

A stand-alone tree demography and landscape structure module for ESM

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A stand-alone tree demography and landscape structure module for Earth system models: integration with global forest data

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Abstract

Poorly constrained rates of biomass turnover are a key limitation of Earth system models (ESM). In light of this, we recently proposed a new approach encoded in a model called Populations-Order-Physiology (POP), for the simulation of woody ecosystem stand dynamics, demography and disturbance-mediated heterogeneity. POP is suitable for continental to global applications and designed for coupling to the terrestrial ecosystem component of any ESM. POP bridges the gap between first generation Dynamic Vegetation Models (DVMs) with simple large-area parameterisations of woody biomass (typically used in current ESMs) and complex second generation DVMs, that explicitly simulate demographic processes and landscape heterogeneity of forests. The key simplification in the POP approach, compared with second-generation DVMs, is to compute physiological processes such as assimilation at grid-scale (with CABLE or a similar land surface model), but to partition the grid-scale biomass increment among age classes defined at sub grid-scale, each subject to its own dynamics. POP was successfully demonstrated along a savanna transect in northern Australia, replicating the effects of strong rainfall and fire disturbance gradients on observed stand productivity and structure.

Here, we extend the application of POP to a range of forest types around the globe, employing paired observations of stem biomass and density from forest inventory data to calibrate model parameters governing stand demography and biomass evolution. The calibrated POP model is then coupled to the CABLE land surface model and the combined model (CABLE-POP) is evaluated against leaf-stem allometry observations from forest stands ranging in age from 3 to 200 yr. Results indicate that simulated biomass pools conform well with observed allometry. We conclude that POP represents a preferable alternative to large-area parameterisations of woody biomass turnover, typically used in current ESMs.

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1 Introduction

Changes in woody biomass storage in forest and savanna ecosystems, including woody ecosystems regenerating on abandoned agricultural lands, are the major driver of the terrestrial carbon sink, which currently amounts to around a quarter of anthropogenic emissions, mitigating climate change (Ahlström et al., 2012; Le Quéré et al., 2013; Pan et al., 2011). Such ecosystem dynamics and their feedbacks to atmospheric carbon content and radiative forcing are represented in Earth system models (ESMs) by incorporating dynamic vegetation models (DVMs). These attempt to describe changes in vegetation biomass components over time as the net effect of the allocation of net primary production (NPP), which increases or decreases biomass pools through phenological (seasonal) cycles of foliage and roots, mortality of plant individuals and disturbances such as wildfires and storms. The first generation DVMs adopted by most current ESMs (Arora et al., 2013) employ large-area parameterisations designed for application on the scales of grid cells 10 s to 100 s of kms on a side. Typically these parameterisations treat carbon flows associated with respiration and mortality as first-order decay processes, expressed as products of pool biomasses and bulk rate parameters independent of age structure (the “Big-Wood” approximation; Wolf et al. 2011). These are computationally-efficient – an important consideration for global-scale applications – but have the disadvantage of not resolving underlying population and community processes such as recruitment, mortality and competition between individuals and species for limiting resources (e.g. Sitch et al., 2003). This lack of mechanistic detail means that the models are unable to directly exploit the wealth of information on forest stand structure and dynamics available from forest inventories that have been used to develop individual-based height-structured models that have been successfully used to simulate forest dynamics at the stand scale since the 1970s (e.g. Botkin et al., 1972; Bugmann, 2001; Smith et al., 2001). Different DVMs have also been shown to simulate widely different patterns and time evolution of biomass pools, especially under future climate projections (Cramer et al., 2001; Friedlingstein

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et al., 2006; Sitch et al., 2008) where models with a conservative response of biomass turnover to climatic forcing tend to retain a net biomass sink over the coming century, whereas others simulate a source or reduced sink by late 21st century (Ahlström et al., 2012). In ESM simulations with an active carbon cycle feedback to climate, such differences translate into divergence in the simulated global climate (Friedlingstein et al., 2006). It has been suggested that the representation of forest dynamics in ESMs may be one of the greatest sources of uncertainty in future climate projections (Purves and Pacala, 2008).

A handful of offline (not coupled to the atmosphere) second generation DVMs exist, that simulate demographic processes and landscape heterogeneity of forests using more explicit approaches that have been demonstrated to accurately replicate forest size structure and successional dynamics as predicted by community ecological theory. Examples include LPJ-GUESS (Smith et al., 2001) and ED (Fisher et al., 2010; Moorcroft et al., 2001). Such approaches are perceived as offering promise as an improved, second generation of DVMs (Fisher et al., 2010; Purves and Pacala, 2008). For studies of global and continental carbon balance, and for coupling to ESMs, however, these models have the potential disadvantage of including stochastic representations of processes such as recruitment, mortality and large-scale disturbance, requiring replication of dynamic objects such as tree individuals and patches, and repeated computations of the same processes as applied to different objects, in order to obtain a representative average for the ecosystem as a whole. As a result these models are demanding both of memory and processing power, and results are not strictly deterministic, which complicates the analysis of results. In addition, the intricate internal representation of stand structure and its integration with plant physiological processes such as carbon assimilation, allocation and phenology implies that the enhancement of existing land surface models lacking or employing simpler parameterisations of vegetation dynamics may be a time-consuming, technically challenging task.

Wolf et al. (2011) recently used global forest inventory data to assess forest biomass allometry in eight global land surface models, including two second generation DVMs.

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Simulated relationships between stem and foliage biomass pools generally conformed poorly with observed allometry, indicative of model failure to consistently reproduce both structural and functional characteristics of vegetation. Best overall performance was noted for the two second generation DVMs (ED and Orchidee-FM), which include an explicit parameterization of crowding mortality and the resultant phenomenon of self-thinning, which strongly controls biomass turnover rates in closed forest ecosystems (Westoby, 1984). The study recommended the use of biomass allometry data from forest inventories as a simple approach to improving the characteristic behaviour of global land surface models with respect to structural dynamics.

To simultaneously address the deficient accuracy of many first generation DVMs, and the technical limitations of current second-generation DVMs, Haverd et al. (2013) proposed a new approach for the simulation of woody ecosystem stand dynamics, demography and disturbance-mediated heterogeneity, designed to be modular, deterministic, computationally-efficient and based on sufficient ecological realism for application at the grid scales typically employed by DVMs and ESMs for continental to global applications. The approach, encoded in a model called Populations-Order-Physiology (POP), and coupled to the CABLE (Wang et al., 2011) LSM, was demonstrated along a savanna transect in northern Australia, successfully replicating the effects of strong rainfall and fire disturbance gradients on observed stand productivity and structure. The key simplification in the POP approach, compared with second-generation DVMs, is to compute physiological processes such as assimilation at grid-scale (with CABLE or a similar land surface model), but to partition the grid-scale biomass increment among age classes defined at sub grid-scale, each subject to its own dynamics.

In the present study, we extend the application of POP to globally-distributed forests, heeding the recommendation of Wolf et al. (2011) to constrain and improve the performance of the model by using allometric scaling relationships from forest inventory data. Thus calibrated, the combined model (CABLE-POP) is evaluated against leaf-stem allometry and total biomass observations from forest stands.

2 Methods

2.1 Models

2.1.1 POP (Populations-Order-Physiology)

POP is described in Appendix 1 of Haverd et al. (2013), and the detailed description (Appendix A) and summary below are largely reproduced from that paper. For the purpose of the present application, that includes closed forest ecosystems, we extended tree mortality in POP to include a crowding component as described below. A Fortran90 version of the POP computer code is included in the Supplement.

