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FullCAM: building capability via data-informed parameters

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Acknowledgments

1 Background

The objective of this study was to draw on recent research and new datasets to update some of the key parameters used in FullCAM for simulation of carbon (C) fluxes within forest systems. This work complements changes made to maximum aboveground biomass calibrations (M, Roxburgh *et al.* 2017); a key parameter used in FullCAMs Tree Yield Formula, TYF.

1.1 Allocation of biomass

How FullCAM simulates allocation of biomass

With the exception of some algorithms used in the predicting accumulation of aboveground biomass via site-productivity modifiers of the Tree Yield Formula (TYF), FullCAM is an empirical model. It does *not* predict the balance between partitioning of photsynthate and turnover of tissues that result in allocation of biomass to components (Thornley 1972; Thornley & Johnson 1990; Bijlsma & Lambers 2000; Yang and Midmore 2005; Barnes *et al.* 2007). For example, in process-based models, foliage and fine roots have a high partitioning of photsynthate, but a relative low allocation of biomass because of high turnover rates of these tissues (e.g. Wardlow 1990; Mooney 1991; Poorter *et al.* 2011). Instead, FullCAM's allocation input table is utilised to apply simple empirically predicted allometric scaling (Cheng & Niklas 2007; Yang & Luo 2011; Niklas & Enquist 2001). This time-series input table specifies biomass allocation for each year of growth, thereby enabling the prediction of how growth is attributed to the six components of biomass over time: stem, branches, bark, foliage, coarse roots and fine roots. There are alternative units of data input available. Generally, the units used in the allocation input table are growth increments of branches, bark, foliage, coarse roots and fine roots components relative to that of the stem, with the input for stem thereby being 1.00 at each time step.

Why accurate simulation of allocation of biomass is important

There are three main reasons why accuracy of the allocation input tables in FullCAM is important, and therefore why it was important to refine these parameters based on a recently expanded datasets of biomass partitioning. Allocation of biomass:

1. Governs the prediction of belowground biomass (BGB). For aboveground biomass (AGB), allocation input tables only adjust the relative allocation to wood, branches, bark and foliage, with the total AGB being set by FullCAM's TYF. In contrast, predicted BGB is determined by allocation to coarse and fine roots as defined in the allocation input table.

2. Determines the management- or disturbance-induced impacts on C stocks. Accurate biomass allocation predictions are important when predicting changes in on-site C stocks following events such as fire, pruning, thinning or harvesting. This is because these events affect the different pools of biomass in different ways.

3. Determine allocation to the fast-turnover pools of foliage and fine roots. For forests with high initial rates of growth (e.g. dense belt plantings), allocation to the high turnover foliage and fine roots components in the first 2-3 years of growth coincided periods of with peak growth rates. Previously under such scenarios, an unrealistically large transfer to C into the debris pool was simulated, thereby highlighting issues with the original defaults for allocation of biomass in some forest systems.

Approach required to revise allocation of biomass parameters

As outlined by DoEE (2016, Section 6.4.2.1 & 6.5.1.1), the original defaults used in the allocation input tables of FullCAM were based on expansion factors reported in Snowdon *et al.* (2000) and Mokany *et al.*

(2006). Each of the 51 different forest types simulated in FullCAM had an input table for allocation of biomass. In addition, the 16 tree species comprising the various hardwood plantations, and the seven tree species comprising the various softwood plantations, had low, medium and high productivity classes in which a multiplier for the allocation of biomass to stem wood was set to 0.95, 1.00 and 1.05, respectively (DoEE 2016). Hence, for plantations, allocation of biomass varied not only with species, but also with productivity.

