Understanding the effect of disturbance on the carbon dynamics of a managed woodland DRAFT

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Key Points:

- No change was found in net ecosystem carbon uptake after selective felling
- Data assimilation was used to investigate effect of this disturbance
- Concurrent reduction in respirations and photosynthesis found to allow for unchanged carbon uptake

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Abstract

The response of forests and terrestrial ecosystems to disturbance is an important process in the global carbon cycle in the context of a changing climate. Disturbance can take many forms, for example; felling, fire and insect outbreak. In current estimates of the global carbon budget, disturbance is one of the least understood components. In this paper, we investigate the effect of the management practice f selective felling on the carbon dynamics of a mature temperate woodland. In order to better understand ecosystem response we use the mathematical technique of data assimilation to combine a diverse set of observations with a mathematical model of ecosystem carbon balance. Data assimilation combines the uncertainty from observations and prior model predictions to find the best possible estimate to the studied system. We develop new data assimilation techniques allowing for the assimilation of daytime and nighttime net ecosystem exchange observations with a daily time-step model. This allows for the assimilation of much otherwise neglected carbon flux information. The presented techniques allow us to estimate the effect of step-changes in ecosystem composition on the parameter and state variables in a modelled estimate of forest carbon balance. These techniques are applicable to other ecosystem models and data assimilation schemes. Previous statistical analyses of eddy covariance data at the study site had suggested that disturbance from selective felling (thinning) resulted in no change to the net carbon uptake of the ecosystem. We show that this is likely due to reduced ecosystem respiration post-disturbance compensating for a reduction in gross primary productivity. Our results support the theory of an upper limit of forest net carbon uptake due to the magnitude of ecosystem respiration scaling with gross primary productivity.

1 Introduction

1.1 Role of disturbance in the global C cycle

Disturbances to terrestrial ecosystems (e.g. felling, fire or insect outbreaks) can have significant effects on net land surface carbon uptake. The response of forests and terrestrial ecosystems to disturbance is one of the least understood components in the global carbon cycle [*Ciais et al.*, 2014]. Land surface models fail to represent the effect of disturbances on long-term carbon dynamics [*Running*, 2008]. The disturbance of forests can have varying degrees of severity; ranging from stand replacing disturbance, where tree

mortality is close to 100%, to non-stand replacing disturbance, where a proportion of total trees are lost.

1.2 Current theories on terrestrial ecosystem response to disturbance

In this paper we investigate the effect of selective felling (thinning) on the carbon dynamics of a mature deciduous forest stand. Thinning is a globally widespread silvicultural practice used to improve ecosystem services or the quality of a final tree crop. The effect of thinning on carbon budgets has largely been ignored [*Liu et al.*, 2011]. It would be logical to assume that after thinning we would see a reduction in the net carbon uptake of an ecosystem. Presumably due to reduced Gross Primary Productivity (GPP) following a reduction in total leaf area and unchanged or heightened ecosystem respiration due to an input of brash and woody debris to the forest floor. However, previous studies, analysing flux-tower eddy covariance records, find no significant change in the observed net ecosystem exchange (NEE) of CO_2 after thinning [*Vesala et al.*, 2005; *Wilkinson et al.*, 2015; *Moreaux et al.*, 2011; *Dore et al.*, 2012]. These studies suggest this is due to increased light availability and reduced competition allowing ground vegetation to display increased GPP and compensate for an increase in heterotrophic respiration post-disturbance.

Other studies have shown a significant reduction in the carbon content of rhizosphere soils following tree felling [*Hernesmaa et al.*, 2005]. It has been shown that tree roots provide a rhizosphere priming effect, greatly increasing the rate of soil organic carbon decomposition [*Dijkstra and Cheng*, 2007], suggesting a decrease in respirations following thinning. This is consistent with work carried out at the study site of focus in this paper, where it has been shown that the magnitude of ecosystem respiration is strongly coupled to the magnitude of GPP [*Heinemeyer et al.*, 2012]. Predictions made by *Kurz et al.* [2008] about the impacts of mountain pine beetle outbreaks in Northern America estimated the migration of forests from sinks to sources of carbon following this insect disturbance. However, the analysis of a diverse set of observations for an area with approximately 70% infested trees by *Moore et al.* [2013] revealed little change in net CO_2 flux, due to concurrent reductions in gross primary productivity and ecosystem respiration. Similar results are also found from large scale tree girdling experiments [*Högberg et al.*, 2001], where 1-2 months after girdling a 54% decrease in soil respiration is observed.

1.3 The role of data assimilation for improving estimates to a system

Data assimilation is a mathematical technique for combing observations with prior model predictions in order to find the best estimate to a studied system. Functional ecology models have been combined with many different observations relevant to the carbon balance of forests [*Zobitz et al.*, 2011; *Fox et al.*, 2009; *Richardson et al.*, 2010; *Quaife et al.*, 2008; *Zobitz et al.*, 2014; *Niu et al.*, 2014]. Leading to improved estimates of model parameter and state variables and reduced uncertainty in model predictions. Although there has been many efforts to model the effect of disturbance on forest ecosystems [*Seidl et al.*, 2011; *Thornton et al.*, 2002], the use of data assimilation has been limited, with only a few examples using satellite data [*Kantzas et al.*, 2015; *Hilker et al.*, 2009]. The authors are not aware of any studies assimilating site level data to quantify disturbance effects. By assimilating observations relevant to post-disturbance ecosystem carbon dynamics with prior model predictions of ecosystem behaviour, we can analyses the retrieved parameters after data assimilation to find the model predicted effects of disturbance.

1.4 What does this paper do?

In this paper we investigate the effect of thinning on the carbon dynamics of the Alice Holt flux site [*Wilkinson et al.*, 2012], a deciduous managed woodland. We investigate an event that occurred in 2014, when one side of the site was thinned and the other side left unmanaged. During this thinning approximately 46% of trees were removed from the studied area. In order to better understand the effect this thinning had on stand structure an intensive field campaign was undertaken in 2015 to measure leaf area index and also estimate woody biomass for both sides of the study site. The site has a flux tower positioned on the boundary between the thinned and unthinned forest. The eddy covariance record of NEE was split between the two sides using a flux footprint model. Previous statistical analysis of a thinning event in 2007 had suggested that there was no change in NEE between the thinned and unthinned sides of the forest post-disturbance [*Wilkinson et al.*, 2015].

We present new methods for the assimilation of daytime and nighttime NEE observations with a daily time-step model, in this case the Data Assimilation Linked Ecosystem Carbon (DALEC2) model [*Bloom and Williams*, 2015]. These methods require no model modification. We combine all available observations for 2015 with prior model predictions

to find two sets of optimised model parameter and initial state values, corresponding to thinned and unthinned sides of the forest. We then use these two versions of the model to seek an explanation for why the net uptake of carbon remains unchanged even after removing a large proportion of the trees from one side. The data assimilation techniques presented in this paper could be applied for similar analyses at other sites and provide a novel method to help elucidate the reasons behind ecosystem responses.