POP is designed to be modular, deterministic, computationally efficient, and based on defensible ecological principles. Parameterisations of tree growth and allometry, recruitment and mortality are broadly based on the approach of the LPJ-GUESS DVM (Smith et al., 2001). The time step (Δt) is one year.

Input variables are annual grid-scale stem biomass increment (ΔC (kgCm^{-2})) and mean return times for two classes of disturbance: (i) “catastrophic” disturbance, which kills all individuals (cohorts) and removes all biomass in a given patch; (ii) “partial” disturbances, such as fire, which result in the loss of a size-dependent fraction of individuals and biomass, preferentially affecting smaller (younger) cohorts. For the present study, we adopt a mean catastrophic disturbance return time of 100 yr, and neglect partial disturbance. Stem biomass increment is provided by the host LSM (here CABLE) or prescribed for stand-alone calibration.

State variables are the density of tree stems partitioned among age/size classes (cohorts) of trees and representative neighbourhoods (patches) of different age-since-last-disturbance across a simulated landscape or grid cell.

POP simulates allometric growth of cohorts of trees that compete for light and soil resources within a patch. The annual stem biomass increment is partitioned among cohorts according to a power function of their current aggregate stem biomass (size), on the assumption that larger individuals preempt resources owing to a larger surface

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area and exploration volume of their resource uptake surfaces (leaves and fine roots), and due to the advantage conferred on taller individuals by the shading of shorter ones in crowded stands (Westoby, 1984). A cohort's share of the total annual biomass increment is divided equally among individuals.

- 5 The mortality parameterization was specifically updated for this study and is therefore described here in detail.

Population dynamics are governed by:

$$\frac{dN_y}{dt} = -(m_{R,y} + m_{C,y})N_y \quad (1)$$

- 10 where N_y is the stem density of the cohort established in year y , and $m_{R,y}$ and $m_{C,y}$ are cohort mortalities (yr^{-1}) due to resource limitation and crowding respectively. N_y is initialised as recruitment density, and is episodically reset (according to disturbance intensity) when the patch experiences disturbance.

- 15 We characterise the response of resource-limitation mortality to growth efficiency (GE, i.e. growth rate as a function of size) by a logistic curve with the inflection point at this threshold:

$$m_{R,y} = \frac{m_{R,\max}}{1 + (\text{GE}_y / \text{GE}_{\min})^\rho} \quad (2)$$

where y is the index for a particular cohort, and

$$20 \text{GE}_y = \Delta C_y / C_y^s \quad (3)$$

$$\frac{\Delta C_y}{\Delta t} = \frac{(C_y / N_y)^s N_y}{\sum (C_i / N_i)^s N_i} \frac{\Delta C}{\Delta t} \quad (4)$$

C_y (kgCm^{-2}) is the stem biomass of the y th cohort, ΔC_y is the annual biomass increment of the y th cohort, ΔC is the grid-cell annual biomass increment, s is set to

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0.75 (Enquist and Niklas, 2001), and $m_{R,max}$ (yr^{-1}) is the upper asymptote for mortality as GE declines, set to 0.3 following (Smith et al., 2001). The exponent p , assigned a default value of 5, governs the steepness of the response of m_R to GE around $GE = GE_{min}$. For this study GE_{min} was set to its calibration value of 0.015, as determined previously by optimisation against Northern Australian tree basal area data (Haverd et al., 2013).

The additional crowding mortality component ($m_{C,y}$) was included to allow for self-thinning in forest canopies. Self thinning is dependent on the assumption that some trees (within a cohort) have a slight advantage in pre-empting resources, creating a positive feedback to their growth, and ultimately resulting in death of the most suppressed individuals. In contrast, in POP, the total stem biomass increment for a cohort is equally partitioned amongst all members. To account for this we use the following new parameterization which emulates the contribution to self-thinning associated with within-cohort competition.

Crowding mortality is expressed as

$$m_{C,y} = \min \left[\frac{1}{\Delta t} \exp(\alpha_C(1 - 1/c_{pc,y}))f_c, \frac{\Delta C_y}{C_y \Delta t} \right] \quad (5)$$

such that it never exceeds growth. Here, $c_{pc,y} = (1 - \exp(-A_{c,y}))$ is crown projective cover; $A_{c,y}$ crown projected area ($\text{m}^{-2} \text{m}^{-2}$) of all crowns in the y th and taller cohorts; α_C a coefficient which determines the onset of crowding mortality with respect to c_{pc} and f_c is a tunable scaling factor. α_C was set to 10.0, corresponding to an onset of crowding mortality at $c_{pc} \sim 0.8$. This value implies that crowding mortality is insignificant in the Australian savanna simulations, thus retaining the validity of the parameters relating to $m_{R,y}$ in Eq. (2) as used in the earlier study of (Haverd et al., 2013). Crown projected area is evaluated as

$$A_{c,y} = N_y k_{allom} D_y^{k_{rp}} \quad (6)$$

where N_y is stem density (m^{-2}); D_y is stem diameter at breast height (m), and k_{allom} and k_{rp} are parameters set to respective values of 200 and 1.67, based on literature values compiled by Widłowski et al. (2003).

Additional mortality occurs as a result of disturbances replicate patches representing stands of differing age since-last-disturbance are simulated for each grid cell. It is assumed that each grid cell is large enough to accommodate a landscape in which the frequency of patches of different ages follows a negative exponential distribution with an expectation related to the current disturbance interval. This assumption is valid if grid cells are large relative to the average area affected by a single disturbance event and disturbances are a Poisson process, occurring randomly with the same expectation at any point across the landscape, independent of previous disturbance events. To account for disturbances and the resulting landscape structure, state variables of patches of different ages are averaged, and weighted by probability intervals from the negative exponential distribution. The resultant weighted average of, for example, total stem biomass or annual stem biomass turnover, is taken to be representative for the grid cell as a whole.

2.1.2 CABLE-POP

CABLE is a global land surface model consisting of five components (Wang et al., 2011): (1) the radiation module describes direct and diffuse radiation transfer and absorption by sunlit and shaded leaves; (2) the canopy micrometeorology module describes the surface roughness length, zero-plane displacement height, and aerodynamic conductance from the reference height to the air within canopy or to the soil surface; (3) the canopy module includes the coupled energy balance, transpiration, stomatal conductance and photosynthesis of sunlit and shaded leaves; (4) the soil module describes heat and water fluxes within soil and snow at their respective surfaces; and (5) the CASA-CNP biogeochemical model (Wang et al., 2010). In this study,

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we used CABLE-2.0 with the default the soil module replaced by the SLI soil model (Haverd and Cuntz, 2010).

As illustrated in Fig. 1, coupling between CABLE and POP is achieved by exchange of two variables: CABLE supplies annual stem biomass increment to POP and POP returns an annual stem biomass loss to CABLE. To convert between stem biomass (POP) and tree biomass (CABLE), we assume a ratio of 0.7, a representative average for forest and woodland ecosystems globally (Poorter et al., 2012). The resulting tree biomass turnover is applied as an annual decrease in the CABLE tree biomass pool, and replaces the default fixed biomass turnover rate.

