

Dear Editor,

We thank the referees for their time and comments.

We would like to make a strong argument that this paper is an important contribution to the literature because it presents measurements of all the major components of NPP and respiration, AND compares them to the flux tower data, AND does this at seasonal resolution. The comparison between biometric and flux tower data provides an important cross-validation of the results which could not be achieved in any other way and strengthens the overall credibility of the science. Seasonal resolution is important within temperate forests to developing process understanding and identifying key sensitivities. We argue below that this has hardly been done for a temperate deciduous woodland, and include a table of previous studies to support our argument. Furthermore, we argue that our field site (ancient woodland) represents an important but understudied forest type that is distinct in characteristics from either old-growth or secondary forest. All these points make this paper a significant contribution to the literature that warrants publication in a high quality journal such as *Biogeosciences*.

Our responses to the reviewers' comments on our discussions manuscript are detailed here. Each reviewer's comments are addressed in turn, in the order in which they were received. Reviewers' comments are in *italics* our response is in normal type.

Dr. Werner Kutsch

Referee comment

The authors start their paper with the statement: "There exist very few comprehensive descriptions of the productivity and carbon cycling of forest ecosystems." Well, maybe they have a very special definition the term 'comprehensive' but I suppose that this statement does not stand a 'comprehensive' recherche of the existing literature. I have already published carbon balances including GPP and NPP in 2001 and 2005 and there is a huge database that was compiled and published by Sebastiaan Luysaert in 2007ff that shows that there are many data around. The authors should not ignore that because it devalues their otherwise very interesting study.

Author Response

The key point is the definition of comprehensive. In the context of this paper, we intend comprehensive to be sites where the major components of NPP and autotrophic respiration are estimated, giving a "bottom-up" estimate of carbon expenditure, and at the same time a "top-down" estimate of carbon intake from flux tower measurements. We accept the reviewer's point that we should have put this study in better context of what exists in the literature. To this end we include a table (Table 1., see below) that summarises the studies that we have found for temperate broadleaved woodlands (including those cited in the Luysaert et al 2007 paper; this table can be included in a revised version of the manuscript). We think we have identified all of the major published studies, although would happily include others if reviewers feel we have missed a study.

This table demonstrates that (i) a number of studies have reported components of NPP; (ii) very few studies have reported "bottom-up" biometric estimates of ecosystem autotrophic respiration and GPP (the excellent studies by Dr Kutsch being

a notable exception); (iii) very few sites report an eddy covariance estimate of GPP in conjunction with biometric estimates of NPP (the sites reported by Kutsch et al. again being an exception). Moreover, we could only find a few studies (e.g. Lavigne et al. 1997; Law et al. 1999) that explore the seasonal variation in respiration using both eddy covariance and bottom-up approaches – and these are both in coniferous forests.

In summary, we argue that the current study is an important contribution to the literature for temperate broadleaved forests because

1. It reports bottom-up estimates of the major components of NPP and R_{auto} to arrive at an estimate of GPP (previously it seems that only the Kutsch et al. sites have reported this for a temperate broadleaved woodland).
2. It compares the bottom-up results with an eddy covariance estimate of GPP and shows good agreement (none of the other sites in our table appear to do this). This allows the eddy covariance derived GPP to be partitioned into components.
3. It partitions ecosystem respiration into the various autotrophic and heterotrophic components.
4. It compares the seasonal variation in ecosystem respiration in bottom-up and top-down approaches and shows good agreement (none of the reported studies have done this). This allows the seasonal variation in respiration to be partitioned, and shows some surprises, such as the large role for stem respiration.
5. It does all this for an ancient woodland ecosystem; many previous temperate studies (especially in the US) have been on secondary forest (see discussion on definition of ancient woodland, below).

Based on the points above we would argue that this paper is an interesting and significant contribution to the literature. We recognise that we should have put this study in better context to the literature, have done so in preparing this response, and would include this context and table in our revised version.

Dr. Gerhard Wieser

Referee comment

This is a valuable paper on carbon fluxes in a temperate broad-leave woodland comparing eddy flux measurements with chamber based measurements of various ecosystem fluxes. The latter data were combined with woody biomass data for scaling up to the tree and finally to the stand level. This approach is not new although references to this method are missing. Nevertheless, concerning scientific questions I hardly can see a discussion of their results in the context of the broad body of literature recently published with respect to GPP, NPP and Reco among various woody-plant systems within different climatic regions.