2 Observation and data assimilation methods

2.1 Alice Holt research forest

Alice Holt Forest is a research forest area managed by the UK Forestry Commission located in Hampshire, SE England. Forest Research has been operating a CO_2 flux measurement tower in a portion of the forest, the Straits Inclosure, since 1998. It is one of the longer forest site CO_2 flux records, globally. The Straits Inclosure is a 90 ha area of deciduous broadleaved plantation woodland on a surface water gley soil, which has been managed for the past 80 years. The majority of the canopy trees are oak (*Quercus robur* L.), with an understory of hazel (*Corylus avellana* L.) and hawthorn (*Crataegus monogyna* Jacq.); but there is a small area of conifers (*Pinus nigra* J. F. Arnold) within the tower measurement footprint area in some weather conditions. Further details of the Straits Inclosure site and the measurement procedures are given in *Wilkinson et al.* [2012], together with analysis of stand-scale 30 minute average net CO_2 fluxes (NEE) measured by standard eddy covariance methods from 1998-2011.

As part of the management regime, the Straits Inclosure is subject to thinning; whereby a proportion of trees are removed from the canopy in order to reduce competition and improve the quality of the final tree crop. At the Straits an intermediate thinning method is used with a portion of both subdominant and dominant trees being removed from the stand [*Kerr and Haufe*, 2011]. The whole of the stand was thinned in 1995. Subsequently the Eastern side of the Straits was thinned in 2007 and then the Western side in 2014. The flux tower at the site is situated on the boundary between these two sides, allowing for the use of a footprint model to split the flux record and analyse the effect of this disturbance on carbon fluxes at the site. In *Wilkinson et al.* [2015] a statistical analysis of the eddy covariance flux record found that there was no significant effect on the net carbon uptake of the Eastern side after thinning in 2007. In this paper we focus on the effect of distur-

137 bance on the Western side after thinning in 2014. We therefore refer to the Western side

138 as thinned and the Eastern side as unthinned.

2.2 Observations

140 In order to assess the effect the 2014 thinning had on the Straits Inclosure, an inten-

141 sive field campaign was undertaken in 2015 to measure leaf area index and also estimate

142 woody biomass. From the site we also have a long record of flux data as discussed in sec-

143 tion 2.1. These observations span both the thinned and unthinned sides of the forest and

144 give us two distinct sets of observations describing both thinned and unthinned.

2.2.1 Flux tower eddy covariance

146 The Straits Inclosure flux tower provides us with half-hourly observations from Jan-

147 uary 1999 to December 2015, these consist of the NEE fluxes and meteorological driv-

148 ing data of temperature, irradiance and atmospheric CO_2 concentration for use in the

149 DALEC2 model. The NEE data is subject to u^* filtering and quality control procedures

150 as described by *Papale et al.* [2006], but is not gap-filled. The resultant half-hourly NEE

151 dataset is then split between observations corresponding to the Western thinned and East-

152 ern unthinned sides of the site using a flux-footprint model, see *Wilkinson et al.* [2015] for

153 more details.

154 In data assimilation NEE observations are usually averaged daily for use with daily

155 time-step functional ecology models. To compute daily NEE observations we take the

156 mean over the 48 measurements made each day, selecting only days where there is no

157 missing data. As we have been strict on the quality control of the flux record and not al-

158 lowed any gap filling this presents a problem in the number of NEE observations available

159 to us. By splitting the flux record between two sides we retrieve very few total daily ob-

160 servations of NEE. In order to address this we instead compute day and nighttime NEE

161 fluxes (NEE_{day} and NEE_{night} respectively) for use in data assimilation. To compute

162 daytime or nighttime NEE observations, we take the mean over the half-hourly day or

163 nighttime (calculated using a solar model) measurements, again only taking periods where

164 there are no gaps in the data so that we are only considering true observations. This pro-

165 vides us with many more observations for assimilation after data processing, as seen in

166 table 1. Because we are averaging over shorter time periods we have a smaller probability

of gaps and erroneous data. We see that we have many more daytime NEE observations than nighttime, as we tend to have much more turbulent air mixing in daylight hours. In section 2.3.2 we give details of how we relate these twice daily observations of NEE to a daily time-step model.

Table 1. Number of observations of NEE, NEE_{day} and NEE_{night} for East and West sides of the Straits Inclosure for the year 2015.

Sector	NEE	NEE_{day}	NEE_{night}
Unthinned (E)	8	43	10
Thinned (W)	8	49	24

In *Richardson et al.* [2008] the error in observations of daily NEE is found to be between 0.2 to 0.8 g C m^{-2}day^{-1}. *Richardson et al.* [2008] also show that flux errors are heteroscedastic. In *Williams et al.* [2005] errors in NEE are assumed to be constant and set at 0.5 g C m^{-2}day^{-1}. To account for the heteroscedastic nature of NEE errors we define an error function that scales between 0.5 to 0.8 g C m^{-2}day^{-1} based on the magnitude of the observation. This function is defined as $0.5 + 0.03|\text{NEE}_{\text{day}}^{i}|$ g C m^{-2}day^{-1}, where $|\text{NEE}_{\text{day}}^{i}|$ is the magnitude of the daytime NEE observation. *Raupach et al.* [2005] comment that nighttime measurements of NEE are much more uncertain than daytime measurements. This is difficult to quantify, but here we assume that nighttime flux errors are 3 times the magnitude of daytime errors. We therefore have the error function of $1.5 + 0.09|\text{NEE}_{\text{night}}^{i}|$ g C m^{-2}day^{-1}, where $|\text{NEE}_{\text{night}}^{i}|$ is the magnitude of the nighttime NEE observation. We also include correlations in time between the errors in our observations of NEE, as discussed in *Pinnington et al.* [2016].

2.2.2 Leaf area index

As part of the work undertaken for this paper; to assess the impact of the 2014 thinning, three transects were established in the Straits Inclosure for intensive sampling during 2015. A total of 435 sampling points were marked at 10 m apart, using a GPS unit and fluorescent tree spray paint. Measurements of peak LAI (July 2015 - September 2015) were made using both a ceptometer and hemispherical photography. The transects were

walked twice with the ceptometer, sampling every 10 m, giving 870 readings in total. Hemispherical photographs were taken every 50 m as shown in Figure 1, giving 89 photographs in total.

The ceptometer is used with an additional Photosynthetically Active Radiation (PAR) sensor. We measure below canopy PAR using the ceptometer while logging above canopy PAR using a data logger and PAR sensor positioned outside the canopy. We can then estimate LAI using the above and below canopy readings and a set of equations relying on some assumptions [*Fassnacht et al.*, 1994]. For the hemispherical photographs, we use the HemiView software [*Rich et al.*, 1999] which can calculate the proportion of visible sky as a function of sky direction (gap fraction) this can then be used to calculate LAI [*Jonckheere et al.*, 2004].