CABLE-POP was run off-line at $1^\circ \times 1^\circ$ spatial resolution for gridcells containing the locations of forests in the Cannell–Usoltsev (C–U) database (see Sect. 2.2 on data below). Simulations were forced using GSWP-2 3 hourly meteorology for the 1986–1995 period (Dirmeyer et al., 2006). Leaf Area Index was prescribed using a monthly climatology from the MODIS Collection 5 product (Ganguly et al., 2008). Vegetation cover was prescribed as one of three of the CABLE plant functional types: evergreen Needleleaf; Evergreen Broadleaf or Deciduous Broadleaf. Needleleaf and broadleaf were distinguished based on the classification in the C–U database. All needleleaf forests were assumed evergreen and broadleaf forests were classified as deciduous or evergreen according to the larger area fraction specified in the vegetation distribution dataset by Lawrence et al. (2012). In cases with no information on either, a distinction was made by the location, with broadleaf forests north of 17° N assumed deciduous.

The modelling protocol was as follows: (i) CABLE soil moisture and temperature were initialised by running CABLE (without CASA-CNP) once for 10 yr (using the 10-yr meteorological data record); (ii) CABLE (without CASA-CNP) was run a second time for 10 yr from this initial state, this time with daily forcing inputs to CASA-CNP being saved, namely gross primary production, soil moisture and soil temperature; (iii) CASA-CNP was run for 400 yr (40×10 yr of repeated forcing) at daily time-step, with POP being called annually and initial biomass stores set to zero.

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2.2 Data

Forest inventory data for total biomass, stem biomass, foliage biomass and stem density were sourced from the Biomass Compartments Database (Teobaldelli, 2008). This database contains data from around 5790 plots and represents a harmonized collection of existing datasets (Cannell, 1982; Usoltsev, 2001), covering the temperate and boreal forest region globally. The data include the following compartments: stem, bark, branches, foliage, roots, fruits, dead wood and understorey. Latitudes and longitudes were rounded to the nearest degree centred on the half-degree and the data were separated into broadleaf and needleleaf groups, with “mixed forest” sites removed. Latitude/longitude duplicates were then removed separately for each of the needleleaf and broadleaf subsets, leaving all but one randomly selected occurrence in each $1^\circ \times 1^\circ$ gridcell. Data for a small number of tropical sites in the database were omitted as they did not contain all data required for our analysis. For comparison with model output, the data were further filtered, such that only plots with data for stem biomass, foliar biomass, stem density and age were retained, leaving 178 broadleaf plots and 304 needleleaf plots. Hereafter we refer to the data for these plots as the “C–U data”. Their locations are denoted in Fig. 2. Average stem biomass M_{stem} (kg tree^{-1}) and foliar biomass M_{fol} (kg tree^{-1}) per tree were obtained by dividing the bulk quantities by stem density (N). Total biomass per tree (M) was estimated as the sum of woody, foliar and fine root biomass, assuming allometric ratios of stem biomass to total woody biomass (0.7) (Widlowski et al., 2003), and fine root to foliar biomass (1.0) (Luyssaert et al., 2007).

In this study, we use the C–U database in three ways: (i) to construct a biomass-density ($\log(M)$ vs. $\log(N)$) plot for the purpose of calibrating the crowding mortality component of POP (Sect. 2.3 below); (ii) To construct leaf-stem allometry plots ($\log(M_{fol})$ vs. $\log(M_{stem})$) for the purpose of evaluating the CABLE-POP scaling exponent (slope) relating M_{fol} to M_{stem} , and for tuning the CABLE allocation coefficients to

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leaves and stems, to which the intercept is sensitive. (Sect. 3 below); (iii) to evaluate CABLE-POP predictions of stem biomass directly against data. (Sect. 3 below).

2.3 Calibration

The crowding mortality component of the POP model was calibrated using average biomass per tree (M) (kg dry matter per tree) and stem density (N) (trees ha^{-1}) data from the combined broadleaf and needleleaf data-sets. These variables can be plotted in the form of the self-thinning “law” (e.g. Westoby, 1984):

$$\log_{10}(M) = \alpha + \beta \log_{10}(N) \quad (7)$$

which describes the ageing trajectory of forest stands after they exit the initial density-independent growth phase and before the stand is sufficiently self-thinned that mortality becomes density-independent. (Hereafter all log functions refer to \log_{10}). The self-thinning part of the trajectory forms the upper bound of a plot of $\log(M)$ vs. $\log(N)$ (Fig. 3), with points below this upperbound resulting from young stands in the density-independent growth phase and additional disturbance-related mortality beyond that described by self-thinning. Thirty evenly-spaced points along this upper bound were selected for POP calibration. The coefficients in Eq. (7) were estimated from these points using reduced major axis (rma) regression (e.g. Sokal and Rohlf, 1995, Sect. 14.13) and treated as observations. The corresponding model observables were constructed from stand-alone POP simulations of stands with the same age and CABLE-estimated annual stem increment (hereafter StemNPP) as the observations, and with a high initial stem density (3 individuals m^{-2}) to accelerate the progress of young stands towards self-thinning behaviour. The residuals between modelled and observed coefficients of Eq. (7) were minimised by optimising the f_c parameter (Eq. A19) using the PEST parameter estimation software (Doherty, 2004) which implements the Levenberg–Marquardt down-gradient search algorithm. This returned a value of $f_c = 0.013 \pm 0.007$ (1σ). All other POP parameters were held fixed at their prior values (Haverd et al., 2013) to ensure that the model parameter set is equally valid for the savanna landscape (to

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(with density highly dependent on initial stem density, the variability of which is not captured in POP); (ii) very old stands of declining biomass in which N is decreasing while M is approximately constant (The total biomass of a very old stand ultimately declines, in part due to reduced productivity arising from physiological decline and nutrient limitations (Dewar, 1993; Gower et al., 1996). In a global context, this effect will be important mainly in the few global regions in which natural disturbance regimes and human management scarcely limit mean stand age. For this reason, and in the interest of model parsimony, we do not attempt to represent a declining biomass trend in very old stands here.); (iii) stands which have undergone managed thinning, particularly prevalent amongst needleleaf stands. Hence the discrepancy between linear fits to the predictions and observations (Table 1) is expected.

In contrast, the linear fits to the CABLE-POP predictions and observations in the leaf-stem allometry plots ((iii) and (iv)) (See also Table 1) agree very well, and generally better than the corresponding fits derived for other LSMs by Wolf et al. (2011). Note here that M_{fol} and M_{stem} are average foliage and stem biomass per tree (kg DM tree^{-1}).

As noted by Wolf et al. (2011), a major impediment to validating models directly against measured biomass is the need to consider the many idiosyncrasies of each forest stand (eg species mix; climate; water/nutrient limitations; timing of disturbances; management). Nonetheless CABLE-POP simulations of biomass in broadleaf forest stands (Fig. 4v) are largely unbiased (slope = 0.94 ± 0.04 when intercept set to zero) and capture a high proportion of the variance ($r^2 = 0.57$). Total biomass in needleleaf stands (Fig. 4vi) is less well predicted (slope = 0.94 ± 0.3 when intercept set to zero; $r^2 = 0.23$), a likely consequence of intensive management, particularly deliberate thinning. This is done for economic reasons (e.g. Aruga et al., 2013) or to promote stand health (e.g. Ronnberg et al., 2013) and would reduce tree-density while leaving the average stem-biomass initially unaffected, resulting in a shift to the right for affected stands in Fig. 4ii (consistent with the high density of outliers). This would also explain the overestimation of low biomass stands by CABLE-POP in Fig. 4vi because biomass would be removed in the early stages of a stand. Furthermore, as stated by

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Law et al. (2013), multi-stage thinning can also lead to an enhanced storage of long-term biomass, which explains why CABLE-POP overestimates the younger stands' biomass but does not reach the maximum values of the Needleleaf stands in the C–U data.

