Biogeosciences

Inter-annual variation of carbon uptake by a plantation oak woodland in south-eastern England

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Abstract. The carbon balance of an 80-yr-old deciduous oak plantation in the temperate oceanic climate of the south-east of Great Britain was measured by eddy covariance over 12 yr (1999–2010). The mean annual net ecosystem productivity (NEP) was $486\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$ (95 % CI of $\pm 73\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$), and this was partitioned into a gross primary productivity (GPP) of $2034 \pm 145\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$, over a $165\,(\pm 6)$ day growing season, and an annual loss of carbon through respiration and decomposition (ecosystem respiration, R_{eco}) of $1548 \pm 122\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$. Although the maximum variation of NEP between years was large ($333\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$), the ratio of R_{eco}/GPP remained relatively constant (0.76 ± 0.02 CI). Some anomalies in the annual patterns of the carbon balance could be linked to particular weather events, such as low summer solar radiation and low soil moisture content (values below 30 % by volume). The European-wide heat wave and drought of 2003 did not reduce the NEP of this woodland because of good water supply from the surface-water gley soil. The inter-annual variation in estimated intercepted radiation only accounted for $\sim 47\,\%$ of the variation in GPP, although a significant relationship ($p < 0.001$) was found between peak leaf area index and annual GPP, which modified the efficiency with which incident radiation was used in net CO_2 uptake. Whilst the spring start and late autumn end of the net CO_2 uptake period varied substantially (range of 24 and 27 days respectively), annual GPP was not related to growing season length. Severe outbreaks of defoliating moth caterpillars, mostly *Tortrix viridana* L. and *Operophtera brumata* L., caused considerable damage to the forest canopy in 2009 and 2010, resulting in reduced GPP in these two years. Inter-annual variation in the sensitivity of R_{eco} to temperature was found to be strongly related to summer soil moisture content. The eddy covariance estimates of NEP closely matched mensuration-based estimates, demonstrating that this forest was a substantial sink of carbon over the 12-yr measurement period.

1 Introduction

Many terrestrial ecosystems, including forests, are sinks for carbon (C) (Unger et al., 2009), and globally between 1990 and 2007 forests were estimated to have a net sequestration of $1.1 \pm 0.8\,\mathrm{Pg\,C\,yr^{-1}}$ (Pan et al., 2011), equivalent to one-seventh of emissions from fossil fuel combustion and cement production (Reich, 2011). Forests therefore have a fundamental role in helping to regulate atmospheric CO_2 concentrations, and an improved understanding of the underlying processes is needed to inform the development of climate change mitigation strategies (Nabuurs et al., 2007). In the medium to long term, a growing forest stand will be a net carbon sink, but at shorter timescales and as they react to unfavourable weather conditions, they can also act as a source (Valentini et al., 2000). For example, the severe drought and extreme high temperatures experienced in Europe over the summer of 2003 led to an estimated net release from the continent's forests of $0.5\,\mathrm{Pg\,C\,yr^{-1}}$ (Ciais et al., 2005). Forest disturbance, changes in local climate or in phenology may also lead to a long-term forest carbon sink temporarily becoming a carbon source (Powell et al., 2006; Pereira et al., 2007; Noormets et al., 2008).

While forest mensuration methods are well suited to quantifying the long-term growth of forest stands (e.g. at 5 yr intervals), the infrequency with which measurements are

usually made means that they are unable to give reliable information about inter-annual variation in growth rates. Furthermore, as mensuration methods typically show only the net effect on the tree components, they do not give information about the C balance of whole ecosystems or about the effects of disturbance and recovery. Networks of long-term, continuous, direct measurements of CO_2 fluxes using the eddy covariance method have become a powerful tool in improving the understanding of C exchange between forests and the atmosphere (Baldocchi et al., 2001), and provide valuable information relating to their daily and seasonal changes and about the impact of management. Our understanding of the size of sink and extent of inter-annual variation is increasing as data from eddy covariance studies in forests in excess of 10 yr duration become available (e.g. Ito et al., 2005; Dunn et al., 2007; Ilvesniemi et al., 2009). Key aspects now being revealed include the following: impacts of climate change (Urbanski et al., 2007); the role of weather anomalies (Saigusa et al., 2008; Teklemariam et al., 2009); effects of pests and diseases (Allard et al., 2008) and the role of management (Saunders et al., 2012).

In this paper we present the results from 12 yr (1999–2010) of eddy covariance measurements of CO_2 flux above an 80-yr-old lowland oak woodland in a mild, temperate, oceanic climate in south-eastern England. The annual sums of net ecosystem productivity (NEP) and its component assimilatory (gross primary productivity, GPP) and respiratory fluxes (ecosystem respiration, R_{eco}) are given. The paper also examines the causes of inter-annual variability of the partitioned fluxes, and assesses the relationship with key climatic and biotic drivers.

2 Materials and instrumentation

2.1 Site description

The site is located in the Straits Inclosure, Alice Holt Research Forest, UK (51°07′ N, 0°51′ W), close to the Alice Holt Research Station in south-eastern England (Fig. 1). The site is affiliated with the FLUXNET network and is also included in several other monitoring and research projects: it is a Level-II observation plot of the European network (ICP Forests) programme (http://icp-forests.net) and a UK Environmental Change Network (ECN) site (http://www.ecn.ac.uk). The inclosure is a flat area with an elevation of 80 m; the surrounding landscape consists of mixed lowland woodland and both arable and pasture agricultural land. The site is managed by Forest Research, the research agency of the British Government's Forestry Commission.

Early maps and records show that the western half of the Straits Inclosure was wooded in 1787, with the eastern part under agricultural management. The whole 90-ha inclosure was planted in the 1820s with oak (Schlich, 1905)
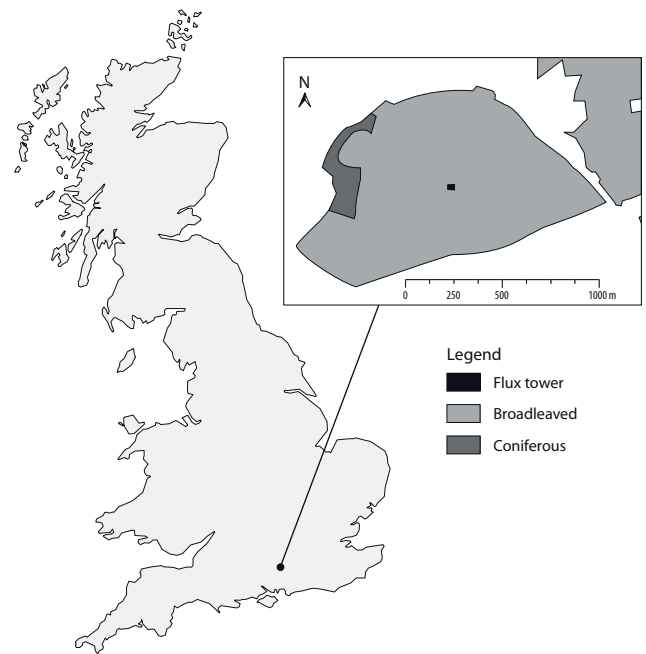

Fig. 1. Map of Great Britain with inset figure showing the location and layout of the Straits Inclosure.

and then replanted in the 1930s so that it is now a relatively homogeneous forest block managed as a commercial lowland oak forest. The main tree species is *Quercus robur* L., but other species, including European ash (*Fraxinus excelsior* L.), *Q. petraea* (Mattuschka) Liebl. and *Q. cerris* L., are present. There is a small area of mixed conifers consisting of Corsican pine (*Pinus nigra* subsp. *laricio* Maire.) and Scots pine (*Pinus sylvestris* L.) at the north-west edge of the woodland, and isolated pockets of Japanese red cedar (*Cryptomeria japonica* (L.f.) D. Don) are also present in the eastern area. The understorey is dominated by hazel (*Corylus avellana* L.) and hawthorn (*Crataegus monogyna* Jacq.; Pitman and Broadmeadow, 2001). The soil is a surface-water gley (Pyatt, 1982), with a depth of 80 cm to the C horizon of the Cretaceous clay. Soil pH is 4.6 and 4.8 in the organic and mineral horizons respectively, and the soil organic C stock measured in the top 30 cm in 2004 was 87 t C ha^{-1} (Benham et al., 2012), and to 1 m depth in 1997 was 157 t C ha^{-1} (Table 3.7; Morison et al., 2012). Periodic tree measurements have been carried out at seven vegetation sampling plots as part of the ECN monitoring programme (Table 1). In addition, 18 forest mensuration plots (8 m in radius) were established in the western half of the inclosure during 2009; a density of 450 canopy trees per hectare was recorded, with a basal area of 29.7 m^2. In the recent past, different parts of the site have been thinned in 1991, 1995, 2000 and 2007.

