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Variability of phenology and fluxes of water and carbon with observed and simulated soil moisture in the Ent Terrestrial Biosphere Model (Ent TBM version 1.0.1.0.0)

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Abstract

The Ent Terrestrial Biosphere Model (Ent TBM) is a mixed-canopy dynamic global vegetation model developed specifically for coupling with land surface hydrology and general circulation models (GCMs). This study describes the leaf phenology submodel implemented in the Ent TBM version 1.0.1.0.0, coupled to the carbon allocation scheme of the Ecosystem Demography (ED) model. The phenology submodel adopts a combination of responses to temperature (growing degree days and frost-hardening), soil moisture (linearity of stress with relative saturation), and radiation (light length). Growth of leaves, sapwood, fine roots, stem wood, and coarse roots is updated on a daily basis. We evaluate the performance in reproducing observed leaf seasonal growth as well as water and carbon fluxes for four plant functional types at five Fluxnet sites, with both observed and prognostic hydrology, and observed and prognostic seasonal leaf area index. The phenology submodel is able to capture the timing and magnitude of leafout and senescence for temperate broadleaf deciduous forest (Harvard Forest and Morgan–Monroe State Forest, US), C3 annual grassland (Vaira Ranch, US), and California oak savanna (Tonzi Ranch, US). For evergreen needleleaf forest (Hyytiäla, Finland), the phenology submodel captures the effect of frost-hardening of photosynthetic capacity on seasonal fluxes and leaf area. We address the importance of customizing parameter sets of vegetation soil moisture stress response to the particular land surface hydrology scheme. We identify model deficiencies that reveal important dynamics and parameter needs.

1 Introduction

Phenological timing remains a major weakness These models integrate biophysical of land surface dynamic global vegetation models (DGVMs) that are coupled to general circulation models (GCMs), and a primary cause of uncertainty in predicting the trajectory of global atmospheric CO_2 (Friedlingstein et al., 2006, 2014). Seasonal variation of vegetation foliage, i.e., leaf phenology, determines the timing and duration of the photosynthetically active canopy, influencing stomatal activity, surface albedo and surface roughness (Jolly and Running, 2004). Thus, it plays a crucial role in the exchange of water, energy and carbon between land and the overlying atmosphere. For example, an observational study in a deciduous forest in the Northeastern US showed that the interannual variability of gross primary productivity is associated with timings of leaf-out and leaf senescence (Goulden et al., 1996), and light-controlled leaf phenology was suggested as a key controlling factor responsible for increasing carbon and water fluxes from land to the atmosphere during the dry season in the Amazon rainforests (Hutyra et al., 2007; Kim et al., 2012). Phenology is also tightly connected to other ecosystem processes, exerting strong controls on the amount of assimilated carbon that is subsequently utilized for plant growth and reproduction. Kramer (2000) showed that phenology could have effects on the species composition of temperate-zone deciduous forests and the geographical distribution of species since difference in phenological response leads to difference in light availability and therefore growth in mixed species stands.

Given the strong interactions between phenology and other land surface and ecosystem processes, phenology has a potential to affect both weather and climate. Seasonal variation in vegetation characteristics have been shown to significantly influence summer precipitation and temperature in the US (Dirmeyer, 1994; Xue et al., 1996), and enhance or weaken the feedbacks between soil moisture and precipitation in the continental interior of North America depending on soil moisture conditions and season (Kim and Wang, 2007). Levis and Bonan (2004) demonstrated that the coupling between phenology and the atmosphere is critical for models to capture seasonal weather evolution. In addition, phenology is one of the vegetation traits most responsive to climate change (Badeck et al., 2004; Richardson et al., 2013). The seasonal cycle of measured atmospheric CO_2 concentration in Hawaii and Alaska shows advances of about 7 days in the timing of spring CO_2 uptake since the early 1960s, suggesting early beginning of the growing season in response to increases in temperature (Keeling et al., 1996). A number of ground- and satellite-based direct observations also show earlier spring leafout in response to climate change during the course of the 20th century due to earlier spring warming (Menzel, 2000; Stöckli and Vidale, 2004), and later spring leafout has also been detected (Bradley et al., 1999; Zhang et al., 2007). Tightly linked to phenology, plant carbon allocation, that is, distribution of assimilated carbon among the plant parts, also responds to environmental and climate conditions (such as increases in air temperature, changes in precipitation patterns and elevated atmospheric CO_2 concentration). For example, Pumpanen et al. (2012) observed that root biomass and the rate of photosynthesis for silver birch, Norway spruce and Scots pine seedlings increase with higher soil temperature, yet a simultaneous increase in both photosynthesis and respiration rates results in no change in net CO_2 exchange and total seedling biomass.

To incorporate the active role of vegetation phenology in climate modeling, terrestrial biosphere models (TBMs) or Dynamic Global Vegetation Models (DGVMs) have been developed and coupled to General Circulation Models (GCMs) (e.g., Foley et al., 1996; Sitch et al., 2003; Bonan and Levis, 2006; Cox, 2001; Dunne et al., 2013). These models integrate biophysical and biogeochemical processes and sometimes biogeography, allowing prediction of transient terrestrial ecosystem responses (Cramer et al., 2001; Friedlingstein et al., 2006). TBMs have been parameterized on the basis of local, regional, or global scale studies. Such models have been evaluated at continental and global scales in most cases, and it is has become common to evaluate the models at the individual field scale (e.g., Delire and Foley, 1999; Arora and Boer, 2005; Krinner et al., 2005; Kucharik et al., 2006; Friend et al., 2007; Stöckli et al., 2008; Bonan et al., 2011). Still, parameterizations for vegetation processes (such as phenology and carbon allocation) implemented in TBMs are often limited to local-scale derivations due to the lack of high-quality global scale observations of vegetation structure and function together with meteorological conditions. Kucharik et al. (2006) evaluated the Integrated Biosphere Simulator (Stephens and Kevin R. Gurney) (Foley et al., 1996) at AmeriFlux forest sites by comparing simulated vegetation structure, phenology, soil temperature and carbon and water exchange against their measurements. Arora and Boer (2005) evaluated the phenological timings as well as leaf area index and stem/root biomass of the Canadian Terrestrial Ecosystem Model for five plant functional types at field sites over the globe, including cold deciduous broadleaf trees in the Eastern US and Germany, dry deciduous trees in Mexico, evergreen broadleaf trees in Amazon, and deciduous needleleaf trees in Siberia. Stöckli et al. (2008, 2011) performed data assimilation of satellite-observed phenology to constrain parameters globally in the prognostic phenology model of Jolly et al. (2005). They encountered poorer skill with the timing of senescence and with the tropics, the arctic, and drought-induced phenology in Mediterranean ecosystems, where Jolly et al's atmospheric bioclimatic index did not capture perhaps belowground drivers or radiation sensitivity.

Richardson et al. (2012) conducted an inter-comparison of phenology predictions of eleven TBMs (and three biophysics models with prescribed phenology) at five deciduous broadleaf and five evergreen needleleaf Fluxnet (Baldocchi et al., 2001) sites as part of the North American Carbon Program. They found that, for deciduous forests, most consistently predicted an earlier onset of the growing season and later fall senescence than observed, resulting in over-prediction of gross primary productivity (GPP) by $+160\pm145\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$ during the spring transition period and $+75\pm130\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$ during the autumn transition period (13 and 8 % annual productivity, respectively); meanwhile, most models under-predicted the magnitude of peak growing degree day (GDD) sums, while those that explicitly or implicitly included a chilling requirement did relatively well in capturing the onset of LAI and GPP for deciduous and evergreen forests, compared to simple temperature threshold schemes. For the timing of deciduous autumn senescence and evergreen photosynthetic deactivation, temperature thresholds combined with a shorter photoperiod produced a range of success. Richardson et al. (2013) performed a further review of the state of phenology representation in DGVMs and conclude that more data in general are needed to obtain a mechanistic understanding of drivers of phenology and its feedbacks with climate to be able to advance beyond current paradigms.

This is a site-based model evaluation study for the Ent[1] Terrestrial Biosphere Model's (Ent TBM version 1.0.1.0.0. Enumeration is in order for different levels of dynamics and different physics versions available for each of these. In order, the digits denote: (1) Primary biophysics (leaf, soil biogeochemistry) and base release version (1: leaf biophysics as described in Schmidt et al., 2014; soil biogeochemistry described in this paper). (2) Canopy radiative transfer (0: two-stream as described in Schmidt et al. 2014; 1: ACTS model (Ni-Meister et al., 2010; Yang et al., 2010); (3) Leaf phenology (0: prescribed from satellite data; 1: prognostic, this paper); (4) Carbon allocation/growth (0: allocation with prognostic phenology, without structural growth, this paper; 1: allocation with structural growth). (5) Ecosystem dynamics (0: none; 1: Ecosystem Demography scheme).) coupled phenology/growth schemes. This evaluation is a necessary task before introducing prognostic phenology into global simulations coupled with a GCM atmosphere in order to enable modeling of interactive phenology and climate. We do not offer yet a new paradigm, but the phenological timing schemes provide a synthesis a variety of approaches in the literature to capture the full combination of climatological drivers thus far known to be essential for each type of phenology, and introduce some new functional representations to do so. These are coupled to growth algorithms from the Ecosystem Demography (ED) model (Moorcroft et al., 2001) that account for both the geometric and mass allometry of plant functional types.

In this paper, we describe the Ent TBM's phenology and allometry scheme coupled to the ED carbon allocation scheme, and evaluate their performance at Fluxnet sites (Baldocchi et al., 2001), focusing on seasonal and inter-annual variations of LAI and carbon and water fluxes. We compare site simulations using both observed soil moisture and that modeled by a land surface hydrology model coupled to the Ent TBM. The phenology schemes synthesize several observational data sets, combining both climate responses and a carbon balance approach, described in detail below. Here we evaluate the performance for temperate broadleaf deciduous forest, C3 annual grass-

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[1] Ent is not an acronym but the name of a sentient species of tree in J. R. R. Tolkien's fantasy novels, *The Lord of the Rings*.

land, evergreen needleleaf forest, and tree/grass savanna (mixed drought deciduous broadleaf and C3 annual grassland). Through these evaluations, we are interested in quantifying the accuracy of the current model at the site level, and we identify ecosystem processes needing further improvement, with regard to both plant growth dynamics and the representation of soil moisture.

2 Model descriptions

2.1 Land Surface Model (LSM) of the NASA GISS GCM

The Ent TBM can be run with observed soil moisture and temperature, and canopy temperature inferred from eddy flux measurements of sensible heat fluxes, or, given precipitation and air temperature, it can obtain modeled soil moisture, temperature, and canopy temperature, if run coupled to a land surface hydrology model. For the coupled mode, we use the land model of the National Aeronautics and Space Administration (NASA) Goddard Institute for Space Studies (GISS) general circulation model (GCM) (Schmidt et al., 2006). The NASA GISS GCM land hydrology consists of six soil layers down to 3.5 m depth based on Rosenweig and Abramopoulos (1997), with updates described in Schmidt et al. (2006, 2014). The land surface model (LSM) computes the fluxes of heat and water vapor to the atmosphere, and the energy balance of the soil and vegetation canopy. Surface runoff is calculated based on saturation and infiltration capacity of the upper soil layer. The underground runoff is computed according to a formulation of Abramopoulos et al. (1988), which takes into account the average slope and the density of underground sinks in the cell. When running the Ent TBM coupled to the GISS LSM, soil physics parameters are taken from the land surface mapped datasets of the GISS LSM.