Author Response

We are pleased that Dr. Wieser considers this a valuable paper. We agree that our discussion of the context of the results is too limited (see response to Referee 1 above), also that references to support our methods are needed in some places. We would happily remedy these points in a revised version of the manuscript. We can also extend this by placing the temperate woodland studies in a global biome context.

Anonymous Reviewer

Referee comment

General comments: This is an occasionally useful addition to the literature on forest carbon cycling that uses standard measurement methods and many modeled inputs to construct a short-term carbon budget for an English deciduous woodland. Its pairing with eddy covariance results provides a potentially useful constraint on the annual flux estimates, although the lack of plot location information relative to the flux footprint compromises this comparison. The seasonal dynamics and annual NPP, Reco, and GPP estimates are unsurprising, but the relative contribution of ecosystem components to these estimates is. Particularly, the low relative contribution of soils and the high relative contribution of stems to Reco and the low ecosystem carbon use efficiency.

Author Response

The flux tower is located in the centre of the one hectare study, and hence we believe the biometric plot provides a reasonable sample of the tower footprint (see footprint analysis in companion paper by Thomas et al.). There is only limited “modelling” of inputs in our carbon budget, beyond using a mass conservation approach to estimate root production (a frequently used approach) and application of temperature correction and light inhibition to the leaf respiration estimates.

The seasonal dynamics may be “unsurprising” but we argue that (to the best of our knowledge) no previous studies have looked at this using bottom-up and top-down approaches at stand level in a broadleaf forest. It is using this approach that reveals surprises that would have otherwise been missed and this is a significant part of the novelty of this paper.

Referee comment

Given the scarcity of belowground measurements in this study and the many assumptions involved with scaling point measurements of stem ‘respiration’ to entire trees and stands, the component data presented in Table 2 must be viewed skeptically. The reported error estimates to these numbers unfortunately have little bearing on their accuracy.

Author Response

It is challenging to measure and scale stem respiration, and the potential systematic errors can affect accuracy. That is precisely why the inclusion of a top-down constraint adds value, and the seasonal (rather than annual) time resolution adds value. By showing (we think for the first time) that the seasonal bottom-up components sum up to the eddy covariance estimate, we argue that we do seem to be capturing the big picture of the major components of respiration. Of course it is possible that opposing biases cancel each other and this should be recognised, but the most parsimonious explanation is that both top-down and bottom-up approaches are broadly correct, greatly increasing confidence in both approaches. The fact that this combination of approaches also seems to work in other forest ecosystems (e.g. tropical forests: Malhi et al. 2009, *Global Change Biology*) also increases confidence that this is a good approach for integrating and reconciling both biometric and eddy covariance studies.

Referee comment

Specific comments: The authors’ statement in the abstract that there are ‘very few comprehensive descriptions of the productivity and carbon cycling of forest ecosystems’ simply is untrue. A little time spent in the publications section of the

Fluxnet website (which is itself incomplete) will reveal a wealth of forest carbon cycling information, comprehensive and otherwise. It is interesting that nothing from the many studies conducted at Harvard Forest are referenced in this paper.

Author Response

See our response to referee 1 above. We recognise that we did not put this study in enough context of the available literature. However, as we have argued in response to Referee 1, there genuinely are very few comprehensive descriptions of the productivity and C cycling of temperate deciduous semi natural ecosystems. We checked through the list of Fluxnet publications online (2006-2010) as suggested by the Anonymous Reviewer; none dealt with the NPP of mixed deciduous temperate woodland, or integrated NPP, autotrophic respiration and flux tower measurements to provide a comprehensive description of the forest carbon cycle.

Referee comment

In the Methods section, 'companion papers' are mentioned, but never listed. We are given one dissertation and a submitted manuscript. This is not helpful.

Author Response

The challenge here is that the other papers have been submitted to other journals and have yet to be accepted (one, on soil respiration, has been accepted). We welcome the Editor's advice. We can either include references to the papers as "submitted", or refer to the completed PhD Thesis (Fenn 2009, Oxford University) from which this work derives, or cite 'unpublished analysis'. The reference to the companion Thomas et al. paper (which focuses on the eddy covariance analysis) has been kept.

We note that no criticism is made of the detail of the methods themselves by the Anonymous Reviewer, so it is hoped that these are sufficient for potential study replication. However, we would be willing to include more methodological detail as an appendix if the Editor considers this useful.