Eddy covariance measurements of CO_2, sensible heat and water vapour flux were carried out at 28 m above ground level on a free-standing 26-m-high square-section mast (Gigalite 4, Litestructures Ltd, Pontefract, UK) located near to

Table 1. Mean annual biometric mensuration data for understorey and canopy tree species at the Straits Inclosure, Alice Holt Forest, for the period 1994–2011.

Year	Shrubs			Canopy Trees	
	Crataegus monogyna	*Corylus avellana*	*Ilex aquifolium*	*Fraxinus excelsior*	*Quercus robur*
Height (m)					
1994	3.5	6.8	Na	17.8	16.1
2002	3.9	7.4	5.4	19.9	19.6
2011	7.4	6.2	8.6	21.6	21.1
Diameter (cm)					
1994	6.0	6.4	Na	20.8	22.5
2002	4.6	6.0	7.5	23.9	28.6
2011	7.3	4.9	11.6	26.5	29.6

Na = not available

the centre of the inclosure (Fig. 1) providing a fetch over the woodland of 500 m, 700 m, 350 m and 600 m to the N, E, S and W respectively. Additional measurements of climatic variables were recorded from the mast or from the ground nearby (see below). The long-term mean (1971–2000) screen annual air temperature was 9.6°C and the mean annual precipitation 779 mm at the UK Meteorological Office affiliated weather station, Alice Holt, Farnham (51°10′ N, 0°51′ W), approximately 1.8 km from the measurement site.

2.2 Instrumentation

Half-hourly fluxes of energy (sensible and latent heat), momentum, CO_2 and water vapour have been measured continuously using the eddy covariance technique (Moncrieff et al., 1997) since 1998. The system is comprised of a three-dimensional sonic anemometer (model Solent R2, Gill Instruments, Lymington, UK) measuring wind vector components and a closed-path infrared CO_2 and H_2O analyser (IRGA, model LI-6262 until October 2005, LI-7000 thereafter, LI-COR Inc., Lincoln, NE USA) measuring atmospheric CO_2 and H_2O concentrations. Pure nitrogen was used as the zero CO_2 concentration gas flowing through the IRGA reference cell. Sample air was drawn from the inlet port at a point close to the sonic anemometer (horizontal separation of ∼ 10 cm) using a sample tube (Dekabon Ltd., Glasgow, UK) with an internal diameter of 6.15 mm, through two inline 1 micron PTFE Teflon filters (Gelman Acro 50) at a rate of 5.5 L min^{-1} by a small pump (Capex V2 SE, Charles Austen Pumps, Byfleet, Surrey, UK). Calibration of the IRGA using a reference standard gas was performed weekly. The raw high frequency data (20.8 Hz) were logged using the EdiSol software (Moncrieff et al., 1997), and for this study were available from 1 January 1999 through to 31 December 2010. The system was powered by battery, charged by solar panels and wind turbines until 31 May 2005, when mains power

was installed, resulting in significant improvements to data collection.

Supporting environmental measurements recorded at the site included the following: wind speed and direction (model WA15, Vaisala, Helsinki, Finland), wet and dry bulb air temperature (model DTS-5, ELE International, Loveland, USA), above and below canopy solar radiation (tube solarimeters, Delta-T Devices, Cambridge, UK), global solar radiation (model CM2, Kipp & Zonen B.V., Delft, Netherlands), net radiation (model DRN-301, ELE International, Loveland, USA), soil heat flux (model HFP01, Campbell Scientific Ltd, Loughborough, UK), soil temperature at 10 cm depth (2K Thermistor, Delta-T Devices) and soil moisture (model ThetaProbe ML2, Delta-T Devices). All measurements were logged at 10 s intervals, and half-hourly averages recorded using data loggers (DT 500, dataTaker, Thermo Fisher Scientific, Australia).

Leaf area index (LAI) was assessed using litterfall traps located within the Level-II forest-intensive monitoring plot approximately 450 m from the flux tower. Canopy litterfall (leaves, twigs, frass, acorns, etc.) was collected in 10 cone-shaped traps held above the ground vegetation at height of 1.5 m, each with a collecting surface area of 0.33 m^2, and distributed randomly within the monitoring plot. Small cloth bags attached to the traps were collected every two weeks during the summer and autumn and subsequently sorted into their constituents. Leaf surface area was measured using a leaf area meter (model MK2, Delta-T Devices), and peak leaf areas back-calculated from cumulative litterfall (ICP Forests, 2004). Although the forest intensive monitoring plot has been subjected to a slightly different management regime than other areas of the forest, a comparison with litterfall traps from the area surrounding the mast (data not shown) indicates that the LAI values derived here give a good representation of the relative change in canopy density between years.

2.3 Calculation of CO_2 fluxes

The raw eddy covariance data files were re-processed with the Edinburgh University micrometeorological software tool EdiRe (http://www.geos.ed.ac.uk/abs/research/micromet/EdiRe) following the basic procedures used in the CarboEurope project (Aubinet et al., 2000). Two-angle velocity signal coordinate rotation was applied to ensure that the vertical velocity signal was orthogonal to the plane of mean air flow. The lag time of the sample from the intake point to the cell of the closed-path analyser was determined by maximising the covariance between the vertical wind velocity and scalar concentration. Virtual temperature derived from the speed of sound was corrected for water vapour (Hignett, 1992). In order to account for flux loss caused by signal damping inside the tube, limited time response and sensor separation, etc, the usual spectral corrections were applied (Moore, 1986; Leuning and Moncrieff, 1990; Lenschow and Raupach, 1991; Massman, 1991) to

compute the corrected CO_2 and water vapour fluxes. In addition, an angle of attack correction was applied to correct for sonic anemometer velocity calibration errors at large ($> \pm 40$ degrees) angles of attack (Van der Molen et al., 2004).

Half-hourly net ecosystem exchange (NEE, μmol m^{-2} s^{-1}) was calculated using the corrected CO_2 flux, F_c as NEE $= F_c + S_c$, where $F_c = \overline{w'c'}$ is the covariance between the vertical wind velocity and the atmospheric CO_2 concentration, and Sc the rate of change in CO_2 storage per unit ground area in the air column below the eddy covariance IRGA intake. The storage term was estimated by the simple approach using only the change in CO_2 concentration measured at 28 m (Hollinger et al., 1994; Greco and Baldocchi, 1996):

$$S_c = \frac{\Delta c(z)}{\Delta t} \Delta z, \tag{1}$$

where $\Delta c(z)$ is the change in CO_2 molar density at height z, Δt the time period (30 min) and Δz the height of the eddy covariance sensor above ground (28 m).

After calculation of corrected NEE, and manual filtering of data for instrument failures and system maintenance, data filters were applied in order to remove extreme spikes, which were assumed to be not biologically valid data, an approach similar to that proposed by Papale et al. (2006) and Thomas et al. (2011). For each calendar year, NEE data were firstly split into either positive or negative values. Positive values greater than the mean positive value for the whole year plus three standard deviations were removed and the same approach applied to all negative values. A secondary stage data filter was then applied, removing positive values that were greater than the mean monthly value for that half-hourly period plus three standard deviations, and negative values less than the mean monthly value minus three deviations. Despiking filters were also applied to the latent heat flux (< -100 or > 400 W m^{-2}) and to the sensible heat flux (< -500 or > 500 W m^{-2}) NEE data when either of these criteria occurred were also removed.

A flux footprint probability analysis was carried out using the "footprint" calculation tool within EdiRe, which applies the model of Kormann and Meixner (2001) to a user-specified fetch. On average 65 % of the daytime flux originated within ~ 450 m of the tower, but at night this increased to ~ 600 m. Therefore, it is likely that a majority of the daytime flux originated from within the oak forest, particularly as the longest possible target fetch extends to over 800 m towards to the south-west of the tower, which is also the predominant (24.6 %) wind direction. However, we cannot exclude the possibility that fluxes were influenced by the adjoining agricultural land, especially when nighttime conditions were combined with southerly wind directions.

2.4 Gap filling

In order to create the continuous flux dataset required for carbon budgeting, and as an input for the partitioning of CO_2 fluxes, it was necessary to replace the missing and deleted values with appropriate values ("gap-filling"). The marginal distribution sampling (MDS) method described in Reichstein et al. (2005) and accessed through the on-line CarboEurope gap filling tool was used (http://www.bgc-jena.mpg.de/~MDIwork/eddyproc/index.php). Whilst similar to the lookup table method (Falge et al., 2001), this approach also considers the temporal auto-correlation of the fluxes, replacing missing data with an average value under similar meteorological conditions. This method was chosen because it is widely accepted and has been employed by both CarboEurope and FLUXNET (Moffat et al., 2007; Papale et al., 2006). Half-hourly NEE values were screened against a friction velocity (u^*) threshold using the method described by Reichstein et al. (2005) and implemented through the on-line gap filling tool. The dataset is split into six temperature categories of equal sample size and then further subdivided into 20 classes based on u^* values. The u^* threshold for each temperature class is calculated as the u^* class where the nighttime flux reaches more than 95 % of the average flux within the higher u^* classes. The final threshold is defined as the median of the thresholds, and this procedure is applied to the subsets of four 3-month periods to account for seasonal variation of vegetation structure. The mean u^* threshold for the period 1999–2010 calculated using this method was 0.17 m s^{-1}. Where it is not possible to calculate a u^* threshold, a default value of 0.4 m s^{-1} is used.

