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 remains in plant biomass 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 fixed C allocation scheme with two variants, 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.

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 sites. Understanding the controls of turnover will be critical to improving long-term C processes in LSMs.

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 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). 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 turnover times (e.g. stem) have a higher standing biomass than the plants that allocate a greater proportion of C to tissues with short 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.

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 (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 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) 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).

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, 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). 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, 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).

To quantify aboveground biomass at all of the sites, we surveyed each forest 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. 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.

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 (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:

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

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, we calculated the allometric parameters a_1, a_2 and a_3 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).

2.4 Alternative C allocation structures and parameterizations

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.

The alternative dynamic C allocation 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 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"). 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 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 parameterizations are shown in Table 2.

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 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):

$$SLA(x) = SLA_0 + mx \qquad (2)$$

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:

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

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).

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 Testing allocation schemes in CLM4.5

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 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).

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:

$$dB_i/dt = a_i NPP - u_i B_i$$

(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

5   rate we used equation (4) as a 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 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

10   over time based on different turnover rates with the aboveground biomass increments estimated from tree-ring data for our sites between 1980 and 2011.

3 Results

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

15   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).

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

20   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

25   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 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).

3.5 C allocation scheme and its effects on C_{stem}/C_{leaf} ratio and 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).

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 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, 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 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 CLM 4.5. 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

5   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

10   None of the allocation schemes simultaneously matched observed evergreen and deciduous forest 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

15   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

20   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).. 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

25   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 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 $Cm^{-2}year^{-1}$.

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

30   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). 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

5 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).

Although in reality, root function is 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 two separate functional trade-offs

10 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

15 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). 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).

20 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).

4.3 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

25 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 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) that adds an extra layer of complexity in diagnosing the impact of an incorrect representation of

30 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.

4.4 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, realistic C_{stem}/C_{leaf} ratios are produced in CLM4.5 at sites where the D-CLM4.5 NPP_{stem}/NPP_{leaf} ratio is similar to the values in the D-Litton scheme (Fig. 8). Any overestimation of allocation to stem is compounded because stem C has a longer turnover time that leaf C (Schulze et al., 2000; Xia et al., 2015; Song et al., 2016). 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 and allocation to leaf and root should increase, to match observed biomass.

4.5 C allocation scheme and 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). Aboveground NPP in the D-CLM4.5 scheme from the deciduous sites, including UMBS, Morgan Monroe, Harvard Forest, and Duke hardwoods (Megonigal et al., 1997; Curtis et al., 2002) was consistently 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). 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).

4.6 Conclusions and perspectives

Our results highlight the importance of evaluating the C allocation scheme and the stem turnover in LSMs using 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. We were unable to distinguish between the allocation schemes using eddy flux data alone.

Data on different carbon pools is sparse, but very useful in parameterizing allocation schemes. 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. Fixed allocation schemes 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. Stem turnover in CLM4.5 may approximate steady state conditions at large scales, and so 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 consistent with observations. It is possible to estimate equilibrium turnover rates from mean stand age derived from

tree ring estimates; this could be a promising technique to approximate the duration of carbon storage 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 the two schemes both use low NPP, regardless of cause, as a proxy for resource limitation (Fig. S1). Cohort representation in the model would enable ontogenetic changes in allocation but would not avoid the problem that these dynamic schemes cause sites 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). 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 shown in Table 2. The code modifications and parameter files for this paper are available 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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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	-92.2000	38.7441	Wood and	n.a.	n.a.	1980-2013	2006-2012	n.a.	n.a.

Site	Lon	Lat	Reference						
Ozark (MOz)			Gu, 2016						
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.

15 **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.

Allometric parameter	Definition (parameter name)	C allocation scheme			
		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	$\dfrac{0.25 - 8e^{-05} \times NPPann}{0.17 + 0.0001158 \times NPPann}$	0.27	0.27
a_3	Ratio of new stem: new leaf carbon allocation (stem_leaf)	$\dfrac{2.7}{1 + e^{-0.004 \times (NPPann - 300)}} - 0.4$	$\dfrac{0.17 + 0.0001158 \times NPPann}{0.26}$	1.76	1.4

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 (see Fig S1).

