

The Carbon Cycle of a Maritime Ancient Temperate Broadleaved Woodland at Seasonal and Annual Scales

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ABSTRACT

This study compares different approaches to quantifying the carbon cycle in a temperate deciduous forest at Wytham Woods in England, which is unusual in its maritime climate and mixed age structure, reflecting low levels of past management. We tested whether eddy covariance and biometric measurements gave consistent estimates of woodland productivity and ecosystem respiration at monthly and annual timescales. Biometric methods estimated gross primary productivity (GPP) as $22.0 \pm 1.6 \text{ Mg C ha}^{-1} \text{ y}^{-1}$, close to the eddy covariance GPP value of $21.1 \text{ Mg C ha}^{-1} \text{ y}^{-1}$. Annual ecosystem respiration (R_{ECO}) was similar, at $20.3 \pm 1.5 \text{ Mg C ha}^{-1} \text{ y}^{-1}$ for biometric and $19.8 \text{ Mg C ha}^{-1} \text{ y}^{-1}$ for eddy covariance. The seasonal cycle of monthly biometric and eddy covariance R_{ECO} estimates also closely matched. Net primary productivity (NPP) was $7.0 \pm 0.8 \text{ Mg C ha}^{-1} \text{ y}^{-1}$, 37% of

which was allocated below ground. Leaf fluxes were the greatest component of NPP and R_{ECO} . Ecosystem carbon-use efficiency (CUE = NPP/GPP) was 0.32 ± 0.04 ; low compared to many temperate broadleaved sites but close to values for old-growth sites. This may reflect the age of some trees, and/or the oceanic climate with relatively mild winters during which there can be substantial autotrophic maintenance respiration in winter but negligible growth. This study demonstrates that biometric measurements can provide robust estimates of site productivity and respiration and that eddy covariance and bottom-up measurements can be combined on seasonal and interannual timescales to enable a detailed understanding of the forest carbon cycle.

Key words: GPP; NPP; ecosystem respiration; component; CUE; allocation.

Received 16 July 2013; accepted 22 May 2014

Electronic supplementary material: The online version of this article (doi:10.1007/s10021-014-9793-1) contains supplementary material, which is available to authorized users.

Author contributions YM, MM and CL conceived the work. KMF carried out the fieldwork with assistance where noted in the acknowledgements. KMF analysed the field data and wrote the paper under supervision by YM and MM. MT analysed the eddy covariance data. CL and MT provided comments on the paper.

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INTRODUCTION

Forest carbon (C) cycling is important in the context of global environmental change. To understand, scale and model the terrestrial C cycle, detailed information is needed on the production, allocation and cycling of C in contrasting forest ecosystems. To determine an ecosystem's productivity and respiration, its net carbon dioxide (CO₂) flux can be measured above the canopy by eddy

covariance and ecosystem gross primary productivity (GPP) and respiration (R_{ECO}) inferred, with some limited assumptions. Alternatively, ecosystem productivity and R_{ECO} can be measured by summing individual production and respiration terms. Whilst eddy covariance has been successfully used in many ecosystems (Falge and others 2002; Baldocchi 2008), providing continuous flux monitoring, many sites are unsuitable, having insufficient fetch or uneven terrain. In such sites, measurements of individual components of net primary productivity (NPP) and R_{ECO} can be used (with appropriate estimates for unmeasured variables if necessary) to quantify ecosystem productivity and R_{ECO} . Moreover, measuring individual components is also complementary to eddy covariance, identifying critical processes and providing understanding of the system beyond total GPP and R_{ECO} . This is important for understanding how changes in factors such as climate, species composition and management may influence C dynamics at different sites.

Studies comparing ‘bottom-up’ biometric and flux chamber measurements with ‘top down’ eddy covariance data have been carried out in a limited number of sites, including temperate deciduous forest (Curtis and others 2005), boreal forest (Black and others 2007), a chronosequence of fire-disturbed boreal sites (Goulden and others 2011), tropical rainforest (Chambers and others 2004; Malhi and others 2009) and *Pinus strobus* L. temperate forest (Peichl and others 2010). Table 1 lists all such studies in temperate deciduous woodlands. Notably absent from the list are low-management ancient woodlands, and sites from maritime climates with mild winters. Temperate woodlands constitute approximately 14% of the world’s forests (Malhi and others 1999, after Dixon and others 1994), but can vary greatly (plantation, natural, deciduous, evergreen, stand age, soil type, species) so C cycle estimates are needed for a broad sample of forests, with information on how individual C budget components vary on an intra- and/or interannual basis.

Here we present monthly and annual biometric data for the major components of productivity and respiration in an ancient semi-natural deciduous woodland in southern Britain which is protected for conservation and not actively managed. Two key features of this site compared to previously studied temperate forests are the maritime climate with relatively mild winters, and the relatively low amount of past disturbance. The fairly undisturbed nature of this site provides a useful comparison to studies on younger temperate forest stands

(Table 1) which are regrowing from past clearance, and where the soil has been disturbed during planting or harvest. As forests age, the NPP:GPP ratio may be expected to decrease as NPP declines, whilst autotrophic respiration (R_{AUTO}) increases with the higher costs of maintaining higher biomass (DeLucia and others 2007). By examining the partitioning of C to growth and respiration at an ancient temperate woodland we hope to understand where less managed temperate broadleaved forest systems fit within our current understanding of the temperate forest C cycle.

We report biometric measurements of the major productivity and respiration components at this site, and compare annual total fluxes with ecosystem fluxes from eddy covariance data. Specifically we aimed to:

- (1) Produce monthly estimates of the main components of ecosystem productivity and respiration to determine their seasonality and comparative magnitude.
- (2) Estimate annual total ecosystem net primary productivity and autotrophic and heterotrophic respiration and their partitioning between various components.
- (3) Compare these biometric estimates of site productivity and respiration with independent eddy covariance measurements.
- (4) Determine whether, at this relatively undisturbed ‘ancient woodland’ site, patterns of carbon allocation to productivity and respiration align with current understanding.
- (5) Examine the role that a relatively mild maritime winter climate has on ecosystem respiration and carbon-use efficiency.

METHODS

Methods are described briefly below, with greater detail in the Supplementary Online Material.

Site Description

All measurements were conducted in a 1 ha plot in Wytham Woods, Oxfordshire, UK (1°19′W 51°46′N; UK National Grid: SP 46 08) (Kirby and Thomas 2000). This plot is part of an 18 ha plot surveyed in 2008 and 2010 for the Smithsonian Global Earth Observation network (<http://www.sigeo.si.edu>) and was divided into 25 20 m-by-20 m subplots to aid measurement point replication.