Expansion factors reviewed by Snowdon *et al.* (2000) and Mokany *et al.* (2006) were useful to provide guidance on broad estimates of total AGB relative to stem wood, or of the ratio of BGB_C:AGB. Since then, new datasets from Australian forests have become available to inform comprehensive empirical models of allocation of biomass. The approach used in this study was to analyses these new collated datasets on allocation of AGB and BGB components of trees and shrubs. In this analysis, three main considerations were required:

1. *Influence of forest type.* To account for differences in allocation between forest types, three separate datasets on AGB and BGB sampling were collated:
    I. Mixed-species environmental plantings (which contain many species of both trees and shrubs), and plantations of mallee eucalypt trees. A large database of biomass sampling and analysis for these systems was already conducted by Paul & Waterworth (2015), and so was briefly outlined here.
    II. Native forests or woodland systems, grouped into those from low rainfall regions (mean annual rainfall, MAR<500 mm yr^{-1}) or high rainfall regions (MAR≥500 mm yr^{-1}). These datasets were collated by Paul *et al.* (2016).
    III. Other monoculture tree plantations, grouped into hardwoods (e.g. *Eucalyptus globulus, E. grandis, E. pilularis* etc.) or softwoods (e.g. *Pinus radiata, P. pinaster* etc.). These datasets were also collated by Paul *et al.* (2016).

2. *Influence of climate and management factors.* While allometric equations using the diameter of the stem to predict *total* AGB or BGB are generic in that they are relatively insensitive to regional variations in climate and stand management (Paul *et al.* 2016), this is not the case when such allometric equations are developed to predict *components* of biomass; they are less generalizable (e.g. Forrester *et al.* 2017). For example, biomass partitioning has been shown to vary with stand age, height, soil moisture and fertility, and climate factors (e.g. Hui *et al.* 2014). This suggests that for FullCAM to accurately predict biomass of components across different forest types, the allocation input tables used in FullCAM need to be informed by empirical allometrics models that account for such impacting factors.

3. *Scaling-up to the individual- to stand-scale.* As FullCAM models the stand as a whole, the allocation input tables are required to be at the stand-scale. However, measurements of biomass components are made at the scale of the individual tree or shrub. Factors influencing allocation at the stand-scale (e.g. stand density, mix of species) may differ to those influencing allocation at the individual-scale (e.g. size). For mixed-species plantings such as environmental plantings, or for native systems, a two-step process to estimation of stand-scale allocation of biomass is therefore required; (i) analysis at the individual-scale, and; (ii) applying these to the stand-scale based on the species mix and their densities/size.

1.2 Litter fall

How FullCAM simulates litter fall

In FullCAM turnover parameters (% DM yr^{-1}) are used to simulate turnover of branches, bark and foliage, and slough of coarse and fine roots. There is much more data available on litter fall than the more resource-intensive process to measure of root slough. Hence, the approach used to revise root turnover

rates is outlined separately (see Section 1.4), with the focus here being on dataset collation from litter trap studies that monitored turnover of branches, bark and foliage.

There are two other processes of note in FullCAM with regard to turnover:

1. Turnover of stem wood is modelled separately via FullCAM's tree mortality parameters. These mortality parameters are generally rarely utilised, e.g. DoEE (2016). This is because FullCAM's TYF already inherently encompasses natural cycles of mortality-regeneration given these yields are calibrated to observations of AGB in remnant native forests or woodlands, with such stands having been naturally impacted by disturbances such as fire and prolonged droughts (Roxburgh *et al.* 2017). In addition, simulated events of fire or thinning enable the explicit simulation of stem mortality, thereby providing a more realistic 'disturbance-event-based' simulation of mortality of stems.

2. FullCAM had functionality for the user to input a maximum (or cap) on the AGB, such that when the model predicts AGB accumulation values that are in excess of this maximum value, each pool of biomass are assumed to 'drop' the excess C into turnover. This was assumed to occur for all pools of biomass: stem wood; branches; bark; foliage, and; coarse and fine roots. However, given recent work to significantly improve the confidence in FullCAM-predicted maximum AGB (Roxburgh *et al.* 2017), and given that this process of simulation of turnover to facilitate the a user-imposed 'cap' of AGB is unrealistic, this functionality was recently removed in FullCAM.