2.2 Ent Terrestrial Biosphere Model (Ent TBM)

The Ent TBM is a standalone model developed specifically for coupling the fluxes of water, energy, carbon, and other trace gases between LSMs and GCMs. It is structured like the Ecosystem Demography (ED) model (Moorcroft et al., 2001) for simulating competition in mixed canopies and disturbance dynamics by representing vertical canopy structure through ensemble cohorts of identical individuals, and horizontal heterogeneity via subgrid patch communities. The specifications of canopy geometry and allometry of biomass pools are consistent with indvidual ellipsoidal crown geometry that is integrated with the coupled phenology/growth model. This paper presents simulations of seasonal variation in leaf area and mass and in fluxes of CO_2, water vapor, and sensible and latent heat of both transpiration and ground evaporation.

Figure 1 shows a conceptual diagram of the Ent model, and how it is coupled with a GCM (or off-line meteorological forcings) and an LSM. Ent's biophysics modules operate at the physical time step of the GCM or LSM. The photosynthetic uptake of carbon utilizes the well-known photosynthesis model of Farquhar et al. (1980) and Farquhar and von Caemmerer (1982) coupled with the stomatal conductance model of Ball and Berry (Ball et al., 1987), while Ent uses its own cubic solution for these coupled equations. Canopy radiative transfer is optionally modeled as in Friend and Kiang (2006) for homogeneous canopies, or as in Ni-Meister et al. (2010) and Yang et al. (2010) for clumped canopies. In this paper, in lieu of detailed site allometric and canopy structure data, we utilize the homogeneous canopy radiative transfer scheme. Carbon uptake is accumulated over a day so that carbon allocation to growth, phenological behavior, and mortality are updated once per day. An individual plant has distinct biomass pools, including a "labile" or carbohydrate reserve pool into which photosynthetic uptake and retranslocated carbon are accumulated; "active" pools consisting of foliage, fine roots, a reproductive pool, and, for woody plants, live sapwood, and "dead" pools consisting of dead stem wood and coarse roots. Autotrophic respiration is the sum of maintenance respiration as function of biomass and temperature, "activity growth respiration" as function of gross assimilation, and tissue growth respiration as a function of amount of new growth.

Ent takes its meteorological drivers and hydrological balance at the grid cell or catchment zone scale of the LSM and subgrid heterogeneity is represented as dynamic patches of vegetation communities, comprised of cohorts of plants that are ensembles of identical individuals (patch and community dynamics are not part of this study). The biomass pools and geometry of an individual woody plant are illustrated in Fig. 2 canopy conductances from each patch are summed to the grid cell or catchment zone level to couple with the atmosphere. Also, root density vertical profile distributions in Ent are used to calculate a depth-weighted average of soil moisture stress. These profiles are a modification of those in Rosenzweig and Abramopoulos (1997), with details given in the Appendix A.

The Ent TBM is designed to support a flexible number of plant functional types (PFTs). A parameter set for 17 PFTs has been developed, as listed in Table 1; however, we note that only a subset of these PFTs is evaluated here according to data availability, and the others must be approximated from the available similar types and theoretical/empirical relations from the literature. Following the rationale first advocated by Defries et al. (1995) and adopted by all vegetation models since then to varying degrees, Ent's PFTs distinguish photosynthetic pathway (C3 and C4), phenological type (evergreen, cold deciduous and drought deciduous), leaf type (broadleaf and needleleaf), growth form (tree, shrub, and herbaceous), and cultivated (herb crops). In addition, to better capture community dynamics in mixed canopies, if parameter sets are provided, Ent has the capability to distinguish early and late successional species through differences in leaf life span, following the approach of the Ecosystem Demography (ED) model (Moorcroft et al., 2001), which is based on leaf physiological relations found in Reich et al. (2007).

To capture total net carbon fluxes, the Ent TBM incorporates the code implementation of CASA' from the Community Land Model 3.0 (CLM 3.0, Randerson et al. 2009; Doney et al., 2006; code kindly supplied by Jasmin John), which is based on the Carnegie-Ames-Stanford-Approach of Potter et al. (1993). For the Ent TBM, the CASA' temperature and soil moisture responses of respiration were replaced with functions derived from new fits to field data of Del Grosso et al. (2005). Details are provided in the Supplement.

As mentioned earlier, the Ent TBM can be run in several different modes of coupling: (1) a stand-alone mode when the meteorological (e.g., radiation, precipitation, air temperature, air pressure, humidity and wind) and land conditions (e.g., soil moisture and soil temperature, and canopy temperature) are provided ("Ent-standalone"), (2) a mode coupled with a LSM for prognostic soil moisture and temperature given meteorological forcings ("Ent-LSM"), and (3) a fully coupled mode with an atmospheric GCM. Ent-standalone and Ent-LSM modes can be used for site-specific simulations or regional/global simulations using observed meteorological and soil moisture data.

The Ent TBM can also be run with different levels of vegetation dynamics turned on or off. In a biophysics-only mode, canopy structure and leaf area are prescribed, to simulate only fluxes of water vapor, carbon dioxide, and other trace gases. In an "active biomass" phenology-only mode, canopy stem structure is prescribed and static, while seasonal leaf and fine root dynamics are prognostic, and carbon that would have been allocated to stem and coarse root growth instead is allocated to litter. In a phenology-woody growth mode, in addition to leaf phenology, stem and coarse root growth are also enabled. In an ecosystem-dynamics mode, mortality and disturbance ensure that plants cannot grow indefinitely and are subject to succession and cover change (ecosystem dynamics are not covered in this paper).

2.3 Plant growth submodel

The plant growth submodel integrates phenological timing and allocation of carbon to growth and litter fluxes (background litterfall and seasonal), and respiration fluxes tied to tissue growth. The phenology scheme determines the phenological status of plants based on various environmental and climate rules studies, which determine budburst, frost-hardening, and senescence according to the phenological types of plants such as drought-deciduousness and cold-deciduousness. The carbon fixed over the course of each day from photosynthesis is accumulated and placed into a labile carbohydrate reserve pool. Carbon from the labile pool is then allocated once per day into different plant pools of foliage, sapwood, heartwood, fine root and coarse root as well as a reproductive pool according to empirical allometric relationships and leaf phenological status. In addition, tissue lost to background litter fluxes is replenished, and respiration fluxes are produced from growth of any tissue. A portion of litterfall is retranslocated back to the labile pool.

In the Ent TBM, the carbon allocation scheme takes a traditional approach of "static allocation", based on fixed allometric relationships between different pools. Adopted from approaches of the ED models (Moorcroft et al., 2001; Medvigy et al., 2009). Appendix B provides the descriptions of the ED allocation scheme, which treats "active" and "dead" biomass pools as bulk sinks, with modifications for Ent. We identified some deficiencies of the ED allocation scheme, and suggest future work for improvement in Sect. 5. Also note that Appendix C provides the biophysical, phenological and allocation parameter values used in this study.

Full prognostic growth entails growth of woody structure and the size of woody plants, which would require in addition full mortality and establishment dynamics so that there is not unlimited growth; these population and community dynamics will be presented in future papers. This study focuses on the "active biomass" performance of Ent given seasonal phenology, keeping woody structure static, allocating the amount that would have gone to growth instead to litterfall.

2.4 Phenology

Prognostic phenology models have been developed to predict phenological response of vegetation to climate based on empirical evidence, as a process-based treatment is still beyond current understanding (Sala et al., 2012). The commonly used climatic rule-based approach accounts for temperature, soil moisture, and day length controls on phenology, to predict leaf-on and leaf-off, with these controls often represented as a cumulative functions of one or several climate variables that reach an empirically defined threshold (White et al., 1997). Another approach is based on plant carbon status (Bonan et al., 2003), and predicts leaf-out and senescence on the basis of potential positive carbon assimilation, which is in turn is affected by temperature, moisture, and sometimes nutrient conditions.

All of the above approaches require empirical parameterization of the responses to climate, and a model scheme that is independent of PFT or geographical variation is still a research goal. Jolly et al. (2005) have proposed a very simple and promising bioclimatic Growing Season Index (GSI) for phenology based on linear relations to minimum temperature, photoperiod, and vapor pressure deficit (VPD, as a proxy for soil moisture), which seems to perform well compared to satellite observations at diverse sites. However, it performs less well for arid systems for which VPD may not be a good indicator of available deep soil moisture, and it is not able to capture any seasonal moisture or light sensitivity that has been observed in ntropical evergreen forests (Stockli et al., 2011).

The phenology scheme in the Ent TBM provides a synthesis, and combines the climatic rule-based approach and carbon balance for deciduous plants to determine the timings and rates of leaf out and leaf senescence by integrating several different modeling studies (Bonan et al., 2003; Botta et al., 2000; Foley et al., 1996; White et al., 1997). We present a diversity of PFTs, adding those with known behaviors that depart from common representations of cold, drought, or light responses. While globally applicable parameterizations of phenology may still be elusive, where available in the literature, we draw from wide surveys that attempt to extrapolate to the global scale.

For deciduous plants, we use parameterizations by Botta et al. (2000), who examined the possibility of extrapolating existing local models for leaf onset date to the global scale by retrieving leaf onset dates from the NOAA/AVHRR satellite normalized difference vegetation index (NDVI). They identified appropriate leaf onset date models and estimated their parameters for each biome, which are implemented in other ecosystem models (Medvigy et al., 2008). We also make use of parameterizations of White et al. (1997) who developed a regional phenology model for the US, predicting timings of leaf onset and offset for drought deciduous trees and grasses based on the satellite NDVI at the 20 km resolution. Their prediction errors are ∼ 1 week, and maximum expected errors are 10–14 days.

For evergreen vegetation, the Ent TBM includes frost-hardening for boreal evergreen plants. The frost-hardening (also called winter cold-hardening) involves physiological changes to protect the plant from chilling injury and freezing injury, leading to a downgrading of leaf photosynthetic capacity as well as tissue turnover and respiration. Coniferous vegetation in the boreal zone has a clear annual cycle of photosynthetic activity, with photosynthesis low or zero during the winter, increasing during the spring, peaking during the summer, and decreasing during the fall. While part of the cycle is due to direct responses to PAR and air temperature, the inherent photosynthetic capacity of needles also changes (Makela et al., 2004). Therefore, the models that do not account for cold-hardening and de-hardening will over-predict the uptake of carbon by photosynthesis for boreal systems during the late fall through early spring. This study implements a frost-hardening algorithm based on Hanninen and Kramer (2007), Makela et al. (2006) and Repo et al. (1990), who developed a model of the frost-hardiness of the stems of Scots pine seedlings.

In the Ent TBM, several "phenological factors", ϕ_x, as well as physiological stress factors, β_x, are calculated for seasonal environmental cues from various climate measures x. These include air and soil temperature history (cumulative number of growing degree days and of chilling days), day-length and soil moisture. The phenological factors control the allocation of assimilated carbon, while the physiological stress factors affect the efficiency of carbon uptake, and all range from 0 to 1 on a daily basis. Different rules apply to the different PFTs, according to phenotype (woody plant cold-deciduous, cd, drought-deciduous, dd, evergreen, ev, tropical radiation phenology, tr; and cold deciduous herbs, c, whether annual or perennial).