Table 1. Studies of temperate deciduous woodlands which have both above and below ground NPP estimates and eddy covariance measurements of GPP and/or R_{ECO} . Errors, where provided, are ± 1 standard error. # indicates that the values are calculated from data presented in the referenced study.

Biometric NPP	Biometric ANPP	Biometric BNPP	Biometric GPP	Biometric R_{ECO}	Eddy Flux GPP	Eddy Flux NEE	Eddy Flux R_{ECO}	Location	Ecosystem	Study
			All	Mg C ha ⁻¹	yr ⁻¹					
7.04 \pm 0.84	4.42 \pm 0.26	2.62 \pm 0.80	20.3 \pm 1.0	18.9 \pm 1.7	21.1	1.2	19.8	Wytham, UK	Temperate mixed deciduous	This study & companion paper
17.7	13.9	3.7	-	-	-	-	-	De Inslag, Belgium	Temperate <i>Quercus robur</i> L. stand	Curiel Yuste et al. (2005)
7.27	5.39	1.88 #	-	-	-	5.77	-	Walker Branch, USA	Eastern Broadleaf Forest (Oceanic)	Curtis et al. (2005)
10.49	5.29	5.20	-	-	-	2.36	-	Morgan Monroe State Forest, USA	Eastern Broadleaf Forest (Continental)	Curtis et al. (2005)
5.65	3.20	2.45	-	-	-	2.00	-	Harvard Forest, USA	Lower Mississippi Riverine Forest	Curtis et al. (2005)
6.39	3.38	3.01	-	-	-	1.67	-	University of Michigan Biological Station, USA	Laurentian Mixed Forest	Curtis et al. (2005)
5.11	3.00	2.11	-	-	-	2.20	-	Willow Creek, USA	Laurentian Mixed Forest	Curtis et al. (2005)
11.32 (0.57)	10.44 (0.53)	0.88 (0.13)	-	-	-	-	-	POPFACE site, Italy	<i>Populus alba</i> , control.	Gielen et al. (2005)
14.94 (0.04)	13.76 (0.17)	1.18 (0.13)	-	-	-	-	-	POPFACE site, Italy	Calculated for 2nd year, 3 rd year	
14.37(0.31)	13.40 (0.42)	0.98 (0.11)	-	-	-	-	-	POPFACE site, Italy	<i>P. nigra</i> , control.	Gielen et al. (2005)
19.83 (0.13)	17.81 (0.49)	2.02 (0.15)	-	-	-	-	-	POPFACE site, Italy	Calculated for 2nd year, 3 rd year	
11.310 (0.35)	10.31(0.31)	1.00 (0.24)	-	-	-	-	-	POPFACE site, Italy	<i>P. x euramericana</i> , control.	Gielen et al. (2005)
15.33 (0.71)	13.51 (0.70)	1.82 (0.17)	-	-	-	-	-	POPFACE site, Italy	Calculated for 2nd year, 3 rd year	
6.54 \pm 0.76	3.45 \pm 0.60 (including groundflora)	3.09 \pm 0.46	-	-	-	-	-	University of Michigan Biological Station, USA	Reference 85 year old temperate/boreal mixed	Gough et al.(2007)
6.56	5.49 #	1.07	10.47	6.98	-	-	-	Bornhöved Lake District, Germany	Temperate <i>Fagus sylvatica</i> L. (mean)	Kutsch et al. (2001)
8.43	5.38 #	3.05	21.50	17.94	-	-	-	Bornhöved Lake District, Germany	Temperate <i>Alnus glutinosa</i> (mean)	Kutsch et al. (2001)
11.30	8.87 #	2.16 #	-	-	17.94	-	12.35	Kannenbruch Forest, Germany	Temperate <i>Quercus robur</i> L.	Kutsch et al. (2005)
7.02	5.45 #	1.57 #	-	-	14.70	-	11.74	Kannenbruch Forest, Germany	Temperate <i>Fagus sylvatica</i> L.	Kutsch et al. (2005)
6.71	4.54 #	2.20 #	-	-	15.94	-	14.01	Kannenbruch Forest,	Temperate <i>Alnus glutinosa</i>	Kutsch et al. (2005)

