

# Thinning effects on the net ecosystem carbon exchange of a Sitka spruce forest are temperature-dependent

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## ARTICLE INFO

### Article history:

Received 5 July 2011

Received in revised form 4 January 2012

Accepted 10 January 2012

### Keywords:

Sitka spruce

Forest thinning

Carbon stocks and fluxes

Net primary productivity

Eddy covariance

Net ecosystem exchange

Gross primary productivity

Ecosystem respiration

## ABSTRACT

Commercial forest plantations need to be actively managed, through tree removal, in order to improve wood quality, maintain productivity and provide an economic return, although this could compromise an important role for forests in carbon sequestration and greenhouse gas mitigation. The impact of forest thinning on net primary productivity (NPP) and net ecosystem exchange (NEE) was assessed using a combination of biometric and eddy covariance (EC) techniques. Two thinning operations were performed in close succession, which reduced the basal area of the stand by 17% and 11% and removed a timber volume of 48 m<sup>3</sup> ha<sup>-1</sup> and 50 m<sup>3</sup> ha<sup>-1</sup>, respectively. Annual rates of NPP ranged from 13.24 (±3.96) to 18.94 (±4.88) t C ha<sup>-1</sup> and 13.22 (±3.72) to 17.77 (±5.30) t C ha<sup>-1</sup> for the pre- and post-thinning periods, respectively. Estimates of NEE varied between 8.44 (±1.34) to 8.87 (±1.48) t C ha<sup>-1</sup> and 6.75 (±1.19) to 10.33 (±1.41) t C ha<sup>-1</sup> in the pre- and post-thinning periods. Forest thinning did not have a significant impact on carbon stocks or fluxes when pre-thinning (2002–2006) and post-thinning (2007–2009) estimates of NPP and NEE were compared, however the range of inter-annual variability in NEE increased after thinning. The partitioning of annual NEE carbon budgets into gross primary productivity (GPP) and ecosystem respiration ( $R_{eco}$ ) together with an analysis of key physiological parameters suggested that the impacts of forest thinning are largely dependent on temperature. An expected decrease in GPP after the initial thinning in 2007 was not observed due, in part, to the higher mean annual air temperatures and incident photosynthetic active radiation (PAR) and a compensatory increase in photosynthesis by the remaining trees. A continual decline in  $R_{eco}$ , was observed in the years subsequent to the first thinning and was attributed to both biomass removal and climatic factors.

Inter-annual variations in climate had a significant impact on NEE, GPP and  $R_{eco}$ . Annual mean air temperature, total precipitation and total incident PAR were all shown to influence the processes driving CO<sub>2</sub> exchange. Overall, these results suggest that the impacts of the thinning practices, as implemented in this study, are dependent on climate and under similar conditions are unlikely, in the short-term, to compromise a role for forest ecosystems in carbon sequestration and greenhouse gas mitigation.

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## 1. Introduction

Forest ecosystems represent a significant terrestrial carbon store, where the majority of carbon sequestered is held within the woody biomass (Scott et al., 2004). Current forest management strategies that involve variable thinning regimes have been designed to enhance the timber yield and economic returns over the length of the forest rotation. In addition, policy-driven research has identified a potential for using forests to mitigate and offset greenhouse gas (GHG) emissions through increased carbon sequestration and the utilisation of forest products and residues.

For example, the replacement of carbon intensive construction materials with timber-based products and the use of forests or forest residues for bioenergy production may reduce anthropogenic carbon dioxide (CO<sub>2</sub>) emissions (Eriksson, 2006). Forest plantations, therefore, have the ability to play an important role in the mitigation of, and adaptation to, global climate change. However, management strategies, such as thinning that reduce the amount of standing biomass, may in the short-term compromise rates of carbon assimilation and negate a dual role for forests for both timber production and carbon sequestration.

In Europe, Sitka spruce (*Picea sitchensis* (Bong.) Carr.) represents an important commercial tree species due mainly to its high productivity (Berhofer et al., 2003). This is particularly the case in Ireland where Sitka spruce accounts for approximately 50% of the total forest area as either mono-species or mixed stands (National

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Forest Inventory, 2007). Plantation forests such as these receive regular management, including thinning, throughout the rotation, in order to maximise the value of the timber produced. In Ireland the most common thinning practice used in Sitka spruce plantations for the first timber removal is the line and selection technique, where initially every seventh row of trees are harvested followed by the removal of selected trees on each side of the thinning line (Joyce and O'Carroll, 2002). This type of combined selective and systematic thinning is undertaken for economic reasons and to facilitate access into the stand while also improving the timber quality of the remaining trees. Subsequent thinnings are purely selective, using the access routes created during the first thinning. The thinning regimes applied are commonly derived from the Forestry Commission yield models for forest management (Edwards and Christie, 1981) and also increasingly from Irish dynamic yield models (Broad and Lynch, 2006). There are however, site-specific instances where the thinning guidelines are not adhered to, such as in areas that may be susceptible to windthrow or where it is not economically viable to thin. Such instances of low or no-thin management may have further implications for long-term carbon sequestration.

Biomass removal through forest thinning represents an early economic return that discounts the net profit of the stand over the length of the rotation and increases the volume and economic quality of the remaining trees as a consequence of the re-distribution of resources, such as light, water and nutrients (Thornley and Cannell, 2000). The thinning process opens the forest canopy resulting in modifications in air and soil temperature, vapor pressure deficit, light penetration, intercepted rainfall and soil water content (Norman and Jarvis, 1974; Black et al., 1980; Wang and Jarvis, 1990; Hale, 2003; Ma et al., 2004; Vesala et al., 2005). Many practical investigations into the silvicultural response of tree growth and yield to different thinning regimes have been undertaken over the past two centuries (Nilsson et al., 2010), although the results differ considerably depending on species, geographic location, climate and the timing and intensity of forest thinning (Thornley and Cannell, 2000; Homyack et al., 2004; Makinen and Isomaki, 2004; Sullivan et al., 2006; Nilsson et al., 2010). In addition, the prediction of growth and yield responses to forest management may be problematic as many models may not be adequately calibrated for a particular management practice (Roberts and Harrington, 2008). Even fewer studies have investigated the impacts of forest thinning on both the long-term carbon pools as well as the more transient ecosystem scale fluxes between these pools. The establishment of long-term monitoring networks, such as Fluxnet, Ameriflux and CarboEurope-IP, have considerably improved our understanding of ecosystem scale carbon fluxes (Baldocchi et al., 2001; Dolman et al., 2008). Several flux based studies have reported on the significant impacts of forest disturbance through harvest (Amiro et al., 2006; Payeur-Poirier et al., 2011) fire (Mkhabela et al., 2009) insect infestation (Brown et al., 2011) and extreme climatic variability (Schwalm et al., 2010; Keith et al., 2011) on ecosystem scale carbon budgets. However, there is a need to further assess the impacts of forest management practices on both timber production and GHG mitigation given the potential multi-functional role of forest plantations.