Why accurate simulation of litter fall is important

In FullCAM, the TYF models empirically observed *yields* of accumulation of biomass (Roxburgh *et al.* 2017). Hence, as outlined above (Section 1.1), in contrast to process-based models (e.g. 3PG) that explicitly simulate net primary production, in FullCAM, live pools of AGB and BGB are simulated independently of turnover, with additional C effectively being 'created' via assumptions made regarding turnover rates. Hence, in FullCAM, turnover inputs are very important given they contribute to the assumptions about net primary production, or the net 'capture' of C from plants on-site.

Having accurate simulation of rates of litter fall is therefore important in FullCAM as they affect the predicted input of C into debris: a significant C stock under forests. Furthermore, litter fall rates not only influence the amount of C entering the debris, but also the composition of the debris pool with regard to the relative contribution of decomposable debris (e.g. foliage litter) and more resistant debris (e.g. deadwood). Depending on its size and composition, the debris pool can make a significant contribution to net emissions following harvesting or fire events. The size and composition of the debris pool in turn also affects the input of C into soil: another significant C stock under forests.

Approach required to revise litter fall parameters

The original values applied to turnover rates of each plant component are shown in Table 6.14 of DoEE (2016). It was therefore timely to revise these input parameters given a recent review of litter trap field studies (Paul *et al.* 2017b; England *et al.* 2017) greatly expanded a previous Australian database of turnover rates under forests (Paul *et al.* 2004; Paul and Polgase 2004a).

1.3 Decomposition of litter

How FullCAM simulates decomposition of litter

Although modelling the inputs of C to the debris is relatively straightforward (simple turnover rates), modelling the outputs of C is relatively complicated. There are three separate processes, and corresponding sets of FullCAM parameters, that drive rates of decomposition of debris:

1. Substrate quality, i.e. the potential split of debris into decomposable (fast decomposing) and resistant (slow decomposing) pools;

2. Breakdown rates (% DM yr^{-1}) of the various pools of debris, both above the ground in the litter, and below the ground as dead roots, and;

3. Climate impacts, i.e. the influence of temperate and rainfall on these rates of decomposition.

There is much more data available on decomposition of litter (which tends to occur largely on the soil surface) than that available on root decomposition (which occurs within the soil, and probably varying greatly with soil depth). Measurement of root decomposition is much more resource-intensive than measurement of litter decomposition. Hence, the approach used to revise root decomposition rates was outlined separately (see Section 1.4), with the focus here being on dataset collated from litter bag studies that monitored decomposition of deadwood, bark litter and foliage litter.

Why accurate simulation of decomposition of litter is important

As per litter fall (Section 1.2), having accurate simulation of rates of litter decomposition is important in FullCAM as it affect both the size and composition of the debris pool: a significant C stock under forests, and one influencing emissions following harvesting or fire events. Additionally, decomposition of debris is particularly important as it affects the emissions of CO_2-C on decomposition, and thereby the C remaining on-site post decomposition that is assumed to become the soil C input. Indeed, the impact of the C inputs to the soil via changes in debris and its decomposition, and how this is influenced by land use or management, will have a significant impact on net sequestration of C in soil (e.g. Paul and Polglase 2004b).

Approach required to revise litter decomposition parameters

As outlined by DoEE (2016, e.g. Table 6.15), the original decomposition rates for the different pools of debris were drawn from the best available information, including Mackensen *et al.* (2003), Mackensen and Bauhaus (1999), O'Connell (1997) and Paul and Polglase (2004a). But recent work on reviewing field studies with litter bags (England *et al.* 2017) has greatly expanded the database of forest litter decomposition rates based on that previously available. Given this, it was timely to revise these input parameters.