Figure 5 shows biomass component fractions extracted from CABLE-POP patch-scale simulations, and compared with estimates derived from the Cannell and Usoltsev databases by Wolf et al. (2011). The CABLE-POP simulations reproduce the major features of the data, particularly the sharp decline in the fraction of foliage biomass, and the relatively large foliage biomass fraction associated with Needleleaf stands compared to Broadleaf stands. The root component is dominated by the coarse root fraction, which in our simulations was a constant proportion of woody biomass. Therefore we do not expect CABLE-POP to reproduce the observed decline in root : shoot ratio with total biomass.

4 Discussion

4.1 POP mortality dynamics

Figure 6 illustrates the dynamic behaviour of POP mortality via stand-alone POP simulations of two undisturbed patches with low and high extremes of annual stem biomass increment: $\text{StemNPP} = 0.05 \text{ kgCm}^{-2}\text{yr}^{-1}$ (low production) and $\text{StemNPP} = 0.20 \text{ kgCm}^{-2}\text{yr}^{-1}$ (high production). For reference, CABLE simulations of the C–U stands give average annual stem biomass increments of $(0.17 \pm 0.06 \ 1\sigma)$ (Broadleaf) and $(0.16 \pm 0.05 \ 1\sigma)$ (Needleleaf) $\text{kgCm}^{-2}\text{yr}^{-1}$. Figure 6i shows the ageing trajectory of each patch in biomass-density space, with points representing every fifth year. The low-production patch exhibits an initial increase in density as recruitment augments the population during initial years (Fig. 6vii), before rapidly transitioning to a regime of declining stem density, characterised by a slope of -1 , as resource-mediated stress induces mortality, cancelling any net increase in stand biomass (Fig. 6v). The ageing tra-

gent property in POP – increases with stand age before reaching an equilibrium value which differs between stands of differing productivity. In accordance with the discussion of Wolf et al. (2011), this suggests that Big-Wood models cannot be expected to perform well for globally important young forest stands, instead being more applicable to relatively rare older stands at equilibrium biomass.

A second limitation of Big-Wood models, also emphasized by Wolf et al. (2011), is that they are not readily amenable to validation against forest inventory data, such as those used in this study. This is because they do not carry information about tree density. Wolf et al. attempted to circumvent this problem by applying a fit to biomass-density ($\log(M)$ vs. $\log(N)$) as a post-hoc estimate of density, which was then used to evaluate component biomass per tree, as required e.g. for the leaf-stem allometry plots (Fig. 4iii and iv). (Results are denoted other LSMs in these plots.) N was thus estimated using:

$$\log(N) = -\alpha/(\beta + 1) + \log(M \times N)/(\beta + 1) \quad (8)$$

Where $M \times N$ is total biomass, and β , α are the slope and intercept of a reduced major axis regression fit to $\log(M)$ vs. $\log(N)$ observations for the whole (global) dataset (Fig. 4). As an approach for estimating N at a grid cell level, this assumes that forests throughout the world are following the same log density-log biomass trajectory. We suggest this is unlikely, as individual stands may be expected to follow different trajectories depending on productivity and age, as illustrated in Fig. 6 and discussed above. We applied Eq. (8) to CABLE-POP gridcell estimates of total biomass to derive a post-hoc prediction of stem density, and hence average foliage and stem biomass per tree, analogous to the approach of Wolf et al. (2011). Results are shown in Fig. 7, and indicate that the grid-cell results (deduced via Eq. (8) with $\alpha = 6.22$ and $\beta = -1.32$ (Wolf et al., 2011, Table 5)) lie on a significantly different line to the patch-level CABLE-POP simulations (individual points shown in Fig. 4iii,(iv)), for which the internal model stem density was used to deduce average foliage and stem biomass per tree. The same was true when values of $\alpha = 6.9$ and $\beta = -1.44$ were used, corresponding to a fit to $\log(M)$

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vs. $\log(N)$ used in the present study (Fig. 3). Allometric data from global forest inventories are thus of limited value for evaluating/constraining Big-Wood models, which do not carry number-density information.

DVMs and biogeochemical LSMs coupled to Earth system models or forced by GCM climate fields and applied globally typically show relatively good agreement with one another and with observation-based estimates of present-day ecosystem carbon balance and flux components (NPP, heterotrophic respiration and net ecosystem C balance) (e.g. Anav et al., 2013; Sitch et al., 2008). When simulations are extended into an emissions-driven future climate projection, however, the predicted global fluxes diverge markedly between models, both in the magnitude and shape (sign, timing of change) of the subsequent trajectory (Ahlström et al., 2012; Anav et al., 2013). One cause of such divergence is that models, many employing a Big-Wood simplification for biomass dynamics, differ markedly in terms of woody biomass turnover and its response to future climate and CO_2 forcing. This in turn affects the rate of transfer of carbon to litter and soil organic carbon pools, where it subsequently decomposes (also with model-dependent turnover rates), returning carbon to the atmosphere as CO_2 . In projections with ESMs that account for carbon cycle feedbacks, this translates into divergence in the simulated climate (Friedlingstein et al., 2006, 2013). We concur with Wolf et al. (2011) and argue that Big-Wood models lack ecological realism and cannot be expected to simulate woody biomass turnover in a realistic manner under changing climate forcing. They should be phased out from use in carbon cycle studies.

5 Conclusion

The approach presented and demonstrated in this paper offers a potential alternative, suitable as a replacement for the Big-Wood approximation in large-scale models. Individual and population growth are treated separately, thus overcoming the main pitfall of the Big-Wood approach. Coupled to a biogeochemical land surface model, able to prognose woody biomass productivity at stand (or grid cell) level, POP may be cali-

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brated and evaluated against forest inventory data, as demonstrated in this study. This is achieved without a marked increase in model complexity or computational demand, thanks to a modular design that separates the role of the parent land surface model (prognosing whole-ecosystem production) and the population dynamics model (partitioning the production among cohorts, computing mortality for each, and returning the stand-level integral as whole-ecosystem biomass turnover to the parent model) (Fig. 1).

The present paper focuses on stand-level demographics and its influence on the accumulation and turnover of stem carbon biomass. At the landscape level, the incidence and intensity of disturbance events such as wildfires, storms or anthropogenic interventions such as forest harvest or land use conversions provide an additional, regionally important control on biomass accumulation and turnover (Shevliakova et al., 2009). Such landscape-level effects are accounted for by our model, for example along a rainfall-mediated wildfire and biomass gradient in savannah vegetation of northern Australia (Haverd et al., 2013).

Appendix A

Detailed description of POP

A1 State variables and governing equation

In POP, state variables are the sub-gridscale (patch-specific) densities of woody plant individuals N_y (m^{-2}) in age/size classes, with an arbitrary number of age/size cohorts, where y is the simulation year in which the cohort was created.

Population dynamics are governed by:

$$\frac{dN_y}{dt} = -(m_{R,y} + m_{C,y})N_y \quad (\text{A1})$$

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where $m_{R,y}$ and $m_{C,y}$ are cohort mortalities (yr^{-1}) due to resource limitation and crowding respectively. N_y is initialised as recruitment density, and is episodically reset (according to disturbance intensity) when the patch experiences disturbance. Below, we describe the formulations of: recruitment; biomass accumulation (partitioning of grid-scale stem increment amongst cohorts); cohort structure; mortality, disturbance and landscape heterogeneity. The model time-step (Δt) is 1 yr.

