

Abstract

There exist very few comprehensive descriptions of the productivity and carbon cycling of forest ecosystems. Here we present a description of the components of annual Net Primary Productivity (NPP), Gross Primary Productivity (GPP), autotrophic and heterotrophic respiration, and ecosystem respiration (R_{ECO}) for a temperate mixed deciduous woodland at Wytham Woods in southern Britain, calculated using “bottom-up” biometric and chamber measurements (leaf and wood production and soil and stem respiration). These are compared with estimates of these parameters from eddy-covariance measurements made at the same site. NPP was estimated as $7.0 \pm 0.8 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$, and GPP as $20.3 \pm 1.0 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$, a value which closely matched to eddy covariance-derived GPP value of $21.1 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$. Annual R_{ECO} was calculated as $18.9 \pm 1.7 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$, close to the eddy covariance value of $19.8 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$; the seasonal cycle of biometric and eddy covariance R_{ECO} estimates also closely matched. The consistency between eddy covariance and biometric measurements substantially strengthens the confidence we attach to each as alternative indicators of site carbon dynamics, and permits an integrated perspective of the ecosystem carbon cycle. 37% of NPP was allocated below ground, and the ecosystem carbon use efficiency (CUE, = NPP/GPP) calculated to be 0.35 ± 0.05 , lower than reported for many temperate broadleaved sites.

1 Introduction

Forest carbon cycles are a topic of immense interest in the context of global environmental change, but to date there have been few comprehensive descriptions of the production, allocation and cycling of carbon within particular forest systems. To determine an ecosystem's productivity and respiration, its flux of CO_2 can be measured directly above canopy via eddy covariance, or as a summation of the individual cycle components; the individual production and respiration terms. Whilst the eddy

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covariance method has been successfully deployed in many ecosystems (Falge et al., 2002), providing continuous monitoring of the fluxes to and from the system, many sites are unsuitable for this method, having insufficient fetch or uneven topography that render micrometeorological approaches problematic. In such sites the measurement of individual components, such as stem growth, can be used, (with appropriate estimates for unmeasured variables if necessary) to quantify ecosystem productivity and respiration. Measuring individual components is also complimentary to the eddy covariance approach as it provides a far greater understanding of the system beyond total values of Gross Primary Productivity (GPP) and ecosystem respiration (R_{ECO}), allowing critical processes and their sensitivities to be identified. This is important for understanding how changes in factors such as climate, species composition and management may influence carbon dynamics at different sites, and how carbon dynamics may alter with changes in these factors.

Each method for measuring the contribution of individual components has associated errors and inaccuracies, in both the collection of data, or in scaling up to ecosystem scale. By comparing the magnitude and seasonality of the fluxes as measured by either method, potential sources of error can be identified, and to some extent quantified.

In this study we present monthly and annual data for the major components of productivity and respiration at a site of ancient semi-natural deciduous woodland in southern Britain. For each component an appropriate frequency of measurement was chosen to enable production of monthly estimates of carbon uptake or release, and so determine the effect of this system's seasonality on its annual carbon cycle. The seasonal nature of deciduous forests, with periods of dormancy and growth generally coinciding with changes in temperature and photoperiod, results in seasonal variation in the uptake and release of C by individual carbon cycle components during the year. Eddy covariance data were collected over the same period and provide an independent data set on the seasonality and magnitude of whole-system C flux (companion paper by Thomas et al., 2010).

There have been very few comprehensive descriptions of forest carbon cycles, using both “bottom-up” biometric and flux chamber measurements and “top down” eddy covariance methods (Curtis et al., 2002; Ehman et al., 2002; Griffis et al., 2004; Malhi et al., 2009) and this is the one of the first, to our knowledge, which presents detailed biometric measurements of productivity and respiration, and compares annual totals with eddy covariance data, for a temperate mixed deciduous forest site in Europe (Valentini et al., 1996). Our aims here are 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 respiration and their partitioning between various components.
- (3) Compare these biometric and chamber estimates of site productivity and respiration with independent eddy covariance measurements, and check for completeness in our description of the forest carbon cycle.

2 Methods

This paper draws on and integrates work described in companion papers (based on Fenn 2010; PhD Thesis), focussed on intensive measurements at this study site, over the period 2005–2008. These papers explore in detail our measurements of total and partitioned soil respiration, (Fenn et al., 2010), tree stem respiration and growth, and allocation of above ground primary productivity. The methods involved for these components will therefore not be covered in full detail here, but sufficient detail on methods and additional methods needed to fill in other C cycle components, and to scale up to plot level, are given.

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2.1 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). The site is divided into 25 subplots, 20 m×20 m, used to structure the placement of multiple measurement points for some methods. The site is ancient semi-natural woodland, UK National Vegetation Classification community W8 *Fraxinus excelsior* – *Acer campestre* – *Mercurialis perennis* woodland (Hall et al., 2004). The term “ancient woodland” means that the site has had a continuity of tree cover though recorded history (since approximately 1600, Peterken and Game, 1984). It has however been managed throughout this periods, including by timber removal and the species composition has changed over time (Morecroft et al., 2008). Over approximately the last 40 years the plot and most of the surrounding area in the flux footprint have been subject to minimum intervention with no silvicultural management.