Although near-continuous meteorological data were collected, the occasional short-term gaps of < 1 h were filled by manual interpolation. Longer-term gaps in the meteorological data, caused by battery or logging failure, were filled using data from an automatic weather station at the nearby Alice Holt Research Station. Over the 12-yr period maintenance, data logging and power failure problems resulted in a mean annual loss of 18.5 % of total available flux data. Quality control, primary, secondary and LE/H despiking routines removed a further 2.6 %, whilst u^* filtering removed 17.1 %, resulting in a mean annual quality-controlled CO_2 flux data availability of 61.8 % (Table 2), and exceeding 50 % in all years.

2.5 CO_2 flux partitioning

The half-hourly quality-controlled NEE data were partitioned into gross primary productivity (GPP) and ecosystem respiration (R_{eco}) using the on-line CarboEurope gap filling tool (Reichstein et al., 2005). The dataset is split into 10-day consecutive periods, and R_{eco} is estimated using the Lloyd–Taylor regression model (Lloyd and Taylor, 1994) between nighttime CO_2 flux (global solar radiation < 20 W m^{-2}) and air temperature. The estimated value of R_{eco} is then assigned

Table 2. Sources of annual data loss of CO_2 flux measurements for the period 1999–2010 at the Straits Inclosure, Alice Holt Forest and quality-controlled (QC) data availability (%).

Year	Power/ logging failure	QC/ despiking	u^* filtering	QC flux data
1999	13.9	2.3	17.7	66.1
2000	21.7	2.5	15.5	60.3
2001	27.0	2.5	11.0	59.5
2002	24.9	2.3	13.9	58.9
2003	18.8	3.1	23.3	54.8
2004	13.0	3.5	15.2	68.3
2005	8.2	3.9	12.7	75.2
2006	23.7	0.1	14.2	62.1
2007	19.5	2.3	19.2	59.0
2008	12.9	5.3	30.2	51.5
2009	23.9	2.3	18.5	55.3
2010	15.0	0.8	13.7	70.5
Mean	18.5	2.6	17.1	61.8

to the central time point of the averaging interval and linearly interpolated between time points. GPP is subsequently calculated as the difference between NEE and R_{eco}. By convention, NEP was defined as opposite in sign to NEE (Fig. 2).

3 Results and analysis

3.1 Climatic conditions

The average annual cycles of daily maximum air temperature (T_{max}), minimum air temperature (T_{min}) and incident solar radiation (S_g) recorded at the flux site are shown in Fig. 3a and the average daily soil moisture content and mean monthly precipitation from the nearby Alice Holt Research station in Fig. 3b. Collectively these illustrate the oceanic climate of the region, typified by mild winters, cool summers and a relatively uniform distribution of precipitation throughout the year. Using the Köppen climate classification system, the region is classified as "Cfb". The long-term (1971–2000) mean annual precipitation of 779 mm was exceeded in 8 out of the 12 yr, with the highest recorded amount falling in 2002 (1046 mm) and the lowest in 2005 (590 mm). The mean annual above-canopy solar radiation receipts were lowest in 2002 (253 W m^{-2}) and highest in 2006 (319 W m^{-2}). Long-term observations (1948–2009) from the Alice Holt weather station near the site have demonstrated a warming in mean surface air temperature (data not shown) of $\sim 0.2\,°C$ per decade, with higher rates of warming in winter and summer than in spring and autumn. Whilst there has been no overall change in annual precipitation, there has been a slight reduction in summer and an increase in winter levels over this period.
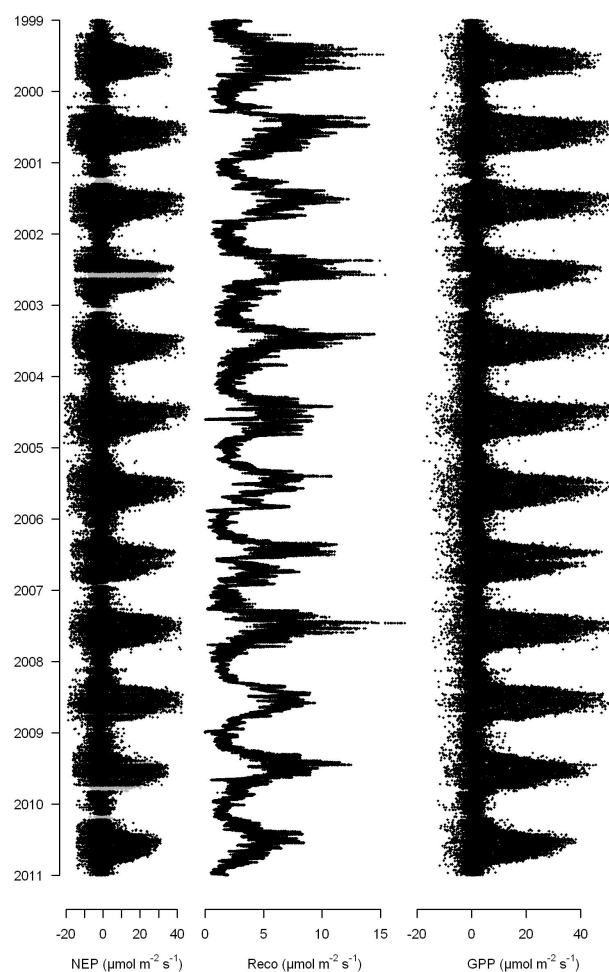

Fig. 2. Half-hourly average values of quality-controlled (black symbols) and gap-filled (gray symbols) NEP, R_{eco} and GPP for the period 1999–2010, at the oak plantation, Straits Inclosure, Alice Holt Forest.