Forest thinning is initially expected to have a negative impact on stand-level productivity, as the removal of aboveground photosynthetic material may reduce potential rates of carbon assimilation, while the decomposition of woody debris may increase carbon losses from the ecosystem (Nilsson et al., 2010). The extent of this is, however, likely to depend on the intensity and type of thinning management applied and how rapidly the growth and carbon uptake of the remaining trees can compensate for any reduction in the productivity of the stand. Furthermore, the role of inter-annual climatic variability on the physiological response of a forest stand to thinning is also of particular importance. Year to year variations

in key climatic parameters, such as temperature, photosynthetic active radiation (PAR) and precipitation that drive rates of net stand carbon uptake and respiratory carbon losses, may alter the response of a forest to thinning.

Additional information is also needed on the key physiological and biochemical processes that underpin the carbon cycle in forests and how they are affected by management practices. Not only are decreases in net canopy photosynthesis and thus gross primary productivity (GPP) likely with such disturbance, but the autotrophic ( $R_a$ ) and heterotrophic ( $R_{het}$ ) components of ecosystem respiration ( $R_{eco}$ ) may also be altered due to a reduction in maintenance respiration, decomposition of harvest residues and changing litterfall and root exudate supply (Amiro et al., 2006; Kowalski et al., 2004). Furthermore, changes in nutrient availability and input after thinning (Vesterdal et al., 1995; Blanco et al., 2009) may modify the contribution of both GPP and  $R_{eco}$  to net ecosystem carbon exchange (NEE). The temporal scale over which these processes change will also influence both the short and long term carbon sequestration potential of forests and may have additional implications for forest management. Other flux-based studies have reported conflicting effects of forest thinning, with neutral (Vesala et al., 2005) or negative (Kolari et al., 2004; Scott et al., 2004) impacts on ecosystem scale carbon fluxes immediately after thinning, while Sullivan et al. (2008) reported a decrease in soil  $CO_2$  efflux in the first year following thinning.

In this paper, we assess the impacts of forest thinning on the carbon budget through both biometric and micrometeorological measurement techniques. Measurements of standing biomass, biomass increment and canopy phenological traits are reported in addition to the surface exchange of  $CO_2$  measured using eddy covariance (EC) techniques. Our principal hypothesis was that forest thinning and the associated removal of biomass would result in a decrease in both the  $CO_2$  sink strength and the net primary productivity (NPP) of the ecosystem. It was also expected that the application of two thinning cycles in relatively close succession would limit the recovery of net canopy photosynthesis and carbon accumulation when compared to pre-thinning levels. The information presented in this paper provides an assessment of the impact of forest thinning on C-sequestration and addresses the potential consequences of the multifunctional role of forests in both GHG mitigation and timber production.

## 2. Materials and methods

### 2.1. Study site

Micrometeorological and biometric measurements have been made since 2002 on a Sitka spruce first rotation plantation (Dooary Forest), growing on a wet mineral soil located in Co. Laois in the Irish midlands (52°57'N, 7°15'W; 30-year mean temperature 9.3 °C; 30-year mean precipitation 850 mm; altitude 260 m). The forest is state owned and managed by Coillte, a semi-state company involved in forest-based land management. The forest stand was planted in 1988 with a stocking density of 2300 stems per hectare and is made up of two adjacent compartments covering an approximate total area of 42 ha. All site-specific characteristics and measured variables can be found in Table 1.

The first thinning event took place between December 2006 and January 2007 using a line and selection technique. Trees from all size classes were harvested and a thinning ratio of 0.85 was applied, based on the mean basal area of trees harvested in relation to the mean basal area of trees remaining in the stand. Trees were felled, de-limbed and sectioned using a mechanical harvester. A forwarder was then used to collect the harvested timber, which was transported to the forest edge from where it was removed from the

**Table 1**  
Biometric and micrometeorological flux characteristics of the Doory forest stand (2002–2009).

Measured variables	2002	2003	2004	2005	2006	2007	2008	2009
Tree density (number ha <sup>-1</sup> )	2367	2367	2367	2367	2367	1768	1768	1345
Basal area (m <sup>2</sup> ha <sup>-1</sup> )	31.34	33.64	40.29	46.83	48.16	39.82	43.90	39.25
Leaf area index (m <sup>2</sup> m <sup>-2</sup> )	4.09	4.41	5.11	5.77	5.94	4.85	5.28	4.61
Tree height (m)	7.6	8.9	9.7	11.3	11.9	13.1	13.7	14.6
EC measurement height (m)	15	15	15	18	18	18	21	21
Live biomass increment (t C ha <sup>-1</sup> )	n.d.	10.26	15.54	10.65	15.99	-13.03	11.29	-11.13
Dead biomass increment (t C ha <sup>-1</sup> )	n.d.	-1.00	0.87	0.6	-0.03	-2.45	-0.36	-0.45
Litterfall (t C ha <sup>-1</sup> )	n.d.	3.55	2.10	2.23	1.81	1.71	1.21	1.33
Fine Root Production (t C ha <sup>-1</sup> )	n.d.	0.43	0.43	0.48	0.49	0.44	1.08	1.08
Thinning removal (t C ha <sup>-1</sup> )	0	0	0	0	0	9.92	0	10.49
Thinning residue <sup>a</sup> (t C ha <sup>-1</sup> )	0	0	0	0	0	17.82	0	16.45
NPP (t C ha <sup>-1</sup> yr <sup>-1</sup> ) <sup>b,c</sup>	n.d.	13.24 (±3.96)	18.94 (±4.88)	13.96 (±7.73)	18.26 (±7.32)	14.41 (±5.09)	13.22 (±3.72)	17.77 (±5.30)
NEE (t C ha <sup>-1</sup> yr <sup>-1</sup> ) <sup>d,e</sup>	8.45 (±1.66)	8.87 (±1.48)	8.44 (±1.34)	8.72 (±1.60)	8.81 (±1.09)	10.33 (±1.41)	6.75 (±1.19)	8.14 (±1.94)
GPP (t C ha <sup>-1</sup> yr <sup>-1</sup> ) <sup>d</sup>	21.22	22.68	22.65	23.97	25.02	24.75	19.49	19.04
R <sub>eco</sub> (t C ha <sup>-1</sup> yr <sup>-1</sup> ) <sup>d</sup>	12.77	13.81	14.21	15.25	16.21	14.42	12.74	10.90

<sup>a</sup> Includes litter associated with thinning residues.

<sup>b</sup> Data derived from biometric measurements.

<sup>c</sup> Values in parenthesis indicate the standard error associated with the NPP calculation.

<sup>d</sup> Data derived from EC measurements.

