June 14, 2017

Dear Editor,

Thank you very much for your letter (gmd-2017-74). Following the reviewers' suggestions we have revised the manuscript. Below are our detailed replies to the issues

1) Point by point response to issues raised by the reviewer 1
2) Point by point response to issues raised by the reviewer 2
3) A marked-up version of the manuscript to illustrate changes

Referee gmd-2017-74-RC1 (Anonymous Referee #1)

This paper assesses the validity of the carbon allocation scheme in the Community Land Model (CLM4.5) against a range of data sets, primarily from flux towers in North America. Two alternative schemes are also introduced as tested against the same data sources.

In general I found this to be a robust piece of model-data comparison, using novel observations and with high relevance to contemporary issues in land surface model development. It also identifies some significant failings of the existing model and suggests schemes that would lead to improvements. I think the organization of the text could be slightly improved upon, but otherwise I have no major concerns here.

We are very pleased that the reviewer finds this work to be robust, relevant and useful in highlighting some new issues in model development. We have attempted to re-organize the text as per the reviewers recommendations.

General points; Throughout the manuscript, there is a tendency to refer to the CLM4.5 as simply 'CLM'. This should be corrected to, wherever possibly, only using CLM4.5, since all other versions of CLM woud produce substantially different findings to those presented here.

We have replaced "CLM" with "CLM4.5" throughout the manuscript. We have modified the legends of the Figures to use "CLM4.5" instead of simply "CLM".

In general, much of the writing in this paper leaves the reader in suspense about the purpose of the paragraph until the end, which makes it hard to follow. I suggest trying to reverse the logic of the paragraph/sections, adding the purpose of the argument much nearer the beginning, and then backing up with the text that follows.

We have revised much of the manuscript for clarity. We have reviewed the opening sentences of each paragraph in an attempt to make the topic clearer. The details of the changes are captured in specific comments below.

For example, one major change is the introduction of a paragraph at the start of the methods that provides a guide to the reader.

Specific Points P1L34: The 'fixed scheme' is introduced as two seperate schemes, one for evergreen and one for deciduous, but given that (P6L23) these differences are derived only from the model parameters, and thus do not require and structural modifications, I would see this as one and not two seperate 'schemes'.

We used the word 'scheme' in the hopes of avoiding confusion with 'structure' and to avoid saying "different structures and parmeterizations" throughout the manuscript. We acknowledge that our schemes are not all structurally distinct and we have altered the phrasing to make clear that different allocation schemes arise from different structures and parameterization.

For example:

Page 3: "...to study the effects of alternative C allocation structures and parameterizations…"

Section 2.4 is now titled "2.4 Alternative C allocation structures and parameterizations"

In section 2.4 we now introduce the fixed "schemes" as follows:
"In addition to the dynamic C allocation structure in CLM4.5 (Oleson et al., 2013), we implemented an alternative dynamic (Litton et al., 2007), and two fixed (Luyssaert et al., 2007) C allocation parameterizations with the same structure."
And just below...
"The two alternative fixed C schemes have the same structure but different allocation parameterizations and were based on observed values reported by Luyssaert et al. (2007), which were converted accordingly to the allometric parameters used in CLM. One of the C allocation parameter sets was representative of temperate evergreen forests (named "F-Evergreen") and the other of temperate broadleaf deciduous forests (named "F-Deciduous")."

Also in the description of model experiments 2.6
"Each experiment represents a different allocation scheme. For experiment 1 we used the original dynamic C allocation structure in CLM4.5 (D-CLM4.5; see Sect. 2.3). For experiment 2, we used the alternative dynamic C allocation structure based on Litton et al. (2007) (D-Litton, see Sect. 2.4). For experiments 3 and 4, we used a fixed C allocation structure representative of evergreen (F-Evergreen) and deciduous (F-Deciduous) forests, respectively (Luyssaert et al. 2007 – see Sect. 2.4)."

We think that this avoids confusion and respects the conventional use of the terms "structure" and "parameterization".
P2L10: The last sentence of this paragraph (That coud be done by: : :) is too vague and should be modified to include specific recommendations.
We have modified it and the end of this paragraph now reads:
"We identified key structural and parameterization deficits that need refinement to improve the accuracy of LSMs in the near future. These include changing how C is allocated in fixed and dynamic schemes based on data from current forest syntheses and different parameterization of allocation schemes for different forest types."
P2L11-13: This reads as somewhat circular (we need to look at biomass data to get biomass correct)? Maybe remove the very last phrase?
We have modified this and the section now reads:
"Our results highlight the utility of using measurements of aboveground biomass to evaluate and constrain the C allocation scheme in LSMs, and also the need for empirical estimates of C turnover rate. Revising these will be critical to improving long-term C processes in LSMs."

P3L1: Do all LSMs do this? What are the exceptions?
No, not all LSMs do this - we re-wrote this section based on the recommendation below. Please see our response to comment P3L1-17

We opted not to include a list, since it would be complicated by lots of variants and option in models - here is a truncated list based on the papers we cite.
Terrestrial biosphere models with fixed schemes: CLM, MEL, ED, IBIS, CASA, JSBACH, Triffid, CABLE, EALCO, GDAY
Terrestrial biosphere models with functional relationships or resource dependent schemes: Orchidee variants, CASA variants , LPJ Guess variants, ISAM, TECO, SDGVM
For changes in response to this reviewer comment please see the response below to P3L1-17
P3L1-17: This long paragraph is somewhat difficult to navigate and could do a better job of clearly introducing the focus of his paper. I suggest splitting it into at least two paragraphs, and making clear what is the focus of this paper early on in each paragraph.
We rewrote this section in two paragraphs. We believe it now better introduces the study. It now reads as follows:

“Allocation of C between pools in terrestrial ecosystems is poorly represented in LSMs (Delbart et al., 2010; Malhi et al., 2011; Negron-Juarez et al., 2015). Some LSMs use fixed ratios for each Plant Functional Type (PFT), while other models use allocation fractions that are altered by environmental conditions (Wolf et al. 2011; DeKauwe et al 2014). Though many LSMs use the same fractional allocation for both evergreen and deciduous forests, global syntheses show differences in inferred C allocation patterns, for example, the percentage of NPP allocated to leaves that is greater in deciduous than in evergreen forests (Luyssaert et al., 2007). In part this is because it is difficult to measure allocation to different pools at ecosystem or landscape scales and instead we infer what partitioning was required to result in different biomass pools. While eddy covariance observations can be used to parameterize and benchmark LSMs either at single sites or, using geospatial scaling methods, across regions or the globe (Baldocchi et al., 2001; Friend et al., 2007; Randerson et al., 2009; Zaehle and Friend 2010; Mahecha et al., 2010; Bonan et al., 2011), these data inform fluxes in and out but do not provide information on allocation between pools (Richardson et al., 2010).
Studies focusing simultaneously on C pools, fluxes and allocation are relatively rare (Wolf et al., 2011; Xia et al., 2015; Bloom et al., 2016; Thum et al., 2017), in part because collecting biometric data in addition to flux data is very labour intensive. Some forest inventory data includes estimates of the average biomass within the leaf, wood and root pool, and these can be used to parameterize and benchmark models (Caspersen et al., 2000; Brown, 2002; Houghton, 2005; Keith et al., 2009). The AmeriFlux network provides a rare opportunity to investigate forest allocation processes because gross primary productivity and respiration fluxes are quantified continuously. However, measurements of pool sizes in leaves, stems etc. are less available at these sites and so have been less frequently explored.”

P3L22: What are ‘biometric data’ in this context?
We clarify that biometric data in this context refers to aboveground biomass and leaf area index. It now reads as follows:
“We collated biometric data (aboveground biomass and leaf area index), where available, for AmeriFlux sites and supplemented these data with novel aboveground biomass estimates from tree-ring data for AmeriFlux sites (Alexander et al., in review).”

P4L8: Is there a reference for the L2 product? I wouldn’t assume that everyone is 100% familiar with this.

Yes, the reference is as follows:
Boden, T. A., Krassovski, M., & Yang, B. The AmeriFlux data activity and data system: an evolving collection of data management techniques, tools, products and services. Geoscientific Instrumentation, Methods and Data Systems, 2(1), 165-176, 2013
A pdf of this paper is available here: http://www.geosci-instrum-method-data-syst.net/2/165/2013/gi-2-165-2013.pdf

We have included the reference and website as follows:
To quantify carbon flux into and out of the different forests, eddy covariance measurements were collated from the AmeriFlux L2 gap-filled data product (Boden et al. 2013, http://ameriflux.lbl.gov/data/download-data/) for all sites, except for Niwot Ridge where only the AmeriFlux L2 with-gaps data product was available and there we used the REddyProc package (Reichstein et al., 2005) to gap-fill and partition the data (Table 1).

P4L14: Why construct these historical biomass datastreams? Why not just use current biomass estimates? A motivation needs to come before any of this.

Biomass observations are not available from the site PIs for all sites, so we collected dbh and tree ring increments for all the sites. Furthermore growth increment rather than static surveys can be informative for evaluating dynamic allocation schemes.
We have added the following text:
"To quantify aboveground biomass at all of the sites, we surveyed each forest between 2012 and 2014 and calculated above-ground biomass between 1980 and 2011 (Table 1) using a dendrochronological sampling technique (Dye et al., 2016; Alexander et al., in review). This provided a reconstruction of year-to-year variability in diameter at breast height (dbh) of trees and biomass inferred from allometric regressions. "
P4L24: I'm guessing allometric assumptions have huge impacts on stem carbon estimates and thus on the rest of the results? These should be discussed somewhere.

Theses assumptions are discussed at length in Dye et al. (2016) and Alexander et al. (2017) and in a forthcoming analysis on data assimilation with CLM. Here we include:
"At Harvard and Howland, tree-ring reconstructed biomass was compared to biomass estimated from permanent plots established in 1969 and 1989 respectively; tree-ring biomass increment estimates fell within the 95% confidence intervals of biomass estimated from 30 the permanent plots (Dye et al., 2016). Both permanent plots and tree-ring reconstructed biomass are dependent on allometric equations which contributes to uncertainty in these values."
P5L6: After all the discussion of biomass estimates, more detail is needed on the leaf C methodologies, since that is non-trivial as well.

NEE, LAI and a small number of above-ground biomass estimates are available from the AmeriFlux network and so we reference the protocols and sources for these data. The tree ring based estimates of biomass are novel and so we explain their generation.

We have rewritten this section to make this origin of these data clear:

To quantify the how much carbon was stored in aboveground woody biomass and leaf biomass in these forests we collated already existing biomass and LAI estimates from the AmeriFlux network; these were available for only some sites and years (Table 1). In-situ measured LAI was available from AmeriFlux data for some sites (Table 1), and we used the annual maximum LAI for all the available measurements in each year. We used leaf C-LAI ratio from the AmeriFlux sites with simultaneous measurements of LAI and leaf C during the same year (Table 1). The Cstem/Cleaf ratio, which was derived from AmeriFlux data with Cstem and Cleaf estimates for the same year, was only available for a subset of sites and years (Table 1).

P5L9: Not necessary to say PTCLM was used, since this isn't a different model, and makes it seem like it might be.
We have removed the mention of PTCLM
P5L15: 'dead' stem and root pools are a little confusing. Are these heartwood, or in the litter pool? This needs to be disambiguated.
We do not refer to litter pools, only to leaf, stem and root pools. We refer to Oleson et al. 2013 to help clarify these concepts
"CLM4.5 includes the following plant tissue types: leaf, stem (live and dead stem), coarse root (live and dead coarse root), and fine root (Oleson et al., 2013)."
P5L17:
I think all these a1, a2, a3 references should have the numbers in subscript.
a_1, a_2, *and* a_3 *references have the numbers in subscript as in Oleson et al. (2013)*
P5L30: What is the purpose of fitting these parameters for a broad range of NPP?
In the two dynamic schemes, allocation varies with respect to NPP. We thought it prudent to illustrate this effect so that readers could see the effect of low and high NPP on the paramters.

We converted the allometric parameters to allocation coefficients because these are easier to interpret than the parameters.
We have rephrased to make this year.
"To account for the range of NPP found in temperate forests, we calculated the allometric parameters a1, a2 and a3 for a broad range of NPP, and then converted the allometric parameters to allocation coefficients for each plant tissue using the C allometry in the model (Oleson et al., 2013). We illustrate in one figure the effect of annual NPP on C allocation to each plant tissue in D-CLM4.5 (Fig. S1)."

P6L24-27:This section seems like results.
The text has been moved to section 3.3, in the Results section.
P6L30: This sentence make it seem like SLA is prognostic when it is actually fixed.

We have now clarified that SLA is a critical and fixed parameter:
"CLM4.5 uses a prognostic canopy model, with feedbacks between GPP and LAI acting through allocation to leaf C and SLA and with SLA being a critical fixed parameter in this feedback pathway (Thornton and Zimmermann, 2007)."
P7L10: There should be units for these parameters here.
We have included the units for parameters m and SLA_0
P7L25: What optimization approach? Did you use the adjusted parameters in all of the allocation model simulations, or in a new set of simulations?
We clarified that the optimization approach was based on least squares. We used the optimized parameters for temperate forests in all of the allocation schemes simulations (D-CLM4.5, D-Litton, F-Deciduous, and F-Evergreen). We used the default parameter values for m and SLA_0 *for evergreen forests in all of the allocation schemes simulations.*

"and used an optimization approach based on least squares that combined the range of parameter values and Eq. (3) to find the best combination of values for the two parameters given the leaf C-LAI observations at our sites."
And
"After optimizing the parameters m and SLA0, we used m=0.0010 and SLA0=0.024 for deciduous forests. For evergreen sites, we could not optimize the parameters m and SLA0 due to the limited number of leaf C-LAI observations available. All model experiments were carried out after SLA optimization."

P7L27: Is the model emulator 'just' equation 4, or is there more to it that needs explaining?
We have clarified that the model emulator was equation 4 (and altered the start of the section to clarify purpose.
"We estimated a range of plausible, site specific stem turnover rates using equation (4) below because, at individual research forest stands, rates of tree mortality may or may not reflect averages rates across larger areas".
And just below…
"To optimize the stem turnover rate we used equation (4) as a model emulator to modify the default stem turnover rate (2%) to within a range of 0 to 2% (van Mantgem et al., 2009; Brown and Schroeder, 1999); for the rest of plant pools we used the default turnover rate in the model."
P7L26: Why are you optimizing turnover? Again, are these new numbers used in all the simulations? There needs to be a better overall narrative connecting the different parts of the methods section.
We have added a section directly under "METHODS" which serves to explain the overall methods narrative.

“We implemented the CLM4.5 model – a well-established and commonly used LSM, at nine different forest sites (2.1) and compiled observation of C fluxes, C pools, LAI, and the Cstem/Cleaf ratio (2.2) to evaluate alternative C allocation structures and parameterizations (2.3 & 2.4). We re-parameterized the Specific Leaf Area (SLA) based on available observations (2.5) before implementing four CLM4.5 model experiments designed to examine the impact of the different C allocation structures and parameterizations (2.6). Finally to investigate the potential effects of site variation in woody turnover we estimated plausible site-specific turnover rates (2.7).“

We have re-ordered the methods to make the distinction between CLM4.5 simulations and model emulator studies more explicit.
The newly numbered section “2.7 Sensitivity of biomass increment to stem turnover rate” contains the following text to explain the purpose of this analysis:

“We estimated a range of plausible, site specific stem turnover rates using equation (4) below because, at individual research forest stands, rates of tree mortality may or may not reflect averages rates across larger areas. LSMs typically are run at scales that are coarser than individual forest sites and use aggregate estimates for C pool turnover.”.

P8L5: There needs to be a motivation statement at the beginning of this section, otherwise one has to read all the way through to figure out where the argument is going…

This section may be useful to some readers in understanding the effects of changes in allocation on the aboveground biomass at the start of the runs. However it’s length and complexity detract from the main message of the paper and so we have opted to move it to the supplemental material.

The aboveground biomass in equilibrium conditions will depend on aboveground NPP (ANPP), the NPPstem/NPPleaf ratio (or astem/aleaf ratio) and the turnover rates for leaf and stem (uleaf and ustem).

P8L23: These also seem like results.

This section may be useful to some readers in understanding the effects of changes in allocation on the aboveground biomass at the start of the runs. However it’s length and complexity detract from the main message of the paper and so we have opted to move it to the supplemental material.

P9L19: CLM was already introduced much earlier.

This reference to CLM has been removed

P10L6: Why use the CRUNCEP data when these are Ameriflux sites for which meteorological observations are typically available? I don’t think this means that the simulations need re-doing, since this paper is focused on relative allocation schemes, but I do think that some more discussion of the potential for errors when comparing site level data and a model driven with reanalysis would be appropriate.

AmeriFlux sites extend only a decade or so, but changes in biomass are slow relative to ecosystem exchange. To explore the results of slowly changing processes we extended model runs to 30 years which requires using CRUNCEP or some other reanalysis climate. We have added an explanation to this section

“The standard climate forcing provided with the model is the 1901-2013 CRUNCEP dataset. While meteorological data is available at the AmeriFlux sites, this data extends only as long at the eddy covariance observations which is less than a decade in several cases. To explore the effects of allocation on slowly changing C pools like woody biomass, we extended model runs to 30 years which requires using CRUNCEP or some other reanalysis climate. “

P11L19: This sentence is confusing. State which values -were- used, not which ones were not…

Comments P11L19 and P11L21 are addressed together (see below)

P11L21: I don't understand this 'turnover effect' from this sentence. What are the max and min tem turnover rates?

We have re-written this entire paragraph as follows:

"The stem turnover rate that best matched the biomass accumulation rate estimated from the tree ring reconstructions varied by site and was always lower than the default rate of 2% year-1 used in CLM4.5 (Fig 7). As expected, changing the turnover rate had the largest influence at sites with the highest average NPP. Biomass accumulation in the D-Litton scheme was less sensitive to changes in turnover rate compared to the D-CLM scheme (compare Fig 7b to 7a). The F-Deciduous and F-Evergreen parameterization were similar in their sensitivity to changes in turnover rate (compare Fig 7c to 7d)."

P12L10: In general this discusión section is rather too long and could do with focusing more coherently on the important findings of the study.

We have re-organized and shorted specific sections to clarify the most important findings. See in particular the response to "P15L30: This is an important point, maybe highlight more in the abstract, conclusions, etc."

P12L14: What are 'initial' biomass estimates in this context?

We have rephrased and referred to the relevant figure (Fig 5) to clarify meaning and context.

"....it produces lower, and more credible aboveground biomass estimates at the start of the simulation for these forests (Fig. 5a) and matches the biometric estimates of C partitioning between leaf and stem (Fig. 8a)."

P12L16: Couldn't there be different parameters for dec and evergreen plants within the Litton scheme? Why not propose the ideal scheme within this paper?

The relationships in Litton et al (2007), we used to derive the D-Litton structure and parameters were for all forest types. Litton et al (2007) were unable to find differences between forest types in these relationships and so we are reluctant to suggest differential parameterization of this model structure without potential parameters.

P12L28: This sentence is confusing. Why mix the reporting for the evergreen and deciduous forests up like this?

We agree - we have clarified as follows:

"None of the allocation schemes simultaneously matched observed evergreen and deciduous forest aboveground biomass."

P12L30: Which version of CLM did Hudiberg et al. use?

Hudiburg et al. 2013 used CLM4 .

We have rewritten this sentence as follows: "These results are in line with previous findings in evergreen Oregon forests where CLM4.0 also underestimated aboveground biomass at most sites (Hudiburg et al., 2013)."

P13L6: These comparisons with other models are somewhat distracting all the way through this section. I'm not sure it's particularly relevant, given that a) there's no real reason to imagine that there would be a systematic bias and b) the illustrations given are not wide-ranging enough to demonstrate one. I'd suggest moving all that material to its own section or removing it entirely.

Allocation schemes among these different models are relatively simple and quite similar in structure. Also while the sites we evaluated are not comprehensive, the resources used to parameterize the schemes are quite wide ranging (Litton et al., 2007; Luyssaert et al., 2007) - we think that it is useful to include Table 3, but we agree that there is some confusion here. We *have re-organized this section and gathered comparisons into section "4.2 C allocation scheme: implications for C pools"*

P13L5: This seems to suggest that Litton is better but only because of the existing biases in NPP?
We cannot exclude this possibility. We try to evaluate whether NPP or stem turnover is overestimated in section 4.5. But note that Fig 8 suggests that the Litton is also better at predicting partitioning between stem and leaf C on average.
P13L11: What exactly is being suggested here? I feel like it needs a specific equation.
We have rephrased for clarity:
"Our results suggest that it is necessary to improve the D-CLM4.5 scheme for temperate forests; for evergreen forests the D-Litton scheme could be modified from a linear to a non-linear scheme to increase allocation to stem for sites with mean annual NPP<500 g Cm-2year-1."
P14L3: Is the ORCHIDEE bias for the same reason? There are lots of ways to get a high LAI bias!
PENDING
The ORCHIDEE model did not have the identical problem. The point we were addressing here is strong and obvious bias/model inconsistency should be dealt with before you evaluate model changes. To clarify this point, we have re-phrased as follows:
"Clear and persistent model-data discrepancies in LAI also needed to be addressed in the ORCHIDEE LSM prior to any evaluation of model changes (Thum et al., 2017). Site specific estimates of SLA and LAI would be very useful for optimizing parameters within their observed range and allow mechanistic processes controlling allocation to leaves in the model to be assessed."

P14L5L: This root allocation discussion perhaps need to be in its own section (and maybe could be removed since the datasets used here don't really address root allocation per se).
We do not wish to remove this section because any change in allocation to stem and leaf must have an impact on allocation to roots. This section has been renumbered "4.2 C allocation scheme: implications for C pools" and we think that roots should be included here as one of three major C pools we discuss in the paper.We think that it We have shortened this paragraph and included a reference to Weng et al., 2015 in response to the reviewers later comment on optimization.
P14L26-: This discussion of 'initial conditions' might also be removed, since 1) this study doesn't really look into initial condition variability 2) it thus doesn't show any sensitivity to initial conditions, 3) what 'initial conditions' are isn't defined here and 4) the derivation of all of the equilibrium biomass pools earlier terms rather undermines the notion that initial conditions might be important. The IC study used by Kay et al. in particular, illustrates extreme sensitivity to very minor perturbations of atmospheric initialization, but this is not really relevant to the problems presented here. IC sensitivity is possible in a model like CLM, due to positive feedbacks between low canopy LAI and surface temperature, nitrogen acquisition, etc. but that is not a feature of this analysis.

Our manuscript deals only with the land surface portion of the model. The biomass at time 0 will strongly influence biomass at any time in the future. The different allocation schemes result is different biomass estimates (leaf and woody) and since the C fluxes are in some measure proportional to pool sizes we think it is important to discuss this. We mean to refer to the value of the various C pools at the start of the evaluation runs (1980). We have clarified to avoid confusion with initial atmospheric conditions in studies like Kay et al.

"There is an increasing awareness in Earth system modeling of the critical role of initial conditions (including the initial size of C pools - examined in this study) that adds an extra layer

of complexity in diagnosing the impact of an incorrect representation of physical processes on the transient simulation (Kay et al., 2015; Fisher et al., 2015).”

P15L15: This referente to Xia is confusing. This is with a model other than CLM4.5, but which one? I’d suggest removing it, since structural modifications of one model are not necessarily relevant to another.

We have clarified the reference to Xia and explained 1) that the allocation scheme is very similar to the fixed schemes presented in our study and 2) that when challenged with data they come to the same conclusion as we do.
We also found important overestimations of aboveground biomass for deciduous forests with D-CLM4.5, and therefore suggest that the NPPstem/NPPleaf ratio in the model is one of the primary factors contributing to these overestimations of biomass.
Overestimation of allocation to stem was also found using the IBIS model, where a fixed allocation scheme with terms for allocation to leaf, stem and root, which sum to 1, was found to overestimate allocation to stem (Xia et al., 2015). The fractional allocation to stem in IBIS was reduced from 0.5 to 0.36 when the scheme was optimized against satellite LAI observations (Xia et al., 2015). Similarly, our results suggest that allocation to stem in D-CLM4.5 should decrease, whereas allocation to leaf and root should increase, in order to align simulated and observed biomass.

