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Effects of management thinning on CO₂ exchange by a plantation oak woodland in south-eastern England

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Abstract

Forest thinning, which removes some individual trees from a forest stand at intermediate stages of the rotation, is commonly used as a silvicultural technique and is a management practice that can substantially alter both forest canopy structure and carbon storage. Whilst a proportion of the standing biomass is removed through harvested timber, thinning also removes some of the photosynthetic leaf area and introduces a large pulse of woody residue (brash) to the soil surface which potentially can alter the balance of autotrophic and heterotrophic respiration. Using a combination of eddy covariance (EC) and aerial light detection and ranging (LiDAR) data, this study investigated the effects of management thinning on the carbon balance and canopy structure in a commercially managed oak plantation in the south-east of England. Whilst thinning had a large effect on the canopy structure, increasing canopy complexity and gap fraction, the effects of thinning on the carbon balance were not as evident. In the first year post thinning, Net Ecosystem Exchange (NEE) was unaffected by the thinning, suggesting that the better illuminated ground vegetation and shrub layer partially compensated for the removed trees. NEE was reduced in the thinned area but not until two years after the thinning had been completed (2009); initially this was associated with an increase in ecosystem respiration (R_{eco}). In subsequent years, NEE remained lower with reduced carbon sequestration in fluxes from the thinned area, which we suggest was in part due to heavy defoliation by caterpillars in 2010 reducing GPP in both sectors of the forest, but particularly in the east.

1 Introduction

In England, woodlands cover 10.0 % of the land surface area, with the majority (0.78 Mha) comprising broadleaved woodland (Forestry Commission, 2013). The total carbon stock in the forest biomass was estimated to be 105.4 MtC in 2011 (Forestry Commission, 2014), with 27.7 and 77.7 MtC in conifer and broadleaved woodlands

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areas. For this study, neither of these approaches were available, and so the area and extent of the thinning operation was deliberately manipulated so that the EC tower was sited near to the line dividing the treatment and control portions of the forest.

Assessing the impacts of management thinning on the Net Ecosystem Exchange (NEE) of a forest stand is further complicated because NEE is the small difference between ecosystem respiration (R_{eco}) and Gross Primary Productivity (GPP), both of which are much larger components; a small shift in the balance between these will therefore have a large effect on NEE. Furthermore, the ways R_{eco} and GPP are affected by thinning will differ; for example, thinning changes the canopy density, altering the soil temperature and moisture conditions (e.g. Tang et al., 2005; Olajuyigbe et al., 2012) and affecting the soil component of R_{eco} . Vesala et al. (2005) found that whilst there was no reduction in the size of the carbon sink of a boreal Scots pine (*Pinus sylvestris* L.) stand in Finland following thinning, increases in ground vegetation photosynthesis and heterotrophic respiration were offset by decreases in canopy GPP and in both above- and below-ground autotrophic respiration. Amiro et al. (2010) published a comprehensive study tracking changes in net ecosystem productivity (NEP) across a variety of different forest types following a range of disturbance events. All three conifer forests studied that were subjected to thinning showed relatively short-term impacts on the carbon balance following a decrease in NEP in the year of disturbance. Other studies in managed forests have shown that NEP rates are sustained following thinning of canopy trees (e.g. Granier et al., 2008), which is often attributed to increased growth by sub-canopy plants after dominant canopy trees have been removed (Moreaux et al., 2011; Dore et al., 2012). Many of these studies are concerned with coniferous forests with very different seasonal dynamics to the deciduous oak woodland found in much of lowland England.

Airborne light detection and ranging (LiDAR) is a remote sensing method capable of producing three-dimensional models of large areas of landscape with sub-metre accuracy and has been used to measure forest height for more than a decade (e.g. Yu et al., 2003). In recent years, its application in forest inventories has become com-

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mon practice, particularly in northern European countries, where the method is used to quickly cover large areas at a high spatial resolution (Næsset, 2004; Maier et al., 2006). Additionally, the ability to view the resulting data in a variety of ways removes the problems associated with illumination and shadowing seen with standard aerial photography. By carrying out airborne LiDAR surveys before and after a management thinning operation, it is possible to quantify the changes in the forest canopy structure.

The aim of this study was to examine the effects of management thinning on the factors determining the carbon balance of a plantation deciduous oak woodland in southern England. Our hypotheses were that the removal of pre-selected trees from the woodland during a thinning operation would lead to an initial reduction in GPP. As thinning also increases the amount of woody debris and other litter components on the forest floor, an increase in R_{eco} was also expected. Together, these changes would result in a large decrease of NEE during the immediate period after thinning, which would be followed by a recovery of NEE to pre-thin rates over a period of time, possibly several years, although we could not predict the timescale. The results here describe the changes in NEE and its components before and up to five years after the thin.

2 Materials and Instrumentation

2.1 Site description

The eddy covariance measurement site is located in the Straits Inclosure, Alice Holt Research Forest, UK ($51^{\circ}09' \text{N}$; $0^{\circ}51' \text{W}$), close to the Alice Holt Research Station in south-eastern England (Fig. 1a). The inclosure is a flat area with an elevation of 80 m above mean sea level; the surrounding landscape consists of mixed lowland woodland and both arable and pasture agricultural land. The whole 90 ha inclosure was planted in the 1820s with oak (Schlich, 1905) and then replanted in the 1930s. 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

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area (4.6 ha) 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). Prior to this study, the whole of the stand was previously thinned in 1995.