A2 Recruitment

A new cohort is created each year, with density (may be zero) given by:

$$N_y(y) = N_{\max}\mu(F) \quad (\text{A2})$$

where N_{\max} is the maximum establishment density expected under optimal conditions for seedling growth with assumed value of 0.2 m^{-2} . F is a proxy for growth conditions in the seedling layer, expressed as a fraction of optimum, set here as a function of (patch-dependent) stem biomass C (kg C m^{-2}), with an exponent of $2/3$ accounting for the proportional increase in resource-uptake surfaces (leaves and fine roots) relative to stem biomass assuming no change in linear proportions with size:

$$F = \exp\left(-0.6C^{2/3}\right) \quad (\text{A3})$$

The function $\mu(F)$ is a non-rectangular hyperbola, modified following Fulton (1991) to account for the reduction of recruitment to the adult population under conditions of growth suppression in the seedling population (essentially enhanced seedling mortality due to resource stress).

$$\mu(F) = \exp\left[\alpha\left(1 - \frac{2\theta}{F + 1 - \sqrt{(F + 1)^2 - 4\theta F}}\right)\right] \quad (\text{A4})$$

where θ is a shape parameter set to 0.95 and α is a shape parameter in the range 0.1–10 with higher values corresponding to a greater suppression of recruitment (e.g. in shade-intolerant tree species). A value of 3.5 fitted to data for Norway spruce (a shade-tolerant boreal tree) (Fulton, 1991) is adopted as a default value.

5 **A3 Biomass partitioning**

Stem biomass increment for each patch ΔC (kgCm^{-2}), is assumed equal to the grid-scale value, accumulated over the POP model time step $\Delta t(y)$. It is partitioned among cohorts as a basis for the characterisation of structure, in turn affecting survivorship and growth. An assumption may be made that individuals capture resources in a varying proportion to their size, following a power relationship to biomass with an exponent (s). As resource uptake, and therefore productivity, is essentially linked to surface area (of leaves and roots), and assuming no change in linear proportions with growth, then an exponent of 2/3 may be assumed.

On this basis, annual stem biomass increment may be partitioned among cohorts in proportion to the population-weighted current biomass of individuals within each cohort:

$$\frac{\Delta C_y}{\Delta t} = \frac{(C_y/N_y)^s N_y}{\sum (C_i/N_i)^s N_i} \frac{\Delta C}{\Delta t} \quad (\text{A5})$$

where C_y is the stem biomass summed across individuals of cohort N_y .

20 **A4 Cohort structure**

Cohort structure is characterised by height and canopy cover. Height (H_y , m) is determined from stem biomass by the allometric relations:

$$H_y = kD_y^{2/3} \quad (\text{A6})$$

(Huang et al., 1992; Smith et al., 2001), where D_y is mean tree stem diameter in m. A default value of 50 is chosen for the scaling coefficient k based on fitting Eq. A6 to height-diameter data for European tree species synthesised in Widłowski et al., 2003.

$$V_y = H_y \frac{\pi}{4} D_y^2 \quad (\text{A7})$$

(volume V_y of a cylinder, m^3 ; π the ratio of the circumference to the radius of a circle)

$$C_y N_y^{-1} = V_y \cdot \rho_w \quad (\text{A8})$$

(absolute stem biomass for an individual in cohort N_y , with wood density ρ_w set here to 300 kg m^{-3} .)

Combining Eqs. (A6)–(A8),

$$H_y = k^{3/4} \left(\frac{4C_y}{\pi \cdot N_y \rho_w} \right)^{1/4} \quad (\text{A9})$$

A5 Mortality

Mortality is defined as a proportional reduction in cohort density (Eq. A9). Adapting and simplifying the approach of the LPJ-GUESS DVM (Smith et al., 2001) we aggregate multiple causes of mortality in real tree stands within a generalised “resource limitation” mortality that increases with size (and therefore age) and under conditions of declining productivity, whether caused by interference in resource uptake among neighbours (Westoby, 1984), abiotic factors such as drought, or secondary biotic factors (e.g. pathogen attacks) (Franklin et al., 1987). Resource limitation leads to a decline in growth efficiency (GE, i.e. growth rate as a function of size), characterised by the ratio of stem biomass increment to current stem biomass for a given cohort. Below a certain threshold GE_{\min} , mortality increases markedly (Pacala et al., 1993). We characterise the response of resource-limitation mortality to growth efficiency by a logistic

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curve with the inflection point at this threshold:

$$m_{R,y} = \frac{m_{R,\max}}{1 + (GE_y/GE_{\min})^\rho} \quad (\text{A10})$$

where $GE_y = \Delta C_y / C_y^s$, s takes the same value as in Eq. (A5), and $m_{R,\max}$ is the upper asymptote for mortality as GE declines, set to 0.3 yr^{-1} following (Smith et al., 2001). The exponent ρ , assigned a default value of 5, governs the steepness of response around $GE = GE_{\min}$ which may be regarded as a calibration parameter.

An additional crowding mortality component ($m_{C,y}$) is included to allow for self-thinning in forest canopies. Self thinning is dependent on the assumption that some trees (within a cohort) have a slight advantage in pre-empting resources, creating a positive feed-back to growth, and ultimately resulting in death of the most suppressed individuals. In contrast, in POP, the total stem biomass increment for a cohort is equally partitioned amongst all members. Therefore we require the following new parameterization which emulates the contribution to self-thinning associated with within-cohort competition.

Crowding mortality is expressed as

$$m_{C,y} = \min \left[\frac{1}{\Delta t} \exp(\alpha_C(1 - 1/c_{pc,y}))f_c, \frac{\Delta C_y}{C_y \Delta t} \right] \quad (\text{A11})$$

such that it never exceeds growth. Here $c_{pc,y} = (1 - \exp(-A_{c,y}))$ is crown projective cover; $A_{c,y}$ crown projected area ($\text{m}^{-2} \text{m}^{-2}$) of all crowns in the y th and taller cohorts; α_C a coefficient which determines the onset of crowding mortality with respect to c_{pc} and f_c is a tunable scaling factor. α_C was set to 10.0, corresponding to an onset of crowding mortality at $c_{pc} \sim 0.8$. This value was chosen to be sufficiently high such that crowding mortality is insignificant in the Australian savanna simulations (Haverd et al., 2013), thus retaining the validity of the parameters relating to m_R in Eq. (A10) as

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used in this earlier study. Crown projected area is evaluated as

$$A_{c,y} = N_y k_{\text{allom}} D_y^{k_{\text{rp}}} \quad (\text{A12})$$

where N_y is stem density (m^{-2}); D_y is stem diameter at breast height (m), and k_{allom} and k_{rp} are parameters set to respective values of 200 and 1.67, based on literature values compiled by Widlowski et al. (2003).

Additional mortality occurs as a result of disturbances, see below.

A6 Disturbance and landscape heterogeneity

Landscape heterogeneity is accounted for by simulating a number of patches (within a grid-cell) which differ by age (time since last disturbance). Each grid-cell state variable (eg stem biomass) is computed as a weighted mean of the patch state-variables, with patch-weight corresponding to the probability (p) of the patch occurring in the landscape. Disturbance is treated as a Poisson process, with time (x) since last disturbance distributed exponentially amongst the patches, according to the grid-cell mean disturbance interval (λ):

$$p(x) = \lambda \exp(-\lambda x) \quad (\text{A13})$$

In this work we held λ fixed in time, but it could also be prescribed a time-dependent variable.