P15L25: What happens at the other sites?
Unfortunately, we have no observations from the other sites.
P15L30: This is an important point, maybe highlight more in the abstract, conclusions, etc.
We have been more explicit in this finding in the abstract
“Our results highlight the utility of using measurements of aboveground biomass to evaluate and constrain the C allocation scheme in LSMs, and suggest that stem turnover is overestimated by CLM4.5 for these Ameriflux forests.“
...and 4.5 Conclusions and Perspectives we state:
“Finally, we show that information on stem turnover rate, which varies with forest age and successional status, is important to interpret the success or failure of different model schemes at forest sites. Default stem turnover in CLM4.5 may approximate steady state conditions at large scales but it is inconsistent with forests which are not at steady state. Decreasing the stem turnover rate from 2% yr-1 to plausible values consistent with their successional status yielded aboveground biomass accumulation rates more consistent with observations.”

Also see the response to comment P16L6
P16L6: This long discussion of Harvard forest rather detracts from why turnover is hard to estimate from the tree ring data? Stem turnover can surely be estimated from permenant sample plot data instead? Further, this whole discussion is really about how plot level observations (rather than the type of observations) are altered by disturbance history. Big leaf models implicitly aggregate all successional stages together, and so comparison with individual sites is problematic, which is a good argument for using site-specific stem mortality estimates. I think this argument could be made clearer, and shorter!
This section has been re-organized in an attempt highlight that NPP and turnover are likely overestimated as the reviewer asked in comment P15L30. It has also been shortened by 200 words

The paragraph now reads:
“It is likely that CLM4.5 overestimates stem turnover at these sites. Currently, CLM4.5 assumes a stem mortality rate of 2% yr-1 that is higher than published tree mortality rates for forests in

the USA (van Mantgem et al., 2009; Brown and Schroeder, 1999; Runkle, 1998). When considering large geographic scales the 2% yr-1 rate of stem turnover may be reasonable but at individual sites this may be a poor approximation. The Harvard Forest, for example, is at the end of the stem exclusions stage of forest development and, there has been little to no canopy disturbance since the time of the 1969 census. As such, the tree-ring biomass increment estimates at Harvard assume zero mortality between 1980 and 2012. This assumption appears solid as it results in no significant difference between tree-ring reconstructed biomass increment and the repeated measurements from permanent plots over the last 40 years (Dye et al., 2016). We thus decreased stem mortality rate from 2% yr-1 to published ranges of tree mortality (between 0 and 1.5% yr-1), to estimate plausible stem turnover rates for each site and scheme. The resulting ranges of aboveground biomass increment overlapped with the observed aboveground biomass increment estimated from tree-ring data, for nearly all the carbon allocation schemes (see Fig. 7). For Harvard forest the turnover rate that most consistent with the tree ring reconstruction was never zero, which indicates that both NPP and turnover are overestimated for this site in all the allocation schemes. A different turnover rate was required for each site and C allocation scheme to match the observed aboveground biomass increment but in each case it was below the default 2% value. Our analysis suggests that when using AmeriFlux sites to inform models, or other site level observations, taking note of site specific rates of stem turnover is prudent.“

P16L17: The ‘large geographical scales’ phrase is repeated from several lines earlier .

The second instance has been removed in the revision

P16L18: In CLM, land use change is considered separately from natural ecosystem physiology.

In this sentence we were referring to the “real” ecosystem C turnover rate, which will encompass all the things that are mentioned, including LC change. However the reference has been removed in the revised paragraph in response to P16L6.

P16L21: Published where? And what numbers were used where? This is too vague of a description.

The references are now included. They are van Mantgem et al., 2009; Brown and Schroeder, 1999; Runkle, 1998 - see the revised paragraph quoted in response to P16L6

P17L8: I’m not sure that the allocation schemes disagree, they are just different…Can this be rephrased?

We have used the word differ instead.

P17L6: The dynamic allocation schemes could be interpreted as plausibly operating at a cohort scale, but also could be interpreted entirely at the landscape scale. This secton introduces the idea that cohort representation is needed, but then discusses coherent patterns in the site-level stem/leaf ratios, underminng that argument.

Thanks for pointing this out - that was the not the emphasis we were trying to convey. We mean to suggest that Cohort representation could remove the conflation of ontogeny (forest stands change allocation as they mature) with resource optimization (trees allocate resources to maximize growth) that is inherent in the D-CLM scheme. We agree that the order of paragraphs is not helpful. We have moved this paragraph to the end of the paper.

P17L14: Better representation of veg dynamic and functional root representation are very different ambitions for LSMs, and have very different implications for allocation schemes. ED-like models, for example, already use allocation schemes that map onto changing stem/leaf ratios with tree size, but these are inappropriate for big leaf models. Some models (LM3-PPA) already have functional roots and change allocation to the acoordingly. It seems like this topic (how to move forward with allocation schemes) is introduced too suddenly in the conclusions, when it might be a better topic for a discussion section evaluating the potential for alternative model improvements to have better connections to data?

We agree that these two developments have different implications for allocation schemes, this is why they must be considered together in the perspectives section. While different dynamic allocation schemes might "work" for a given model configuration, none of the current working schemes appear to represent the actual ecological process. We have changed the topic sentence moved this perspective to the end of the conclusions and perspectives section as a 'closing thought'.
The line of reasoning is introduced earlier in the discussion -re: root function - at the end of 4.2 "However, some studies suggest that this trade-off includes fine roots (Wolf et al., 2011; Malhi et al., 2011; Chen et al., 2013), probably due to the co-limitation of productivity by resources captured aboveground (e.g. light) and belowground (e.g. nutrients and water) (Dybzinski et al., 2011; Weng et al., 2015). These growth drivers also vary with time and across spatial ecological gradients (Guillemot et al., 2015). In CLM4.5 employed here, the roots control water uptake but are not related to nutrient uptake which limits the potential for dynamic responses to nutrients and CO2 concentrations (Atkin, 2016 De Kauwe et al., 2014; Hickler et al., 2015; Sevanto and Dickman 2015). Root functionality in LSMs could be enhanced by improving parameterization within models and introducing new components such as dynamic root distribution and root functional traits linked to resource extraction (Warren et al., 2015; Brzostek et al., 2014; Shi et al., 2016; Phillips et al., 2016; Brzostek et al., 2017; Iversen et al., 2017)."

Note - we have now included the reference to Weng et al 2015 in that section.

Re cohorts - we have re-written the paragraph as follows:
"Ecological theory suggests that dynamic allocation probably reflects whatever resource is most limiting but developing allocation schemes for LSMs that respond to resource limitation is challenging. The two dynamic allocation schemes reflect forest stand development to some extent i.e. as trees get bigger (and can grow more) they tend to invest more in stem and less in leaves. However the two schemes also use low NPP as a proxy for resource limitation, but they differ on how allocation changes as a function of NPP (Fig. S1). This is a problem because these dynamic schemes cause sites that have low NPP to perpetually allocate more resources to leaves and roots while sites with high NPP perpetually allocate less resources to leaves and roots (Fig. S1). Cohort representation in the model could help deal with this problem by treating allocation caused by low resources differently from early development. As coupled C-N and functional root subroutines are developed for LSMs (Shi et al., 2016), and with better representation of vegetation dynamics (Fisher et al., 2015), we could imagine a dynamic allocation scheme for CLM4.5 based on whether above ground (light) or below ground (water and nutrients) are limiting."

Referee gmd-2017-74-RC2 (Anonymous Referee #2)

I would only like to add to the comments of the other reviewer the following remarks:
Given that the concept "residence time" is ambiguous (see Sierra 2016 GlobChangBiol, doi: 10.1111/gcb.13556), it would add clarity to the paper if the authors shortly defined the concept.

To avoid the muddle discussed in Sierra et al 2016, we have removed the term residence time from the manuscript, we have defined our use of turnover time and used this term throughout.

In the abstract we rephrase the term as follows:

“How carbon (C) is allocated to different plant tissues (leaves, stem and roots) determines how long C remains in plant biomass and thus remains a central challenge for understanding the global C cycle.”

In the introduction we have also rephrased for clarity
“The amount of carbon stored in biomass is dependent how photosynthetically fixed carbon is allocated between C pools and how long these pools persist (Bloom et al., 2016; Koven et al., 2015; De Kauwe et al., 2014). How long-lived different plant pools are (leaf, stem, and root) influences whether ecosystems are projected to act as C sources or sinks (Delbart et al., 2010; Friend et al., 2014).”

In the methods describing our turnover time experiments we include this sentence:
“Here we define turnover time as the total C pool divided by the rate of C input or output.”

In section 4.6 we replace the term residence time with turnover
“The processes controlling turnover times influence C storage capacity, but turnover is not well constrained in models (Friend et al., 2014; Chen et al., 2015; Sierra et al 2016).”

Some sentences need revision because they are not clear, for example: P2L9-10: in "That could be done..." is not clear if "could" is pointing to events in the past or the future. P3L4-5 P4L12: I would suggest to remove "but not for all" P4L25-6 P8L6: I would suggest to remove "then" P6L17-21

Several of these instances have been revised as part of our re-organization in response to reviewer 1, specific changes are below.

RE: P2L9-10 We have changed as follows:
“We identified key structural and parameterization deficits that need refinement to improve the accuracy of LSMs in the near future. These include changing how C is allocated in fixed and dynamic schemes based on data from current forest syntheses and different parameterization of allocation schemes for different forest types.”
P3L4-5 P4L12: I would suggest to remove "but not for all"

"but not for all" does not occur on P3L4-5
P4L12 -"but not for all" has been removed, the sentence now reads:
“While partitioning and uncertainty analysis were available from the FLUXNET2015 dataset (http://fluxnet.fluxdata.org/data/fluxnet2015-dataset/) only for some sites, we opted to use only AmeriFlux L2 data and process all sites using the same protocol.”

P4L25-6 P8L6: I would suggest to remove "then"
“then” does not occur on P4L25-6

P8L6 - “then” has been removed (Note this section has now been moved to the supplementary section).

Other comments: The reference of figure 1 in P10L15 does not match the actual figure: (a) NEE (b) GPP (c) Respiration. Also, from the figure it indeed seems like an overestimation of NEE instead of an underestimation.
The reference of Figure 1 has been modified to match the actual figure and the sentence has been corrected:

“When compared to observations from the AmeriFlux sites, D-CLM4.5 usually net ecosystem exchange (NEE; Fig. 1a) through an overestimation of GPP (Fig. 1b), and ecosystem respiration (Fig. 1c).”

In P15L20-3, is it possible that the comparisson of predictions of aboveground biomass increment (dynamic) with static observations = rings have caused the observed underestimation? Perhaps the comparison is not valid.

We are confident that these comparisons are valid. Aboveground biomass increment varies year by year. Ring width also varies year by year. Potential discrepancies and inconsistencies are discussed at length in section 4.5

I agree with P16L29-30 in that it should be clear what the turnover rate actually comprises. However, in equation 4 it is clear that u_i is the rate at which material leaves B_i, so all C releases (respiration, litterfall, etc.) are necessarilly lumped together in this parameter, unless they are independently specified.

Respiration is independently specified but mortality and woody litterfall are not.

To clarify the CLM technical note states:

“Allocation of available carbon on each time step is prioritized, with first priority given to the demand for carbon to support maintenance respiration of live tissues (section 13.7). Second priority is to replenish the internal plant carbon pool that supports maintenance respiration during times when maintenance respiration exceeds photosynthesis (e.g. at night, during winter for perennial vegetation, or during periods of drought stress) (Sprugel et al., 1995). Third priority is to support growth of new tissues, including allocation to storage pools from which new growth will be displayed in subsequent time steps.”

“Whole-plant mortality is estimated on each time step, and is treated simply as a percentage of total mass in each vegetation pool lost to litter and coarse woody debris pools on an annual basis.”

In a renamed section 2.7 Sensitivity of biomass increment to stem turnover rate we clarify the definition:

“In CLM4.5 the stem turnover rate is dominated by how much woody C is lost each year through senescence (mortality and litter). Here we use the definition of turnover as the total carbon pool divided by the total input and output (Sierra et al 2016). We estimated a range of plausible, site specific stem turnover rates using equation (4) below because, at individual research forest stands, rates of tree mortality may or may not reflect averages rates across larger areas.”

We have reworded this section:

“Some of the aforementioned processes are already partially incorporated in LSMs, in particular land use and land cover change, but the lack of a mechanistic representation of the remaining processes is therefore indirectly represented in stem turnover rates. The processes controlling turnover times influence C storage capacity, but turnover is not well constrained in models (Friend et al., 2014; Chen et al., 2015; Sierra et al 2016). ”

Finally, for Scientific Reproducibility, consider publishing the code in a repository.

Code for CLM4.5 is available through the NCAR CESM code repository. Source modifications and parameterizations will be placed on a publically available code repository and the link will be provided in the final manuscript.

Page 16

“The code for CLM version 4.5 (CLM4.5) is available (registration required) at https://svn-ccsm-models.cgd.ucar.edu/cesm1/release_tags/cesm1_2_1. The allometric parameters used for the different

C allocation schemes used in this study with CLM4.5 are shown in Table 2. The code modifications and parameter files for this paper are available from https://github.com/davidjpmoore/gmd-2017-74. "

Evaluating the effect of alternative carbon allocation schemes in a land surface model (CLM4.5) on carbon fluxes, pools and turnover in temperate forests

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Abstract. How carbon (C) is allocated to different plant tissues (leaves, stem and roots) determines how long C ~~residence~~ remains in plant biomass ~~time~~ and thus remains a central challenge for understanding the global C cycle. We used a diverse set of observations (AmeriFlux eddy covariance tower observations, biomass estimates from tree-ring data, and Leaf Area Index (LAI) measurements) to compare C fluxes, pools, and LAI data with those predicted by a Land Surface Model (LSM), the Community Land Model (CLM4.5). We ran CLM4.5 for nine temperate (including evergreen and deciduous) forests in North America between 1980 and 2013 using four different C allocation schemes: i) Dynamic C allocation scheme (named "D-CLM4.5") with one dynamic allometric parameter, which allocates C to the stem and leaves to vary in time as a function of annual Net Primary Production (NPP). ii) An alternative dynamic C allocation scheme (named "D-Litton"), where, similar to (i) C allocation is a dynamic function of annual NPP, but unlike (i) includes two dynamic allometric parameters involving allocation to leaves, stem and coarse roots iii-iv) A~~Two~~ fixed C allocation scheme with two variants~~s~~, one representative of observations in evergreen (named "F-Evergreen") and the other of observations in deciduous forests (named "F-Deciduous"). D-CLM4.5 generally overestimated Gross Primary Production (GPP) and ecosystem respiration, and underestimated Net Ecosystem Exchange (NEE). In D-CLM4.5, initial aboveground biomass in 1980 was largely overestimated (between 10527 and 12897 gCm^{-2}) for deciduous forests, whereas aboveground biomass accumulation through time (between 1980 and 2011) was highly underestimated (between 1222 and 7557 gCm^{-2}) for both evergreen and deciduous sites due to a lower stem turnover rate in the sites than the one used in the model. D-CLM4.5 overestimated LAI in both evergreen and deciduous sites because the leaf C-LAI relationship in the model did not match the observed leaf C-LAI relationship at our sites. Although the four C allocation schemes gave similar results for aggregated C fluxes, they translated to important differences in long-term aboveground biomass accumulation and aboveground NPP. For deciduous forests, D-Litton gave more realistic C_{stem}/C_{leaf} ratios and strongly reduced the overestimation of initial aboveground biomass, and aboveground NPP for deciduous forests by D-CLM4.5. We identified key structural and parameterization deficits that need refinement to improve the accuracy of LSMs in the near future. These include changing how C is allocated in fixed and dynamic schemes based on data from current forest syntheses and different parameterization of allocation schemes for different forest types~~That could be done by addressing some of the current model assumptions about C allocation and the associated parameter uncertainty~~.

Our results highlight the ~~importance~~ utility of using measurements of aboveground biomass~~ data~~ to evaluate and constrain the C allocation scheme in ~~the model~~LSMs, and suggest that stem turnover is overestimated by CLM4.5 for these Ameriflux ~~forests~~sites~~also the need forin particular, the sensitivity to empirical estimates of the stemC turnover rate~~. ~~Revising these~~Understanding the controls of turnover will be critical to improving long-term C processes in LSMs~~, and improve their projections of biomass accumulation in forests~~.

1 Introduction

Over the last half century, on average a little more than a quarter of global CO_2 emissions were absorbed by terrestrial carbon (C) sinks (Le Quéré et al., 2015), with forests accounting for most (Malhi et al., 2002; Bonan, 2008; Pan et al., 2011; Baldocchi et al., 2016). The interannual variability in the land C sink is high, representing up to 80% of annual CO_2 emissions (Le Quéré et al., 2009). The mechanism by which forests accumulate C is through photosynthetic uptake and allocation of the C to biomass in different plant pools (leaf, stem and root). The C stored in biomass stocks are determined mainly by the C fluxes and the C allocation amongst plant pools.

The amount of carbon stored in biomass is dependent ~~Recent modeling studies have shown that simultaneous consideration of C allocation and residence times is crucial to better understand their combined effects on biomass accumulation~~how photosynthetically fixed carbon is allocated~~ion~~ between C pools and how long these pools persist (Bloom et al., 2016; Koven et al., 2015; De Kauwe et al., 2014). How long-lived ~~Carbon residence time in the~~ different plant pools are (leaf, stem, and root) influences whether ecosystems are projected to act as C sources or sinks (Delbart et al., 2010; Friend et al., 2014). Once C is taken up by the plant, the carbon is allocated either to short-lived leaf or fine-root tissues, or to longer lived woody tissues. Here we use turnover time of C in a plant pool as the total carbon pool divided by the total flux into or out of the pool (Sierra et al. 2016). Plants that allocate a greater proportion of C to tissues with long ~~residence~~ turnover times (e.g. stem) have a higher standing biomass than the plants that allocate a greater proportion of C to tissues with short ~~residence~~ turnover times (e.g. leaf). Ecological theory suggests that variation in C allocation to different plant pools is governed by functional trade-offs (Tilman, 1988); with plants investing in either aboveground or belowground tissues depending on which strategy would maximise growth and reproduction. If the functional trade-off hypothesis is relevant at forest or regional scales, land surface models (LSMs) for forests should represent it using dynamic C-allocation schemes, which are responsive to above (e.g. light) and belowground (e.g. water or nutrients) factors that limit growth.

Allocation of C between pools in terrestrial ecosystems is poorly represented in LSMs (Delbart et al., 2010; Malhi et al., 2011; Negron-Juarez et al., 2015). Some LSMs use fixed ratios for each Plant Functional Type (PFT), while other models use allocation fractions that are altered by environmental conditions (Wolf et al. 2011; DeKauwe et al 2014). Though many LSMs use the same fractional allocation for both evergreen and deciduous forests, global syntheses show differences in inferred C allocation patterns, for example, the percentage of NPP allocated to leaves that is greater in deciduous than in evergreen forests (Luyssaert et al., 2007). In part this is because it is difficult to measure allocation to different pools at ecosystem or landscape scales and instead we infer what partitioning was required to result in different biomass pools. While eddy covariance observations can be used to parameterize and benchmark LSMs either at single sites or, using geospatial scaling methods, across regions or the globe (Baldocchi et al., 2001; Friend et al., 2007; Randerson et al., 2009; Zaehle and Friend 2010; Mahecha et al., 2010; Bonan et al., 2011), these data inform fluxes in and out but do not provide information on allocation between pools (Richardson et al., 2010).

Studies focusing simultaneously on C pools, fluxes and allocation are relatively rare (Wolf et al., 2011; Xia et al., 2015; Bloom et al., 2016; Thum et al., 2017), in part because collecting biometric data in addition to flux data is very labour intensive. Some forest inventory data includes estimates of the average biomass within the leaf, wood and root pool, and these can be used to parameterize and benchmark models (Caspersen et al., 2000; Brown, 2002; Houghton, 2005; Keith et al., 2009). The AmeriFlux network provides a rare opportunity to investigate forest allocation processes because gross primary productivity and respiration fluxes are quantified continuously. However, measurements of pool sizes in leaves, stems etc. are less available at these sites and so have been less frequently explored. ~~Currently, many LSMs use a simplistic approach of allocating C between pools using fixed ratios (e.g. fixed coefficient models) (De Kauwe et al., 2014) for each Plant Functional Type (PFT), assuming that allocation fractions are not affected by environmental conditions. A global syntheses of evergreen and deciduous forests show differences in inferred C allocation patterns, for example, the percentage of NPP allocated to leaves that is greater in deciduous than in evergreen forests (Luyssaert et al., 2007), though many LSMs use the same fractional allocation for both of these forest types. LSMs poorly represent observed relationships between productivity and different pools of biomass within tropical forests (Delbart et al., 2010; Malhi et al., 2011; Negron-Juarez et al., 2015). Eddy covariance observations are commonly used to parameterize and benchmark LSMs either at single sites or, using geospatial scaling methods, across regions or the globe (Baldocchi et al., 2001; Friend et al., 2007; Randerson et al.,~~

~~2009; Zaehle and Friend 2010; Mahecha et al., 2010; Bonan et al., 2011). Biosphere-atmosphere fluxes indicate the balance between the amount of CO_2 entering the system through assimilation (e.g. photosynthesis) and the amount of CO_2 leaving the system through respiration (e.g. ecosystem respiration) but do not provide information on allocation between pools (Richardson et al., 2010). Studies that focus on C allocation to the different plant pools are not common (e.g. Gower et al., 2001; Franklin et al., 2012). It is difficult to measure allocation to different pools at ecosystem or landscape scales and instead we infer what partitioning was required to result in different biomass pools. Some forest inventory data includes estimates of the average biomass within the leaf, wood and root pool, and these can be used to parameterize and benchmark models (Caspersen et al., 2000; Brown, 2002; Houghton, 2005; Keith et al., 2009). Studies focusing simultaneously on C pools, fluxes and allocation are relatively rare (Wolf et al., 2011; Xia et al., 2015; Bloom et al., 2016; Thum et al., 2017), in part because collecting biometric data in addition to flux data is very labour intensive.~~

In this study, we evaluate mechanisms by which C is stored over multiple decades in plant biomass using corresponding eddy covariance flux towers and biometric measurements of C storage in different pools. We collated biometric data (~~e.g.~~ aboveground biomass and leaf area index), where available, for AmeriFlux sites and supplemented these data with novel aboveground biomass estimates from tree-ring data for AmeriFlux sites (Alexander et al., in review). We evaluate two dynamic C allocation schemes (Oleson et al., 2013; Litton et al., 2007) and two fixed C allocation schemes (Luyssaert et al., 2007) within the Community Land Model (CLM4.5) against C fluxes, stocks, and Leaf Area Index (LAI) data at nine temperate North American forest ecosystems.

2 Methods

We ~~used~~implemented the CLM4.5 model – a well-established and commonly used LSM, at nine different forest sites (2.1) and compiled observation of C fluxes, C pools, LAI, and the C_{stem}/C_{leaf} ratio (2.2) ~~as a platform to implement~~ to ~~study the effects of~~evaluate ~~the~~ alternative C allocation ~~schemes, described above~~structures and parameterizations (2.3 & 2.4)~~, and compared the resultant model simulations of C fluxes, C pools, LAI, and the C_{stem}/C_{leaf} ratio with available observations (2.2)~~. ~~Because we implemented the model at particular sites we~~ ~~w~~We re-parameterized the Specific Leaf Area (SLA) based on available observations (2.5) before implementing four CLM4.5 model experiments designed to examine the impact of the different C allocation structures and parameterizations (2.6). Finally to investigate the potential effects of site variation in woody turnover we~~(2.5) and~~ ~~attempted to~~ estimated plausible site-specific turnover rates (2.~~6~~7). ~~We then implemented Ffour experiments were designed to betterexamine understand the impact of the different C allocation schemes (2.7). All modelling experiments were run for nine sites, including four evergreen and five deciduous forests (see Table 1). For evergreen sites, we used the default leaf C-LAI relationship in CLM4.5, whereas for deciduous forests we used the optimized leaf C-LAI relationship (Sect. 2.5).~~

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~~For experiment 1 we used the original dynamic C allocation scheme in CLM4.5 (D-CLM4.5; see Sect. 2.3). For experiment 2, we used the alternative dynamic C allocation scheme based on Litton et al. (2007) (D-Litton, see Sect. 2.4). For experiments 3 and 4, we used a fixed C allocation scheme representative of evergreen (F-Evergreen) and deciduous (F-Deciduous) forests, respectively (Luyssaert et al. 2007 – see Sect. 2.4).~~

~~The standard climate forcing provided with the model is the 1901-2013 CRUNCEP dataset. The CRUNCEP dataset has been used to force CLM for studies of vegetation growth, evapotranspiration, and gross primary production (Mao et al., 2012; Mao et al., 2013; Shi et al., 2013; Chen et al., 2016), and for the TRENDY (trends in net land-atmosphere carbon exchange over the period 1980-2010) project (Piao et al., 2012).~~

~~In all the experiments, we spun-up the model for each site and C allocation scheme using 1901-1920 CRUNCEP climate and assuming pre-industrial atmospheric CO_2 concentration in order to bring all above- and belowground C pools to equilibrium. We used the initial conditions resulting from the spin-up to perform a 1901-2013 transient run (e.g. 1901-2013 CRUNCEP transient climate, transient atmospheric CO_2 concentration). Observations were compared with model outputs for the period between 1980 and 2013.~~

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2.1 Study sites

Nine temperate forests widely distributed throughout the USA were selected for this study, including four evergreen (Niwot Ridge, Valles Caldera Mixed Conifer, Howland Forest, and Duke Forest Loblolly Pine) and five deciduous forests (University of Michigan Biological Station, Missouri Ozark, Harvard Forest, Morgan Monroe State Forest, and Duke Forest Hardwoods) (Table 1). All the selected forests are AmeriFlux sites (http://ameriflux.lbl.gov/), a network of eddy covariance sites measuring ecosystem C, water, and the energy fluxes in North and South America. AmeriFlux datasets provide central connections between terrestrial ecosystem processes and climate responses from site to continental scale, and are part of FLUXNET, a global network of eddy covariance measurements being made on all continents.