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% - ~20%	~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% - ~46%	~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) ~45-50% as mean values for temperate forests (Gill and Finzi, 2016)	~40% - ~34%	~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)

FIGURES
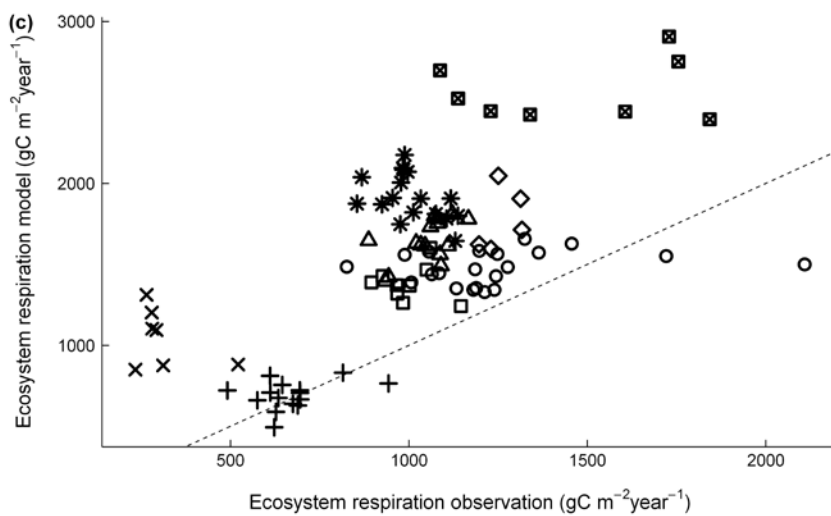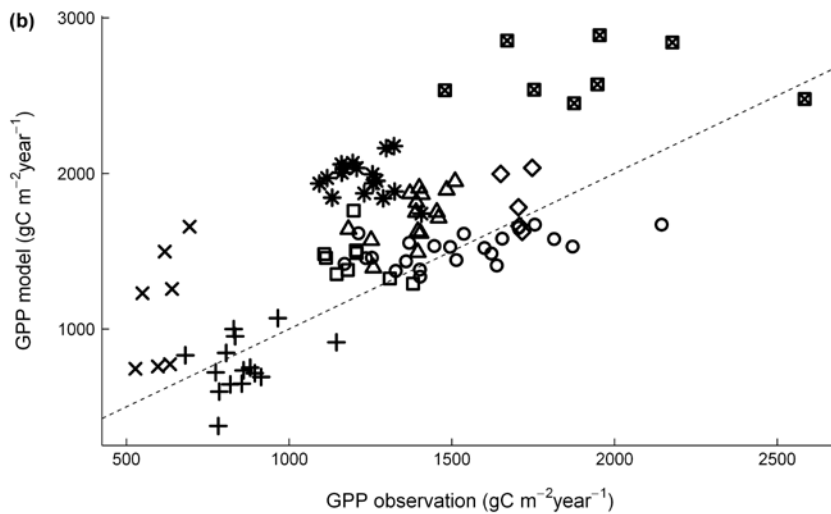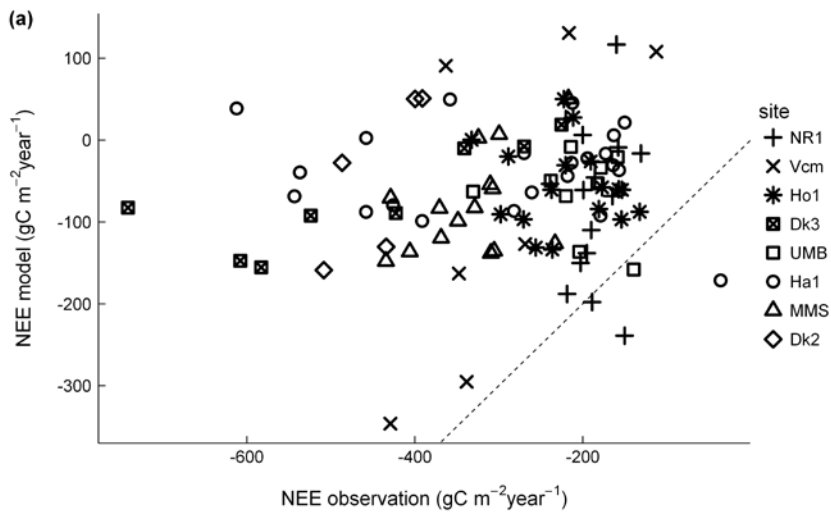
Figure 1 Comparisons between (a) NEE, (b) GPP and (c) ecosystem respiration in observations and model (D-CLM4.5). All fluxes were