The majority of trees (>10 cm diameter at breast height, dbh) in the study plot are sycamore *Acer pseudoplatanus* 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. The ground vegetation is predominantly dogs' mercury *Mercurialis perennis* L. with stinging nettle *Urtica dioica* L., bluebells *Hyacinthoides non-scripta* L. Chourad ex Rothm. in spring and pendulous sedge *Carex pendula* Huds.

The soil is mostly a stagni-vertic cambisol, derived from clay, with areas of arenihaplic luvisols and calcaric cambisols (FAO/UNESCO classification from Beard 1993). Meteorological data have been recorded on site since 1992 as part of the UK Environmental Change Network (ECN) monitoring programme (Morecroft et al., 1998). For the period 1993–2008 mean annual precipitation was 725.8 mm, mean annual temperature was 10.1 °C, mean air temperature of the warmest month (from hourly mean temperatures) was 16.7 °C for both July and August, and mean coolest month temperature (from hourly mean temperatures) was 4.4 °C (December).

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2.2 Wood production

Tree growth was measured for a subsample of trees (280 out of 466) over 10 cm dbh. Monthly measurements of dbh change were taken from dendrometer bands (adapted from Keeland and Young, 2005) using 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 3 February 2007 and last on 12 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.

Dendrometer measurements were scaled up to estimates of tree aboveground dry woody biomass (ABW, kg) using species-specific allometric equations (Eqs. 1–3) for *A. pseudoplatanus*, *F. excelsior* and *Q. robur*, where c is trunk circumference (cm) at breast-height.

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

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

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

These equations were calculated by Bunce (1968) for trees harvested at Meathop Wood, a site similar to Wytham in species composition. Mean coefficients from these three equations were used for the remaining species (contributing 8% of the individuals in the plot) which were almost all small trees.

ABW was converted to mass of carbon by taking the fractional carbon content of dry wood to be 0.469 ± 0.008 , 0.491 ± 0.005 and $0.474 \pm 0.005 \text{ g C g}^{-1}$ ABW for *A. pseudoplatanus*, *F. excelsior* and *Q. robur*, respectively, from data obtained at Wytham (Butt et al., 2009), and the mean value of $0.477 \pm 0.003 \text{ g C g}^{-1}$ ABW for the remaining species.

Mean biomass increment per tree of *A. pseudoplatanus*, *F. excelsior*, *Q. robur*, and the

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remaining species grouped together, was then calculated, and multiplied by the number of individuals of each species, to produce the plot-level estimate of annual wood production ($\text{Mg C ha}^{-1} \text{ yr}^{-1}$).

2.3 Root production

5 Fine root production ($\text{NPP}_{\text{fineroot}}$) was not directly measured, but rather estimated using a mass balance approach, where belowground C input (root mortality and material carried down from the litter layer) is assumed equal to the belowground carbon outputs (SOM respiration, and dissolved organic C in water, DOC), plus any change in soil C stocks:

$$10 \text{NPP}_{\text{fineroot}} + (\text{NPP}_{\text{litter}} \cdot F_{\text{LITTER}}) + (M_{\text{AG}} \cdot F_{\text{CWD}}) + M_{\text{BG}} = R_{\text{SOM}} + (F_{\text{DOC}} + \Delta C) \quad (4)$$

Equation (4) can be rearranged as in Eq. (5), to allow calculation of $\text{NPP}_{\text{fineroot}}$ from the other components.

$$\text{NPP}_{\text{fineroot}} = R_{\text{SOM}} - (\text{NPP}_{\text{litter}} \cdot F_{\text{LITTER}}) - (M_{\text{AG}} \cdot F_{\text{CWD}}) - M_{\text{BG}} + F_{\text{DOC}} + \Delta C \quad (5)$$

15 R_{SOM} is the heterotrophic respiration of the soil excluding the litter layer and was directly measured through a soil partitioning experiment (see below). $\text{NPP}_{\text{litter}}$ is the canopy (leaves, flowers and fruit) litterfall and F_{LITTER} is the fraction of this litter entering the soil (as opposed to being respired in situ in the litter layer). M_{AG} is the above-ground biomass lost in tree mortality in $\text{Mg C ha}^{-1} \text{ yr}^{-1}$, the mean production of above-ground Coarse Woody Debris (CWD) over the four years of this study, and F_{CWD} is the fraction of this CWD entering the soil (as opposed to being respired in situ in the CWD). M_{BG} is the below ground biomass lost in tree mortality, all of which enters the soil. Here we assume that the dissolved organic C leakage (F_{DOC}) and the net change in soil stocks (ΔC) are both zero, or at least negligible compared to the overall internal carbon cycle of the forest.

25 The terms F_{litter} and F_{CWD} are poorly quantified. For lowland Amazonian forests, Malhi et al. (2009) estimated F_{CWD} as 0.24 ± 0.15 . It is unclear how these value

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extrapolates to a temperate context, but it seems very likely that more than half the litter and CWD is broken down by in situ heterotrophic decomposition (by macrofauna, fungi and bacteria) rather than transport to the soil organic matter matrix. Hence we assume $F < 50\%$ and apply broad error bars to reflect the high uncertainty, i.e. F_{litter} and $F_{\text{CWD}} = 0.25 \pm 0.25$. The value of F_{litter} only has a moderate influence on our overall NPP estimates and the value of F_{CWD} has almost negligible influence as the input of CWD is so small at this site.