2.2 Observations

We compiled different data streams from diverse sources for the sites (Table 1) for benchmarking C fluxes, C pools, and LAI in the model experiments. Some of the data were only available for a subset of sites and years (Table 1).

To quantify carbon flux into and out of the different forests, ~~E~~eddy covariance ~~tower data~~measurements were~~ were derived~~ collated from the AmeriFlux L2 gap-filled data product (Boden et al. 2013, http://ameriflux.lbl.gov/data/download-data/) for all sites~~ (Table 1)~~, except for Niwot Ridge where only the AmeriFlux L2 with-gaps data product was available and there we used the REddyProc package (Reichstein et al., 2005) to gap-fill and partition the data (Table 1). Half-hourly eddy covariance flux data were aggregated to annual values at all sites. While partitioning and uncertainty analysis were available from the FLUXNET2015 dataset (http://fluxnet.fluxdata.org/data/fluxnet2015-dataset/) only for some sites, ~~but not for all,~~ we opted to use only AmeriFlux L2 data and process all sites using the same protocol.

To quantify the how much carbon was stored in aboveground woody biomass and leaf biomass in these forests we collated already existing biomass and LAI estimates from the AmeriFlux network; these were available for only some sites and years (Table 1). In-situ measured LAI was available from AmeriFlux data for some sites (Table 1), and we used the annual maximum LAI for all the available measurements in each year. We used leaf C-LAI ratio from the AmeriFlux sites with simultaneous measurements of LAI and leaf C during the same year (Table 1). The C_{stem}/C_{leaf} ratio, which was derived from AmeriFlux data with C_{stem} and C_{leaf} estimates for the same year, was only available for a subset of sites and years (Table 1).

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To quantify ~~A~~aboveground biomass at all of the sites, we surveyed each forest and calculated above-ground biomass between 1980 and 2011 ~~was estimated for all sites~~ (Table 1) using a dendrochronological sampling technique (Dye et al., 2016; Alexander et al., in review). This ~~, to~~provided a reconstruction of year-to-year variability in diameter at breast height (dbh) of trees and biomass inferred from allometric regressions. Briefly, the dbh of trees within a 20-m diameter plot were measured; all trees above 10 cm in diameter were sampled within 13 m and trees larger than 20 cm dbh were sampled in the remainder of the plot. In Valles Caldera, rather than subsampling within a 20-m plot, all trees were sampled from two central locations until fifty samples were collected from each location following Babst et al., (2014). At the Niwot site, a point-center-quarter method (Stearns, 1949; Cottam et al., 1953) was used to estimate stand density and to select individuals for sampling. Species, dbh and canopy position were recorded for each tree within the plots. Increment cores were dried, mounted, and sanded using standard dendrochronological procedures (Stokes and Smiley, 1968). Increments were first visually crossdated (Douglass, 1941) and then measured under a binocular microscope and statistically crossdated using COFECHA software (Holmes, 1983; Grissino-Mayer, 2001). Ring widths were scaled to dbh and allometric equations (Jenkins et al., 2004; Chojnacky et al., 2014) were applied to estimate biomass through time. When available site/region specific allometric equations were applied, and generalized species level allometric equations were used where these were not available. Trees that were sampled but lacked sufficient tree-ring data were gap-filled with a generalized additive mixed model to account for their biomass on the landscape (Alexander et al., in review). At Harvard and Howland, tree-ring reconstructed biomass was compared to biomass estimated from permanent plots established in 1969 and 1989 respectively; tree-ring biomass increment estimates fell within the 95% confidence intervals of biomass estimated from the permanent plots (Dye et al., 2016). Both permanent plots and tree-ring reconstructed biomass are dependent on allometric equations which contributes to uncertainty in these values.

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~~Biometric estimates of aboveground biomass were also available for some sites and years from the AmeriFlux network (Table 1). The C_{stem}/C_{leaf} ratio, which was derived from AmeriFlux data with C_{stem} and C_{leaf} estimates for the same year, was only available for a subset of sites and years (Table 1).~~

~~In-situ measured LAI was available from AmeriFlux data for some sites (Table 1), and we used the annual maximum LAI for all the available measurements in each year. We used leaf C-LAI ratio from the AmeriFlux sites with simultaneous measurements of LAI and leaf C during the same year (Table 1).~~

2.3 C allocation scheme in CLM

The Community Land Model (CLM version 4.5) was used to simulate C fluxes, C pools and LAI at single points (~~PTCLM;~~ Oleson et al., 2013). CLM4.5 is a component of the Community Earth System Model (CESM1.2) of the National Center for Atmospheric Research (Oleson et al., 2013).

CLM4.5 assumes that vegetated surfaces are comprised of different Plant Functional Types (PFTs). Our sites had two different PFTs: “needleleaf evergreen tree – temperate” for evergreen forests and “broadleaf deciduous tree – temperate” for deciduous forests.

CLM4.5 includes the following plant tissue types: leaf, stem (live and dead stem), coarse root (live and dead coarse root), and fine root (Oleson et al., 2013). The model calculates carbon allocated to new growth based on three allometric parameters that relate allocation between tissue types (Oleson et al., 2013): a_1 (ratio of new fine root: new leaf carbon allocation); a_2 (ratio of new coarse root: new stem carbon allocation); and a_3 (ratio of new stem: new leaf carbon allocation). CLM4.5 has a dynamic allocation scheme (named “D-CLM4.5”), which is described in Oleson et al. (2013), that includes one dynamic allometric parameter (as function of annual NPP) and two constant allometric parameters. In D-CLM4.5 (see Table 2), for the PFTs in our sites a_1 and a_2 are constant (a_1=1, a_2=0.3), whereas a_3 is a dynamic parameter defined by the following equation:

$$a_3 = \frac{2.7}{1+e^{-0.004*(NPPann-300)}} - 0.4 \qquad (1)$$

where *NPPann* is the annual sum of NPP of the previous year. The above equation for a_3 increases stem allocation relative to leaf when annual NPP increases. For instance, when annual NPP is 0 $gCm^{-2}year^{-1}$, a_3 is 0.20 (e.g. 0.2 units of C allocated to stem for 1 unit of C allocated to leaf), whereas when NPP is close to 1000 $gCm^{-2}year^{-1}$ or greater, a_3 is constrained to not exceed 2.2 (e.g. 2.2 units of C allocated to stem for 1 unit of C allocated to leaf). Therefore, when annual NPP is relatively close to 1000 $gCm^{-2}year^{-1}$ or greater the C allocation scheme becomes fixed with the following values for the parameters: a_1=1, a_2=0.3, and a_3=2.2. To account for the range of NPP found in temperate forests, ~~For a broad range of annual NPP values,~~ we calculated the allometric parameters a_1, a_2 and a_3 for a broad range of NPP, and then converted the allometric

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parameters to allocation coefficients for each plant tissue using the C allometry in the model (Oleson et al., 2013). We illustrate in one figure the effect of annual NPP on C allocation to each plant tissue in D-CLM4.5 (Fig. S1).

2.4 Alternative C allocation ~~schemes~~structures and parameterizations

In addition to the dynamic C allocation ~~scheme~~ structure in CLM4.5 (Oleson et al., 2013), we implemented an alternative dynamic (Litton et al., 2007), and two fixed (Luyssaert et al., 2007) C allocation ~~schemes~~parameterizations with the same structure.

The alternative dynamic C allocation ~~scheme~~ structure (named “D-Litton”) was based on carbon partitioning data along an annual GPP gradient from Litton et al. (2007), and it considered two dynamic allometric parameters. We adapted the original equations reported in Litton et al. (2007), converted the GPP gradient to a NPP gradient with the general assumption that NPP=0.5×GPP (Waring et al., 1998; Gifford, 2003), and used the modified equations to calculate the allometric parameters used in CLM4.5. The partitioning between coarse root and fine root was not provided, and we used the default value for parameter a_1 (a_1=1). The other allometric parameters (a_2 and a_3) were dynamic, and the equations used for them are shown in Table 2.

The two ~~two~~ alternative fixed C schemes have the same structure but different allocation ~~schemes~~ parameterizations and were based on observed values reported by Luyssaert et al. (2007), which were converted accordingly to the allometric parameters used in CLM. One of the C allocation ~~schemes~~ parameter sets was representative of temperate evergreen forests (named “F-Evergreen”) and the other of temperate broadleaf deciduous forests (named “F-Deciduous”). Similarly to Litton et al. (2007), Luyssaert et al. (2007) only provided total root allocation without considering coarse and fine root, but the default value for parameter a_1 (a_1=1) was not possible in some cases. We thus initially used a range of possible values for parameter a_1 (a_1=1, a_1=0.75 and a_1=0.5) for model runs. When based on the values in Luyssaert et al. (2007) allocation to leaf was lower than total root allocation, we used the default value for parameter a_1 (a_1=1 for F-Evergreen); but when based on the values in Luyssaert et al. (2007) allocation to leaf was higher than total root allocation, the a_1 parameter had to be lower than 1. This was the case for the F-Deciduous C allocation ~~scheme~~parameterization, and because a_1=0.75 gave unrealistic aboveground:belowground ratios, we used a_1=0.5. The allometric parameters used for the F-Evergreen and F-Deciduous C allocation ~~scheme~~ parameterizations are shown in Table 2.

~~D-CLM and the alternative C allocation schemes have important differences in C allocation to each plant tissue (see Fig. S1). Some of the main differences between D-CLM, and the alternative C allocation schemes, include increased allocation to leaf, and decreased allocation to stem, especially in D-Litton at sites with low mean annual NPP (see Fig. S1).~~

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2.5 LAI in CLM

CLM4.5 uses a prognostic canopy model, with feedbacks between GPP and LAI acting through allocation to leaf C and ~~Specific Leaf Area (SLA),~~ SLA and with SLA being a critical fixed parameter in this feedback pathway ~~-~~(Thornton and Zimmermann, 2007). The model assumes a linear relationship between SLA and the canopy depth (x):

$$SLA(x) = SLA_0 + mx \tag{2}$$

where SLA_0 (m^2 one-sided leaf area gC^{-1}) is a fixed value of SLA at the top of the canopy, *m* is a linear slope coefficient, and *x* is the canopy depth expressed as overlying leaf area index (m^2 overlying one-sided leaf area m^{-2} ground area). LAI is calculated for a given leaf C (C_L) using the following equation:

$$LAI = \frac{SLA_0[\exp(mC_L) - 1]}{m} \tag{3}$$

where m (m^2 ground area gC^{-1}) and SLA_0 (m^2 one-sided leaf area gC^{-1}) are different parameters for each PFT. In the case of temperate evergreen forests the default values for m and SLA_0 in CLM4.5 are 0.00125 and 0.010; whereas for temperate broadleaf deciduous forests m= 0.004 and SLA_0=0.030 (Oleson et al., 2013).

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We compared leaf C-LAI data from available sites with the leaf C-LAI relationship in the model. For deciduous sites, we optimized the model parameters based on observed leaf C-LAI. To avoid using unrealistic values for the parameters m and SLA_0, we took a range of possible values for both parameters from Thornton and Zimmermann (2007), and used an optimization approach based on least squares that combined the range of parameter values and Eq. (3) to find the best combination of values for the two parameters given the leaf C-LAI observations at our sites. After optimizing the parameters m and SLA_0, we used m=0.0010 and SLA_0=0.024 for deciduous forests. For evergreen sites, we could not optimize the parameters m and SLA_0 due to the limited number of leaf C-LAI observations available. All model experiments were carried out after SLA optimization.

~~2.6 Turnover rate and aboveground biomass increment~~

~~LSMs typically are run at scales that are coarser than individual forest sites and use aggregate estimates for C pool turnover. However, at individual research forest stands, rates of tree mortality may or may not reflect averages rates across larger areas. CLM4.5, like many models, is based on differential equations for the calculation of changing biomass with time, which can be expressed as:~~

~~$dB_i/dt = a_i\,NPP - u_i B_i$~~ ~~(4)~~

~~where *i* is a given plant pool; B_i is the biomass of that pool; dB_i/dt is the biomass increment with time for each plant pool; a_i is the allocation coefficient to that plant pool (allocation coefficients for all pools combined sum to 1); and u_i is the turnover rate for each component. We considered leaf, stem, coarse root and fine root as plant pools. To optimize the stem turnover rate we used a model emulator with the above equation to modify the default stem turnover rate (2%) to within a range of 0 to 2% (van Mantgem et al., 2009; Brown and Schroeder, 1999); for the rest of plant pools we used the default turnover rate in the model. In the model emulator, the annual NPP input was derived from the model for a given site using the default stem turnover (2%), and the initial biomass for each plant pool was derived from the model with a particular carbon allocation scheme. We compared the differences in aboveground biomass (leaf and stem) increment over time based on different turnover rates with the aboveground biomass increments estimated from tree-ring data for our sites between 1980 and 2011.~~

~~2.7 C allocation scheme effect on initial aboveground biomass and C_{stem}/C_{leaf} ratio~~

~~We To evaluate compared the effect of different C allocation schemes in initial aboveground biomass in equilibrium and we also compared them with tree-ring estimates of aboveground biomass data for 1980. The C allocation scheme used had has a strong influence on initial aboveground biomass and the C_{stem}/C_{leaf} ratio, which can be explained with Eq. (4). When the model is in equilibrium conditions, then $dB_i/dt=0$ in Eq. (4), and denoting B_{stem} with C_{stem}, and B_{leaf} with C_{leaf}:~~

~~$a_{stem}NPP = NPP_{stem} = u_{stem}C_{stem}$~~ ~~(5)~~

~~$a_{leaf}NPP = NPP_{leaf} = u_{leaf}C_{leaf}$~~ ~~(6)~~

~~After dividing Eq. (5) by Eq. (6):~~

~~$a_{stem}/a_{leaf} = NPP_{stem}/NPP_{leaf} = \left(C_{stem}/C_{leaf}\right)\times\left(u_{stem}/u_{leaf}\right)$~~ ~~(7)~~

~~$C_{stem}/C_{leaf} = \dfrac{\left(NPP_{stem}/NPP_{leaf}\right)}{\left(u_{stem}/u_{leaf}\right)}$~~ ~~or~~ ~~$C_{stem}/C_{leaf} = \dfrac{\left(a_{stem}/a_{leaf}\right)}{\left(u_{stem}/u_{leaf}\right)}$~~ ~~(8)~~

~~In D-CLM4.5 $NPP_{stem}/NPP_{leaf} \approx 2$ and $a_{stem}/a_{leaf} \approx 2$ for evergreen sites in favorable conditions (e.g. mean annual NPP ≈ 1000 $gCm^{-2}year^{-1}$) and for deciduous sites; u_{stem}/u_{leaf}=0.02 for deciduous and u_{stem}/u_{leaf}=0.06 for evergreen forests. Therefore, in D-CLM4.5 $C_{stem}/C_{leaf} \approx 33$ for evergreen sites in favorable conditions; and $C_{stem}/C_{leaf} \approx 100$ for deciduous sites.~~

~~Because the alternative C allocation schemes have different NPP_{stem}/NPP_{leaf} ratio than the one in D-CLM4.5, they showed different C_{stem}/C_{leaf} ratio, despite having the same u_{stem}/u_{leaf} . We compared the C_{stem}/C_{leaf} ratio from the four C allocation schemes with available observations for the sites (Table 1).~~

~~In reference to the initial aboveground biomass (leaf+stem), we can use Eq. (4), and assuming equilibrium conditions, dB_i/dt=0, then:~~

~~$a_{leaf}NPP + a_{stem}NPP = u_{leaf}C_{leaf} + u_{stem}C_{stem}$ (9)~~

~~$ANPP = u_{leaf}C_{leaf} + u_{stem}C_{stem} = C_{stem}(u_{stem} + u_{leaf}C_{leaf}/C_{stem})$ (10)~~

~~$C_{stem}^{*} = ANPP/(u_{stem} + u_{leaf}C_{leaf}/C_{stem}) = ANPP/u_{stem}(1+(NPP_{leaf}/NPP_{stem}))$ (11)~~

~~Similarly to Eq (10),~~

~~$ANPP = u_{leaf}C_{leaf} + u_{stem}C_{stem} = C_{leaf}(u_{leaf} + u_{stem}C_{stem}/C_{leaf})$ (12)~~

~~$C_{leaf}^{*} = ANPP/(u_{leaf} + u_{stem}C_{stem}/C_{leaf}) = ANPP/u_{leaf}(1+(NPP_{stem}/NPP_{leaf}))$ (13)~~

~~Hence,~~

~~$C_{aboveground}^{*} = C_{leaf}^{*} + C_{stem}^{*} = ANPP/u_{leaf}(1+(NPP_{stem}/NPP_{leaf})) + ANPP/u_{stem}(1+(NPP_{leaf}/NPP_{stem}))$ (14)~~

~~where C_{stem}^{*}, C_{leaf}^{*}, and $C_{aboveground}^{*}$ refer to stem C, leaf C and aboveground C in equilibrium conditions, respectively. Therefore, the aboveground biomass in equilibrium conditions will depend on aboveground NPP (*ANPP*), the NPP_{stem}/NPP_{leaf} ratio (or a_{stem}/a_{leaf} ratio) and the turnover rates for leaf and stem (u_{leaf} and u_{stem}). We compared the effect of different C allocation schemes in initial aboveground biomass in equilibrium and we also compared them with tree-ring estimates of aboveground biomass data for 1980.~~

2.~~8~~6 Testing allocation schemes in CLM4.5 ~~Model experiments~~

All CLM4.5 modelling experiments were run for nine sites, including four evergreen and five deciduous forests (see Table 1). For evergreen sites, we used the default leaf C-LAI relationship in CLM4.5, whereas for deciduous forests we used the optimized leaf C-LAI relationship (Sect. 2.5).

Each experiment represents a different allocation scheme. For experiment 1 we used the original dynamic C allocation ~~scheme~~structure in CLM4.5 (D-CLM4.5; see Sect. 2.3). For experiment 2, we used the alternative dynamic C allocation ~~scheme~~structure based on Litton et al. (2007) (D-Litton, see Sect. 2.4). For experiments 3 and 4, we used a fixed C allocation ~~scheme~~structure representative of evergreen (F-Evergreen) and deciduous (F-Deciduous) forests, respectively (Luyssaert et al. 2007 – see Sect. 2.4).

The standard climate forcing provided with the model is the 1901-2013 CRUNCEP dataset. While meteorological data is available at the AmeriFlux sites, this data extends only as long at the eddy covariance observations which is less than a decade in several cases. To explore the effects of allocation on slowly changing C pools like woody biomass, we extended model runs to 30 years which requires using CRUNCEP or some other reanalysis climate. The CRUNCEP dataset has been used to force CLM for studies of vegetation growth, evapotranspiration, and gross primary production (Mao et al., 2012; Mao et al., 2013; Shi et al., 2013; Chen et al., 2016), and for the TRENDY (trends in net land-atmosphere carbon exchange over the period 1980-2010) project (Piao et al., 2012).

In all the experiments, we spun-up the model for each site and C allocation scheme using 1901-1920 CRUNCEP climate and assuming pre-industrial atmospheric CO_2 concentration in order to bring all above- and belowground C pools to equilibrium. We used the initial conditions resulting from the spin-up to perform a 1901-2013 transient run (e.g. 1901-2013 CRUNCEP transient climate, transient atmospheric CO_2 concentration). Observations were compared with model outputs for the period between 1980 and 2013.

2.7 Sensitivity of biomass increment to stem turnover rate

In CLM4.5 the stem turnover rate is dominated by how much woody C is lost each year through senescence (mortality and litter). Here we define turnover time as the total C pool divided by the rate of C input or output. We estimated a range of plausible, site specific stem turnover rates using equation (4) below because, at individual research forest stands, rates of tree mortality may or may not reflect averages rates across larger areas. LSMs typically are run at scales that are coarser than individual forest sites and use aggregate estimates for turnover of different C pools. CLM4.5, like many models, is based on differential equations for the calculation of changing biomass with time, which can be expressed as:

$$dB_i/dt = a_i\,NPP - u_i B_i \quad (4)$$

where i is a given plant pool; B_i is the biomass of that pool; dB_i/dt is the biomass increment with time for each plant pool; a_i is the allocation coefficient to that plant pool (allocation coefficients for all pools combined sum to 1); and u_i is the turnover rate for each component. We considered leaf, stem, coarse root and fine root as plant pools. To optimize the stem turnover rate we used equation (4) as a ~~model emulator~~simplified offline model to modify the default stem turnover rate (2%) to within a range of 0 to 2% (van Mantgem et al., 2009; Brown and Schroeder, 1999); for the rest of plant pools we used the default turnover rate in the model. In the ~~model emulator~~simplified offline model, the annual NPP input was derived from the model for a given site using the default stem turnover (2%), and the initial biomass for each plant pool was derived from the model with a particular carbon allocation scheme and parameterization. We compared the differences in aboveground biomass (leaf and stem) increment over time based on different turnover rates with the aboveground biomass increments estimated from tree-ring data for our sites between 1980 and 2011.

~~We used the CLM4.5 model – a well-established and commonly used LSM, as a platform to implement the alternative C allocation schemes, described above, and compared the resultant model simulations of C fluxes, C pools, LAI, and the C_{stem}/C_{leaf} ratio with available observations. Four experiments were designed to better understand the impact of the different C allocation schemes. All modelling experiments were run for nine sites, including four evergreen and five deciduous forests (see Table 1). For evergreen sites, we used the default leaf C-LAI relationship in CLM4.5, whereas for deciduous forests we used the optimized leaf C-LAI relationship (Sect. 2.5).~~

~~For experiment 1 we used the original dynamic C allocation scheme in CLM4.5 (D-CLM4.5; see Sect. 2.3). For experiment 2, we used the alternative dynamic C allocation scheme based on Litton et al. (2007) (D-Litton, see Sect. 2.4). For experiments 3 and 4, we used a fixed C allocation scheme representative of evergreen (F-Evergreen) and deciduous (F-Deciduous) forests, respectively (Luyssaert et al. 2007 – see Sect. 2.4).~~

~~The standard climate forcing provided with the model is the 1901-2013 CRUNCEP dataset. The CRUNCEP dataset has been used to force CLM for studies of vegetation growth, evapotranspiration, and gross primary production (Mao et al., 2012; Mao et al., 2013; Shi et al., 2013; Chen et al., 2016), and for the TRENDY (trends in net land-atmosphere carbon exchange over the period 1980-2010) project (Piao et al., 2012).~~

~~In all the experiments, we spun-up the model for each site and C allocation scheme using 1901-1920 CRUNCEP climate and assuming pre-industrial atmospheric CO_2 concentration in order to bring all above- and belowground C pools to equilibrium. We used the initial conditions resulting from the spin-up to perform a 1901-2013 transient run (e.g. 1901-2013 CRUNCEP transient climate, transient atmospheric CO_2 concentration). Observations were compared with model outputs for the period between 1980 and 2013.~~

3 Results

3.1 Carbon fluxes, and pools in D-CLM4.5

When compared to observations from the AmeriFlux sites, D-CLM4.5 usually net ecosystem exchange (NEE; Fig. 1a) through an ~~overestimated~~ overestimation of GPP (Fig. 1b~~a~~), and ecosystem respiration (Fig. 1c).~~, and underestimated net ecosystem exchange (NEE; Fig. 1ab).~~

Initial aboveground biomass in 1980 showed contrasting patterns in D-CLM4.5 for evergreen and deciduous forests. At evergreen sites, aboveground biomass in 1980 was underestimated at sites with mean annual NPP<500 $gCm^{-2}year^{-1}$ (NR1 and Vcm) and overestimated at the site with mean annual NPP>500 $gCm^{-2}y^{-1}$ (Ho1; Fig. 2a). Aboveground biomass in 1980 was largely overestimated at all deciduous sites (between 10527 and 12897 gCm^{-2}) (Fig. 2a). The accumulated aboveground biomass between 1980 and 2011 was largely underestimated in the model (difference between observations and model ranged between 1222 and 7557 gCm^{-2}, depending on the site) (Fig. 2b).