From combinations of the above factors, the Ent TBM determines an overall "phenological status," Phenostatus$_\text{p}$, where p is the phenotype; this status indicator controls the timing and rate of carbon transfer between the labile and active carbon pools and hence the seasonal variation in leaf area index (LAI), fine roots, and sapwood. For plants with seasonal leaf-out and senescence, $\text{Phenostatus}_\text{p}$ is 1 for the leaf-off season, 2 for the leaf-up period, 3 for the peak foliage period, and 4 for the senescent period. For evergreen plants, $\text{Phenostatus}_\text{p}$ is a constant of 1, but seasonal variation in photosynthetic capacity is subject to frost-hardening and light controls, treated as a physiological stress factor. Below we itemize these variables and equations in the Ent phenology scheme.

2.4.1 Seasonal day length

The trend in length of day (ld) is used to determine which season it is, or, rather, which half of the year it is. If day length is decreasing, then it is the latter half of the year, and “fall” may be allowed to commence, depending on other climate variables of phenological factors.

2.4.2 Cold deciduous woody plants

During the winter, the phenological status of cold-deciduous trees and shrubs, $\text{Phenostatus}_\text{cd}$, is 1, for no foliage. Leaf-out ($\text{Phenostatus}_\text{cd} = 2$) occurs once the cumulative number of growing degree days (GDD) exceeds its critical number (GDD_crit), which is determined with a function of cumulative number of chilling days (NCD) (Botta et al., 2000). The 10 day running average of air temperature (T_{10}) is used to calculate GDD and NCD on a daily basis with the base temperature (T_base) of 5 °C as follows:

$$\text{GDD} = \max \sum (0, T_{10} - T_\text{base}). \tag{1}$$

$$\text{NCD} = \text{NCD} + 1 \ \text{if} T_{10} < T_\text{base}. \tag{2}$$

GDD and NCD are reset to be zero at the beginning of the winter season. The function for $\mathrm{GDD}_{\mathrm{crit}}$ is expressed as follows:

$$\mathrm{GDD}_{\mathrm{crit}} = \mathrm{GDD}_{\mathrm{intercept}} + \mathrm{GCC}_{\mathrm{slope}} \exp(\mathrm{NCD}_{\mathrm{multi}} \cdot \mathrm{NCD}), \tag{3}$$

where the constant values of $\mathrm{GDD}_{\mathrm{intercept}}$, $\mathrm{GDD}_{\mathrm{slop}}$ and $\mathrm{NCD}_{\mathrm{multi}}$ are provided in Table 2.

Once leaf-out starts, trees take a number of degree days ($\mathrm{GDD}_{\mathrm{length}}$) to reach the phenologically unconstrained status (Foley et al., 1996). We introduce an approach to scale the departure of GDD from $\mathrm{GDD}_{\mathrm{crit}}$ with $\mathrm{GDD}_{\mathrm{length}}$, and thus ϕ_{GDD} ranges from 0 to 1:

$$\begin{aligned} \varphi_{\mathrm{GDD}} &= \frac{\mathrm{GDD} - \mathrm{GDD}_{\mathrm{crit}}}{\mathrm{GDD}_{\mathrm{length}}} && \text{when } \mathrm{GDD} < \mathrm{GDD}_{\mathrm{crit}}, \\ \varphi_{\mathrm{GDD}} &= 0 && \text{otherwise.} \end{aligned} \tag{4}$$

When $\phi_{\mathrm{GDD}} = 1$, then the $\mathrm{Phenostatus}_{\mathrm{cd}}$ switches to 3, peak foliage. Full or peak foliage may also occur when carbon allocation to foliage reaches the maximum supported by the available sapwood.

Fall senescence ($\mathrm{Phenostatus}_{\mathrm{cd}} = 4$) can commence in response to shortening day length (“fall”) and decreased air temperature, in a modification of White et al. (1997) and Jolly et al. (2005). Leaves start dropping once air temperature or day length decreases down to threshold values (i.e., T_{max} and $\mathrm{Id}_{\mathrm{max}}$); full senescence finally occurs when air temperature or day length decrease further down to the minimum thresholds (i.e., T_{min} and $\mathrm{Id}_{\mathrm{min}}$). The phenological factor with respect to air temperature, ϕ_{T}, is:

$$\begin{aligned} \varphi_{\mathrm{T}} &= \min\left(1, \frac{T_{10} - T_{\mathrm{min}}}{T_{\mathrm{max}} - T_{\mathrm{min}}}, \frac{\mathrm{Id} - \mathrm{Id}_{\mathrm{min}}}{\mathrm{Id}_{\mathrm{max}} - \mathrm{Id}_{\mathrm{min}}}\right) && \text{when } T_{10} < T_{\mathrm{max}} \text{ or } \mathrm{Id} < \mathrm{Id}_{\mathrm{max}}, \\ \varphi_{\mathrm{T}} &= 0 && \text{otherwise.} \end{aligned} \tag{5}$$

T_{max}, T_{min}, $\mathrm{Id}_{\mathrm{max}}$ and $\mathrm{Id}_{\mathrm{min}}$ are constants, with values provided with references in Table 2.

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2.4.3 Cold deciduous herbaceous plants

Phenological status of cold-deciduous (annual or perennial) herbaceous plants, $\text{Phenostatus}_\text{c}$, is well captured with functions based on soil temperature (TS), while that of cold-deciduous woody plants is with air temperature (White et al., 1997). Similarly to Eqs. (1) and (4) for cold deciduous trees, the soil growing degree days (SGDD) of soil temperature (TS_{10}) is calculated with the base temperature constant (TS_base) of 0 °C. Grasses generate leaves once SGDD exceeds its PFT-dependent critical number (SGDD_crit) and the phenology factor for SGDD, ϕ_SGDD, becomes 1 or greater, as follows:

$$\begin{aligned} \varphi_\text{SGDD} &= \frac{\text{SGDD} - \text{SGDD}_\text{crit}}{\text{SGDD}_\text{length}} && \text{when SGDD} > \text{SGDD}_\text{crit}, \\ \varphi_\text{SGDD} &= 0 && \text{otherwise.} \end{aligned} \qquad (6)$$

While White et al. (1997) derived SGDD_crit as a logistic function of mean annual soil temperature, here we simplify it with three different numbers for different grass types as provided in Table 2. The parameters for ϕ_SGDD were fit to observations at Barrow, Alaska, for arctic C3 grass; the values for C3 and C4 grasses are drawn from White et al. (1997).

Grasses begin fall senescence in response to decreased soil temperature. Leaves start dropping once soil temperature decreases down to a given threshold, TS_max; grasses complete senescence when soil temperature decreases further down to the critical threshold, TS_min:

$$\begin{aligned} \varphi_\text{TS} &= \min\left(1, \frac{\text{TS}_{10} - \text{TS}_\text{min}}{\text{TS}_\text{max} - \text{TS}_\text{min}}\right) && \text{when } \text{TS}_{10} < \text{TS}_\text{max}, \\ \varphi_\text{TS} &= 0 && \text{otherwise.} \end{aligned} \qquad (7)$$

See Table 2 for constant values of TS_max and TS_min.

2.4.4 Drought deciduous woody and herbaceous plants

Drought deciduousness is determined based on a 10 day running average of the physical time step (~ half-hourly) plant water stress factor β. This factor is the same used to scale stomatal conductance for water stress, and is determined by a linear response between PFT-dependent critical relative soil moisture (volumetric soil moisture/saturated volume) points for the plant, at which water stress begins, s_*, and at which wilting occurs, s_{wilt}, (Rodriguez-Iturbe et al., 2001):

$$\beta = \frac{S - S_{\text{wilt}}}{S_* - S_{\text{wilt}}}. \tag{8}$$

$\beta = 1$ when the plant is unstressed, and $\beta = 0$ at the wilting point. For 6 soil layers in the LSM, β is calculated for the soil moisture in each layer, and averaged weighted by layer thickness and relative root mass fraction, giving the overall β experienced by the plant.

The phenological factor for water stress, φ_β, is determined by a linear response to the 10 day running average (Foley et al., 1996) of water stress, β_{10}, to $\beta_{\max}$ and $\beta_{\min}$, which represent similarly 10 day running averages of water stress experienced before the onset of drought-induced senescence and at full senescence:

$$\varphi_\beta = \left(\frac{\beta_{10} - \beta_{\min}}{\beta_{\max} - \beta_{\min}}\right)^{\beta_{\text{resis}}}. \tag{9}$$

When β_{10} goes below a minimum ($\beta_{\min}$), plants completely senesce in response to drought ($\varphi = 0$); when β_{10} is above a maximum ($\beta_{\max}$), plants do not experience drought ($\varphi = 1$); when β_{10} is between $\beta_{\min}$ and $\beta_{\max}$, the sensitivity of plant to water availability is controlled by the resistance factor (β_{resis}). The values of s_*, s_{wilt}, $\beta_{\min}$, $\beta_{\max}$ and β_{resis} are provided in Table 2.

2.4.5 Frost-hardening in evergreen cold-climate plants

Boreal plants undergo winter frost-hardening, which involves physiological changes to protect the plant from chilling injury and freezing injury. Following Repo et al. (1990), the state of frost hardiness S_h (°C) is modeled as follows:

$$\frac{\mathrm{d}S_\mathrm{h}}{\mathrm{d}t} = \frac{1}{\tau}[(a \cdot T_{10} + b) - S_\mathrm{h}]. \tag{10}$$

where τ is a PFT-specific time constant, and the term $a \cdot T_{10} + b$ is the stationary frost hardiness, where a and b are PFT-specific parameters for the linear relationship between stationary frost hardiness and air temperature (Hanninen and Kramer, 2007). S_h can be thought of as an aggregated measure of the state of the physiological leaf processes that determine the photosynthetic capacity (Makela et al., 2004).

The state of frost hardiness is then used to adjust the maximum photosynthetic capacity $V_{\mathrm{c}_\mathrm{max}}$, which is an approach similar to the work of Makela et al. (2006). However, we convert from S_h to a dimensionless factor that can take values from 0 to 1. This frost hardiness factor f_frost, is expressed as:

$$f_\mathrm{frost} = \frac{1}{S_\mathrm{h,\,max}}(S_\mathrm{h} - T_0). \tag{11}$$

where T_0 is a threshold value of cumulative mean temperature at which photosynthesis starts and $S_\mathrm{h,\,max}$ is the maximum value of S_h (see Table 2 for constants). We implement the first-order Euler scheme to solve Eq. (10) and the resulting f_frost is used to adjust $V_{\mathrm{c}_\mathrm{max}}$.

3 Experiments

We performed a series of numerical experiments with Ent in different model modes in order to evaluate leaf seasonal dynamics, including leaf phenology and related water and carbon fluxes. We performed simulations for each site with observed soil moisture (hereafter denoted "Ent" mode), and LSM modeled soil moisture ("LSM" mode); and with observed LAI (without allocation of assimilated carbon to growth) ("oveg") and dynamically modeled LAI (via carbon allocation) ("dveg"), giving four experiments, Ent-oveg, Ent-dveg, LSM-oveg, and LSM-dveg (Table 3). In the biophysics-only mode, the observed LAI is prescribed and related active carbon allocations are calculated according to that LAI. In the "active biomass" phenology mode, the leaf phenology and active carbon allocation are dynamically simulated. The Ent TBM was evaluated at the following Fluxnet sites: cold deciduous broadleaf forests at Morgan Monroe State Forest (MMSF), Indiana, US and Harvard Forest, Massachusetts, US; C3 annual grassland at the Vaira Ranch, California, US; drought deciduous broadleaf oaks at the Tonzi Ranch, California, US; and evergreen needleleaf forest at Hyytiala, Finland (Table 4). For MMSF and Harvard Forest, the model was forced with 6 and 9 years' worth of drivers, respectively. In these two sites, continuous soil moisture measurements throughout the rooting depth were not available, so only Ent-LSM simulations were performed. For Vaira, Tonzi and Hyytiala, the model was forced with a year's worth of tower-measured meteorological drivers as well as observed soil temperature and moisture.