The climate regime is mild temperate oceanic, 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. Further site-specific details can be found in Wilkinson et al. (2012).

Between June and August 2007, the eastern half of the woodland (approx. 47.5 ha) was selectively thinned (Fig. 1a) using an “intermediate” thinning procedure, (see introduction) resulting in an open forest canopy with a uniform stand structure (Kerr and Haufe, 2011). Pre-selected trees (based on stem form and position within the canopy) were felled, de-limbed and sectioned using mechanical harvesters. The merchantable stem wood with a diameter > 7.0 cm was subsequently collected and transported to the forest roadside using a forwarder, before being removed from the forest by timber haulage lorries. This harvesting technique resulted in substantial disturbance to the understorey and shrub layer. Whilst all of the remaining woody debris was left on the site, some of it was collected and used to construct “brash mats” for machinery movement in order to minimise damage and compaction to the soil, especially in areas of heavy traffic. Mensuration surveys carried out after the thinning in 2009 (western half) and 2011 (eastern half) showed 453 and 354 trees ha⁻¹ respectively, a difference in stand density of approx 22 % (Table 1).

2.2 Micrometeorological measurements and flux calculations

Eddy covariance (EC) measurements of energy flux (sensible and latent heat), momentum, net ecosystem exchange (NEE) and water vapour flux have been made

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2.3 Flux data processing and treatment separation

Following the calculation of corrected NEE and in order to remove extreme spikes, which were assumed not to be biologically valid, a data filter was applied using an approach similar to that proposed by Papale et al. (2006) and Thomas et al. (2011). For each calendar year, NEE data were first split into positive or negative values. Positive values more 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 subsequently applied, which removed positive values more 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.

Thirty minute average flux data (including additional meteorological data such as air temperature, humidity and incident solar radiation (S_g)) were separated into two sectors according to wind direction: data that were collected when the wind direction was between 315° and 170° were classified as “east sector” (the area that was thinned in 2007), and data collected when the wind direction was between 170° and 315° were classified as “west sector” (unthinned area). Table 2 summarises the data availability after this classification into the two sectors. Thirty minute NEE fluxes for both sectors were subsequently gap filled using the marginal distribution sampling method Reichstein et al. (2005) to allow the calculation of annual totals, and partitioned into the component fluxes of R_{eco} and GPP using the on-line eddy covariance gap filling and partitioning tool (<http://www.bgc-jena.mpg.de/~MDIwork/eddyproc/index.php>). In brief, this uses the night-time fluxes and their response to temperature to estimate respiration during the day.

2.4 Model parameters

In order to examine changes in the physiological drivers of the carbon balance, original (quality controlled, but not gap-filled or flux partitioned) daytime and night-time 30 min average NEE data were separated and analysed independently.

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The temperature sensitivity of ecosystem respiration for each sector of the forest was determined using an exponential equation fitted to the average half hourly night-time NEE and air temperature for each corresponding period:

$$R_s = K_1 \exp(K_2 T_{\text{air}}) \quad (1)$$

5 where R_s is the night-time NEE and T_{air} is the night-time air temperature at 26 m. Data fitted to this function were limited to night-time condition only where the mean half hourly $S_g < 20 \text{ W m}^{-2}$ and the quality control flag calculated by EddyPro according to the Mauder and Foken (2004) method was equal to zero.

10 The relationship between summer (July and August) daytime NEE and S_g was modelled using a rectangular-hyperbolic function:

$$\text{NEE} = \left[\frac{(\varepsilon \cdot \text{NEE}_{\text{max}} \cdot S_g)}{(\varepsilon \cdot S_g + \text{NEE}_{\text{max}})} \right] + R_d \quad (2)$$

where NEE_{max} is the asymptotic CO_2 assimilation rate, ε is the incident quantum yield (initial slope of the light response curve), and R_d is respiration in the dark. Data fitted to the light response model were limited to periods where the mean half hourly $S_g > 15$ 20 W m^{-2} , air temperature was between 18–23 °C and the quality control flag (Mauder and Foken, 2004) was equal to zero.

2.5 LiDAR measurements and calculation of vegetation structure

20 The aerial photograph taken after thinning (Fig. 1a) and mensuration surveys revealed substantial spatial heterogeneity within the forest block and showed large differences in forest structure between the two sectors. Changes in canopy top height and gap fraction were assessed using airborne LiDAR surveys conducted over two flight campaigns for the whole of Alice Holt forest (800 ha) by the Unit for Landscape Modelling (ULM), (Dept. of Geography, University of Cambridge). The first was in early November 2006,

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prior to the thinning and the second in August 2009, two years after the thinning. Due to the mild autumn in 2006 both surveys were completed whilst the forest had a fully developed canopy. A LiDAR system (ALTM 3033, Optech Incorporated, Ontario, Canada) flown at an altitude of 1000 m above ground level and with a scan angle $\pm 15^\circ$ was used along a series of overlapping transects designed to cover the whole forest. The system combined a pulse rate of 33 kHz and an overlap of 50 % between swaths, resulting in a point density of 2 to 4 points m^{-2} , which was used to generate a virtual cloud of 3-D data points with an accuracy of ± 15 cm root mean square (RMS). The first and last pulse return data were used to generate a Digital Surface Model (DSM) which included the tree cover and a Digital Terrain Model (DTM) representing the ground surface. These data were provided by the ULM as raster elevation models with a 0.5 m cell size. By subtracting the DTM from the DSM using GIS software (ArcGIS 10, Esri, Redlands, California, USA), Canopy Height Models (CHM) for each survey were created. Furthermore, by subtracting the 2006 DSM from the 2009 DSM, a model of change between the two surveys was also created (Fig. 1b).

