervals generates a total annual estimate of carbon uptake of 3.6 Mg C ha⁻¹ for 2008, 33% greater than using 30 min intervals. This difference can be accounted for by the mean 30 min and 60 min CO₂ fluxes, which are -0.53 and -0.74 μmol CO₂ m⁻² s⁻¹ respectively. This may result from the detection of lower frequency turbulence when longer averaging intervals are used (Malhi et al., 2004) although increasing averaging periods can enhance advection problems. Some authors present annual carbon fluxes in cumulative NEE, which were ~75% of NEP estimates for our 2008 results. However,

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using NEP as corrected GPP minus respiration may give a more accurate impression of net carbon sequestration by providing further correction for erroneous night-time values. It is worth highlighting the impacts of removing negative night-time CO₂ fluxes. Including these values produced an estimated carbon sink of 8.2 Mg C ha⁻¹ for 2008, which seems implausible when compared to other biometric data (see Sect. 4).

3.3.4 Meteorological drivers and canopy physiological parameters

Correlating CO₂ fluxes with individual meteorological variables is difficult due to strong temporal auto-correlations associated with the seasonal cycle that hinder identification of specific causal factors. Solar radiation was found to be the primary driver of photosynthesis with $R^2=0.35$ for the positive non-linear relationship between all half hourly daytime solar radiation and NEE data. Analysis of daytime data from summer months when the tree canopy was in full leaf produced the highest R^2 values between these two variables ($R^2=0.53$). Despite a linear response of CO₂ fluxes to low levels of solar radiation (<100 W m⁻²), the overall curved fit and levelling-off of CO₂ uptake rates above 700–800 W m⁻² indicates when carboxylation becomes limiting. The CO₂ compensation point (when canopy uptake equals ecosystem respiration) occurs at ~60 W m⁻². The zero solar radiation intercept is at an NEE of 2.3 μmol CO₂ m⁻² s⁻¹ representing net release of CO₂ to the atmosphere similar to the mean night-time respiration of 2.4±0.06 μmol CO₂ m⁻² s⁻¹. Night-time fluxes showed unexpectedly weak but significant increases in NEE (respiration) with increasing soil temperature over the study period ($R^2=0.11$, $P<0.001$), with a slightly stronger relationship during the spring months ($R^2=0.17$, $P<0.001$).

The theoretical maximum quantum yield for photosynthesis in C₃ species is about 0.06 mol CO₂ per mol of absorbed photons (Farquhar et al., 1980). The maximum observed yield can be estimated using the slope of the light-response curve at low solar radiation (5 to 100 W m⁻²), when photosynthesis is restricted by photon availability rather than other limiting factors that become more influential at higher insolation.

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Assuming that Photosynthetic Active Radiation (PAR) in $\mu\text{mol photons m}^{-2} \text{s}^{-1} = 2.16 \times$ solar radiation in W m^{-2} (Weiss and Norman, 1985) and that absorbed PAR = $0.9 \times$ incident PAR (as the average solar albedo of temperate deciduous forests is $\sim 12\%$) linear regression through all data at low solar radiation gives an apparent yield of 0.024 ± 0.002 (95% confidence) mol CO_2 per mol of absorbed photon, or 40% of the theoretical maximum. Monthly variation in quantum efficiency is shown in Table 2 and Fig. 8, along with monthly averaged GPP and NEE values that represent maximum photosynthetic rate.

The quantum efficiency approaches theoretical maximum values in both years but with different timing, with a late summer peak in August 2007, and a sharp early summer peak in June 2008. The photosynthetic capacity (GPP under high light) shows a more consistent peak at about $30 \mu\text{mol CO}_2 \text{ m}^{-2} \text{s}^{-1}$ over June–August in both years. This peak is relatively late after canopy leaf-out, and may reflect the late and secondary leafing of the oak canopy which adds to canopy photosynthetic capacity while the sycamore and ash canopies have not begun to decline substantially in photosynthetic capacity. Photosynthetic capacity declines strongly in September, preceding most litterfall (October/November), suggesting that leaf senescence strongly affects photosynthetic capacity well before leaf abscission. Quantum efficiency over the study site for the months of June to September was found to be greater than the values obtained from leaf observations on sunny days for oak and sycamore (0.029 ± 0.007 and 0.021 ± 0.006 mol CO_2 per mol of absorbed photon respectively) made by Morecroft and Roberts (1999), where corresponding maximum irradiance saturated photosynthetic rates were estimated at approximately 10.4 and $3.5 \mu\text{mol CO}_2 \text{ m}^{-2} \text{s}^{-1}$ respectively.

Other authors have found NEP in temperate deciduous forests to be sensitive to rainfall and Vapour Pressure Deficit (VPD) during the summer months (Valentini et al., 2000; Knohl et al., 2003; Urbanski et al., 2007). The symmetrical rise and fall of diurnal changes in NEE in summer months suggests that water deficiency was not a limiting factor in the summers of 2007 and 2008 and comparison of 30 min residual daytime flux data against rainfall and vapour pressure deficit produced weak coefficient of

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determination values, typically $R^2 < 0.01$ even when analysed on a monthly or seasonal basis or warm days only where hourly air temperatures reached $>20^\circ\text{C}$. Pulses of respiration following precipitation (Huxman et al., 2004) were not observed at Wytham, with declining NEP during sustained heavy rainfall caused by a lack of insolation resulting from heavy cloud cover. Comparison of 30 min residual daytime flux data against soil and air temperature also produced weak coefficient of determination values, where $R^2 < 0.01$. For daily averaged daytime data, the strongest relationships between meteorological variables and residual fluxes were found for spring and autumn, recording $R^2 = 0.23$ and 0.20 ($P < 0.001$) respectively for linear increases in air temperature and respiration and $R^2 = 0.56$ and 0.34 ($P < 0.001$) respectively for linear increases in soil temperature and respiration at 300 mm. During the summer months weak relationships between residual flux data and meteorological variables were calculated, where typically $R^2 < 0.05$.