Disturbances (periodic events that recur randomly at the local scale, destroying all (catastrophic disturbance) or a fraction of biomass (partial disturbance) in a patch) significantly affect biomass residence time, vegetation structure and thereby resource use and productivity at a large spatial scale. At the level of a grid cell or large landscape, patches of different ages (years since last disturbance) should occur at frequencies corresponding to the expected likelihood of a local disturbance sometime in the corresponding period, given a known expected disturbance return time. The latter is prescribed in this work, but could be computed prognostically, e.g. by a wildfire module incorporated within CABLE.

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A partial disturbance event in an affected patch is simulated by removing a size-dependent fraction of the biomass (and hence stems) in each cohort. In this work this fraction is specified using an observation-based relationship between tree size and the probability of tree survival following a fire of specified intensity (see Appendix A3). Following either type of disturbance event (catastrophic or partial), recruitment occurs and the patch persists in the landscape and its age since the particular type of disturbance is set to zero.

Importantly, patch weightings by age are evaluated after growth, recruitment, non-disturbance related mortality and disturbance. It is particularly important that the weightings be calculated after disturbance: otherwise patches of age zero would not be represented.

Vegetation structure changes more from year to year early in vegetation development following a disturbance than later. After a period corresponding to a few average tree generation times, a steady state is reached with no further net changes in vegetation structure (provided there are no trends in forcing data). To strike a balance between computational efficiency and “accuracy” in characterising landscape structure, we simulate patches with a sequence of ($n_{\text{age_max}} = 5\text{--}7$) maximum ages with equally-spaced cumulative probabilities (assuming an exponential distribution of patch ages, with expected value equal to the mean disturbance interval). To ensure a wide spread of ages in any given year, we additionally simulate ($n_{\text{patch_reps}} = 4\text{--}7$) replicate patches for each maximum age, with the first disturbance occurring in year $1a, 2a, 3a \dots n_{\text{patch_reps}}a$, and thereafter every “ $n_{\text{patch_reps}}a$ ” years (where “ $n_{\text{patch_reps}}a$ ” is the maximum age of the patch).

A7 Patch weightings

Each patch is characterised by time since last disturbance and its weighting in the landscape is given by the probability of this age occurring in an exponential distribution. When two disturbance types (catastrophic and partial) are considered, each patch is characterised by two ages corresponding to times since each disturbance type and two

weights, one for each age. The patch weighting is then the product of the weights for each age, divided by the number of patches with the same combination of two ages, and normalised such that patch weights sum to one.

We evaluate weights for each unique time since each disturbance as follows: First we construct an ordered list of n_{age} unique ages since last disturbance. Each unique age a_i is associated with lower and upper integer bounds ($b_{l,i}$ and $b_{u,i}$), spanning the range of ages to be represented by a_i . These bounds are set as follows:

$$b_{l,i} = \begin{cases} 0, & i = 1 \\ a_i, & i > 1, a_{i-1} = a_i - 1 \\ b_{u,i-1} + 1, & i > 1, a_{i-1} \neq a_i - 1 \end{cases} \quad (\text{A14})$$

$$b_{u,i} = \begin{cases} 0, & a_i = 0 \\ a_i, & (i = 1, a_i > 0) \text{ or } (i > 1, a_{i-1} = a_i - 1) \\ \text{int}[(a_i + a_{i+1})/2], & 1 < i < n_{\text{age}} \\ a_i, & i = n_{\text{age}} \end{cases} \quad (\text{A15})$$

The weighting for each age a_i is evaluated as the sum of the exponential frequencies, $w = \lambda \exp(-\lambda x)$ (where λ is the expectation value of the time since disturbance and x the integral age), of integral ages from $b_{l,i}$ to $b_{u,i}$ inclusive.

A8 Tree foliage projective cover

Tree foliage projective cover is calculated following (Haverd et al., 2012) as $1 - P_{\text{gap}}$, where P_{gap} is defined here the probability of radiation penetrating the entire canopy from directly above (i.e. zero zenith angle):

$$P_{\text{gap}} = e^{-\lambda A_c (1 - P_{\text{wc}})} \quad (\text{A16})$$

In Eq. (A23), λ is the number density of crowns; A_c is the projected area of a crown envelope (i.e. an opaque crown) and P_{wc} is the mean expected gap (or porosity) through

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a single crown or partial crown. The overbar denotes a mean over the distribution of crown heights and dimensions: thus $\overline{A_c(1 - P_{wc})}$ is the mean area of the projected objects that fill the crown volume. Crowns are approximated as spheroids. We assume that crown horizontal and vertical diameters are monotonic functions of tree height (h), such that the mean projected area is:

$$\overline{A_c(1 - P_{wc})} = \int_{h_{\min}}^{h_{\max}} A_c(h)(1 - P_{wc}(h))\rho(h)dh \quad (\text{A17})$$

where $\rho(h)$ is the tree height probability distribution and h_{\min} and h_{\max} are the lower and upper extremes of the tree heights. The crown porosity P_{wc} is approximated as:

$$P_{wc} \approx e^{-GF_a s_{\text{mean}}}. \quad (\text{A18})$$

Here G is the projection of the leaf area in the direction of the beam (assumed here to be 0.5, corresponding to a spherical leaf angle distribution) and s_{mean} is the mean path length through the crown approximated as

$$s_{\text{mean}} = V/A_C \quad (\text{A19})$$

with V the crown volume and F_a is the foliage area volume density, equated here with the ratio of tree LAI to total crown volume. We assumed a vertical to horizontal crown radius ratio of 1.5.

Supplementary material related to this article is available online at <http://www.biogeosciences-discuss.net/11/2343/2014/bgd-11-2343-2014-supplement.zip>.

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Table 1. Reduced major axis regression coefficients associated with biomass-density, leaf-stem allometry and stem biomass plots of Fig. 4.

	slope	intercept	R^2	N
$\log(M)$ vs. $\log(N)$, C–U (BL)	-1.63 ± 0.07	6.95 ± 0.24	0.70	178
$\log(M)$ vs. $\log(N)$, CABLE-POP (BL)	-1.91 ± 0.05	8.47 ± 0.17	0.90	178
$\log(M)$ vs. $\log(N)$, C–U (NL)	-1.57 ± 0.06	6.7 ± 0.18	0.66	304
$\log(M)$ vs. $\log(N)$, CABLE-POP (NL)	-1.52 ± 0.02	6.99 ± 0.09	0.92	304
$\log(M_{\text{fol}})$ vs. $\log(M_{\text{stem}})$, C–U (BL)	0.69 ± 0.02	-0.89 ± 0.04	0.84	178
$\log(M_{\text{fol}})$ vs. $\log(M_{\text{stem}})$, CABLE-POP (BL)	0.64 ± 0.02	-0.96 ± 0.02	0.85	178
$\log(M_{\text{fol}})$ vs. $\log(M_{\text{stem}})$, C–U (NL)	0.74 ± 0.02	-0.60 ± 0.04	0.79	304
$\log(M_{\text{fol}})$ vs. $\log(M_{\text{stem}})$, CABLE-POP (NL)	0.68 ± 0.01	-0.59 ± 0.02	0.94	304
*CABLE-POP stem-biomass vs. CU stem-biomass (BL)	0.94 ± 0.04	0	0.57	178
*CABLE-POP stem-biomass vs. CU stem-biomass (NL)	0.99 ± 0.04	0	0.24	304

* Standard linear regression, with intercept forced through zero.