1.4 Parameters influencing soil C

How FullCAM simulates soil C under forests

In FullCAM, predicted stocks of soil C are the result of the balance between predicted inputs of C to the soil from decomposition of debris, and the predicted output of C due to turnover of soil pools. The latter process of soil C turnover (i.e. and therefore loss of CO_2-C from the soil C pools) is simulated in FullCAM using the RothC sub-model. RothC simulates pools of differing rates of decomposition. The inert soil C pool (IOM) changes relatively little, but can be determined via measurement (Baldock *et al.* 2013a,b). The two largest pools (RPM and HUM) have the slowest rates of decomposition, and are the most important to parameterise, with this being facilitated via their measurement (Baldock *et al.* 2013a,b). The two smallest pools (BIO and DPM) have high rates of turnover, and are relatively unimportant to parameterise. Like decomposition of debris, turnover of pools of soil C are influenced by climate in accordance with RothC algorithms. However, in the RothC sub-model, turnover rates of pools of soil C are also influenced by the clay content of the soil.

Why accurate simulation of soil C is important

Soil is the largest stock of C in many forests, and many pools of soil C significantly change in response to land use change, or changes in management. However, the modelling of stocks of soil C is complicated

given: (i) stocks are the balance of C inputs from debris decomposition, and outputs from turnover of soil pools, and; (ii) many of the important processes influencing soil C are difficult to measure. Indeed, there is a paucity of data for inputs such as root turnover and decomposition, the fraction of C lost as CO_2 on decomposition. Having measurements of the various pools of soil C simulated by FullCAM (e.g. the RothC sub-model's IOM, RPM and HUM pools, Baldock *et al.* 2013a,b) has been essential to facilitate constraining the calibration of some of these 'difficult-to-measure' parameters (e.g. Paul and Polglase 2004b; Paul *et al.* 2017b).

Approach required to revise litter parameters influencing soil C

A recent national study of soil C changes following reforestation with environmental plantings (Paul *et al.* 2017b) greatly expanded the datasets available from long-term irrigation and fertiliser trials in temperate plantations (Paul *et al.* 2004; Paul and Polgase 2004a). In these studies, measurements of pools of soil C (i.e. IOM, RPM and HUM) were made. These datasets on pools of soil C, together with measurements of biomass, litter fall and litter mass, were utilised to constrain calibration of root turnover and decomposition, and CO_2-C loss on decomposition. In other words, the approach used was to effectively 'tune' rates of root turnover and decomposition, and the fraction of CO_2-C loss on decomposition, to ensure that predicted pools of soil C match that observed, while at the same time constraining predictions of biomass, litter fall and litter mass to that observed. The general approach used was to:

1. Provide justification for parameters of root turnover and decomposition, and CO_2-C loss on decomposition, with constant values being applied across forest types unless there was evidence otherwise.

2. Maintain the RothC parameters constant across the various forest calibration sites, while at the same time also making these parameters consistent with those recently derived for a wide range of Australian agricultural soils (Chappel and Baldock 2013; DoEE 2016, Table 6.B.5).

1.5 Initialising pools of biomass and debris

How FullCAM initialises simulations

When simulating a planting or regeneration event, estimates of the initial pools of biomass are assumed to be relatively small, and vary with stocking (DoEE 2016). However, when simulating an existing mature forests, initial biomass estimates are large, and are populated for each location in Australia based on the empirical calibrations of *M* in the TYF (Roxburgh *et al.* 2017). Here we focus on the initial composition of the pools of biomass in response to revisions made to partitioning assumptions (Section 1.1), not the *total* AGB per se. For the composition of initial forest biomass, there are alternative options available for the units in which these initial values are entered. As a default, the units required are the percentages of maximum tree biomass that is allocated to stem, branches, bark, foliage and coarse and fine roots. These values correspond to the nominated age of the stand at the start of simulation.

In terms of initial pools of debris pools, values required in FullCAM were the actual C masses of the decomposable and resistant pools of deadwood, bark litter, leaf litter, coarse dead roots and fine dead roots. If turnover and decomposition parameters are revised (Sections 1.2 and 1.3), these initial pools of debris will also require updating.

In FullCAM, inputs are required for the initial C stocks in each pool of biomass, debris and soil. As described by DoEE (2016), the initial pools of soil C are currently estimated using a national soil carbon map (Viscarra-Rossel *et al.* 2006; Hicks *et al.* 2015). Further work is required to revise these initial pools of soil C in accordance with the assumed historic land use and management regimes associated with each location. Such further improvements are currently under consideration.