To allow a detailed analysis of the vertical change in forest height and gap frequency between 2006 and 2009, each CHM was converted to a 1 m cell size and then spatially split into a 1 ha grid. Canopy top height histograms (bin size = 50 cm) were calculated for each grid cell, based on the 10 000 values $hectare^{-1}$. Frequencies were then averaged for all the grid cells within each sector. Grid cells at the interface between the thinned and unthinned areas of the forest were excluded from the analysis, as were those cells that contained, either wholly or partially, areas of the surrounding agricultural land. All analyses were conducted using R software (R Development Core Team, 2011).

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3 Results

3.1 Climatic conditions

The prevailing wind direction at the site is from the south west, so more of the data come from periods when the wind is from the west (unthinned) sector (Table 2). As the meteorological conditions associated with easterly and westerly winds differ, the flux data recorded from the two sectors did not reflect the same meteorological conditions (Fig. 2). Mean canopy level annual air temperature (2004–2012) was slightly warmer when air flow was from the west sector (10.8 °C) than from the east sector (9.6 °C).

The mean diurnal course of air temperature over the bi-monthly winter periods of November–December and January–February were generally warmer when airflow was from the more usual west rather than the east. The largest difference in winter air temperature was observed in January–February 2012: a period of cold weather from the start of February, dominated by easterly conditions, persisted over the southern UK for about two weeks this was also associated with snowfall to parts of the region (Fig. 3a). Conversely, mean summer air temperatures (during daylight hours) were generally higher when airflow was from the east than from the west, as occurred in 2004. Incident solar radiation and relative humidity were generally very similar when air flow was from either sector (Fig. 2).

3.2 Variation in NEE, GPP and ecosystem respiration

The mean (not gap-filled) diurnal course of NEE (Fig. 3b) indicated that the forest generally acted as a CO₂ source for the bi-monthly periods of November–December, January–February and March–April, although in exceptionally warm and early springs such as 2007 the forest became a weak CO₂ sink for a few hours around noon. Both sectors of the forest were a strong CO₂ sink from May through to October, although there was considerable variation between years. In some periods, when temperature and insolation conditions were very similar for each sector, NEE patterns were also

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similar (e.g. May–June 2007, and March–April 2012). In other periods with similar temperature and insolation, NEE was different, for example, in July–August 2012.

The annual gap-filled totals of NEP and its component partitioned fluxes (R_{eco} and GPP) were calculated for both sectors of the forest (Fig. 4). Before the thinning the annual GPP was slightly higher (+6 %) in fluxes from the west than those from the east sector (mean difference 2004–2007 = $121.3 \text{ g C m}^{-2} \text{ yr}^{-1}$; SE 33.2). After the thinning, the difference increased (mean difference 2008–2012 = $238 \text{ g C m}^{-2} \text{ yr}^{-1}$; SE 88.6) and annual GPP was higher in the west sector in all years, apart from 2009. Heavy defoliation by caterpillars (Wilkinson et al., 2012) occurred in 2010 reducing GPP in both sectors of the forest, but particularly in the east. Prior to thinning the annual R_{eco} was similar in both sectors of the forest (mean difference 2004–2007 = $26.3 \text{ g C m}^{-2} \text{ yr}^{-1}$; SE 58.1). In the first year after thinning (2008) R_{eco} was slightly lower (−12 %) in the east than the west however, a year later, in 2009, R_{eco} increased substantially (+34 %) in the east compared to the west, but in subsequent years it dropped in the east (mean difference 2010–2012 = $80.0 \text{ g C m}^{-2} \text{ yr}^{-1}$; SE 56.0).

NEP was also generally larger in the west sector than the east prior to the thinning (mean difference 2004–2007 = $95.3 \text{ g C m}^{-2} \text{ yr}^{-1}$; SE 36.09). In 2007, the year of the thinning, NEP was substantially higher for both sectors, which was a result of the weather in that year, with a longer growing season (19 days longer than the average) and high peak LAI (see Wilkinson et al., 2012). From 2009 onwards there was a substantial increase in the ratio of R_{eco} to GPP in the east which was not evident in the west sector (Fig. 4d), resulting in much larger differences in NEP between the two sectors after thinning (mean difference 2009–2012 = $318.3 \text{ g C m}^{-2} \text{ yr}^{-1}$; SE 39.5).

3.3 Effects of thinning on ecosystem respiration

As expected for a temperate, deciduous forest, there was a large annual cycle in R_{eco} , with a peak in May–August, (Fig. 5a–c) but varying substantially year to year with weather conditions, particularly precipitation and temperature. Before thinning, annual R_{eco} patterns were similar between sectors (e.g. Fig. 5a, 2006) but after thinning R_{eco}

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was usually higher in the east sector (e.g. Fig. 5b, 2009), particularly in the warmer summer period. As weather conditions differed for fluxes measured for east and west, we compared the underlying relationships of R_{eco} with temperature between sectors.

As an assessment of the sensitivity of R_s to air temperature using the coefficients of the exponential function revealed important differences between sectors (Table 3). Overall Q_{10} was generally higher when airflow was from the west sector (mean = 4.14; SD = 1.42) than from the east (mean = 2.41; SD = 0.51) however there were deviations from this most notably in 2009 and 2010. The largest differences in R_s (highest in the east) between the two sectors occurred in 2009, two years after the thinning. This was the only year during which there was a constant positive offset in the sensitivity of R_s to air temperature between the two sectors (Fig. 5h).