<sup>e</sup> Values in parenthesis indicate the range based on the 95% confidence interval associated with the sampling uncertainty.

site and taken to the local sawmill. Residues produced during each thinning operation (all non-timber material that was not removed during the harvest) were placed in the harvested rows to produce a brush mat that was used to reduce soil disturbance due to the harvesting machinery. A second, selective thinning took place in November 2008 where generally larger trees were removed from the stand resulting in a thinning ratio of 1.37. During the second thin the harvester and forwarder accessed the stand using the previously created thinning lines in order to minimise any further soil disturbance and compaction, as is normal practice on soils of low load bearing capacity (Booth et al., 2009).

## 2.2. Meteorological measurements

An automated weather station controlled by a CR10X datalogger (Campbell Scientific, Shepshed, England) was used to record meteorological parameters, including air temperature, relative humidity (HMP45C, Vaisala, Helsinki, Finland), wind speed and direction (Wind Monitor, RM Young, Traverse City, Michigan, USA), precipitation (Tipping bucket rain gauge, RM Young, Traverse City, Michigan, USA), net radiation (NR-Lite, Kipp & Zonen, Delft, The Netherlands), incident irradiance (Quantum sensor, Skye Instruments, Llandrindod, Wales), canopy reflected irradiance (Skye quantum sensor, installed facing the forest canopy), transmitted irradiance (measured using an array of Skye quantum sensors installed at the forest floor, located within the remaining forest block between the thinning rows), total, direct and diffuse photosynthetically active radiation (BF3, Skye Instruments, Llandrindod, Wales), soil heat flux (HFPO1 Hukseflux, Delft, The Netherlands), soil temperature (105E, Campbell Scientific, Shepshed, England) and soil moisture content (CS616 Water Reflectometer, Campbell Scientific, Shepshed, England). All atmospheric sensors were installed above the forest canopy and were maintained at a height of approximately 2 m below the EC sensors. Soil temperature was measured using thermocouples buried at 10 cm intervals from the soil surface to a depth of 1 m. Soil heat flux plates were buried at a depth of 5 cm, and soil water reflectometers measured the water content of the soil between 0 and 20 cm.

## 2.3. Biometric measurements

Biometric surveys were undertaken annually during winter or non-growing periods (November–March) on four permanently established 0.05 ha plots within the footprint of the EC flux tower.

Tree and crown height were measured using a laser hypsometer (Laser Technology Inc., CO, USA) and stem diameter at 1.3 m (dbh) was calculated from the circumference measured using a 1 m girth tape. During the establishment of the biomass plots all measured trees were marked with paint at 1.3 m to ensure that subsequent dbh measurements were made at the same point on the stem of individual trees. The change in living biomass ( $\Delta B$ ; Eq. (1)) was determined from annual biometric surveys of the fixed plots within the forest stand, where the tree height and diameter at breast height of individual trees were measured and the living biomass was calculated using site-specific biomass equations for Sitka spruce (Black et al., 2007; Tobin and Nieuwenhuis, 2007). Total stand biomass included all aboveground biomass and belowground root material to a minimum diameter of 2 mm. Attached dead branch biomass (AGD) was calculated from a model derived from data in Tobin et al. (2006), supplemented with more recent site-specific data. Fine root data from 2002 to 2007 were taken from Saiz et al. (2006) and Black et al. (2007) while estimates for 2008 and 2009 were determined using in-growth cores sampled during the current study. Litterfall data were derived from monthly collections made at the site since 2003.

Estimates of leaf area index (LAI) were determined by converting needle biomass to a projected stand level leaf area using a mean half-surface specific leaf area from scanned branches taken from destructive biomass samples located outside of the inventory plots (Tobin et al., 2006). Inventory based estimates of annual NPP was determined as:

$$\text{NPP} = \Delta B + \Delta \text{AGD} + D_a + D_b + \text{Th}_{\text{rem}} + \text{Th}_{\text{res}} \quad (1)$$

where  $\Delta B$  is the change in the living biomass,  $\Delta \text{AGD}$  is the change in dead material still attached to the tree,  $D_a$  is aboveground litterfall,  $D_b$  is belowground fine root production,  $\text{Th}_{\text{rem}}$  accounts for the removal of biomass in harvested wood and  $\text{Th}_{\text{res}}$  represents the harvest residues remaining in the forest. Losses due to herbivory, volatile organic compound emissions, or dissolved carbon losses were not accounted for in this study.

## 2.4. Micrometeorological measurements

Measurements of NEE were made using the closed path EC technique. The instrumentation consisted of a three dimensional sonic anemometer (Solent R3, Gill Instruments, Lymington, UK) and a closed path infra-red gas analyser (LI-7000, LI-COR Lincoln, Nebraska, USA). The EC data were collected using the Edisol

system as described by Moncrieff et al. (1997) and the fluxes of CO<sub>2</sub> ( $F_c$ ), water vapor, latent and sensible heat were calculated over 30 minute periods using the EdiRe software (Moncrieff et al., 1997). The gas analyser was calibrated bi-weekly, using oxygen free nitrogen to set the zero calibration and a 401  $\mu\text{mol mol}^{-1}$  CO<sub>2</sub> standard to set the span of the gas analyser. Additional information on the instrumentation, data processing and flux calculations can be found in Black et al. (2007). Net ecosystem exchange of CO<sub>2</sub> ( $F_{\text{NEE}}$ ) between the forest and the atmosphere was calculated as the sum of  $F_c$  and the change in CO<sub>2</sub> storage within the forest canopy beneath the EC instrumentation. In this study, canopy CO<sub>2</sub> storage was calculated from the change in the mixing ratio of CO<sub>2</sub> measured at the height of the EC instrumentation (Morgenstern et al., 2004; Humphreys et al., 2006).

The study site used for EC measurements is comprised of two adjacent forest compartments. The first compartment has approximate dimensions of 516 m  $\times$  500 m (~25.8 ha), with the longest edge orientated in the east-west direction, while the second compartment has approximate dimensions of 650 m  $\times$  250 m (~16.2 ha), with the longest edge orientated in the north-south direction. The flux tower is located in the north-eastern corner of the first compartment in order to avail of the maximum possible fetch from the predominant south westerly wind direction. Footprint analyses were applied based on the flux footprint model of Kormann and Meixner (2000) and the half-hourly flux measurements were discarded when greater than 10% of the measured flux was derived from outside the area of interest. The peak location of the flux footprint ( $x_{\text{max}}$ ) and the scaled cumulative flux footprint, representing the distance from which 90% of the flux was derived ( $x_{\text{R90}}$ ), were also determined for a range of wind vectors based on the footprint parameterisation model of Kljun et al. (2004). The maximum possible fetch,  $x_{\text{max}}$ , and  $x_{\text{R90}}$  for each wind vector are as follows; 0–90° (250 m;  $x_{\text{max}}$  173 m;  $x_{\text{R90}}$  470 m), 90–180° (930 m;  $x_{\text{max}}$  171 m;  $x_{\text{R90}}$  467 m), 180–270° (585 m;  $x_{\text{max}}$  189 m;  $x_{\text{R90}}$  516 m), 270–365° (250 m;  $x_{\text{max}}$  170 m;  $x_{\text{R90}}$  466 m). The greatest amount of data rejection based on the footprint analyses occurred when the flux data were derived from a northerly wind direction; however such conditions only constituted a relatively small amount (~8%) of the total data collected.