3.2 Annual cycle of carbon fluxes

Substantial seasonal and inter-annual variations in component fluxes were measured (Fig. 2). In order to describe the mean annual carbon cycle for each of these components, data from all 12 yr were pooled (Fig. 3c). Over the winter period (December, January, February), GPP was close to zero and started to rise slowly from around day of year (DOY) 50 as a result of early bud break and leaf expansion of the shrub layer, exploiting available light. At approximately DOY 100 GPP started to rise more rapidly, coinciding with bud break and expansion of the tree canopy, peaking at around DOY 170, with a mean summer (June, July and August) value of 13.5 g C m^{-2} d^{-1}. A reduction in GPP started around DOY 200 as mean solar radiation levels declined (Fig. 3a); this reduction accelerated around the beginning of October ($\sim$ DOY 280), corresponding with the start of canopy senescence.
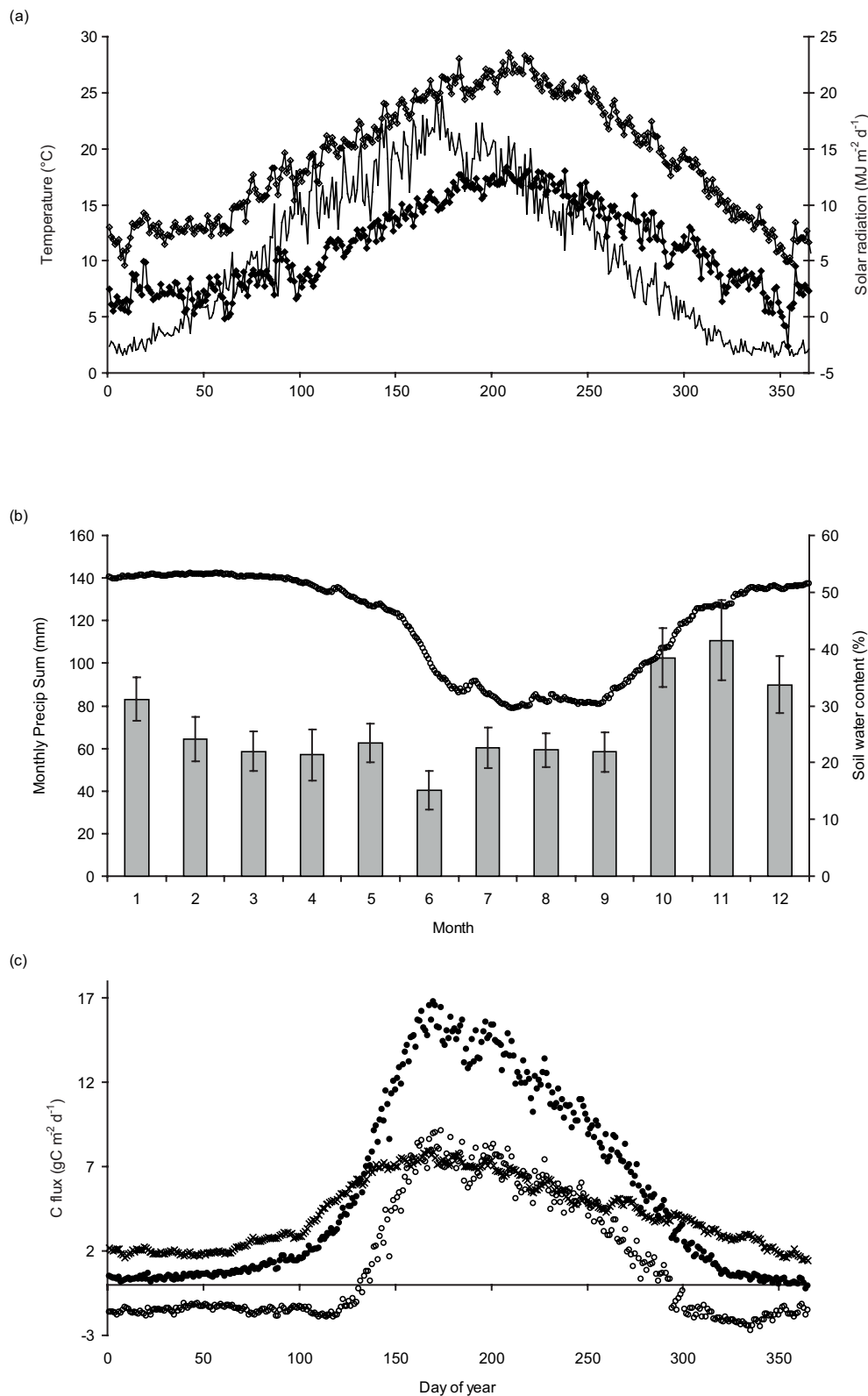
Fig. 3. Average annual cycle of key climatic variables and CO_2 flux components between 1999–2010 for the oak plantation at the Straits Inclosure, Alice Holt Forest: **(a)** T_{max} (open symbols), T_{min} (closed symbols) and incident solar radiation (solid line); **(b)** mean monthly precipitation (error bars represent ± 1 standard error, $n = 12$) and volumetric soil water content recorded under grass nearby (open symbols); and **(c)** daily GPP (solid circles), R_{eco} (crosses) and NEP (open circles).
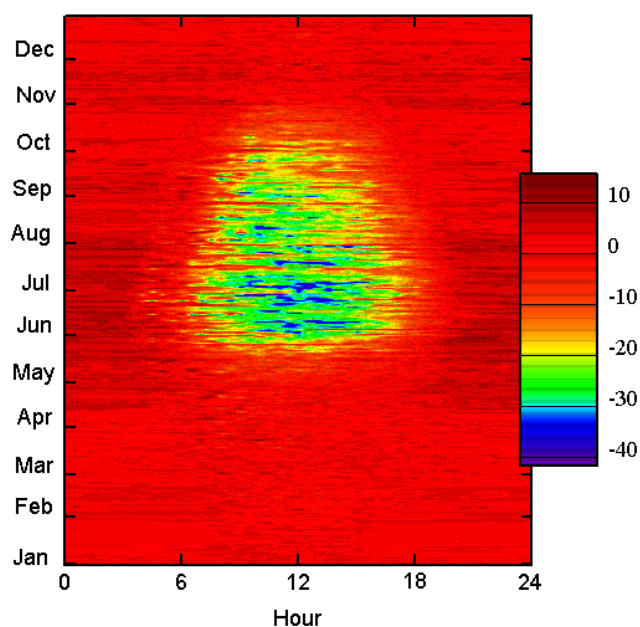
Fig. 4. A typical (2003) net ecosystem exchange (NEE) "fingerprint" plot showing diurnal (x-axis) and seasonal (y-axis) CO_2 fluxes (μmol m^{-2} s^{-1}) for the oak plantation at the Straits Inclosure, Alice Holt Forest, generated by the CarboEurope on-line gap filling and partitioning tool.

R_{eco} also demonstrated a strong seasonal cycle (Fig. 3c), with the lowest fluxes occurring over the cooler winter period at a mean rate 2.0 g C m^{-2} d^{-1}. R_{eco} stayed low until approximately DOY 70, when it began to increase slowly at first and more rapidly from DOY 100, coinciding with increases in air and soil temperature. The highest R_{eco} occurred during the warm summer months between DOY 145 and 200, with a mean summer rate of 6.7 g C m^{-2} d^{-1}. The NEP of an ecosystem is determined by the relative balance of GPP and R_{eco}. In this study daily NEP remained negative until on average DOY 132; prior to this point small increases in GPP and R_{eco} effectively cancel each other out, ensuring that NEP remains constant until approximately DOY 115. During spring (DOY 115-150) as the increase in GPP exceeded losses through R_{eco}, daily NEP rapidly turned from being negative (a CO_2 source) to positive (a CO_2 sink); over the summer, high levels of GPP relative to R_{eco} resulted in a mean NEP of 6.8 g C m^{-2} d^{-1}. On a daily timescale the forest continued to act as a net CO_2 sink until on average DOY 297, after which it reverted to being a source. Over the 12-yr measurement period, mean daily winter (December–February) NEP was -1.6 g C m^{-2} d^{-1}.

The diurnal and seasonal changes of NEE for a typical year (2003) are shown in the "finger print" plot (Fig. 4). Maximum CO_2 sequestration occurred during spring and summer daylight hours (green through to dark blue). The asymmetrical shape of the NEE "pulse" within the year was caused by the rapid increase in net CO_2 uptake in the spring followed
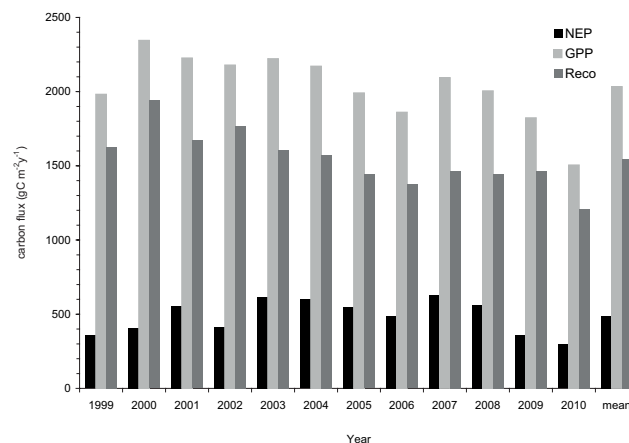

Fig. 5. Annual sum of NEP, GPP and R_{eco} for the period 1999–2010 at the oak plantation, Straits Inclosure, Alice Holt Forest

by a more gradual decline at the end of the growing season. In addition, higher CO_2 uptake fluxes are evident during the morning than in the afternoon during September, indicating the possibility of moisture stress.

3.3 Inter-annual variation in NEP, GPP and R_{eco}

The carbon budget and partitioned fluxes were calculated for each year of the study period (Fig. 5 and Table 3). Annual NEP varied from 296 g C m^{-2} yr^{-1} (2010) to a maximum of 629 g C m^{-2} yr^{-1} (2007), with a 12-yr average of 486 $\pm$ 73 g C m^{-2} yr^{-1} (95 % CI). The maximum year-to-year variation in NEP was therefore 333 g C m^{-2} yr^{-1}. The growing season length (GSL), here defined as the number of days between the first and last day where the integrated 3-day NEP was positive (a net sink of carbon), also varied considerably from year to year (Table 4). The average GSL was 165 days, ($\pm$6 days, 95 % CI); the longest GSL occurred in 2007 (186 days) and the shortest in 2005 (153 days).

The inter-annual variation in the calculated R_{eco} was large (from a minimum of 1210 to a maximum of 1940 g C m^{-2} yr^{-1}, Table 3), and the standard deviation (SD) was larger than that for NEP (192 and 115 g C m^{-2} yr^{-1}, respectively, Table 3). Annual GPP ranged from 1506 g C m^{-2} yr^{-1} (2010) to 2346 g C m^{-2} yr^{-1} (2000), with SD = 223 g C m^{-2} yr^{-1}. As R_{eco} is driven in part by preceding GPP, it could be argued that the NEP budget for any given year should be calculated over the growing season year (i.e. 1 April through to 31 March in the following year). However, our results show that this approach had very little effect on the annual sums in most years, and only in 2005 was there a noticeable difference (Table 3).