aggregated to annual. Dashed line is 1:1 relationship between observations and model. Observations are from the AmeriFlux L2 data product.
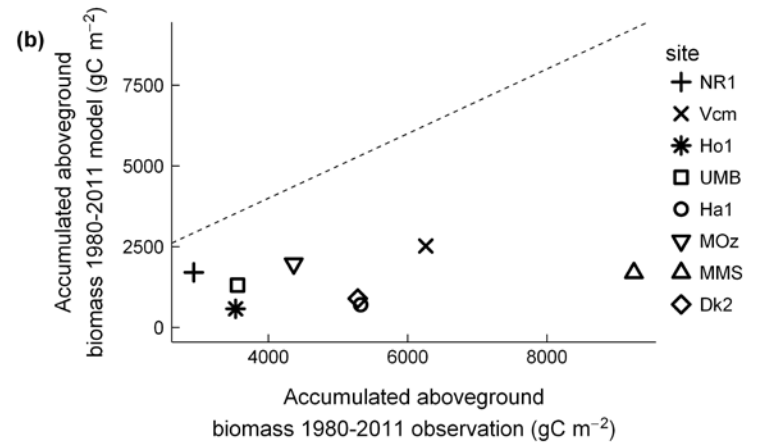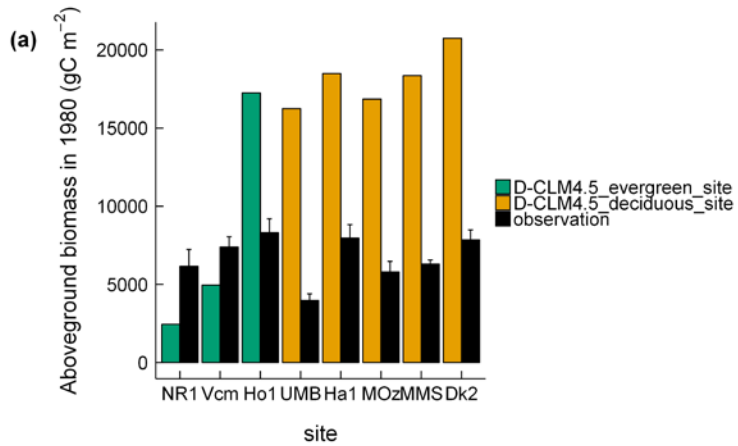
Figure 2 Comparisons between (a) observed and modeled (D-CLM4.5) aboveground biomass in 1980; (b) observed and modeld (D-CLM4.5) accumulated aboveground biomass between 1980-2011. Dashed line is 1:1 relationship between observations and model. Observations (estimates of aboveground biomass from tree-ring 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).