Six litter traps were also established at points along the transects allowing for comparison with the other methods. These were sampled throughout the season in 2015. We found the litter trap derived LAI was always greater than LAI estimates derived from optical methods, as expected [*Bréda*, 2003]. From the sampling of the litter traps we also have estimates to leaf mass per area for use in data assimilation. As the 6 litter traps are not enough to describe the LAI for the research site [*Kimmins*, 1973], we used estimates from the ceptometer and hemispherical photographs for data assimilation. We take the weighted average of the hemispherical photograph and ceptometer estimated LAI to find an LAI of 4.42 with a standard error of 0.07 for the Eastern unthinned section of forest, and an LAI of 3.06 with a standard error of 0.07 for the Western thinned section of forest. We are assimilating the mean of 299 LAI observations in the unthinned and 225 in the thinned section of forest. Consequently the appropriate representation of error for data assimilation is the standard error of the mean. From our litter trap observations we find a leaf mass per area of 29 g C m^{-2} for both sides of the forest.

2.2.3 Woody biomass

The method of Point-Centred Quarters (PCQ) was used to conduct a biomass survey as specified in *Dahdouh-Guebas and Koedam* [2006]. 114 points were sampled along the three transects measuring the Diameter at Breast Height (DBH) and the density of trees. We then used allometric relationships between DBH and total above ground biomass and coarse root biomass, found in work carried out by Forest Research and in *McKay et al.*
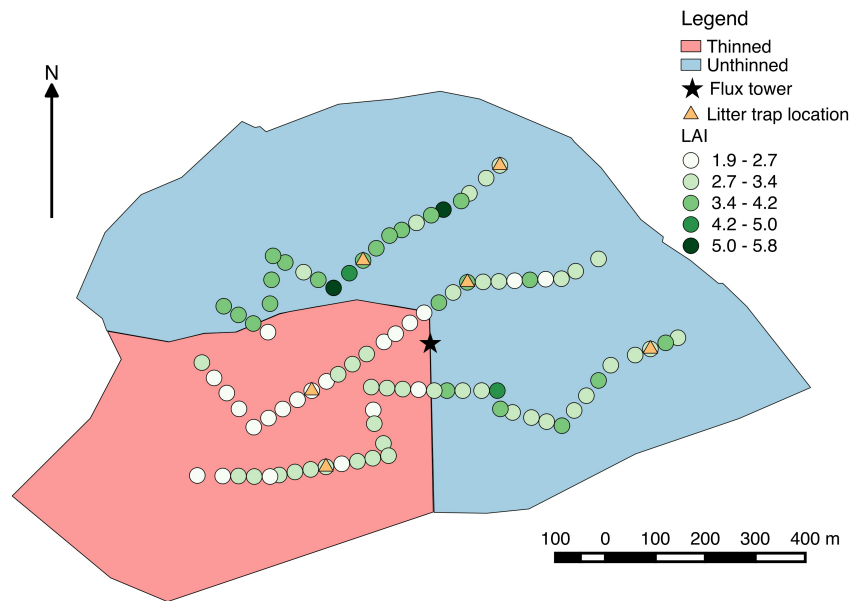
Figure 1. Hemispherical photograph derived LAI for the Straits Inclosure at 50m intervals along three transects.

[2003], to find an estimate to total woody and coarse root carbon. We can see these observations in table 4, we have made the assumption that 50% of dry plant mass is carbon.

Forest Research also carry out their own mensuration studies at the site. One such study was carried out of the Western side after the thinning at a similar time to our own PCQ measurements and found a tree density of 225 ha^{-1} and an average DBH of 32 cm, which are in close agreement to our own estimates in table 4. This gives us confidence that past measurements before the thinning will also be representative of the methods we have used. From 2009, measurements from Forest Research found the Western side to have a tree density of 418 ha^{-1} and an average DBH of 27.73 cm. This suggests that approximately 46% of trees have been removed during thinning. From these estimates we can also see the effect thinning has on the type of trees found at the site. The amount of trees per hectare has dropped dramatically after thinning but the mean DBH has increased, indicating that smaller subdominant trees have been removed. The mean DBH on the Eastern side is greater still, indicating that the thinning that took place in 2007 of the Eastern side has allowed the dominant trees to grow as a result of reduced competition.

240

Table 2. Point-centred quarter method observations for 2015.

Sector	Tree density (ha^{-1})	Mean DBH (cm)	Estimated Woody biomass and coarse root carbon (g C m^{-2})
Unthinned (E)	272	34.12	13130
Thinned (W)	225	32.85	9908

241   **2.3 Model and data assimilation**

242   *2.3.1 DALEC2 ecosystem carbon model*

243   The DALEC2 model is a simple process-based model describing the carbon dynam-

244   ics of a forest ecosystem [*Bloom and Williams*, 2015]. The model is constructed of six

245   carbon pools (labile (C_{lab}), foliage (C_f), fine roots (C_r), woody stems and coarse roots

246   (C_w), fresh leaf and fine root litter (C_l) and soil organic matter and coarse woody debris

247   (C_s)) linked via fluxes. The aggregated canopy model (ACM) [*Williams et al.*, 1997] is

248   used to calculate daily gross primary production (GPP) of the forest, taking meteoro-

249   logical driving data and the modelled leaf area index (a function of C_f) as arguments.

250   Figure 2 shows a schematic of how the carbon pools are linked in DALEC2, full model

251   equations can be found in the appendix, section A: .
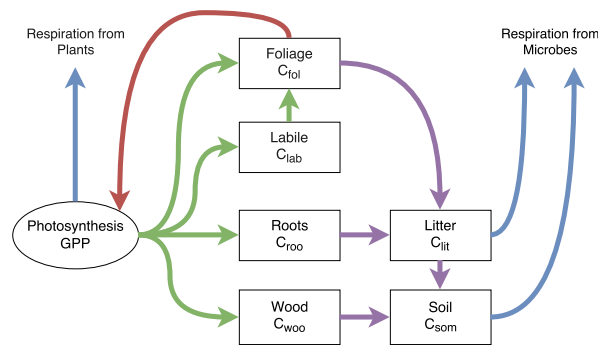
252   **Figure 2.** Representation of the fluxes in the DALEC2 carbon balance model. Green arrows represent C al-

253   location, purple arrows represent litter fall and decomposition fluxes, blue arrows represent respiration fluxes

254   and the red arrow represents the influence of leaf area index in the GPP function.

255 ### *2.3.2 Data assimilation*

256   We implement Four-Dimensional Variation data assimilation (4D-Var) with the DALEC2

257 model for joint parameter and state estimation. In 4D-Var we aim to find the parameter

258 and initial state values such that the model trajectory best fits the data over some time

259 window, given some prior information about the system. This prior information takes the

260 form of an initial estimate to the parameter and state variables of the model, $\mathbf{x}^b$, valid at

261 the initial time. This prior is assumed to have unbiased, Gaussian errors with known co-

262 variance matrix $\mathbf{B}$. Adding the prior term ensures that our problem is well posed and that

263 we can find a locally unique solution [*Tremolet*, 2006]. The prior used in this paper is

264 derived from the assimilation of eddy covariance data from previous years and can be

265 found in table A.1. In 4D-Var we aim to find the parameter and initial state values that

266 minimises the weighted least squares distance to the prior, while minimising the weighted

267 least squares distance of the model trajectory to the observations over the time window

268 $t_0,\ldots,t_N$ [*Lawless*, 2013]. We do this by finding the state $\mathbf{x}^a$ at time t_0 that minimises

269 the cost function

270
$$J(\mathbf{x}_0) = \frac{1}{2}(\mathbf{x}_0 - \mathbf{x}^b)^T \mathbf{B}^{-1}(\mathbf{x}_0 - \mathbf{x}^b) + \frac{1}{2}\sum_{i=0}^{N}(\mathbf{y}_i - \mathbf{h}_i(\mathbf{x}_i))^T \mathbf{R}_i^{-1}(\mathbf{y}_i - \mathbf{h}_i(\mathbf{x}_i)), \qquad (1)$$

271 where $\mathbf{x}_0$ is the vector of parameter and initial state values to be optimised, $\mathbf{h}_i$ is the ob-

272 servation operator mapping the parameters and state to the observations $\mathbf{y}_i$ and $\mathbf{R}_i$ is the

273 observation error covariance matrix. Further details of the implemented data assimila-

274 tion scheme and specification of prior and observational errors can be found in *Pinnington*

275 *et al.* [2016].