Coarse woody root production ($\text{NPP}_{\text{coarse root}}$) was taken to be 20% of above ground woody production (Giardina and Ryan, 2002), equal to the ratio of below-ground to above-ground woody biomass typically found in temperate deciduous forests, with a conservative error estimate of $\pm 15\%$, i.e. 0.20 ± 0.15 . Similarly, we assume $M_{\text{BG}} = (0.20 \pm 0.15) \times M_{\text{AG}}$.

2.4 Leaf production

Annual leaf production was determined by catching subsamples of the leaves falling in autumn in litter traps, and scaling up to the 1 ha plot. A 0.25 m^2 litter trap was placed in each of the 25 subplots in October 2006; they remained in place to catch leaves falling in the autumns of 2007 and 2008. Traps were emptied every two weeks; the leaves were sorted into species before drying for 48 h at $75\text{--}80^\circ\text{C}$ and weighing.

The Specific Leaf Area (SLA; area/mass) for each species were determined by measuring the leaf area of several subsamples of each species' leaf litter, prior to leaf drying and weighing (Scion Image, Maryland, USA). The LAI of each species per sample session could then be calculated, and the total LAI of each species estimated by reverse cumulative summing of the litter caught (i.e. summing the shed LAI over preceding weeks.)

The seasonality of leaf production and canopy decline was recorded using the optical LAI-2000 method (LiCor, Lincoln, NE, USA). In autumn measurements were taken on the same days as litter traps were emptied to allow calibration of the optical method with actual leaf area measurements. The calibrated peak LAI value ($\text{m}^2 \text{ m}^{-2}$) was taken to

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represent the total amount of leaves collected in the traps, and the relationship between the two used to estimate leaf production in the preceding months. This assumed that no new leaves were produced once peak canopy cover had been achieved and that only a very small amount of leaf material had been lost to herbivory, or that the two balance. *Q. robur* is known to have a second flush of leaves “Lammas leaves”, but the consistency of our summer LAI values after May suggests that this assumption is reasonable.

2.5 Leaf respiration

Night-time measurements of leaf respiration were made for sun and shade leaves of sycamore and oak at this site in a previous study (Stokes, 2002). These measurements were used in Eq. (6), to estimate hourly leaf respiration at each hour t (R_t , $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ h}^{-1}$) for the study plot during 2008. Night time leaf respiration (R_n , $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) is calculated as from Eq. (7).

$$R_t = (R_n \cdot Q_{10})^{[(T_2 - T_1)/10]} \quad (6)$$

$$R_n = \{F_{\text{sun}}[(A_{\text{sun}} + Q_{\text{sun}}/2)]\} + \{F_{\text{shade}}[(A_{\text{shade}} + Q_{\text{shade}})/2]\} \quad (7)$$

T_1 is air temperature at time of measurement ($^{\circ}\text{C}$), T_2 is hourly mean temperature ($^{\circ}\text{C}$) at time t and Q_{10} is assumed to be 2 (i.e. respiration rate doubles for every 10°C increase in air temperature). F_{sun} and F_{shade} are the fraction of sun and shade leaves in the canopy. Using a sun-leaf SLA of 10 or less (Stokes, 2002) and the distribution of oak leaf SLA in sun-exposed and shaded layers of the canopy (Roberts et al., 1999), F_{sun} was estimated to be 39% and F_{shade} 61%. A_{sun} and A_{shade} , and Q_{sun} and Q_{shade} are the measured values of night-time leaf dark respiration ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) of *A. pseudoplatanus* sun and shade, and *Q. robur* sun and shade leaves, respectively.

The daytime respiration rate (R_d) cannot simply be assumed to be equal to the temperature-corrected night respiration (R_n); light inhibits dark respiration (Sharp et

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al., 1984), so R_n must be adjusted for the hours of daylight. The degree of this inhibition varies with species, leaf age, level of irradiance and temperature (Villar et al., 1995; Atkin et al., 2000). A previous study estimated the degree of inhibition of dark respiration in a deciduous shrub (*Lepechinia fragans*) as $61.8 \pm 4.7\%$ (i.e. $R_d = 38.2 \times R_n$, Villar et al., 1995); this value was used here, as to our knowledge, no data exist for the species in this study. Malhi et al. (2009) applied photoinhibition of 67% for daytime leaf respiration of tropical trees. Night was defined as the hours when total solar radiation $< 20 \text{ W m}^{-2}$, as measured at the Upper Seeds meteorological station.

Once the adjustments for photoinhibition were made to daytime hourly leaf respiration, hourly values could be summed to produce monthly and annual estimates of total leaf respiration. Our assumptions around leaf respiration (the degree of photoinhibition, the fraction of sun and shade leaves, the fraction of leaves in each species, and the temperature sensitivity) all contain potential systematic uncertainty. To be conservative we apply a large uncertainty bound of 50% for the leaf respiration estimates and propagate these through our calculations. Leaf respiration is the largest source of uncertainty in our “bottom-up” quantification of the carbon cycle; it is however based on in situ measurements of the same species. The mean of the standard errors reported by Stokes (2002) for other photosynthesis measurements of the same species was $\pm 40\%$.