Anomalies from the long-term monthly means in GPP, R_{eco} and associated environmental variables were calculated (Fig. 6). GPP was high during the spring and summer of 2000 probably because of the combined effect of high peak LAI (7.7 m^2 m^{-2}) and average solar radiation receipts. GPP was

Table 3. Annual values 1999–2010 of carbon flux components for the oak plantation at the Straits Inclosure in Alice Holt Forest. Radiation-use efficiency (RUE) is calculated as GPP/incident solar radiation. NEP_{gsy} is the sum of NEP in the growing season year, i.e. 1 April through to 31 March in the following year. Peak LAI was back calculated from cumulative LAI measured using litterfall traps sampled bi-weekly.

Year	NEP $g\,C\,m^{-2}$	R_{eco} $g\,C\,m^{-2}$	GPP $g\,C\,m^{-2}$	R_{eco}/GPP	NEP/GPP	RUE $g\,C\,MJ^{-1}$	NEP_{gsy} $g\,C\,m^{-2}$	Peak LAI $m^2\,m^{-2}$
1999	357	1625	1983	0.820	0.180	0.486	345	6.49
2000	406	1940	2346	0.827	0.173	0.616	405	7.72
2001	557	1670	2227	0.750	0.250	0.575	538	6.94
2002	412	1767	2180	0.811	0.189	0.554	426	5.52
2003	617	1606	2223	0.722	0.278	0.542	613	6.17
2004	600	1573	2172	0.724	0.276	0.563	585	6.55
2005	551	1441	1992	0.723	0.277	0.510	630	4.97
2006	488	1374	1862	0.738	0.262	0.464	466	5.42
2007	629	1466	2094	0.700	0.300	0.529	664	6.47
2008	563	1442	2006	0.719	0.281	0.520	518	6.21
2009	359	1465	1824	0.803	0.197	0.458	367	4.4
2010	296	1210	1506	0.804	0.196	0.414	321	4.18
Mean	486	1548	2034	0.762	0.239	0.520	490	5.92
SEM*	33.3	55.6	65.8	0.01	0.01	0.02	34.0	0.32
SD	115	192	223	0.01	0.05	0.04	117.67	1.05

* SEM = standard error of the mean

Table 4. Onset of growing season (OGS), end of growing season (EGS) and growing season length (GSL) defined by the start and end of net CO_2 uptake, at the Straits Inclosure, Alice Holt Forest.

Year	OGS (DOY)	EGS (DOY)	GSL (days)
1999	132	297	165
2000	135	291	156
2001	132	303	171
2002	135	291	156
2003	126	300	174
2004	132	291	159
2005	141	294	153
2006	138	312	174
2007	117	303	186
2008	129	297	168
2009	129	285	156
2010	132	297	165
Mean	132	297	165
SEM	1.8	2.1	2.8
SD	6.1	7.2	9.9

not adversely affected by the major Europe-wide drought year in 2003, and the year had the second highest GPP sum over the entire 12-yr period probably because of the above-average solar radiation levels. Although 2003 had the lowest precipitation total, this followed a wet end to 2002 (Fig. 6a) and soil moisture (Fig. 6c) did not start to decline below the long-term monthly mean until July. Precipitation was also lower than average for most of 2005; although summer soil moisture levels did not fall as low as in 2003, the decline started a month earlier in the year, which combined with the lower levels of solar radiation caused a reduction in summer GPP in 2005. It is likely that low R_{eco} values in late summer/early autumn, as occurred in 2003, 2005 and 2006, can be attributed to low soil moisture levels (Fig. 6c).

GPP was low in 2009 and 2010 because of considerable damage to the forest canopy following a major outbreak of defoliating moth caterpillars, mostly *Tortrix viridana* L., but also *Operophtera brumata* L., early in the year (Pitman et al., 2010). This was despite an increase in incident solar radiation of 4 % in 2009 and 7 % in 2010 received during the May to July period of each year. The infestation caused a reduction in peak LAI values (Table 3) from the long-term mean of 26 % in 2009 (4.40 $m^2\,m^{-2}$) and 30 % in 2010 (4.18 $m^2\,m^{-2}$), which resulted in a reduction of GPP by 5 % in 2009 and 33 % in 2010.

The overall time trends in annual GPP, R_{eco} and NEP were tested by linear regression against year. Although there was no apparent long-term trend in the annual NEP ($p = 0.89$), this resulted from similar significant decreases in both GPP ($-46.1\,g\,C\,m^{-2}\,yr^{-1}$, standard error (s.e.) 13.7, $p < 0.01$) and R_{eco} ($-44.7\,g\,C\,m^{-2}\,yr^{-1}$, s.e. 9.2, $p < 0.001$) over time. If the last two annual values from the insect-affected years of 2009 and 2010 were omitted, there was a significant positive trend in NEP ($+21.0\,g\,C\,m^{-2}\,yr^{-1}$, s.e. 8.5, $p < 0.05$), because the declining trend in GPP was reduced to $-24.2\,g\,C\,m^{-2}\,yr^{-1}$, although the declining trend in R_{eco} was not affected ($-45.2\,g\,C\,m^{-2}\,yr^{-1}$, s.e. 12.2, $p < 0.01$). However, none of these changes in slope when 2009 and 2010 values were omitted were significant because of their large standard errors.
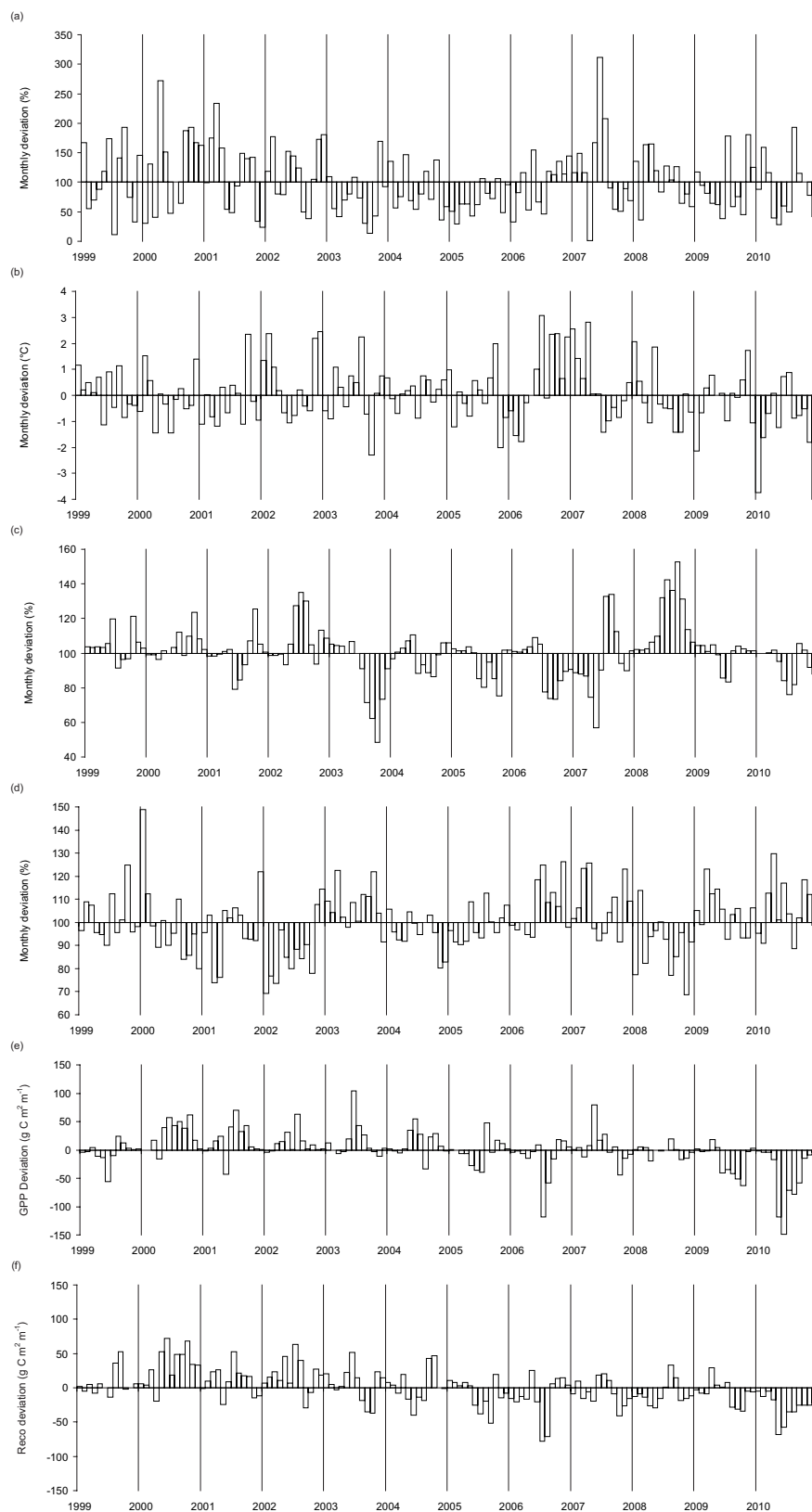
Fig. 6. Deviation from the 12-yr monthly average (1999–2010) for key climatic variables and partitioned CO_2 flux components at the oak plantation woodland, Straits Inclosure, Alice Holt Forest: **(a)** precipitation, **(b)** air temperature, **(c)** soil moisture, **(d)** solar radiation, **(e)** GPP and **(f)** R_{eco}.
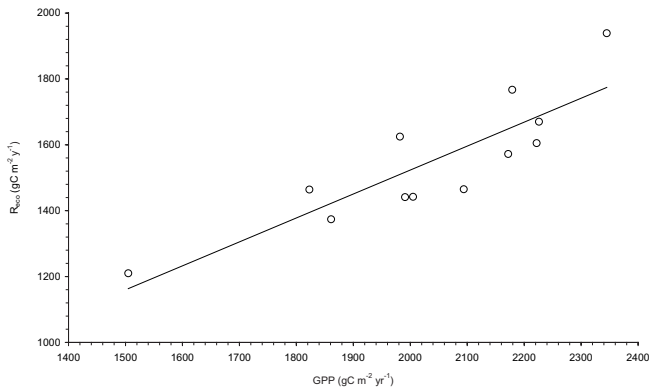
Fig. 7. Relationship between annual R_{eco} and annual GPP ($r^2 = 0.74$, $p < 0.001$).