3.4 Effects of thinning on canopy NEE light response

The maximum rate of light saturated photosynthesis (NEE_{max}) and incident quantum yield (ε) were determined from a light response function (Eq. 2) fitted to the summer (July and August) daytime NEE flux data for both forest sectors (Fig. 6) in a 5 °C range (18–23 °C). Differences in NEE_{max} were observed between the east and west sectors both before and after thinning (data not shown). Although both sectors followed the same general inter-annual pattern, there was no clear change (in either sector) after thinning. The values of NEE_{max} were generally larger (more negative) than the maximum observed rates of daytime NEE, due to an over estimation of NEE_{max} by the rectangular-hyperbolic model therefore NEE at S_g 800 W m⁻² (NEE_{800}) was considered a better indication of the maximum rate of light saturated NEE. NEE_{800} was consistently smaller (less negative) in the fluxes observed from the east sector (Fig. 7a) than from the west from the start of the observation period through to 2007, the year of the treatment (mean difference 2004–2007 = 3.85 $\mu\text{mol m}^{-2} \text{s}^{-1}$; SD = 0.92), but there was no reduction in NEE_{800} in 2008. There was a small increase (2.2 and 2.1 $\mu\text{mol m}^{-2} \text{s}^{-1}$) in NEE_{800} in the east relative to the west in 2009 and 2010 respectively. In 2011 and 2012 the two sectors returned to their pre-thinning ranking. Incident quantum yield (Fig. 7b)

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was generally much larger (more negative) when fluxes were from the west than from the east (except for 2007 and 2012) indicating that this area of the forest used low radiation levels more efficiently. Although R_d (respiration in the dark) estimated from the light response curves in the east sector was usually about half the value of that in the west sector there was substantial inter-year variation and no clear change was associated with thinning (Fig. 7c).

3.5 Changes in canopy height and gap fraction

The canopy top height derived from the first return data from the LiDAR survey showed that the two sectors of forest had similar canopy height distributions in 2006, before thinning (Fig. 8a and b), but with some differences in detail. The small peak in frequency between 5 and 10 m height in the west in 2006 (Fig. 8a) is from areas of the forest which were undergoing succession development following previous disturbance events. By 2009 these areas of the forest had grown and are evident as heterogeneous patches in Fig. 1b. In both sectors, the canopy height distribution profile changed, in the west this was because of growth, whilst in the east, the thinning operation had a substantial effect. Prior to the thinning both maximum and mean canopy heights were similar in both sectors (Table 4). Between 2006 and 2009, the maximum canopy height increased in the west sector by 0.9 m, but was reduced slightly in the east sector by 0.1 m. Over the same time period mean canopy top height also increased in the west sector by 0.95 m and reduced in the east sector by 1.4 m.

Changes in the canopy height distribution profiles were also observed (Fig. 8c and d). The elevation relief ratio, E (Pike and Wilson, 1971) reflects the degree to which the outer canopy surfaces are in the upper ($E > 0.5$) or lower ($E < 0.5$) portion of the height range is defined as:

$$25 \quad E = \frac{h_{\text{mean}} - h_{\text{min}}}{h_{\text{max}} - h_{\text{min}}} \quad (3)$$

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where h_{mean} , h_{min} , and h_{max} are the mean, minimum and maximum canopy heights respectively. E was reduced substantially in the east because of the larger proportion of lower top heights, while there was only a small increase in E in the west (Table 4). The canopy top height distribution also showed a relatively small increase in the proportion of canopy > 15 m in height between 2006 and 2009 in the west (+6.2%) but a substantial reduction in the east (−13.7%) as a result of the thinning operation.

The LiDAR survey also showed that canopy complexity across the upper-most surface of the forest in the east sector increased following the thinning operations. The relative variability in canopy height (indicated by the coefficient of variation) increased substantially (Table 4) in the east but not in the west. After thinning there was a large increase in the frequency of gaps in the forest canopy (canopy top height < 1 m) in the east sector but not the west, because of the removal of canopy trees (compare Fig. 8d). Gaps in the forest canopy were relatively uniformly distributed throughout the whole east sector and increased from a total area of 1.13 ha (3.1 % of the eastern area) in 2006 to 2.16 ha (6.6 %) in 2009. Over the same period there was a small decrease in the total area of gaps in the forest canopy in the west, which measured 0.89 ha (2.47 % of the total western area) in 2006 and 0.85 ha (2.35 %) in the 2009 surveys (Fig. 1b).

4 Discussion

Surprisingly, effects of the thinning procedure in 2007 on carbon balance were not clearly evident. In part, this might have been because of our experimental approach. We used eddy covariance measurements at one location near the boundary between the thinned and unthinned sectors in order to determine the CO_2 fluxes, because of the relatively small size of the forest block and being restricted to only one tower and EC system. The effects of thinning are partly obscured by: (a) the differences in weather conditions when airflow is from either sector (Fig. 2), (b) existing heterogeneity in fluxes from different parts of the forest prior to thinning (Fig. 4), (c) the substantial inter-annual variation in component CO_2 fluxes (evident in Fig. 4); and (d) the limited data availability

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for each sector, which after classification and quality control can be as low as 22.5 % (Table 2). However there was no evident bias in the data availability (e.g. day or night, or seasonal distribution) that might have affected our gap-filled annual total CO₂ flux component estimates. The main difference in CO₂ flux between the two sectors after thinning was substantially lower NEE in fluxes from the east (Fig. 4c) although this was only observed from 2009 onwards.