19.37 ± 1.10	15.94 ± 0.67 #	344 ± 0.11	-	-	-	-	-	Germany	(L.) Gaertn. / <i>Fraxinus excelsior</i> L.	
5.74 (tree census)	5.32 #	0.42 (coarse roots)	-	-	-	-	-	Oak Ridge National Environmental Research Park, USA	<i>Liquidambar styraciflua</i> FACE (ambient CO ₂ , mean 1998-2000)	Norby et al. (2002)
8.8 to 14.1	5.6 to 8.5	1.5 to 7.7	-	-	-	-	-	Takayama Forest Research Station, Japan	Secondary temperate mixed deciduous	Ohtsuka et al. (2005)
-	-	-	-	-	-	2.42	11.5	Ashiu Forest, Japan	Cool temperate deciduous on N gradient	Tateno et al. (2004)
8.02	3.45 #	4.57 (fine roots)	-	-	10.16 (GEP)	4.72 (NEP)	5.44	Harvard Forest, USA	Temperate mixed <i>Quercus rubra</i> , <i>Acer rubrum</i> , & coniferous spp.	Urbanski et al. (2007)
								Collelongo, Italy	Temperate, mainly <i>Fagus sylvatica</i> L.	Valentini et al. (1996)

Referee comment

The Morecroft et al. 2008 paper cited as providing background information on the site is missing from the cited literature list.

Author Response

The Morecroft et al. (2008) reference has been added to the list and the Stokes et al. (2010) reference updated from "In Press".

Referee comment

A general problem is that we are given virtually no information on stand characteristics in this paper: stand area, tree age distribution, total basal area, maximum LAI, position relative to the flux tower, etc.

Author Response

Information on total basal area, maximum LAI and position of the flux tower has been added to the Methods section. Stand area of 1 ha was already given in the submitted manuscript. Tree size distributions, as a basic proxy for tree age distributions, of the three main species are given in Table 2.

Referee comment

For many readers, 'ancient woodland' suggests something like 'old growth forest', but that evidently is not the case here. Indeed, the trees in this stand may be relatively young.

Author Response

Ancient woodland has a specific definition in the UK, being that which has had a continuity of forest cover (i.e. no clear felling) since 1600 (the approximate date of the earliest reliable records for most sites) (Peterken & Game 1984). Forest management has taken place during this time and the site was maintained as coppice with (mainly *Q. robur*) standards but returned to high forest in the twentieth century. This twentieth century growth has resulted in some young trees being present; the DBH range of trees studied, as an approximate indicator of age, can be seen in Table 2. Even in undisturbed ancient woodland, natural mortality and regeneration will mean trees of a range of ages may be present.

It is important to understand that in various parts of the temperate zone, including the UK, there is a long history of forest management and true old growth or virgin forest is effectively absent. Ancient woodland (and similar designations) represent the most valuable conservation sites and are of great interest as relatively stable communities with a semi-natural composition and undisturbed soils.

Hence ancient woodland is not old-growth forest, but is land that has, almost certainly, had continuous tree cover (and associated features, such as unploughed soils) over most of the Holocene. As such it is a forest type that is distinct from both old-growth forest and usual secondary forest; these features also make the current study a novel contribution to the literature.

Referee comment

How representative is the 1 ha plot studied here to the rest of this forest?

Author Response

Figure 3 in a report on the Wytham Smithsonian CTFS site (Butt et al. 2009, <http://www.eci.ox.ac.uk/publications/downloads/butt09-wythamwoods.pdf>) contains the 1 ha study plot in the top left (north west) corner of a larger 18 ha (300 m by 600 m) plot. This figure provides the species of all trees over 1 cm DBH, showing the 1

ha plot to be homogeneous in terms of tree species with surrounding forest for approximately 300m in the south-west direction. The surrounding forest is also similar to that of the plot in the east and south-east directions. Directly to the north there is a beech (*Fagus sylvatica* L.) plantation. The majority of eddy covariance fluxes are brought with the prevailing winds from the south-west of the plot (companion paper by Thomas et al.). We can include this context in a revised paper.

Referee comment

For the allometric equations used to estimate tree biomass, were the size of harvested trees comparable to those in the study plot? These equations may be very problematic if larger trees are being measured for DBH than were harvested and weighed (a common occurrence).