For the Ent vs. LSM simulations for annual grass phenology, it was necessary to tailor the soil moisture stress parameterst to the different metrics of soil moisture. The phenological timings of grasses depend on the soil moisture condition while an LSM-derived soil moisture is a model-specific index of soil wetness, not a physical quantity that can be directly validated with field measurements (Koster et al., 2009). The thresholds for the root water stress factor (β in Eq. 8) that was used to model drought-deciduous behavior of grasses (volumetric soil moisture at onset of stress and at wilting point) were derived from the observed soil moisture and fluxes, such that these parameters were in a sense tuned to the site as well as to the type of soil moisture measurement. In this study, we therefore tuned the parameters for LSM to better capture the phenological behaviors.

For diagnostics for model performance, we examined observed monthly LAI, and monthly sums of gross primary production (GPP), ecosystem respiration (R_E), net ecosystem productivity (NEP = GPP – R_E) and total evapotranspiration (ET). For potentially water-limited sites, we examined the modeled volumetric soil moisture and Ent's plant water stress factor. For observed R_E, the values are inferred from nighttime respiration and its sensitivity to soil temperature, while the modeled values result from both autotrophic and soil respiration. Soil carbon as a driver of soil respiration was initialized from site measured soil carbon, with litterfall from the model as inputs on a daily basis (soil carbon was not driven to equilibrium).

4 Results

4.1 Cold deciduous woody plants

4.1.1 Phenology

We evaluated the model performance for cold deciduous woody plants at two sites, Morgan–Monroe State Forest (MMSF) in Indiana, and Harvard Forest.

Figure 3 and Table 5 show the simulated variations of the leaf elongation factor (ratio of LAI to the maximum LAI of the year) in comparison to observations. First, it is clear that gradual nature of changes in LAI during spring and fall were not captured in the model because the phenology factor serves as an on-/off cue between environmental thresholds, while growth rate with the ED scheme is limited only by carbon availability, which is generally not limiting in trees (Sala et al., 2012). At both sites, the inter-annual variations of leaf-on timings in the spring were better captured than those of the leaf-off timings in the fall. At Harvard Forest, the dates with the elongation factor of 0.5 in spring showed a correlation coefficient (R) of 0.85 and a root mean squared error (RMSE) of 3.00 days, while the dates with an elongation factor of 0.5 in fall showed R of 0.04 and an RMSE of 15.09 days.

4.1.2 Fluxes

In MMSF, the predicted NEP reasonably followed the observed NEP (Schmid et al., 2000; Dragoni et al., 2007) with correlation coefficients ranging from 0.86 to 0.94, while the peak NEP in summer was slightly underestimated compared to the observed (Fig. 4 and Table 6). However, the partitioning of NEP into GPP and R_E were both larger in the model compared to the Fluxnet data product.

In Harvard Forest, the default simulations (LSM-dveg and LSM-oveg) showed underestimated NEP compared to the flux tower observations due to simulated water stress (Fig. 5). As it is known that the cold deciduous plants in Harvard Forest do not experience water stress, no root water stress ($\beta = 1$ in Eq. 8) is assumed for additional simulations (LSM-dvegNS and LSM-ovegNS). With the prescribed water stress factor of 1, the model captured the observed NEP reasonably and overestimated GPP and RE compared to observations, similar to MMSF simulations.

The ET in both LSM simulations were overestimated compared to the flux tower observations in MMSF and Harvard Forest. These discrepancies might be attributed to both model and data errors. In the model, the higher estimated GPP (although we cannot confirm this) may lead to the overestimated ET to some extent, since higher photosynthesis corresponds to higher canopy conductance and hence more transpiration. In addition, it is well known that eddy flux measurements do not close the energy balance (Wilson et al., 2002). The sum of latent, sensible and ground heat is generally smaller than the net shortwave radiation, which is often caused by measurement errors of latent heat (i.e., ET) and sensible heat (Aranibar et al., 2006), leading to imbalance in measured net radiation of as much as 20 %. The LSM simulated peak ET is within 70 % of measurements.

4.2 Drought deciduous herbaceous plants

4.2.1 Phenology

We evaluated the model performance for drought deciduous herbaceous and woody plants at two sites, the Vaira Ranch and Tonzi Ranch in California. The Vaira Ranch is on C3 annual grassland ecosystem, and the Tonzi Ranch is on an oak/grass savanna ecosystem, close by the Vaira Ranch. At both sites, the timings of C3 annual grasses' green-up and senescence are mainly controlled by soil moisture in a Mediterranean climate, in which precipitation and temperature are seasonally out of phase. Grasses are active during the winter rains, but slightly cold limited in activity, then with spring warming, growth and activity increase, followed by rapid senescence that closely tracks soil moisture dry-down in the late spring, and full senescence by the beginning of the dry, hot summer. At the Tonzi Ranch, the oaks have the opposite seasonality to the C3 grasses. The oaks leaf out at the end of winter rains around March, when grasses have reached their peak, and then the trees start gradually losing their leaves around the beginning of July due to drought stress. Their complete leaf-off appears to be cued by November cold or fog, but this latter cue would not be considered a stress factor and is not well understood.

At both Vaira and Tonzi Ranches, Ent-dveg and LSM-dveg reasonably captured these phenological timings (Fig. 6). The growth rate for herbaceous plants (i.e., increase in LAI during the growing season) reflected the net carbon assimilation each day, and slightly lagged observations at the beginning of the growing season in the model. Simulated soil moisture clearly decreased much more slowly in LSM-dveg during the late spring dry-down compared to the observed volumetric soil moisture that was used to drive Ent-dveg.

4.2.2 Fluxes

For carbon fluxes at the Vaira Ranch, the model simulations generally followed the observed seasonality, although the late leaf-off in LSM-dveg leads to overestimation of carbon uptake significantly, and the observed abrupt increase in R_E in the beginning of the growing season was not captured in all cases (Fig. 7 and Table 6). Xu and Baldocchi (2004) suggest that the large pulse of R_E is the consequence of quickly stimulated microbial activity in decomposition after rain events during the dry season. In the Ent TBM, the soil moisture dependency of decomposition is parameterized as a linear function of soil saturation percent (S) with a plateau when $S > S_{opt}$ (70 %). This response is derived from raw data of soil respiration responses to temperature and moisture in grassland and winter wheat soils from Del Grosso et al. (2005). Most likely, the damped response is because the Ent TBM does not model a separate litter layer on top of the soil, and litter quality may not be well parameterized to allow for fast turnover. As this is a soil model issue, further analysis is worthy of a separate study.

At the Tonzi Ranch, the simulated NEP resulted in an RMSE of ~ 0.4 compared to the observed flux (Fig. 7 and Table 6). During the late spring soil moisture dry-down period, the grasses senesced and the oaks retained their leaves. The oaks started reducing their carbon assimilation due to water stress, as the Ball–Berry slope (m; slope for stomatal conductance) is scaled linearly with the water stress in the model. In reality, the oaks at Tonzi adjust their osmotic potential to maintain their water potential, so their leaf water potential is not linear with soil moisture (Kiang, 2002). Therefore even with the reasonable LAIs in Ent-oveg, Ent-dveg and LSM-dveg, the underestimated NEP and GPP in the summer are to be expected, lacking a non-linear response function. Meanwhile, the overestimated LAI in LSM-dveg clearly led to overestimated NEP and GPP. Furthermore, we found the soil biogeochemistry model did not capture the soil respiration pulses after the rainfall, as in Vaira.

The model reasonably captured the observed seasonality of ET with an R of ~ 0.9 in Vaira and ~ 0.8 in Tonzi, while the R values for carbon fluxes were much lower.

The water fluxes were not much different between LSM-dveg vs. LSM-oveg, while the carbon fluxes were significantly different due to different LAIs between the two. The differences in transpiration, resulting from different LAIs, were compensated by evaporation, leading to a relative small discrepancy in ET between the two experiments. Furthermore, the amplitudes (difference between the maximum and the minimum) of ET were clearly damped in the model, with underestimated peak fluxes during the growing season and overestimated fluxes during the non-growing season. In particular, the noticeable amount of ET occurred during the non-growing season in Vaira, suggesting the partitioning of ET into evaporation and transpiration should be further investigated.

4.3 Frost-hardening in evergreen cold-climate plants

4.3.1 Phenology

At Hyytiala, the vegetation type is boreal evergreen needleleaf (Scots pine), and the phenological behavior of interest is frost-hardening, which lowers photosynthetic capacity in the winter. Variation in LAI is modeled solely via the plant's carbon balance and not with any other phenological cues for growth or senescence. The seasonal variation of LAI at this forest site is not well documented. For observed LAI, we used the site investigator's description of a constant minimum all-sided needleleaf LAI (75 % of maximum) in January–May, linear increase over June to its maximum of 3.9, remaining at the maximum LAI during July–September, linear decline to its minimum in October, and a constant minimum LAI in November–December (P. Kolari,personal communication, 2007; Ilvesniemi and Liu, 2001).

Simulated LAIs (Ent-dveg and LSM-dveg) (Fig. 8) were almost constant at 4 $m^2 m^{-2}$ throughout the year, without much decrease during the winter. For evergreen plants, LAI variations in the model reflect the change in foliage carbon balance, as the phenological factor for evergreens remains 1 all the time. Thus, the relatively constant LAIs mean no significant carbon losses during the winter in the model. Based on additional Ent-dveg and LSM-dveg without frost-hardening (not shown), we found that such discrepancy in LAI between observation and simulation itself did not influence the predicted water and carbon fluxes noticeably.

4.3.2 Fluxes

Modeled frost-hardening in the spring improved the predicted seasonality of NEP markedly in both Ent and LSM simulations (Fig. 9 and Table 6). Frost-hardening suppressed photosynthetic capacity during the winter (particularly in February–April) and therefore GPP and NEP. It also suppressed transpiration and thus ET, but a relatively small difference in ET was detected between the simulations with and without the frost-hardening scheme.

With regard to the differences between the Ent-standalone and Ent-LSM models (Ent-dveg vs. LSM-dveg), we found the magnitude of NEP was overestimated in Ent-dveg due to high simulated GPP and underestimated in LSM-dveg due to low soil moisture. During the growing season, the observed volumetric soil moisture was above $\sim 0.35\,\mathrm{m}^3\,\mathrm{m}^{-3}$, and the resulting root water stress factor was 1 (completely unstressed) most of the time in Ent-dveg (driven with the observed soil moisture and temperature). However, the predicted volumetric soil moisture was below $\sim 0.25\,\mathrm{m}^3\,\mathrm{m}^{-3}$ during the growing season in the top 3 soil layers and the plants roots experienced an average water stress factor of 0.68. Such underestimated soil moisture in the Ent-LSM led to low estimates of NEP.