3.4 Environmental controls of GPP, R_{eco} and NEP

NEP is the relatively small difference between the two much larger fluxes of GPP and R_{eco} (Baldocchi, 2008), which were shown to be tightly correlated (Fig. 7 and Table 3), with a mean R_{eco}/GPP ratio of 0.76 ($\pm$ 0.03 CI). Therefore, in order to understand the possible causes of inter-annual variation in NEP, it is necessary to explore the causes of variation in GPP and R_{eco}.

On an annual time scale, GPP was weakly correlated with mean annual air temperature ($r^2 = 0.27$, $p < 0.1$) but not with growing season incident solar radiation ($r^2 = 0.13$, $p > 0.1$) or GSL ($r^2 < 0.1$, $p > 0.1$) (data not shown). Therefore radiation use efficiency (RUE = GPP/incident solar radiation) varied between years (mean = 0.52 g C MJ^{-1}, 12 % CV, Table 3). There was a stronger correlation between GPP and intercepted solar radiation ($S_g{}^i$, $r^2 = 0.46$, $p < 0.05$, Fig. 8a) resulting in less interannual variation in radiation use efficiency calculated on an intercepted basis (mean = 0.88 g C MJ^{-1}, 8.5 % CV). The strongest correlation was between annual GPP and peak LAI ($r^2 = 0.70$, $p < 0.001$, Fig. 8b). Peak LAI showed a significant linear decline over time (-0.208 LAI yr^{-1}, $r^2 = 0.51$, $p < 0.01$), and this resulted in reduced fractional radiation interception and reduced annual GPP and R_{eco} over time. Resulting seasonal differences in RUE for years of contrasting LAI are illustrated in Fig. 9 . The year with highest observed LAI, 2000, had a higher than average RUE during the June–October period; conversely, 2009 with low LAI showed a below average RUE.

Coefficients of an exponential function were derived by fitting monthly R_{eco} and mean monthly air temperature (Table 5). The high overall degree of correlation (mean $r^2 = 0.82$) within each year is not surprising given the method by which R_{eco} was estimated (see Sect. 2.5). However, this approach is useful in highlighting the variation in response between years. Figure 10 shows the relationship for years of contrasting R_{eco}, i.e. high (2000 and 2002) and
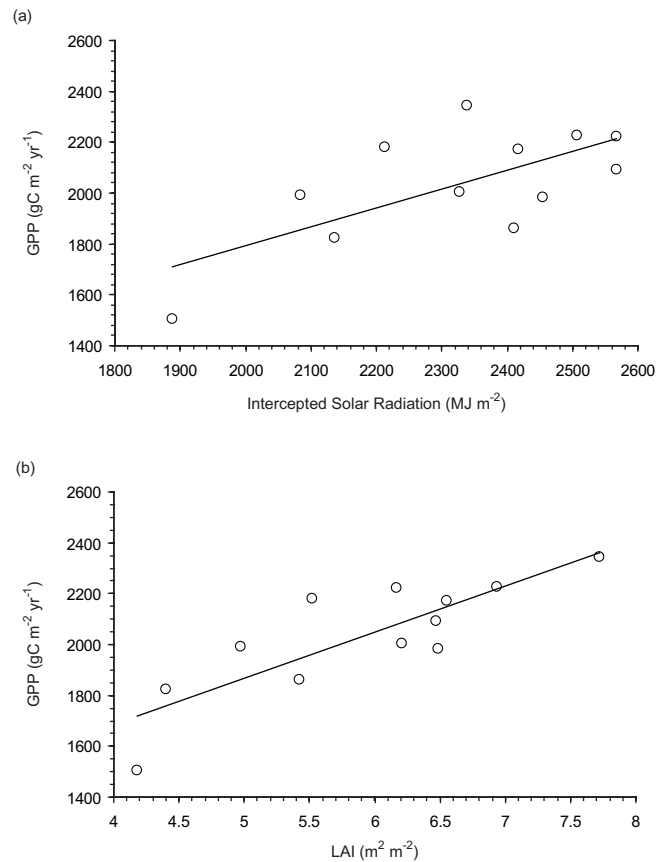

Fig. 8. Relationship between **(a)** annual GPP and intercepted solar radiation ($r^2 = 0.46$, $p < 0.05$) and **(b)** annual GPP and peak LAI ($r^2 = 0.7$, $p < 0.001$).
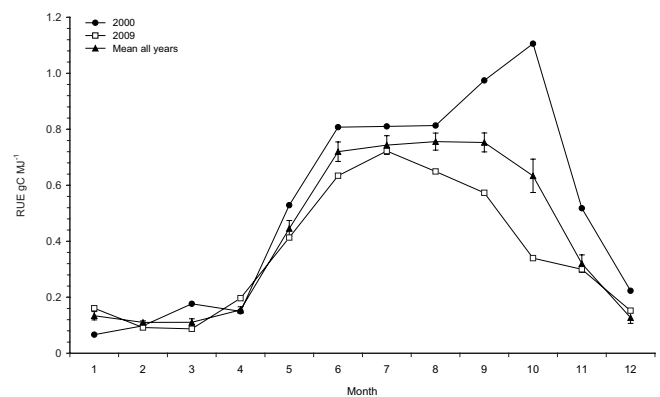

Fig. 9. Monthly RUE for contrasting years of high GPP (2000) and low GPP (2009).

low (2006 and 2010). It is evident that the years of high annual R_{eco} showed an enhanced sensitivity of monthly R_{eco} to temperature and, conversely, a lower sensitivity during the years of low annual R_{eco}. When the monthly R_{eco} values are separated between growing season (May–October, inclusive) and non-growing season months, it becomes clear

Table 5. Coefficients of an exponential model-fitted monthly R_{eco} to mean monthly air temperature, calculated mean Q10 values and r^2 values for the Straits Inclosure, Alice Holt Forest. r^2 values are also shown for exponential regressions for the non-growing (November–March) and growing (April–October) season months, separately.

Year	Intercept	e	r^2	Q10	Non-growing season r^2	Growing season r^2
1999	36.12	0.114	0.895	3.13	0.973	0.537
2000	41.89	0.119	0.815	3.30	0.469	0.110
2001	40.80	0.108	0.881	2.95	0.936	0.571
2002	35.04	0.122	0.740	3.38	0.878	0.242
2003	49.51	0.084	0.688	2.32	0.692	0.319
2004	41.25	0.100	0.836	2.73	0.925	0.001
2005	47.66	0.081	0.719	2.26	0.864	0.009
2006	38.69	0.086	0.655	2.37	0.751	0.200
2007	19.79	0.155	0.924	4.72	0.525	0.739
2008	24.77	0.139	0.948	4.01	0.676	0.969
2009	36.88	0.103	0.777	2.81	0.801	0.207
2010	39.90	0.088	0.934	2.41	0.765	0.768
Mean	38.22	0.107	0.818	3.00	0.771	0.389
SEM	2.53	0.01	–	0.22	–	–
SD	8.77	0.62	–	0.78	–	–

Fig. 10. Relationship between the monthly sum of R_{eco} and mean monthly air temperature for years of high (2000 and 2002; $r^2 = 0.75$) and low (2006 and 2010; $r^2 = 0.78$) annual R_{eco}.

that the relationship with temperature is much more consistent in the non-growing season (Table 5). In several years there is no evident relationship between growing season R_{eco} and temperature, suggesting that other factors are more influential, accounting for the reduction in sensitivity to temperature shown in Fig. 10. This sensitivity when quantified as the apparent Q10 value was found to be strongly related to the mean summer (July–September) soil moisture content (Fig. 11, $y = 0.099x - 0.06$; $r^2 = 0.78$). This analysis indicates that high rates of R_{eco} occur at this site under the combined conditions of high air and soil temperature and higher than average summer soil moisture.