3.2 LAI and C_{stem}/C_{leaf} in D-CLM4.5

D-CLM4.5 overestimated LAI relative to in-situ LAI measurements (Fig. 3a). We compared the leaf C-LAI relationship with the observed leaf C-LAI and found important differences, especially for deciduous sites (Fig. 3b). We optimized the parameters m and SLA_0 based on available observations for two deciduous sites (Fig. 3b). The modified LAI was closer to the LAI values measured in-situ for all five deciduous sites (Fig. 3c).

The C_{stem}/C_{leaf} ratio in the model was dramatically different from the observations (Fig. 4). The model overestimated the C_{stem}/C_{leaf} ratio in one of the two years with available data for two evergreen sites, and all the 19 years with available data for two deciduous sites (Fig. 4; Table 1).

3.3 Carbon fluxes, pools and LAI in the alternative C allocation schemes

D-CLM4.5 and the alternative C allocation schemes have important differences in C allocation to each plant tissue (see Fig. S1). Some of the main differences between D-CLM4.5, and the alternative C allocation schemes, include increased allocation to leaf, and decreased allocation to stem, especially in D-Litton at sites with low mean annual NPP (see Fig. S1).

The accumulated annual C fluxes (GPP, ecosystem respiration, and NEE) from 1980 to 2011 gave comparable results for the four C allocation schemes (Suppl. Fig. 2). However, the C allocation schemes resulted in differences larger than 5000 gCm^{-2} in long-term aboveground biomass accumulation for all the sites (Fig. 5a and 5b). All C allocation schemes overestimated aboveground biomass in 1980 in all the sites, except in evergreen sites with mean annual NPP<500 $gCm^{-2}year^{-1}$ (NR1 and

Vcm), where only the F-Deciduous allocation overestimated aboveground biomass (Fig. 5a). The D-Litton allocation scheme underestimated aboveground biomass in 1980 at all evergreen sites and, despite overestimating it at all deciduous sites, this scheme gave the closest values to the observations (Fig. 5a). Similar results were found for mean aboveground biomass between 2002 and 2011 (Fig. 5b). Despite the differences in the total aboveground biomass, aboveground biomass annual increment in all the C allocation schemes was lower than that estimated from tree-ring data and accumulated aboveground biomass between 1980 and 2011 was therefore strongly underestimated assuming a mortality rate of 2% year^{-1} (Fig. 5c).

The C allocation schemes showed differences of up to 10% in allocation to leaf, which produced large differences in LAI values (from ~20 to ~4.5) between allocation schemes (Fig. 6). In particular the F-Deciduous allocation gave high and unrealistic LAI values at evergreen sites (LAI ~ 20; Fig. 6), where the leaf C-LAI relationship was not optimized. At deciduous sites, using the optimized leaf C-LAI relationship, the highest LAI values were ~10 (Fig. 6). The F-Deciduous allocation had an allocation to leaf that was ~10% greater than the one in D-CLM; however, the F-Deciduous allocation scheme with optimized LAI gave very similar LAI values to the D-CLM without optimizing the leaf C-LAI relationship (Fig. 6).

3.4 Turnover rate and its effect on accumulated aboveground biomass through time

The stem turnover rate that best matched the biomass accumulation rate estimated from the tree ring reconstructions varied by site and was always lower than ~~When using stem turnover rates lower than~~the default rate of 2% year^{-1} ~~(the default value~~ used in CLM4.5 (Fig 7)~~), the modeled accumulated aboveground biomass between 1980 and 2011 was closer to the observed values for all the C allocation schemes (Fig. 7a, 7b, 7c, 7d).~~. As expected, changing the turnover rate had the largest influence at sites with the highest average NPP~~Overall, the turnover effect (difference in accumulated aboveground biomass between minimum and maximum stem turnover rate – see Section 2.6) was relatively low in the evergreen sites with annual NPP<500 g Cm^{-2}year^{-1} (between 1999 and 3928 gCm^{-2} in D-CLM4.5), but it was relatively high in evergreen sites with annual NPP>500 g Cm^{-2}year^{-1} and in the deciduous sites (between 10779 and 14342 gCm^{-2} in D-CLM4.5) (Fig. 7a, 7b, 7c, 7d)~~. ~~Relative to D-CLM4.5,~~Biomass accumulation in the D-Litton scheme was less sensitive to changes in turnover rate compared to the D-CLM scheme (compare Fig 7b to 7a). The ~~considerably reduced the turnover effect for evergreen sites with annual NPP>500 g Cm^{-2}year^{-1} and deciduous sites (between 6395 and 9543 gCm^{-2}), whereas the~~ F-Deciduous and F-Evergreen ~~scheme~~ parameterization were similar in their sensitivity to changes in ~~increased the~~ turnover rate (compare Fig 7c to 7d)~~effect for evergreen sites with annual NPP<500 g Cm^{-2}year^{-1} (between 5115 and 7130 gCm^{-2})~~.

3.5 C allocation scheme and its effects on C_{stem}/C_{leaf} ratio and initial ~~initial~~ aboveground biomass

The partitioning between leaf and stem C at these sites was best predicted by the D-Litton scheme (Fig 8). For the range of annual NPP values at our sites (NPP<1500 gCm^{-2}year^{-1}), the NPP_{stem}/NPP_{leaf} ratio was the lowest in the D-Litton scheme (Fig. 8b), which therefore resulted in the lowest C_{stem}/C_{leaf} ratios amongst the four C allocation schemes (Fig. 8a). The

C_{stem}/C_{leaf} ratios from the D-Litton scheme were also the closest to the observed values at all the sites with mean annual NPP> 500 g Cm^{-2}year^{-1} (Fig. 8a). The NPP_{stem}/NPP_{leaf} ratio was overestimated in D-CLM4.5, and it caused overestimations in the C_{stem}/C_{leaf} ratio, which ranged between 33 and 56 for deciduous sites (Fig. 4, Fig. 8a). ~~For the range of annual NPP values at our sites (NPP<1500 gCm^{-2}year^{-1}), the NPP_{stem}/NPP_{leaf} ratio was the lowest in the D-Litton scheme (Fig. 8b), which therefore resulted in the lowest C_{stem}/C_{leaf} ratios amongst the four C allocation schemes (Fig. 8a). The C_{stem}/C_{leaf} ratios from the D-Litton scheme were also the closest to the observed values at all the sites with mean annual NPP> 500 g Cm^{-2}year^{-1} (Fig. 8a).~~

Initial aboveground biomass showed different patterns between evergreen and deciduous sites (Fig. 9a, 9b). Whereas for evergreen sites with annual NPP<500 g Cm^{-2}year^{-1}, there was some overlap between modeled and observed initial aboveground biomass, for deciduous sites modeled initial aboveground biomass was strongly overestimated (between 10527 and 12897 gCm^{-2}) in D-CLM4.5 (Fig. 5a, Fig. 9b). The D-Litton scheme reduced the initial aboveground biomass relative to D-CLM4.5, but still with a positive bias (between 5040 and 6859 gCm^{-2}) (Fig 5a, Fig. 9b).

4 Discussion

From the four C allocation schemes used, two were based on fixed coefficients (Luyssaert et al., 2007), whereas the other two were dynamic based on optimisation of resources (Oleson et al., 2013; Litton et al., 2007). Of these schemes, the dynamic scheme based on D-Litton performed better than the other three. Though this scheme is imperfect, we note that on average it produces lower, and more credible ~~initial~~ aboveground biomass estimates at the start of the simulation for these forests (Fig. 5a) and matches the biometric estimates of C partitioning between leaf and stem (Fig. 8a). The evergreen and deciduous forests appear to allocate carbon differently and for situations where a fixed scheme is preferred our results favour the adoption of separate schemes for evergreen and deciduous forests. Below we discuss these findings in detail and make some recommendations for future development of allocation schemes.

4.1 C allocation scheme: implications for C flux, ~~C pools~~ and LAI

The C allocation scheme does not strongly influence annual GPP, ecosystem respiration, and NEE over 34 years of accumulated effect (Fig. S2); the ~~general over-estimate~~overestimation of GPP and ecosystem respiration in Fig. 1 was common to all allocation schemes. GPP was also overestimated in previous versions of CLM (Bonan et al., 2011; Lawrence et al., 2011). Despite revisions of the model structure in previous versions of CLM, and that the GPP bias was found to be most pronounced in the tropics (Lawrence et al., 2011), our results show that the GPP is still overestimated in temperate forests with ~~the current version of~~ CLM 4.5~~(CLM4.5)~~. Our results support the recommendation by Thornton and Zimmerman (2007) that additional measurements are required to establish the variability of SLA(x) within and between

PFTs. Maximum LAI values reported for temperate evergreen and deciduous forests are 15 and 8.8, respectively (Asner et al., 2003). Realistic C allocation schemes (e.g. Litton et al., 2007; Luyssaert et al., 2007) in CLM4.5 combined with the default values for the parameters SLA_0 and m resulted in unrealistically high – sometimes >20 – estimates of maximum annual LAI values when implementing alternative C allocation schemes in CLM4.5. When using the optimized parameters in conjunction with the alternative allocation schemes, LAI always remained below 10. Clear and persistent model-data discrepancies in LAI also needed to be addressed in the ORCHIDEE LSM prior to any evaluation of model changes (Thum et al., 2017). -Site specific estimates of SLA and LAI would be very useful for optimizing parameters within their observed range and allow mechanistic processes controlling allocation to leaves in the model to be assessed.

4.2 C allocation scheme: implications for C pools

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None of the allocation schemes simultaneously matched observed ~~When comparing estimated and modeled aboveground biomass values for the different sites, we found contrasting patterns for e~~evergreen and deciduous forest~~s~~ aboveground biomass. D-CLM4.5 underestimated the modeled aboveground biomass for evergreen sites with mean annual NPP<500 g Cm^{-2}year^{-1}, but overestimated it for deciduous sites. These results are in line with previous findings in evergreen Oregon forests where CLM4.0 also underestimated aboveground biomass at most sites (Hudiburg et al., 2013). The strong overestimation in biomass at temperate deciduous sites is due to the fact these sites had a higher mean annual NPP and therefore a higher allocation to stem in D-CLM4.5 than the evergreen sites. A similar pattern has been found in other models, in which a high allocation to stem results in an overestimation of aboveground biomass (e.g. Song et al., 2016). In a comparison between observations and CMIP5 Earth System Models for tropical forests, the high CLM-based biomass values were attributed to the high stem allocation relative to observations (Negron-Juarez et al., 2015). D-CLM4.5 stem C allocation has a value of ~46% when annual NPP is close to or greater than 1000 g Cm^{-2}year^{-1}, while forest data syntheses indicate that 20-35% are more plausible for sites with similar mean annual NPP to our sites (Litton et al., 2007). Other LSMs have an even higher allocation to stem of 45-50% for temperate forests (Table 3; Ise et al., 2010, Xia et al., 2015).~~A similar pattern has been found in other models, such as IAP-DGVM1.0, which also had a high allocation to stem that resulted in an overestimated aboveground biomass (Song et al., 2016). Our results support this point: our temperate deciduous sites, which generally had a higher mean annual NPP and therefore a higher allocation to stem in D-CLM4.5 than our evergreen sites, showed a strong overestimation of aboveground biomass~~. Our results show that an alternative scheme (D-Litton, based on Litton et al., 2007), which greatly reduced allocation to stem compared with D-CLM4.5, provided more realistic estimates of aboveground biomass for deciduous sites (Fig. 5a and 5b). However, the D-CLM4.5-based estimates of aboveground biomass were closer to the observed values than those from the D-Litton scheme for evergreen sites with mean annual NPP<500 g Cm^{-2}year^{-1} (NR1 and Vcm). Our results suggest that it is necessary to improve the D-CLM4.5 scheme for temperate forests; for evergreen forests~~, and that~~ the D-Litton scheme ~~can~~ could be modified ~~adapting the equations used here to~~from a linear to a non-linear ~~equations~~ scheme to increase allocation to stem for sites with mean annual NPP<500 g Cm^{-2}year^{-1}.

LSMs tend to overestimate allocation to stem in temperate forest syntheses and therefore underestimate allocation to leaves. C allocation to leaf in D-CLM4.5 is probably underestimated when mean annual NPP is relatively close to or greater than 1000 g Cm^{-2}year^{-1}. In other LSMs carbon allocation to leaf shows broad ranges (~19-30%; Table 3; Ise et al., 2010; Xia et al., 2015). The D-CLM4.5 scheme is dynamic with changing C but functions as a fixed scheme at higher NPP values (Fig. S1), which means that at many sites the allocation to leaf is 20% in this scheme, which is ~5-10% lower than available data suggests for deciduous sites (Table 3; Litton et al., 2007; Luyssaert et al., 2007; Wolf et al., 2011). ~~When compared to syntheses of temperate forests, LSMs tend to underestimate allocation to leaves and overestimate allocation to stem. We designed the D-Litton, F-Deciduous and F-Evergreen schemes to match recent syntheses (Table 3). However, C allocation to leaf in D-CLM4.5 is probably underestimated when mean annual NPP is relatively close to or greater than 1000 g Cm^{-2}year^{-1}. In other LSMs carbon allocation to leaf shows broad ranges (~19-30%; Table 3; Ise et al., 2010; Xia et al., 2015). The D-CLM4.5 scheme is dynamic with C but functions as a fixed scheme at higher NPP values (Fig. S1) which means that at many sites allocation to leaf is 20% in this scheme, which is ~5-10% lower than available data suggests for deciduous sites (Table 3; Litton et al., 2007; Luyssaert et al., 2007; Wolf et al., 2011). Similarly, D-CLM4.5 stem C allocation has a value of ~46% when annual NPP is close to or greater than 1000 g Cm^{-2}year^{-1}, while forest data syntheses indicate that 20-35% are more plausible for sites with similar mean annual NPP to our sites (Litton et al., 2007). Other LSMs have an even higher allocation to stem of 45-50% for temperate forests (Table 3; Ise et al., 2010, Xia et al., 2015).~~

There is reasonable agreement across LSMs on how much carbon is allocated to roots; however, root biomass is difficult to measure accurately and data are sparse. Allocation to root and stem are variable between sites, and conditions that favour high productivity increase partitioning to stem and decrease partitioning to root (Litton et al., 2007). D-CLM4.5 allocates 34-40% of carbon to roots, which is similar to most other models (Table 3). The partitioning between fine and coarse root is absent from most syntheses but empirical studies show a wide range in allocation of C belowground and are generally higher than LSMs (Table 3; Nadelhoffer and Raich, 1992, Gower et al., 2001, Newman et al., 2006, Luyssaert et al., 2007, Litton et al., 2007, Wolf et al., 2011; Gill and Finzi, 2016).

~~There is reasonable agreement across LSMs on how much carbon is allocated to roots, however root biomass is difficult to measure accurately and data are rare. Allocation to root and stem are variable between sites, and conditions that favour high productivity increase partitioning to stem and decrease partitioning to root (Litton et al., 2007). D-CLM4.5 allocates 34-40% of carbon belowground which is similar to other models (Table 3), though notably larger than IBIS (~20%; Xia et al., 2015). The partitioning between fine and coarse root is absent from most syntheses but empirical studies show a wide range in allocation of C belowground and are generally higher than LSMs (Table 3; Nadelhoffer and Raich, 1992, Gower et al., 2001, Newman et al., 2006, Luyssaert et al., 2007, Litton et al., 2007, Wolf et al., 2011; Gill and Finzi, 2016).~~

~~Our results support the recommendation by Thornton and Zimmerman (2007) that additional measurements are required to establish the variability of SLA(x) within and between PFTs. Maximum LAI values reported for temperate evergreen and deciduous forests are 15 and 8.8, respectively (Asner et al., 2003). The standard leaf C-LAI relationship resulted in unrealistically high – sometimes >20 – estimates of maximum annual LAI values when implementing alternative C~~

~~allocation schemes in CLM~~4.5~~. When using the optimized parameters in conjunction with the alternative allocation schemes, LAI always remained below 10. Realistic C allocation schemes (e.g. Litton et al., 2007; Luyssaert et al., 2007) in CLM~~4.5 ~~combined with the default values for the parameters *SLA₀* and *m* can give unrealistic LAI values. Unrealistic simulations of LAI also had to be addressed prior to using aboveground biomass data to optimize allocation parameters in the ORCHIDEE LSM (Thum et al., 2017). Site specific estimates of SLA and LAI would be very useful for optimizing parameters within their observed range and allow mechanistic processes controlling allocation to leaves in the model to be assessed.~~

Although in reality, root function is ~~extremely dynamic~~complex, the controls of root dynamics and function are highly simplified in LSMs (Warren et al., 2015). It has been suggested that resource allocation is controlled by ~~the functional trade-off hypothesis (Tilman, 1988) does not occur directly as a trade-off between leaf and fine root, but instead from~~ two separate functional trade-offs between leaf or fine roots and their supporting woody organs (Chen et al., 2013). If this is correct, LSMs should use an allocation scheme based on at least two (or probably three) dynamic allometric parameters, instead of the D-CLM4.5 which is based only on one dynamic allometric parameter (*a3*). Here, we implemented an allocation scheme (D-Litton) that included two dynamic allometric parameters (*a2* and *a3*) based on Litton et al., (2007), assuming that the ratio between allocation to leaf and fine root (*a1*) is constant. However, some studies suggest that this trade-off includes fine roots (Wolf et al., 2011; Malhi et al., 2011; Chen et al., 2013), probably due to the co-limitation of productivity by resources captured aboveground (e.g. light) and belowground (e.g. nutrients and water) (Dybzinski et al., 2011; Weng et al., 2016~~5~~). ~~Furthermore, this complexity is enhanced by the fact that the relative influences of the~~These growth drivers ~~strongly~~ also vary with time and across spatial ecological gradients (Guillemot et al., 2015). In ~~the version of CLM (~~CLM4.5~~)~~ employed here, the roots control water uptake but are not related to nutrient uptake which limits the potential ~~. Understanding the mechanisms responsible for these multiple trade-offs and integrating them in the C allocation schemes of models is critical for accurate predictions of changes in carbon sequestration, including CO_2 impacts on forest productivity and allocation~~for dynamic responses to nutrients and CO2 concentrations (Atkin, 2016 De Kauwe et al., 2014; Hickler et al., 2015; Sevanto and Dickman 2015)~~, and for determining the extent of atmospheric CO_2 accumulation in the coming decades (Atkin, 2016)~~. Root functionality in LSMs could be enhanced by improving parameterization within models and introducing new components such as dynamic root distribution and root functional traits linked to resource extraction (Warren et al., 2015; Brzostek et al., 2014; Shi et al., 2016; Phillips et al., 2016; Brzostek et al., 2017; Iversen et al., 2017). ~~More pProcess based root dynamics in LSMs could can enable functional trade-offs to be used as a method to optimize constrain allocation between to roots and aboveground pools (Weng *et al.*, 2015).~~

4.~~2~~3 C allocation scheme: implications for steady state aboveground biomass

Initial conditions in LSMs are usually obtained by spin-up methods that perform long simulations until the model reaches a steady state, a point when C pool sizes remain constant over long periods of repeated climate forcing (Xia et al., 2012). The simulation critically depends on the initial values and flawed initial conditions may produce a model output that can be

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severely biased or unrealistic (Yang et al., 1995; Cosgrove et al., 2003; Rodell et al., 2005; Li et al., 2009). There is an increasing awareness in Earth system modeling of the critical role of initial conditions (including the initial size of C pools - examined in this study) ~~in model behaviour~~ that adds an extra layer of complexity in diagnosing the impact of an incorrect representation of physical processes on the transient simulation (Kay et al., 2015; Fisher et al., 2015). Our results reinforce that concern by showing that with the same climate forcing different C allocation schemes within the same LSM can produce strongly differing initial conditions for aboveground biomass (Fig. 9). In Sect. 2.7, we provide an explanation for the variability in steady state aboveground biomass depending on the C allocation scheme used in CLM4.5.

4.~~3~~ 4 C allocation scheme: implications of the NPP_{stem}/NPP_{leaf} ratio

The NPP_{stem}/NPP_{leaf} ratio in the model (*a3* parameter) is one of the primary factors contributing to overestimations of biomass. While the D-Litton scheme best approximates the average ratio of stem C to leaf C, ~~The NPP_{stem}/NPP_{leaf} ratio (*a3* parameter) used in CLM~~4.5~~ has two important implications. Firstly, for the residence time given for the plant pools in CLM~~4.5~~, the NPP_{stem}/NPP_{leaf} ratio in D-CLM~~4.5~~ is causing an overestimation of C_{stem}/C_{leaf} ratio when compared to observations (see also Sect. 2.7). We show that it is possible to simulate more~~ realistic C_{stem}/C_{leaf} ratios are produced in CLM4.5 ~~by~~ at sites where~~decreasing~~ the D-CLM4.5 NPP_{stem}/NPP_{leaf} ratio ~~in the model from values >2 to values ~1 or ~1.25,~~is similar to the values in the D-Litton scheme (~~see~~ Fig. 8~~b~~). ~~The second implication is that~~Any overestimation of allocation to stem is compounded because stem C has a longer ~~residence~~turnover time that leaf C ~~if CLM~~4.5~~ overestimates the NPP_{stem}/NPP_{leaf} ratio, it will also overestimate aboveground biomass due to the long residence time of stem~~ (Schulze et al., 2000; Xia et al., 2015; Song et al., 2016). ~~We also found important overestimations of aboveground biomass for deciduous forests with D-CLM~~4.5~~, and therefore suggest that the NPP_{stem}/NPP_{leaf} ratio in the model is one of the primary factors contributing to these overestimations of biomass.~~ Overestimation of allocation to stem was also found using the IBIS model, where a fixed allocation scheme with terms for allocation to leaf, stem and root, which sum to 1, was found to overestimate allocation to stem (Xia et al., 2015). The fractional allocation to stem in IBIS was reduced from 0.5 to 0.36 when the scheme was optimized against satellite LAI observations (Xia et al., 2015).~~Although several ecosystem models (e.g. Hyland, IBIS, Biome-BGC, VISIT) allocate most of the carbon to stem for deciduous forests (Xia et al., 2015), allocation to stem was considerably reduced after constraining the allocation parameters in the model with satellite data (Xia et al., 2015).~~ Similarly, our results suggest that allocation to stem in D-CLM4.5 should decrease and ~~e, whereas~~ allocation to leaf and root should increase, ~~in order to align simulated and~~to match observed biomass.

4.54 C allocation scheme and ~~residence time for~~ stem turnover rate: implications for accumulated aboveground biomass

Regardless of allocation scheme, CLM4.5 overestimates aboveground NPP and underestimates aboveground biomass increments (Fig 5c), this suggests that the stem turnover rate is overestimated in the model. The underestimation of increment can be attributed to an inaccurate representation of production in the model, an inaccurate representation of turnover time of the plant pools, or both (Friend et al., 2014; Koven et al., 2015). ~~When comparing average annual aboveground biomass increment derived from the four C allocation schemes with aboveground biomass increments reconstructed from tree rings for the period between 1980 and 2011, we found that it was underestimated at all sites. The underestimation can be attributed to an inaccurate representation of production in the model, an inaccurate representation of turnover time of the plant pools in the model, or both (Friend et al., 2014; Koven et al., 2015). For deciduous sites, when comparing a~~Aboveground NPP in the D-CLM4.5 scheme ~~with available aboveground NPP~~ from ~~some of our~~ the deciduous sites, including UMBS, Morgan Monroe, Harvard Forest, and Duke hardwoods (Megonigal et al., 1997; Curtis et al., 2002)~~, the model~~was consistently ~~overestimated aboveground NPP relative to~~higher than the observations. The D-Litton scheme, however, resulted in aboveground NPP estimations that were consistently closer to the observations (data not shown). These results suggest that, in temperate deciduous forests, the D-CLM4.5 scheme is overestimating allocation to stem, and underestimating allocation to roots, as previously found in other models like IBIS (Xia et al., 2015).