4 Discussion

4.1 Comparison with biometric data

Our study area in Wytham Woods was found to be a carbon sink, sequestering approximately $1.24 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ between May 2007 and April 2009. Larger estimates of carbon sequestration were produced using hourly averaging intervals. This suggests the detection of low frequency turbulent fluxes, but these results may be more vulnerable to advection biases and detection of flux beyond the study site (Malhi et al., 2004). Validation of eddy covariance findings is provided by comparison with stock-based assessments of the carbon budget at Wytham. Biometric assessments of NEP at thirty-two 10 m^2 plots in Wytham were generated using allometric equations (Bunce, 1968) relating tree girth to biomass between 2005 and 2008 for the main tree species of ash, sycamore and oak. The results show an increase in stored aboveground biomass carbon of $4.2 \pm 0.8 \text{ Mg C ha}^{-1}$ over the 3 years, or approximately

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1.4±0.3 Mg C ha⁻¹ yr⁻¹. More detailed sampling of 466 trees within a 1 ha plot close to the flux tower (SP 457 089) shows an increase in carbon content stored in above-ground biomass of 1.4 Mg C ha⁻¹ in 2008 (Fenn, unpublished data). Both stock-based estimates for 2008 are lower than the eddy covariance equivalent of 2.7 Mg C ha⁻¹.
 5 Some of this variation may be accounted for by including belowground biomass (approximately 20% of above-ground live biomass in temperate broadleaf woodlands; Jackson, 1996), increasing the estimated uptake rate to 1.7±0.3 Mg C ha⁻¹ yr⁻¹. Furthermore, soils may be accumulating carbon if recovering from historical management practices, or possibly losing carbon in response to long-term warming. Eddy covariance,
 10 Annual eddy covariance estimates of GPP and R_e are validated by biometric and chamber measurements of 20.3±1.0 and 18.9±1.7 Mg C ha⁻¹ yr⁻¹ respectively (Fenn et al., 2010).

Importantly, the findings of these “top-down” and “bottom-up” studies also complement one another on a monthly basis as shown by respiration estimates in Fig. 7; both approaches indicate the same magnitude and timing of seasonal variation. The biometric estimates of respiration justify our approach to remove negative night-time fluxes. Although advection effects were not accounted for directly, negative night-time CO₂ fluxes could be related to the advection of CO₂ away from the flux tower resulting
 20 from the undulating topography at Wytham. Here, the size of downward wind vectors would negate and surpass the upward wind vector, creating an apparent negative flux. It can be argued that removing the effects of advection (such as negative night-time CO₂ fluxes) indirectly helps correct for advection.

4.2 Comparison with other woodlands

25 Analysis of wind data and the estimated flux footprint suggests net sequestration within disturbed ancient deciduous woodland. To understand the context of such findings, it is necessary to compare our estimates to other eddy covariance based temperate

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deciduous woodland studies. Whilst it is important to note that timings of data collection and processing methods may vary between sites, Fig. 9 plots annual GPP, R_e and NEP according to annual mean temperature and total precipitation at sites across the globe to provide insights into the influence of climatic factors upon carbon budgets. Of particular interest is Alice Holt in Hampshire, one of the few other sites in the UK where eddy covariance has been used to estimate carbon budgets in mature deciduous woodland. Here, between 1999 and 2006, average NEP was $\sim 4.4 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ (Read et al., 2009). Partitioned Alice Holt flux data from 2000 (validated by stock-based measurements) estimates GPP at $\sim 14 \text{ Mg C ha}^{-1}$ and R_e at $10.2 \text{ Mg C ha}^{-1}$ (Broadmeadow and Matthews, 2003). With similar species composition to Wytham Woods, it is likely that greater NEP at Alice Holt resulted from more intensive commercial management practices over the last few decades (Benham, 2008). The removal and regeneration of understory shrubs or introduction of saplings is likely to increase the rate of CO_2 assimilation from the atmosphere (Ryan et al., 1997). Both GPP and R_e estimates at Wytham are substantially higher than other sites (Fig. 9, Table 3). Hence the higher fluxes at Wytham relative to mainland Europe cannot simply be explained by climatic factors.

Only a few of these sites are not actively managed. Unmanaged forest sites in Fig. 9 include a 250 year-old temperate deciduous beech forest in central Germany with a carbon uptake of 4.9 Mg C ha^{-1} (cumulative NEE; Knohl et al., 2003), a large uptake supported by other research sites at beech forests around the globe (e.g. Valentini et al., 1996). An unmanaged mixed temperate forest in northeast China, parts of which are estimated to be greater than 450 years old, yielded an estimated carbon sink of around $2 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ (Guan et al., 2006), with vapour pressure deficits acting to restrict further carbon assimilation. Although NEP may decline with stand age (Ryan et al., 1997), mature temperate deciduous forests still have the potential to act as carbon sinks through natural regeneration, diversity of vegetation age and species turnover (Luyssaert et al., 2008) and possibly increased tree growth through CO_2 fertilisation, earlier bud-break or increased nutrient availability.

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The relatively large GPP estimates at Wytham and observed net sequestration of carbon may partially result from past management history. It is difficult to assess the degree to which the “ancient” sections of the forest are still adjusting to the influence of practices such as selective felling or coppicing which ceased 40 to 100 years ago (Gibson, 1986), but it is clear that the Woods are not in an equilibrium state even after 100 years. Such legacy effects are an important issue when calculating possible baselines and carbon stock changes under carbon forestry schemes (Böttcher et al., 2008). In advanced unmanaged forest such as the ancient areas of Wytham small-scale disturbances such as wind-throw, infestation, or fungal attack can facilitate new recruitment and thus biomass accumulation. Tree-falls caused by the storms of 1987 and 1990 are thought to have opened the canopy at Wytham, facilitating the growth of ash and sycamore in the gaps created (Kirby et al., 1996). Numbers of fallow deer (*Dama dama* L.) and Chinese muntjac (*Muntiacus reevesi* Ogilby) in the Woods have declined since populations boomed in the 1990s, due to regular culling (Mihok et al., 2009) and rabbit populations crashed following myxomatosis in the 1950s. Although reduced browsing pressure may have aided the regeneration of saplings and shrubs, anecdotal evidence of slow growth (Mihok et al., 2009) suggests that established vegetation may account for the majority of the net carbon uptake in Wytham Woods.