The majority of trees (10 cm or greater diameter at breast height, DBH) are sycamore *Acer pseudo-*

Table 1. Studies of Temperate Deciduous Woodlands Which Have Both Above (ANPP) and Belowground (BNPP) Estimates, and Eddy Covariance Measurements of GPP/NEE and/or R_{ECO} , for the Same Time Period

Location	Ecosystem	Time period	Biometric NPP (Mg C $ha^{-1} y^{-1}$)	Biometric ANPP (Mg C $ha^{-1} y^{-1}$)	Biometric BNPP (Mg C $ha^{-1} y^{-1}$)	Biometric GPP (Mg C $ha^{-1} y^{-1}$)	Biometric R_{ECO}
Collelongo, Italy	Temperate <i>Fagus sylvatica</i> L.	1993	8.02	3.45 #	4.57 (fine roots)	-	-
Harvard Forest, USA	Lower Mississippi Riverine Forest	1999 (wood)	5.65	3.20	2.45	-	-
Kannenbruch Forest, Germany	Temperate <i>Q. robur</i> L.	2002	11.03	8.87 #	2.16 #	-	-
Kannenbruch Forest, Germany	Temperate <i>Fagus sylvatica</i> L.	2002	7.02	5.45 #	1.57 #	-	-
Kannenbruch Forest, Germany	Temperate <i>Alnus glutinosa</i> (L.) Gaertn./ <i>Fraxinus excelsior</i> L.	2002	6.71	4.54 #	2.20 #	-	-
Morgan-Monroe State Forest, USA	Eastern Broadleaf Forest (Continental)	1998–1999 (wood)	10.49	5.29	5.20	-	-
Morgan-Monroe Forest, USA	Mixed deciduous	1998–1999	9.54 # (1998) 9.67 # (1999)	5.15 # 5.31 #	4.39 # 4.36 #	-	-
University of Michigan Biological Station, USA	Laurentian Mixed Forest	1999 (wood)	6.39	3.38	3.01	-	-
University of Michigan Biological Station, USA	Reference 85-year-old temperate/boreal mixed	1999–2003	6.54 ± 0.76 (mean)	1.73 ± 0.10 (mean)	0.40 ± 0.02 (mean)	-	-
Walker Branch, USA	Eastern Broadleaf Forest (Oceanic)	1993–1999 (wood)	7.27	5.39	1.88 #	-	-
Willow Creek, USA	Laurentian Mixed Forest	1989–1999 (wood)	5.11	3.00	2.11	-	-
Wytham, UK	Temperate mixed deciduous	2008 all	7.04 ± 0.84	4.42 ± 0.26	2.62 ± 0.80	21.99 ± 1.61	20.26 ± 1.53
Synthesis of sites	Temperate humid deciduous		7.38 ± 0.55				11.04 ± 2.60

Table 1. continued

Location	Ecosystem	Time period	Biometric ANPP/ BNPP #	CUE #	Eddy flux GPP (Mg C ha ⁻¹ y ⁻¹)	Eddy flux NEE (Mg C ha ⁻¹ y ⁻¹)	Eddy flux R _{Eco} (Mg C ha ⁻¹ y ⁻¹)	Reference
Collelongo, Italy	Temperate <i>Fagus sylvatica</i> L.	1993	0.75	0.79	10.16 (GEP)	4.72 (NEP)	5.44	Valentini and others (1996)
Harvard Forest, USA	Lower Mississippi Riverine Forest	1999 (wood)	1.31	-	-	2.00	-	Curtis and others (2002)
Kannenbruch Forest, Germany	Temperate <i>Q. robur</i> L.	2002	4.11	0.61	17.94	-	12.35	Kutsch and others (2005)
Kannenbruch Forest, Germany	Temperate <i>Fagus sylvatica</i> L.	2002	3.47	0.48	14.70	-	11.74	Kutsch and others (2005)
Kannenbruch Forest, Germany	Temperate <i>Alnus glutinosa</i> (L.) Gaertn./ <i>Fraxinus excelsior</i> L.	2002	2.06	0.42	15.95	-	14.01	Kutsch and others (2005)
Morgan-Monroe State Forest, USA	Eastern Broadleaf Forest (Continental)	1998–1999 (wood)	1.02	-	-	2.36	-	Curtis and others (2002)
Morgan-Monroe Forest, USA	Mixed deciduous	1998–1999	1.17	-	-	2.37	-	Ehman and others (2002)
University of Michigan Biological Station, USA	Laurentian Mixed Forest	1999 (wood)	1.12	-	-	1.67	-	Curtis and others (2002)
University of Michigan Biological Station, USA	Reference 85-year-old temperate/boreal mixed	1999–2003	3.78 ± 0.49 (mean)	-	-	0.80 to 1.77 (NEP)	-	Gough and others (2008)
Walker Branch, USA	Eastern Broadleaf Forest (Oceanic)	1993–1999 (wood)	2.87	-	-	5.77	-	Curtis and others (2002)
Willow Creek, USA	Laurentian Mixed Forest	1989–1999 (wood)	1.42	-	-	2.20	-	Curtis and others (2002)
Wytham, UK	Temperate mixed deciduous	2008 all	1.69 ± 0.52	0.32 ± 0.04	21.1	1.2	19.8	This study and Thomas and others (2011)
Synthesis of sites	Temperate humid deciduous		0.54		13.75 ± 56	3.11 ± 0.38 (NEP)	10.48 ± 2.60	Luyssaert and others (2007)

Errors, where provided, are ±1 standard error.

*The values are calculated from data presented in the referenced study. ANPP/BNPP for each site is also calculated from the presented data. CUE is Biometric NPP/Eddy GPP except for Wytham.

platanus L. (323; 70%) and ash *Fraxinus excelsior* L. (80; 17%); the remainder being pedunculate oak *Quercus robur* L. (24; 5%), hawthorn *Crataegus monogyna* L., hazel *Corylus avellana* L., blackthorn *Prunus spinosa* L. and field maple *Acer campestre* L. Total basal area was 32.9 m² in spring 2007, with 23.1 m² (70%) of this being *A. pseudoplatanus*. Peak leaf area index (LAI), calculated cumulatively from litter trap collections, was 7.8 m² m⁻² in 2008. DBH ranges for *A. pseudoplatanus*, *F. excelsior* and *Q. robur* are in Table S1 of the Supplementary Material.

The site is ancient semi-natural woodland, UK National Vegetation Classification community W8 *Fraxinus excelsior*–*Acer campestre*–*Mercurialis perennis* woodland (Hall and others 2004). ‘Ancient woodland’ means a site that has had continuous forest cover through recorded history (since approximately 1600, Peterken and Game 1984) and often much longer. Most ancient woodland, including Wytham Woods, has been managed throughout this period, including by timber removal. This site was managed as coppice with standards (a mixture of trees cut regularly to produce poles and a smaller number allowed to grow to full height), for long periods but returned to full height trees in the twentieth century. The species composition has changed over time, particularly with an increase in *A. pseudoplatanus* (Morecroft and others 2008), but the site has consistently been forested and the soil subject to little disturbance. Tree cover has very likely been continuous throughout the Holocene, albeit with turnover in tree species. For approximately the last 40 years, the plot and most of the surrounding area in the flux footprint have had minimum intervention with no silvicultural management.

The ground vegetation is predominantly dogs’ mercury *Mercurialis perennis* L. with stinging nettle *Urtica dioica* L., bluebells *Hyacinthoides non-scripta* L. Chourad ex Rothm. and pendulous sedge *Carex pendula* Huds. The site is similar in tree species composition for over 300 m to the south-west, south and east. Directly north is a beech (*Fagus sylvatica* L.) plantation. The flux tower is near the plot centre with a footprint within 600 m of the tower, mainly to the south-west, the prevailing wind direction (Thomas and others 2011). The whole forest covers approximately 400 ha (Morecroft and others 2008).