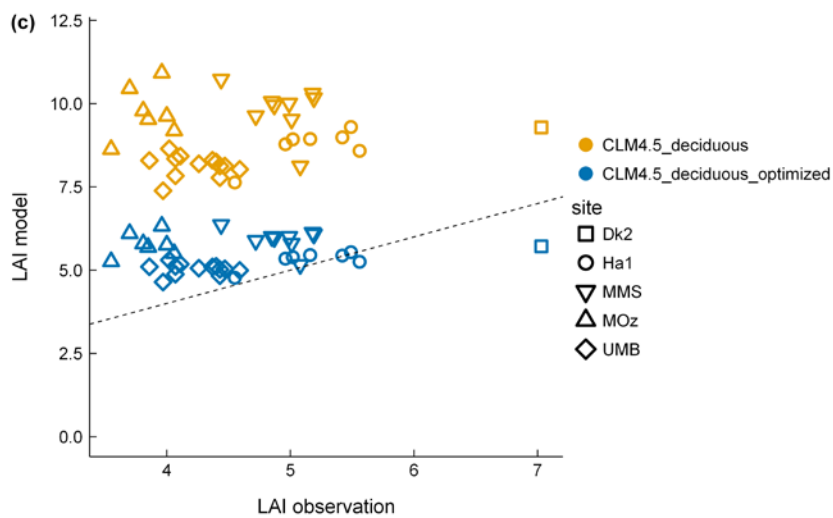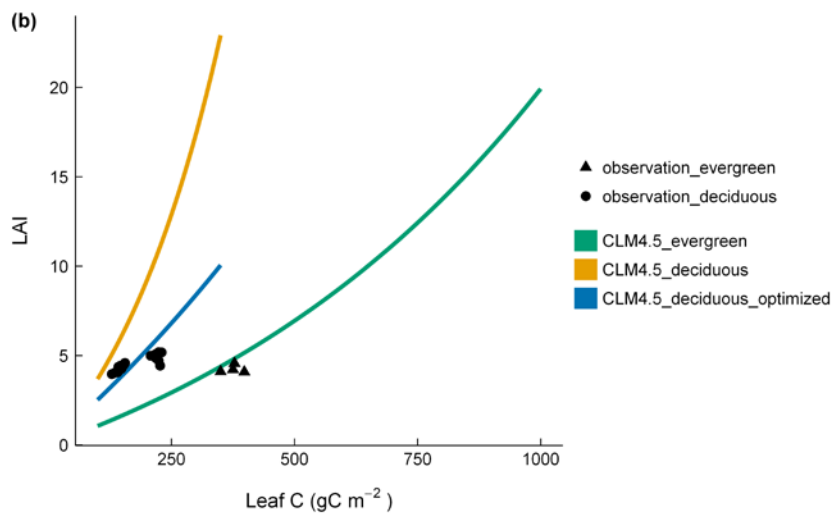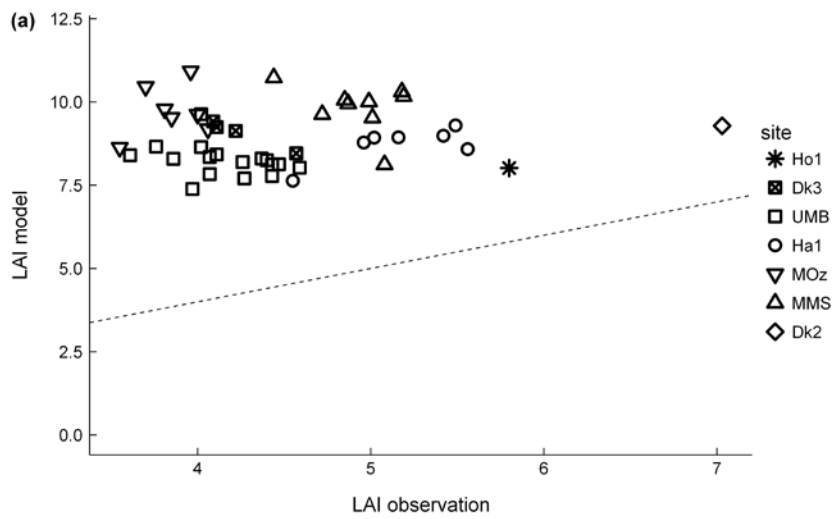
Figure 3 Comparisons between (a) LAI measured in-situ and LAI in the model; (b) Relationship between Leaf C and LAI in: CLM4.5 for deciduous forests, observations for deciduous forests, optimized Leaf C-LAI relationship for deciduous forests, CLM4.5 for evergreen forests, and observations for evergreen 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.
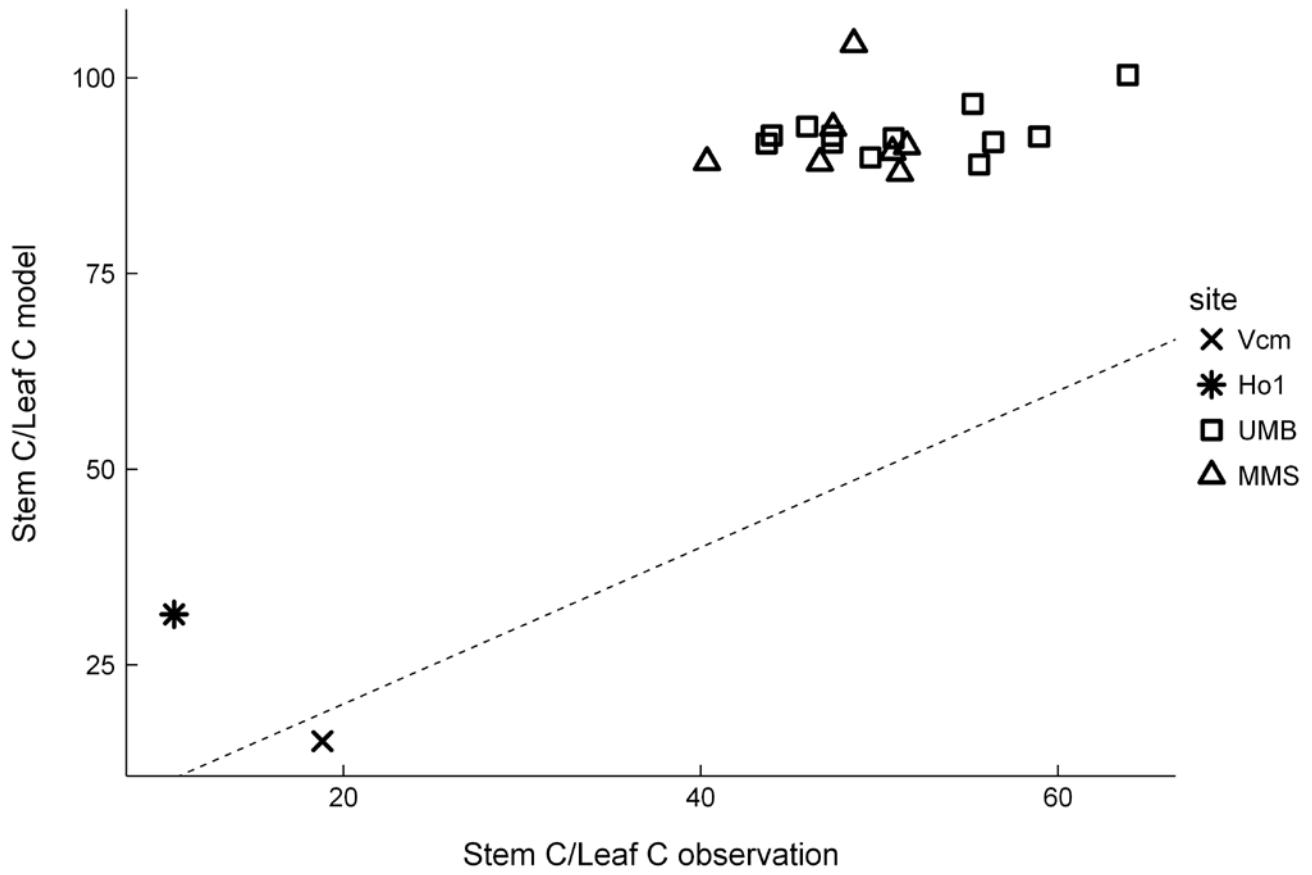