5 Conclusions

The carbon balance of a temperate deciduous broadleaved forest has been estimated using two years of eddy covariance CO₂ flux data. We detected some interannual variability in NEP, driven by changes in R_e resulting from seasonal fluctuations in weather conditions, whilst GPP was similar between years. At 21.1 Mg C ha⁻¹ yr⁻¹ GPP was larger than thus far reported at other temperate deciduous forest sites. This is possibly a result of the UK’s maritime climate (mild winters) and a negligible influence of water stress upon photosynthesis for the majority of the study period. Our eddy covariance estimates for both GPP and R_e closely matched with biometric and chamber

data, increasing the confidence in the use of either technique to estimate carbon budgets. Wytham Woods was a considerable carbon sink of $\sim 1.2 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ between May 2007 and April 2009. This estimate is validated by similar findings using stock-based measurements and is likely to be conservative since inclusion of negative night-time flux values or low frequency turbulence calculates greater net carbon uptake.

Recent net sequestration of carbon despite probably reflects the legacy of past management techniques at Wytham. Although our study doesn't necessarily add to the growing database of mature forests achieving net sequestration, it still provides another reason for the protection of temperate deciduous woodland as anthropogenic CO_2 emissions continue to rise. The response of the terrestrial biosphere to projected future climates will determine the degree to which temperate deciduous forests can ameliorate future emissions. One could speculate that Wytham has the potential to be a larger carbon sink under projected warmer springs, especially with a potential "CO₂ fertilisation effect". However, Broadmeadow et al. (2005) suggest that species such as oak and ash could be adversely affected by warmer summers, whereas sycamore may struggle to compete if droughts increase in frequency and magnitude (Morecroft et al., 2008). Continued research at sites such as Wytham will help build long term datasets to partition the effects of ecosystem dynamics (such as phenology and growing season length), environment (CO₂ fertilisation, nitrogen deposition) and climate change, upon terrestrial carbon budgets at forest sites.

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Nomenclature

- NEE = Net Ecosystem Exchange of C between atmosphere and vegetation (negative NEE indicates net sequestration of C).
- GPP = Gross Primary Productivity, assimilation of C by photosynthesis (GPP is ≥ 0 by definition).
- R_e = Ecosystem Respiration (autotrophic + heterotrophic), loss of C from the ecosystem to the atmosphere (R_e is > 0).
- NEP = Net Ecosystem Productivity, the difference between GPP and R_e fluxes (positive NEP indicates net sequestration of C).
- PAR = Photosynthetically Active Radiation.

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Table 1. Classification of woodland in terms of management history at Wytham (adapted from Morecroft et al., 2008).

| Woodland classification | Description |
|---|--|
| Undisturbed ancient semi-natural woodland | <ul style="list-style-type: none"> – Woodland hosting continuous forest cover since ~1600. – Largely unmanaged for the past 40–100 years. – Dominant species are hazel and oak, with ash present. |
| Disturbed ancient woodland | <ul style="list-style-type: none"> – Ancient forest more recently modified by human management, but which has not been clearfelled. – Natural regeneration in areas of timber extraction. – Localised planting, with hazel and oak dominant and sycamore present. |
| Secondary woodland | <ul style="list-style-type: none"> – Former grassland areas, that have naturally reverted to closed canopy woodland over the last 200 years. – Limited localised timber extraction and planting. – Dominant species are ash and sycamore with some oak. |
| 19th century plantations | <ul style="list-style-type: none"> – Former open/grassland areas planted in the 19th century. – Ornamental, widely spaced trees with little management in recent decades. – Beech is the dominant species. |
| 20th century plantations | <ul style="list-style-type: none"> – Plantations created between 1950–1970 on grassland or cleared ancient woodland. – Plantations consist mainly of oak, beech and exotic conifers. |

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Table 2. Monthly calculations for light use efficiency in Wytham Woods. Quantum efficiency is in units of mol CO₂ per mol of absorbed photon. Blanks indicate too few data to generate quantum efficiency estimates via linear regression.

| Solar radiation (W m ⁻²): | | 5 to 100 | >500 | |
|---------------------------------------|-----------|--|--|--|
| Year | Month | Quantum efficiency (± standard error) | Average GPP (μmol CO ₂ m ⁻² s ⁻¹) | Average NEE (μmol CO ₂ m ⁻² s ⁻¹) |
| 2007 | May | 0.021±0.017 | 24.5±0.63 | -17.3±0.69 |
| | June | 0.039±0.011 | 31.5±0.59 | -21.8±0.58 |
| | July | 0.047±0.011 | 31.1±0.39 | -20.5±0.39 |
| | August | 0.052±0.008 | 25.9±0.51 | -15.5±0.43 |
| | September | 0.047±0.007 | 19.8±0.73 | -14.3±0.69 |
| | October | 0.018±0.008 | 24.5±1.55 | -10.3±1.47 |
| | November | 0.008±0.010 | | |
| | December | 0.008±0.008 | | |
| 2008 | January | 0.018±0.011 | | |
| | February | 0.014±0.005 | 4.3±1.44 | -0.6±1.45 |
| | March | 0.005±0.007 | 4.1±0.34 | -1.2±0.44 |
| | April | 0.017±0.008 | 9.5±0.31 | -5.0±0.34 |
| | May | 0.046±0.006 | 24.9±0.51 | -15.3±0.57 |
| | June | 0.062±0.010 | 30.2±0.34 | -21.1±0.32 |
| | July | 0.030±0.013 | 29.1±0.51 | -20.2±0.50 |
| | August | 0.040±0.009 | 27.7±0.52 | -19.7±0.61 |
| | September | 0.037±0.011 | 19.5±0.72 | -15.4±0.72 |
| | October | 0.019±0.007 | 14.3±0.58 | -7.8±0.72 |
| | November | 0.013±0.008 | | |
| | December | 0.018±0.006 | | |
| 2009 | January | 0.006±0.008 | | |
| | February | 0.005±0.004 | 0.6±0.54 | 1.3±0.57 |
| | March | 0.004±0.005 | 2.4±0.13 | 1.3±0.17 |
| | April | 0.022±0.009 | 12.2±0.43 | -7.1±0.52 |
| ALL DATA | | 0.024±0.002 | 22.9±0.25 | -15.0±0.21 |

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Table 3. Collection of flux data from temperate deciduous or semi deciduous woodland across the globe. NEP, GPP and R_e in $\text{Mg C ha}^{-1} \text{yr}^{-1}$. NEE used where NEP unavailable.