276   In this paper we assimilate day and nighttime NEE in order to increase the number

277 of observations available to us and also better partition our modelled estimate of GPP and

278 total ecosystem respiration, as discussed in section 2.2.1. As the DALEC2 model runs at

279 a daily time step, this requires us to relate the daily parameter and state values from the

280 model to the twice-daily observations of NEE. We do this by writing two new observation

281 operators, one relating the model state and parameters to daytime NEE, and the other to

282 nighttime NEE. The NEE of CO_2 at any given time is the difference between GPP and

283 ecosystem respiration. For an observation of total daily NEE on day i we have,

284
$$NEE^i = -GPP^i(C_{fol}^i, \Psi) + f_{auto}GPP^i(C_{fol}^i, \Psi) + \theta_{lit}C_{lit}^i e^{\Theta T^i} + \theta_{som}C_{som}^i e^{\Theta T^i}, \qquad (2)$$

where all terms have the same meaning as described in section A: , with term one being gross primary productivity, term two corresponding to autotrophic respiration and term three and four corresponding to heterotrophic respiration. For total daytime NEE we have,

$$NEE_{day}^i = -GPP^i(C_{fol}^i, \Psi) + \delta_{day} f_{auto} GPP^i(C_{fol}^i, \Psi) + \delta_{day} \theta_{lit} C_{lit}^i e^{\Theta T_{day}^i} + \delta_{day} \theta_{som} C_{som}^i e^{\Theta T_{day}^i}$$
(3)

where δ_{day} is the day length, expressed as $\frac{\text{number of daylight hours}}{24}$, and T_{day}^i is the mean daytime temperature. Here we still have the same term for GPP as in equation (2) as all photosynthesis occurs during daylight hours, the respirations are then scaled by the length of daylight hours. For nighttime NEE we have,

$$NEE_{night}^i = \delta_{night} f_{auto} GPP^i(C_{fol}^i, \Psi) + \delta_{night} \theta_{lit} C_{lit}^i e^{\Theta T_{night}^i} + \delta_{night} \theta_{som} C_{som}^i e^{\Theta T_{night}^i} \quad (4)$$

where δ_{night} is the night length, expressed as $\frac{\text{number of night hours}}{24}$, and T_{night}^i is the mean nighttime temperature. Here we no long have a term for GPP as no GPP will occur during the night. The respirations are again scaled by night length as in equation (3). Day length and night length are calculated using a solar model here, but could also be estimated using the record of incident solar radiation from the flux tower. These new observation operators allow for assimilation of day/nighttime NEE without the need for model development and can be applied to other ecosystem models to allow for the assimilation of finer temporal resolution eddy covariance data and possible improvements to the partitioning of photosynthesis and ecosystem respiration. From section 3 we can see that these modified observation operators allow our model to predict both daytime and nighttime NEE accurately.

2.4 Experimental setup

Using the prior model estimate specified in table A.1, we run two data assimilation experiments for the years window of 2015. In the first experiment we assimilated all data available (as specified in section 2.2) for the unthinned Eastern section of forest. In the second experiment we assimilate all data available for the thinned Western section of forest. Combining these two distinct sets of observations with our prior model using 4D-Var data assimilation allows us to retrieve two unique sets of parameter and initial state values, corresponding to the thinned and unthinned sections of the site. This allows us to judge the effect the thinning in 2014 had on the carbon dynamics of the forest in 2015. We do this by analysing the optimised parameter and initial state values for the thinned

315 and unthinned sections of the forest and also considering the model predictions of differ-

316 ent variables for each side post-disturbance.

317   **Table 3.**   Combination of observations used in data assimilation experiments.

Experiment	NEE	LAI	C_{woo}
A	×		
B	×	×	
C	×	×	×

3 Results

319   In Figure 3 we show the observations and model trajectories after assimilation for

320 both thinned and unthinned sections of the forest site. We can see that we fit all the ob-

321 servations well after assimilation. We have confidence in our results as we know that even

322 assimilating a single year of data we can accurately describe the carbon uptake of the site

323 for a long time period (15 years) into the future [*Pinnington et al.*, 2016]. From Figure **??**

324 and **??** the modified observation operators presented in section 2.3.2 have allowed our

325 model to represent both daytime and nighttime NEE well.

327   From Figure **??** and **??** the distinct difference in stand structure is clear with re-

328 duced LAI and woody carbon for the thinned area. The model predicted time of green-

329 up and senescence in LAI is consistent with phenocam observations made by Forest Re-

330 search at the site (maybe include phenocam plot for 2015 in sup. material?). In Figure **??**

331 we see that both model predicted and observed net carbon uptake of both the thinned and

332 unthinned is very similar. The model predictions of NEE_{day} are overlapping for most of

333 the 2015 window. However, in Figure **??** we see that our model predicts reduced reduced

334 NEE_{night} for the thinned compared to unthinned, here NEE_{night} correspond to ecosystem

335 respiration as no GPP occurs during the night.

341   In Figure 4 we show the model predicted GPP and ecosystem respiration (including

342 its partitioning between autotrophic and heterotrophic) for both thinned and unthinned af-

343 ter data assimilation. Figure **??** shows the model predicting a reduction in GPP following

344 a reduction in leaf area for the thinned. In order to compensate for this reduced GPP, in

Table 4. Total annual fluxes for 2015 after assimilation (g C m^{-2}).

Unthinned side			
	Experiment A	Experiment B	Experiment C
NEE	−379 ± 147	−425 ± 156	−426 ± 154
GPP	1648 ± 193	2191 ± 147	2193 ± 141
RT	1267 ± 186	1766 ± 175	1767 ± 176
Thinned side			
	Experiment A	Experiment B	Experiment C
NEE	−394 ± 117	−421 ± 111	−420 ± 110
GPP	1976 ± 153	1855 ± 118	1856 ± 119
RT	1582 ± 162	1435 ± 132	1436 ± 132

Figure **??** we see the thinned is demonstrating reduced total ecosystem respiration, this allows the thinned to still do the same net carbon uptake as the unthinned (seen in Figure **??**), as net ecosystem carbon uptake = - GPP + ecosystem respiration. From Figure **??** and **??** we see that heterotrophic respiration sees the greatest reduction compared to the unthinned, however autotrophic respiration is also reduced.