The pre- and post-thinning LiDAR surveys indicated that whilst canopy top height distributions were comparable in 2006, the thinning operations in 2007 had a large effect on the canopy structure of the east sector, resulting in a more complex canopy with a wider range of top heights and a larger total area of gaps. The complexity of the forest canopy at our site, as a result of variability in gaps and a dense understorey, contrasts with other published studies using LiDAR at other deciduous forest sites (Wasser et al., 2013). Whilst we acknowledge that the 2009 LiDAR survey was not immediately after the thinning, our estimate of the change in canopy gap fraction may be an under representation. Firstly, LiDAR pulses have a relatively large footprint (~ 25 cm in diameter) and therefore gaps in the canopy would need to be larger than this in order to be recognised as a gap. Secondly, off-nadir pulses are more likely to produce a canopy height return than they are to penetrate to ground level. Our approach used only the first and last return signals of the LiDAR data, so the canopy height model showed only the uppermost component of the forest canopy. As such, some of the changes in the understorey canopy during thinning may have been masked by the vertical overlap of the understorey vegetation and upper canopy. Whilst we acknowledge that an analysis of full wave-form or multiple return data (Mallet and Bretar, 2009) may provide more detailed information about the canopy's 3-D structure, we maintain that the approach adopted here provided a useful assessment of the changes to the forest canopy due to the thinning operations.

The parameters obtained from the summer NEE light response curves did not support our hypothesis that tree thinning would lead to a reduction in NEE through a loss of canopy photosynthetic area, although there is substantial variation in the data and

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5 Conclusions

This study has investigated the effects of management thinning on the carbon balance of deciduous oak woodland in south-eastern England. LiDAR data were used to assess changes in the forest canopy, while EC was used to measure changes in the carbon balance. Management thinning reduced the mean canopy top height and resulted in a forest canopy with a wider top height range and more gaps. The impacts of management thinning on the carbon balance were not clearly evident although NEE was lower in fluxes from the thinned area from 2009 onwards, two years after the thinning. The sensitivity of photosynthetic parameters in the first year after thinning, 2008, suggests that newly exposed ground vegetation and shrub layers receiving better illumination compensated for the removed trees. The R_{eco} component increased in the thinned area but not until two years after the thinning had been completed and was associated with an increase in the sensitivity of R_{eco} to temperature.

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Acknowledgements. This work was funded by the Forestry Commission, and this paper is an output of the Managing Forest Carbon Programme. We are grateful to the local Forestry Commission staff for allowing and facilitating the research in the Straits Inclosure. We are indebted to Bernard Devereux, Gabriel Amable and Ed Wyer from the Unit of Landscape Modelling, Cambridge University for acquiring and processing the LiDAR data. We wish to acknowledge

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the help of many Forest Research colleagues who have helped on this work over the years, and particularly Mark Broadmeadow who initiated the project and set up the eddy covariance CO₂ flux site.

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Table 1. Results of tree mensuration surveys carried out in 2009 (west sector) and 2011 (east sector) at the Straits Inclosure, Alice Holt Forest. In the east sector 26 circular plots were measured each with a radius of 12.6 m, whilst in the west sector, 18 plots were measured each with a plot radius of 8 m. Plots locations were selected using a stratified grid basis to ensure the heterogeneity of the forest structure was measured; figures in brackets are standard error.

All trees		Oak trees only	
		Density (trees ha ⁻¹)	Mean diameter at breast height (cm)
East	354	23.9 (0.55)	30.0 (0.53)
West	450	26.6 (0.57)	26.8 (0.57)

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Table 2. Annual eddy covariance CO₂ flux data capture, data availability following de-spiking, following footprint and u^* quality checks, and resulting data availability for the east and west sectors (all in %) over the period 2004–2012 at the Straits Inclosure, Alice Holt Forest.

Year	Total data Capture	De-spiked data	Footprint/ u^* Quality check	East sector	West sector
2004	87.4	85.4	67.1	26.2	40.9
2005	91.4	89.3	68.8	30.9	37.9
2006	78.5	74.1	58.3	25.2	33.1
2007	76.2	74.7	56.9	23.6	33.3
2008	81.7	80.3	64.8	22.5	42.3
2009	73.4	72.2	56.7	27.9	28.8
2010	92.8	90.8	69.9	37.5	32.5
2011	86.4	84.4	66.5	28.7	37.8
2012	82.1	80.4	64.0	27.4	36.7
Mean	83.0	81.2	63.7	27.7	35.9

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Table 3. Night-time ecosystem respiration (R_s) coefficients and the estimated Q_{10} values derived from fitting an exponential equation to half hourly night-time NEE and air temperature values over the period 2004–2012 at the Straits Inclosure, Alice Holt Forest.