Why accurate initialisation is important

Clearly, the size of the initial stocks of C are important when simulating changes in these stocks due to a change in land use or management. However, the composition of these stocks is also very important. For example, when simulating the biomass residues following a post-clearing fire, a relatively high proportion of the deadwood and dead root are assumed to remain in the debris pool when compared to other component of biomass. Similarly, a relatively high proportion foliage and bark litter is assumed to be incorporated into the inert pool of soil when compared to other components of the debris pool. Therefore, we would expect that net emissions resulting from post-clearing fires is highly sensitive to not only the total size, but also the initial composition of the biomass and debris pools.

For debris pools, it is also of paramount importance that the composition of these pools is also reflective of the state of equilibrium for the given site quality and climate. Otherwise, the predicted changes in C stocks of debris and soil may be attributable to the fact that the pool composition is changing simply due to its equilibrating to the site quality and climate, with little of this change being attributable to the actual change in land use or management *per se*.

Approach required to update initialisation

In FullCAMs database, there are 51 different forest types, each having a nominated stand age if assumed to be present at the start of a simulation. The original model parameters for the composition of biomass pools were based on the original allocation parameters. As outlined by DoEE (2016, Table 6.41), the original initial amount of forest debris for each forest type was based upon model simulations run to equilibrium. These estimates were cross-checked with published estimates of debris in Australian forests (Hingston *et al.* 1981; Mackensen and Bauhus 1999; Murphy *et al.* 2002; Griffin *et al.* 2002; Harms and Dalal 2003; Harms *et al.* 2005; Woldendorp and Keenan 2005). Here, a similar approach was used to initialise biomass and debris pools following the revision to the parameters governing the prediction of biomass (Section 1.1) or debris (Sections 1.2-1.3).