The soil is mostly stagni-vertic cambisol, derived from clay, with areas of arenic-haplic luvisols and calcareous cambisols (FAO/UNESCO classification, Beard 1993). Meteorological data have been recorded at the wood since 1992 for the UK

Environmental Change Network (ECN) program (Morecroft and others 1998). For 1993–2011, mean annual total precipitation was 714 ± 29 mm, mean annual temperature 10.0 ± 0.1°C, mean air temperature of the warmest month (from hourly means) 16.6 ± 0.3°C (July), and mean coolest month temperature (from hourly means) 4.2 ± 0.4°C (December).

Wood Production

Point Measurements

Tree growth was measured monthly for a subsample of 280 trees from the plot total of 466 over 10 cm DBH, using dendrometer bands (adapted from Keeland and Young 2009) and vernier-gauge callipers to a precision of 0.5 mm in circumference (<0.2 mm in diameter). Measurements started in 2006; the first measurements reported here were taken on 3rd February 2007 and last on 12th December 2008. No measurements were made in January and February 2008 when growth rates were very low; December–March total growth was assumed to be evenly apportioned between January, February and March.

Scaling

Dendrometer measurements were scaled up to estimates of tree aboveground dry woody biomass (ABW, kg) using species-specific allometric equations (equations 1–3) for *A. pseudoplatanus*, *F. excelsior* and *Q. robur*, where c is trunk circumference (cm) at breast height (Bunce 1968). For the 39 trees of other species, DBH was converted to ABW using equation 4, with coefficients that are means of those in equations 1–3.

$$A. pseudoplatanus \text{ ABW} = \exp^{(-5.644074 + (2.5189 * (\ln c))} \quad (1)$$

$$F. excelsior \text{ ABW} = \exp^{(-5.308133 + (2.4882 * (\ln c)))} \quad (2)$$

$$Q. robur \text{ ABW} = \exp^{(-5.284602 + (2.4682 * (\ln c)))} \quad (3)$$

$$\text{Other species ABW} = \exp^{(-5.41227 + (2.491767 * (\ln c)))} \quad (4)$$

ABW was converted to g C using dry wood fractional C contents of 0.47 ± 0.01, 0.49 ± 0.01 and 0.47 ± 0.01 g C g⁻¹ ABW (mean ± SE) for *A. pseudoplatanus*, *F. excelsior* and *Q. robur*, respectively, from data obtained at Wytham (Butt and others 2009), and the mean of 0.48 ± 0.003 g C g⁻¹ ABW for the remaining species. Mean biomass increment

per tree of *A. pseudoplatanus*, *F. excelsior*, *Q. robur* and the remaining species was calculated and multiplied by the number of individuals of each species, to estimate plot-level annual wood production (NPP_{WOOD} , $\text{Mg C ha}^{-1} \text{y}^{-1}$).

Root Production Using TBCA

Fine root production (NPP_{ROOT}) was not directly measured, but estimated using total belowground C allocation (TBCA) from measured inputs and respiration rates (Davidson and others 2002; Giardina and Ryan 2002). This assumes soil C is at or near steady state, a reasonable assumption at this site as the soil has had little disturbance over many decades. Wytham Wood's history is well documented (Savill and others 2010) showing historical low-impact management followed by no intervention since the 1950s.

Using TBCA, belowground C input (root mortality, litter-derived material) is assumed to equal belowground C output (SOM respiration, dissolved organic C in water), plus any change in soil C stocks:

$$\begin{aligned} \text{NPP}_{\text{ROOT}} + (\text{NPP}_{\text{LITTER}} \cdot F_{\text{LITTER}}) + (M_{\text{AG}} \cdot F_{\text{CWD}}) \\ + M_{\text{BG}} = R_{\text{SOM}} + (F_{\text{DOC}} + \Delta C). \end{aligned} \quad (5)$$

R_{SOM} is soil heterotrophic respiration excluding the litter layer and was directly measured in a soil CO_2 efflux partitioning experiment ("Soil CO_2 Efflux" section). $\text{NPP}_{\text{LITTER}}$ is canopy litter-fall (leaves, flowers, fruit) and F_{LITTER} the fraction entering the soil (rather than respired in the litter layer). M_{AG} is the mean annual production of aboveground coarse woody debris (CWD) over the 3 years, calculated from mortality recorded in DBH surveys as $0.045 \pm 0.045 \text{ Mg C ha}^{-1} \text{y}^{-1}$. F_{CWD} is the CWD fraction entering the soil, so the CWD fraction respired, R_{CWD} , is therefore the M_{AG} not entering the soil, that is $M_{\text{AG}} - F_{\text{CWD}}$.

F_{LITTER} has been estimated at 0.2 (20% of litter) for *Fagus sylvatica* in France (Ngao and others 2005), 0.67 ± 0.12 for *Populus nigra* in Italy (Rubino and others 2010) and >0.16 for sugar maple in North America (Fahey and others 2011). F_{CWD} has been estimated as 0.24 ± 0.15 for lowland Amazonian forests (Malhi and others 2009). It is unclear how these values extrapolate to this mixed-species temperate context, but observation suggests that as the soil is mineral without a thick organic layer, over half the litter and CWD is probably broken down in situ by heterotrophic decomposition (R_{CWD}), rather than transported to the soil

organic matter (SOM) matrix. Hence we assume $F < 0.50$ and apply broad error bars to reflect the high uncertainty, that is F_{LITTER} and $F_{\text{CWD}} = 0.25 \pm 0.25$. F_{LITTER} has only a moderate influence on our overall NPP estimates and F_{CWD} has almost negligible influence as CWD input is small here.

M_{BG} is belowground biomass lost in tree mortality, all of which enters the soil. We assume that DOC leakage (F_{DOC}) and net change in soil C stocks (ΔC) are both negligible compared to the overall internal forest C cycle. Respiration of root exudates is assumed indistinguishable from root autotrophic respiration and excluded from equation 5. Equation 5 can be rearranged as equation 6, to calculate NPP_{ROOT} from the other components:

$$\begin{aligned} \text{NPP}_{\text{ROOT}} = R_{\text{SOM}} - (\text{NPP}_{\text{LITTER}} \cdot F_{\text{LITTER}}) - (M_{\text{AG}} \cdot F_{\text{CWD}}) \\ - M_{\text{BG}} + F_{\text{DOC}} + \Delta C. \end{aligned} \quad (6)$$

Coarse woody root production ($\text{NPP}_{\text{CWRROOT}}$) was taken as 20% of aboveground woody production (Curtis and others 2002; Giardina and Ryan 2002), equal to the ratio of belowground to aboveground woody biomass typically found in temperate deciduous forests, with a conservative error estimate of $\pm 15\%$, that is, 0.20 ± 0.15 . Similarly, we assume $M_{\text{BG}} = (0.20 \pm 0.15) \times M_{\text{AG}}$.

Reproductive Structure Production

Reproductive structure (flower and fruit) production ($\text{NPP}_{\text{REPRODUCTIVE}}$) was estimated using litter traps to collect samples which were scaled up to the 1 ha plot. One 0.25 m^2 litter trap was installed per subplot in October 2006; they remained to catch reproductive structures and leaves falling in 2007 and 2008. Reproductive structures were sorted by species and their dry weight determined after drying for 48 h at $75\text{--}80^\circ\text{C}$. The litter trap estimate may be an underestimate, as fruits can be taken before they fall by birds and squirrels and eaten or stored.

Leaf Production

Annual leaf production (NPP_{LEAF}) was determined by sampling autumn leaf-fall using litter traps ("Reproductive Structure Production" section), and scaling up to 1 ha by area multiplication. Traps were emptied fortnightly; the leaves sorted by species, dried for 48 h at $75\text{--}80^\circ\text{C}$, then weighed.