Figure 4 Comparisons between Cstem/Cleaf ratio for the D-CLM4.5 scheme and AmeriFlux observations. Dashed line is 1:1 relationship between observations and model. Observations (Cstem and Cleaf) are from the AmeriFlux database.
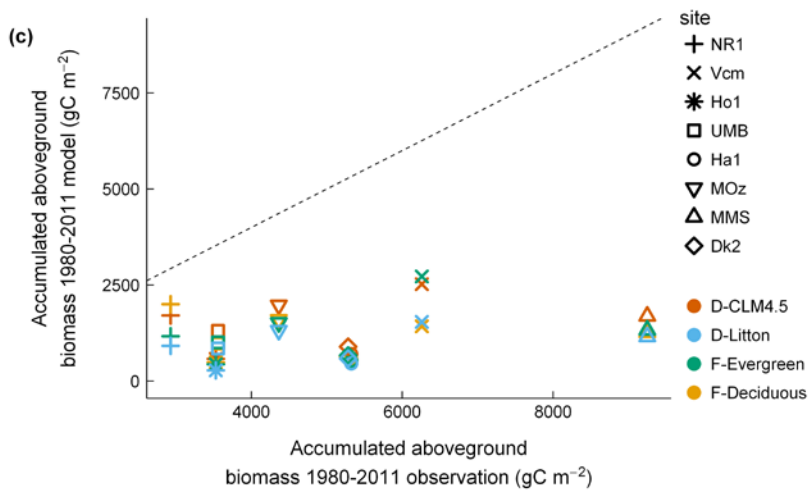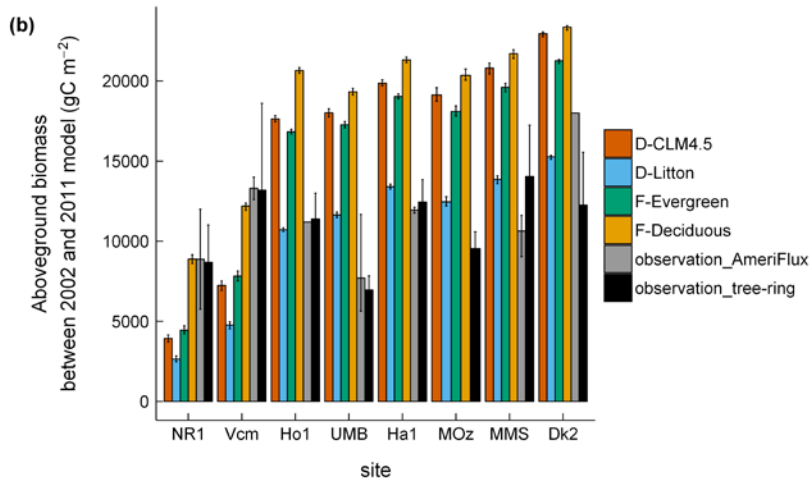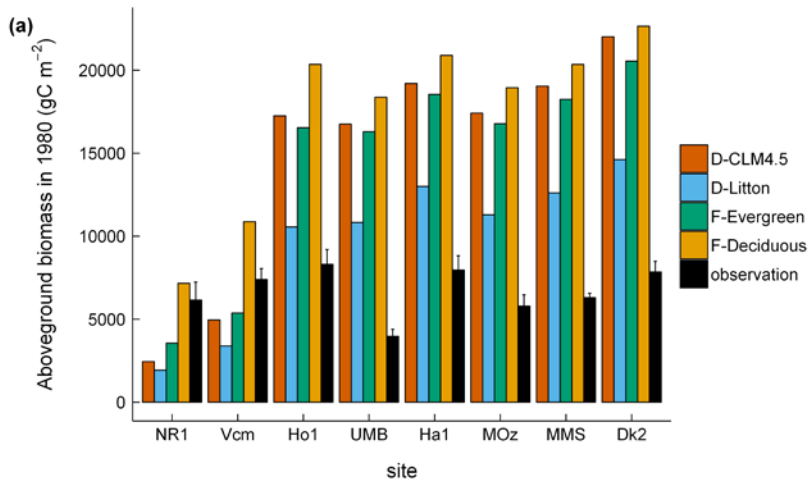
Figure 5 (a) Comparisons between observed and modeled aboveground biomass in 1980 for the four C allocation schemes; (b) Comparisons between mean observed and modeled aboveground biomass between 2002 and 2011 for the four C allocation schemes; (c) Comparisons between observed and modeled accumulated 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).