Figure 7 shows the change in parameter and initial state values for thinned and unthinned after assimilating the 2015 data. It is important to note this is the difference when compared to our prior model estimate, which was found by assimilating only eddy covariance data from previous years, and a single observation of leaf mass per area estimated from Forest Research litter traps. We therefore expect changes in parameter and state values for both thinned and unthinned, as we are assimilating new data streams. This is particularly noticeable in the carbon pool state members in Figure 7. Constraints on the carbon pool state members are provided by the assimilated observations of woody biomass and coarse roots (C_{woo}), LAI and leaf mass per area (c_{lma}). LAI and c_{lma} give us a constraint on foliar carbon (C_{fol}) as LAI = $\frac{C_{fol}}{c_{lma}}$. We can see the values for the model predicted carbon pools are as we might expect with the thinned having less carbon in all
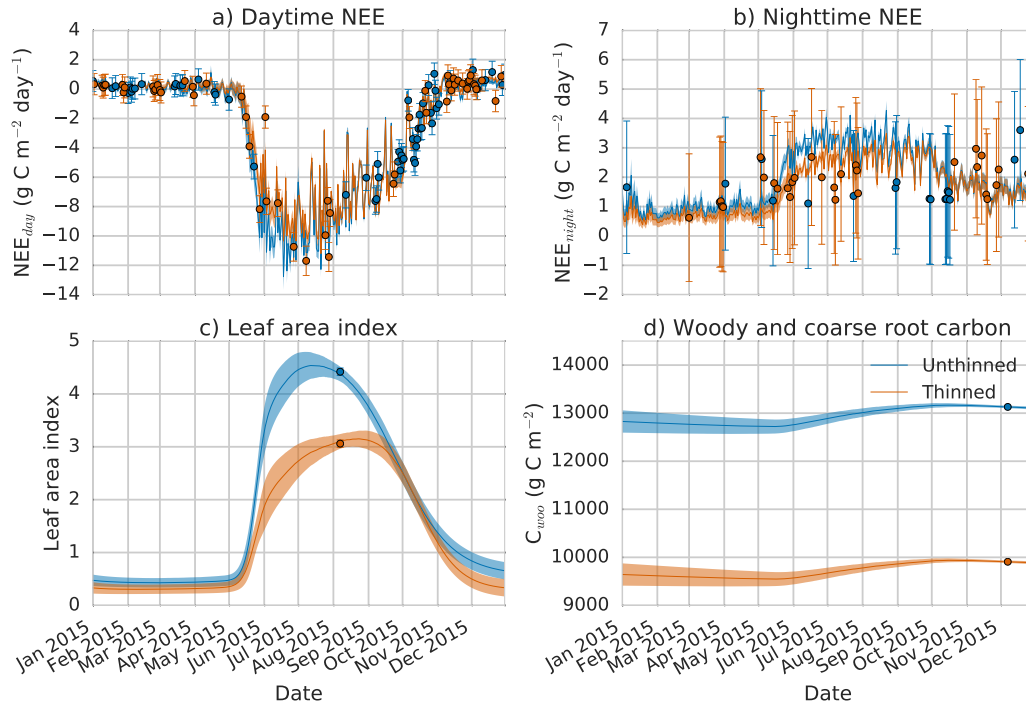
Figure 3. 2015 unthinned and thinned side observations and model trajectories after assimilation for experiment C. Blue line: model trajectory after assimilation of unthinned data, blue shading: uncertainty in model trajectory after assimilation (± 1 standard deviation), blue dots: unthinned observations with error bars, orange line: model trajectory after assimilation of thinned data, orange shading: uncertainty in model trajectory after assimilation (± 1 standard deviation), orange dots: thinned observations with error bars.
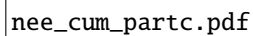
pools compared to the unthinned. For litter carbon (C_{lit}) it is possible that the input of brash and woody debris may compensate for the reduction in input of leaf litter on the thinned side. However, this woody debris is much less readily decomposed and so possibly has little impact in the year after thinning. We also see a large difference in the predicted soil carbon content (C_{som}) between the two model predictions. This is consistent with studies analysing soil carbon contents after felling [*Hernesmaa et al.*, 2005].

For the parameters the biggest changes appear to be in the litter mineralisation parameter (θ_{min}) and the fraction of GPP allocated to foliage (f_{fol}). θ_{min} is a parameter that our results are relatively insensitive to, as it is a very slow process which we do not have much information about after assimilating only a single years data. Our model predicted LAI seems unaffected by f_{fol}, as we are modelling a deciduous forest it relies more on the flow of labile carbon to the leaves at green-up than the input of GPP, this

flux_compc.pdf

Figure 4. 2015 unthinned and thinned side model trajectories after assimilation for experiment C. Blue line: model trajectory after assimilation of unthinned data, blue shading: uncertainty in model trajectory after assimilation (± 1 standard deviation), orange line: model trajectory after assimilation of thinned data, orange shading: uncertainty in model trajectory after assimilation (± 1 standard deviation).

can be seen in equations (A.2) and (A.3) in the appendix. We also see a distinct difference in the parameter controlling the rate of soil carbon turnover (θ_{som}), with this parameter being smaller for the thinned side of the forest. This could occur due to a reduction in the priming of rhizosphere soils [*Dijkstra and Cheng*, 2007], since almost half of the trees have been lost in the thinned section.
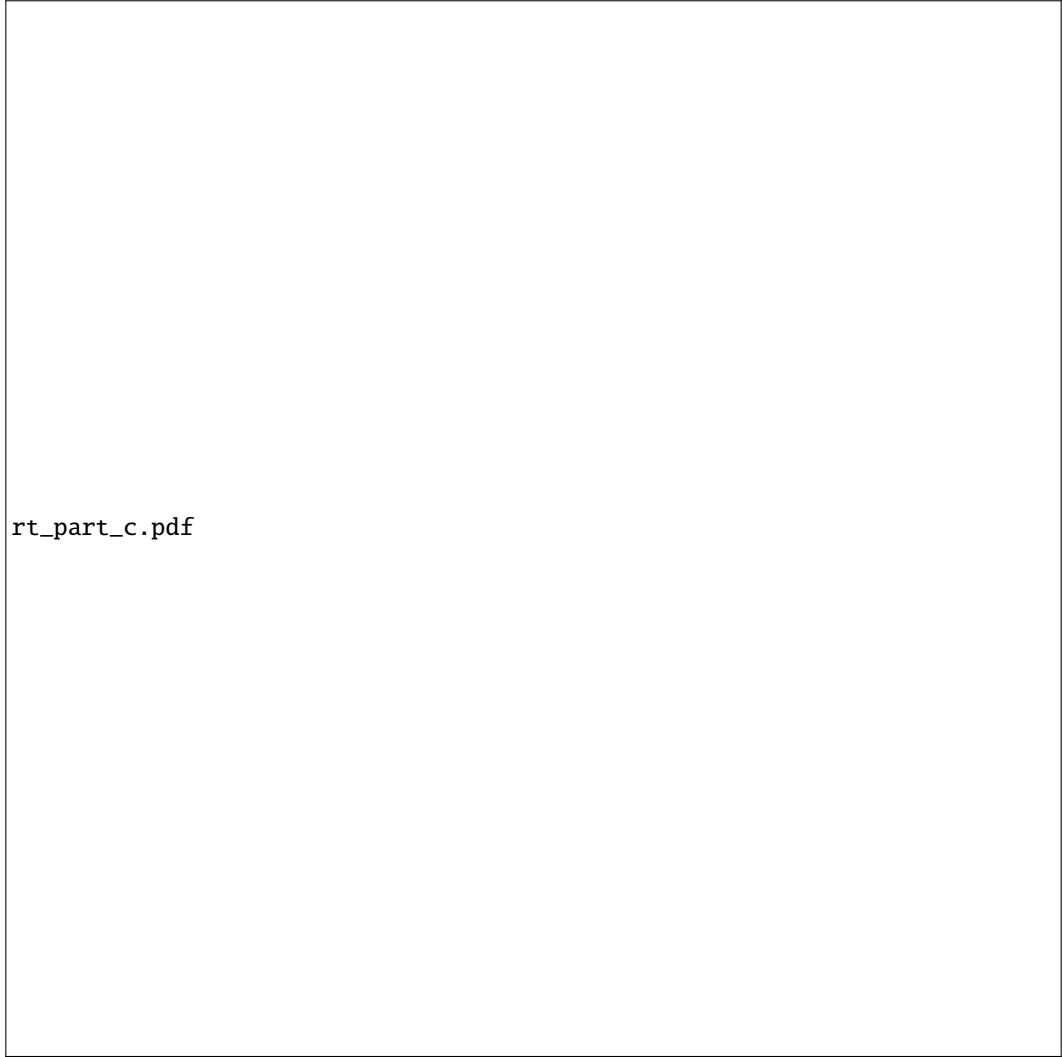
nee_cum_partc.pdf