Specific leaf area (area/mass; SLA, $\text{m}^2 \text{kg}^{-1}$) for each species was determined by measuring the leaf area of several subsamples of each species' leaf litter, before drying and weighing (Scion Image, Maryland, USA). The LAI of each species per

Table 2. Annual NPP of Each Measured Component for 2007 and 2008, Calculated Belowground Components for 2008

Component (Mg C ha ⁻¹ y ⁻¹)	2007	2008
NPP _{WOOD}	1.25 ± 0.11	1.65 ± 0.16
NPP _{LEAF}	1.84 ± 0.15	2.40 ± 0.20
NPP _{LEAF} assuming 10% herbivory	2.04 ± 0.15	2.67 ± 0.20
NPP _{REPRODUCTIVE}	0.32 ± 0.03	0.37 ± 0.07
NPP _{AG} (aboveground)	3.41 ± 0.19	4.42 ± 0.26
NPP _{COROOT}	0.25 ± 0.19	0.33 ± 0.25
NPP _{FROOT}	–	2.29 ± 0.76
NPP _{BG} (belowground)	–	2.62 ± 0.80
NPP _{TOTAL}	–	7.04 ± 0.84
GPP	–	21.99 ± 1.61
NPP _{BG} /NPP _{AG}	–	0.59 ± 0.18
NPP _{BG} /NPP _{TOTAL}	–	0.37 ± 0.12
NPP _{AG} /NPP _{TOTAL}	–	0.62 ± 0.08
CUE _{ECO} (NPP _{TOTAL} /GPP)	–	0.32 ± 0.04

Plot total annual NPP and GPP, the ratio of below- to aboveground NPP, proportions of NPP allocated below- and aboveground, and the plot carbon-use efficiency (CUE) for 2008. All values are given ±1 standard error.

sample session was calculated from the total sample weights, and total LAI of each species estimated by reverse cumulative summing.

Herbivory was not measured, but work at similar sites has estimated it at 8–11.5% of NPP_{LEAF} on *Q. robur* (Crawley 1985) and 1–1.6 or 6–10%, respectively, on ant-foraged and non-ant-foraged *A. pseudoplatanus* (Whittaker and Warrington 1985). Here NPP_{LEAF} was calculated assuming zero and 10% herbivory (Table 2). Only the measured (no herbivory) value was used to calculate aboveground (NPP_{AG}) and total NPP (NPP_{TOTAL}).

Leaf Respiration

Night-time leaf respiration measurements were previously made for sun and shade leaves of *A. pseudoplatanus* and *Q. robur* at Wytham (Stokes 2002). The steps to incorporate these measurements into this study, using Q₁₀ relationships, fractions of sun and shade leaves and area scaling, are detailed in the Supplementary Material.

Stem CO₂ Efflux

Monthly stem CO₂ efflux measurements from eight *F. excelsior* and eight *A. pseudoplatanus* trees were taken from April to November 2008. Measurements were made using a portable infra-red gas analysis (IRGA) system (EGM-4 and SRC-1 soil chamber, PP Systems, UK), with an adaptor custom-made to fit PVC ‘collars’ on each tree (50 mm high × 65 mm diameter pipe, Marley, UK). The collars were attached throughout the study using non-setting putty (Plumbers’ Mait, Bostik Ltd, UK)

to allow tree diameter changes. Point measurements were scaled to plot level using a literature stem area value. Further details on the point measurements and scaling are given as Supplementary Material.

There is debate in the literature on the origin of CO₂ effluxing from tree stems (Teskey and McGuire 2002; Teskey and others 2008). If a fraction of stem efflux originates from soil heterotrophic respiration, it would artificially inflate our estimates of autotrophic respiration and hence GPP. Eddy covariance R_{ECO} estimates are unaffected, being at the ecosystem scale (increased stem efflux is balanced by reduced soil efflux). To indicate this uncertainty of origin, we refer to ‘stem CO₂ efflux’ rather than ‘stem respiration’, but label it R_{STEM} to show it is a component of R_{ECO} .

Soil CO₂ Efflux

Point Measurements

Soil CO₂ efflux measurements were made using a portable IRGA and soil CO₂ efflux chamber (EGM-4 and SRC-1 soil chamber, PP Systems, UK) with a custom-made adaptor for fixed soil ‘collars’. One measurement was made per subplot, per session, except in the four plot corners where three measurements were taken to quantify local-scale variability. All measurements were combined to generate the plot mean CO₂ efflux rate (μmol - CO₂ m⁻² s⁻¹). Surface litter was removed before efflux measurements as litter cover varied seasonally.

To determine the contribution of autotrophic and heterotrophic components to total soil efflux, we used micromesh bags to partition root and rhizosphere, mycorrhizal and SOM components (Plastok Ltd, UK) (Moyano and others 2007, 2008; Heinemeyer and others 2007; Fenn and others 2010). The bags were installed in nine of the 25 subplots (a *t* test paired by month showed no significant difference in mean efflux between the nine and 25 subplots, $P = 0.38$) and enclosed a core of soil *in situ*, from which CO₂ efflux measurements were taken fortnightly between 15th April 2008 and 26th November 2008 (the growing season) (Fenn and others 2010). The mean percentage contributions to R_{SOIL} of each component were then calculated.

Mean soil temperature over 0–150 mm depth (Digital Waterproof Thermometer, Barnstead International, USA) and volumetric soil water content over 0–200 mm depth (Hydrosense meter, Campbell Scientific, Australia) were measured within 2 m of respiration collars during each total and partitioned soil CO₂ efflux measurement.

Scaling

Monthly total soil CO₂ efflux was calculated from mean monthly efflux rate ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), the number of seconds per month, and plot area (1 ha), using a similar method as for stem CO₂ efflux. Calculating monthly efflux allowed seasonal changes in soil CO₂ efflux rate to be accounted for without a Q_{10} equation which may not sufficiently represent the effects of seasonal changes in plant activity and soil moisture. These monthly rates were then summed to annual total soil efflux (R_{SOIL}). More details are given in Fenn and others (2010).

Summation of Biometric Components to $\text{NPP}_{\text{TOTAL}}$, R_{ECO} and GPP

Once the point measurements of each component had been scaled to plot level they were summed to produce estimates of monthly and annual $\text{NPP}_{\text{TOTAL}}$ and R_{ECO} and annual GPP using the following equations:

$$\begin{aligned} \text{NPP}_{\text{TOTAL}} &= \text{NPP}_{\text{AG}} + \text{NPP}_{\text{BG}} \\ &= \text{NPP}_{\text{LITTER}} + \text{NPP}_{\text{WOOD}} \\ &\quad + \text{NPP}_{\text{FROOT}} + \text{NPP}_{\text{CROOT}} \end{aligned} \quad (7)$$

$$\begin{aligned} R_{\text{ECO}} &= R_{\text{AUTO}} + R_{\text{HET}} \\ &= R_{\text{LEAF}} + R_{\text{STEM}} + R_{\text{SOIL}} + R_{\text{CWD}} + R_{\text{LITTER}} \end{aligned} \quad (8)$$

where

$$R_{\text{SOIL}} = R_{\text{MYC}} + R_{\text{RRHIZ}} + R_{\text{SOM}} \quad (9)$$

$$\text{GPP} = \text{NPP}_{\text{TOTAL}} + R_{\text{AUTO}}. \quad (10)$$

Equation 10 assumes C gain through photosynthesis equals C use through respiration of GPP. It also assumes negligible interannual variation in internal photosynthate storage.