It is likely that CLM4.5 overestimates stem turnover at these sites. Currently, CLM4.5 assumes a stem mortality rate of 2% yr^{-1} that is higher than published tree mortality rates for forests in the USA (van Mantgem et al., 2009; Brown and Schroeder, 1999; Runkle, 1998). When considering large geographic scales the 2% yr^{-1} rate of stem turnover may be reasonable but at individual sites this may be a poor approximation. The Harvard Forest, for example, is at the end of the stem exclusions stage of forest development and, there has been little to no canopy disturbance since the time of the 1969 census. As such, the tree-ring biomass increment estimates at Harvard assume zero mortality between 1980 and 2012. This assumption appears solid as it results in no significant difference between tree-ring reconstructed biomass increment and the repeated measurements from permanent plots over the last 40 years (Dye et al., 2016). We thus decreased stem mortality rate from 2% yr^{-1} to published ranges of tree mortality (between 0 and 1.5% yr^{-1}), to estimate plausible stem turnover rates for each site and scheme. The resulting ranges of aboveground biomass increment overlapped with the observed aboveground biomass increment estimated from tree-ring data, for nearly all the carbon allocation schemes (see Fig. 7). For Harvard forest the turnover rate that most consistent with the tree ring reconstruction was never zero, which indicates that both NPP and turnover are overestimated for this site in all the allocation schemes. A different turnover rate was required for each site and C allocation scheme to match the observed aboveground biomass increment but in each case it was below the default 2% value. Our analysis suggests that when using AmeriFlux sites to inform models, or other site level observations, taking note of site specific rates of stem turnover is prudent.

Given the high uncertainty associated with turnover relative to production, it has been suggested that research priorities should move from production to turnover (Friend et al., 2014). Our results show the need for improvements of models in carbon turnover processes, a current limitation in state-of-the-art LSMs (Thurner et al., 2017).Tree-ring widths can provide reliable estimates of biomass increment but repeated surveys of forests are required to estimate stem turnover in non-equilibrium stands (Alexander et al., in review; Dye et al., 2016; Klesse et al., 2016; Babst et al., 2014).~~Given that the model overestimates aboveground NPP and underestimates aboveground biomass increments, this suggests that the stem turnover rate is overestimated in the model. Given the high uncertainty associated with turnover relative to production, it has been suggested that research priorities should move from production to turnover (Friend et al., 2014). It is possible that CLM4.5 - at least for deciduous sites - overestimated aboveground NPP as well as stem turnover.~~ ~~Turnover of biomass in forests includes annual loss of leaf, root and woody litter as well as tree mortality.~~ However, whole ecosystem C turnover will encompass processes other than mortality, including disturbances, land use and land cover change (Masek et al., 2008; Erb et al., 2016; Thurner et al., 2017). Some of the aforementioned processes are already partially incorporated in LSMs, in particular land use and land cover change, but the lack of a mechanistic representation of the remaining processes is therefore indirectly represented in stem turnover rates. The processes controlling turnover times influence C storage capacity, but turnover is not well constrained in models (Friend et al., 2014; Chen et al., 2015; Sierra et al 2016).~~Some of the aforementioned processes are already partially incorporated in LSMs, in particular land use and land cover change, but the lack of a mechanistic representation of the remaining processes is therefore indirectly represented in stem turnover rates. These turnovers influence C residence time, a key factor that determines C storage capacity, but it is not well constrained in models (Friend et al., 2014; Chen et al., 2015) and often inexpertly defined (Sierra et al 2016).~~ ~~Tree-ring widths are measured with high precision and can thus result in reliable estimates of biomass increment (Alexander et al., in review; Dye et al., 2016; Klesse et al., 2016; Babst et al., 2014), but turnover is difficult to estimate from these data because of how they are influenced by stand age and disturbance history. The Harvard Forest, for example, is at the end of the stem exclusions stage; some secondary regeneration has begun. And, there has been little to no canopy disturbance since the time of the 1969 census. Thus, most of the mortality is self-thinning or thinning from below and the canopy has been stable. The loss of most trees through self-thinning are relatively small loses in terms of biomass and competition. As such, the tree-ring biomass increment estimates at Harvard and Howland assume zero mortality between 1980 and 2012, resulting in no significant difference between tree-ring reconstructed biomass increment and the repeated measurements from permanent plots over the last 40 years (Dye et al., 2016). Currently, CLM4.5 assumes a stem mortality rate of 2% yr^{-1} that is higher than published tree mortality rates for forests in the USA (van Mantgem et al., 2009; Brown and Schroeder, 1999; Runkle, 1998). When considering whole ecosystem C turnover over large geographic scales the 2% yr^{-1} rate of stem turnover may be reasonable. If we assume that tree-ring increment is a good proxy for biomass increment over this time window (Dye et al., 2016; Klesse et al., 2016), and the model captures the observed biomass increment from tree-rings, then the model can be used to estimate reasonable turnover rates for stems. Over large geographic scales a 2% yr^{-1} stem turnover rate may be reasonable. However, whole ecosystem C turnover will encompass processes other than mortality, including disturbances,~~

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~~land use and land cover change (Masek et al., 2008; Erb et al., 2016; Thurner et al., 2017) – such processes are partially incorporated in LSMs, but some impacts of these processes are also implicitly represented in stem turnover rates. Some of the aforementioned processes are already partially incorporated in LSMs, in particular land use and land cover change, but the lack of a mechanistic representation of the remaining processes is therefore indirectly represented in stem turnover rates. We thus decreased stem mortality rate from 2% yr^{-1} to published ranges of tree mortality (between 0 and 1.5% yr^{-1}), and the resulting ranges of aboveground biomass increment included the observed aboveground biomass increment, which was estimated from tree-ring data, for all the carbon allocation schemes (see Fig. 7a, 7b, 7c, and 7d) except in evergreen sites with mean annual NPP<500 g $Cm^{-2}year^{-1}$ with the D-Litton scheme. This suggests that D-Litton is underestimating aboveground NPP at these sites as pointed out in Sect. 4.2 (Fig. 7b). However, a different turnover rate was required for each site and C allocation scheme to match the observed aboveground biomass increment. Our analysis suggests that when using AmeriFlux sites to inform models, or other site level observations, taking note of site specific rates of stem turnover is prudent. Our results show the need for improvements of models in carbon turnover processes, a current limitation in state-of-the-art LSMs (Thurner et al., 2017). Furthermore, we should be clear what we are referring to when considering turnover rate in the models, and be careful not to use this parameter to account for missing processes or scaling issues (Thum et al., 2017).~~

4.6~~5~~ Conclusions and perspectives

Our results highlight the importance of evaluating the C allocation scheme and the stem turnover in LSMs using ~~biometric data~~measures of C stocks in addition to flux data. The four C allocation schemes translated to important long-term differences in C accumulation in aboveground biomass, but gave similar results for short term C fluxes. ~~There is no way~~We were unable to distinguish between the allocation schemes using eddy flux data alone.

~~Developing allocation schemes for LSMs is challenging. The two dynamic allocation schemes reflect forest stand development to some extent i.e. as trees get bigger (and can grow more) they tend to invest more in stem and less in leaves. The two schemes also use low NPP as a proxy for resource limitation, but they disagree on how allocation changes as a function of NPP (Fig. S1). However, these schemes and many other LSMs do not have a way to consider cohorts of trees. This problem is highlighted in the different performance of the D-CLM4.5 scheme at high and low NPP; sites that have low NPP perpetually allocate more resources to leaves and roots while sites with high NPP perpetually allocate less resources to leaves and roots (Fig. S1). This increases the NPPstem/NPPleaf ratio with increasing NPP (Fig. 8b), and it causes the overestimation of the Cstem/Cleaf ratio relative to observations (Fig. 8a) at most of the sites (except at low NPP sites; NPP<500 gC $m^{-2}year^{-1}$). Ecological theory suggest that dynamic allocation probably reflects whatever resource is most limiting. As coupled C-N and functional root subroutines are developed for LSMs with better representation of vegetation dynamics (Fisher et al., 2015), we could imagine a dynamic allocation scheme based on whether above ground (light) or below ground (water and nutrients) are limiting.~~

Data on different carbon pools is sparse, but very useful in parameterizing allocation schemes. ~~the non-physiological components of LSMs.~~ We found that site specific SLA was a pre-requisite to evaluating the different allocation schemes; large scale databases might be exploited to better estimate this relationship. ~~Also, f~~Fixed allocation schemes ~~are unable to capture~~preclude dynamic changes in allocation in response to varying water and nutrient availability at seasonal to interannual timescales (De Kauwe et al., 2014) but they have the advantage of simplicity. If fixed allocation schemes are used in land surface modelling, we suggest different schemes for evergreen and deciduous forests, and that databases like Litton et al. (2007) and Luyssaert et al. (2007) can be used to parameterize them.

Finally, we show that information on stem turnover rate, which varies with forest age and successional status, is important to interpret the success or failure of different model schemes at forest sites. ~~forest age and successional status is important to interpret the success or failure of different model schemes at forest sites. Some~~Stem turnover ~~aspects of~~ in~~LSMs~~ CLM4.5 ~~are most consistent with ecological processes that~~ may approximate steady state conditions at large scales, and so ~~are~~ is inconsistent with forests which are not at steady state. Decreasing the stem turnover rate from 2% yr^{-1} to plausible values consistent with their successional status yielded aboveground biomass accumulation rates ~~more~~ consistent with observations. It is possible to ~~coarsely~~ estimate equilibrium turnover rates from mean stand age derived from tree ring estimates; this could be a promising technique to ~~more firmly estimate~~approximate the duration of carbon ~~residence~~ storage ~~times~~ in temperate forests though equilibrium assumptions are problematic.

Ecological theory suggests that dynamic allocation probably reflects whatever resource is most limiting but developing allocation schemes for LSMs that respond to resource limitation is challenging. The two dynamic allocation schemes reflect forest stand development to some extent i.e. as trees get bigger (and can grow more) they tend to invest more in stem and less in leaves. However t~~T~~he two schemes ~~also~~ both use low NPP, regardless of cause, ~~-~~as a proxy for resource limitation~~, but they -differ on how allocation changes as a function of NPP~~ (Fig. S1). Cohort representation in the model would enable ontogenetic changes in allocation but would not avoid the~~HoweverThis is a~~ problem ~~because,~~ that these dynamic schemes cause sites ~~that have~~with low average NPP to perpetually allocate more resources to leaves and roots while sites with high average NPP perpetually allocate less resources to leaves and roots (Fig. S1). ~~Cohort representation in the model could help deal with this problem. This increases the NPPstem/NPPleaf ratio with increasing NPP (Fig. 8b), and it causes the overestimation of the Cstem/Cleaf ratio relative to observations (Fig. 8a) at most of the sites (except at low NPP sites; NPP<500 gC m^{-2}year^{-1}).~~ As coupled C-N and functional root subroutines are developed for LSMs (Shi et al., 2016), and with better representation of vegetation dynamics (Fisher et al., 2015), we could imagine a dynamic allocation scheme for CLM4.5 based on whether above ground (light) or below ground (water and nutrients) are limiting.

Code availability

The code for CLM version 4.5 (CLM4.5) is available (registration required) at https://svn-ccsm-models.cgd.ucar.edu/cesm1/release_tags/cesm1_2_1. The allometric parameters used for the different C allocation schemes used in this study with CLM4.5 are ~~available~~ shown in Table 2. ~~The optimized parameters, based on observations, for the leaf C-LAI relationship for temperate deciduous forests in CLM~~4.5 ~~are available in Sect. 2.5.~~ The code modifications and parameter files for this paper ~~is~~ are available ~~upon request, contacting the corresponding author~~from https://github.com/davidjpmoore/gmd-2017-74.

Data availability

The data for this paper is available upon request, contacting the corresponding author.

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References

Alexander RM., Rollinson, C.R., Babst, F., Trouet, V. and Moore, D.J.P. Uncertainty in tree-ring based aboveground biomass estimates does not substantially alter growth-climate relationships. Trees-Struct. Funct., in review.

Asner, G.P., Scurlock, J.M., and Hicke, J.A.: Global synthesis of leaf area index observations: implications for ecological and remote sensing studies. Global Ecol. Biogeogr., 12, 191-205, 2003.

Atkin, O.: New Phytologist: bridging the 'plant function–climate modelling divide'. New Phytol., 209, 1329-1332, 2016.

Babst, F., Bouriaud, O., Papale, D., Gielen, B., Janssens, I.A., Nikinmaa, E., Ibrom, A., Wu, J., Bernhofer, C., Köstner, B., Grünwald, T., Seufert, G., Ciais, P., and Frank, D.: Above-ground woody carbon sequestration measured from tree rings is coherent with net ecosystem productivity at five eddy-covariance sites. New Phytol., 201, 1289-1303, 2014.

Baldocchi, D., Falge, E., Gu, L., Olson, R., Hollinger, D., Running, S., Anthoni, P., Bernhofer, C., Davis, K., Evans, R., Fuentes, J., Goldstein, A., Katul, G., Law, B., Lee, X., Malhi, Y., Meyers, T., Munger, W., Oechel, W., Paw U, K.T., Pilegaard, K., Schmid, H.P., Valentini, R., Verma, S., Vesala, T., Wilson, K., and Wofsy, S.: FLUXNET: a new tool to study the temporal and spatial variability of ecosystem-scale carbon dioxide, water vapor, and energy flux densities. B. Am. Meteorol. Soc., 82, 2415-2434, 2001.

Baldocchi, D., Ryu, Y., and Keenan, T.: Terrestrial carbon cycle variability [version 1; referees: 2 approved]. F1000Research, (F1000 Faculty Rev), doi:10.12688/f1000research.8962.1, 2016.

Blanken, P.: AmeriFlux US-NR1 Niwot Ridge Forest (LTER NWT1), doi:10.17190/AMF/1246088, 2016.

Bloom, A.A., Exbrayat, J.F., van der Velde, I.R., Feng, L., and Williams, M.: The decadal state of the terrestrial carbon cycle: global retrievals of terrestrial carbon allocation, pools, and residence times. P. Natl. Aca. Sci., 113, 1285-1290, 2016.

Boden, T. A., Krassovski, M., & Yang, B. The AmeriFlux data activity and data system: an evolving collection of data management techniques, tools, products and services. Geosc~~ientific~~, Instru~~mentation~~, Methods and Data Systems, 2(1), 165-176, 2013

Bonan, G.B.: Forests and climate change: forcings, feedbacks, and the climate benefits of forests. Science, 320, 1444-1449, 2008.

Bonan, G.B., Lawrence, P.J., Oleson, K.W., Levis, S., Jung, M., Reichstein, M., Lawrence, D.M., and Swenson, S.C.: Improving canopy processes in the Community Land Model version 4 (CLM4) using global flux fields empirically inferred from FLUXNET data. J. Geophys. Res., 116, G02014, doi:10.1029/2010JG001593, 2011.

Brown, S.: Measuring carbon in forests: current status and future challenges. Environ. Pollut., 116, 363-372, 2002.

Brown, S.L., and Schroeder, P.E.: Spatial patterns of aboveground production and moratlity of woody biomass for Eastern U.S. forests. Ecol. Appl., 9, 968-980, 1999.

Caspersen, J.P., Pacala, S.W., Jenkins, J.C., Hurtt, G.C., Moorcroft, P.R., and Birdsey, R.A.: Contributions of land-use history to carbon accumulation in US forests. Science, 290, 1148-1151, 2000.

Brzostek, E.R., Fisher, J.B., and Phillips, R.B.: Modeling the carbon cost of plant nitrogen acquisition: mycorrhizal trade-offs and multipath resistance uptake improve predictions of retranslocation. J. Geophys. Res. Biogeosci., 119, doi:10.1002/2014JG002660, 2014.

Brzostek, E.R., Rebel, K.T., Smith, K.R., and Phillips, R.P.: Integrating mycorrhizae into global scale models: a journey toward relevance in the Earth's climate system. In: Johnson, N.C., Gehring, C., and Jansa, J. Eds. Mycorrhizal mediation of soil: fertility, structure, and carbon storage. Elsevier, 479-499, 2017.

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Chen, M., Melaas, E.K., Gray, J.M., Friedl, M.A., and Richardson, A.D.: A new seasonal-deciduous spring phenology submodel in the Community Land Model 4.5: impacts on carbon and water cycling under future climate scenarios. Glob. Change Biol., 22, 3675-3688, 2016.

Chen, G., Yang, Y., and Robinson, D.: Allocation of gross primary production in forest ecosystems: allometric constraints and environmental responses. New Phytol., 200, 1176-1186, 2013.

Chen, Y., Xia, J., Sun, Z., Li, J., Luo, Y., Gang, C., and Wang, Z.: The role of residence time in diagnostic models of global carbon storage capacity: model decomposition based on a traceable scheme. Scientific Reports, 5, 16155, doi:10.1038/srep16155, 2015.

Chojnacky, D.C., Heath, L.S., and Jenkins, J.C.: Updated generalized biomass equations for North American tree species. Forestry, 87, 129-151, 2014.

Cosgrove, B.A., Lohmann, D., Mitchell, K.E., Houser, P.R., Wood, E.F., Schaake, J.C., Robock, A., Sheffield, J., Duan, Q., Luo, L., Higging, R.W., Pinker, R.T., and Tarpley, J.D.: Land surface model spin-up behavior in the North American Land Data Assimilation System (NLDAS). J. Geophys. Res., 108, 8845, doi:10.1029/2002JD003316, 2003.

Cottam, G., Curtis, J.T., and Hale, B.W.: Some sampling characteristics of a population of randomly dispersed individuals. Ecology, 34, 741-757, 1953.

Curtis, P.S., Hanson, P.J., Bolstad, P., Barford, C., Randolph, J.C., Schmid, H.P., and Wilson, K.B.: Biometric and eddy-covariance based estimates of annual carbon storage in five eastern North American deciduous forests. Agr. Forest Meteorol., 113, 3-19, 2002.

De Kauwe, M.G., Medlyn, B.E., Zaehle, S., Walker, A.P., Dietze, M.C., Wang, Y.-P., Luo, Y., Jain, A.K., El-Masri, B., Hickler, T., Warlind, D., Weng, E., Parton, W.J., Thornton, P.E., Wang, S., Prentice, I.C., Asao, S., Smith, B., McCarthy, H.R., Iversen, C.M., Hanson, P.J., Warren, J.M., Oren, R., and Norby, R.J.: Where does the carbon go? A model-data intercomparison of vegetation carbon allocation and turnover processes at two temperate forest free-air CO_2 enrichment sites. New Phytol., 203, 883-899, 2014.

Delbart, N., Ciais, P., Chave, J., Viovy, N., Malhi, Y., Le Toan, T.: Mortality as a key driver of the spatial distribution of aboveground biomass in Amazonian forest: results from a dynamic vegetation model. Biogeosciences, 7, 3027-3039, 2010.

Douglass, A.E.: Crossdating in dendrochronology. J. Forest., 39, 825-831, 1941.

Dybzinski, R., Farrior, C., Wolf, A., Reich, P.B., and Pacala, S.W.: Evolutionarily stable strategy carbon allocation to foliage, wood, and fine roots in trees competing light and nitrogen: an analytically tractable, individual-based model and quantitative comparisons to data. Am. Nat., 177, 153-166, 2011.

Dye, A., Barker Plotkin, A., Bishop, D., Pederson, N., Poulter, B., and Hessl, A.: Comparing tree-ring and permanent plot estimates of aboveground net primary production in three eastern U.S. forests. Ecosphere, 7, e01454, 2016.

Erb, K.-E., Fetzel, T., Plutzar, C., Kastner, T., Lauk, C., Mayer, A., Niedertscheider, M., Körner, C., and Haber, H.: Biomass turnover time in terrestrial ecosystems halved by land use. Nat. Geosci., 9, 674-678, 2016.

Fisher, R.A., Muszala, S., Verteinstein, M., Lawrence, P., Xu, C., McDowell, N.G., Knox, R.G., Koven, C., Holm, J., Rogers, B.M., Spessa, A., Lawrence, D., and Bonan, G.: Taking off the training wheels: the properties of a dynamic vegetation model without climate envelopes, CLM4.5(ED). Geosci. Model Dev., 8, 3593-3619, 2015.

Franklin, O., Johansson, J., Dewar, R.C., Dieckmann, U., McMurtrie, R.E., Brannstrom, A., and Dybzinski, R.: Modelling carbon allocation in trees: a search for principles. Tree Physiol., 32, 648-666, 2012.

Friend, A.D., Arneth, A., Kiang, N.Y., Lomas, M., Ogée, J., Rödenbeck, C., Running, S.W., Santaren, J.-D., Sitch, S., Viovy, N., Woodward, F.I., and Zaehle, S.: FLUXNET and modeling the global carbon cycle. Glob. Change Biol., 13, 610-633, 2007.

Friend, A.D., Lucht, W., Rademacher, T.T., Keribin, R., Betts, R., Cadule, P., Ciais, P., Clark, D.B., Dankers, R., Falloon, P.D., Ito, A., Kahana, R., Kleidon, A., Lomas, M.R., Nishina, K., Ostberg, S., Pavlick, R., Peylin, P., Schaphoff, S., Vuichard, N., Warszawski, L., Wiltshire, A., and Woodward, F.I.: Carbon residence time dominates uncertainty in terrestrial vegetation responses to future climate and atmospheric CO_2. Proc. Natl. Aca. Sci., 111, 3280-3285, 2014.

Gifford, R.M.: Plant respiration in productivity models: conceptualisation, representation, and issues for global-terrestrial carbon-cycle research. Funct. Plant Biol., 30, 171-186, 2003.

Gill, A.I., and Finzi, A.C.: Belowground carbon flux links biogeochemical cycles and resource-use efficiency at the global scale. Ecol. Lett., 19, 1419-1428, 2016.

Gough, C.M., Bohrer, G., and Curtis, P.S.: AmeriFlux US-UMB University of Michigan Biological Station. doi: 10.17190/AMF/1246107, 2016.

Gough, C.M., Flower, C., Volgel, C.S., Dragoni, D., and Curtis, P.S.: Whole ecosystem labile carbon production in a north temperate deciduous forest. Agr. Forest Meteorol., 149, 1531-1540, 2009.

Gough, C.M., Hardiman, B.S., Nave, L.E., Bohrer, G., Maurer, K.D., Vogel, C.S., Nadelhoffer, K.J., and Curtis, P.S.: Sustained carbon uptake and storage following moderate disturbance in a Greta Lakes forest. Ecol. Appl., 23, 1202-1215, 2013.

Gower, S.T., Krankina, O., Olson, R.J., Apps, M., Linder, S., and Wang, C.: Net primary production and carbon allocation patterns of boreal forests ecosystems. Ecol. Appl., 11, 1395-1411, 2001.

Grissino-Mayer, H.D.: Evaluating crossdating accuracy: a manual and tutorial for the computer program COFECHA. Tree-Ring Research, 57, 205-221, 2001.

Guillemot, J., Martin-StPaul, N.K., Dufrêne, E., François, C., Soudani, K., Ourcival, J.M., and Delpierre, N.: The dynamic of the annual carbon allocation to wood in European tree species is consistent with a combined source–sink limitation of growth: implications for modelling. Biogeosciences, 12, 2773-2790, 2015.

Hickler, T., Rammig, A., and Werner, C.: Modelling CO_2 impacts on forest productivity. Current Forestry Reports, 1, 69-80, 2015.

Hollinger, D.: AmeriFlux US-Ho1 Howland Forest (main tower), doi:10.17190./AMF/1246061, 2016.

Holmes, R.L.: Computer-assisted quality control in tree-ring dating and measurement. Tree-Ring Bulletin, 43, 69-78, 1983.