2.6 Stem respiration

Monthly stem respiration measurements from eight *F. excelsior* and eight *A. pseudoplatanus* trees were taken from April to November 2008 (Fenn et al., 2010). The chosen trees had diameters at breast height (dbh) ranging between 22.0–40.6 and 16.3–60.1 cm for the two species, respectively, representing the range of tree size of these two species at this site.

Measurements were taken at fixed points on each tree, using PVC “collars” (50 mm high \times 65 mm diameter PVC pipe, Flowline, Marley, Maidstone, UK) attached for the duration of the study, using non-setting putty (Plumbers’ Mait, Evostik, Bostik Ltd,

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Leicester, UK) to allow change in tree diameter. The collars were fixed on south-facing areas of stem with no wounds or growing/dormant buds, which were flat enough to accommodate the collars and as close as possible to breast height (1.3 m).

Respiration measurements were made using a portable infra-red gas analysis system (EGM-4 and SRC-1 soil chamber, PP Systems, Hitchin, UK), with an adaptor custom-made to fit the collars. To maximise comparability between measurement sessions, all measurements were taken between 09:00 and 13:00 GMT.

Respiration rates in $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ were scaled up to plot-level estimates of monthly and annual stem respiration ($\text{Mg C ha}^{-1} \text{ y}^{-1}$) using Eq. (8) (Whittaker and Woodwell, 1967), which calculates tree stem and branch surface area (S , cm^2) from stem and branch woody biomass (ABW, g).

$$\log_{10} S = 1.2980 + 0.8259 \log_{10} \text{ABW} \quad (8)$$

This equation was derived from the relationship between stem and branch surface area and woody biomass in woody temperate species (*Quercus alba*, *Q. coccinea*, *Q. ilicifolia*, *Liriodendron tulipifera*, *Pinus rigida*, *P. echinata*, *Rhododendron maximum*, *Gaylussacia baccata* and *Vaccinium vacillans*), harvested at the Brookhaven National Laboratory and Oak Ridge National Laboratory centres, US. No dbh data were collected in January and February 2008, so zero growth was assumed for these winter months and the March 2008 ABW values were used for January and February. The Stem Area Index (SAI) of this plot was calculated to be $1.94 \text{ m}^2 \text{ m}^{-2}$.

The calculated stem area for each tree in each month was then multiplied by the stem CO_2 efflux rate for that month. For *A. pseudoplatanus* and *F. excelsior* their species-specific stem efflux rates were used, for all other species a mean of these rates was used. These rates were summed to produce monthly and annual estimates of stem respiration (R_{STEM}).

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2.7 Soil respiration

Soil CO₂ efflux measurements were made using a portable infra-red gas analysis system and soil CO₂ efflux chamber (PP Systems, Hitchin, UK) modified with a custom-made adaptor to fit soil “collars” used as fixed measurement points. One measurement was carried out per subplot, per session, except in the four corners of the plot where three were taken to check for measurement consistency. The mean of these replicates was taken with each of the other individual measurements to generate the plot mean CO₂ efflux rate, used in the subsequent analysis. Soil respiration measurements were made from 13 February to 23 November 2007, and 1 April to 14 December 2008. To approximate the efflux in the missing winter months the mean of all measurements made on 30 November 2006 and 13 February 2007 were used for January 2007, and of 23 November and 1 April 2008 for December 2007 to April 2008. As winter efflux rates are low compared to those in summer it is hoped that any inaccuracies arising from this estimation method have little effect on annual Reco. Mean monthly total soil respiration used all measurements taken within each month, excluding the extra corner measurements. Surface litter was removed prior to efflux measurements as the amount of litter varied seasonally over the year.

We partitioned total soil CO₂ efflux into root and rhizosphere, mycorrhizal, and SOM components using micromesh bags (Plastok Ltd, Birkenhead, UK) (Moyano et al., 2007, 2008; Heinemeyer et al., 2007) 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, $P=0.38$). The bags enclosed a core of soil in-situ, from which CO₂ efflux measurements were repeatedly taken throughout the 2008 growing season (Fenn et al., 2010). Two mesh sizes were used producing three ‘partitions’ of soil CO₂ efflux. From these partitions, the relative contributions of heterotrophic respiration of soil organic matter (R_{SOM}), mycorrhizas (R_{MYC}) and roots and their rhizosphere (R_{RRHIZ}) to total soil CO₂ efflux (R_{SOIL}) can be determined by subtraction. Both mesh sizes allow the passage of water.

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Mesh bags were installed in January 2008, to allow the soil within them to equilibrate with the surrounding soil before the growing season brought an increase of soil respiratory activity. CO₂ efflux measurements were made approximately every two weeks between 15 April 2008 and 26 November 2008.

Mean soil temperature over 0–150 mm depth (Digital Waterproof Thermometer, Barnstead International, Dubuque, 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.