Figure 5. 2015 unthinned and thinned side model trajectories for cumulative NEE and its partitioning after assimilation for experiment C. Solid line cumulative NEE, dotted line: cumulative ecosystem respiration, dashed line: cumulative GPP. Colour and shading has the same meaning as in Figure 3.

4 Discussion

In this paper we have used data assimilation to combine observations and prior model predictions of ecosystem carbon balance in order to understand how the state of an ecosystem might be altered after a disturbance event. We find no significant change in net carbon uptake for the studied ecosystem following stand thinning, where approximately 46% of trees were removed. This is consistent with other studies of ecosystem carbon dynamics following thinning. We find evidence that reductions in GPP following a decrease in total leaf area post-thinning are being offset by simultaneous reductions in ecosystem

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rt_part_c.pdf
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Figure 6.   2015 unthinned and thinned side model trajectory for cumulative total ecosystem respiration and
its partitioning after assimilation for experiment C.

respiration. This is in contrast to current suggestions that reduced canopy photosynthesis
is compensated for by increased GPP by ground vegetation post-thinning [*Vesala et al.*,
2005; *Wilkinson et al.*, 2015; *Moreaux et al.*, 2011; *Dore et al.*, 2012]. However does sup-
port work investigating the effect of insect disturbance [*Moore et al.*, 2013].

Our results show a decrease in both autotrophic and heterotrophic respirations fol-
lowing thinning. Autotrophic respiration has both above and below ground components,
whereas heterotrophic respiration is mainly from soils and litter. There is no set definition
for below ground autotrophic respiration but it is often characterised as respiration from
roots, mycorrhizal fungi and other micro-organisms dependent on the priming of soils
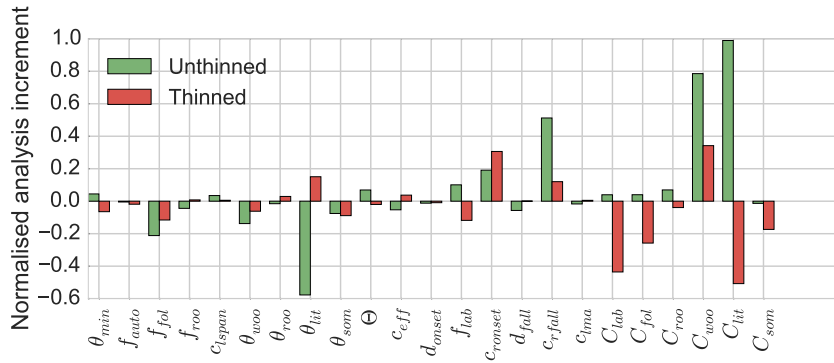
Figure 7. Normalised analysis (posterior model) increment ($\frac{(\mathbf{x}^a - \mathbf{x}^b)}{\mathbf{x}^b}$) for the East and West experiments. Explanation of parameter and state variable symbols in table A.1.

with labile carbon compounds from roots. It has been shown recently that deep root systems and their influences may be more widespread than previously thought [*Pierret et al.*, 2016]. Heterotrophic respiration is respiration by microbes not directly dependent on autotrophic substrate, however the largest fraction of heterotrophic respiration is based on the decomposition of young organic matter (e.g. leaves and fine roots) whose availability also depends on the GPP of an ecosystem [*Janssens et al.*, 2001]. We find the largest decreases in heterotrophic respiration compared to autotrophic respiration. While it has been shown that heterotrophic respiration can decrease after disturbance events [*Bhupinder-pal et al.*, 2003], it is possible we overestimate the reduction in heterotrophic respiration and underestimate the reduction in autotrophic respiration. This is understandable as we have assimilated no data on this partitioning. Also our model description of autotrophic respiration is simple (described as a constant fraction of GPP) and therefore the models heterotrophic component might compensate and in this instance describe the behaviour of mycorrhizal fungi and other microbes commonly categorised in the autotrophic component of respiration.

In a study measuring soil CO_2 fluxes over 4 years at the Straits Inclosure (the study site in this paper) *Heinemeyer et al.* [2012] showed a large 56% contribution of autotrophic respiration (characterised as root and mycorrhizal respiration) to total measured soil respiration. *Heinemeyer et al.* [2012] also suggested that mycorrhizal fungi play a role in priming the turnover of soil organic carbon by other microbes, with evidence from other studies [*Talbot et al.*, 2008]. *Högberg and Read* [2006] find similar figures for the autotrophic contribution to total soil respiration, with around half or more of all soil respiration be-

ing driven by recent photosynthesis. *Heinemeyer et al.* [2012] discuss the possibility of this tight coupling between GPP and ecosystem respiration leading to an upper limit for forest CO_2 uptake due to increased GPP leading to increased respiration, this is also discussed by *Heath et al.* [2005]. Our results support this theory, as we see ecosystem respiration scaling with GPP after approximately 46% of trees are removed from the study site, meaning that we find no significant change in net ecosystem carbon uptake after thinning.