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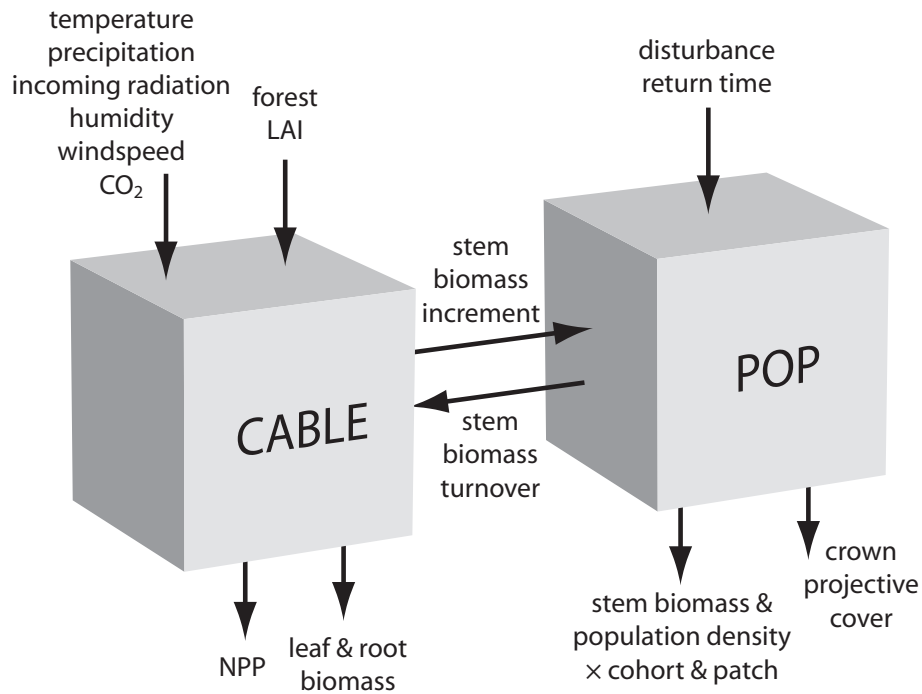


Fig. 1. Coupling of CABLE and POP, along with key inputs and outputs.

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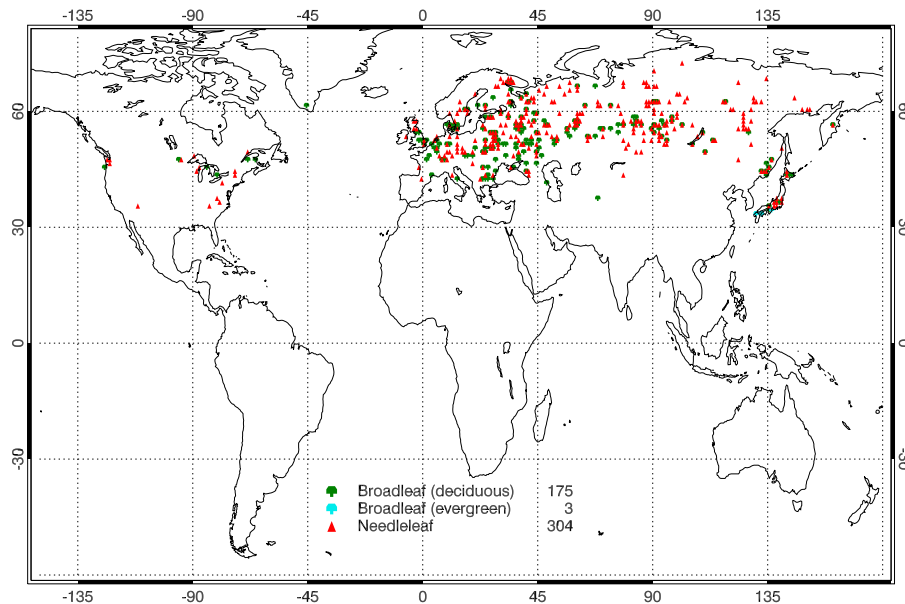


Fig. 2. Locations of forest stands used for CABLE-POP calibration and evaluation.

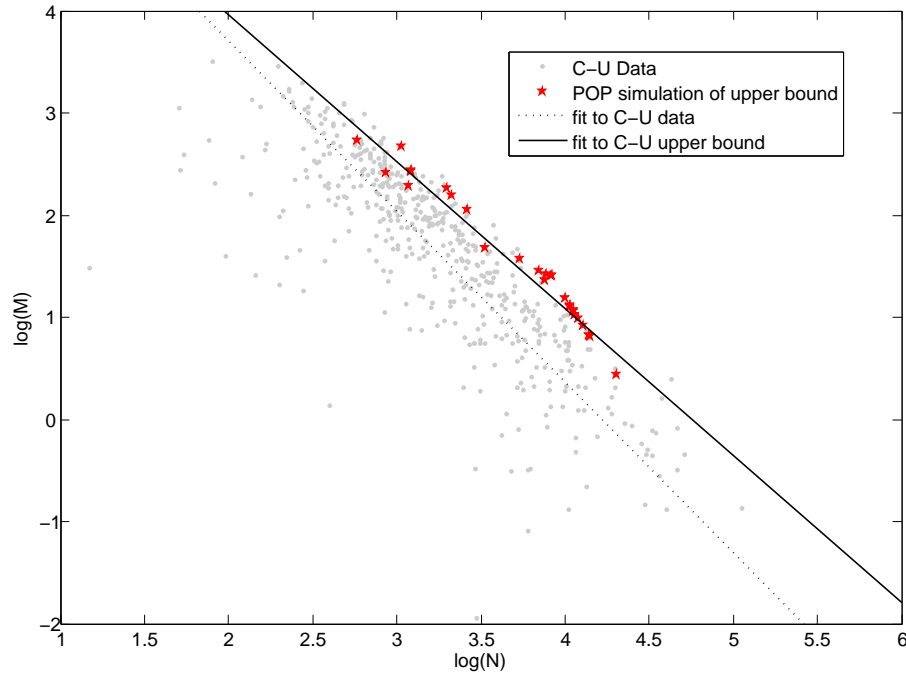


Fig. 3. POP calibration. Biomass-density plot, showing all the points in the CU data; a linear fit to all the CU-data; a linear fit to 30 data points lying along the upper-bound; POP simulations of patches with the same age and StemNPP as the 30 data points lying along the upper bound.

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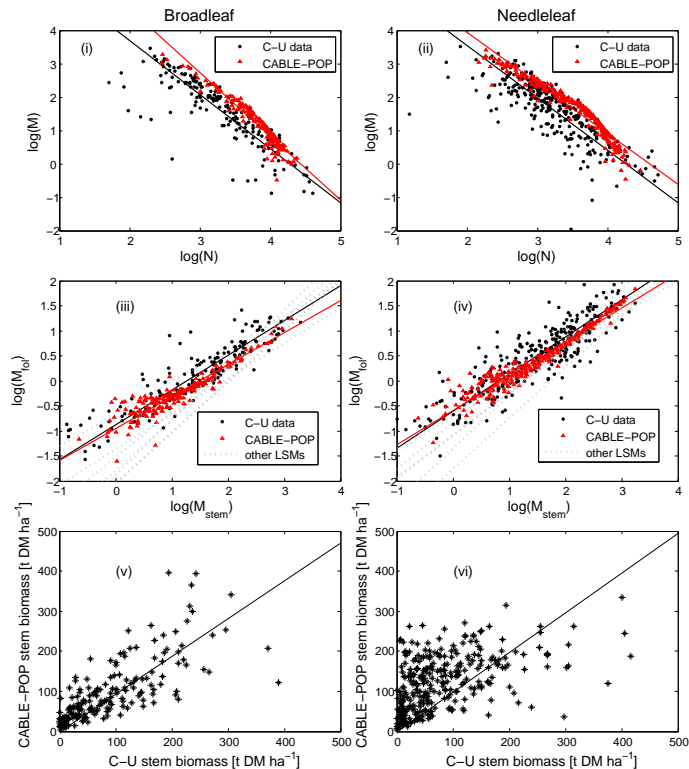