2 Methods

2.1 Allocation of biomass

2.1.1 Above-ground biomass components

Datasets on AGB biomass were collated from across numerous different studies; some of which had coarse AGB partitioned into only bole and crown components, while others had detailed AGB partitioning which included stem wood, bark, branches and foliage. Here, the bole is defined as stem wood together with the larger >20-50 mm diameter branches that could easily be separated from the crown by technicians using loppers. As shown in Fig. 1, the bole is comprised of bark and bough (= branches of various size classes greater than 20 mm diameter). The crown is made up of 'twigs' (<20 mm diameter branches) and foliage.
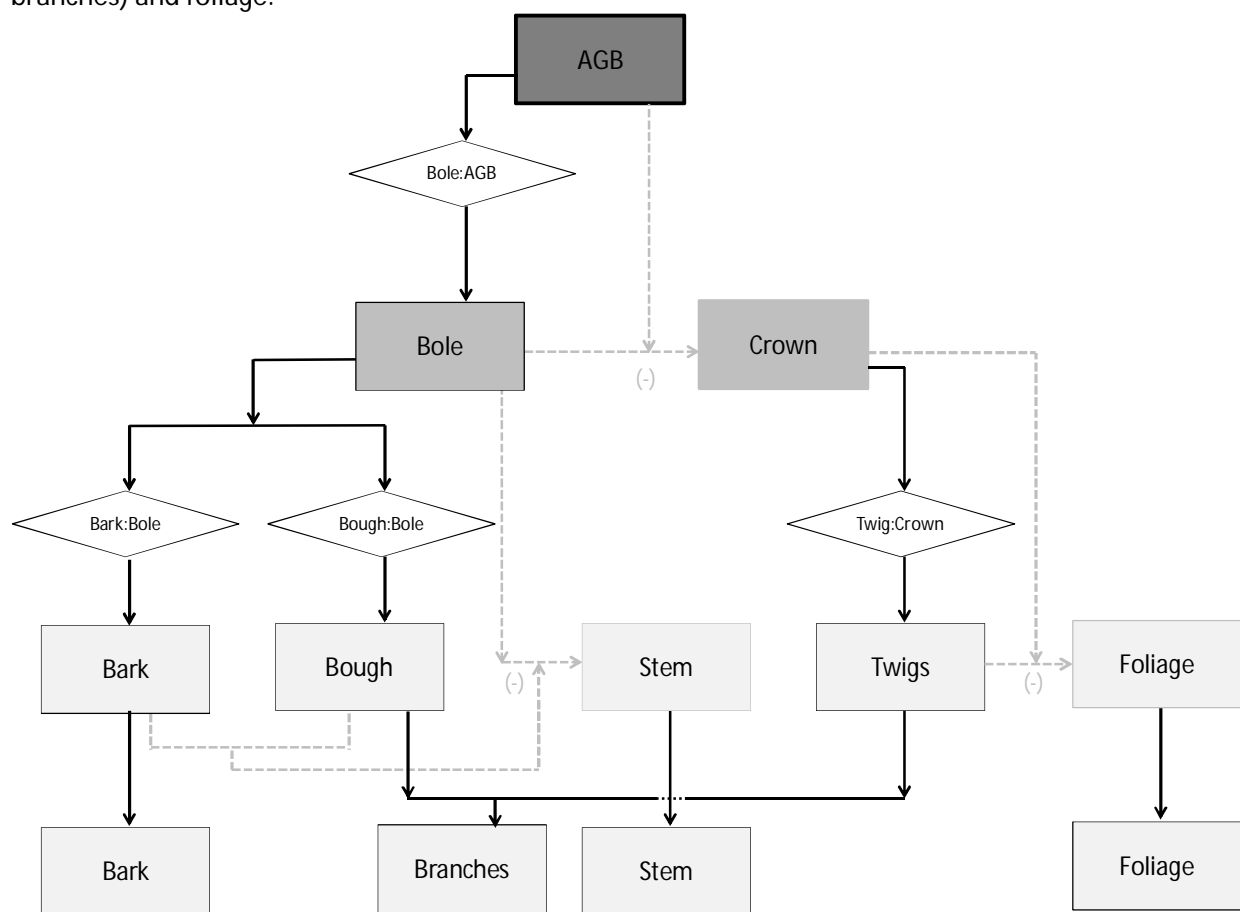
Figure 1: Procedure used to partition AGB into components of bark, branches, stem and foliage. Diamond shapes represent the four different models derived to allocate AGB into these components.

Given the differences in the types of data available for different forest types, these datasets were analyses separately as described below.

Environmental and mallee plantings

There has already been significant investment in the analysis of AGB allocation of these types of plantings (Paul & Waterworth 2015). In this relatively detailed study, there were two distinct steps undertaken to improve FullCAM-predictions of stand-scale allocation of biomass of mixed-species environmental plantings and mallee eucalypt plantings:

1. Collating datasets of components of biomass from individual trees or shrubs that had been destructively sampled. This dataset, together with including auxiliary data (e.g. stand age, stand density, climatic conditions etc.) were used to develop empirical models for biomass partitioning at the scale of the individual tree or shrub;

2. Application of these individual-scale empirical models to datasets of plot- and site-based inventories of stem diameters obtained from a diversity of forest types. Statistical analysis were then used to develop empirical models for allocation at the stand-scale.

There were 1,401 measurements of one or more components of AGB of an individual tree or shrub (Table 1). A majority of these data (68%) included information on the split between canopy and bole, with the remainder of the datasets having more detailed partitioning data.

These datasets were compiled in terms of Bole:AGB (N=1,334), Bough:Bole (N=73), Bark:Bole (N=183), and Twigs:Crown (N=498), with these partitioning terms being used to provide estimates of all four components of the AGB (Fig. 1).