As noted above, annual NEP did not show any clear trends over time. While annual NEP sums were related to neither the single variables of annual incident radiation (S_g), precipitation (P), average air temperature, mean summer soil moisture content (SM) nor peak leaf area index, NEP was weakly related to intercepted radiation, $S_g{}^i$ ($r^2 = 0.421$, $p < 0.05$). When possible drivers were analysed with multiple regression, the best linear model derived was NEP $\propto S_g{}^i + P + SM$ ($r^2 = 0.715$, $p = 0.014$), accounting for more than 70 % of the variation in NEP.

3.5 NEP comparison with biometric-based estimates

Regular tree mensuration assessments have been carried out as part of the ECN vegetation monitoring protocol (Sykes and Lane, 1996) in plots within the potential EC (eddy covariance) footprint (Table 1), therefore enabling a comparison with the EC-based estimates of NEP. The mensuration data were used to estimate stem volumes and above-ground biomass, using empirical biometric relation-
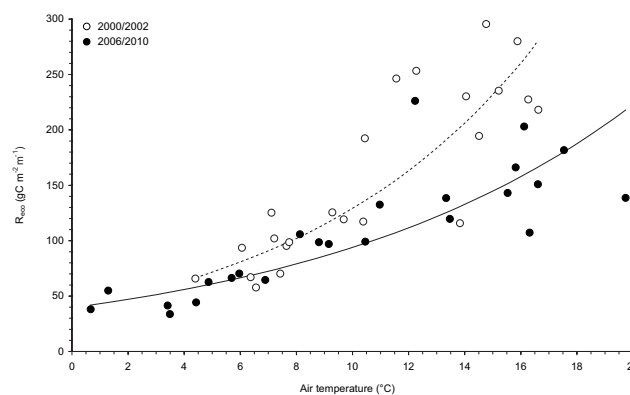
ships derived from sets of 10 oak trees harvested and weighed in the inclosure in both 2005 and in 2009. Assuming a C content of dry weight of 50 % (Broadmeadow and Matthews, 2003) gives a mean annual estimated increase between 1997 and 2011 in above-ground biomass of 260 g C m^{-2} yr^{-1} (canopy trees only). Using relationships found by McKay et al. (2003) specifically for oak trees, the below-ground biomass increment was estimated as 87 g C m^{-2} yr^{-1}. Thus the mean annual (biometric) estimated C uptake was 347 g C m^{-2} yr^{-1}, 71 % of the mean NEP estimated from EC fluxes (486 g C m^{-2} yr^{-1}).

4 Discussion

4.1 Annual C budget of woodlands in Britain and Ireland

Using eddy covariance (EC) measurements we have provided a 12-yr time series of partitioned forest CO_2 fluxes and quantified the inter-annual variation of these partitioned fluxes (Fig. 5) for a managed oak woodland in south-eastern England, revealing important differences in their seasonal phase and amplitude (Fig. 3c). Although the accuracy of eddy covariance measurements in establishing C balances has been questioned because of the problems of filling inevitable data gaps, the various methodological corrections required, difficulties in measuring nighttime fluxes, and advection problems, some comparisons have shown good agreement with direct measurements of changes in C stocks (Gough et al., 2008; Thomas et al., 2011). Whilst we do not have the detailed representative component stock change estimates, as in the exemplary work by Butt et al. (2009) or Gough et al. (2008), the available mensuration data suggest NEP values that are similar, but 29 % lower than those estimated by eddy covariance (EC). However, this biometric estimate includes neither the substantial C uptake by the woody understorey, which might be ~ 10 % (Moore et al., 2007), nor any
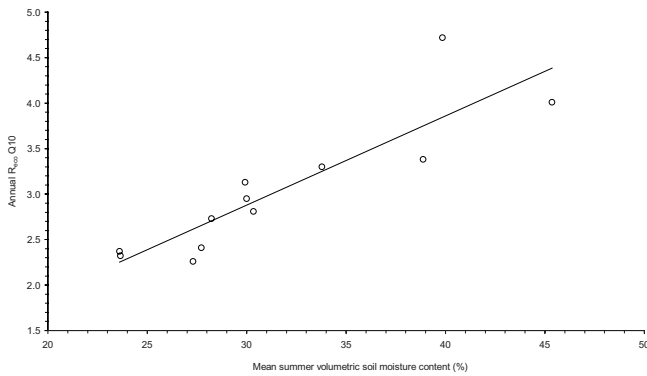
Fig. 11. Relationship between annual R_{eco} Q10 and summer volumetric soil moisture content measured at a depth of 10 cm at the Alice Holt Research Station ($r^2 = 0.78$, $p < 0.001$). Annual Q10 values were calculated from the coefficients of an exponential function fitted to monthly R_{eco} and mean monthly air temperature.

increase in soil organic C content, estimated in this woodland to be 34 g C m^{-2} yr^{-1} (Benham et al., 2012), about 7 % of EC NEP. If these components are included, agreement to within 10–15 % gives some confidence in the NEP values derived from EC data, given the low precision of the biometric approach.

Between 1999 and 2010, the forest acted as a substantial net C sink with a mean NEP of 486 g C m^{-2} yr^{-1}, further evidence that temperate deciduous woodlands actively contribute to the global terrestrial C sink (Luyssaert et al., 2007). Furthermore, the results from this study provide a good basis for understanding the processes of CO_2 exchange within deciduous woodlands under British conditions, which to date have been poorly characterised. Despite the fact that there are more than 30 forest EC flux sites (Clement et al., 2012) currently active across Europe, Britain has only a few, of which only two can be considered long-term studies, (i.e. > 5 yr): this Alice Holt site, and the Griffin Forest site in central Scotland, located in a Sitka spruce (*Picea sitchensis* (Bong.) Carr.) plantation, established in 1997 (Clement et al., 2012). Between 1997 and 2001, average NEP of that young coniferous forest was 721 g C m^{-2} yr^{-1}, which is substantially larger ($+48$ %) than the NEP observed in the current study. Whilst partitioned flux estimates from Griffin Forest indicate very similar levels of R_{eco} (1533 g C m^{-2} yr^{-1}) to the current study (1548 g C m^{-2} yr^{-1}), despite differing soil types, the longer growing season and higher carbon use efficiency of coniferous forests meant that GPP at Griffin was substantially higher ($+11$ %). Under milder conditions than those experienced at the Griffin Forest site, the NEP of Sitka spruce in Dooary, central Ireland, has been shown to be even higher (830–890 g C m^{-2} yr^{-1}; Black et al., 2007).

Although the mean NEP reported here is at the high end of the range reported from other comparable temperate deciduous or semi-deciduous woodlands (Table 6), it is not the highest and has been exceeded at other European deciduous

sites. NEP of 660 g C m^{-2} yr^{-1} was reported at the Collelongo Forest site in Italy (Valentini et al., 2000) and NEP of 550 g C m^{-2} yr^{-1} from an oak sub plot at the Kannenbruch Forest in Germany (Kutsch et al., 2005). However, it should be noted that both of these values were derived from much shorter time series than this study, and in half the 12 yr at Alice Holt the NEP was between 550 and 650 g C m^{-2} yr^{-1} (Table 3).

A site where comparable EC flux measurements have been made in deciduous woodland is that at Wytham Woods in Oxfordshire (Thomas et al., 2011), where a relatively short-term study showed very similar rates of GPP to this study (2110 g C m^{-2} yr^{-1}). It is noteworthy that the Straits site shows one of the larger mean annual GPP values in any of the long-term temperate or boreal forests so far reported (see Table 6). Only the two evergreen conifer plantations at Griffin and Dooary have higher GPP values. However, substantially higher R_{eco} rates at Wytham Woods (1980 g C m^{-2} yr^{-1}) resulted in a much lower mean annual NEP (130 g C m^{-2} yr^{-1}). The Straits Inclosure and Wytham Woods have had contrasting histories; whereas our study site has been managed as commercial forest, with regular interventions, it is likely that the higher levels of R_{eco} observed at Wytham Woods are a result of less intensive management over the last few decades (Kirby, 2010), resulting in greater levels of decomposing deadwood and possibly higher level of heterotrophic respiration due to enhanced soil activity and C levels.

No trend in NEP was observed at our site over the 12 yr, although there were declining trends in both GPP and R_{eco}. Recent data for 2011 are consistent with these trends. This contrasts with the observed increasing NEP trend of 23 g C m^{-2} yr^{-1} observed over 14 yr in a similarly aged beech stand in Denmark, attributed to increasing GPP (Pilegaard et al., 2011).