EDDY COVARIANCE ESTIMATES OF GPP AND R_{ECO}

Eddy covariance data collection began in June 2007; the data used here are from this date to 31st December 2008. The instrumentation, a Solent R2 3D sonic anemometer (Gill Instruments, UK) and LiCOR 7500 open-path infra-red gas analyzer (LiCOR Instruments, USA), is 25 m above the ground on a tower close to the plot centre. Raw data at a frequency of 0.05 s (20 Hz) were recorded on a CR3000 logger (Campbell Scientific, USA). Details of the analysis and results are presented by (Thomas and others 2011) and summarised briefly here. Primary raw data processing used the EdiRe software (<http://www.geos.ed.ac.uk/abs/research/micromet/EdiRe/>) with the standard 30-min averaging interval. Standard corrections for open-path IRGAs were also made in EdiRe, including Webb–Pearman–Leuning air-density effects corrections (Webb and others 1980) and vertical wind signal rotation.

Secondary processing, including removal of CO₂, LE and H flux spikes, and a negative bias to night-time values was then carried out. Data gaps thus created were filled by Marginal Distribution Sampling (<http://www.bgc-jena.mpg.de/bgc-mdi/html/eddyproc/index.html>, Reichstein and others 2005).

To correct for any night-time lateral drainage of CO₂, the friction velocity correction of Goulden and others (1996) was applied, following the method of Reichstein and others (2005). GPP, R_{ECO} and net ecosystem productivity (NEP) were then estimated using the CarboEurope partitioning tool (Reichstein and others 2005), with GPP being $\text{NEP} - R_{\text{ECO}}$.

Data Analysis

All data processing and statistical analyses were carried out using Microsoft Excel 2003 (Microsoft Corp., 1985–2003) and SPSS version 16.0 for Windows (SPSS Inc., 1989–2007). Standard errors were propagated to annual and plot level using the standard error propagation methods (for details see the Supplementary Material).

RESULTS

Meteorological Conditions

Total annual rainfall was 777.6 mm in 2007 and 863.6 mm in 2008, both wetter than the 1993–2010 average of 714 mm. Annual mean temperature was 10.3°C in 2007 and 9.7°C in 2008 compared to the 1993–2011 mean of $10.0 \pm 0.1^\circ\text{C}$. Peak summer temperature was reached in August 2007 and July 2008, with 27.4 and 26.7°C, respectively. These months were the warmest in their respective years, with mean monthly temperatures of 15.7 and 16.0°C for 2007 and 2008, respectively; below the mean temperature of the warmest month of $16.6 \pm 0.3^\circ\text{C}$ (1993–2011 warmest month is July). The two sampling years therefore had cooler and wetter summers than the preceding 18 years, but warmer-than-average spring and autumn in 2007.

NPP

$\text{NPP}_{\text{TOTAL}}$ was $7.04 \pm 0.84 \text{ Mg C ha}^{-1} \text{ y}^{-1}$ for 2008 and mainly aboveground; the production of leaves, ABW and reproductive structures contributed approximately 60%. The largest component was NPP_{LEAF} at $2.40 \pm 0.20 \text{ Mg C ha}^{-1} \text{ y}^{-1}$ (Table 2), so

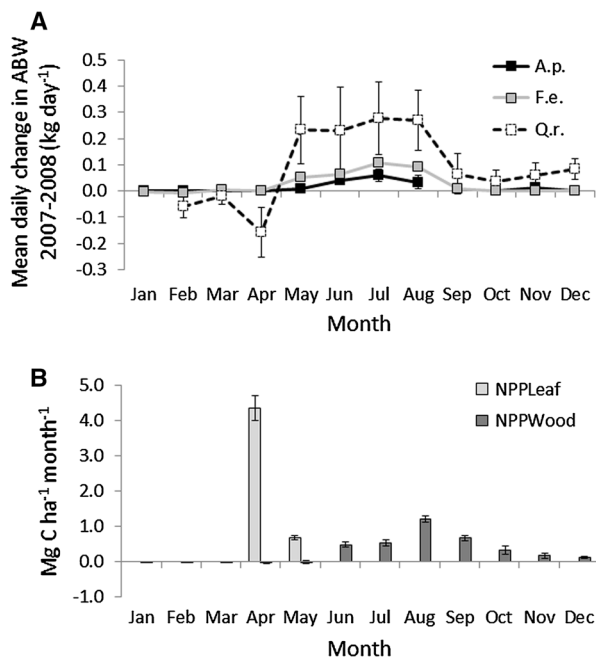


Figure 1. **A** Mean monthly wood production (kg day^{-1}) for the three main species at the site, averaged for the 2 years 2007 and 2008. *A.p.*, *Acer pseudoplatanus*; *F.e.*, *Fraxinus excelsior*; and *Q.r.*, *Quercus robur*. **B** Monthly NPP of leaves and wood ($\text{Mg C ha}^{-1} \text{ month}^{-1}$). Error bars indicate ± 1 standard error of the mean.

aboveground NPP (NPP_{AG}) was mostly the production of short-lived structures, rather than long-lived wood. Whilst deciduous tree leaf production in any given year requires remobilization of resources stored the previous growing season, we accounted for this production in the year the leaves were produced. Some trunk expansion occurs during canopy development, but significant wood production begins once the canopy is established and photosynthesizing, increasing to a peak in July then decreasing through autumn (Figure 1).

NPP_{AG} was similar in 2007 and 2008, though greater in 2008 for all components (Table 2). 2007 NPP_{LEAF} and NPP_{WOOD} were approximately 76% of that in 2008. Absolute allocation to $\text{NPP}_{\text{REPRODUCTIVE}}$ was not significantly different between years, so a greater proportion of $\text{NPP}_{\text{TOTAL}}$ in the less productive 2007 season.

Respiration Components

Measurements throughout 2008 showed clear seasonality of CO_2 efflux from soil and stems. The exact seasonality differed, however, with peak efflux in June for soil ($1.9 \pm 0.2 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), July for *F. excelsior* ($4.7 \pm 0.5 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) and August for *A. pseudoplatanus* ($1.7 \pm 0.5 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$). The two species also differed in efflux magnitude, with *F. excelsior* having a greater rate than *A. Pseudoplatanus*—and soil—from May to October (Figure S2 in Supplementary Material).

Ecosystem Respiration

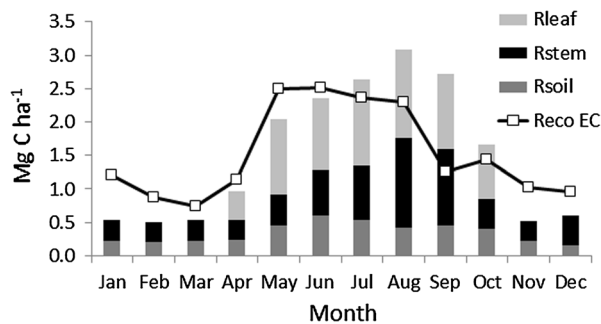
Biometric total R_{ECO} for 2008 was $20.3 \pm 1.5 \text{ Mg C ha}^{-1} \text{ y}^{-1}$. The largest R_{ECO} component was R_{LEAF} , at $7.2 \pm 1.4 \text{ Mg C ha}^{-1} \text{ y}^{-1}$ in 2008 (Table 3), 35.3 \pm 4.4% of R_{ECO} . R_{STEM} is the second greatest contributor at $6.9 \pm 1.2 \text{ Mg C ha}^{-1} \text{ y}^{-1}$ and assumed to continue throughout winter dormancy, at a reduced rate, reflecting maintenance respiration as the lack of transpiration in these leafless months suggests no xylem transport of soil CO_2 . R_{STEM} and R_{LEAF} are influenced by temperature and tree growing season, with R_{LEAF} , by definition, only occurring when leaves are present and metabolically active.