In addition to biomass of components, auxiliary information were collated on key aspects of the stand from which the individual was harvested. These included:
1. Growth habit, defined as either a mallee, other tree or shrub;
2. Stand age;
3. Mean annual rainfall (MAR, mm yr^{-1}) that occurred over the years during which the stand was growing;
4. Stand density (individuals ha^{-1});
5. Planting configuration (i.e. belt or bock planting as defined by Paul *et al.* 2014ab), and;
6. Proportion of eucalypts (or dominant trees) in the stand from which the individual was harvested (PropEuc), and/or the species planted if the forest was a monoculture planting.

Stepwise Generalised Linear Modelling (GLM) using least squares means was used to assess which factors had a statistically significant impact on Bole:AGB, Bough:Bole, Bark:Bole, and Twigs:Crown, with the denominator of these fractions being used as the primary explanatory variable, but with the above six auxiliary variables being utilised to explore whether they improved the efficiency of prediction. Natural log transformations were used for AGB and stand age explanatory variables. Second order interactions were considered. Non-significant terms were systematically removed from the model fit starting with the higher-order interactions until a final parsimonious model was produced. Residuals from the model were inspected for a normal and heterogeneous distribution without influential outliers.

Once the individual-level analysis was completed to determine factors influencing allocation, stand-based estimates of AGB components could be generated. This was done using 1,127 stand-level inventories of stem diameters (and associated predictions of AGB, Paul *et al.* 2013a,b; Table 2). For each of these stands, the individual-scale models predicting AGB allocation were applied to predict stand-scale estimates of Bole:AGB, Bough:Bole, Bark:Bole, and Twigs:Crown. Given allocation is most variable within younger stands, the focus of this database was younger stands; typically <15 years. The stand-scale auxiliary data available included those listed above.

As at the individual-scale, there are factors likely to influence AGB allocation at the stand-scale. Hence, as described for the individual-scale, at the stand-scale, GLM was utilised to derive the allocation ratio models based on total AGB and the stand-scale auxiliary data (auxiliary variables 1-5 listed above).

Table 1. For environmental or mallee plantings, the number of individual trees and shrubs included in the dataset that represented different species and/or growth-habits. HR ad LR indicates individuals were sampled from stands from regions of high and low rainfall (MAR>500 or <500 mm yr^{-1}), respectively. The subscript 'Trees' and 'Mix' indicate that individuals were sampled from stands were PropEuc>0.75 and PropEuc<0.75, respectively. Data were collected from 15 different sources as described in detail by Paul & Waterworth (2015).

Type	Mallee		Other tree		Shrubs	
	N	Sites	N	Sites	N	Sites
HR$_{Tree}$	24	5	352	25	33	10
HR$_{Mix}$	NA	NA	92	14	53	10
LR$_{Tree}$	494	40	83	9	10	3
LR$_{Mix}$	NA	NA	166	12	94	16
Total	*518*	*45*	*693*	*60*	*190*	*39*

Table 2. Number of mallee and environmental planting stands included in the stand-based analysis of AGB allocation, where HR and LR indicate stands from regions of high and low rainfall (MAR>500 or <500 mm yr^{-1}), respectively. The subscript 'Trees' and 'Mix' indicate stands where PropEuc>0.75 and PropEuc<0.75, respectively. Data were collected from numerous different sources as described in detail by and Paul & Waterworth (2015).

Type	Mallee plantings	Environmental plantings
	N	N
HR$_{Tree}$	76	90
HR$_{Mix}$	NA	159
LR$_{Tree}$	315	273
LR$_{Mix}$	NA	214
Total	*391*	*736*

Native forests, woodlands and shrublands

Despite the vast diversity of native systems across high and low rainfall regions of Australia, biomass datasets were only available for 2,408 individuals sampled from a few hundred sites (Paul *et al.* 2016; Paul *et al.* 2017a). These individuals were categorised into four different plant functional types:

1. Typically single- stemmed hardwood trees from the genus *Eucalyptus* and closely related genera of *Corymbia* and *Angophora* (F$_{Euc}$);

2. Multi-stemmed hardwood (angiosperm) trees, including mallees from the genus Eucalyptus, and trees from the genus *Acacia* (F$_{Multi}$);

3. Other tree species that typically have single stems and relatively high wood density (mean 0.67 g cm^{-3}) (F$_{Other-H}$), and;

4. Shrubs or small trees characterized by being relatively short (generally <2 m height) and typically multi-stemmed or highly branched, with a relatively small (<7 cm) stem diameter (F$_{Shrub}$).