| Label | Country | Forest | Authors | NEP | GPP | R_e | Mean temp ($^{\circ}\text{C}$) | Annual ppn (mm) | Years of data | Forest description |
|-------|---------|-------------------------------------|---|------|------|-------|----------------------------------|-----------------|---------------|---|
| A | Italy | Collelongo | (Valentini et al., 2000) | 6.6 | 13.0 | 6.4 | 6.2 | 1180 | 1 | Broadleaf deciduous woodland |
| B | Germany | Kannenbruch | (Kutsch et al., 2005) | 5.5 | 17.9 | 12.4 | 8.4 | 714 | 1 | Oak subplot |
| C | Germany | Hainich | (Knohl et al., 2003) | 4.9 | 15.6 | 10.7 | 8.3 | 992 | 2 | Beech dominated deciduous |
| D | Belgium | – | (Valentini et al., 2000) | 4.4 | 14.5 | 10.1 | 7.5 | 792 | 1 | Mixed + broadleaf deciduous temperate |
| E | UK | Alice Holt | (Broadmeadow and Matthews, 2003; Read et al., 2009) | 3.8 | 14.0 | 10.2 | 10.5 | 800 | 1 | Broadleaf deciduous woodland |
| F | USA | Morgan Monroe State Forest, Indiana | (Curtis et al., 2002) | 3.5 | – | – | 11.1 | 1010 | 4 | Eastern broadleaf forest (continental) oak, maple, blackgum, pine |
| G | USA | Synthesis of global data | (Luyssaert et al., 2007) | 3.1 | 13.8 | 10.5 | Varied | Varied | – | Temperate humid deciduous |
| | | Harvard Forest, New England | (Urbanski et al., 2007) | 2.5 | 14.0 | 11.5 | 8.5 | 1050 | 13 | Mixed deciduous forest red oak, red maple, red and white pine |
| H | USA | Walker Branch, Tennessee | (Curtis et al., 2002) | 2.5 | – | – | 13.8 | 1350 | 6 | Eastern broadleaf forest oceanic oak, maple, blackgum, pine |
| I | France | Hesse | (Granier et al., 2000) | 2.3 | 11.3 | 9.0 | 9.2 | 820 | 1 | Broadleaf deciduous temperate, mainly Beech |
| J | Japan | Tomakomai National Forest | (Hirata et al., 2007) | 2.1 | 16.7 | 14.6 | 6.2 | 1040 | 3 | Temperate larch plantation |
| K | Denmark | Zealand | (Pilegaard et al., 2001) | 1.8 | 13.1 | 11.2 | 8.1 | 510 | 2 | Beech |
| L | China | Changbai Mountain | (Guan et al., 2006) | 1.8 | – | – | 3.6 | 695 | 1 | Mixed temperate pine, maple, liden, ash, oak |
| M | Canada | Ontario | (Lee et al., 1999) | 1.7 | – | – | 6.6 | 798 | 3 | Mixed temperate forest, aspen, maple, cherry, ash, pine |
| N | UK | Wytham Woods | This study | 1.3 | 21.1 | 19.8 | 9.7 | 900 | 2 | Broadleaf deciduous woodland |
| O | Japan | Yamashiro | (Kominami et al., 2008) | 0.9 | – | – | 15.5 | 1450 | 1 | Warm temperate mixed forest |
| P | China | Laoshan | (Saigusa et al., 2008) | 0.2 | 14.0 | 13.8 | 5.0 | 640 | 1 | Larch |
| Q | Belgium | Campine region, De Inslag | (Carrara et al., 2004) | –0.9 | 12.4 | 13.3 | 9.8 | 750 | 5 | Mixed temperate woodland, pine and oak |

Legend

-  Flux_tower_location
-  Ancient semi-natural woodland
-  Disturbed ancient semi-natural woodland
-  Plantation (1800s)
-  Plantation (1900s)
-  Secondary woodland

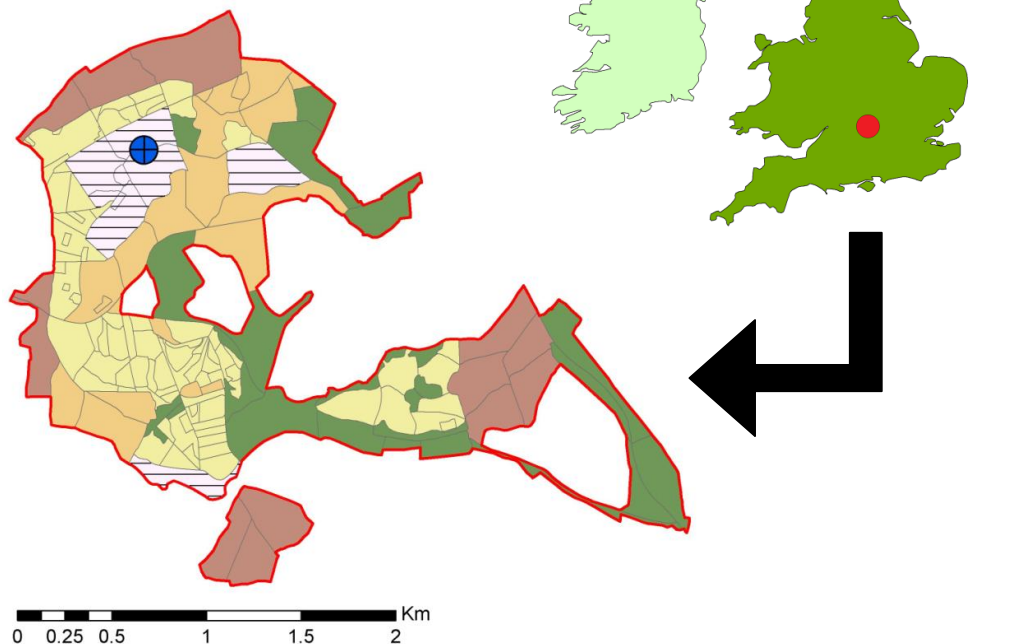


Fig. 1. Study site location in the UK and map of Wytham Woods showing woodland types.

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Fig. 2. South-facing aspect from the flux tower, with an insert looking up the flux tower from ground level. Sources: CEH and author.