The clear seasonal R_{ECO} cycle produced when the components are combined (Figure 2) is similar to the independent eddy covariance R_{ECO} estimate (Figure 2), except in September, when eddy covariance records a drop in R_{ECO} not reflected in the biometric measurements, which produce a monthly sum 1.16 Mg C (116%) greater than the tower. From January to December 2008, the mean

Table 3. Annual Respiration of Each Measured Component and Plot Total Annual Ecosystem Respiration, R_{ECO} , Estimated by Chamber Methods and Eddy Covariance

Respiration component ($\text{Mg C ha}^{-1} \text{y}^{-1}$)	2008
R_{RRHIZ}	0.88 ± 0.25
R_{MYC}	0.34 ± 0.10
R_{SOM}	2.89 ± 0.25
R_{SOIL}	4.11 ± 0.01
R_{STEM}	6.89 ± 1.17
R_{LEAF}	7.16 ± 2.86
R_{LITTER}	2.08 ± 0.69
R_{CWD}	0.03 ± 0.01
R_{AUTO}	14.73 ± 0.92
R_{HET}	5.31 ± 0.76
R_{ECO} biometric	20.3 ± 1.5
R_{ECO} tower	19.8

R_{SOIL} for 2007 was $4.12 \pm 0.01 \text{ Mg C ha}^{-1} \text{y}^{-1}$. R_{RRHIZ} , R_{MYC} , and R_{SOM} are respiration from roots and the rhizosphere, mycorrhizas and soil organic matter decomposition, respectively, which sum to total soil respiration, R_{SOIL} . R_{STEM} is total stem CO_2 efflux and R_{LEAF} , R_{LITTER} , R_{CWD} , R_{AUTO} , and R_{HET} are respiration from leaves, litter, coarse woody debris, all autotrophic components, and all heterotrophic components, respectively. Values are ± 1 standard error, where relevant.

**Figure 2.** Contribution of R_{LEAF} , R_{STEM} , and R_{SOIL} to R_{ECO} , per month, for 2008 with R_{ECO} derived from eddy covariance estimates (R_{ECO} EC). R_{LITTER} and R_{CWD} are not included as they cannot be estimated on a monthly basis.

monthly difference between the methods was $0.01 \pm 0.6 \text{ Mg C}$ or $6.2 \pm 13.7\%$ of monthly tower-measured efflux (Figure 2).

During winter, some autotrophic and heterotrophic respiration continues because of the relatively mild maritime climate. For November to March inclusive, when the trees are leafless, soil CO_2 efflux produced $1.0 \pm 0.04 \text{ Mg C ha}^{-1}$ and stem CO_2 efflux $1.7 \pm 0.83 \text{ Mg C ha}^{-1}$.

Carbon Cycle of the Forest Plot

Figure 3 illustrates each component contribution to the plot C cycle. Aboveground components contribute most to both productivity and respiration, as

NPP_{LEAF} , NPP_{WOOD} and R_{LEAF} , R_{STEM} and R_{LITTER} , respectively (Tables 3, 4). Leaves contribute the greatest portion of both $\text{NPP}_{\text{TOTAL}}$ (34.1%) and R_{ECO} (35.3%) (2008 data). We estimated GPP as $21.99 \pm 1.61 \text{ Mg C ha}^{-1} \text{y}^{-1}$. The carbon-use efficiency (CUE), the proportion of GPP used for biomass production rather than respiration, was 0.32 ± 0.04 . This was calculated including light-inhibited daytime foliar respiration; if daytime foliar respiration is taken as zero, as in previous work (for example, Ryan and others 1997), we obtain a similar CUE of 0.35 ± 0.05 .

DISCUSSION

Productivity

Annual $\text{NPP}_{\text{TOTAL}}$, $7.0 \pm 0.8 \text{ Mg C ha}^{-1} \text{y}^{-1}$ for 2008, lies within the range in Table 1, which varies from $5.11 \text{ Mg C ha}^{-1} \text{y}^{-1}$ for a mixed forest (Curtis and others 2002) to $11.03 \text{ Mg C ha}^{-1} \text{y}^{-1}$ for a *Quercus robur* stand (Kutsch and others 2005). This $\text{NPP}_{\text{TOTAL}}$ is also close to a mean of $7.38 \pm 0.55 \text{ Mg C ha}^{-1} \text{y}^{-1}$ for deciduous temperate humid forests calculated by (Luyssaert and others 2007). This mean was calculated from a database of forests ranging from boreal evergreen (mean NPP $2.71 \pm 0.17 \text{ Mg C ha}^{-1} \text{y}^{-1}$) to tropical evergreen ($8.64 \pm 0.96 \text{ Mg C ha}^{-1} \text{y}^{-1}$).

DeLucia and others (2007) also compiled production values for a range of sites and ecosystem types, with mean temperate deciduous woodland NPP being $13.0 \text{ Mg C ha}^{-1} \text{y}^{-1}$; nearly twice that reported here. This high NPP compared to Wytham may result from the relatively young age of many of the temperate deciduous sites previously reported. Comparing the NPP of our ancient woodland to these and other values reported for managed temperate deciduous forests of $17.7 \text{ Mg C ha}^{-1} \text{y}^{-1}$ (Curiel Yuste and others 2005a), a 60-plus-year-old *Q. robur*-dominated stand in Belgium), and 2.7 and $3.8 \text{ Mg C ha}^{-1} \text{y}^{-1}$ (for two consecutive years, Ehman and others 2002 at a mixed deciduous forest of 60- to 80-year-old trees, USA), demonstrates that relatively unmanaged temperate woodlands can be relatively productive in global terms.

Aboveground NPP was greater in 2008 than 2007, possibly as the 2008 summer was wetter and warmer than in 2007. It is interesting that both NPP_{WOOD} and NPP_{LEAF} were greater in 2008 relative to 2007, and to an equal extent (approximately 30% increase from 2007 to 2008), but that $\text{NPP}_{\text{REPRODUCTIVE}}$ increased by only half this (15% of 2007 greater in 2008). This interannual differ-