Year	K_1 East	K_1 West	K_2 East	K_2 West	Q_{10} coefficient East	Q_{10} coefficient West	R^2 East	R^2 West
2004	1.747	1.123	0.076	0.115	2.14	3.16	0.32	0.40
2005	1.857	1.253	0.066	0.099	1.94	2.68	0.39	0.39
2006	1.383	1.110	0.084	0.014	2.31	2.82	0.41	0.38
2007	1.698	0.816	0.067	0.132	1.97	3.75	0.24	0.32
2008	1.536	0.729	0.083	0.139	2.29	4.00	0.36	0.45
2009	1.407	1.189	0.095	0.086	2.58	2.36	0.39	0.26
2010	1.366	1.437	0.077	0.066	2.16	1.93	0.32	0.26
2011	1.263	0.791	0.079	0.118	2.19	3.25	0.22	0.37
2012	1.309	0.768	0.099	0.035	2.71	3.86	0.39	0.39

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Table 4. Results of aerial LiDAR surveys before and after thinning calculated from first and last return data at a point density of 2 points m⁻² and extracted from a 1 ha gridded canopy height model at the Straits Inclosure, Alice Holt Forest.

Year	Sector	Maximum height (m)	Mean height (m)	S.D of mean height	C.V.	Elevation relief ratio (E)	% of canopy > 10 m	% of canopy > 15 m
2006	West	25.7	15.0	5.04	0.34	0.58	81.9	66.3
2006	East	26.0	15.0	5.03	0.34	0.57	84.5	65.3
2009	West	26.6	15.9	4.99	0.32	0.59	85.8	72.5
2009	East	25.9	13.6	6.19	0.46	0.52	73.6	51.7

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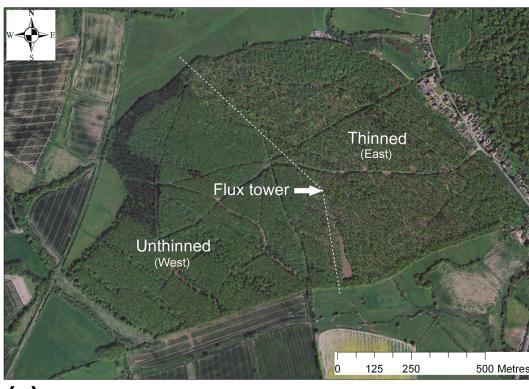


Figure 1. (a) Aerial photograph of the Straits Inclosure, Alice Holt Forest. Bluesky International Ltd[®]/Getmapping PLC. (b) Change in canopy height between November 2006 and August 2009 calculated using aerial LiDAR data at the Straits Inclosure, Alice Holt Forest.

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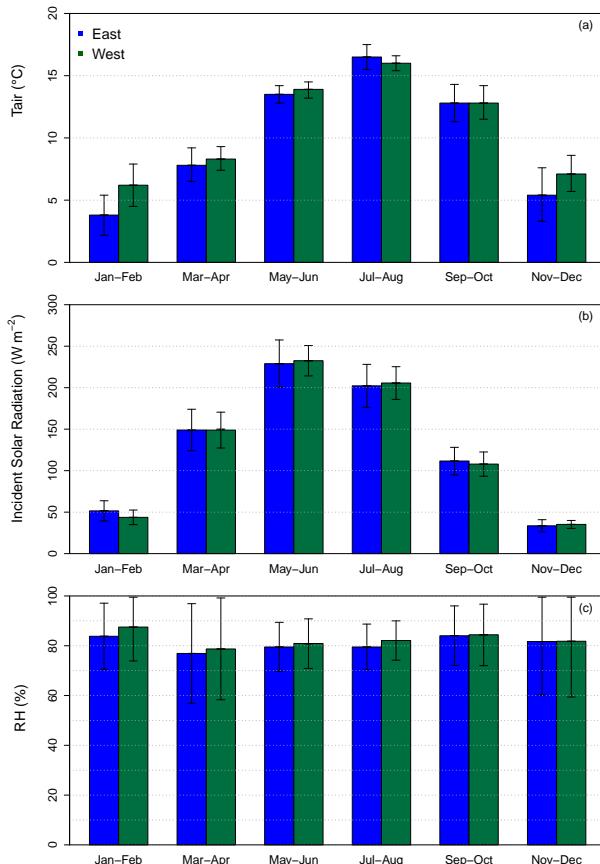


Figure 2. Average bi-monthly values (2004–2012) for the key climatic variables of (a) air temperature (b) incident solar radiation, S_g and (c) relative humidity for the east (blue) and west (green) sectors, error bars represent ± 1 standard deviation ($n = 7$) at the Straits Inclosure, Alice Holt Forest.

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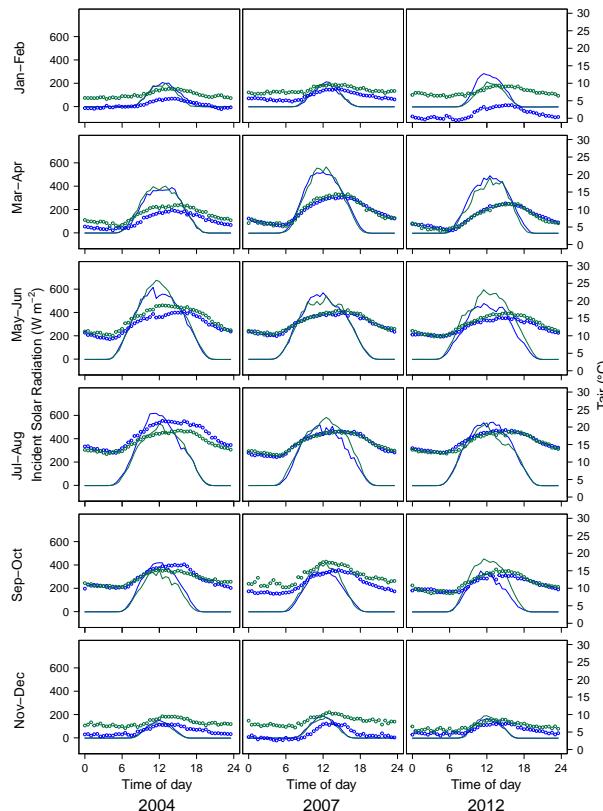


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Figure 3. (a) Average bi-monthly diurnal curve of incident solar radiation, S_g for east sector (blue solid line) and west sector (green solid line) and air temperature for east sector (blue open circles) and west sector (green open circles) for 2004, 2007 and 2012 at the Straits Inclosure, Alice Holt Forest. **(b)** Mean bi-monthly diurnal curve of net ecosystem exchange for east sector (blue solid line) and west sector (green solid line) for 2004, 2007 and 2012, + symbols represent $\pm 1\text{SE}$ at the Straits Inclosure, Alice Holt Forest.