4.2 Inter-annual variation in NEP, GPP and R_{eco}

Understanding of the sources of inter-annual variation in NEP, GPP and R_{eco} within forest ecosystems is improving as the number of EC forest sites where multi-year records are available increases. In this study, the 12-yr measurement period showed quite high inter-annual variations in NEP, GPP and R_{eco} (SD of 115, 223 and 192 g C m^{-2} yr^{-1} respectively). This may be because of the influence of the variable temperate oceanic climate, but it may also be because the length of record means that there is an increased likelihood of including anomalous or extreme climate years and episodes of biotic stresses such as pests and diseases. Although the variation in GPP and R_{eco} is large compared to similar sites across a range of forest types (Table 6), the close linkage between R_{eco} and GPP resulted in smaller variation in NEP, similar to that found at other sites (Table 6).

Within temperate forests a number of biotic and abiotic factors have been shown to have a controlling effect on GPP,

Table 6. Published multi-annual values of NEP, GPP and R_{eco} for a range of temperate and boreal forest ecosystems

Site	Country	No of years	Measurement period	NEP g C m^{-2} yr^{-1}	GPP g C m^{-2} yr^{-1}	R_{eco} g C m^{-2} yr^{-1}	Forest Type	Authors
Alice Holt	UK	12	1999–2010	486 (115)	2034 (228)	1548 (192)	Temperate deciduous oak plantation	Present study
Griffin	UK	5	1997–2001	721 (60)	2253 (83)	1533 (37)	Temperate conifer plantation	Clement et al. (2012)
De Inslag	Belgium	6	1997–2002	−91 (na)	1234 (na)	1326 (na)	Mixed temperate	Carrara et al. (2003)
Lille Bøgeshov	Denmark	14	1996–2009	156 (103)	1727 (136)	1570 (97)	Temperate beech	Pilegaard et al. (2011)
SMEAR II	Finland	10	1999–2007	206 (38)	1031 (54)	825 (39)	Boreal Scots pine	Ilvesniemi et al. (2009)
Hesse	France	10	1995–2005	386 (171)	1397 (192)	1011 (138)	Temperate beech	Granier et al. (2008)
Puéchabon	France	6[b]	2001–2006	278 (117)	1317 (151)	1018 (68)	Evergreen Mediterranean forest	Allard et al. (2008)
Dooary	Ireland	8	2000–2006[c]	886 (20)	2311 (145)	1445 (133)	Temperate conifer plantation	Saunders et al. (2012)
Borden Forest	Canada	8	1996–2003	141 (112)	1118 (92)	976 (67)	Mixed hardwood and conifer	Teklemariam et al. (2009)
Northern Old Black Spruce	Canada	10	1994–2004	1.8 (41)	706 (57)	713 (79)	Black spruce/veneer bog	Dunn et al. (2007)
Harvard Forest	USA	9	1993–2000	201 (36)	1297 (99)	1099 (91)	Mixed deciduous	Barford et al. (2001)
Harvard Forest[a]	USA	13	1992–2004	245 (100)	1400 (164)	1153 (105)	Mixed deciduous	Urbanski et al. (2007)
Akou	Japan	3	2001–2003	615 (189)	1759 (220)	1144 (135)	Warm temperate evergreen broad-leaved	Kosugi et al. (2005)
Takayama	Japan	9	1994–2002	237 (92)	978 (120)	742 (36)	Cool temperate deciduous forest	Saigusa et al. (2005)
Tomakomai National Forest	Japan	3	2001–2003	212 (44)	1673 (60)	1461 (43)	Larch plantation	Hirata et al. (2007)

Where NEP data were not available, NEE has been used; figures in brackets are standard deviation;
[a] based on ecological year;
[b] of this 9-yr study, only 6 full years of data were available;
[c] based on the pre-thinning period.

including light interception, seasonal phenological development, temperature and moisture availability (Reichstein et al., 2007). The ratio of CO_2 uptake to available light is a key variable, and has been shown to be influenced by a variety of environmental conditions and stresses including stand age, species composition, soil fertility, nutrient status (Gower et al., 1999) and the ratio of diffuse to total incident radiation (Jenkins et al., 2007; Alton, 2008). Here, the annual mean RUE varied between 0.62 and 0.41 g C MJ^{-1} incident radiation (2000 and 2010 respectively; Table 3), averaging 0.52 g C MJ^{-1}. A comparison with other sites is made difficult as there is no common definition of RUE. Some studies have used net primary productivity as the numerator; others have used GPP (Schwalm et al., 2006). In years with low peak LAI, monthly RUE values were low (Fig. 9), particularly later in the year. It is unlikely that, over such monthly periods, variation in the ratio of diffuse to total incident radiation was a major contributor to this effect. Peak LAI explained a large proportion of the inter-annual variation in annual GPP ($r^2 = 0.7$; Fig. 8) because of its direct relationship with light interception and canopy photosynthesis; a similar response to that shown by Longdoz et al. (2010) across a range of forest sites in France. Furthermore, the trend of declining peak LAI over time at this site led to parallel declines in GPP and R_{eco}. We can offer no explanation for this long-term decline in peak LAI. Interestingly, when annual R_{eco} totals are separated into growing season and non-growing sea-

son periods, the declining trend is only found in the growing season R_{eco}, which comprises 71 % (± 3 % CI) of the annual total. This emphasises the strong linkage between R_{eco} and GPP within a growing season.

Growing season length has also been shown to be an important control factor in ecosystem C balance both at the individual site level (e.g. Carrara et al., 2003; Granier et al., 2008) and across a range of forest types (Baldocchi and Xu, 2005). However, at this site neither NEP nor GPP was correlated with onset of growing season or length of growing season. This is similar to the findings of Dunn et al. (2007) who found no correlation between longer growing seasons and net C uptake (at a boreal black spruce forest), which they suggested was due to corresponding increases in ecosystem respiration offsetting increased GPP during longer growing seasons.

The importance of indirect climatic events such as insect-induced canopy defoliation is becoming evident from the growing network of long-term forest EC studies (Allard et al., 2008; Pilegaard et al., 2011). In this study the observed reduction in NEP that occurred in 2009 and 2010 could in part be attributed to the major outbreak of defoliating moth caterpillars, which caused a significant reduction in peak LAI. In addition, there are likely to have been some effects of the oak powdery mildew (*Erysiphe alphitoides*) infection of leaf regrowth on a number of oak trees within the study

area in 2009 and 2010 (Heinemeyer at al., 2012) and the occurrence of a late and damaging air frost on day 127 in 2010.

Understanding the determinants of R_{eco} is complicated because it is governed by several different above- and below-ground processes, each responding to a set of environmental variables. The ratio of R_{eco}/GPP was relatively constant (0.76 ± 0.02 CI) and was similar to the average value of 0.80 reported by Law et al. (2002) for a range of forest types. In the absence of auxiliary measurements, it is impossible to separate total R_{eco} into its different components. However in a parallel study at the same site, between 2007 and 2010, soil CO_2 efflux was estimated to be 740 ± 43 g C m^{-2} yr^{-1} (Heinemeyer at al., 2012), accounting for $\sim 53\%$ of total R_{eco} over the same period. Other studies have estimated a larger contribution by soil autotrophs and heterotrophs to total R_{eco}. For example, Knohl et al. (2008) reported a range of 79–88 % for another temperate deciduous forest. At the annual scale, mean monthly air temperature explained most of the annual variability in R_{eco} ($r^2 = 0.81$, Table 5). Non-growing season (winter) R_{eco} was tightly correlated with air temperature (mean $r^2 = 0.77$), which we attribute to the dominance of heterotrophic respiration during this period. During the growing season the relationship was weaker and varied substantially between years because of the influence of soil moisture. There was more interannual variation in this relationship during the growing season ($r^2 = 0.39$). This type of response has been demonstrated across a range of other forest sites (Law et al., 2002) and is probably because, under conditions of moderate reduced water content, microbial respiration is limited by the diffusion of soluble organic substrates (Epron et al., 1999), particularly in the near-surface layers. The autotrophic respiration component is less likely to be affected by moderate reductions in water content because of the deeper rooting depth (Borken et al., 2006).

The 12-yr continuous dataset presented here for the first time shows that this deciduous forest ecosystem located in southeast Britain acted as a substantial sink for carbon, with a mean up take of 486 g C m^{-2} yr^{-1} (95 % CI of ± 73 g C m^{-2} yr^{-1}). Our EC-based estimates of NEP are relatively closely matched by mensuration-based estimates, providing confidence in our measurements. Year-to-year variation in NEP was largely explained by changes in the contributory, yet opposing, partitioned fluxes of GPP and R_{eco}, and the main biological and environmental drivers of these have been discussed. The study has also identified the important effect that biotic damage such as insect defoliation can have on the carbon flux dynamics of forests.

Copyright statement

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