Author Response

The DBH of *A. pseudoplatanus*, *F. excelsior* and *Q. robur* trees in Meathop wood, on which the allometric equations were based (Bunce 1968), and those from the study plot, are given in Table 2. From this it can be seen that the study trees were within the range of those used for production of the allometric equations, except *A. pseudoplatanus*, where 13 of the 196 trees measured (6.6 %) were below the lower DBH of 11.5 cm.

Table 2. Number and DBH range of *Q. robur*, *F. excelsior* and *A. pseudoplatanus* trees harvested in Meathop wood (Bunce 1968) for allometric equation production, and DBH range of these species measured in this study and on which the allometric equations were used.

	Meathop n	Meathop diameter (cm)	Wytham diameter (cm)
<i>Q. robur</i>	20	14.0 – 162.5	44.83 – 117.82
<i>F. excelsior</i>	15	9.0 – 104.0	9.97 – 41.77
<i>A. pseudoplatanus</i>	10	11.5 – 96.5	9.5 – 67.65

Referee Comment

How were coarse woody debris and reproductive inputs calculated?

Author Response

Coarse woody debris (CWD) production ($\text{Mg C ha}^{-1} \text{ year}^{-1}$) was calculated as equal to trees lost through mortality ($\text{Mg C ha}^{-1} \text{ year}^{-1}$) over the four years of the study (M_{AG} in equations 4 and 5), as explained in section 2.3. M_{AG} was equal to $0.037 \pm 0.018 \text{ Mg C ha}^{-1} \text{ year}^{-1}$. The inputs of this CWD into the soil (F_{CWD}) were taken to be 0.25 ± 0.25 , i.e. somewhere between 0 and 50%; the reasoning behind this conservative estimate is also outlined in section 2.3.

Reproductive inputs were estimated by the mass of reproductive structures collected in the litter traps present in the plot. This is probably an underestimate due to herbivory, in particular of acorns (*Q. robur* nuts). We agree that the explanation of this method was needed, and has now been added as the new section 2.4.

Referee Comment

Were any attempts made to measure herbivore losses? They are assumed to balance new leaf production post canopy closure, but is the LAI 2000 sensitive enough to base this assumption on?

Author Response

Herbivore losses were not measured directly during this study. Crawley (1985) found that *Q. robur* trees lost 8-12% of their foliage to herbivorous insects. Whitaker and Warrington (1985) found *A. pseudoplatanus* leaf loss to herbivory to be 1-1.6% and 6-10% in areas where ants did and did not forage on trees (reduced herbivore load), respectively. Without knowing the herbivore populations during this study, their effect cannot be determined, but taking these previous findings as a guide, actual leaf production could be assumed to be approximately 10% greater than the measured leaf production. We can include this uncertainty in our error propagation calculations in a revised version. No major outbreaks of defoliating insects were noted during the study.

Referee Comment

How sensitive are the daily and seasonal estimates of leaf respiration to the assumption of $Q_{10} = 2$? There are many reports in the literature of significant deviations from that value, with temperature acclimated plants typically having lower Q_{10} and unacclimated plants have a higher Q_{10} .

Author Response

Leaf respiration can have some uncertainty in Q_{10} values. We can include a revision to our error uncertainty propagation using Q_{10} values from 1.5 to 3.0 as possible ranges for the error estimates on leaf respiration.

Referee Comment

The description of methods for measuring stem respiration leave many important questions unanswered. For example, were temperature relationships established or assumed so as to adjust spot measurements for variation in ambient temperatures?

Author Response

We are sorry for being so concise in our description of methods (an as-yet unpublished companion paper focuses entirely on stem respiration). We can include more details in a revised version. Further details are given here.

Measured stem CO_2 efflux was used in a Q_{10} equation, as below, to adjust measured efflux rates for hourly air temperature variation and then create hourly estimates of stem CO_2 efflux throughout the year.

$$R_{\text{STEM}} = (R_M \cdot Q_{10})^{[(T_2 - T_1)/10]}$$

R_M is the mean CO_2 efflux from all trees per measurement session, both *A. pseudoplatanus* and *F. excelsior*. Q_{10} is taken to be 2. Measurement temperature (T_1) was the average air temp ($^{\circ}\text{C}$, from Wytham ECN monitoring) at the time of each monthly measurement session (09:00 to 12:00 on each given day). T_2 was hourly mean air temperature ($^{\circ}\text{C}$, from Wytham ECN site). No efflux data exist for January to March and December, so the mean rate for November and April ($0.53 \mu\text{mol CO}_2 \text{ m}^2 \text{ sec}^{-1}$, monthly means 0.54 and $0.52 \mu\text{mol CO}_2 \text{ m}^2 \text{ sec}^{-1}$ respectively) was used.