Houghton, R.A.: Aboveground forest biomass and the global carbon balance. Glob. Change Biol., 11, 945-958, 2005.

Hudiburg, T.W., Law, B.E., and Thornton, P.E.: Evaluation and improvement of the Community Land Model (CLM4) in Oregon forests. Biogeosciences, 10, 453-470, 2013.

Ise, T., Litton, C.M., Giardina, C.P., and Ito, A.: Comparison of modeling approaches for carbon partitioning: impact on estimates of global net primary production and equilibrium biomass of woody vegetation from MODIS GPP. J. Geophys. Res., 115, G04025, doi:10.1029/2010JG001326, 2010.

Iversen, C.M., McCormack, M.L., Powell, A.S., Blackwood, C.B., Freschet, G.T., Kattge, J., Roumet, C., Stover, D.B., Soudzilovskaia, N.A., Valverde-Berrantes, O.J., van Bodegom, P.M., and Violle, C.: A global fine-root ecology database to address below-ground challenges in plant ecology. New Phytol., doi:10.1111/nph.14486, 2017.

Jenkins, J.C., Chojnacky, D.C., Heath, L.S., and Birdsey, R.A.: Comprehensive database of diameter-based biomass regressions for North American tree species. US Department of Agriculture, Forest Service, Newtown Square, PA, 2004.

Kay, J.E., Deser, C., Phillips, A., Mai, A., Hannay, C., Strand, G., Arblaster, J.M., Bates, S.C., Danabasoglu, G., Edwards, J., Holland, M., Kushner, P., Lamarque, J.-F., Lawrence, D., Lindsay, K., Middleton, A., Munoz, E., Neale, R., Oleson, K., Polvani, L., and Vertenstein, M.: The Community Earth System Model (CESM) large ensemble project. A community resource for studying climate change in the presence of internal climate variability. B. Am. Meteorol. Soc., 96, 1333-1349, 2015.

Keith, H., Mackey, B.G., Lindenmayer, D.B.: Re-evaluation of forest biomass carbon stocks and lessons from the world's most carbon-dense forests. Proc. Natl. Aca. Sci., 106, 11635-11640, 2009.

Klesse, S., Etzold, S., and Frank, D.: Integrating tree-ring and inventory-based measurements of aboveground biomass growth: research opportunities and carbon cycle consequences from a large snow breakage event in the Swiss Alps. Eur. J. For. Res., 135, 297-311, 2016.

Koven, C.D., Chambers, J.Q., Georgiou, K., Knox, R., Negron-Juarez, R., Riley, W.J., Arora, V.K., Brovkin, V., Friedlingstein, P., and Jones, C.D.: Controls on terrestrial carbon feedbacks by productivity versus turnover in the CMIP5 Earth System Models. Biogeosciences, 12, 5211-5228, 2015.

Lawrence, D.M., Oleson, K.W., Flanner, M.G., Thornton, P.E., Swenson, S.C., Lawrence, P.J., Zeng, X., Yang, Z.-L., Levis, S., Sakaguchi, K., Bonan, GB., and Slater, A.G.: Parametrization improvements and functional and structural advances in version 4 of the Community Land Model. Journal of Advances in Modeling Earth Systems, 3, Art. M03001, doi: 10.1029/2011MS000045, 2011.

Le Quéré, C., Raupach, M.R., Canadell, J.G., Marland, G., Bopp, L., Ciais, P., Conway, T.J., Doney, S.C., Feely, R.A., Foster, P., Friedlingstein, P., Gurney, K., Houghton, R.A., House, J.I., Huntingford, C ., Levy, P.E., Lomas, M.R., Majkut, J., Metzl, N., Ometto, J.P., Peters, G.P., Prentice, I.C., Randerson, J.T., Running, S.W., Sarmiento, J.L., Schuster, U., Sitch, S., Takahashi, T., Viovy, N., van der Werf, G., and Woodward, F.I.: Trends in the sources and sinks of carbon dioxide. Nat. Geosci., 2, 831-836, 2009.

Le Quéré, C., Moriarty, R., Andrew, R.M., Canadell, J.G., Sitch, S., Korsbakken, J.I., Friedlingstein, P., Peters, G.P., Andres, R.J., Boden, T.A., Houghton, R.A., House, J.I., Keeling, R.F., Tans, P., Arneth, A., Bakker, D.C.E., Barbero, L., Bopp, L., Chang, J., Chevallier, F., Chini, L.P., Ciais, P., Fader, M., Feely, R.A., Gkritzalis, T., Harris, I., Hauck, J., Ilyina, T., Jain, A.K., Kato, E., Kitidis, V., Klein Goldewijk, K., Koven, C., Lanschützer, P., Lauvset, S.K., Lefèvre, N., Lenton, A., Lima, I.D., Metzl, N., Millero, F., Munro, D.R., Murata, A., Nabel, J.E.M.S., Nakaoka, S., Nojiri, Y., O'Brien, K., Olsen, A., Ono, T., Pérez, F.F., Pfeil, B., Pierrot, D., Poulter, B., Rehder, G., Rödenbeck, C., Saito, S., Schuster, U., Schwinger, J., Séférian, R., Steinhoff, T., Stocker, B.D., Sutton, A.J., Takahashi, T., Tilbrook, B., van der Laan-Luijkx, I.T., van der Werf, G.R., van Heuven, S., Vandemark, D., Viovy, N., Wiltshire, A., Zaehle, S., and Zeng, N.: Global Carbon Budget 2015. Earth System Science Data, 7, 349-396, 2015.

Li, H., Luo, L., Wood, E.F., and Schaake, J.: The role of initial conditions and forcing uncertainties in seasonal hydrologic forecasting. J. Geophys. Res., 114, D04114, doi:10.1029/2008JD010969, 2009.

Livak, M.E.: AmeriFlux US-Vcm Valles Caldera Mixed Conifer, doi:10.17190/AMF/1246121, 2016.

Mahecha, M.D., Reichstein, M., Jung, M., Seneviratne, S.I., Zaehle, S., Beer, C., Braakhekke, M.C., Carvalhais, N., Lange, H., Le Maire, G., and Moors, E.: Comparing observations and process-based simulations of biosphere-atmosphere exchanges on multiple timescales. J. Geophys. Res., 115, G02003, doi:10.1029/2009JG001016, 2010.

Litton, C.M., Raich, J.W., and Ryan, M.G.: Carbon allocation in forest ecosystems. Glob. Change Biol., 13, 2089-2109, 2007.

Luyssaert, S., Inglima, I., Jung, M., Richardson, A.D., Reichstein, M., Papale, D., Piao, S.L., Schulze, E.-D., Wingate, L., Matteucci G., Aragao, L., Aubinet, M., Beer, C., Bernhofer, C., Black, K.G., Bonal, D., Bonnefond, J.-M., Chambers, J., Ciais, P., Cook, B., Davis, K.J., Dolman, A.J., Gielen B., Goulden, M., Grace, J., Granier, A., Grelle, A., Griffis, T., Grünwald, T., Guidolotti, G., Hanson, P.J., Harding, R., Hollinger, D.Y., Hutyra, L.R., Kolari, P., Kruijt, B., Kutsch, W., Lagergren, F., Laurila, T., Law, B.E., Le Maire, G., Lindroth, A., Loustau, D., Malhi, Y., Mateus, J., Migliavacca, M., Misson, L., Montagnani, L., Moncrieff, J., Moors, E., Munger, J.W., Nikinmaa, E., Ollinger, S.V., Pita, G., Rebmann, C., Roupsard, O., Saigusa, N., Sanz, M.-J., Seufert, G., Sierra, C., Smith, M.-L., Tang, J., Valentini, R., Vesala, T., and Janssens, I.A.: CO_2 balance of boreal, temperate, and tropical forests derived from a global database. Glob. Change Biol., 13, 2509-2537, 2007.

Malhi, Y., Doughty, C., and Galbraith, D.: The allocation of net primary productivity in tropical forests. Philos. T. Roy. Soc. B, 366, 3225-3245, 2011.

Malhi, Y., Meir, P., and Brown, S.: Forests, carbon and global climate. Philos. T. Roy. Soc. A, 360, 1567-1591, 2002.

Mao, J., Thornton, P.E., Shi, X., Zhao, M., and Post, W.M.: Remote sensing evaluation of CLM4 GPP for the period 2000 to 2009. J. Climate, 25, 5327-5342, 2012.

Mao, J., Shi, X., Thornton, P.E., Hoffman, F.M., Zhu, Z., Ranga, B., and Myneni, R.B.: Global latitudinal-asymmetric vegetation growth trends and their driving mechanisms: 1982-2009. Remote Sensing, 5, 1484-1497, 2013.

Masek, J.G., Huang, C., Wolfe, R., Cohen, W., Hall, F., Kutler, J., and Nelson, P.: North American forest disturbance mapped from a decadal Landsat record. Remote Sens. Environ., 112, 2914-2926, 2008.

Megonigal, J.P., Conner, W.H., Kroegger, S., and Sharitz, R.R.: Aboveground production in southeastern floodplain forests: a test of the subsidy-stress hyphothesis. Ecology, 78, 370-384, 1997.

Munger, J.W.: AmeriFlux US-Ha1 Harvard Forest EMS Tower (HFR1), doi:10.17190/AMF/1246059, 2016.

Nadelhoffer, K.J. and Raich, J.W.: Fine root production estimates and belowground carbon allocation in forest ecosystems. Ecology, 73, 1139-1147, 1992.

Negron-Juarez, R., Koven, C.D., Riley, W.J., Knox, R.G., and Chambers, J.Q.: Observed allocations of productivity and biomass, and turnover times in tropical forests are not accurately represented in CMIP5 Earth system models. Environ. Res. Lett., 10, 064017, 2015.

Newman, G.S., Arthur, M.A., and Muller, R.N.: Above- and belowground net primary production in a temperate mixed deciduous forest. Ecosystems, 9, 317-329, 2006.

Novick, K.A., and Phillips, R.: AmeriFlux US-MMS Morgan Monroe State Forest, doi:10.17190/AMF/1246080, 2016.

Oishi, C., Novick, K.A., and Stoy, P.: AmeriFlux US-Dk2 Duke Forest-hardwoods, doi:10.17190/AMF/1246047, 2016.

Oleson, K., Lawrence, D.M., Bonan, G.B., Drewniak, B., Huang, M., Koven, C.D., Levis, S., Li, F., Riley, W.J., Subin, Z.M., Swenson, S.C., Thornton, P.E., Bozbiyik, A., Fisher, R., Heald, C.L., Kluzek, E., Lamarque, J.-F., Lawrence, P.J., Leung, L.R., Lipscomb, W., Muszala, S., Ricciuto, D.M., Sacks, W., Sun, Y., Tang, J., and Yang, Z.-L.: Technical Description of version 4.5 of the Community Land Model (CLM), NCAR Technical Note NCAR/TN-503+STR, Boulder, Colorado, 420 pp, 2013.

Pan, Y., Birdsey, R.A., Fang, J., Houghton, R., Kauppi, P.E., Kurz, W.A., Phillips, O.L., Shvidenko, A., Lewis, S.L., Canadell, J.G., Ciais, P., Jackson, R.B., Pacala, S.W., McGuire, A.D., Piao, S., Rautiainen, A., and Hayes, D.: A large and persistent carbon sink in the world's forests. Science, 333, 988-993, 2011.

Phillips, R.P., Ibáñez, I., D'Orangeville, L., Hanson, P.J., Ryan, M.G., and McDowell, N.G.: A belowground prespective on the drought sensitivity of forests: towards improved understanding and simulation. Forest Ecol. Manag., 380, 309-320, 2016.

Piao, S.L., Ito, A., Li, S.G., Huang, Y., Ciais, P., Wang, X.H., Peng, S.S., Nan, H.J., Zhao, C., Ahlströn, A., Andres, R.J., Chevallier, F., Fang, J.Y., Hartmann, J., Huntingford, C., Jeong, S., Levis, S., Levy, P.E., Li, J.S., Lomas, M.R., Mao, J.F., Mayorga, E., Mohammat, A., Muraoka, H., Peng, C.H., Peylin, P., Poulter, B., Shen, Z.H., Shi, X., Sitch, S., Tao, S., Tian, H.Q., Wu, X.P., Xu, M., Yu, G.R., Viovy, N., Zaehle, S., Zeng, N., and Zhu, B.: The carbon budget of terrestrial ecosystems in East Asia over the last two decades. Biogeosciences, 9, 3571-3586, 2012.

Randerson, J.T., Hoffman, F., Thornton, P.E., Mahowald, N.M., Lindsay, K., Lee, Y.-H., Nevison, C.D., Doney, S.C., Bonan, G., Stöckli, R., Covey, C., Running, S.W., and Fung, I.Y.: Systematic assessment of terrestrial biogeochemistry in coupled climate-carbon models. Glob. Change Biol., 15, 2462-2484, 2009.

Reichstein, M., Falge, E., Baldocchi, D., Papale, D., Aubinet, M., Berbigier, P., Bernhofer, C., Buchmann, N., Gilmanov, T., Granier, A., Grünwald, T., Havránková, K., Ilvesniemi, H., Janous, D., Knohl, A., Laurila, T., Lohila, A., Loustau, D., Matteucci, G., Meyers, T., Miglietta, F., Ourcival, J.-F., Pumpanen, J., Rambal, S., Rotenberg, E., Sanz, M., Tenhunen, J., Seufert, G., Vaccari, F., Vesala, T., Yakir, D., and Valentini, R.: On the separation of net ecosystem exchange into assimilation and ecosystem respiration: review and improved algorithm. Glob. Change Biol., 11, 1424-1439, 2005.

Richardson, A.D., Williams, M., Hollinger, D.Y., Moore, D.J.P., Dail, D.B., Davidson, E.A., Scott, N.A., Evans, R.S., Hughes, H., Lee, J.T., Rodrigues, C., and Savage, K.: Estimating parameters of a forest ecosystem C model with measurements of stocks and fluxes as joint constraints. Oecologia, 164, 25-40, 2010.

Rodell, M., Houser, P.R., Berg, A.A., and Famiglietti, J.S.: Evaluation of 10 methods for initializing a land surface model. J. Hydrometeorol., 6, 146-155, 2005.

Runkle, J.R.: Changes in Southern Appalachian canopy tree gaps sampled thrice. Ecology, 79, 1768-1780, 1998.

Schulze, E.-D., Wirth, C., and Heimann, M.: Managing forests after Kyoto. Science, 289, 2058-2059, 2000.

Sevanto, S. and Dickman, L.T. Where does the carbon go?—Plant carbon allocation under climate change. Tree physiol., 35, 581-584, 2015.

Shi, M., Fisher, J.B., Brzostek, E.R., and Phillips, R.P: Carbon cost of plant nitrogen acquisition: global carbon cycle impact from an improved plant nitrogen cycle in the Community Land Model. Glob. Change Biol., 22, 1299-1314, 2016.

Shi, X., Mao, J., Thornton, P.E., and Huang, M.: Spatiotemporal patterns of evapotranspiration in response to multiple environmental factors simulated by the Community Land Model. Environ. Res. Lett., 8, 024012, 2013.

Song, X., Zeng, X.-D., and Li, F.: Evaluation of the individual allocation scheme and its impacts in a dynamic global vegetation model. Atmospheric and Oceanic Science Letters, 9, 38-44, 2016.

Stearns, F.W.: Ninety years change in a northern hardwood forest in Wisconsin. Ecology, 30, 350-358, 1949.

Stokes, M.A., and Smiley, T.L.: An introduction to tree-ring dating. University of Chicago Press, Chicago, Illinois, USA, 1968.

Stoy, P., Oishi, C., and Novick., K.A.: AmeriFlux US-Dk3 Dule Forest – loblolly pine, doi:10.17190/AMF/1246048, 2016.

Thornton, P.E. and Zimmerman, N.E.: An improved canopy integration scheme for a Land Surface Model with prognostic canopy structure. J. Climate, 20, 3902-3923, 2007.

Thum, T., MacBean, N., Peylin, P., Bacour, C., Santaren, D., Longdoz, B., Loustau, D., and Ciais, P.: The potential benefit of using forest biomass data in addition to carbon and water flux measurements to constrain ecosystem model parameters: case studies at two temperate forest sites. Agr. Forest Meteorol., 234, 48-65, 2017.

Thurner, M., Beer, C., Ciais, P., Friend, A.D., Ito, A., Kleidon, A., Lomas, M.R., Quegan, S., Rademacher, T.T., Schaphoff, S., Tum, M., Wiltshire, A., and Carvalhais, N.: Evaluation of climate-related carbon turnover processes in global vegetation models for boreal and temperate forests. Glob. Change Biol., doi: 10.1111/gcb.13660, 2017.

Tilman, D.: Plant strategies and the dynamics and structure of plant communities. Monographs in Population Biology 26. Princeton University Press, Princeton, New Jersey, USA, 1988.

van Mantgem, P., Stephenson, N.L., Byrne, J.C., Daniels, L.D., Franklin, J.F., Fulé, P.Z., Harmon, M.E., Larson, A.J., Smith, J.M., Taylor, A.H., and Veblen, T.T.: Widespread increase of tree mortality rates in the western United States. Science, 323, 521-524, 2009.

Waring, R.H., Landsberg, J.J., and Williams, M.: Net primary production of forests: a constant fraction of gross primary production? Tree Physiol., 18, 129-134, 1998.

Warren, J.M., Hanson, P.J., Iversen, C.M., Kumar, J., Walker, A.P., and Wullschleger, S.D.: Root structural and functional dynamics in terrestrial biosphere models – evaluation and recommendations. New Phytol., 205, 59-78, 2015.

Weng, E., Farrior, C.E., Dybzinski, R. and Pacala, S.W.,~~ 2016.~~ Predicting vegetation type through physiological and environmental interactions with leaf traits: evergreen and deciduous forests in an earth system modeling framework. Glob. Change Biol., doi: ~~Global change biology.~~ 10.1111/gcb.13542, 2016

Wolf, A., Field, C.B., and Berry, J.A.: Allometric growth and allocation in forests: a perspective from FLUXNET. Ecol. Appl., 21, 1546-1556, 2011.

Wood, J.D., and Gu, L.: AmeriFlux US-MOz Missouri Ozark site, doi:10.17190/AMF/1246081, 2016.

Xia, J., Chen, Y., Liang, S., Liu, D., and Yuan, W.: Global simulations of carbon allocation coefficients for deciduous vegetation types. Tellus B, 67, 28016, 2015.

Xia, J.Y., Luo, Y.Q., Wang, Y.-P., Weng, E.S., and Hararuk, O.: A semi-analytical solution to accelerate spin-up of a coupled carbon and nitrogen land model to steady state. Geosci. Model Dev., 5, 1259-1271, 2012.

Yang, Z.-L., Dickinson, R.E., Henderson-Sellers, A., and Pitman, A.J.: Preliminary study of spin-up processes in land surface models with the first stage data of Project for Intercomparison of Land Surface Parameterization Schemes Phase 1(a). J. Geophys. Res., 100, 16553-16578, 1995.

Zaehle, S. and Friend, A.D.: Carbon and nitrogen cycle dynamics in the O-CN land surface model: 1. Model description, site-scale evaluation, and sensitivity to parameter estimates. Global Biogeochem. Cy., 24, GB1005, doi:10.1029/2009GB003521, 2010.

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Table 1. Site general information and observations available. ID refers to site name used in the AmeriFlux network.

Site (ID)	Longitude	Latitude	Reference	C fluxes data	Aboveground biomass (AmeriFlux)	Aboveground biomass (tree-ring)	LAI in-situ data	Leaf C-LAI data	Stem C/Leaf C data
Evergreen									
Niwot Ridge (NR1)	-105.5464	40.0329	Blanken, 2016	1999-2013	2003	1980-2012	n.a.	n.a.	n.a.
Valles Caldera Mixed Conifer (Vcm)	-106.5321	35.8884	Litvak, 2016	2007-2013	2007	1980-2011	n.a.	n.a.	2007
Howland Forest (Ho1)	-68.7402	45.2041	Hollinger, 2016	1996-2004 2006-2013	2003	1980-2012	2006	n.a.	2003
Duke Forest Loblolly Pine (Dk3)	-79.0942	35.9782	Stoy et al., 2016	1998-2005	2001-2005	n.a.	2002-2005	2002-2005	n.a.
Deciduous									
University of Michigan Biological Station (UMB)	-84.7138	45.5598	Gough et al., 2009; Gough et al., 2013; Gough et al., 2016	2005-2013	1998-2011	1980-2013	1997-2013	1998-2009	1998-2009
Harvard Forest (Ha1)	-72.1715	42.5378	Munger, 2016	1992-2013	2006-2008	1980-2012	1998,1999, 2005-2008, 2010	n.a.	n.a.

Missouri Ozark (MOz)	-92.2000	38.7441	Wood and Gu, 2016	n.a.	n.a.	1980-2013	2006-2012	n.a.	n.a.
Morgan Monroe State Forest (MMS)	-86.4131	39.3232	Novick and Phillips, 2016	1999-2013	1999-2005	1980-2013	1999-2006, 2009	1999-2005	1999-2005
Duke Forest Hardwoods (Dk2)	-79.1004	35.9736	Oishi et al., 2016	2001-2005	2002	1980-2013	2006	n.a.	n.a.

Table 2. Allometric parameter values for evergreen and deciduous temperate forests in the C allocation scheme in CLM described in Oleson et al. (2013) (D-CLM4.5); the alternative dynamic C allocation scheme (D-Litton) based on Litton et al. (2007); and the 2 fixed C allocation schemes (F-Evergreen, and F-Deciduous) based on Luyssaert et al. (2007). Allometric parameters represented with numbers indicate constant parameters, whereas equations indicate dynamic parameters. In the equations, *NPPann* is the annual sum of Net Primary Productivity (NPP) of the previous year.

		C allocation scheme			
Allometric parameter	Definition (parameter name)	D-CLM4.5	D-Litton	F-Evergreen	F-Deciduous
a_1	Ratio of new fine root: new leaf carbon allocation (froot_leaf)	1	1	1	0.5
a_2	Ratio of new coarse root: new stem carbon allocation (croot_stem)	0.3	$\frac{0.25 - 8e^{-05} \times NPPann}{0.17 + 0.0001158 \times NPPann}$	0.27	0.27
a_3	Ratio of new stem: new leaf carbon allocation	$\frac{2.7}{1 + e^{-0.004 \times (NPPann - 300)}} - 0.4$	$\frac{0.17 + 0.0001158 \times NPPann}{0.26}$	1.76	1.4

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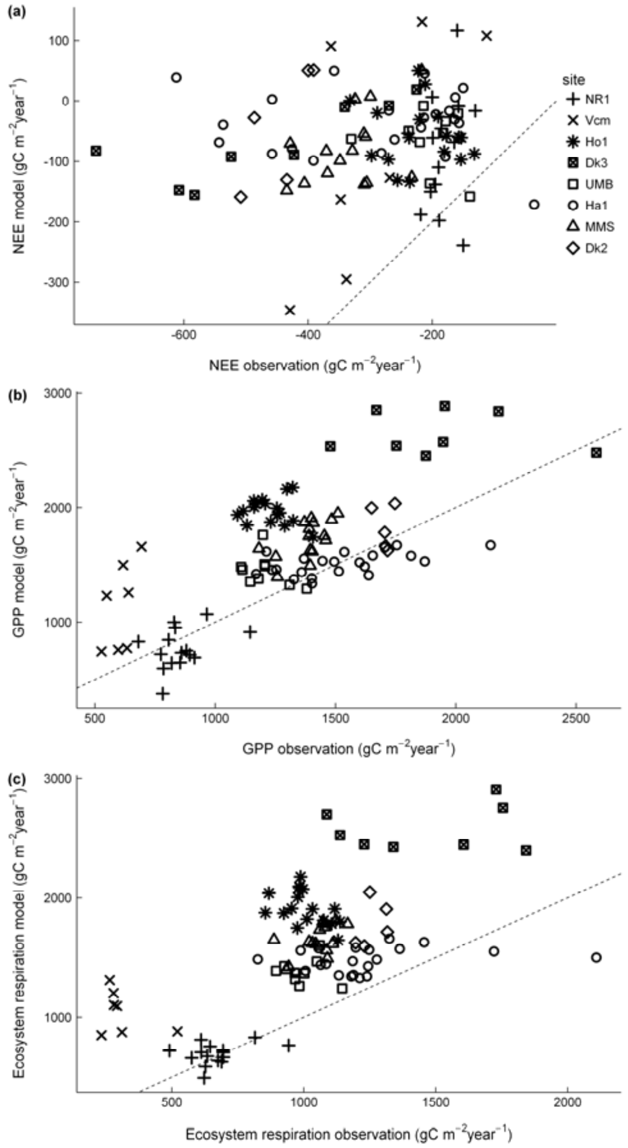
Table 3. Percentage of NPP allocated to the each plant pool (leaf, stem, and belowground) according to observations, the four C allocation schemes used (D-CLM4.5, D-Litton, F_Evergreen, and F-Deciduous), and C allocation schemes of other models.