2.8 Leaf decomposition

Litter bag estimates of monthly leaf litter decomposition were made at this site, following the method of Robertson et al. (1999), to determine the seasonal trend of litter C loss. Over an extended period it is however assumed that litter production and decomposition are in equilibrium. Therefore, using the mass balance approach, the amount of litter C entering the soil annually (S_{LITTER}) can be estimated, using F_{LITTER} estimated as 25%±25% of fallen litter ($\text{NPP}_{\text{LITTER}} = \text{NPP}_{\text{LEAF}} + \text{NPP}_{\text{REPRODUCTIVE}}$, as for root production). The C released to the atmosphere from decompositional respiration of the litter (R_{LITTER}) can also then be estimated, as $\text{NPP}_{\text{LITTER}} - S_{\text{LITTER}}$.

2.9 Eddy covariance estimates of GPP and R_{ECO}

Eddy covariance data collection at the site began in June 2007; the data used here are from this date to 31 December 2008. Details of the analysis methods used and results are described in detail in the companion paper by Thomas et al. (2010). The instrumentation is 25 m above the ground on a tower located close to the centre of the plot. Thomas et al. (2010) estimated GPP and R_{ECO} (and Net Ecosystem Productivity, NEP) from the data using the CarboEurope partitioning tool (Reichstein et al., 2006), with GPP being $\text{NEP} - R_{\text{ECO}}$.

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The eddy covariance derived estimates of GPP and R_{ECO} were then compared with those produced using the biometric and chamber measurements, where the biometric estimate of GPP is calculated as in Eq. (9).

$$\text{GPP} = R_{\text{AUTO}} + \text{NPP}_{\text{total}} \quad (9)$$

5 This assumes that carbon gain through photosynthesis equals carbon use through respiration of NPP. It assumes that there is negligible interannual variation in internal storage of photosynthate, in the form of non-structural carbohydrates.

3 Results

3.1 NPP

10 The largest component of productivity is leaf production, accounting for over half of total NPP (Table 1). Whilst deciduous tree leaf production in any given year requires the remobilisation of resources stored in the previous growing season, this production is here allocated to the year in which the leaves are produced and so that year's NPP. The majority of NPP is above-ground; the production of leaves, wood and reproductive
15 structures, contribute approximately 60% of total NPP. A small amount of trunk expansion occurs during the months of canopy production, but significant wood production begins once the canopy is established and photosynthesising, increasing to a peak in August then decreasing through autumn (Fig. 1).

3.2 Ecosystem respiration

20 The greatest component of R_{ECO} is R_{STEM} , releasing $8.8 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ in 2008 (Table 2), $46.8 \pm 1.3\%$ of total R_{ECO} . R_{LEAF} is the second greatest contributor over the whole year, only producing more Mg C than R_{STEM} during August, the month of highest wood production rate, when R_{STEM} itself drops slightly. R_{STEM} also continues throughout the winter months of dormancy, at a reduced rate, as maintenance respiration. Both

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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 cycle of R_{ECO} produced when the components are combined (Fig. 2a) closely matches the independent estimate of R_{ECO} estimate produced by eddy covariance (Fig. 2b), except in September, when there is a discrepancy between them of 1.19 Mg C.

3.3 Carbon cycle of the forest plot

The above-ground components are the greatest contributors to both productivity and respiration, as NPP_{leaf} , NPP_{wood} and R_{STEM} , R_{LEAF} , and R_{LITTER} , respectively (Table 3). Of these, leaf production contributes the greatest portion of $\text{NPP}_{\text{total}}$ (40.2%), but stem respiration the greatest portion of R_{ECO} (45.6%). The Carbon-Use Efficiency (CUE) of this site, the proportion of GPP used for biomass production rather than respiration, is 0.35 ± 0.05 .

4 Discussion

4.1 Productivity

We estimate the annual NPP of this system at $7.0 \pm 0.8 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$. Studies at temperate deciduous sites using comparable inventory methods are rare, but Ohtsuka et al. (2002) estimated NPP to be $5.7 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ for a site in Japan using a similar methodology to this study. Both sites have been disturbed by some tree removal in the past and now contain secondary growth, whilst remaining as broadleaved deciduous forest. Compared to NPP values reported for managed temperate deciduous forests of $17.7 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ (Curiel Yuste et al., 2005a), $6.3 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ (LeMaire et al., 2005) and 2.7 and $3.8 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ (for two consecutive years; Ehman et al., 2002), this demonstrates that relatively unmanaged woodlands, such as Wytham, can also be quite productive.

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The clear monthly data on woody productivity demonstrate the value of this scale of dendrometer dbh change measurements. The ability of this simple method to detect monthly changes in the growth of these temperate species enabled us to gain clear insight into the seasonality of wood production at this site. Combining dendrometer data with LAI measurements showed how the production of leaves, concentrated in late spring, was immediately followed by an increase in trunk growth, peaking in August.

The production of leaves in deciduous trees requires the reallocation of resources acquired and stored in the previous growing season. In this system leaf production is the greatest component of total NPP, contributing 38% (where leaf production is allocated to the year in which they appear, rather than the previous year), revealing the high level of internal C-cycling within these trees. Stokes et al. (2010) used carbon isotope ($^{13}\text{C}:^{12}\text{C}$) ratios in oak and sycamore leaves at Wytham to show that much of this internal cycling is likely to take place within individual branches, as isotopic signatures of sun and shade branches are maintained.