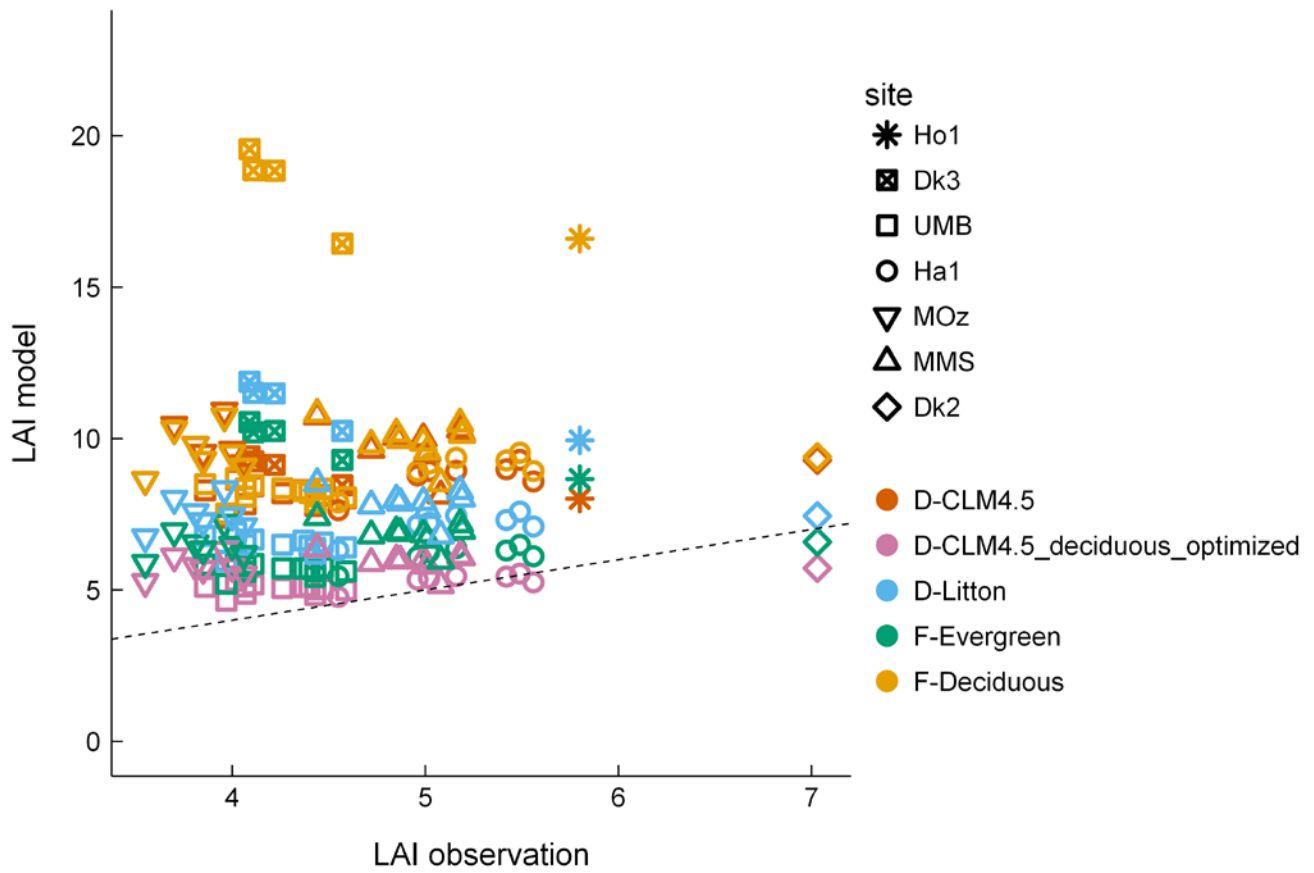
Figure 6 Comparisons between LAI measured in-situ and LAI in the model for the different C allocation schemes (D-CLM4.5_deciduous_optimized refers to the one with the optimized leaf C-LAI relationship for deciduous forests in D-CLM4.5). Dashed line is 1:1 relationship between observations and model. Observations (LAI measured in-situ) are from the AmeriFlux database.
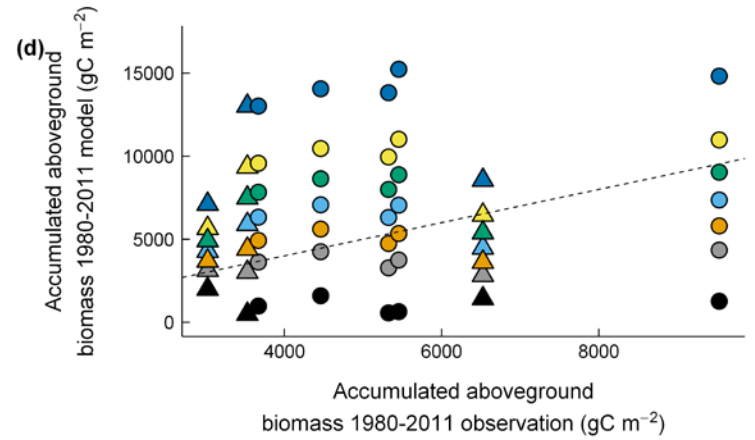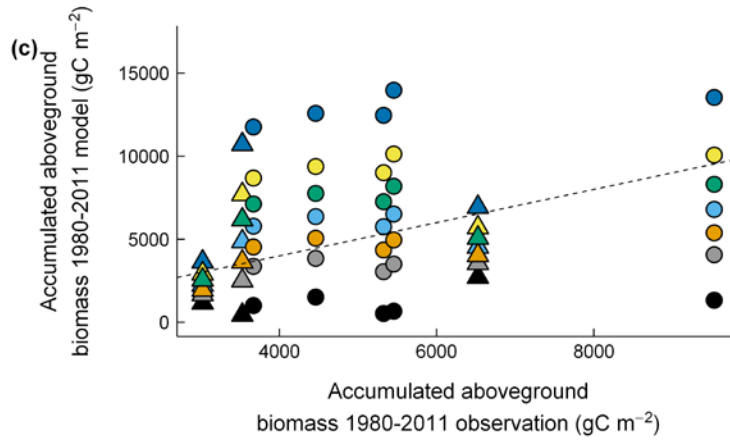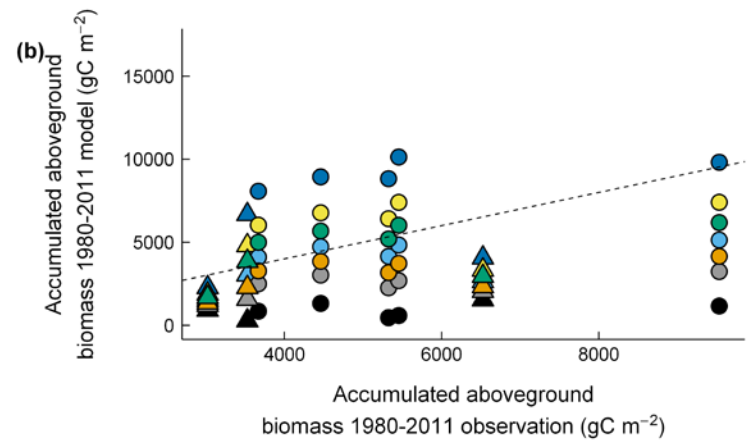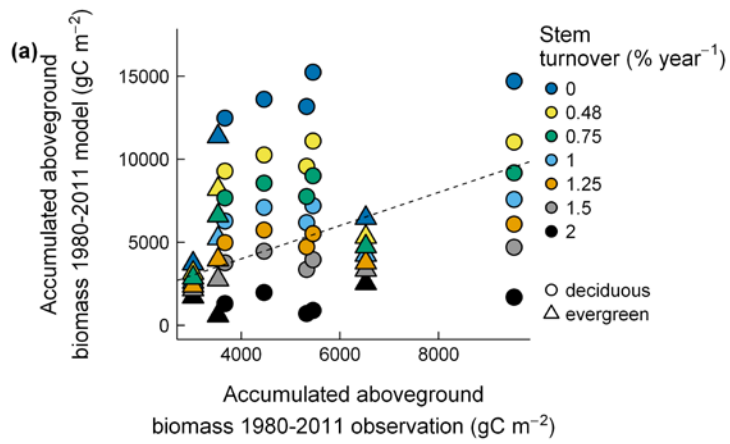