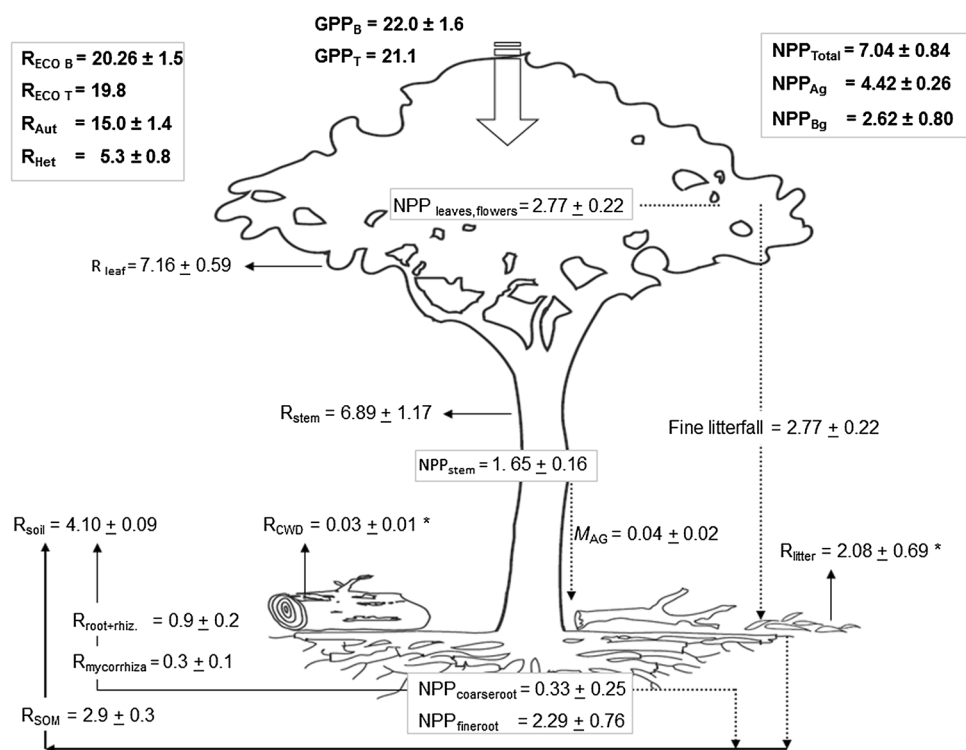


Figure 3. Illustration of the carbon cycle of the site, constructed from the measured components. The partitioning method used allows mycorrhizal respiration and SOM decomposition to be counted as part of total heterotrophic respiration whilst root and rhizosphere respiration, which are inseparable with the mesh bag method used, are taken to be autotrophic * indicates components calculated using mass balance, rather than directly measured.

Table 4. Percentage Contribution of Each Respiration Component, ± 1 Standard Error, to Total R_{ECO} , in This and Previous Studies

R_{ECO} (Mg C ha ⁻¹ y ⁻¹)	R_{SOIL} (%)	R_{STEM} (%)	R_{LEAF} (%)	Biome	Dominant species	Source
20.3 \pm 1.5	20.2 \pm 1.6	34.0 \pm 6.3	35.3 \pm 4.4	Temperate	<i>A. pseudoplatanus</i>	This study
13.8 \pm 0.4	80.9 \pm 0.2	11.1 \pm 0.2	8.0 \pm 0.1	Temperate	<i>Populus tremuloides</i> Michx.,	Calculated mean of 1999–2002 data from Bolstad and others (2004)
11.8 \pm 0.4	75.4 \pm 0.4	19.9 \pm 0.4	4.8 \pm 0.1	Temperate	<i>A. saccharum</i> Marsh.	Calculated mean of 1999–2002 data from Bolstad and others (2004)
9.61	73.2	11.8	15.1	Boreal	<i>P. tremuloides</i> Michx., <i>P. balsamifera</i> L.	Griffis and others (2004)
9.1 \pm 1.15	67	–	–	Temperate	<i>Quercus robur</i> , <i>Pinus sylvestris</i> L.	Curiel Yuste and others (2005b)

R_{SOIL} and R_{DECOMP} for this site are combined (as R_{SOIL}) for ease of comparison with the other studies.

ence in component contributions to NPP would not be captured in a purely eddy covariance study.

The clear monthly dendrometer data on woody productivity demonstrate the value of this temporal resolution of growth measurements and gave an insight into the seasonality of wood production at Wytham. Combining dendrometer and LAI data showed how leaf production, concentrated in late

spring, was immediately followed by an increase in stem expansion (Figure 1). Whilst the three main species showed differences in magnitude and seasonality of stem growth rate, in 2007 and 2008 all species achieved peak growth rate in July. Stem changes at a daily scale have been recorded for *A. pseudoplatanus*, *F. excelsior* and three other deciduous species by Köcher and others (2012). Their data

show a similar overall trend to ours, with the exception that their *A. pseudoplatanus* trees had stopped stem expansion by July.

Leaf production in deciduous trees requires the reallocation of resources acquired and stored in the previous growing season. Here, leaf production is the greatest $\text{NPP}_{\text{TOTAL}}$ component at 38%, allocated to the year in which leaves appear, rather than the previous year when the carbon was fixed. Stokes and others (2010) showed that much of this internal reallocation in *Q. robur* and *A. pseudoplatanus* leaves is likely to take place within individual branches, as isotopic signatures (^{13}C : ^{12}C) of sun and shade branches are maintained.

We estimate that 37% of $\text{NPP}_{\text{TOTAL}}$ was allocated belowground, in the middle of the range of previous findings of 15–55% for a temperate *Quercus* and *Fraxinus* forest (Tateno and others 2004), 54% for a regenerated mixed deciduous temperate site (Newman and others 2006), and 20–74% calculated for the studies referenced in Table 1 (minimum from Kutsch and others 2005, maximum from Gough and others 2008). This substantial component of $\text{NPP}_{\text{TOTAL}}$ (particularly fine root production) can be missed by studies that focus on more easily measurable aboveground components. All studies in Table 1 have this lower allocation to below- than aboveground productivity except one *Fagus sylvatica* stand (Valentini and others 1996).

From scaling biometric measurements, we estimated GPP as $20.99 \pm 1.61 \text{ Mg C ha}^{-1} \text{ y}^{-1}$, close to the $21.1 \text{ Mg C ha}^{-1} \text{ y}^{-1}$ eddy covariance estimate by Thomas and others (2011), providing support that we have included the major components of $\text{NPP}_{\text{TOTAL}}$ or R_{AUTO} and used appropriate scaling. The Thomas and others (2011) paper reports higher GPP and R_{ECO} values for the scaled chamber measurements than we do here. We had previously scaled stem CO_2 efflux measurements to plot level using our stem biomass values in stem surface area equations from the literature derived from species similar to those in our study. The area estimates from this method were very high, so we instead used literature stem area values. This change to stem CO_2 efflux scaling produced a lower plot-level estimate and consequently lower R_{ECO} and GPP estimates than in Thomas and others (2011). Finding a realistic stem CO_2 efflux scaling method was one of the greatest challenges of this study.

Respiration

R_{ECO} was $20.3 \pm 1.5 \text{ Mg C ha}^{-1} \text{ y}^{-1}$ for 2008; approximately 81% greater than the mean R_{ECO} of

$11.04 \pm 2.60 \text{ Mg C ha}^{-1} \text{ y}^{-1}$ calculated by (Luyssaert and others 2007) from a synthesis of temperate forests. It is, however, only slightly higher than our independent eddy covariance estimate of $19.8 \text{ Mg C ha}^{-1} \text{ y}^{-1}$. The closeness of these estimates increases confidence that the major C cycle components are adequately captured by the biometric measurements.

The seasonality of the biometric and eddy covariance R_{ECO} estimates was also close for most months. The largest discrepancy, of 1.5 Mg C, in September (116% of September's tower-measured efflux) may be an artefact of measurement date. Whilst the eddy covariance data are monthly means of continuous measurements, R_{SOIL} was measured fortnightly and R_{STEM} monthly. September covers a transitional period at the end of the tree growing season and possibly the point measurements of R_{STEM} and R_{SOIL} were unrepresentative of the month as a whole.