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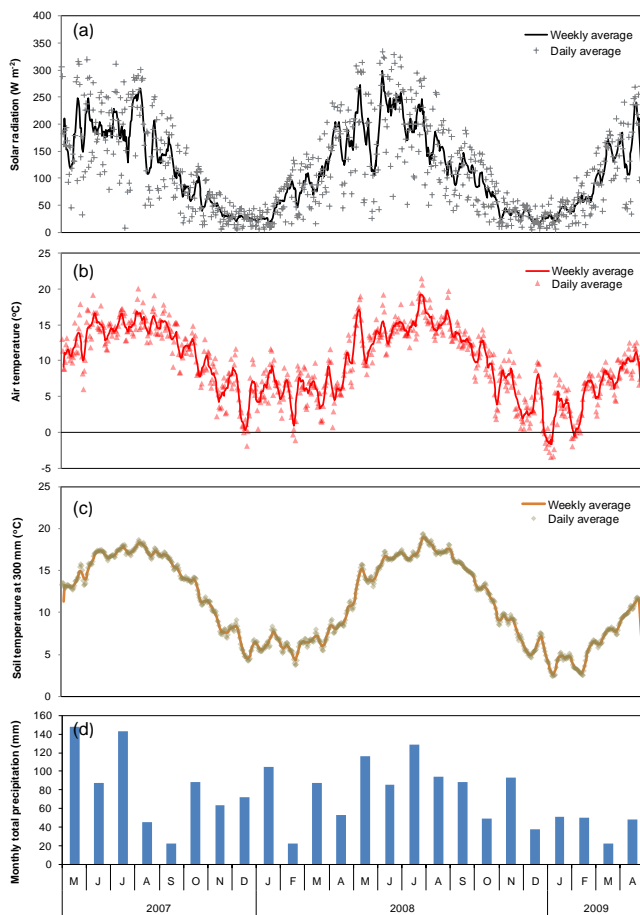


Fig. 3. Variation of **(a)** solar radiation; **(b)** air temperature; **(c)** soil temperature at 300 mm depth; **(d)** monthly total precipitation over the study period.

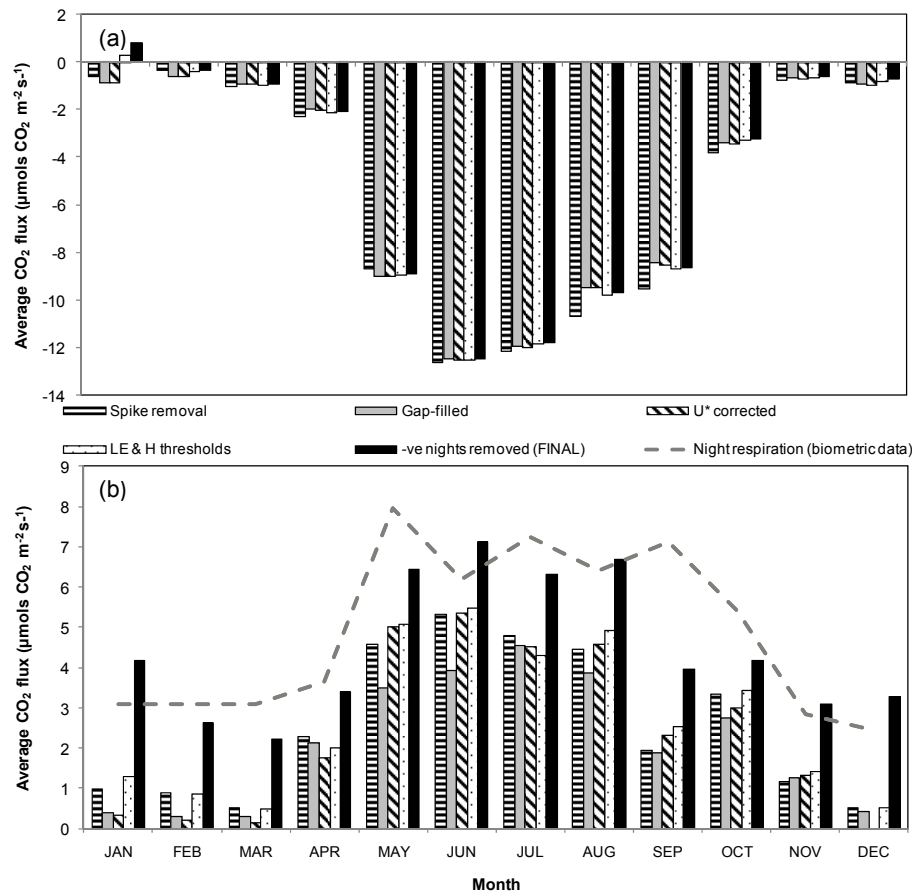


Fig. 4. (a) Day and (b) night-time flux sensitivity attributed with secondary stage processing approaches. Each stage represents cumulative processing approaches with increasing constraints upon the flux data, removing “erroneous” results and replacing with gap-filled data. Biometric estimation of respiration from chamber data (soils, stems and leaves) overlay night time fluxes.

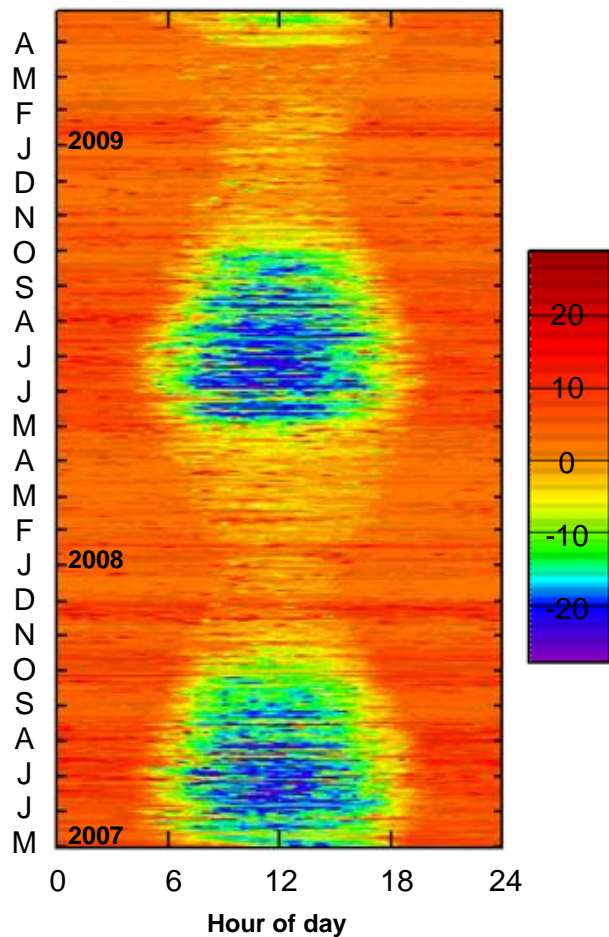


Fig. 5. The Net Ecosystem Exchange (NEE) “pulse” of Wytham Woods showing diurnal (x-axis) and seasonal (y-axis) CO₂ fluxes in $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, generated using CarboEurope’s online partitioning tool.