Figure 7 Comparisons between observed and modeled accumulated aboveground biomass 1980-2011 for (a) D-CLM4.5 allocation scheme; (b) D-Litton allocation scheme; (c) F-Evergreen allocation scheme; (d) F-Deciduous allocation scheme. We assumed different turnover rates for stem from 0 to 2% year-1. Turnover 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.
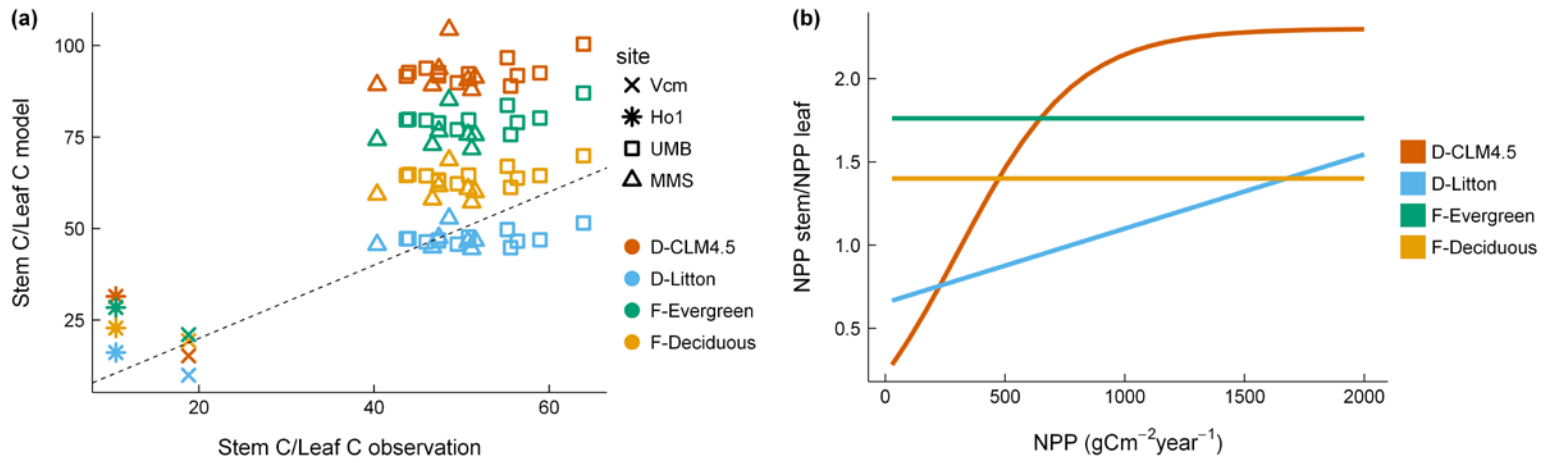
Figure 8 (a) Comparisons between Cstem/Cleaf ratio for the four C allocation schemes and AmeriFlux