Fig. 4. Evaluation of CABLE-POP predictions against Cannell–Usoltsev Data, separated into Broadleaf and Needleleaf classes: **(i)**, **(ii)** Biomass-Density plot; **(iii)**, **(iv)** Leaf-Stem allometry plot (M_{fol} and M_{stem} are average foliage and stem biomass per tree (kg DM tree^{-1})), including results derived for other LSMs by Wolf et al. (2011); **(v)**, **(vi)** Total biomass: predictions vs. observations. In **(i–iv)**, lines denote linear fits to the observations and predictions. Solid lines denote linear regression fits to the data points (see Table 1 for regression coefficients.)

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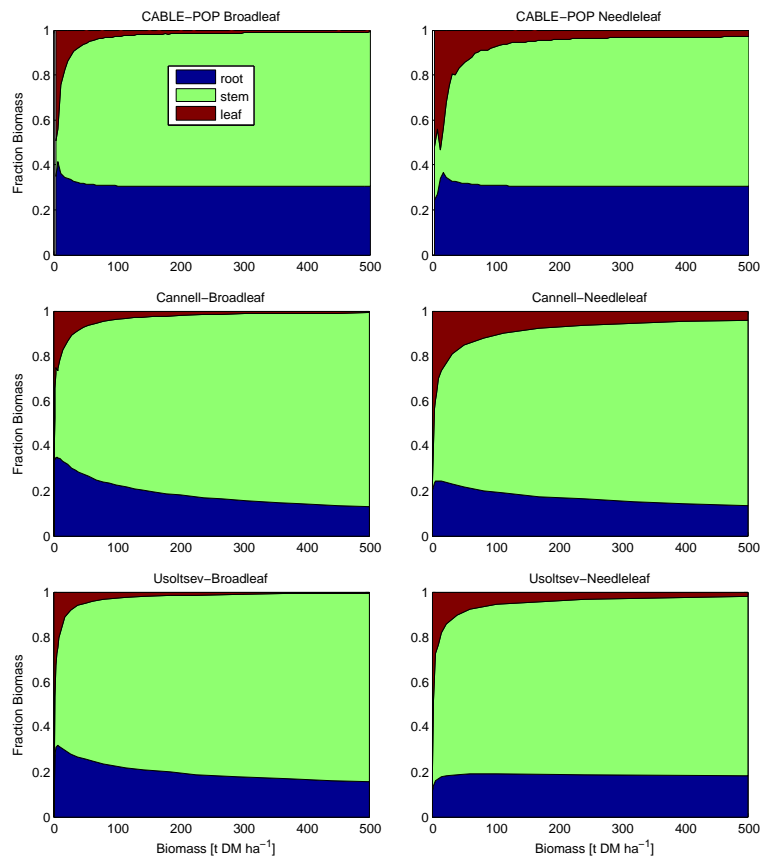


Fig. 5. Biomass component fractions as a function of total biomass: Top: CABLE-POP patches; Middle and Bottom: data-derived estimates reproduced from Wolf et al., 2011.

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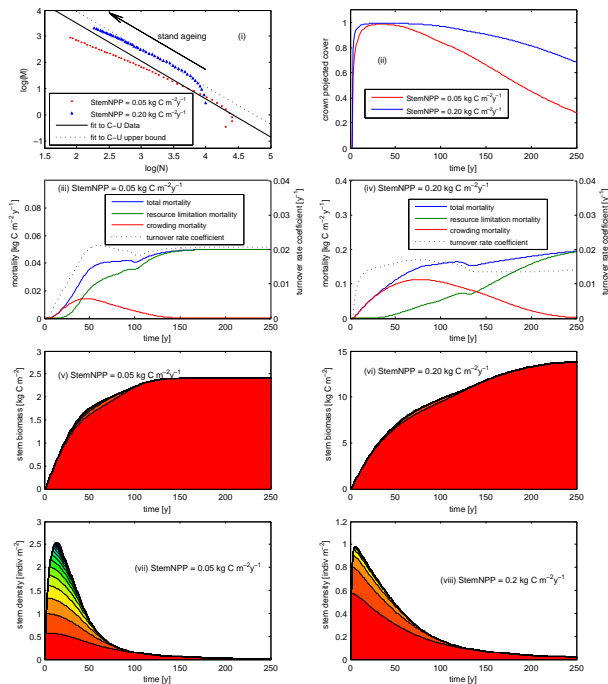


Fig. 6. POP dynamics, as illustrated by undisturbed patch simulations at low and high extremes of annual stem increment ($\text{StemNPP} = 0.05 \text{ kg C m}^{-2} \text{ yr}^{-1}$ and $\text{StemNPP} = 0.20 \text{ kg C m}^{-2} \text{ yr}^{-1}$). (i) Biomass-density plot, showing the ageing trajectories of each patch (every 5th year plotted). Linear fits to the C–U data and its upper bound are shown for reference; (ii) Time course of crown projective cover for each patch; (iii), (iv) Time course of mortality, its components, and turnover rate coefficient for patches with low (iii) and high (iv) annual stem increments; (v), (vi) Time course of stem biomass for patches with low (v) and high (vi) annual stem increments. Solid lines indicate contributions from different cohorts; (vii), (viii) Time course of stem density for patches with low (vii) and high (viii) annual stem increments. Solid lines indicate contributions from different cohorts.

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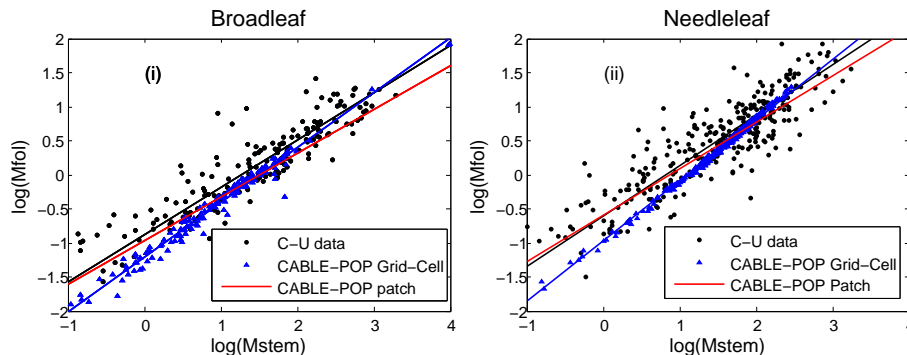


Fig. 7. Leaf-Stem allometry plots for **(i)** Broadleaf and **(ii)** Needleleaf pfts. C–U data and CABLE-POP patch results are the same as in Fig. 4iii and iv. CABLE-POP Grid-Cell results are by deducing stem density from total grid-cell biomass (average over multiple patches, weighted by probability of time since last disturbance with a mean disturbance interval of 100y) via Eq. (8), and using this to compute M_{fol} and M_{stem} from grid-cell foliage and stem biomass components.

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