Studies analysing eddy covariance flux records also find no significant change in the net ecosystem exchange of CO_2 after thinning [*Vesala et al.*, 2005; *Wilkinson et al.*, 2015; *Moreaux et al.*, 2011; *Dore et al.*, 2012]. These studies suggest that this is due to increased GPP by ground vegetation (following increased light availability and reduced competition) compensating for increases in heterotrophic respiration and reduced canopy photosynthesis post-thinning. We do not find evidence to support this and instead suggest that reduced ecosystem respiration is the most important component for the unchanged NEE of the forest following thinning. However, it is important to note that our observations of LAI are made at approximately 1 m above the forest floor. This means that our observations of LAI do not account for ground vegetation and therefore any effect of this ground vegetation is not simulated by our model. Despite this, observations made during multiple walks of the three established transects find no evidence of increased ground vegetation in the year after thinning. In fact much of the ground vegetation and subcanopy was removed during thinning and does not appear to have recovered in the following year. At longer time-scales we believe re-growth of the subcanopy and ground vegetation will play an important role in increased productivity. Our results suggest that this increased productivity would also be met with subsequent increases in ecosystem respiration.

The effect of disturbance is poorly characterised in current land surface and global climate models [*Running*, 2008], it is therefore important to better understand how parameters and carbon pools might change following disturbance. DALEC2 and many other ecosystem models assume that respiration rates are proportional to carbon pool size. It has been suggested that although this assumption works well in equilibrium conditions it may not allow such models to predict ecosystem carbon dynamics following disturbance [*Schimel and Weintraub*, 2003]. The data assimilation techniques in this paper present a way for these simple models to cope with step changes in ecosystem behaviour, by allowing parameters and carbon pools to be updated following disturbance events.

5 Conclusion

In this work we have presented novel methods for understanding ecosystem responses to disturbance by using data assimilation. Assimilating all available data streams after an event of disturbance with a prior model prediction allows us to assess changes to model parameter and state variables due to this disturbance. We have also created modified observation operators to allow for the assimilation of daytime and nighttime NEE observations with a daily time-step model. This negates the need for model modification.

We find no significant change in net ecosystem carbon uptake after a thinning event in 2014 where approximately 46% of trees were removed from the studied area. This was also found to be true when a similar event occurred in 2007 [*Wilkinson et al.*, 2015]. From our optimised model we find that reduced ecosystem respiration is the main reason for this unchanged net ecosystem carbon uptake. So that even for a demonstrated decrease in GPP following thinning, there is no significant change in NEE. We believe this reduction in ecosystem respiration is due to reduced input of autotrophic substrate following thinning, meaning both autotrophic and heterotrophic respiration are reduced. These results support work suggesting that GPP is the dominant driver for ecosystem respiration [*Janssens et al.*, 2001; *Heinemeyer et al.*, 2012; *Bhupinderpal et al.*, 2003; *Högberg and Read*, 2006; *Moore et al.*, 2013]. This has implications on future predictions of land surface carbon uptake and whether forests will continue to sequester atmospheric CO_2 at similar rates, or if they will be limited by increased GPP leading to increased respiration.

A: DALEC2 equations

The model equations for the carbon pools at day i are as follows:

$$GPP^i = ACM(C_{fol}^{i-1}, c_{lma}, c_{eff}, \Psi) \tag{A.1}$$

$$C_{lab}^i = C_{lab}^{i-1} + (1 - f_{auto})(1 - f_{fol})f_{lab}GPP^i - \Phi_{on}C_{lab}^{i-1}, \tag{A.2}$$

$$C_{fol}^i = C_{fol}^{i-1} + \Phi_{on}C_{lab}^{i-1} + (1 - f_{auto})f_{fol}GPP^i - \Phi_{off}C_{fol}^{i-1}, \tag{A.3}$$

$$C_{roo}^i = C_{roo}^{i-1} + (1 - f_{auto})(1 - f_{fol})(1 - f_{lab})f_{roo}GPP^i - \theta_{roo}C_{roo}^{i-1}, \tag{A.4}$$

$$C_{woo}^i = C_{woo}^{i-1} + (1 - f_{auto})(1 - f_{fol})(1 - f_{lab})(1 - f_{roo})GPP^i - \theta_{woo}C_{woo}^{i-1}, \tag{A.5}$$

$$C_{lit}^i = C_{lit}^{i-1} + \theta_{roo}C_{roo}^{i-1} + \Phi_{off}C_{fol}^{i-1} - (\theta_{lit} + \theta_{min})e^{\Theta T^{i-1}}C_{lit}^{i-1}, \tag{A.6}$$

$$C_{som}^i = C_{som}^{i-1} + \theta_{woo}C_{woo}^{i-1} + \theta_{min}e^{\Theta T^{i-1}}C_{lit}^{i-1} - \theta_{som}e^{\Theta T^{i-1}}C_{som}^{i-1}, \tag{A.7}$$

where T^{i-1} is the daily mean temperature, Ψ represents the meteorological driving data used in the *GPP* function and Φ_{on}/Φ_{off} are functions controlling leaf-on and leaf-off. Descriptions for each model parameter used in equations (A.1) to (A.7) are included in table A.1. DALEC2 can be parameterised for both deciduous and evergreen sites with Φ_{on} and Φ_{off} being able to reproduce the phenology of either type of site. The full details of this version of DALEC can be found in *Bloom and Williams* [2015].

Table A.1. Parameter values and standard deviations for prior vector used in experiments.