The influence of friction velocity ( $u_*$ ) on nocturnal NEE measurements was assessed using the methodology of Humphreys et al. (2006) and a  $u_*$  threshold for each dataset was determined. Nocturnal NEE data were rejected when the measured  $u_*$  was lower than the assigned  $u_*$  threshold as these data were assumed to underestimate nocturnal ecosystem respiration.

The quality control procedures associated with the EC flux data were derived from the CarboEurope-IP directive and included tests for stationarity and integral turbulence. In both cases the data were flagged according to the QA/QC directive as being of good, acceptable or poor quality. Poor quality data were not rejected from the data set but were not included in the parameterisation of gap-filling models.

## 2.5. Flux analysis and gap-filling

Short gaps of 0.5–3 h in duration within the EC data as a result of data rejection, equipment calibration, power loss and footprint analysis were filled using linear interpolation techniques. Gaps greater than 3 h in duration were filled using semi-empirical models as described in Falge et al. (2001) and Moffat et al. (2007). Ecosystem respiration was modeled using the Lloyd and Taylor (1994) model (Eq. (2)) describing the relationship between measured nocturnal NEE and the corresponding air temperature.

Daytime ecosystem respiration was determined using this relationship and daytime air temperatures.

$$R_{\text{eco}} = R_{10} e^{E_0 \left[ \frac{1}{283.15 - T_0} - \frac{1}{T - T_0} \right]} \quad (2)$$

where  $R_{10}$  is the respiration rate at 10 °C,  $E_0$  is a derived coefficient for ecosystem respiration,  $T$  is air temperature (K) measured above the forest canopy and  $T_0$  is a best-fit temperature value (K). This relationship was fitted to the data using sum of squares non-linear optimisation.

GPP was derived by initially subtracting the daytime ecosystem respiration from the daytime measured NEE. The daytime GPP was then subdivided into 5 °C temperature classes and modeled using the light response function described in Eq. (3) (Leverenz, 1995).

$$\text{GPP} = \frac{\{(\alpha Q + A_{\text{max}}) - \sqrt{[(\alpha Q + A_{\text{max}})^2 - (4\gamma Q \alpha A_{\text{max}})]}\}}{2\gamma} \quad (3)$$

where  $Q$  is the incident photon irradiance ( $\mu\text{mol}[\text{photon}] \text{m}^{-2} \text{s}^{-1}$ ),  $\alpha$  is the net stand quantum (photon) yield based on incident irradiance ( $\text{mol}[\text{photons}] \text{mol}[\text{CO}_2]^{-1}$ ),  $A_{\text{max}}$  is the maximum assimilation rate ( $\mu\text{mol}[\text{CO}_2] \text{m}^{-2} \text{s}^{-1}$ ) and  $\gamma$  is the convexity coefficient. This relationship was fitted to the data using the sum of squares non-linear optimisation function.

In order to reduce the uncertainty associated with the parameterisation of the gap-filling models due to the thinning events, the data used to constrain the gap filling models were derived from individual annual data sets and specific pre- and post-thin periods. For example, in 2006 the gap filling model parameters were fitted and applied to the EC data collected between January and November in the pre-1st thin period, while the gap filling model parameters applied to EC data collected in December 2006 were derived from post-1st thin data collected in 2007. In 2008, the gap filling model parameters were fitted to the EC data collected between January and October 2008 (data collected prior to the 2nd thin) while the gap-filling parameters applied to the EC data collected in November and December were derived from the 2009 flux data (post-2nd thin).

The net stand physiological characteristics, such as quantum yield ( $\alpha$ ), convexity coefficient ( $\gamma$ ) and maximum CO<sub>2</sub> assimilation rate ( $A_{\text{max}}$ ) were determined by fitting the Leverenz (1995) light response relationship (Eq. (3)), using the sum of squares non-linear optimisation function applied to the high quality flux data measured during the growing season, where the air temperature ranged between 5 and 10 °C. The apparent and inherent quantum yields were determined using incident and absorbed irradiance, respectively.

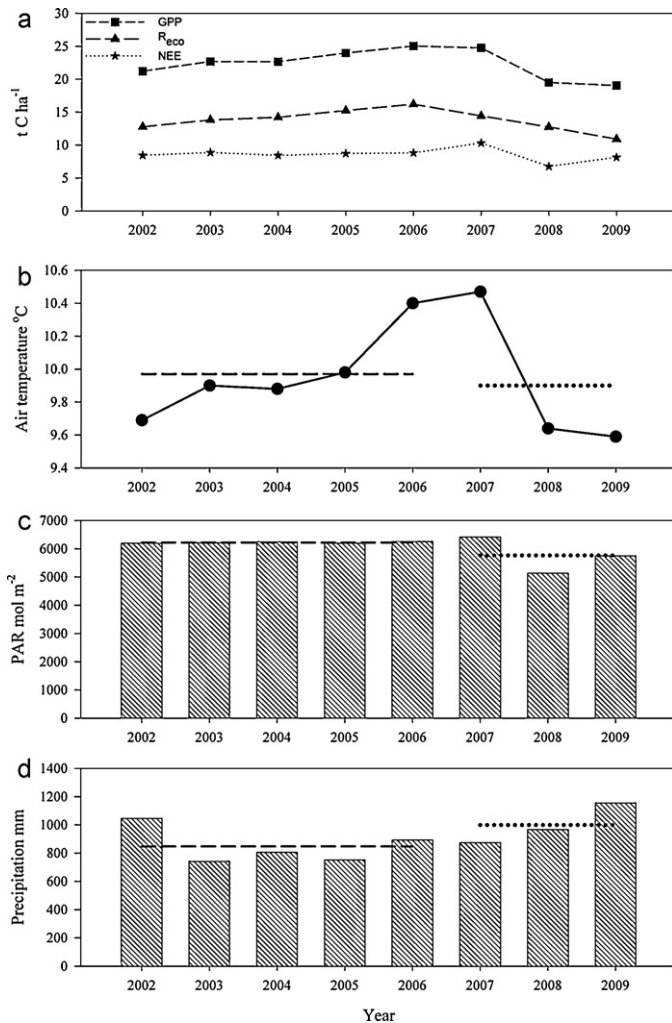
## 2.6. Uncertainty estimates associated with NEE measurements.

The sources of uncertainty within annual estimates of NEE for this site are detailed in Black et al. (2007) and are based on the uniform systematic, selective systematic and sampling uncertainty errors presented by Goulden et al. (1996).