The percentage contribution of each respiration component to R_{ECO} at this site unexpectedly differs from that at other locations, with R_{LEAF} being the greatest contributor here, as opposed to R_{SOIL} elsewhere (Table 4). Our soil respiration measurements scale up to estimates of $4.12 \pm 0.01 \text{ Mg C ha}^{-1} \text{ y}^{-1}$ in 2007 and $4.11 \pm 0.01 \text{ Mg C ha}^{-1} \text{ y}^{-1}$ in 2008, roughly half the 8.09 to $11.94 \text{ Mg C ha}^{-1} \text{ y}^{-1}$ measured by Bolstad and others (2004) for three temperate hardwood sites over 4 years, or the $7.5 \pm 0.45 \text{ Mg C ha}^{-1} \text{ y}^{-1}$, Curiel Yuste and others (2005b) estimated for an oak/deciduous woodland. However, the consistency between years suggests that our data are reliable. Our stem efflux measurements were conversely high compared to the literature, but made with the same portable IRGA system, so the possibility of a calibration error causing low soil efflux measurements is unlikely. Figure S2 of the Supplementary Material presents mean monthly CO_2 efflux for soil alongside those for *A. pseudoplatanus* and *F. excelsior* for comparison of rates without area scaling.

At $20.3 \pm 1.5 \text{ Mg C ha}^{-1} \text{ y}^{-1}$ R_{ECO} was 92.3% of GPP; far above the mean 57% partitioning to R_{ECO} across a review of studies by Litton and others (2007). Additionally, the CUE of this site is 0.32 ± 0.04 (or 0.35 ± 0.05 with zero daytime foliar respiration), lower than (or at the low end of) the 0.34 to 0.83 reported for a range of temperate deciduous forests (DeLucia and others 2007). These comparisons suggest a higher level of autotrophic respiration, R_{STEM} in particular, in relation to production at Wytham, compared to similar sites. This may result from Wytham being an old, relatively undisturbed site, as DeLucia and others (2007)

noted that CUE appeared to decline with stand age, a pattern also suggested for tropical forests by Malhi and others (2009). Hence, the higher CUE reported for many temperate sites may reflect their secondary forest or plantation status. A possible additional factor in the low CUE may be that higher winter autotrophic respiration rates result from the relatively warm winters associated with the maritime climate at this site. During winter, taken here as November to March, inclusive, when the trees are leafless, stem CO₂ efflux is assumed to be the main autotrophic respiration component and produces $1.7 \pm 0.8 \text{ Mg C ha}^{-1} \text{ y}^{-1}$. This is over one-tenth of annual autotrophic respiration, produced during the 'dormant' season.

LIMITATIONS

Interannual differences in weather can cause interannual differences in C uptake and release from individual components of a site's C cycle, and so result in interannual differences in C balance (Ehman and others 2002). The two study years gave similar results and provide a guide to the range and relative magnitudes of the separate components (Figure 3) but a longer term study would build a fuller picture. A further extension would be to include ground flora productivity and respiration measurements, to determine the contribution of these species to site C balance.

Belowground productivity was not directly measured, but estimated using measured parameters in the TBCA method (Davidson and others 2002). One parameter is M_{AG} , the mortality of ABW (and from this M_{BG}). M_{AG} was measured as the trees dying or clearly senescing each year; five individuals in 2006 and zero in 2007 or 2008. All five remained standing throughout the study, but were deemed alive in spring 2006 and so included in the first census. This episodic M_{AG} is reflected by the SE equalling the mean over the three study years. Taking years individually, M_{AG} would range from $0.14 \text{ Mg C ha}^{-1} \text{ y}^{-1}$ in 2006 to $0.00 \text{ Mg C ha}^{-1} \text{ y}^{-1}$ in 2007 and 2008. Using annual M_{AG} in this way would produce negligible effects on NPP_{ROOT} with values of 2.24 ± 0.76 in 2006 and 2.31 ± 0.76 in 2007 and 2008. It must also be recognised that though M_{AG} is averaged across the whole plot, at a lower spatial level it is a heterogeneous parameter at this time-scale. Although the site is established woodland there is currently an increase in tree recruitment following the end of (low-level) management in the 1950s; the site is not at steady state, but approaching it, so NPP_{AG} is currently greater than M_{AG} (by a factor of 100).

The nature of this study requires scaling to transform measurements made at one point in space and time to estimates for the whole plot on a monthly and annual basis. To reflect possible limitations in the scaling methods used, we have applied large error estimates where appropriate; annual leaf respiration and stem CO₂ efflux were assigned very conservative uncertainties. Similarly, unmeasured elements of the C cycle, estimated by reference to previous studies, were also given large error estimates.

Wood production estimates involved allometric equations (Bunce 1968) to produce ABW values from DBH measurements. However, these allometric equations are thought appropriate, being derived for the most numerous species at this site from trees in the same size-range.

Scaled stem CO₂ efflux is a major source of uncertainty. This component, though based on field measurements, relied on a literature stem area estimate to scale these field measurements to plot level. Using a literature stem area rather than one calculated from the trees themselves could have produced an inaccurate estimation of stem efflux; we have tried to reflect this by applying a conservative 50% error to the estimate for each month and propagating this error through to the total annual value. R_{STEM} is therefore our best estimate, based on available data and methods, but this possible caveat must be borne in mind. It is worth noting that the directly measured stem CO₂ efflux values per unit stem area are high (summer mean values are typically $2\text{--}3 \mu\text{mol m}^{-2} \text{ s}^{-1}$). The relatively high annual estimates are therefore thought to mainly result from these high direct measurements, rather than being an artefact of temporal or spatial scaling assumptions. Future work of this kind would benefit greatly from having species-specific allometric equations derived for trees at the measurement site to maximise the accuracy of stem efflux scaling.

CONCLUSIONS

We have quantified many of the forest C cycle components within a coherent framework. The close agreement between annual, and also many monthly, R_{ECO} estimates from biometric and eddy covariance methods give us confidence in the robustness and suitability of the methods used and increases confidence that no large components have been missed. There is also a good agreement between the eddy and biometric estimates of GPP; 21.1 and $22.0 \pm 1.6 \text{ Mg C ha}^{-1} \text{ y}^{-1}$, respectively. These results suggest that, given proper scaling methods,

biometric measurements can provide useful estimates of GPP and R_{ECO} at sites unsuitable for eddy covariance, such as those with a small fetch, or uneven topography. Moreover, they provide much greater insight into the C dynamics of an old and relatively undisturbed forest, including sometimes neglected aspects such as CUE and NPP allocation.

ACKNOWLEDGMENTS

Many thanks to everyone who assisted with this work, in particular Michèle Taylor and NERC for the Upper Seeds meteorological data collected under the ECN program, Dave McNeil for installing and maintaining the eddy covariance equipment, and Dr. Terhi Riutta and Earthwatch-HSBC volunteers for collecting and sorting the autumn 2008 leaf litter. KMF was supported by a NERC Studentship at Oxford University and the Centre for Ecology and Hydrology. Some manuscript editing took place whilst KMF was at SLU, Umeå, Sweden, funded by a Kempe Foundation stipend. YM is supported by the Jackson Foundation, the Oxford Martin School, and an Advanced Investigator Award of the European Research Council. Thorough, constructive comments by reviewers improved this manuscript and are greatly appreciated.

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