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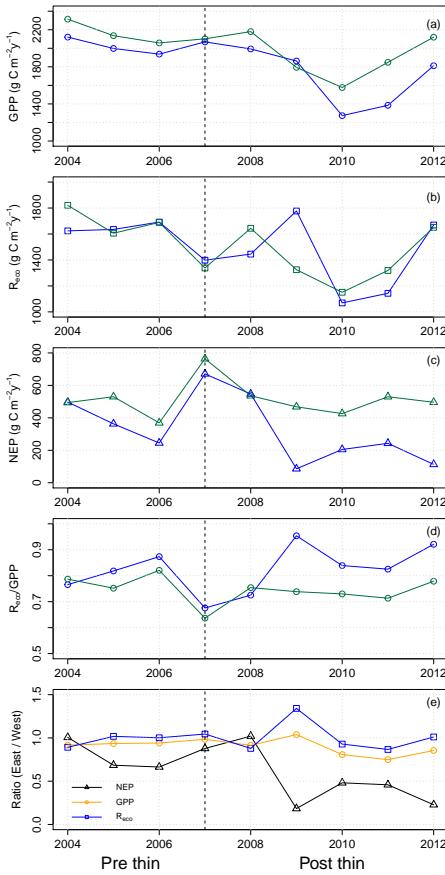


Figure 4. Annual totals of CO_2 flux components for the east sector (blue line and symbols) and west sector (green line and symbols) 2004–2012 for (a) GPP (b) Reco (c) NEP (d) ratio of annual R_{eco} to annual GPP and (e) ratio of east sector to west sector values for each component at the Straits Inclosure, Alice Holt Forest.

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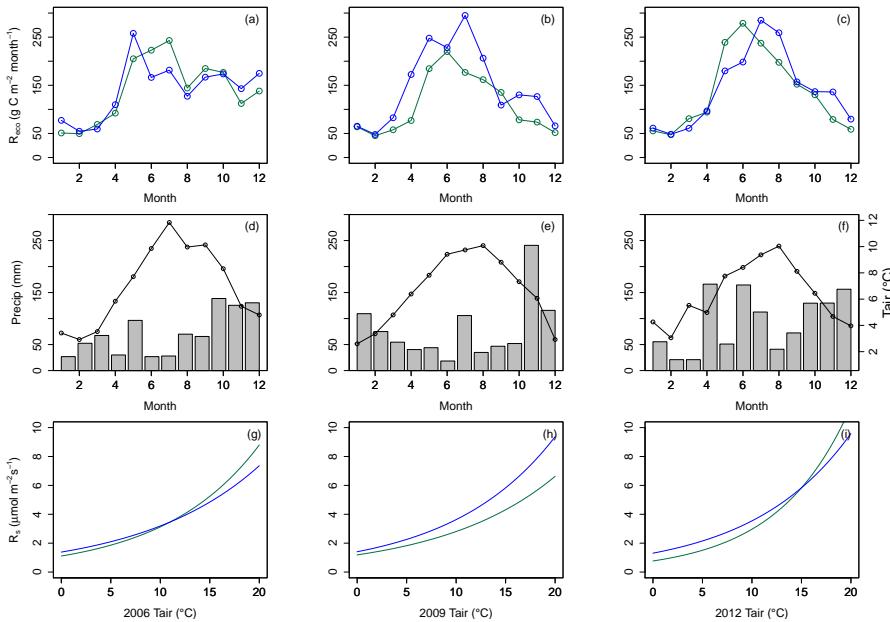


Figure 5. Monthly estimated R_{eco} for the east sector (blue solid line with open circles) and west sector (green solid line with open circles) for (a) 2006 (b) 2009 (c) 2012; monthly mean air temperature (at 26 m height) and monthly precipitation total for (d) 2006, (e) 2009 (f) 2012; modelled temperature response (R_s derived from night-time NEE fluxes only) for east sector (blue solid line) and west sector (green solid line) for (g) 2006 (h) 2009 (i) 2012 at the Straits Inclosure, Alice Holt Forest.