## 2.7. Statistical analysis

The impacts of forest thinning on the response variables NEE, GPP,  $R_{\text{eco}}$  and NPP were analyzed using a Chi square test for generalised linear models (GLMs). Replicated control and treatment plots with respect to the forest thinning management and the EC technique were not available during this study, so the data were divided into two treatment periods, a “pre-thinning” (2002–2006) and a “post-thinning” (2007–2009) period, for subsequent analyses.

The effects of inter-annual climatic variation on the response variables (NEE, GPP,  $R_{\text{eco}}$  and NPP) were also tested using GLMs, in



**Fig. 1.** Annual variation in GPP,  $R_{eco}$  and NEE (a), mean annual air temperature (b), total annual photosynthetic active radiation (c), and total annual precipitation (d), at the Dooley forest site from 2002 to 2009. The dashed and dotted horizontal lines (graphs b–d) represent the pre- and post-thinning mean for each variable, respectively.

which mean annual air temperature, total annual precipitation and total incident PAR were tested separately in relation to each factor.

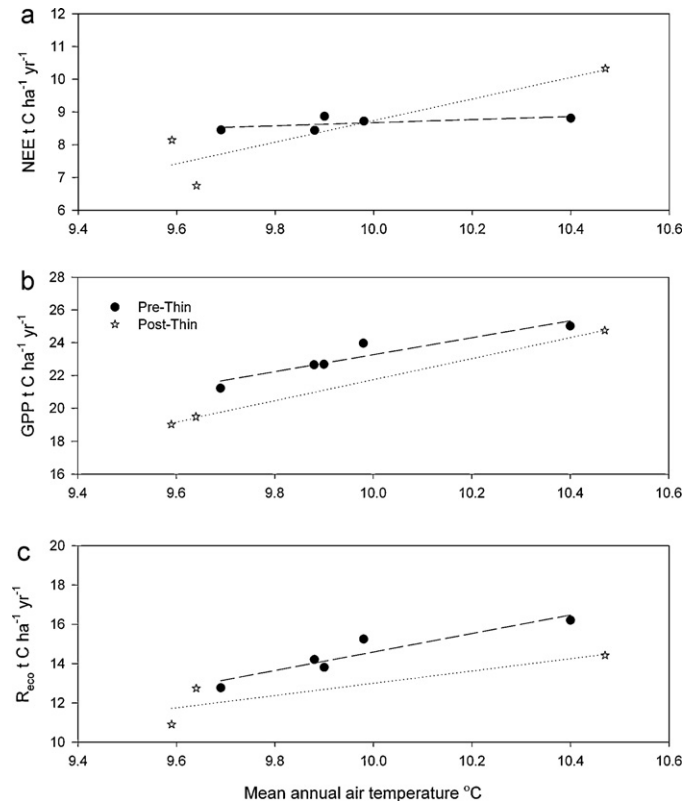
All analyses were conducted using R software (R Development Core Team, 2011).

### 3. Results

#### 3.1. Climate variations from 2002 to 2009

Mean annual air temperature (Fig. 1b) ranged from 9.6 to 10.5 °C over the duration of this study. The mean air temperature for the pre-thinning period (2002–2006) was  $10.0 \pm 0.2$  °C with a small reduction (1%) for the post-thinning period (2007–2009). The flux components, GPP,  $R_{eco}$  and NEE (Fig. 1a) followed a similar pattern to the inter-annual fluctuations in mean air temperature. The highest values for NEE, were associated with the highest mean annual air temperatures (Fig. 1b) and total incident PAR (Fig. 1c).

Total incident PAR (Fig. 1c) showed similar annual values in the pre-thinning years (6192–6258 mol m<sup>-2</sup>) with greater inter-annual differences in the post-thinning years (5135–6414 mol m<sup>-2</sup>). The mean incident PAR was, on average 7.3% lower in the post-thinning years with a considerable reduction (17.5%) in 2008 relative to the



**Fig. 2.** The relationship between mean annual air temperature and NEE (a) [pre-thin:  $y = 0.467x + 4.005$ ;  $R^2 = 0.37$ ; post-thin:  $y = 3.295x - 24.209$ ;  $R^2 = 0.81$ ], GPP (b), [pre-thin:  $y = 5.176x - 28.495$ ;  $R^2 = 0.89$ ; post-thin:  $y = 6.422x - 42.483$ ;  $R^2 = 0.99$ ] and  $R_{eco}$  (c), [pre-thin:  $y = 4.709x - 32.500$ ;  $R^2 = 0.87$ ; post-thin:  $y = 3.127x - 18.274$ ;  $R^2 = 0.77$ ] for the pre-thin (circles) and post-thin (stars) periods.

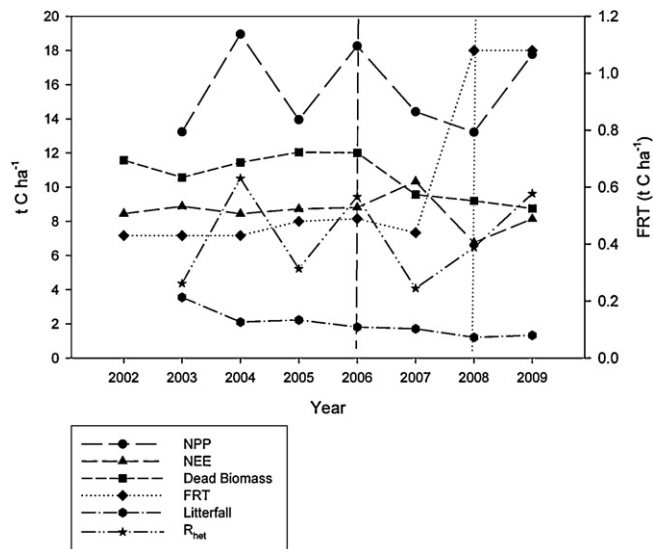
pre-thinning mean. Transmitted radiation increased by 51% and 55% after the first and second thinning events, respectively (Fig. 5).

There was considerable variability in the total annual precipitation (Fig. 1d), which ranged from 742.6 mm to 1132.1 mm, with an average increase of 15.2% in the post-thinning years.

#### 3.2. Inter-annual climatic control on NEE, GPP and $R_{eco}$

The components of NEE, GPP and  $R_{eco}$  increased progressively up to the first thinning event (Table 1; Fig. 1a) and were associated with increasing air temperatures (Fig. 1b). Inter-annual climatic variability had a significant effect on NEE, GPP and  $R_{eco}$  in both the pre and post-thinning years. Temperature had a significant effect on all flux components, NEE ( $P = 0.003$ ), GPP ( $P < 0.001$ ), and  $R_{eco}$  ( $P = 0.001$ ). Variations in PAR also had a significant effect on NEE ( $P < 0.001$ ) and GPP ( $P = 0.001$ ), while precipitation only influenced  $R_{eco}$  ( $P = 0.006$ ).