observations. (b) NPPstem/NPPleaf ratio for the different mean annual NPP values and C allocation schemes. In 8a, dashed line is 1:1 relationship between observations and model. Observations (Cstem and Cleaf) are from the AmeriFlux database.
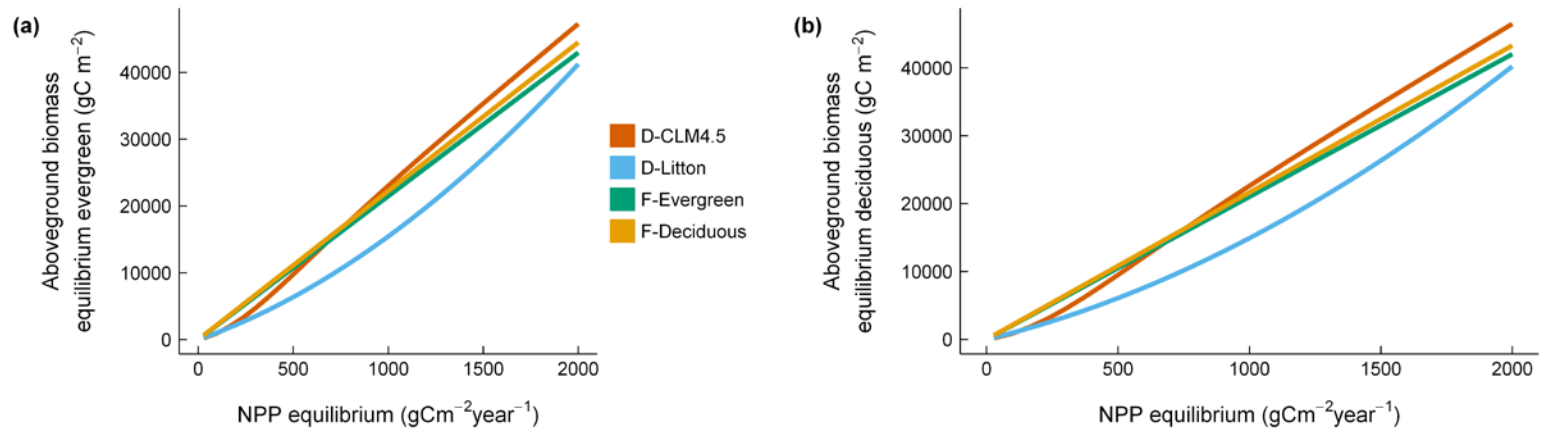
Figure 9 The C allocation scheme determines aboveground biomass C at equilibrium for (a) evergreen and (b) deciduous sites. For the deciduous sites, with NPP at equilibrium conditions, the D-Litton allocation scheme is closer to the observed aboveground biomass values in 1980 (see Fig. 5a).