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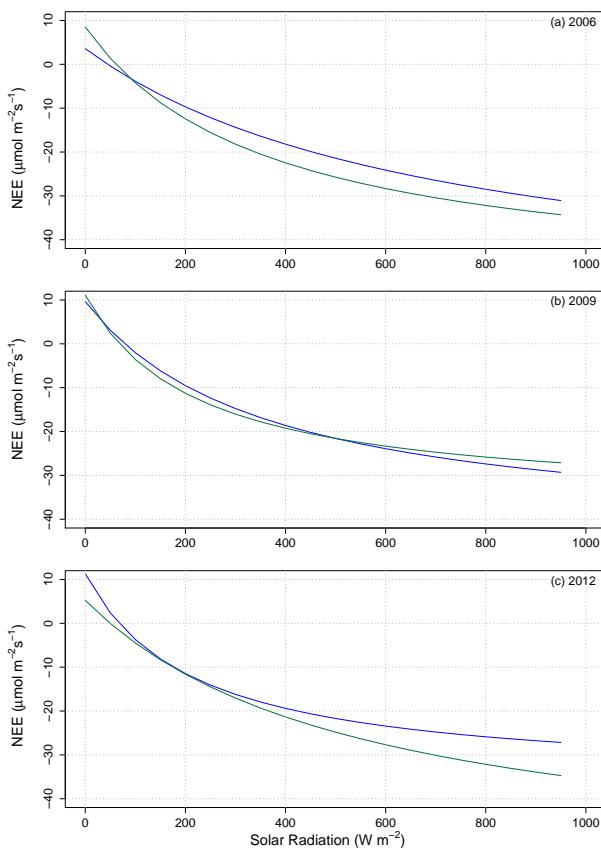


Figure 6. Summer (July and August) daytime modelled light response for the east sector (blue line) and west sector (green line) for the years of **(a)** 2006 **(b)** 2009 **(c)** 2011 at the Straits Inclosure, Alice Holt Forest. Data limited to 18–23 °C air temperature conditions.

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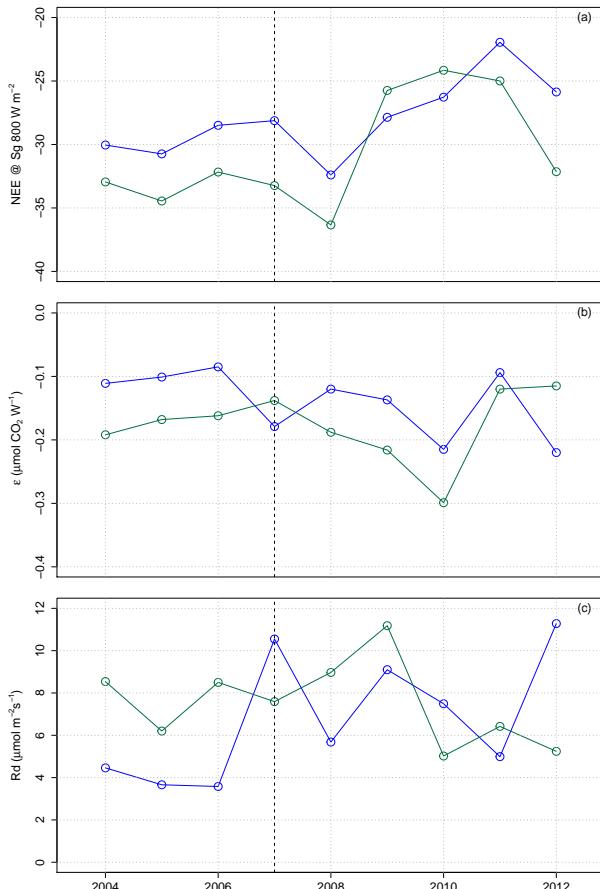


Figure 7. Inter-annual variation in summer (July and August) daytime light response model parameters for (a) NEE_{800} (b) ε and (c) R_d for the east sector (blue line with open circles) and west sector (green line with open circles) at the Straits Inclosure, Alice Holt Forest.

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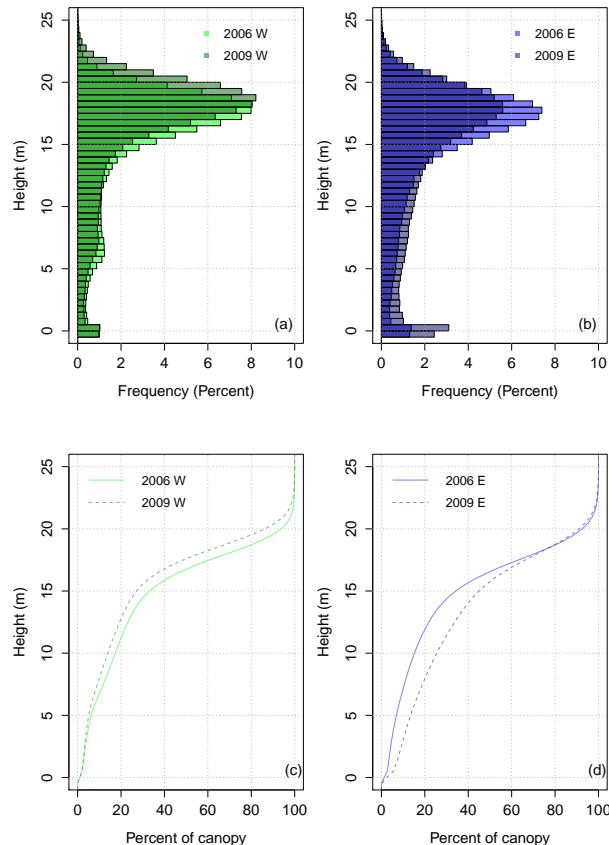


Figure 8. Histograms of canopy top height (m) derived from airborne LiDAR for the east sector (blue bars) and west (green bars) for (a) 2006 and 2009 west sectors, (b) 2006 and 2009 east sectors, cumulative frequency of canopy top height for (c) west sector in 2006 and 2009 and (d) east sector in 2006 and 2009 at the Straits Inclosure, Alice Holt Forest.