Hourly R_{STEM} was then multiplied by the calculated stem area of the plot (1.88 ha) and summed for each month.

The description of this was erroneously missing from section 2.7 of the manuscript, and we are grateful to the Anonymous Reviewer for bringing this to our attention. The version in section 2.7 was left from a previous analysis; this mistake must be attributed to the first author becoming forgetful as her PhD drew to a close!

Referee Comment

How was bole temperature measured (if at all)? Were the south facing measurements (presumably warmer) representative of other sides of the tree?

Author Response

Bole temperature was not regularly measured, but a diurnal cycle of bole temperature on north and south faces of one tree was recorded on 30th October 2008 using thermocouples. Fig. 1 shows the south side of the bole to be slightly higher than the north around late morning and midday on this autumn day, and it can be assumed that the difference is greater on warmer days due to a greater difference in insolation. Assuming that stem respiration, and therefore CO₂ efflux, is locally sensitive to temperature, then the efflux rates reported may be seen as maximum estimates, having all been consistently taken on the south side of the study trees. However, previous work has found CO₂ efflux from branches and twigs to be greater than that of the stem (Ceschia et al. 2002), so in that sense the values here could be an underestimate.

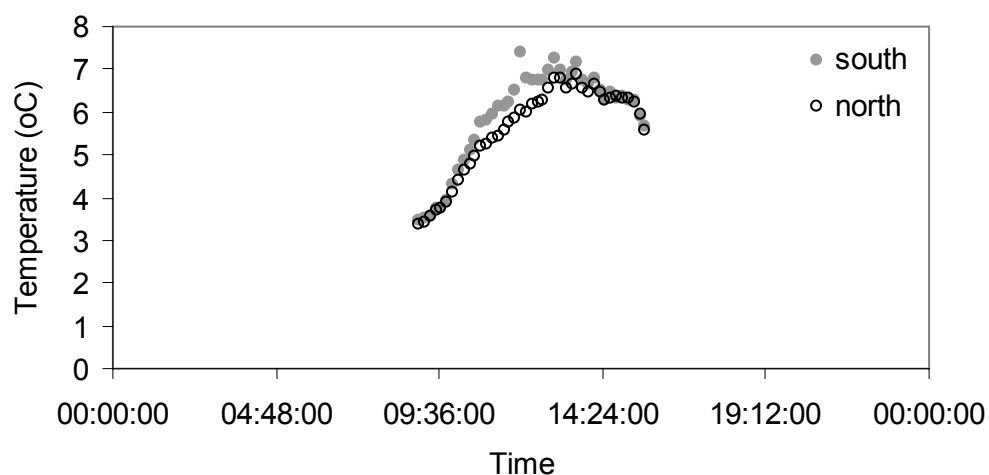


Fig. 1. Bole temperature of a tree in the study plot during daylight hours on 30.10.08.

Referee Comment

Did bole surface CO₂ flux show any relationship to sap flow? If so, it is likely that other sources of CO₂ were contributing to the flux in addition to the underlying sapwood.

Author Response

Sap flow was not measured in this study, so no relationship was established between stem CO₂ efflux and sap flow. We realise that the CO₂ efflux from the stem may result wholly from respiration, or contain some CO₂ diffusing from the transpiration stream (Teskey & McGuire 2002; Teskey et al. 2008), and, to clarify this, the efflux is now only referred to as 'stem CO₂ efflux' throughout the paper. In the discussions manuscript it was referred to as both 'stem respiration' and 'stem CO₂ efflux'; we acknowledge this was ambiguous.

Despite the origin of the CO₂ effluxing from the stems being unknown, the rates presented are as measured effluxing from the trees, and as such are a part of the C cycle of the plot. Our overall bottom-up scaling of respiration is unaffected, as excess CO₂ efflux from stems is balanced by too little efflux from soils. To not

present them due to their origin being unknown would be to miss an element of this cycle.

Referee Comment

Do we have any idea how accurate Equation 8 is in predicting total woody surface area of trees in an ancient woodland? How do their absolute values compare with other reports from deciduous forests of similar basal area?