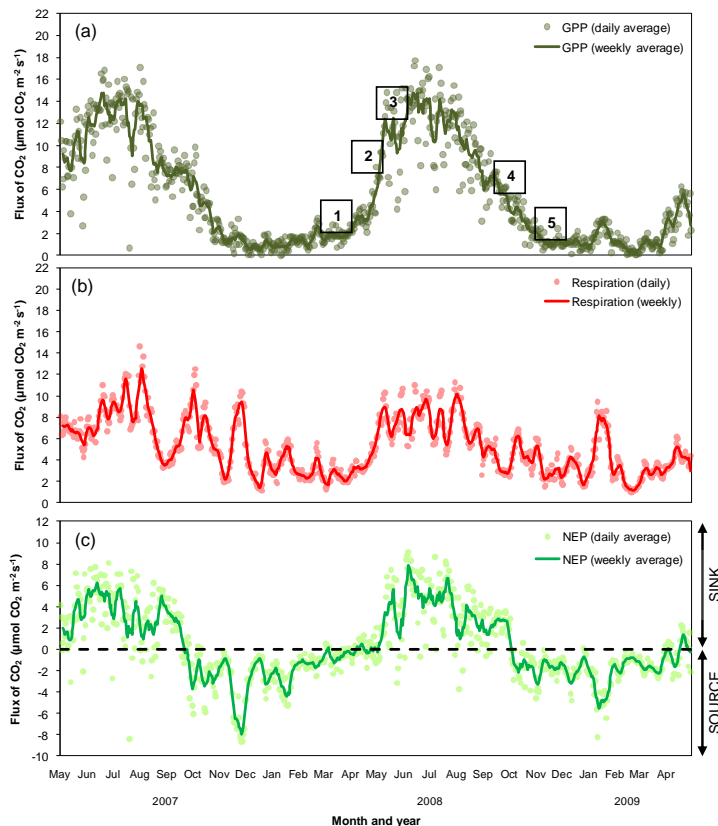


Fig. 6. Partitioned flux from Wytham Woods showing **(a)** Gross Primary Productivity (GPP), **(b)** ecosystem respiration (R_e) and **(c)** Net Ecosystem Productivity (NEP) over the study period. Dots indicate daily mean values, lines trace weekly mean values. Stages of GPP rise have been overlaid; stage (1) suggests the period of ground flora activity, stage (2) the period of rapid canopy leaf-out, and stage (3) the slow rise to mid-summer peak. Stages of GPP decline represent (4) peak litterfall in early to mid October and (5) minimum leaf area index.

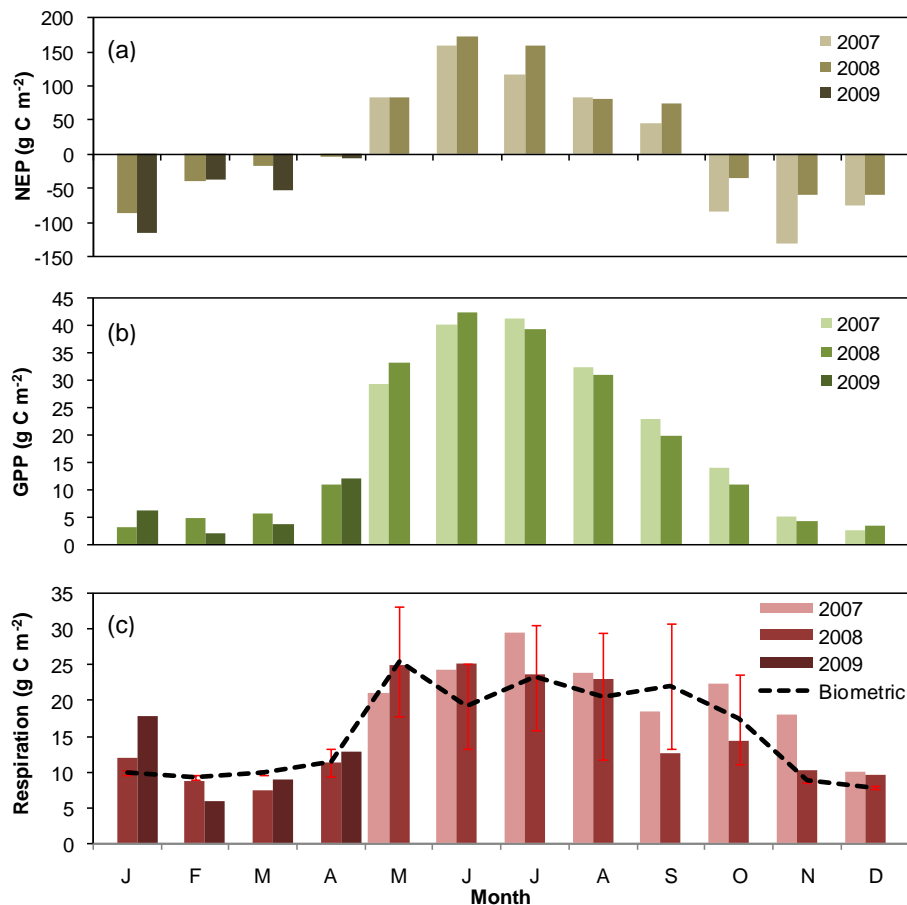


Fig. 7. Monthly total NEP **(a)** and partitioned monthly totals for **(b)** GPP and **(c)** respiration. For R_e , monthly total biometric/chamber estimates of ecosystem respiration during 2008 (Fenn et al., 2010a) with error bars have been overlaid for comparison.