5 Discussion

Our experiments show that phenological timing of leaf-out and senescence can be fairly well captured within 10 days or better of observations for deciduous or annual vegetation when based on cumulative weather statistics (air and soil temperature, growing degree days, day length) derived from observations in the literature. However, the response to soil moisture is sensitive to whether deep root water access is represented to offset soil moisture stress in shallower soil. Also the soil moisture response must be tuned to the given measure or land model, because soil water content as simulated at the spatial resolution of a land surface hydrology model does not correspond well with any field measure of soil moisture (e.g. volumetric water content, matric potential, predawn water potentials). Stomatal conductance and soil respiration are sensitive to soil moisture stress and hence subject to inaccuracy dependent on the soil moisture representation. Meanwhile, we uncovered weaknesses in the representation of particular vegetation processes – autotrophic respiration and ED-based carbon allocation – that, besides differences in simulated LAI at one site, were the primary causes of differences from observed NEP.

5.1 Soil moisture

In Vaira grassland and Tonzi savanna, the phenology parameters, which are based on the plant water stress factor (a function of soil moisture), were derived from the site observations of volumetric soil water content (Eq. 8), and they perform well with observed soil moisture in Ent but not with simulated soil moisture in the LSM. The GISS LSM model predicted the same seasonal trends of soil moisture but higher in magnitude and lower in variability than observations. Koster et al. (2009) point out that simulated soil moisture is a model-specific quantity and thus that can be considered as an “index” of the moisture state. The specific evaporation and runoff formulations, in addition to model-specific soil parameters such as porosity, hydraulic conductivity, wilting point and layer depth defines a dynamic range of soil moisture simulated by the certain model. Therefore the true information content of soil moisture data lies not necessarily in their absolute magnitudes but in their time variability.

Therefore, the current approach using the absolute soil moisture value for water-limited phenology parameterization could be improved by properly mapping the soil moisture values from the field sites into those in the model, or by using the surrogates for the soil moisture, such as VPD as suggested by Jolly et al. (2005). However, Stöckli et al. (2011) note that VPD may not a good indicator of deep soil moisture.

For the trees at MMSF and Harvard Forest, LSM-simulated water stress where the plants should be unstressed indicates that calculating the water stress factor by weighting by root depth distributions does not accurately reflect how trees actually access water. Deep roots generally supply water when shallow layers are dry, and many trees perform hydraulic lift. A future revision of the Ent water stress scheme will account for the ability of plants preferentially to access soil moisture at any depth in the root zone, such that soil moisture stress is not a simple weighted average through the root profile.

While the Fluxnet data have been widely used to evaluate the DGVMs and LSMs recently, we still found the need for more comprehensive measurements at the sites. Specifically, it was very difficult to have continuous soil moisture and temperature together along with measurements with eddy covariance towers; also the detailed tree surveys were not always available. There may be some justification for temperature and day-length phenological parameters to be universal for all PFTs, but primarily drought tolerance is PFT-dependent, as seems to be indicated in the performance of the bioclimatic index of Jolly and Running (2005).

5.2 Photosynthesis and respiration parameters

While site-specific parameters were used according to the data availability in this study, model parameters for biophysics or ecosystem models have been inferred with various mathematical techniques, such as a Monte Carlo simulation (Kleidon and Mooney, 2000), data assimilation with Kalman filtering (Mo et al., 2008; Stöckli et al., 2008), optimization with the Marquardt–Levenberg method (Wang et al., 2007) and optimization with Simulated Annealing method (Medvigy et al., 2009; Kim et al., 2012). In general, vegetation biophysics models can replicate observed canopy fluxes of CO_2 well when the vegetation structure is well-specified, but the same net flux can be predicted from different levels of gross assimilation vs. respiration. The main biophysical parameters common to most models are the maximum leaf photosynthetic carboxylation rate, Vcmax; autotrophic respiration as a function of biomass, temperature, and activity; and leaf litter quality, such as lignin content, for soil respiration. While Vcmax may be precisely measured for a leaf, its value can be highly variable within a plant and seasonally.

Autotrophic respiration can range ∼ 30–80 % of annual GPP for different plant types (Falge et al., 2002). These parameters, however, may not extrapolate to the global scale, and thus future study is necessary to investigate global variation in parameterizations. In general, respiration is poorly understood and cannot be modeled fully mechanistically, but must rely on bulk parameterizations that effectively integrate numerous processes. Researchers have attempted various approaches to grouping some respiratory fluxes (Amthor, 2000; Cannell and Thornley, 2000) as responsive to different drivers, though there is as yet no generally accepted scheme. In Ent, the streams are maintenance respiration that is a function of biomass and responsive to temperature, "light growth respiration" from photosynthetic activity, and "biosynthesis respiration" from growth or turnover of plant tissues.

In Ent, using site-specific parameters for leaf photosynthetic capacity, Vcmax, constant throughout the canopy, we observed a tendency toward higher GPP and higher ecosystem respiration, R_E, compared to that inferred from tower observations when night-time respiration temperature response is used to estimate R_E. These extremes in the two components of the net flux are not necessarily unreasonable, since the Fluxnet respiration product could be underestimated. The R_E data products we used were modeled, as typical, with an exponential equation to fit the measured night-time CO_2 flux as a function of soil temperature (Schmid et al., 2000). Such an estimate excludes daytime root respiration, which increases with photosynthetic activity (Tang and Baldocchi, 2005; Tang et al., 2005). With regard to GPP, recent oxygen isotope work suggests that global gross primary productivity is higher than traditional estimates (Welp et al., 2011). It is a well-known problem in ecosystem science that GPP and respiration cannot be directly partitioned through current measurement methods for net ecosystem exchange, although there are hopes for a solution now possibly with measurements of solar-induced fluorescence (van der Tol et al., 2014).

5.3 Carbon allocation/growth scheme

We also encountered deficiencies in the carbon allocation/growth scheme that we adopted from the ED model. Although the current carbon allocation and growth scheme results in LAI that is reasonable, with some phenological timing issues as noted, the maximum LAI is achieved thanks to a cap on LAI by allometric relations to stem structure and plant density, while the rest of the plant carbon balance is not realistic, particularly with regard to rate of LAI growth, amount of seasonal sapwood growth and conversion to heartwood, accumulation of carbon reserves, and allocation to reproduction. The on/off cues of the Ent phenological factor for cold deciduous trees results in unrealistic fast full leaf-out, which could be rectified by introduction of a physically-based cell growth elongation factor (Lockhart, 1965). We found that the ED scheme's allocation to one live biomass total and then partitioning among the live pools can lead to awkward and unrealistic behaviors for sapwood patterns during spring growth and fall senescence, due to a partitioning scheme for live carbon that does not account for the different seasonal behaviors of each live pool. Making carbon allocation to each live pool independent would be more realistic. Finally, reproduction in ED currently is a fixed fraction of assimilated carbon, which is problematic in the plant's overall carbon balance as a large sink. Recent studies show that reproduction relies heavily on stored carbon, which often accumulates over more than a year, such that growth of other plant tissue is never carbon limited while large stores are kept in reserve. The ED scheme relies on the plant using nearly all stored carbon for deciduous plants each year. Introducing reproductive allocation based on thresholds proposed by Sala et al. (2012) would help rectify Ent's simulated plant carbon balances such that trees are not always reaching the limit of carbon starvation. Besides respiration, plant carbon allocation is currently still poorly understood. However, recent studies with carbon tracers (Epron et al., 2012,) are yielding new insights that could be used to improve growth schemes that continue to be a weakness in dynamic global vegetation models.

6 Conclusions

In this study, we evaluated the Ent TBM focusing on the seasonal dynamics of vegetation leaf as well as carbon and water fluxes. In particular, we took a process-based approach, evaluating the Ent-standalone model with observed LAI and Ent's prognostic active growth submodel with observed soil moisture as well as coupled to the LSM model for prognostic soil moisture, allowing us to identify parameterizations that need to be improved. For herbaceous PFTs whose phenological timings depend on soil water availability, it is inevitable to find errors in phenological timing in Ent-LSM simulations due to the discrepancy in simulated soil moisture in the LSM. Also the predicted LAI of herbaceous PFTs in Ent directly reflects the amount of assimilated carbon on the day and vice versa as herbaceous PFTs allocate assimilated carbon only to active compartments (as they have no structural tissue), and thus any errors in phenological timings propagate into errors in biophysical processes. For tree PFTs, the Ent soil moisture stress scheme should be improved to allow deep soil moisture access to override stress that might result from weighting shallower dry soil layers too strongly.

This study evaluated the phenology and resulting seasonality of fluxes in the limited number of sites, including 4 different PFTs. The Ent PFTs not tested in this study include deciduous needleleaf plants, evergreen broadleaf plants, shrubs, arctic grasses and crops. Future work will involve determining the efficacy of these PFT parameterizations at the global scale, and the possibility of developing some of these parameters as functions of local climate as obtained from either reanalysis data or from GCM climatology. In addition, we have identified deficiencies in the carbon allocation scheme from the ED model that can be rectified in future revision of Ent's growth submodel.

Future work will include development of phenology and allometry parameter sets that are robust at the global scale, and soil moisture stress accounting for deeper soil access. In addition, due to how ED allocates biomass to all live pools (foliage, sapwood, fine roots) combined rather than allowing for separate dynamics, alternative carbon allocation schemes that partition the dynamics of the live tissues must be developed for realistic plant carbon balances. This work sets the foundations for coupled land carbon-GCM simulations that can utilize height-structured canopy data from remotely sensed lidar, to reduce uncertainty in predictions of the land carbon balance through tighter links between seasonal growth dynamics geometrical and biomass allometry of vegetation canopies. Because use of the model at the global scale will involve community users who will contiune to identify parameter sets applicable for more climatically diverse distributions of the Ent TBM's plant functional types, this paper is also written to serve as a detailed reference for these users for appropriate interpretation of model results and parameter adjustment.

Appendix A: Root profiles

Depth profiles of root density are modifications of those in (Rosenzweig and Abramopoulos, 1997), revised to fit the PFT categorizations in the Ent TBM. These are modeled as cumulative normalized root density distributions $F(z)$ of a PFT as:

$$F(z) = a_{\mathrm{PFT}} Z^{b_{\mathrm{PET}}} \tag{A1}$$

where z is soil depth (m), and a and b are PFT-specific parameters, summarized in Table A1. The cumulative distributions are plotted in Since soil layers in the NASA GISS land surface model only are defined down to 3.5 m depth, maximum root depths are limited to this value.

Appendix B: Allocation

The labile carbon reserves in Ent are allocated into different plant biomass pools, including foliage, sapwood, heartwood, fine root and coarse root. In addition, turnover of tissue due to background litter fluxes is replenished from the carbon reserve pool. In nature, plants may allocate biomass to different compartments in response to many different controlling factors, such as light availability and water availability, which alter, for example, root:shoot ratios. Among various carbon allocation modeling approaches with different complexities, many DGVMs take a simple approach to model carbon allocation via empirical and allometric relationships, a traditional “static allocation” approach (Foley et al., 1996; Sitch et al., 2003) while some models parameterize the dependency of carbon allocation on resource availability, “dynamic allocation” approach (Friedlingstein et al., 1999; Arora and Boer, 2005). Although carbon allocation varies with plant status such as size and age, and environmental conditions, the static allocation approach may be justified for models operating at the large scale. If plant productivity is assumed in a steady state, carbon allocation is likely to be in a steady state. Also, spatial variability in environmental factors and their effects on allocation can be averaged. However, the fixed allocation approach is limited in long-term simulations as it lacks response to environmental changes such as climate change and elevated atmospheric CO_2 (Franklin et al., 2012). However, recent models of “dynamic allocation” have been difficult to constrain due to a dearth of observations.