Here 36% of total NPP was allocated belowground, in the centre of the range of previous findings of 15.2–55.1% for a temperate *Quercus* and *Fraxinus* forest (Tateno et al., 2004), 54% for a regenerated mixed deciduous temperate site (Newman et al., 2006) and 27% in a Siberian *Larix* forest. This is a substantial component of NPP (particularly fine root production) that can be missed by traditional studies that have focussed on more easily measurable above-ground components.

4.2 Respiration

The seasonality of the biometric and tower estimates of R_{ECO} was remarkably close for the majority of months. There was a discrepancy in September of 1.19 Mg C, which 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. This is a period of transition at the end of the tree growing season and it is possible that the spot 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 differs from that at other locations which have been measured, with R_{STEM} being the greatest contributor here, as opposed to R_{SOIL} at other sites (Table 4). The very high levels of stem respiration are noteworthy and unusual, particularly given the relatively low values of NPP_{STEM} . Additionally the CUE of this site is 0.35 ± 0.05 , at the low end of the 0.34–0.83 reported for a range of temperate deciduous forests (DeLucia et al., 2007). This suggests that there is a higher level of autotrophic respiration, likely R_{STEM} in particular, compared to production at Wytham, compared to other sites. This may result from higher winter respiration rates as a result of the relatively warm winters associated with the oceanic climate at this site.

Both R_{ECO} and GPP rely on accurate measurements of a large number of parameters, and their accurate up-scaling, and further characterisation of the way these parameters vary between ecosystems would be useful.

5 Conclusions

We have demonstrated the feasibility of quantifying many of the components of the forest carbon cycle within a coherent framework. The close agreement between not just the annual but also monthly R_{ECO} estimates from biometric and eddy covariance methods give us confidence in the robustness and suitability of both the methods used and increases confidence that no large components of the carbon cycle have been missed. There is also a very close agreement between the tower and biometric estimates of GPP; 21.1 and $20.3 \pm 1.0 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$, respectively. These biometric methods can therefore be used with greater confidence at sites unsuitable for eddy covariance, such as those with a small fetch, or uneven topography and in any case provide much greater insight into the carbon dynamics of the forest.

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covariance equipment, and Terhi Riutta and Earthwatch-HSBC volunteers for collecting and sorting the autumn 2008 leaf litter. KMF's D. Phil studentship was funded by the Natural Environment Research Council through the Centre for Ecology and Hydrology.

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Table 1. Annual NPP of each measured component for 2007 and 2008, calculated below-ground components for 2008, plot total annual NPP for 2008.

Component (Mg C ha ⁻¹ yr ⁻¹)	2007	2008
NPP coarse wood	1.25±0.11	1.65±0.16
NPP leaf	1.84±0.15	2.40±0.20
NPP reproductive	0.32±0.03	0.37±0.07
NPP above-ground	3.41±0.19	4.42±0.26
NPP coarse root	0.25±0.19	0.33±0.25
NPP fine root	–	2.29±0.76
NPP below-ground	–	2.62±0.80
NPP total	–	7.04±0.84

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Table 2. Annual respiration of each measured component, plot total annual R_{ECO} Biometric, and eddy covariance estimated R_{ECO} Tower. R_{RRHIZ} , R_{MYC} and R_{SOM} sum to produce R_{SOIL} .

Respiration component (Mg C ha ⁻¹ yr ⁻¹)	2007	2008
R_{RRHIZ}	–	0.9±0.2
R_{MYC}	–	0.3±0.1
R_{SOM}	–	3.0±0.3
R_{SOIL}	4.1±0.0	4.10±0.09
R_{STEM}	8.9±0.1	8.79±0.00
R_{LEAF}	–	4.9±0.1
R_{LITTER}	–	2.08±0.69
R_{CWD}	–	0.03±0.01
R_{AUTO}	–	13.87±0.55
R_{HET}	–	5.41±0.76
R_{ECO} Biometric	–	18.9±1.7
R_{ECO} Tower	–	19.8

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Table 3. Above-, below-ground and total NPP, the ratio of below- to above-ground NPP, proportions of NPP allocated below- and above-ground, GPP and CUE_{eco}.

Component (Mg C ha ⁻¹ yr ⁻¹)	2008
NPP above-ground	4.42±0.26
NPP below-ground	2.62±0.80
NPP total	7.04±0.84
NPP _{bg} /NPP _{ag}	0.59±0.18
NPP _{bg} /NPP _{total}	0.37±0.12
NPP _{ag} /NPP _{total}	0.62±0.08
GPP	20.27±1.00
CUE _{eco} (NPP _{total} /GPP)	0.35±0.04

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Table 4. Percentage contribution of each respiration component to total R_{ECO} , in this and previous studies. R_{SOIL} and R_{DECOMP} for this site are combined for ease of comparison with the other studies.