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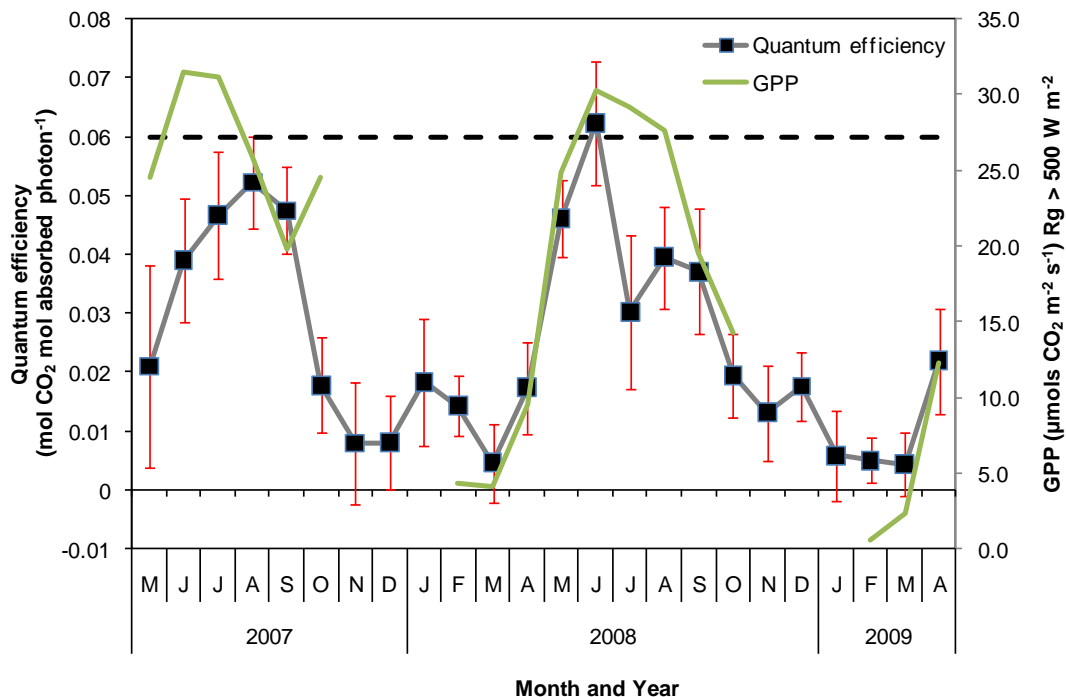


Fig. 8. Variation of quantum efficiency and GPP under high light (solar radiation $>500 \text{ W m}^{-2}$), calculated from monthly data (theoretical maximum quantum efficiency is also shown).

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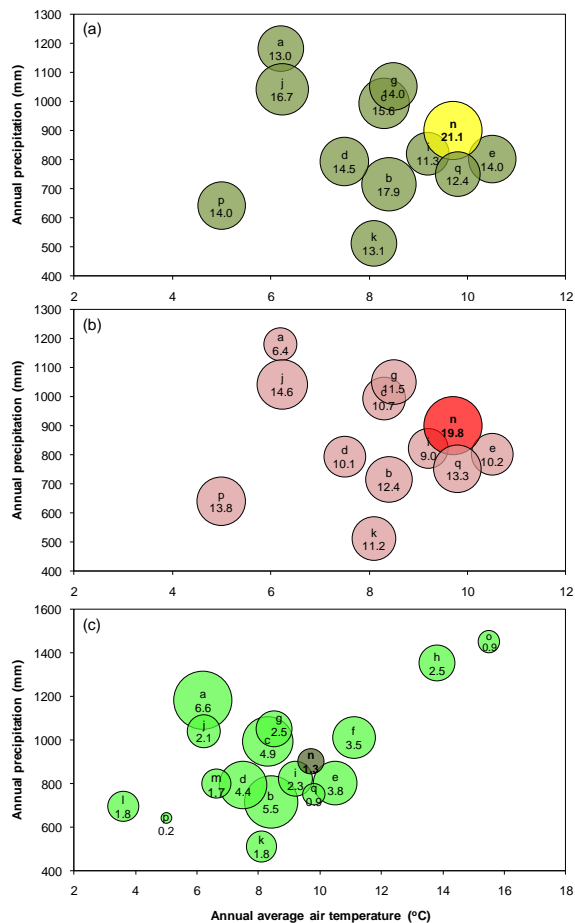


Fig. 9. Average annual (a) Gross Primary Productivity (GPP), (b) ecosystem respiration (R_e) and (c) Net Ecosystem Productivity (NEP) estimates from temperate deciduous forests across the globe in $\text{MgC ha}^{-1} \text{yr}^{-1}$, plotted by site annual mean air temperature and precipitation. Site descriptions are given in Table 3, Wytham Woods is highlighted in each plot.