Author Response

Equation 8, used to scale up from ABW (kg) to stem surface area (m²) was devised by Whitaker and Woodwell (1967) from trees harvested at the Brookhaven and Oak Ridge National Laboratory Centres. It was chosen for use here as it was devised using species similar to those in this study, in particular three *Quercus* species the deciduous *Liriodendron tulipifera* and shrubby *Rhododendron maximum*. It is this species similarity, rather than the woodland classification per se, that we felt to be most important. Ideally individual equations specifically for each of the study species would have been used, but these were not found. As the species are not identical there is room for inaccuracy, but this equation, we believe, provides the best estimate available for our species at the time of analysis. There are very few allometric equations available for stem area for trees.

Referee Comment

Because of these issues, and others, I have little confidence in the scaled measurements of stem respiration reported here.

Author Response

Very few studies have attempted to scale respiration to stand level. The fact that we do so here is noteworthy. Also, we repeat a point we make above, that the patterns agree both in magnitude and seasonal cycle with the eddy covariance-derived respiration fluxes. This provides a crucial extra crux to suggest our scaling is broadly correct. A sceptical reviewer may wish to argue that it is also coincidence with hidden errors cancelling each other, but should at least acknowledge the novelty of comparing with top-down constraints. We would argue that this makes this paper an important contribution to the literature.

Referee Comment

In the Discussion the authors point to their belowground NPP data and remark that traditional studies focus on more easily measured aboveground components. I find this a bit remarkable given that with the exception of soil respiration, virtually all their belowground results are built upon untested model assumptions, rather than direct measurements. We really have no idea how accurate they are.

Author Response

We think “untested model assumptions” is a very unfair description of our belowground NPP estimates; perhaps we failed to provide sufficient detail for the reviewer to understand our approach to below-ground NPP?

Fine root production was estimated using a version of the mass balance or total below ground carbon allocation (TBCA) method, using measured inputs and respiration rates (Davidson et al. 2002; Giardina and Ryan 2002). This approach is thought to be fair in situations where soil C is at or near steady-state (we have no reason to assume otherwise here) and is widely acknowledged to be a reasonable field measurement approach to estimate NPP. Tree mortality and leaf litter available as inputs of C to the soil were based on measured data. The fractions of these

inputs actually entering the soil were unknown, but large, conservative errors were employed to reflect this.

Here coarse root productivity was estimated to be 20% of above ground woody production, this method was also reported in the Curtis et al. (2002) paper, referenced in Table 1. This is a small component and has little influence on our overall budget.

References

- Ceschia, É., Damesin, C., Lebaube, S., Pontailler, J.-Y., Dufrene É.: Spatial and seasonal variations in stem respiration of beech trees (*Fagus sylvatica*). *Annals of Forest Science*, 58, 801-812, 2002
- Crawley, M.: Reduction of oak fecundity by low-density herbivore populations. *Nature, Letters*, 314, 163-164, 1985
- Curiel Yuste, J., Konôpka, B., Janssens, I.A., Coenen, K., Xiao, C.W., Ceulemans, R.: Contrasting net primary productivity and carbon distribution between neighboring stands of *Quercus robur* and *Pinus sylvestris*. *Tree Physiology*, 25, 701-712, 2005
- Curtis, P.S., Hanson, P.J., Bolstad, P., Barford, C., Randolph, J.C., Schmidt, H.P., Wilson, K.B.: Biometric and eddy-covariance based estimates of annual carbon storage in five eastern North American deciduous forests. *Agricultural and Forest Meteorology*, 113, 3-19, 2002
- Davidson, E.A., Savage, K., Bolstad, P., Clark, D.A., Curtis, P.S., Ellsworth, D.S., Hanson, P.J., Law, B.E., Luo, Y., Pregitzer, K.S., Randolph, J.C., Zak, D.: Belowground carbon allocation in forests estimated from litterfall and IRGA-based soil respiration measurements. *Agricultural and Forest Meteorology*, 113, 39-51, 2002
- Giardina, C.P. & Ryan, M.G.: Total belowground carbon allocation in a fast-growing eucalyptus plantation estimated using a carbon balance approach. *Ecosystems*, 5, 487-499, 2002
- Gielen, B., Calfapietra, C., Lukac, M., Wittig, V.E., De Angelis, P., Janssens, I.A., Moscatelli, M.C., Grego, S., Cotrufo, M.F., Godbold, D.L., Hoosbeek, M.R., Long, S.P., Miglietta, F., Polle, A., Bernacchi, C.J., Davey, P.A., Ceulemans, R., Scarascia-Mugnozza, G.E.: *Tree Physiology*, 25, 1399-1408, 2005
- Gough, C.M., Vogel, C.S., Harrold, K.H., Georges, K., Curtis, P.S.: The legacy of harvest and fire on ecosystem carbon storage in a north temperate forest. *Global Change Biology*, 13, 1935-1949, 2007
- Kutsch, W.L., Eschenbach, C., Dilly, O., Middelhoff, U., Steinborn, W., Vanselow, R., Weisheit, K., Wötzel, J., Kappen, L.: The carbon cycle of contrasting landscape elements of the Bornhöved Lake District. *Ecological Studies*, 147, 75-95.
- Luyssaert S., Reichstein M., Schultze E.-D., Janssens I.A., Law B.E., Papale D., Dragoni D., Goulden M.L., Granier A., Kutsch W.L., Linder S., Matteucci G., Moors E., Munger J.W., Pilegaard K., Saunders M. Falge E.M. (2009) Toward a consistency cross-check of eddy covariance flux-based and biometric estimates of ecosystem carbon balance. *Global Biogeochemical Cycles*, 23, 2001