		C allocation scheme				
% Allocation	Observation (Reference)	D-CLM4.5	D-Litton	F-Evergreen	F-Deciduous	Other models (Model; Reference)
% Leaf	~25-30% (Luyssaert et al., 2007) ~26% (Litton et al., 2007) ~25% (Wolf et al., 2011)	~30% in low NPP sites ~20% in high NPP sites	~26%	~25%	~30%	19.8% (VISIT; Ise et al. 2010) 19% for evergreen and 20% for deciduous (BIOME-BGC; Ise et al., 2010) 30% (IBIS; Xia et al., 2015)
% Stem	~41-43% (Luyssaert et al., 2007) ~20-35% in sites with similar NPP to the sites in this study (Litton et al., 2007) ~20-35% (Wolf et al., 2011) ~30-38%; assuming NPP=0.5×GPP (Chen et al., 2013)	~25% in low NPP sites ~46% in high NPP sites	~20-35%	~41%	~43%	50% (VISIT; Ise et al. 2010) 42% for evergreen and 45% for deciduous (BIOME-BGC; Ise et al., 2010) 50% for temperate broadleaf forests (IBIS; Xia et al., 2015)
% Belowground (fine root+coarse root)	~34-37% (Luyssaert et al., 2007) ~39-54% in sites with similar NPP to the sites in this study (Litton et al., 2007) ~50% for temperate forests (Newman et al., 2006)	~40% in low NPP sites ~34% in high NPP sites	~39-54%	~34%	~37%	30.2% (VISIT; Ise et al. 2010) 39% for evergreen and 34% for deciduous (BIOME-BGC; Ise et al., 2010) 20% (IBIS; Xia et al., 2015)

~45-50% as mean values for temperate forests (Gill and Finzi, 2016)

FIGURES


(a)
NEE model (gC m^{-2}year^{-1})
100
0
-100
-200
-300
-600
-400
-200
NEE observation (gC m^{-2}year^{-1})
site
+ NR1
× Vcm
✱ Ho1
⊠ Dk3
□ UMB
○ Ha1
△ MMS
◇ Dk2
(b)
GPP model (gC m^{-2}year^{-1})
3000
2000
1000
500
1000
1500
2000
2500
GPP observation (gC m^{-2}year^{-1})
(c)
Ecosystem respiration model (gC m^{-2}year^{-1})
3000
2000
1000
500
1000
1500
2000
Ecosystem respiration observation (gC m^{-2}year^{-1})

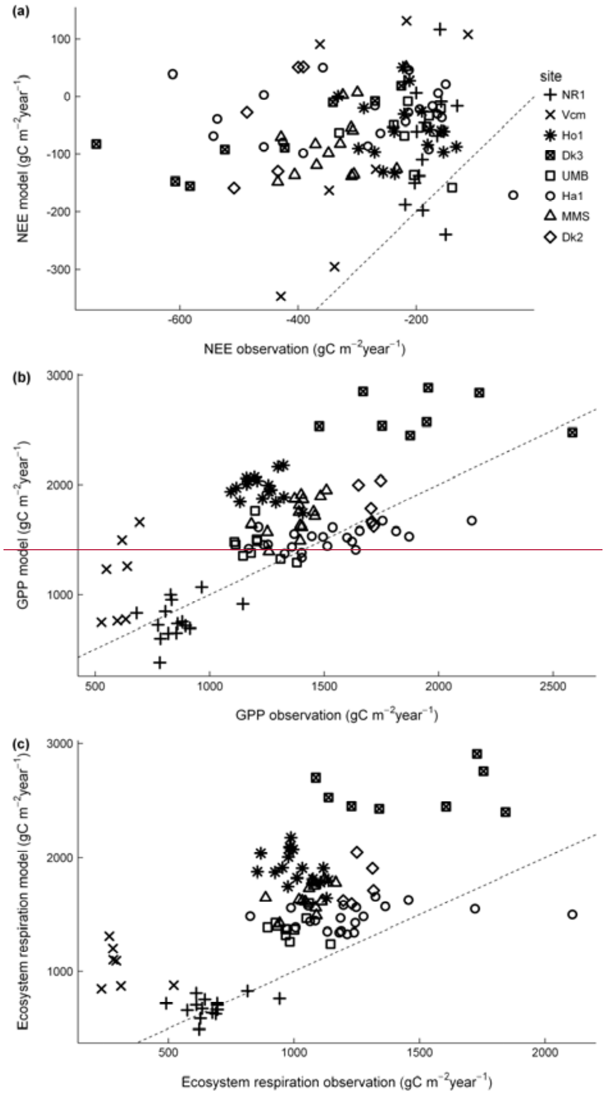
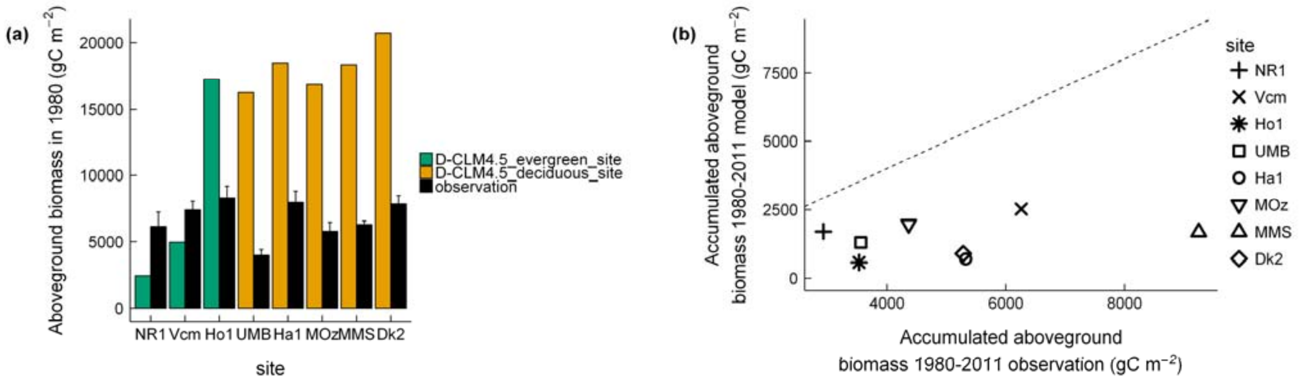

(a)
NEE model (gC m^{-2}year^{-1})
100
0
-100
-200
-300
-600
-400
-200
NEE observation (gC m^{-2}year^{-1})
site
NR1
Vcm
Ho1
Dk3
UMB
Ha1
MMS
Dk2
(b)
GPP model (gC m^{-2}year^{-1})
3000
2000
1000
500
1000
1500
2000
2500
GPP observation (gC m^{-2}year^{-1})
(c)
Ecosystem respiration model (gC m^{-2}year^{-1})
3000
2000
1000
500
1000
1500
2000
Ecosystem respiration observation (gC m^{-2}year^{-1})

Figure 1 Comparisons between (a) NEE, (b) GPP and (c) ecosystem respiration in observations and model (D-CLM4.5). All fluxes were aggregated to annual. Dashed line is 1:1 relationship between observations and model. Observations are from the AmeriFlux L2 data product.


(a)
Aboveground biomass in 1980 (gC m^{-2})
20000
15000
10000
5000
0
NR1 Vcm Ho1 UMB Ha1 MOz MMS Dk2
site
D-CLM4.5_evergreen_site
D-CLM4.5_deciduous_site
observation
(b)
Accumulated aboveground biomass 1980-2011 model (gC m^{-2})
7500
5000
2500
0
4000
6000
8000
Accumulated aboveground biomass 1980-2011 observation (gC m^{-2})
site
NR1
Vcm
Ho1
UMB
Ha1
MOz
MMS
Dk2

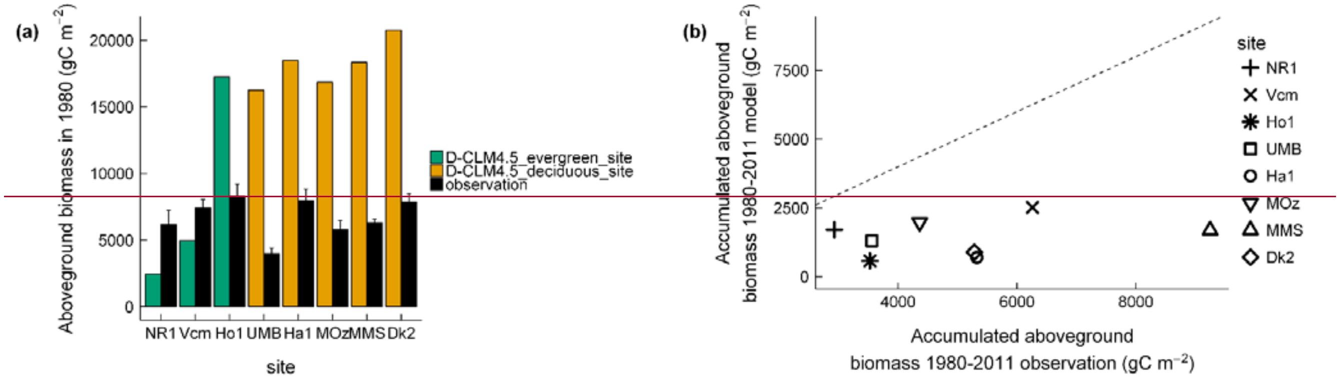
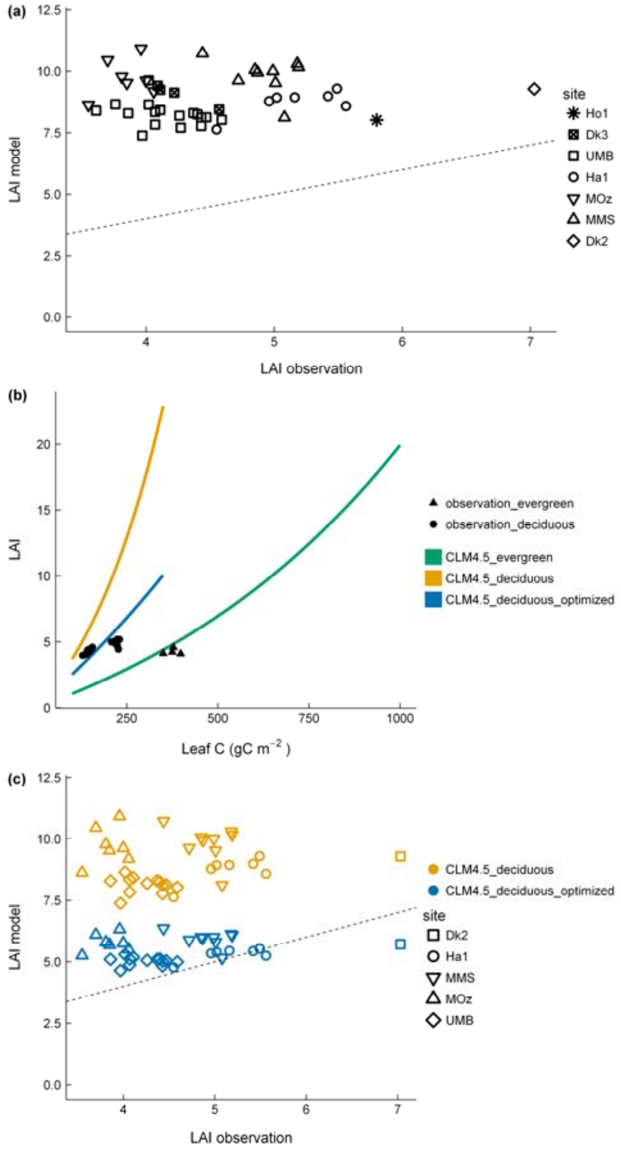

(a)
Aboveground biomass in 1980 (gC m^{-2})
20000
15000
10000
5000
0
NR1 Vcm Ho1 UMB Ha1 MOz MMS Dk2
site
D-CLM4.5_evergreen_site
D-CLM4.5_deciduous_site
observation
(b)
Accumulated aboveground biomass 1980-2011 model (gC m^{-2})
7500
5000
2500
0
4000
6000
8000
Accumulated aboveground biomass 1980-2011 observation (gC m^{-2})
site
NR1
Vcm
Ho1
UMB
Ha1
MOz
MMS
Dk2

Figure 2 Comparisons between (a) observed and modeled (D-CLM4.5) aboveground biomass in 1980; (b) observed and modeld (D-CLM4.5) accumulated aboveground biomass between 1980-2011. Dashed line is 1:1 relationship between observations and model. Observations (estimates of aboveground biomass from tree-ring data) for the Ho1 and Ha1 sites are from Dye et al. (2016), whereas for the rest of sites observations were obtained following the methodology described in Alexander et al. (under review).


(a)
LAI model
LAI observation
12.5
10.0
7.5
5.0
2.5
0.0
4
5
6
7
site
Ho1
Dk3
UMB
Ha1
MOz
MMS
Dk2
(b)
LAI
Leaf C (gC m^{-2})
20
15
10
5
0
250
500
750
1000
observation_evergreen
observation_deciduous
CLM4.5_evergreen
CLM4.5_deciduous
CLM4.5_deciduous_optimized
(c)
LAI model
LAI observation
12.5
10.0
7.5
5.0
2.5
0.0
4
5
6
7
CLM4.5_deciduous
CLM4.5_deciduous_optimized
site
Dk2
Ha1
MMS
MOz
UMB

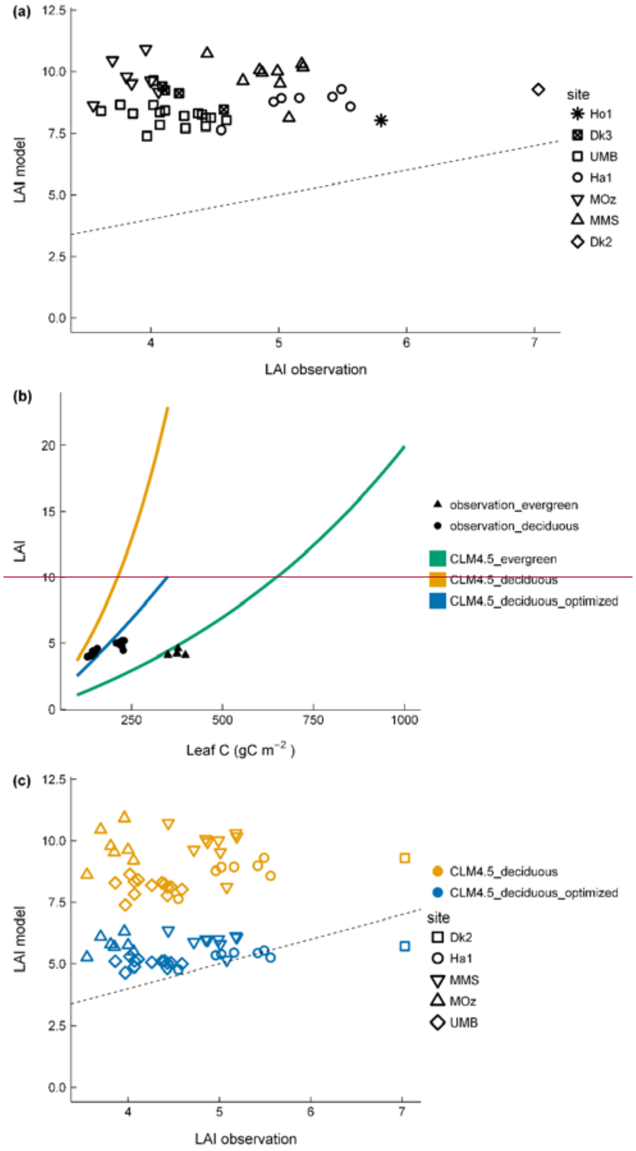
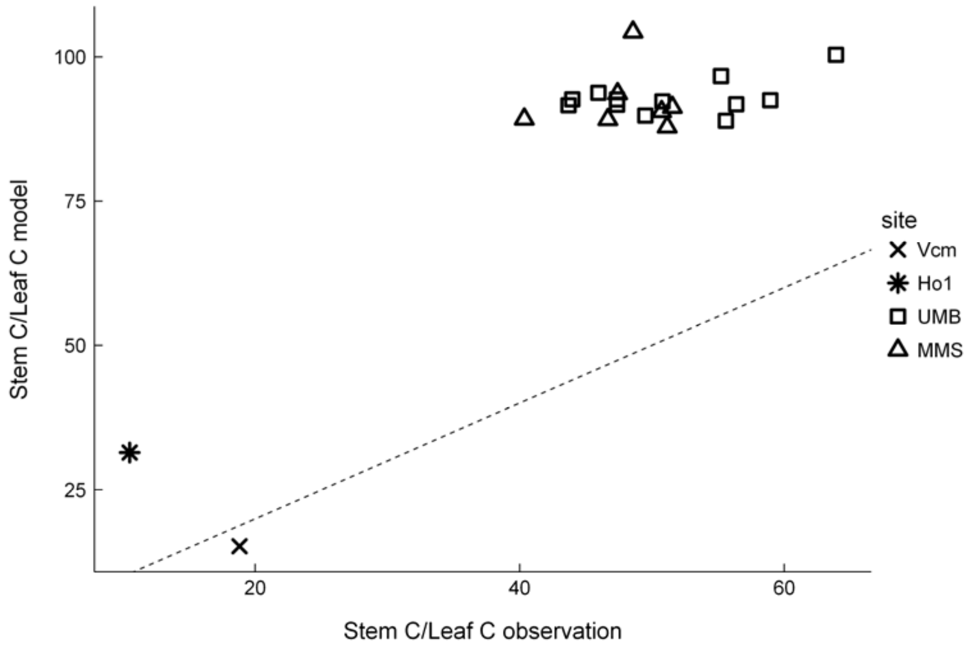

(a)
12.5
10.0
7.5
5.0
2.5
0.0
LAI model
4
5
6
7
LAI observation
site
Ho1
Dk3
UMB
Ha1
MOz
MMS
Dk2
(b)
20
15
10
5
0
LAI
250
500
750
1000
Leaf C (gC m^{-2})
observation_evergreen
observation_deciduous
CLM4.5_evergreen
CLM4.5_deciduous
CLM4.5_deciduous_optimized
(c)
12.5
10.0
7.5
5.0
2.5
0.0
LAI model
4
5
6
7
LAI observation
CLM4.5_deciduous
CLM4.5_deciduous_optimized
site
Dk2
Ha1
MMS
MOz
UMB

Figure 3 Comparisons between (a) LAI measured in-situ and LAI in the model; (b) Relationship between Leaf C and LAI in: CLM4.5 for deciduous forests, observations for deciduous forests, optimized Leaf C-LAI relationship for deciduous forests, CLM4.5 for evergreen forests, and observations for evergreen forests; (c) Comparisons between LAI measured in-situ and LAI in the standard and modified version of the model with optimized parameters for LAI. In 3a and 3c, dashed line is 1:1 relationship between observations and model. Observations (LAI measured in-situ, and Leaf C) are from the AmeriFlux database.


Stem C/Leaf C model
100
75
50
25
20
40
60
Stem C/Leaf C observation
site
Vcm
Ho1
UMB
MMS

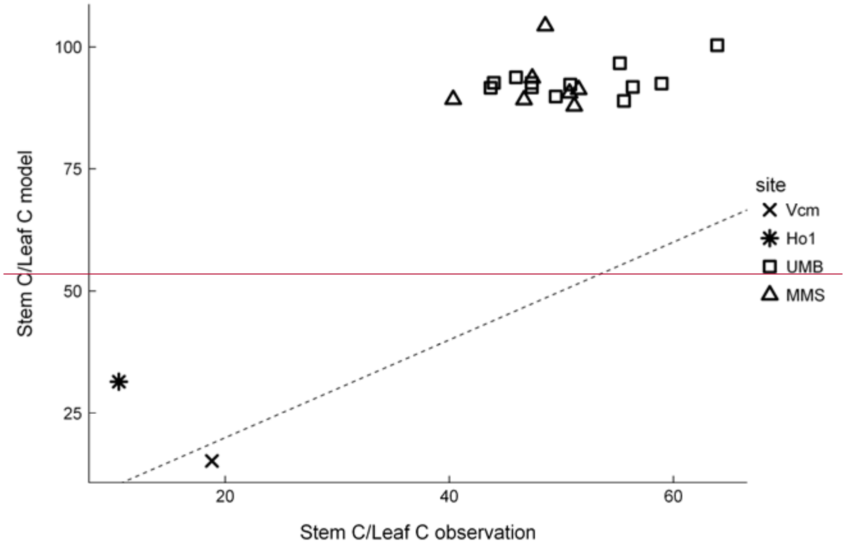
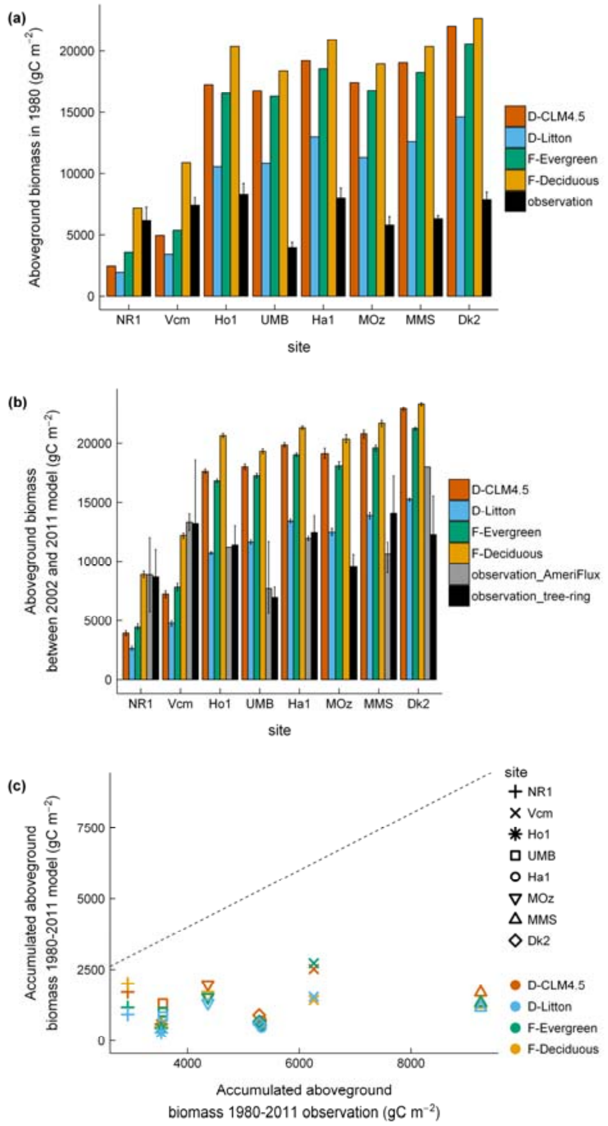


Figure 4 Comparisons between Cstem/Cleaf ratio for the D-CLM4.5 scheme and AmeriFlux observations. Dashed line is 1:1 relationship between observations and model. Observations (Cstem and Cleaf) are from the AmeriFlux database.