In the Ent TBM, the allocation submodel takes a traditional approach of “static allocation”, based on allometric relationships between different pools. Modified from approaches of the ED models (Moorcroft et al., 2001; Medvigy et al., 2009), the scheme allocates the labile carbon to different biomass pools according to empirical allometric relationships and leaf phenological status on a daily basis.

B1 Active biomass

The biomass within each plant is partitioned between an active carbon pool and a structural carbon pool. The active biomass pool (B_{active}) ($\mathrm{kg_{biomass}\ cohort^{-1}}$) is sub-divided into foliage (B_{fol}), sapwood (B_{sw}) and fine roots (B_{froot}) which turn over at different rates, while the structural pool ($B_{\mathrm{structural}}$) consists of heartwood (B_{hw}) and coarse roots (B_{croot}). Grasses do not have the structural pool. The labile biomass (B_{lab}) assimilated on the same day is allocated to the active carbon pool to maintain the size of foliage, sapwood and fine root tissues given their turnover rates, and to accumulate the active carbon up to its maximum.

Thus, the time change of the active pool can be written by

$$\frac{\mathrm{d}B_{\mathrm{active}}}{\mathrm{d}t} = \min[\min(B_{\mathrm{lab}}, \mathrm{CB_d}), B_{\mathrm{active}}^{\mathrm{max}} - B_{\mathrm{active}}] \tag{B1}$$

where $B_{\mathrm{active}}^{\mathrm{max}}$ is the maximum active carbon of each plant, which is determined according to the maximum foliage carbon according to the size of plant, $\mathrm{CB_d}$ is the daily plant carbon balance (i.e., sum of NPP on one day). Then, the allometric relationships are used to sub-divide the active biomass into its components. The foliage biomass is determined according to its phenological status (φ), ranging from 0 (for full senescence) to 1 (full leaf-out), as a proportion of full-leaved foliage biomass, B_{fol}^{*}, so that $B_{\mathrm{fol}} = \varphi B_{\mathrm{fol}}^{*}$. Both the fine root and sapwood biomass are also determined according to their proportional relationships to B_{fol}^{*}. A constant empirical proportionality for fine root (q_{fr}), assumed to be 1, is related as:

$$q_{\mathrm{fr}} = \frac{B_{\mathrm{froot}}}{B_{\mathrm{fol}}^{*}} = 1 \tag{B2}$$

The sapwood biomass is determined according to the pipe-model theory (Shinozaki et al., 1964), which suggests that the total foliage area is proportional to the sapwood cross-sectional area. The ratio between full-leaved foliage area and sapwood area is assumed to be 3900 ($\mathrm{m_{foliage}^{2}\,m_{sapwood}^{-2}}$). This value is adopted from the value used in ED1 (Moorcroft et al., 2001), which follows Rending and Taylor (1989), giving the ratios of foliage area to sapwood area ranging from 3900 to 14 000.These assumptions result in the following relationship:

$$\frac{\text{(foliage area)}}{\text{(sapwood area)}} = \frac{\mathrm{SLA} \cdot B_{\mathrm{fol}}^{*}}{\frac{B_{\mathrm{sw}}}{\rho_{\mathrm{sw}} \cdot h}} = 3900 \tag{B3}$$

where ρ_{sw} is the sapwood density ($\mathrm{kg\,C\,m_{sapwood}^{-3}}$) and SLA is the specific leaf area ($\mathrm{m_{foliage}^{2}\,(kg\,C)^{-1}}$)for each PFT, provided in Table 1. ρ_{sw} is taken to be 500 (kg C $\mathrm{m}^{-3}_{\mathrm{sapwood}}$) (i.e., 0.5 kg C $\mathrm{kg}^{-1}_{\mathrm{biomass}}$ × 1000 $\mathrm{kg}_{\mathrm{biomass}}\,\mathrm{m}^{-3}_{\mathrm{sapwood}}$ for very hard wood). However, we note that there are departures from these constant values. The fraction of dry biomass that is carbon in spruce wood is typically 0.48 (Payne, 2002). Also, Schneider et al. (2011) find the foliage to sapwood area ratio to be closer to 500–600 for Jack pine, with higher values toward the interior of the sapwood that serves older foliage. Calvo-Alvarado et al. (2008) find an increasing linear relation between height and foliage area/sapwood area for Costa Rican rainforest trees, ranging from 500–1500. A consistent rule for this variation has yet to be identified, but it may vary with wood density and anatomy.

Finally, B_{fol} is related to LAI ($\mathrm{m}^{2}_{\mathrm{foliage}}\,\mathrm{m}^{-2}_{\mathrm{ground}}$), measuring the total leaf (i.e., foliage) area per the projected ground area by

$$\mathrm{LAI} = 0.5 \cdot B_{\mathrm{fol}} \cdot \mathrm{SLA} \cdot \mathrm{nplant} \tag{B4}$$

where nplant is the population density of cohorts (# plants $\mathrm{m}^{-2}_{\mathrm{ground}}$), and 0.5 (kg C $\mathrm{kg}^{-1}_{\mathrm{biomass}}$) is to convert SLA in $\mathrm{m}^{2}_{\mathrm{foliage}}\,(\mathrm{kg\,C})^{-1}$ to $\mathrm{m}^{2}_{\mathrm{foliage}}\,\mathrm{kg}^{-1}_{\mathrm{biomass}}$.

B2 Structural and reproductive biomass

Growth of structural tissue is handled as follows. If the stored labile biomass is non-zero, the size of the structural pool of woody plants increases according to the empirical allometric relationships and consequently the size of the active pool increases. Here, the partitioning between B_{active} and $B_{\mathrm{structural}}$ is written by

$$q_{\mathrm{structural}} = \frac{\mathrm{d}B_{\mathrm{structural}}}{\mathrm{d}B_{\mathrm{active}}} = \frac{\frac{\mathrm{dDBH}}{\mathrm{d}B_{\mathrm{active}}}}{\frac{\mathrm{dDBH}}{\mathrm{d}B_{\mathrm{structural}}}} \tag{B5}$$

where DBH is the diameter at breast height and $q_{\mathrm{structural}}$ is the ratio of structural growth to active growth. The derivatives are derived from allometric relationships according to plant size (i.e., DBH, and height) for woody plants. Note herbaceous plants do not have the structural pool, meaning that DBH= 0, $q_{\text{structural}} = 0$, $B_{\text{structural}} = 0$, and $q_{\text{sw}} = 0$. Also, the plant devotes a fixed fraction (q_{repro}) of daily carbon to the reproductive pool and the rest to growth of the active and structural pools. q_{repro} is assumed to be 0.3 for woody plants and 1.0 for herbaceous plants, following the assumptions of ED1 (Moorcroft et al., 2001).

Appendix C: Biophysics, Allocation, and Phenology Parameters

See Tables C1 and C2.

Code availability

The Ent TBM is being developed as a part of NASA GISS ModelE. Version 1.0.0.0.0, Ent biophysics, is available in http://data.giss.nasa.gov/modelE/ (Schmidt et al., 2014). As noted in the main text, users of this version of Ent phenology and growth, version 1.0.1.0.0, are encouraged to use it for site-based studies with parameters derived at the site level, not for global studies. Since Ent TBM v1.0.1.0.0 does not yet apply at the global scale, it is not released yet in ModelE for GCM use, but the code used in this study may be obtained by contacting the corresponding author via email.

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Table 1. Plant Functional Types (PFT) in Ent.

Number	Plant Function Type
1	Evergreen broadleaf early successional
2	Evergreen broadleaf late successional
3	Evergreen needleleaf early successional
4	Evergreen needleleaf late successional
5	Cold deciduous broadleaf early successional
6	Cold deciduous broadleaf late successional
7	Drought deciduous broadleaf
8	Deciduous needleaf
9	Cold adapted shrub
10	Arid adapted shrub
11	C3 grass perennial
12	C4 grass
13	C3 grass annual
14	Arctic C3 grass
15	C3 crops
16	C4 crops
17	Crops broadleaf woody

Table 2. Parameters in phenology submodel.

Parameters	Values	Eq. #	References
$\mathrm{GDD}_{\mathrm{int}}$	−68	(3)	Botta et al. (2000)
$\mathrm{GDD}_{\mathrm{slop}}$	638		
$\mathrm{GDD}_{\mathrm{multi}}$	−0.01		
$\mathrm{GDD}_{\mathrm{length}}$	200	(4)	Derived from observations at MMSF
T_{max}	15	(5)	Adjusted based on Jolly et al. (2005)
T_{min}	5		
$\mathrm{Id}_{\mathrm{max}}$	540		
$\mathrm{Id}_{\mathrm{max}}$	660		
$\mathrm{SGDD}_{\mathrm{crit}}$	100 for arctic C3 grass; 400 for C3 grass; 1400 for C4 grass;	(6)	Arctic C3 grass derived from observations at Barrow, AK C3 annual grass from White et al. (1997)
$\mathrm{SGDD}_{\mathrm{length}}$	50		
$\mathrm{TS}_{\mathrm{max}}$	0	(7)	Derived from observations at Tonzi and Vaira
$\mathrm{TS}_{\mathrm{min}}$	−5		
β_{max}	0.4 for both woody and herbaceous	(8)	Derived from observations at Tonzi
β_{min}	0.0 for woody; 0.2 for herbaceous		
β_{resis}	0.25 for woody; 1.0 for herbaceous		
a	1	(9)	Makela et al. (2006)
b	0		
τ	125 h	(10)	
T_0	−5.9 °C		
$S_{\mathrm{h,\,max}}$	16.8 °C	(11)	Derived from observations at Hyytiala

Table 3. Types of experiments.

	Soil state (moisture and temperature)	Vegetation phenology
Ent-dveg	Prescribed with observation (Ent-standalone)	Prognostic LAI (dynamic "active biomass" phenology)
Ent-oveg	Prescribed with observation (Ent-standalone)	Prescribed with observed LAI
LSM-dveg	Prognostic (Ent-LSM coupled)	Prognostic LAI
LSM-oveg	Prognostic (Ent-LSM coupled)	Prescribed with observed LAI

Table 4. Site descriptions.

	Morgan Monroe State Forest	Harvard Forest	Vaira Ranch	Tonzi Ranch	Hyytiala
Short name	MMS	Ha1	Var	Ton	Hyy
Location	Indiana, USA	Massachusetts, USA	California, USA	California, USA	Hyytiala, Finland
Coordinates	39.32° N, 86.41° W	42.54° N, 72.17° W	38.41° N, 120.95° W	38.43° N, 120.97° W	61.85° N, 24.29° W
Primary reference	Schmid et al. (2000)	Urbanski et al. (2007)	Xu and Baldocchi (2004)	Baldocchi et al. (2004)	Makela et al. (2004)
Data website	http://ameriflux.ornl.gov/fullsiteinfo.php?sid=48	http://ameriflux.ornl.gov/fullsiteinfo.php?sid=50	http://ameriflux.ornl.gov/fullsiteinfo.php?sid=30	http://ameriflux.ornl.gov/fullsiteinfo.php?sid=29	http://www.bgc-jena.mpg.de/public/carboeur/site-details?id=117
Dominant Species	Sugar maple, Tulip poplar	Red oak, Red maple	Purple false brome	Overstory: Blue oak, Understory: Purple false brome	Scots pine, Norway spruce
Ent PFT	6-cold deciduous broadleaf l.s.	5-cold deciduous broadleaf e.s.	13-annual grass	7-drought deciduous Broadleaf & 13-annual grass	4-evergreen needleleaf
Simulation Period	1 Jan 2002–31 Dec 2006	1 Jan 1994–31 Dec 2002	1 Jan 2002–31 Dec 2002	1 Jan 2002–31 Dec 2002	1 Jan 1998–31 Dec 1998
Experiments	LSM-oveg LSM-dveg	LSM-oveg LSM-dveg	Ent-oveg Ent-dveg LSM-oveg LSM-dveg	Ent-oveg Ent-dveg LSM-oveg LSM-dveg	Ent-oveg Ent-dveg LSM-oveg LSM-dveg

Table 5. Correlation coefficients and RMSEs of LAI-based phenological dates between simulations and observations.