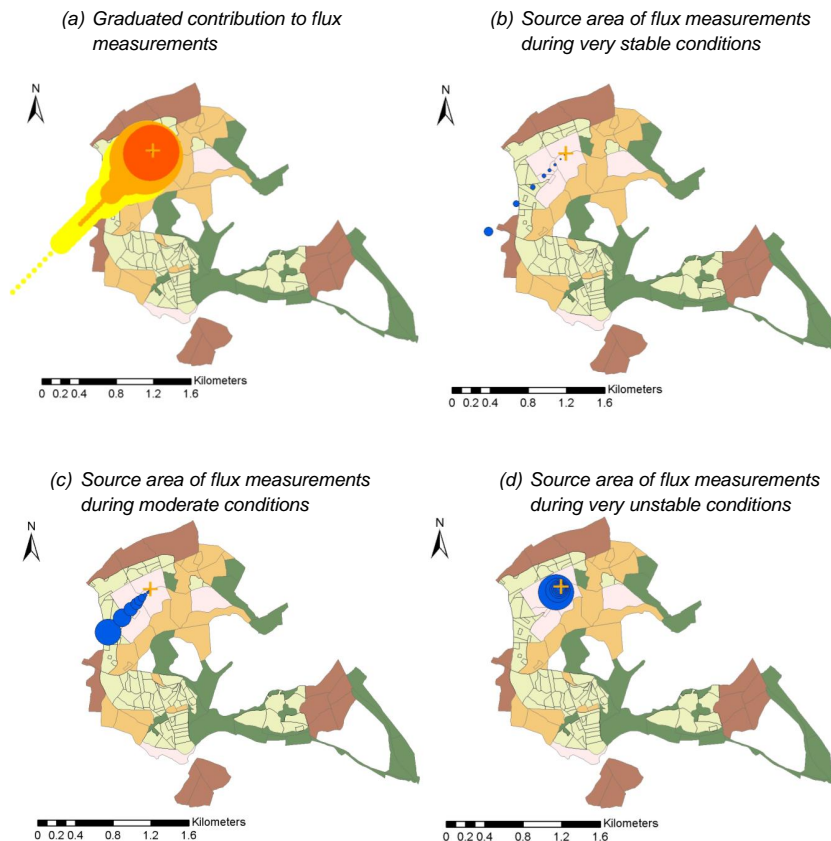


Fig. B1. Estimates of flux tower footprint. Colours in the graduated contribution to flux measurements (a, top left) represent atmospheric stability, whereby red = very unstable ($ZL = -0.5$ m), orange = moderate ($ZL = -0.1$ m) and yellow = very stable conditions ($ZL = -0.001$ m). ZL = flux measurement height/Monin-Obukhov length (based on Schmid and Oke, 1990). Flux tower shown as cross and woodland type types as shown in Fig. 1.

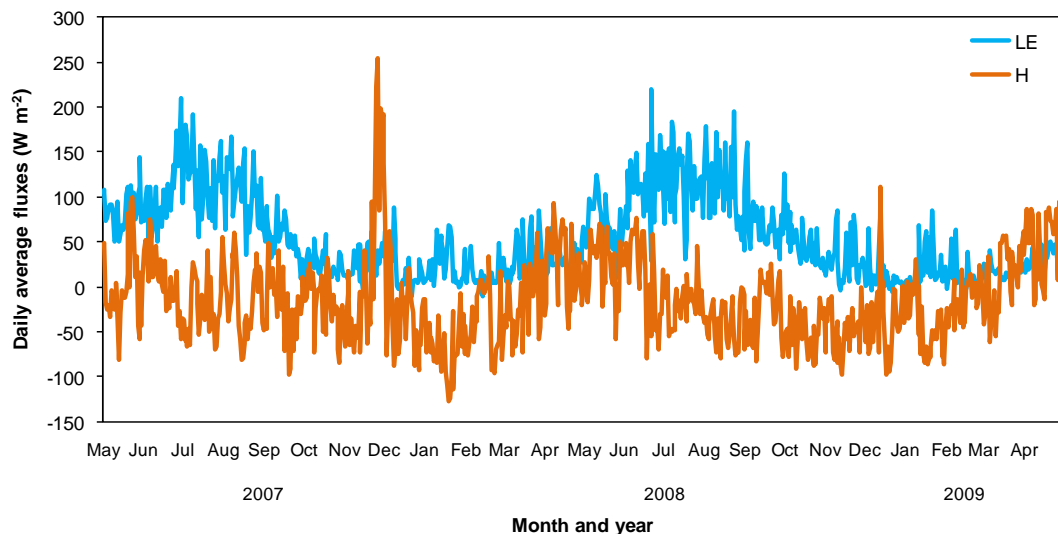


Fig. B2. Daily average fluxes of latent heat (LE) and sensible heat (H) over the study period. Both units are W m^{-2} .

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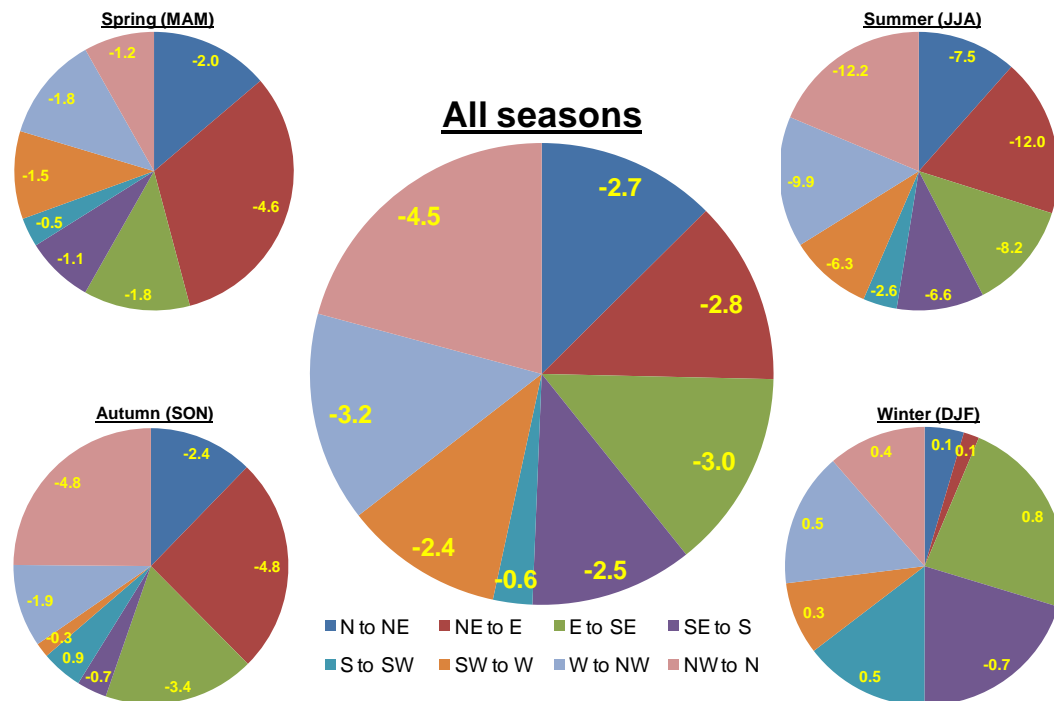


Fig. B3. Seasonal changes in average half-hourly CO₂ flux grouped by wind direction. Larger segments represent greater half-hourly average CO₂ flux detected from the corresponding wind direction and thus upwind vegetation. Total fluxes do not necessarily follow these seasonal patterns since wind direction is not evenly distributed: the prevailing direction is south-westerly.

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