In order to compare the role of inter-annual temperature variability on the response of the forest stand to thinning, linear regression between the flux components (NEE, GPP and  $R_{eco}$ ) and mean air temperatures were used (Fig. 2). The measured post-thin data were compared with the linear extrapolation of the pre-thin relationship between the net stand carbon dioxide flux components and the mean annual air temperature, given the absence of thinning. Based on the magnitude of the difference between the measured post-thin data and the predicted response of the forest stand in the absence of thinning, the first thinning event resulted in a smaller reduction in GPP (3.7%) compared to the reduction in  $R_{eco}$  (13.9%), leading to a 16.2% increase in NEE in this year (2007). In the year subsequent to the first thinning event (2008), GPP was reduced by 8.9% and was associated with lower air temperatures



**Fig. 3.** Annual variation in NPP (circles), NEE (triangles), dead biomass (squares), fine root turnover (diamonds), litterfall (hexagons) and heterotrophic respiration (stars) for the Doory forest stand. The vertical lines indicate the years in which the first (dashed) and second (dotted) thinning events were applied.

and a lower incident PAR (Fig. 1). However, only a small reduction in  $R_{eco}$  was observed (1.2%) resulting in a reduction in NEE of ~21% in this year. After the second thinning event, both GPP (9.9%) and  $R_{eco}$  (13.9%) were further reduced, resulting in a reduction in NEE of 4.1%.

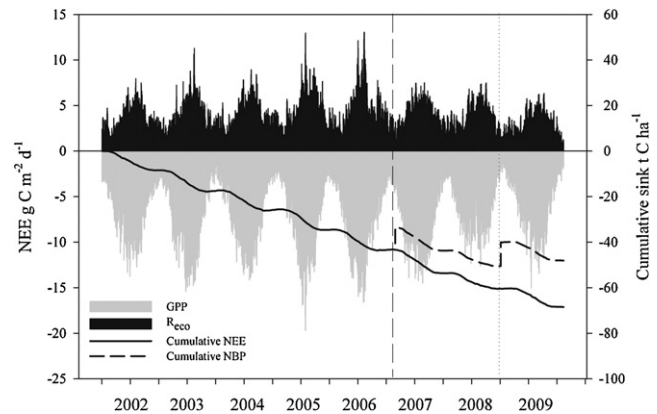
### 3.3. Thinning effects on net ecosystem exchange

The Doory forest acted as a net carbon sink during the experimental period with the NEE sink strength ranging from  $6.75 (\pm 1.19)$  to  $10.33 (\pm 1.41) \text{ t C ha}^{-1} \text{ yr}^{-1}$  (Table 1; Fig. 3). Prior to thinning NEE showed little inter-annual variation, and ranged from  $8.44 (\pm 1.34)$  to  $8.81 (\pm 1.09) \text{ t C ha}^{-1} \text{ yr}^{-1}$ , with a mean NEE of  $8.66 (\pm 1.43) \text{ t C ha}^{-1} \text{ yr}^{-1}$ . After thinning NEE showed increased variability, ranging from  $6.75 (\pm 1.19)$  to  $10.33 (\pm 1.41) \text{ t C ha}^{-1} \text{ yr}^{-1}$ , with a mean value of  $8.41 (\pm 1.42) \text{ t C ha}^{-1} \text{ yr}^{-1}$ . No significant differences were detected between the mean pre and post-thinning values of NEE, however the range of inter-annual variability in NEE was enlarged during the post-thinning period (Fig. 3).

Net primary productivity ranged between  $13.22 (\pm 3.72)$  and  $18.94 (\pm 4.88) \text{ t C ha}^{-1} \text{ yr}^{-1}$  across all years (Table 1; Fig. 3), although no significant differences were detected between the pre ( $16.10 \pm 5.97 \text{ t C ha}^{-1}$ ) and post thinning ( $15.13 \pm 4.70 \text{ t C ha}^{-1}$ ) estimates of mean NPP. The inter-annual variability in NPP and its constituent components are shown in Fig. 3 in addition to NEE and estimates of heterotrophic respiration ( $R_{het}$ ), which was determined as the difference between NPP and NEE. There was considerable inter-annual variability in NPP and  $R_{het}$  in the pre-thinning years, the dead biomass attached to the tree and litterfall both declined after thinning while fine root turnover (FRT) increased considerably after thinning.

Seasonal patterns of NEE were similar across all years (Fig. 4), with peak values for carbon uptake between  $14$  and  $19 \text{ g C m}^{-2} \text{ d}^{-1}$  associated with maximum mean daily temperatures and the highest irradiances. The highest carbon losses ranged between  $7$  and  $13 \text{ g C m}^{-2} \text{ d}^{-1}$  and were associated with higher temperatures and periods of peak plant productivity (Fig. 4).

The cumulative annual carbon sink showed distinct seasonal patterns with net carbon gains during the summers/growing seasons and carbon losses dominating winter periods. An estimate of the net biome productivity (NBP) of the forest over the study period



**Fig. 4.** Net ecosystem carbon exchange at the Doory forest stand from 2002 to 2009. Black shading denotes the daily loss of carbon through ecosystem respiration, gray shading denotes carbon uptake through GPP. The solid black line indicates the cumulative NEE-based carbon sink, while the dashed line indicates the cumulative NBP-based carbon sink, post thinning. The dashed vertical line indicates the timing of the first thin and the dotted vertical line indicates the timing of the second thin.

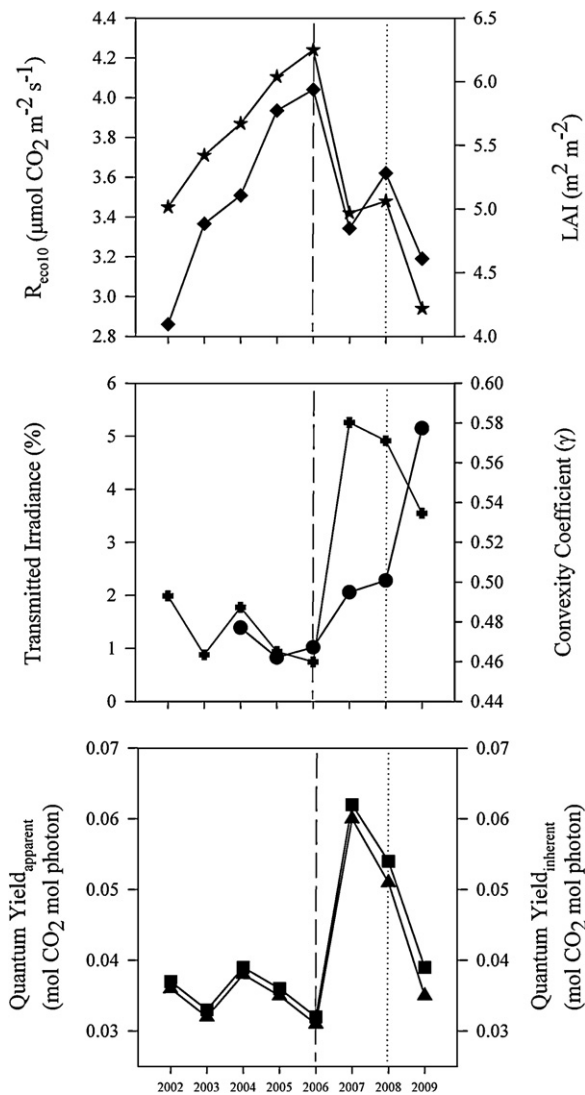
was determined by offsetting the carbon losses associated with timber removal from the site after thinning. The carbon removals, shown in Fig. 4, reduced the carbon sink strength of the forest from  $68.51 \text{ t C ha}^{-1}$  to  $48.1 \text{ t C ha}^{-1}$  over the study period.