Site	Spring Phenology						Fall Phenology					
	20 % LAI		50 % LAI		80 % LAI		80 % LAI		50 % LAI		20 % LAI	
	R	RMSE	*R*	RMSE	*R*	RMSE	*R*	RMSE	*R*	RMSE	*R*	RMSE
MMS (2002–2006)	0.80	3.65	0.36	6.75	0.67	16.44	0.20	27.95	0.46	19.65	0.49	7.67
Ha1 (1994–2002)	0.44	5.71	0.85	3.00	0.44	9.18	0.55	9.91	0.04	15.09	−0.56	17.52

Table 6. Correlation coefficients and RMSEs of daily fluxes between simulations and observations.

Site	Years		NEP (µmol m^{-2} s^{-1})				ET (mm s^{-1})			
			Hourly		Daily		Hourly		Daily	
			R	RMSE	*R*	RMSE	*R*	RMSE	*R*	RMSE
MMS	2002–2006	LSM-dveg	0.86	3.67	0.91	1.31	0.80	67.89	0.85	32.82
		LSM-oveg	0.88	3.59	0.94	1.04	0.79	66.62	0.85	32.12
Ha1	1994–2002	LSM-dveg	0.89	3.03	0.85	1.70	0.79	45.25	0.82	22.46
		LSM-oveg	0.92	2.72	0.92	1.36	0.74	52.12	0.72	29.14
Var	2002	Ent-dveg	0.74	2.92	0.57	1.41	–	–	–	–
		Ent-oveg	0.76	2.81	0.55	1.60	–	–	–	–
		LSM-dveg	0.70	2.57	0.75	1.16	0.84	25.37	0.83	13.46
		LSM-oveg	0.84	2.34	0.72	1.54	0.91	25.73	0.93	11.36
Ton	2002	Ent-dveg	0.42	3.96	0.36	1.51	–	–	–	–
		Ent-oveg	0.44	3.94	0.43	1.50	–	–	–	–
		LSM-dveg	0.41	4.06	0.53	1.37	0.77	5.38	0.83	14.42
		LSM-oveg	0.42	3.99	0.50	1.41	0.76	35.59	0.84	14.40
Hyy	1998	Ent-dveg	0.79	2.63	0.71	1.25	–	–	–	–
		Ent-oveg	0.77	2.90	0.68	1.35	–	–	–	–
		LSM-dveg	0.92	1.66	0.86	0.82	0.87	19.37	0.93	7.89
		LSM-oveg	0.90	1.89	0.82	0.92	0.87	19.30	0.94	7.88

Table A1. Plant functional type parameters for root density distributions.

	Ent plant functional type															
	Evergreen broad		Evergreen needle		Cold-deciduous broad		drought broad	decidciduous needle	shrub cold	shrub arid	grass				crop herb	crop tree
PET	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
a	1.1	1.1	0.25	0.25	0.25	0.25	0.25	0.25	0.8	0.8	0.9	0.9	0.9	0.9	0.9	0.25
b	0.4	0.4	2.0	2.0	2.0	2.0	2.0	2.0	0.4	0.4	0.9	0.9	0.9	0.9	0.9	2.0

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Table C1. Biophysics parameters for Fluxnet sites in this study.

Variable	Definition	Unit	PFT2 TNF	PFT4 Hyytiala	PFT5 Harvard	PFT6 MMSF	PFT7 Tonzi-oaks	PFT13 Tonzi-grass and Vaira
P_{st}	P_{st} – photosynthetic pathway	–	C3	C3	C3	C3	C3	C3
PAR_{absorb}	Leaf PAR absorbance	–	0.90	0.93	0.90	0.90	0.90	0.86
$V_{c_{max}}$	maximum photosynthetic capacity	$\mu mol\, m^{-2}\, s^{-1}$	15.675	40.0	50.0	40	56.4	60.0
m	Slope of Ball–Berry stomatal conductance equations	–	9.0	9.0	9.0	9.0	9.0	11.0
b	Intercept of Ball–Berry stomatal conductance equation	$\mu mol\, m^{-2}\, s^{-1}$	0.002	0.002	0.002	0.002	0.002	0.008

Table C2. Biogeochemical and phenological parameters for Fluxnet sites in this study.

Variable	Defintion	Unit	PFT2 TNF	PFT4 Hyytiala	PFT5 Harvard	PFT6 MMSF	PFT7 Tonzi-oaks	PFT13 Tonzi-grass and Vaira
leaftype	Leaf type	–	broad	needle	broad	broad	broad	grass
h_{wilt}	Wilting point	m	−153.0	−153.0	−500.0	−500.0	−500.0	−2030.0
S_*	Soil moisture stress onset point (fraction of soil volumetric saturation)	–	0.60	0.50	0.50	50.0	0.34	0.65
s_{wilt}	Wilting point (fraction of soil volumetric saturation)	–	0.29	0.25	0.29	0.29	0.28	0.27
sla	Specific leaf area	$\text{m}^2_{\text{leaf}}\,(\text{kg C}_{\text{leaf}})^{-1}$	9.7	9.5	34.5	34.0	8.3	21.6
r	Respiration parameter	–	0.5	1.2	0.6	0.6	0.5	1.2
lrage	Leaf and root litter age	years	3.0	4.0	1.2	0.75	1.2	1.5
woodage	Stem litter age	years	41.0	42.0	58.0	58.0	245.0	UNDEF
lit_C2N	Litter C : N ratio	–	40.0	80.0	57.0	57.0	60.0	50.0
lignin	Lignin content		0.2	0.25	0.2	0.3	0.2	0.1
croot_ratio	Coarse roots:woody stem mass ratio	–	0.75	0.184	0.093	0.093	0.153	0.0
phenotype	Phenological type	–	Ever-green	Cold deciduous	Cold deciduous	Cold deciduous	Drought deciduous	Annual
b1Cf	Parameter 1 for allometric relation between DBH and foliage carbon	–	0.0395	0.045	0.024	0.017	0.0296	0.0800
b2Cf	Parameter 2 for allometric relation between DBH and foliage carbon	–	1.560	1.683	1.860	1.731	1.560	1.000
b1Cd	Parameter 1 for allometric relation between DBH and structural carbon	–	0.1017	0.1617	0.148	0.235	0.0621	0.00001
b2Cd	Parameter 2 for allometric relation between DBH and structural carbon	–	2.306	2.1536	2.411	2.252	2.306	1.000
b1Ht	Parameter 1 for allometric relation between DBH and height	–	34.62	22.79	25.18	23.39	34.62	0.4778
b2Ht	Parameter 2 for allometric relation between DBH and height	–	−0.0232	−0.0445	−0.0496	−0.054	−0.02321	−0.75

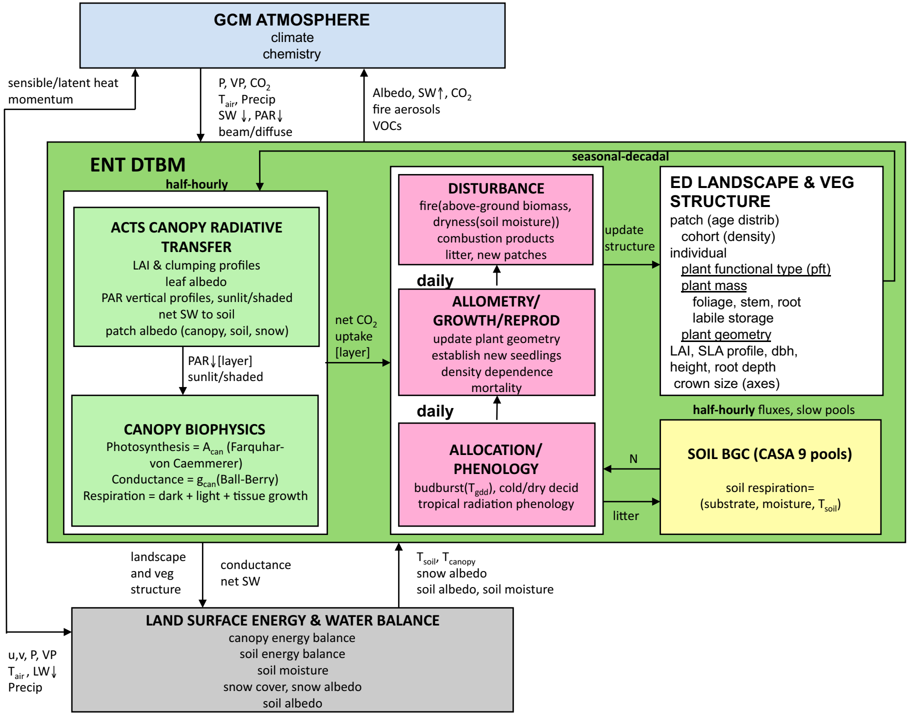

Figure 1. Schematic diagram of the Ent model.

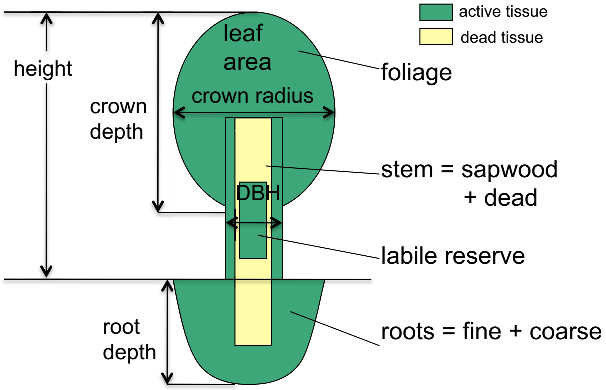

Figure 2. Ent individual plant biomass pools and geometry. Herbaceous plants exclude woody tissue.

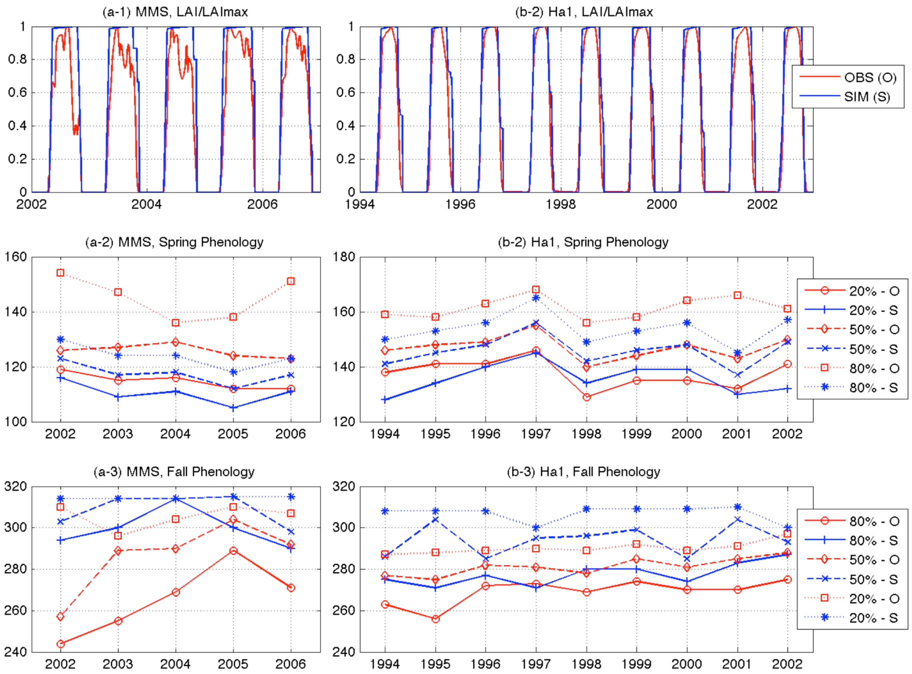

Figure 3. Daily simulated (S) and observed (O) phenology: (top) LAI/LAImax (middle) phenological dates (day of year) for spring leaf-out at percent of maximum; and (bottom) phenological dates (day of year) for fall senescence in MMSF and Harvard Forest. These results show good simulated timing of initial leaf-out and final senescence, but lack of the gradual rate of these, such that maximum leaf-out occurs too soon, and period of peak growth is too long. The gradual behavior could be simulated through a rate constraint.