| Parameter	Description	Prior estimate ($\mathbf{x}^b$)	Standard deviation	Range
θ_{min}	Litter mineralisation rate (day^{-1})	5.471×10^{-4}	2.861×10^{-7}	$10^{-5} - 10^{-2}$
f_{auto}	Autotrophic respiration fraction	4.492×10^{-1}	7.605×10^{-5}	$0.3 - 0.7$
f_{fol}	Fraction of GPP allocated to foliage	4.091×10^{-2}	8.122×10^{-4}	$0.01 - 0.5$
f_{roo}	Fraction of GPP allocated to fine roots	3.700×10^{-1}	1.420×10^{-3}	$0.01 - 0.5$
c_{lspan}	Determines annual leaf loss fraction	1.089×10^{0}	1.164×10^{-3}	$1.0001 - 10$
θ_{woo}	Woody carbon turnover rate (day^{-1})	1.012×10^{-4}	1.274×10^{-9}	$2.5 \times 10^{-5} - 10^{-3}$
θ_{roo}	Fine root carbon turnover rate (day^{-1})	5.411×10^{-3}	5.669×10^{-7}	$10^{-4} - 10^{-2}$
θ_{lit}	Litter carbon turnover rate (day^{-1})	4.387×10^{-3}	7.648×10^{-7}	$10^{-4} - 10^{-2}$
θ_{som}	Soil and organic carbon turnover rate (day^{-1})	1.311×10^{-4}	1.133×10^{-9}	$10^{-7} - 10^{-3}$
Θ	Temperature dependance exponent factor	9.354×10^{-2}	2.854×10^{-5}	$0.018 - 0.08$
c_{eff}	Canopy efficiency parameter	5.618×10^{1}	2.797×10^{0}	$10 - 100$
d_{onset}	Leaf onset day (day)	1.584×10^{2}	5.740×10^{0}	$1 - 365$
f_{lab}	Fraction of GPP allocated to labile carbon pool	7.927×10^{-2}	9.997×10^{-4}	$0.01 - 0.5$
c_{ronset}	Labile carbon release period (days)	1.891×10^{1}	2.519×10^{1}	$10 - 100$
d_{fall}	Leaf fall day (day)	3.049×10^{2}	4.386×10^{1}	$1 - 365$
c_{rfall}	Leaf-fall period (days)	5.447×10^{1}	6.294×10^{1}	$10 - 100$
c_{lma}	Leaf mass per area (g C m^{-2})	2.929×10^{1}	2.975×10^{2}	$10 - 400$
C_{lab}	Labile carbon pool (g C m^{-2})	7.309×10^{1}	1.413×10^{3}	$10 - 1000$
C_{fol}	Foliar carbon pool (g C m^{-2})	1.313×10^{1}	5.668×10^{2}	$10 - 1000$
C_{roo}	Fine root carbon pool (g C m^{-2})	2.103×10^{2}	1.711×10^{4}	$10 - 1000$
C_{woo}	Above and below ground woody carbon pool (gCm^{-2})	7.182×10^{3}	1.707×10^{7}	$100 - 10^{5}$
C_{lit}	Litter carbon pool (g C m^{-2})	1.697×10^{2}	4.190×10^{4}	$10 - 1000$
C_{som}	Soil and organic carbon pool (g C m^{-2})	1.950×10^{3}	7.043×10^{5}	$100 - 2 \times 10^{5}$
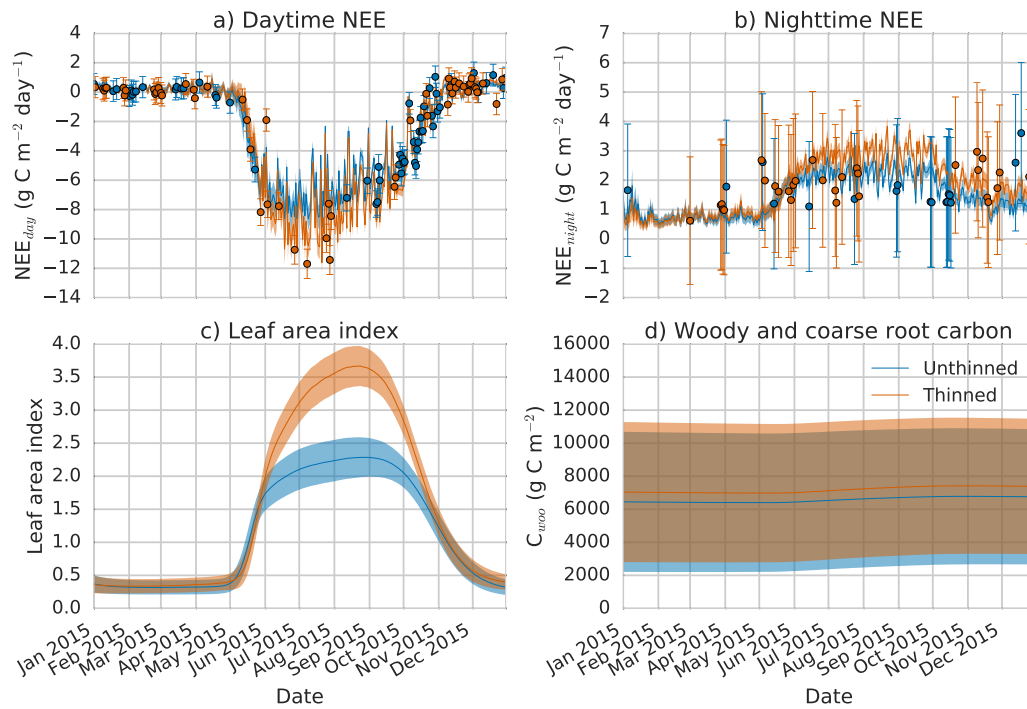
Figure B.1. 2015 unthinned and thinned side observations and model trajectories after assimilation for experiment A. Blue line: model trajectory after assimilation of unthinned data, blue shading: uncertainty in model trajectory after assimilation (± 1 standard deviation), blue dots: unthinned observations with error bars, orange line: model trajectory after assimilation of thinned data, orange shading: uncertainty in model trajectory after assimilation (± 1 standard deviation), orange dots: thinned observations with error bars.

B: Data assimilation experiment plots

C: Phenocam observations

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Figure B.2.   2015 unthinned and thinned side observations and model trajectories after assimilation for experiment B. Blue line: model trajectory after assimilation of unthinned data, blue shading: uncertainty in model trajectory after assimilation (± 1 standard deviation), blue dots: unthinned observations with error bars, orange line: model trajectory after assimilation of thinned data, orange shading: uncertainty in model trajectory after assimilation (± 1 standard deviation), orange dots: thinned observations with error bars.

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pheno_obs.pdf
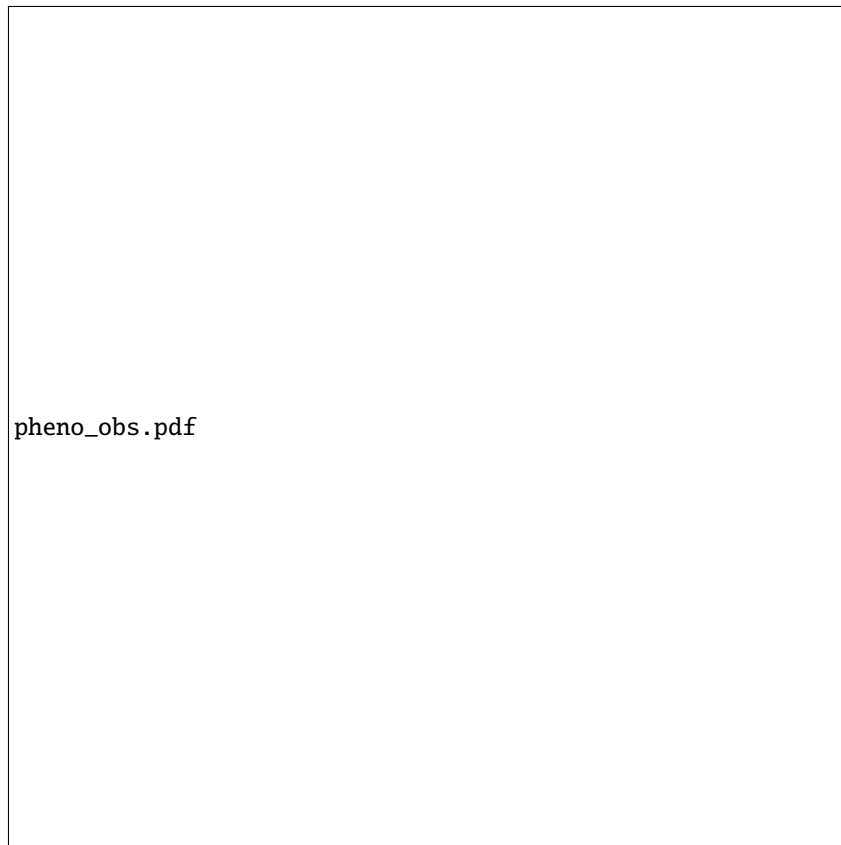
501 **Figure C.1.** Alice Holt phenocam observations of green fraction, calculated for the canopy region of
502 interest using red-green-blue digital numbers for each pixel, see **?** for more details.