The apparent and inherent quantum yield ( $\alpha$ ) and the convexity coefficient ( $\gamma$ ) of the stand for a  $5$ – $10^\circ \text{C}$  temperature range were determined by fitting the Leverenz (1995) light response function (Eq. (3)) to the high quality daytime (GPP) flux data. Prior to thinning  $\alpha_{apparent}$  varied from  $0.031$  to  $0.038 \text{ mol CO}_2 \text{ mol}^{-1} \text{ photon}$  but increased to  $0.060 \text{ mol CO}_2 \text{ mol}^{-1} \text{ photon}$  after the first thin (Fig. 5). The inherent quantum yield followed a similar inter-annual pattern and showed little variation from the  $\alpha_{apparent}$  values in any given year. In 2008  $\alpha_{apparent}$  decreased to  $0.051 \text{ mol CO}_2 \text{ mol}^{-1} \text{ photon}$  and in 2009 returned to pre-thin levels ( $0.035 \text{ mol CO}_2 \text{ mol}^{-1} \text{ photon}$ ). The convexity coefficient prior to thinning varied from  $0.46$  to  $0.49$ , increasing to  $0.58$  after the first thinning event (Fig. 5).

Values for ecosystem respiration at a temperature of  $10^\circ \text{C}$  ( $R_{eco10}$ ), determined by fitting the Lloyd and Taylor (1994) model to the nocturnal flux data, ranged from  $2.94 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  to  $4.24 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  across all years, with the higher values observed prior to the thinning event. Values of temperature-dependent  $R_{eco10}$  followed a similar inter-annual pattern to a number of biometric parameters, including LAI (Fig. 5).

## 4. Discussion

The ability of commercial forest plantations to sequester carbon may be reduced under active management strategies, such as thinning, which are designed to maintain timber production throughout the length of the forest rotation. Estimates of both NEE and NPP for the Doory study site are broadly comparable to other similar forest types across Europe (Berhofer et al., 2003; Medlyn et al., 2005; Forestry Commission, 2009), however, they represent one of the most productive forest types so far reported for this region (Van Dijk and Dolman, 2004; Luysaert et al., 2009a,b). The average NEE at the Doory forest stand over the eight year study period was  $8.39 (\pm 1.46) \text{ t C ha}^{-1}$ , approximately 9% higher than the average NEE reported for a Sitka spruce forest in Scotland of similar age and management (Forestry Commission, 2009). Although the Scottish site was of a lower yield class and associated with a different soil type, it highlights the significant potential for carbon sequestration through Sitka spruce afforestation in Ireland and the United Kingdom.



**Fig. 5.** Annual variation in ecosystem respiration normalised to 10°C (stars), leaf area index (diamonds), transmitted irradiance (circles), convexity coefficient (crosses), net stand apparent quantum yield (triangles) net stand inherent quantum yield (squares). The vertical lines indicate the years in which the first (dashed) and second (dotted) thinning events were applied.

The impacts of thinning practices on both NEE and NPP at the stand level will depend on the thinning intensity, site-specific climatic factors and the extent to which the remaining trees can compensate, in terms of enhanced carbon uptake, for those removed. Previous reports have indicated that forest thinning can have both a positive or neutral effect on net stand productivity and can also alter biomass allocation, as the removal of trees reduces intraspecific competition for resources, such as light, nutrients and water (Valinger, 1993; Mund et al., 2002; Shibuya et al., 2005; Vesala et al., 2005; Sabatia et al., 2010). In the current study, the thinning managements applied reduced the cumulative carbon sink of the stand due to the export of carbon in timber (Fig. 4), but did not significantly affect NPP, NEE, GPP or  $R_{eco}$ .

It might have been expected that the removal of biomass from the stand and the disturbance of the forest canopy would result in significant changes in NEE by altering both GPP and  $R_{eco}$  as has been observed in forests (Amiro et al., 2010) and grassland ecosystems (Soussana et al., 2007) when clear-fell harvest and silage cuts are taken, for example. In this study inter-annual variability in temperature was, in fact, shown to have a greater impact on the

components of NEE than any changes in the physical structure of the stand due to thinning (Fig. 2). Both GPP and  $R_{eco}$  were positively correlated with air temperature in the pre and post-thinning periods (Fig. 2), and the relative impact of forest thinning was shown to be temperature dependant. For example, based on the slope of the linear regressions (Fig. 2) there is evidence that the magnitude of the reduction in GPP is greatest at low temperatures after thinning. A possible explanation for this is that thinning results in the increased exposure of a greater proportion of the canopy foliage to sub-optimal temperatures, which in turn results in a reduction in stand level GPP.

The greatest reductions in  $R_{eco}$  were observed directly after each thinning event, which may be due to the changing contribution of both autotrophic and heterotrophic respiration to  $R_{eco}$ , associated with both biomass removal (Anderson-Teixeira et al., 2011) and a combined reduction in GPP (Woodward et al., 2010).

In this study, the impact of thinning could have either a neutral, negative or positive effect on NEE depending on temperature, which is the most important climatic factor at this forest site (Fig. 2). More information is required to adequately evaluate the influence of this type of forest management on net stand carbon assimilation across a broader geographical range, as the impacts of inter-annual climatic variability need to be identified first, especially where multi-year eddy-covariance data are considered.

Forest thinning practices are designed to open up the forest canopy, increasing light penetration and reducing the proportion of photosynthetically competent material that was previously light-limited. In this study the increase in transmitted light after thinning (Fig. 5) was consistent with similar studies on Sitka spruce (Hale, 2003). The first thinning event resulted in an increase in both the apparent and inherent quantum yield and the convexity coefficient of the stand, for a particular temperature class (Fig. 5), but did not alter the difference between the apparent and inherent quantum yield for any given year (Fig. 5). This indicates that changes in photosynthetic efficiency were not due to an increase in light absorption but due to an inherent change in the photosynthetic efficiency of the remaining trees. The increase in the inherent quantum yield and the convexity coefficient of the stand (Fig. 5) may be due to an increase in the photosynthesis of both existing and new needles (Leverenz, 1995; Ogren, 1993; Reich et al., 1995) and a corresponding reduction in intraspecific competition for resources such as light, nitrogen and water coupled with the improved microclimatic conditions, including an increase in air temperature within the forest canopy (Vesala et al., 2005). Increases in leaf level photosynthesis after thinning have also been reported for a paper birch stand (Wang et al., 1995) and a black walnut stand (Gauthier and Jacobs, 2009), and were attributed to an increase in light penetration and foliar nitrogen concentrations within the canopy.