Lavigne, M.B., Ryan, M.G., Anderson, D.E., Baldocchi, D.D., Crill, P.M., Fitzjarrald, D.R., Goulden, M.L., Gower, S.T., Massheder, J.M., McCaughey, J.H., Rayment, M., Striegl, R.G.: Comparing nocturnal eddy covariance measurements to estimates of ecosystem respiration made by scaling chamber measurements at six coniferous boreal sites. *Journal of Geophysical Research*, 102, 28977-28985, 1997

Law, B.E., Ryan, M.G., Anthoni, P.M.: Seasonal and annual respiration of a ponderosa pine ecosystem. *Global change Biology*, 5, 169-182, 1999

Malhi, Y., Aragão, L.E.O.C., Metcalfe, D.B., Paiva, R., Quesadas, C.A., Almeida, S., Anderson, L., Brando, P., Chambers, J.Q., DaCosta, A.C.L., Hutrya, L.R., Oliveira, P., Patiño, S., Pyle, E.H., Robertson, A.L., Teixeira, L.M.: Comprehensive assessment of carbon productivity, allocation and storage in three Amazonian forests. *Global Change Biology*, 15, 1255-1274, 2009

Norby, R.J., Hanson, P.J., O'Neill, E.G., Tschaplinski, T.J., Weltzin, J.F., Hansen, R.A., Cheng, W., Wullschleger, S.D., Gunderson, C.A., Edwards, N.T., Johnson, D.W.: Net primary productivity of a CO₂-enriched deciduous forest and the implications for carbon storage. *Ecological Applications*, 12, 1261-1266, 2002

Ohtsuka, T., Akiyama, T., Hasimoto, Y., Inatomi, M., Saki, T., Jia, S., Mo, W., Tsuda, S., Koizumi, H.: *Agricultural and Forest Meteorology*, 134, 27-38. 2005

Teskey, R.O. & McGuire, M.A.: Carbon dioxide transport causes errors in estimation of rates of respiration in stems and branches of trees. *Plant, Cell and Environment*, 25, 1571-1577, 2002

Teskey, O.R., Saveyn, A., Steppe, K., McGuire, M.A.: Origin, fate and significance of CO₂ in tree stems. *New Phytologist*, 177, 17-32, 2008

Urbanski, S., Barford, C., Wofsy, S., Kucharik, C., Pyle, E., Budney, J., McKain, K., Fitzjarrald, D., Czkowsky, M., Munger, J.W.: Factors controlling CO₂ exchange on timescales from hourly to decadal at Harvard Forest. *Journal of Geophysical Research*, 112, 2007

Valentini, R., De Angelis, P., Matteucci, G., Monaco, R., Dore, S., Scarascia Mugnozza, G.E.: Seasonal net carbon dioxide exchange of a beech forest with the atmosphere, 2, 199-207, 1996

Whittaker, J.B. & Warrington, S.: An experimental field study of different levels of insect herbivory induced by *Formica rufa* predation on sycamore (*Acer pseudoplatanus*) III. Effects on tree growth. *Journal of Applied Ecology*, 22, 797-811, 1985