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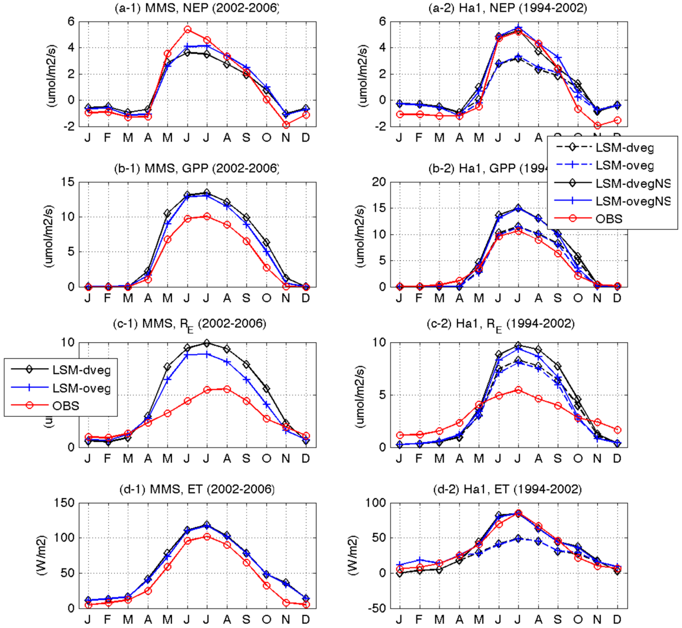

Figure 4. Average monthly fluxes in MMSF for 2002-2006 and Harvard Forest for 1994–2002: **(a)** NEP, **(b)** GPP, **(c)** R_E and **(d)** ET.

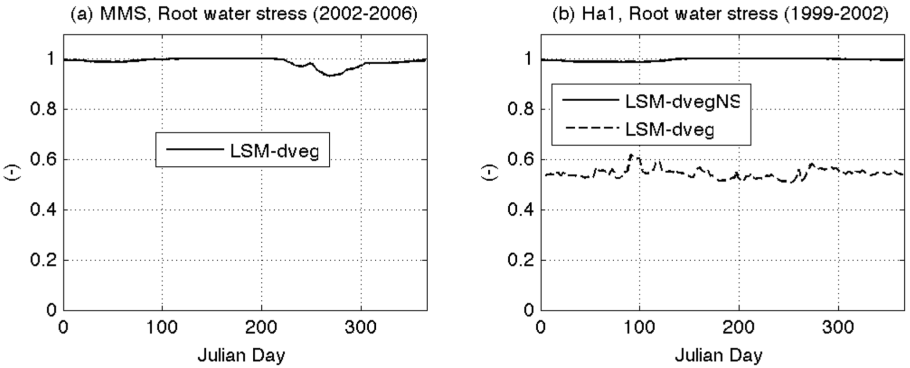

Figure 5. Daily root water stress factor in **(a)** MMSF for 2002–2006 and **(b)** Harvard Forest for 1994–2002.

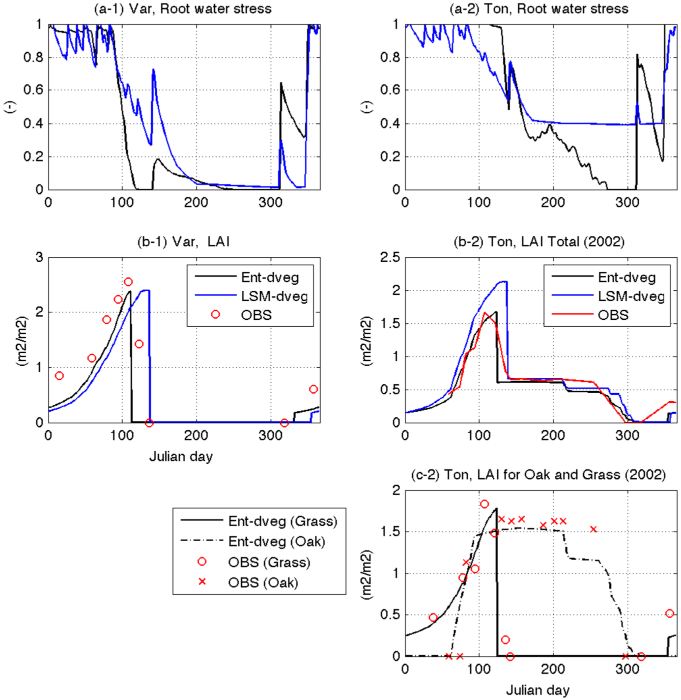

Figure 6. (a) Daily root water stress and **(b–c)** daily LAI in Vaira and Tonzi Ranches for 2002.

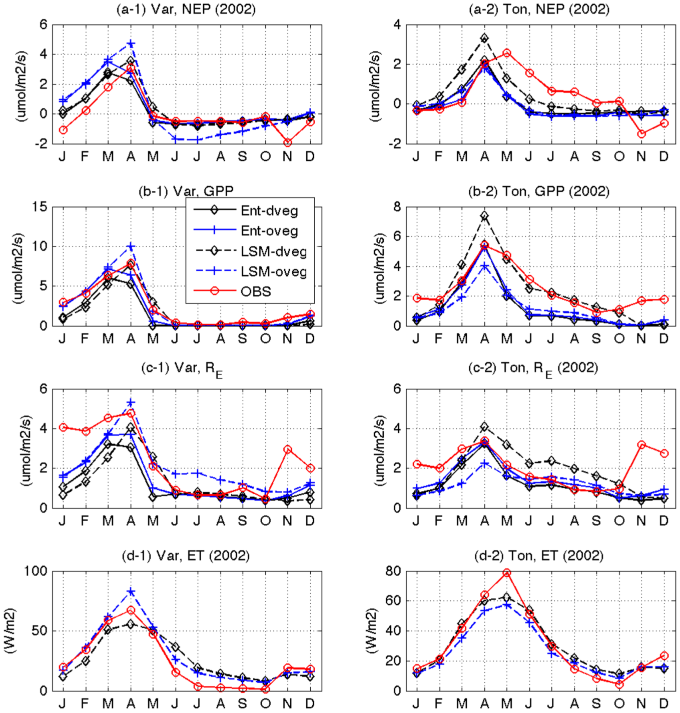

Figure 7. Monthly fluxes in Vaira and Tonzi Ranches for 2002: **(a)** NEP, **(b)** GPP, **(c)** R_E and **(d)** ET.

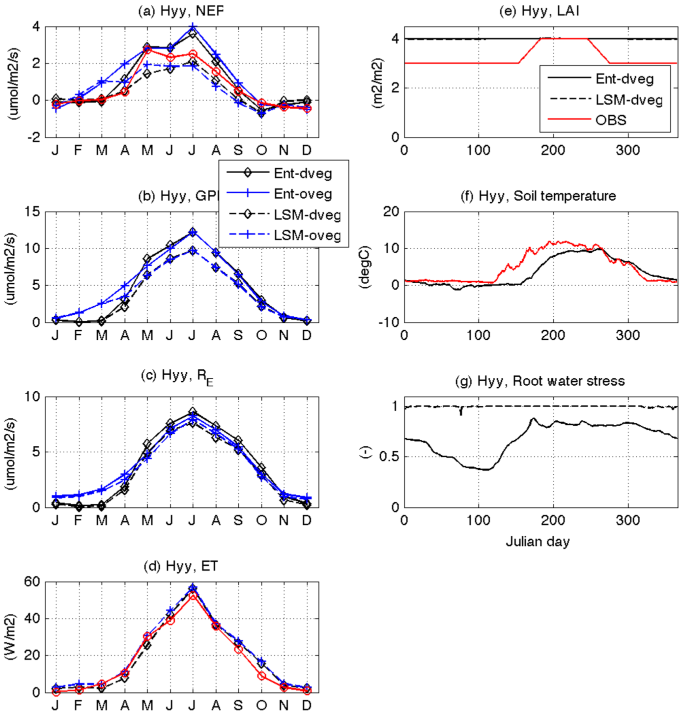

Figure 8. Monthly fluxes and daily states in Hyytiala for 1998: **(a)** NEP, **(b)** GPP, **(c)** R_E, **(d)** ET, **(e)** LAI, **(f)** soil temperature and **(g)** root water stress. Here the observed LAI is assumed based on personal communication with the site investigator, Pasi Kolari.

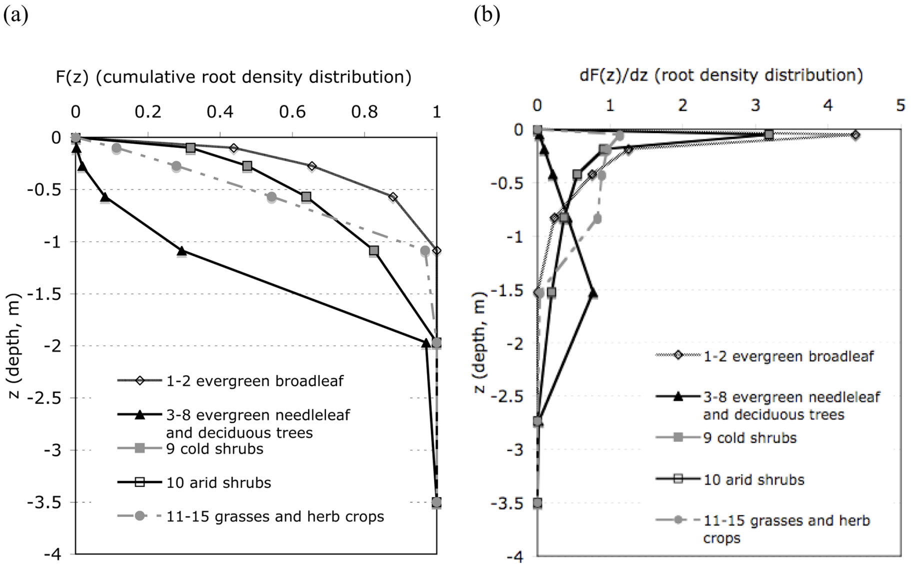

Figure A1. (a) Cumulative root density profile distributions and **(b)** probability density distributions in the EntTBM, modified from (Rosenzweig and Abramopoulos, 1997), by soil depth increments of the NASA GISS GCM land surface model.

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