(a)
Aboveground biomass in 1980 (gC m^{-2})
0
5000
10000
15000
20000
NR1
Vcm
Ho1
UMB
Ha1
MOz
MMS
Dk2
site
D-CLM4.5
D-Litton
F-Evergreen
F-Deciduous
observation
(b)
Aboveground biomass between 2002 and 2011 model (gC m^{-2})
0
5000
10000
15000
20000
NR1
Vcm
Ho1
UMB
Ha1
MOz
MMS
Dk2
site
D-CLM4.5
D-Litton
F-Evergreen
F-Deciduous
observation_AmeriFlux
observation_tree-ring
(c)
Accumulated aboveground biomass 1980-2011 model (gC m^{-2})
0
2500
5000
7500
4000
6000
8000
Accumulated aboveground biomass 1980-2011 observation (gC m^{-2})
site
NR1
Vcm
Ho1
UMB
Ha1
MOz
MMS
Dk2
D-CLM4.5
D-Litton
F-Evergreen
F-Deciduous

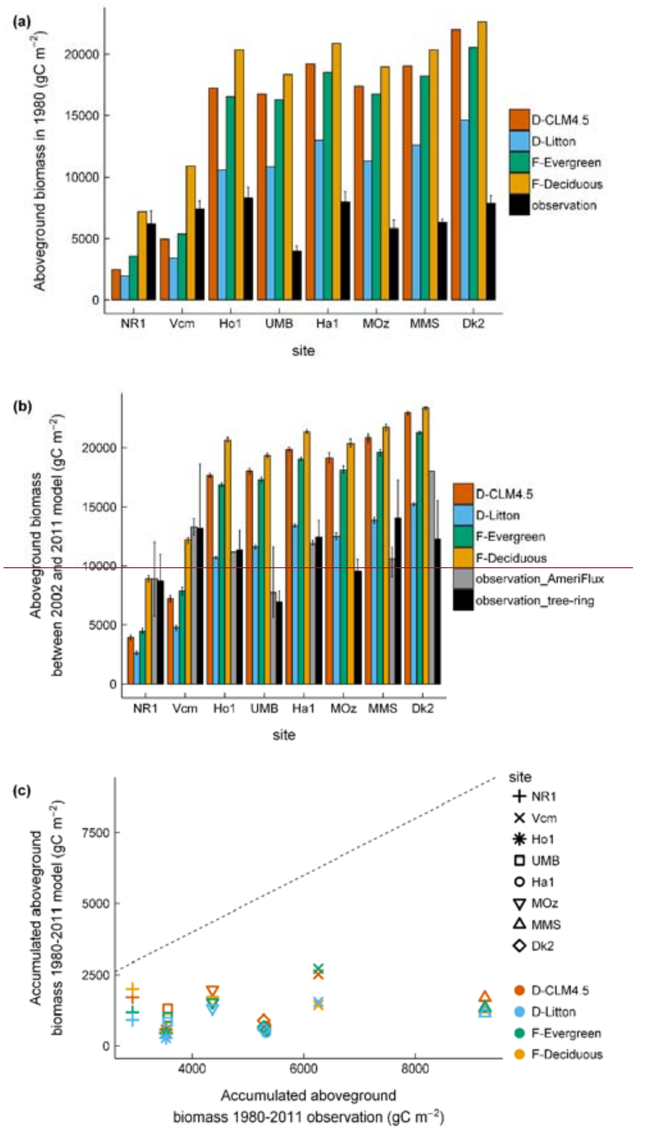
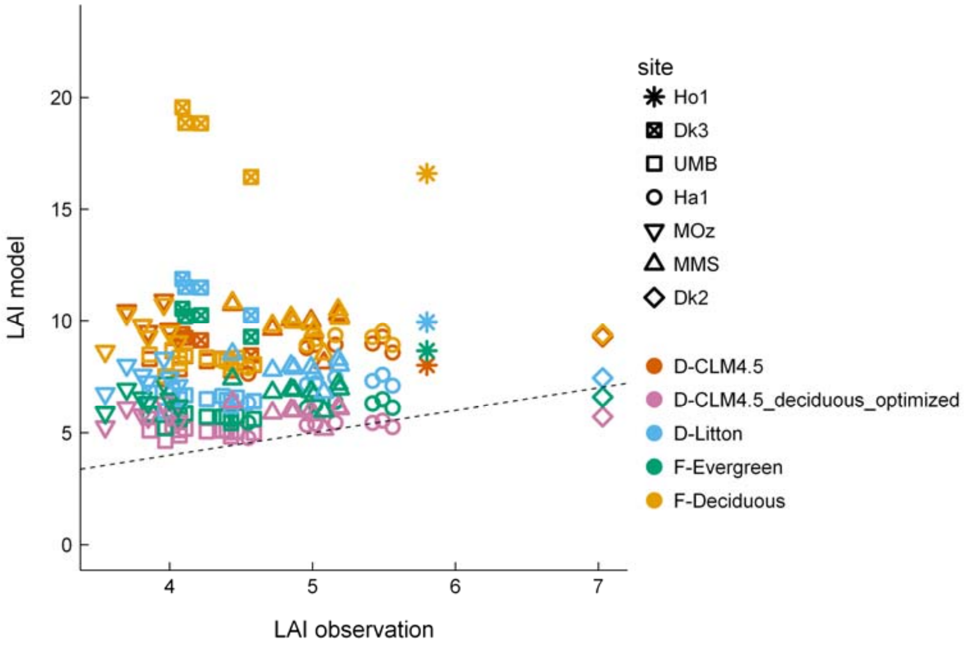

(a)
Aboveground biomass in 1980 (gC m^{-2})
0
5000
10000
15000
20000
NR1
Vcm
Ho1
UMB
Ha1
MOz
MMS
Dk2
site
D-CLM4.5
D-Litton
F-Evergreen
F-Deciduous
observation
(b)
Aboveground biomass between 2002 and 2011 model (gC m^{-2})
0
5000
10000
15000
20000
NR1
Vcm
Ho1
UMB
Ha1
MOz
MMS
Dk2
site
D-CLM4.5
D-Litton
F-Evergreen
F-Deciduous
observation_AmeriFlux
observation_tree-ring
(c)
Accumulated aboveground biomass 1980-2011 model (gC m^{-2})
0
2500
5000
7500
4000
6000
8000
Accumulated aboveground biomass 1980-2011 observation (gC m^{-2})
site
NR1
Vcm
Ho1
UMB
Ha1
MOz
MMS
Dk2
D-CLM4.5
D-Litton
F-Evergreen
F-Deciduous

Figure 5 (a) Comparisons between observed and modeled aboveground biomass in 1980 for the four C allocation schemes; (b) Comparisons between mean observed and modeled aboveground biomass between 2002 and 2011 for the four C allocation schemes; (c) Comparisons between observed and modeled accumulated aboveground biomass 1980-2011 for the four C allocation schemes. Turnover rate for stem in CLM4.5 is 2%. Dashed line is 1:1 relationship between observations and model. Observations ("observation" in 5a, "observation_tree_ring" in 5b, and "accumulated aboveground biomass 1980-2011 observation" in 5c) are aboveground biomass estimates from tree-ring data, which are from Dye et al. (2016) for the Ha1 and Ho1 sites, and following the methodology in Alexander et al. (under review) for the rest of sites. Observations ("Observation_AmeriFlux" in 5b) are aboveground biomass data from the AmeriFlux database, available only for a subset of sites and years (see Table 1).


LAI model
LAI observation
0
5
10
15
20
4
5
6
7
site
Ho1
Dk3
UMB
Ha1
MOz
MMS
Dk2
D-CLM4.5
D-CLM4.5_deciduous_optimized
D-Litton
F-Evergreen
F-Deciduous

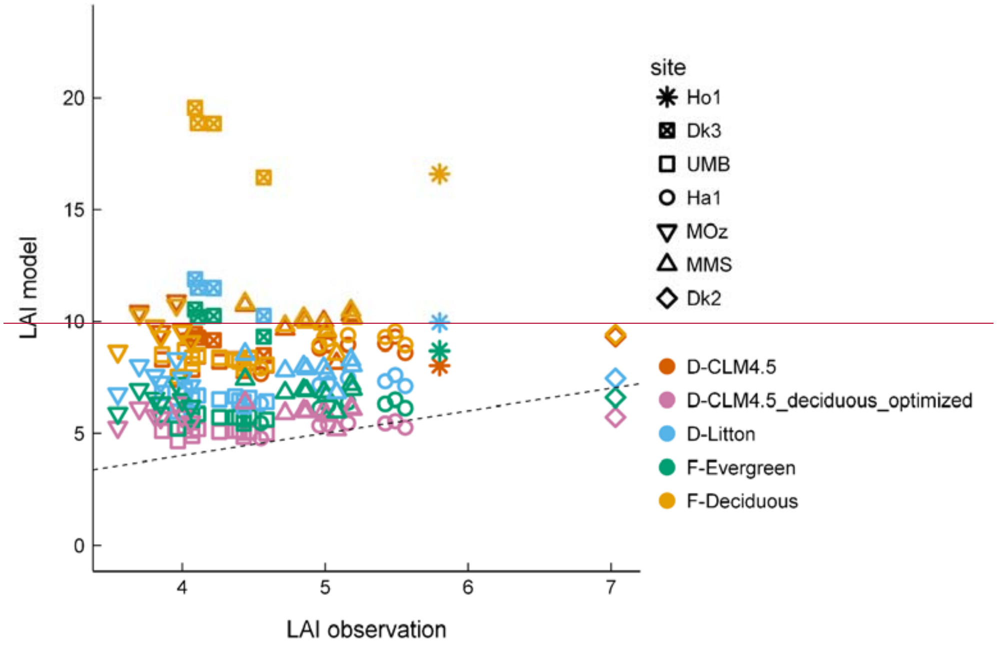
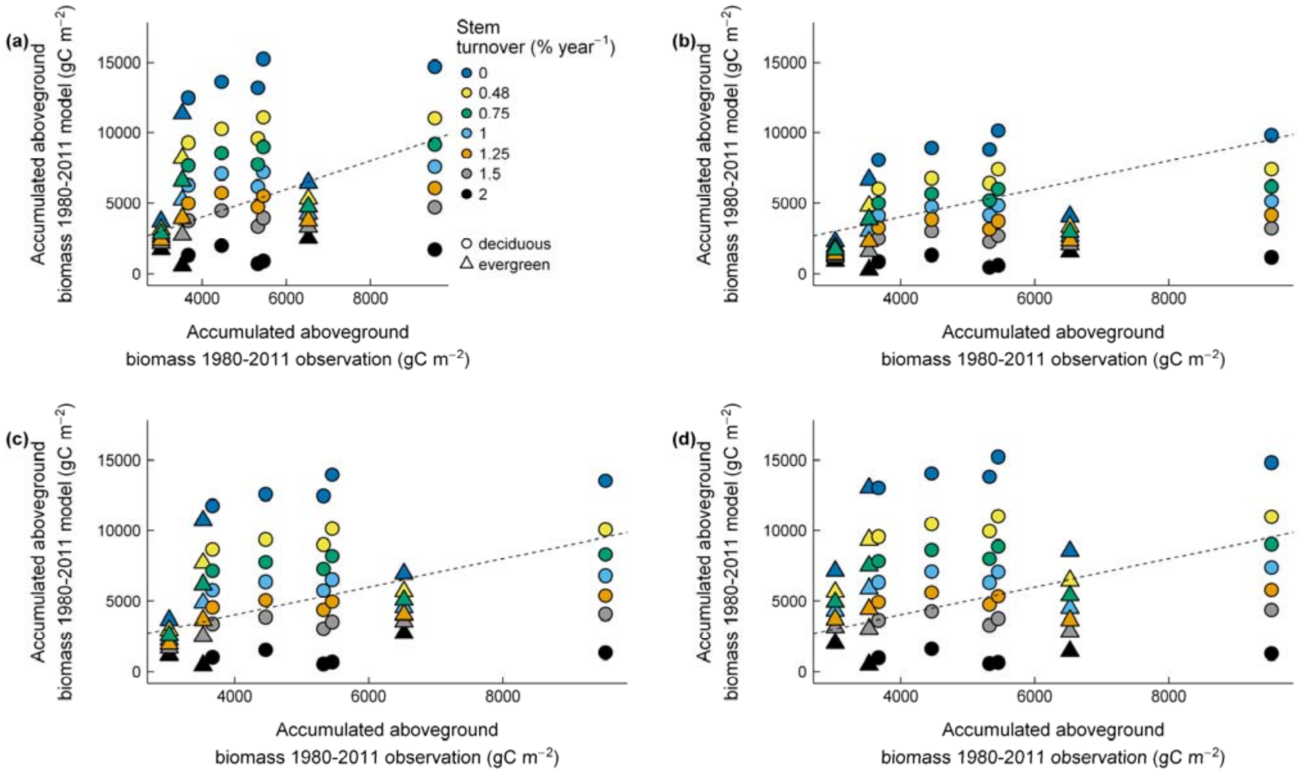


Figure 6 Comparisons between LAI measured in-situ and LAI in the model for the different C allocation schemes (D-CLM4.5_deciduous_optimized refers to the one with the optimized leaf C-LAI relationship for deciduous forests in D-CLM4.5). Dashed line is 1:1 relationship between observations and model. Observations (LAI measured in-situ) are from the AmeriFlux database.


(a)
(b)
(c)
(d)
Accumulated aboveground biomass 1980-2011 model (gC m^{-2})
Accumulated aboveground biomass 1980-2011 observation (gC m^{-2})
0
5000
10000
15000
4000
6000
8000
Stem turnover (% year^{-1})
● 0
● 0.48
● 0.75
● 1
● 1.25
● 1.5
● 2
○ deciduous
△ evergreen

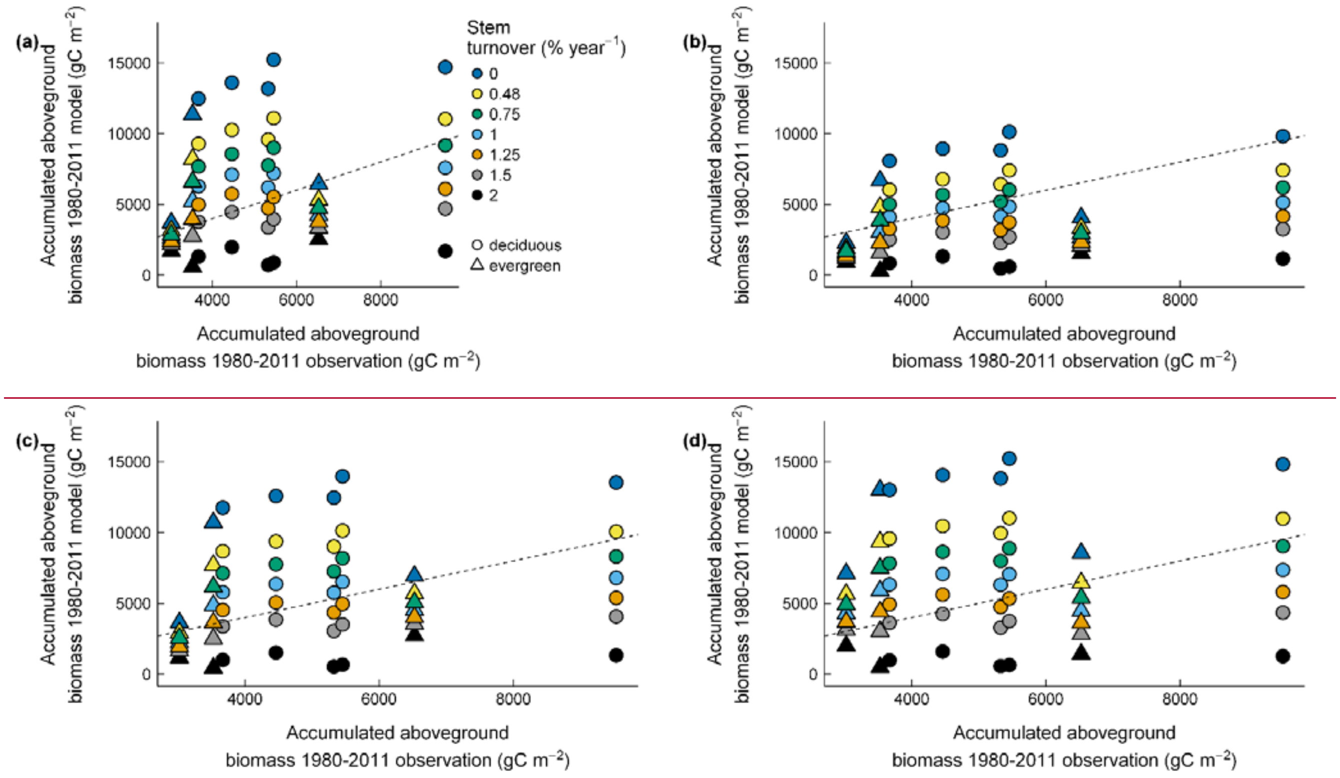
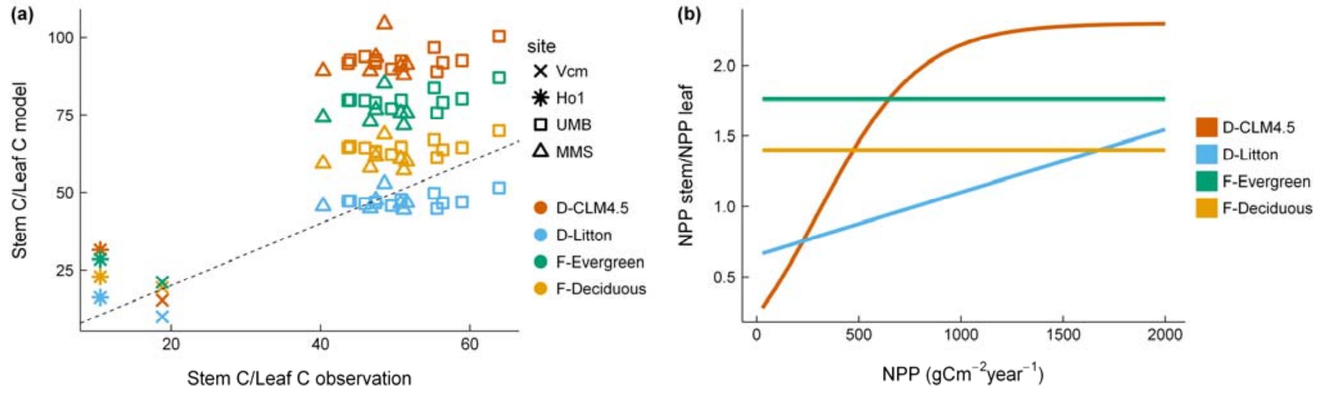

(a)
(b)
(c)
(d)
Accumulated aboveground biomass 1980-2011 model (gC m^{-2})
Accumulated aboveground biomass 1980-2011 observation (gC m^{-2})
0
5000
10000
15000
4000
6000
8000
Stem turnover (% year^{-1})
● 0
● 0.48
● 0.75
● 1
● 1.25
● 1.5
● 2
○ deciduous
△ evergreen

Figure 7 Comparisons between observed and modeled accumulated aboveground biomass 1980-2011 for (a) D-CLM4.5 allocation scheme; (b) D-Litton allocation scheme; (c) F-Evergreen allocation scheme; (d) F-Deciduous allocation scheme. We assumed different turnover rates for stem from 0 to 2% year-1. Turnover rate for stem in the model is 2% year-1. Dashed line is 1:1 relationship between observations and model. Observations (aboveground biomass estimates from tree-ring data) are from Dye et al. (2016) for the Ha1 and Ho1 sites, and following the methodology in Alexander et al. (under review) for the rest of sites.



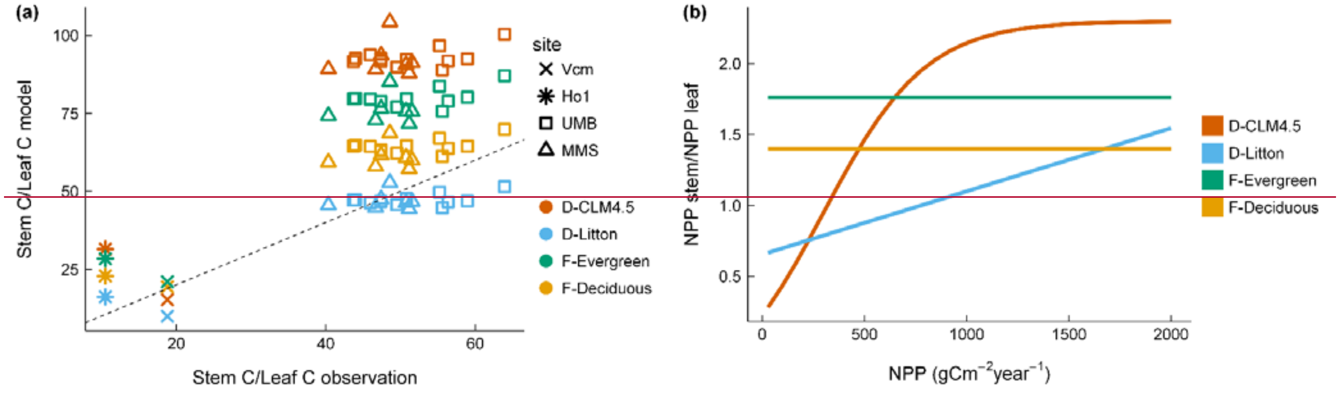
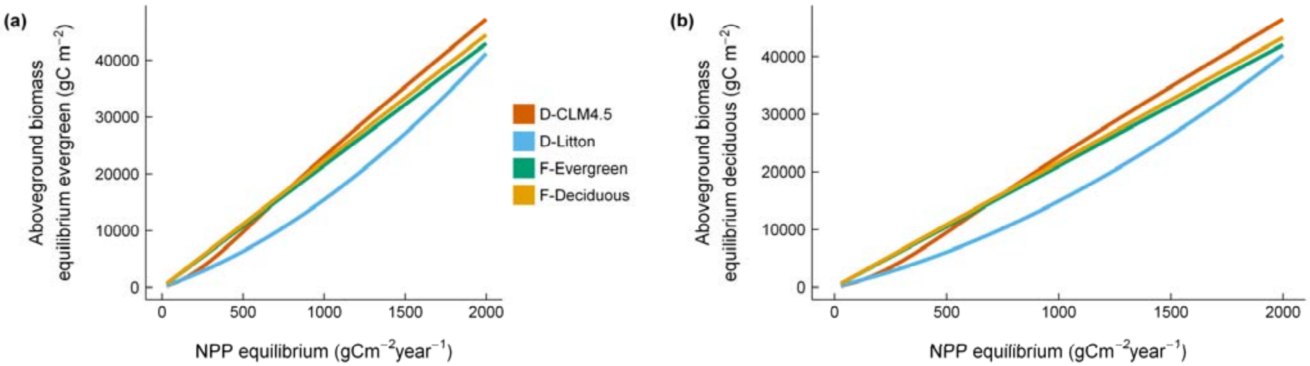


Figure 8 (a) Comparisons between Cstem/Cleaf ratio for the four C allocation schemes and AmeriFlux observations. (b) NPPstem/NPPleaf ratio for the different mean annual NPP values and C allocation schemes. In 8a, dashed line is 1:1 relationship between observations and model. Observations (Cstem and Cleaf) are from the AmeriFlux database.



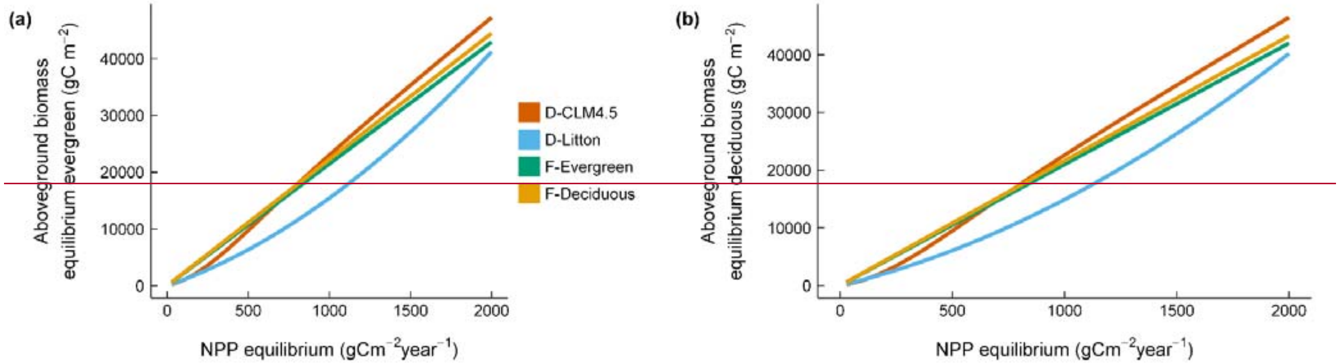


Figure 9 The C allocation scheme determines aboveground biomass C at equilibrium for (a) evergreen and (b) deciduous sites. For the deciduous sites, with NPP at equilibrium conditions, the D-Litton allocation scheme is closer to the observed aboveground biomass values in 1980 (see Fig. 5a).