The second thinning event did not stimulate a similar photosynthetic response (Fig. 5) that, we suggest, is a consequence of the way in which the thinning operations were undertaken. The first, predominantly systematic thinning event, removed entire rows of trees increasing the availability of resources to a greater number of trees in comparison to the second, selective thinning, where only select individual trees within the stand would have been affected.

The increased availability of resources after thinning has also been shown to alter tree allometry and contribute to the enhanced NPP of forest ecosystems (Valinger, 1993; Aber et al., 1998; Mund et al., 2002; Magnani et al., 2007; Campbell et al., 2009). An increase in light penetration and nitrogen availability after thinning enhanced growth in the lower crown of a Scots pine forest (Valinger, 1993), increased needle survival and production in a Sakhalin fir plantation (Shibuya et al., 2005) and increased shoot expansion and total leaf area in a loblolly pine plantation (Tang et al., 1999). In addition, thinning may alter the needle-age distribution of a forest canopy favoring the production of new needles lower

in the canopy that could contribute to a compensatory increase in the photosynthetic response at the stand level (Reich et al., 1995). However, such responses were not directly observed in the biometric surveys undertaken and might be expected to occur over a longer timeframe than reported in the present study.

Estimates of NPP were consistently higher than NEE throughout this study, but the year-to-year trends of both were markedly different (Table 1; Fig. 3). The differences between NPP and NEE can be attributed to carbon losses through heterotrophic respiration ( $R_{\text{het}}$ ) and, based on this definition, the data suggest that both prior to thinning and after the thinning managements had been applied, there was a large degree of variability in  $R_{\text{het}}$ . Carbon losses through  $R_{\text{het}}$  have been shown to vary significantly in response to both changing environmental variables and seasonal and annual variations in photosynthesis, carbon substrate production and utilisation, and total above and below ground carbon stocks (Hogberg et al., 2001; Jassal et al., 2007; Saiz et al., 2007; Anderson-Teixeira et al., 2011). In addition, carbon losses through  $R_{\text{eco}}$  have been shown to be more sensitive to inter-annual climatic variability than photosynthetic assimilation in coniferous forests (Morgenstern et al., 2004; Jassal et al., 2007). In this study the greatest variation in  $R_{\text{het}}$  prior to thinning was observed in the years where the largest increment in total live biomass was recorded (2004 and 2006) resulting in the variation in NPP observed in these years (Table 1; Fig. 3). Climate-dependent increases in biomass, coupled with changing above and below ground phenological characteristics and variation in the mobilisation and utilisation of stored carbohydrates, may have stimulated an increase in the decomposition of soil organic carbon in these years. The reduction in  $R_{\text{het}}$  observed in the year after the first thinning event is most likely due to changing biometric components, such as the reduction in live biomass associated with a systematic thinning event, rather than climate, as the highest mean annual temperatures were recorded in this year, which might otherwise have been expected to increase respiratory carbon losses (Fig. 2). Furthermore, the second selective thinning event did not stimulate a similar response, and  $R_{\text{het}}$  was observed to continually increase in the years after the first thinning event, possibly due to both the recovery of live biomass stocks, including an increase in fine root production after thinning (Table 1; Fig. 3) and also because of short-term increases in the decomposition of the residual material left after thinning.

The beneficial influence of forest thinning on tree growth responses in coniferous forest stands has been highlighted in a number of studies (Makinen and Isomaki, 2004; Sullivan et al., 2006; Roberts and Harrington, 2008). The Forestry Commission yield models (Edwards and Christie, 1981) suggest that a Sitka spruce stand with a yield class of 24 would produce a total timber volume of approximately  $84 \text{ m}^3 \text{ ha}^{-1}$  in the first and second thinning events, respectively. In this study, the first thinning event applied to the Doory forest stand removed a timber volume of  $48 \text{ m}^3 \text{ ha}^{-1}$  (42% lower than prescribed by the Forestry Commission yield models), while the second thinning, applied in close succession to the first, removed a timber volume of approximately  $50 \text{ m}^3 \text{ ha}^{-1}$  (40% lower than prescribed by the Forestry Commission yield models). The reduced thinning intensity applied at the Doory forest represents the site-specific prescriptive management associated with highly productive sites in Ireland, where light thinnings are applied at a greater frequency as dictated by the degree of forest productivity. In addition, lighter initial thinnings maintain the material to supply brush mat construction ensuring protection against soil damage during future management events while also minimising the risks associated with windthrow. Both the biometric and micrometeorological data suggest that the thinning activities applied in this study had little impact on short-term carbon sequestration, while climatic variables had a stronger influence on carbon uptake at this site. The reduction in the cumulative

carbon sink strength of these forests due to the carbon exported in timber may, however, be offset by the utilisation of thinning products or residues as a replacement for fossil fuels or more carbon intensive building materials.

## 5. Conclusions

This study investigated the impacts of forest thinning on standing carbon stocks and surface to atmosphere carbon fluxes. The thinning events did not have a significant effect on rates of carbon sequestration at this site, when pre and post thinning data were compared, however thinning increased the range of inter-annual variability in NEE. The cumulative carbon sink strength was reduced when carbon exports through timber removal were accounted for and any increases in dissolved carbon losses, for instance, that may be associated with forest thinning would need to be considered when calculating a more accurate estimate of the NBP of this ecosystem.

The impacts of the thinning events applied in this study were dependant particularly on temperature, although all climatic variables examined were shown to have a greater impact on the measured carbon pools and fluxes when compared to the disturbance associated with biomass removal through forest thinning. The expected decrease in NEE after thinning was not observed, due largely to the magnitude of the thinning management applied and the redistribution of carbon sources and sinks within the forest ecosystem, in particular the temperature related compensatory increase in photosynthesis by the remaining trees within the stand. The continuation of flux measurements at this site will provide more detailed information regarding the impacts of inter-annual climatic variability on a modified forest stand.

## Acknowledgments

The authors would like to thank the National Council for Forest Research and Development (COFORD) for providing funding for this research, Coillte for providing land access and forest management information, MET Eireann for additional meteorological data and Mr. D. Farrell for his continual logistical support in the field. The authors would also like to acknowledge the extensive contribution made to this paper by the review panel of Agricultural and Forest Meteorology.

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