R_{ECO} (Mg C ha ⁻¹ yr ⁻¹)	R_{SOIL} (%)	R_{STEM} (%)	R_{LEAF} (%)	Biome	Dominant species	Source
18.9±1.7	33.0±4.5	46.8±1.3	20.2±2.7	Temperate	<i>A. pseudoplatanus</i>	This study
13.8±0.4	80.9±0.2	11.1±0.2	8.0±0.1	Temperate	<i>Populus tremuloides</i> Michx.,	Calculated mean of 1999–2002 data from Bolstad et al. (2004)
11.8±0.4	75.4±0.4	19.9±0.4	4.8±0.1	Temperate	<i>A. saccharum</i> Marsh.	Calculated mean of 1999–2002 data from Bolstad et al. (2004)
9.61	73.2	11.8	15.1	Boreal	<i>P. tremuloides</i> Michx., <i>P. balsamifera</i> L.	Griffis et al. (2004)
9.1±1.15	67	–	–	Temperate	<i>Quercus robur</i> , <i>Pinus sylestris</i> L.	Curiel Yuste et al. (2005b)

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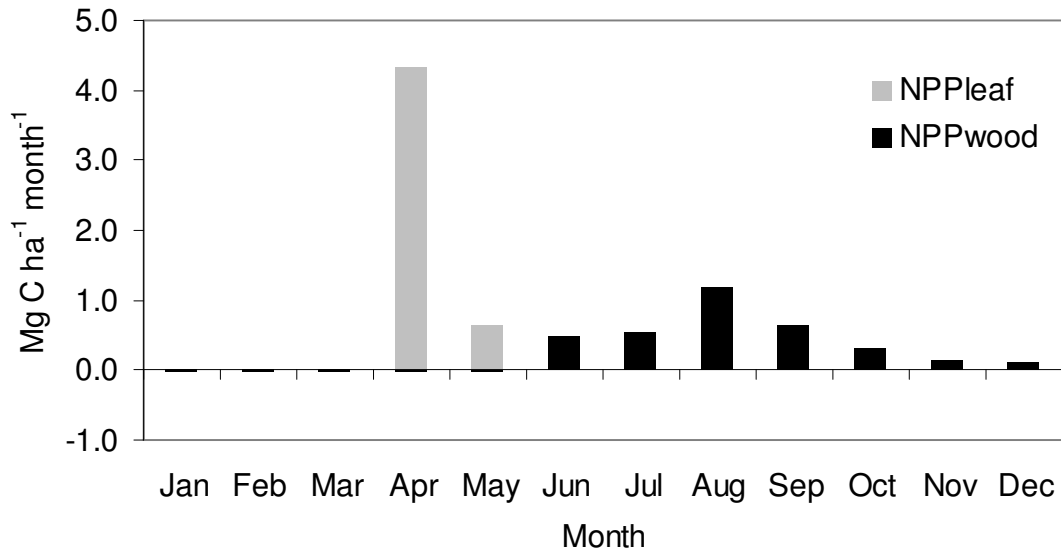



Fig. 1. Seasonality of leaf and wood production ($\text{Mg C ha}^{-1} \text{ month}^{-1}$). Grey bars indicate leaf production, black bars indicate above-ground woody biomass production.

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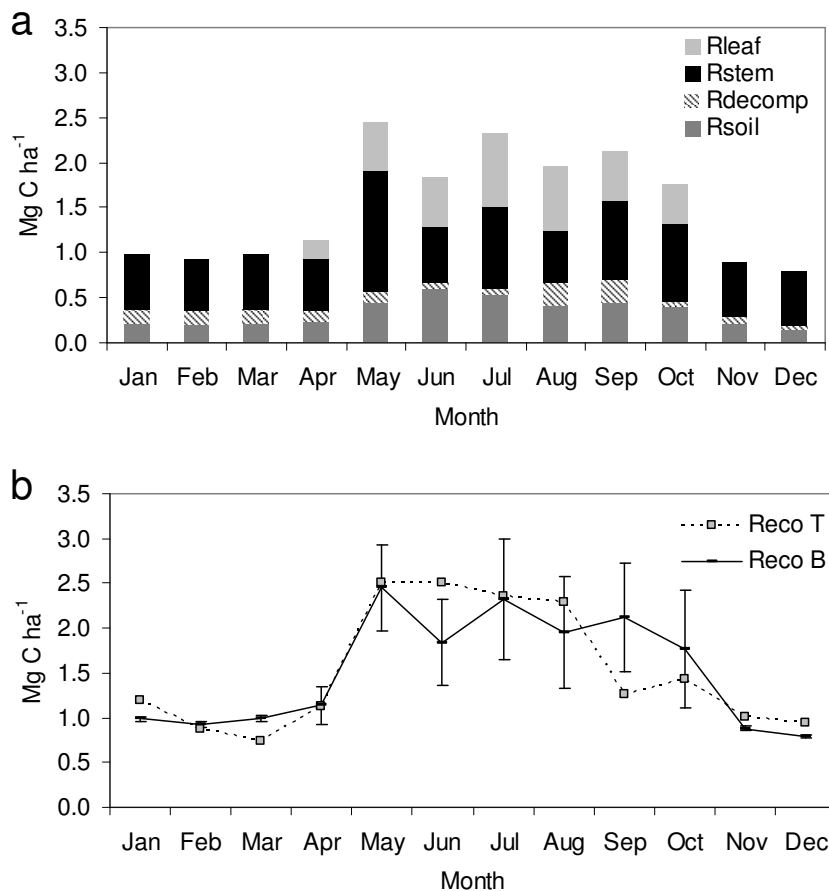


Fig. 2. (a) Contribution of each R_{ECO} component, per month, for 2008. (b) Comparison of biometrically calculated 2008 R_{ECO} with that derived from eddy covariance estimates. R_{litter} and R_{CWD} are not included as they cannot be estimated on a monthly basis.

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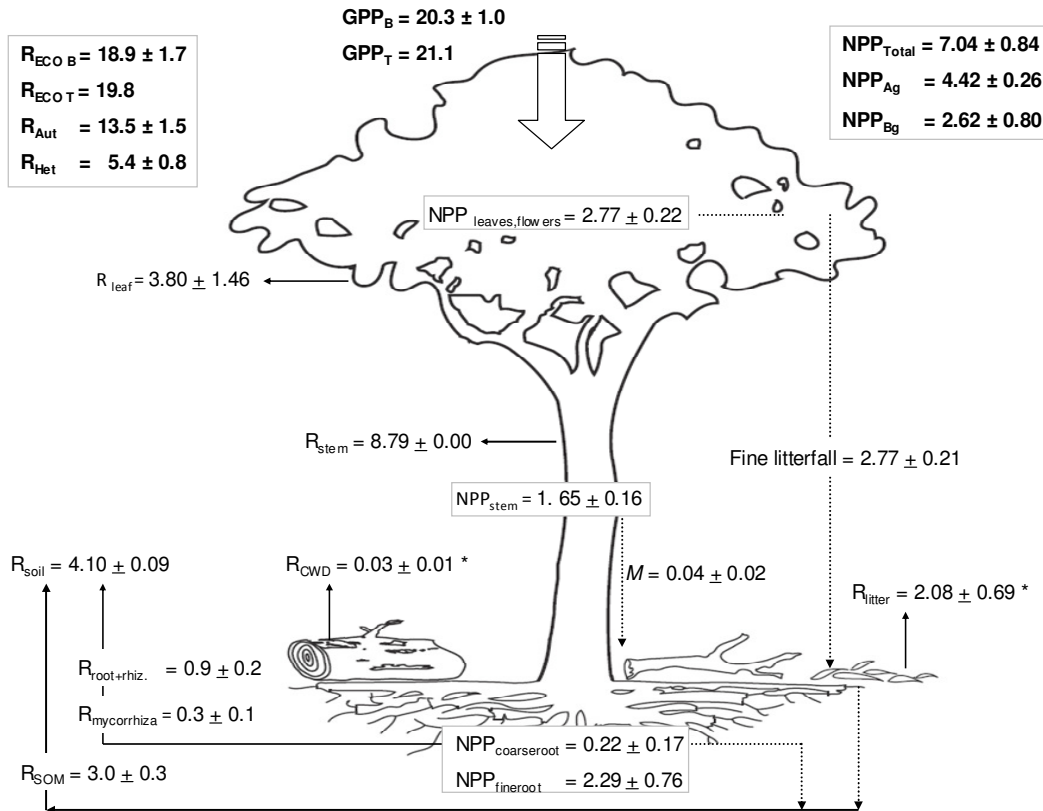


Fig. 3. Illustration of the carbon cycle of the site, constructed from the measured components. All soil respiration components are treated as heterotrophic respiration as root and rhizosphere contributions could not be separated. * indicates components calculated using mass balance, rather than directly measured.

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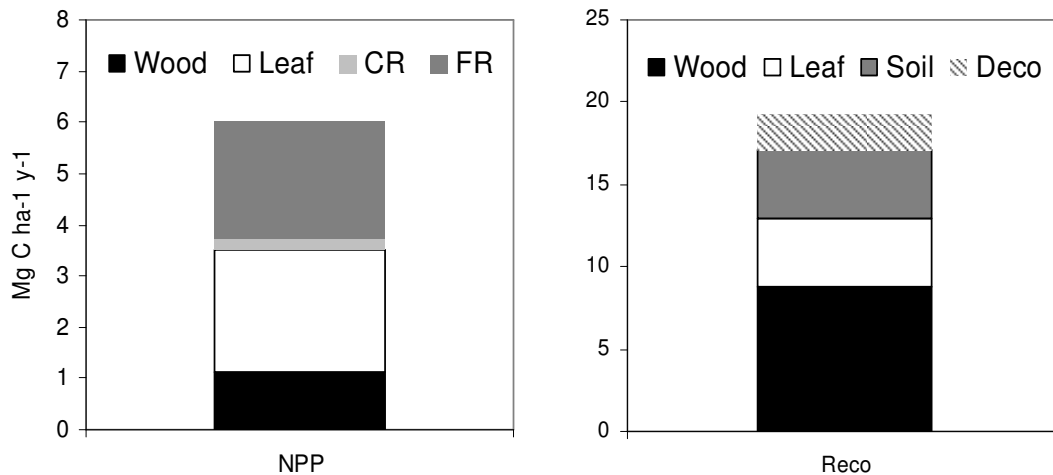


Fig. 4. Relative contributions of each component measured to NPP or R_{ECO} .

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