Just under half (46%) of the individual-scale datasets were partitioned for AGB in such a way that the biomass of Bole and Crown components could be estimated, with the remainder being partitioned into one or more other components of AGB; namely stem wood, bark, branches or foliage (Fig. 1).

Allometry of biomass of individuals from native forests or woodlands was found to be consistent with those from younger stands of environmental plantings (Paul *et al.* 2016). Furthermore, unlike for environmental plantings (Paul & Waterworth 2015), comprehensive data collation and subsequent analysis of biomass allocation has yet to be undertaken to inform accurate estimates of allocation of biomass for the large diversity of native ecosystems across Australia (i.e. varying greatly in their composition of plant functional types, stand densities and site qualities). Until such comprehensive datasets are available to inform the impacts of these factors on biomass, empirical models predicting AGB

allocation were not developed as per environmental plantings, and only broad assumptions regarding biomass allocation in native systems could be made.

Hence, the approach used was to use collated datasets from various individual trees or shrubs sampled from native systems (Table 3) to provide estimates of typical biomass partitioning in these systems. These estimates were used to verify whether the stand-scale models derived for environmental plantings were adaptable for application to predict AGB allocation in native systems. For both high and low rainfall regions, the average (and standard deviation, SD) ratios observed for Wood:AGB, Bark:AGB, Branch:AGB, Foliage:AGB and Bole:AGB (Table 3) were compared to that predicted using typical simulations of mature (100 year old) stands. Assumptions made in this approach were that:

1. Native forests from regions of relatively high rainfall (>500 mm yr^{-1}) will have different allocation of biomass to native woodland/shrubland systems from regions of relatively low rainfall (<500 mm yr^{-1}). Therefore, the analysis here considered these two broad classes of native ecosystems; high rainfall forests (N=1,478) and low rainfall woodland/shrublands (N=930) (Table 3).

2. Data available from these sampled individuals (Table 3) were representative (in size and mix of plant functional types) of what would be observed in mature stands from these respective regions. This assumption was necessary given the paucity of data informing the variability between different stands in terms of their mix of plant functional types.

3. When adapting and validating stand-based empirical models based on environmental plantings to predict AGB allocation of mature native systems, three key assumptions were made:

   a. *Generic rates of growth.* Rates of biomass accumulation were based on current FullCAM defaults. Hence, regardless of the type of native forests, woodland or shrubland, the *G* and *y* parameters in the TYF were consistently 10 years and 1.00, respectively.

   b. *Ratio of trees to shrubs within the stand.* Growth rates in the empirical AGB allocation models were also influenced by the assumed PropEuc>0.75 within the stand. Native forests (where MAR≥500 mm yr^{-1}) were represented by environmental plantings with PropEuc>0.75, while woodlands or shrublands (where MAR<500 mm yr^{-1}) were represented by environmental plantings with PropEuc<0.75. This was because data from Table 3 suggests that in regions of high rainfall, the F_{Euc} plant functional type is highly dominant, averaging 91% of the individuals sampled. In contrast, in regions of low rainfall, F_{Euc} was less dominant, averaging only 32% of the individuals sampled.

   c. *Stand density inputs.* Growth rates in the empirical AGB allocation models were also influenced by the assumed stocking rates within the stand. Stand density was taken to be the lowest available stand density category; <500 individuals ha^{-1}. This was because when compared to high stand density plantations managed for biomass or wood products, native ecosystems tend to have moderate-low stand densities, particularly in mature self-thinned ecosystems.

Table 3. Number of datasets collated (N) on individual tree or shrub biomass derived from biomass sampling under a range of locations (Sites) within native forests or woodlands in regions of Australia. Datasets were collected from 46 and 7 different sources for regions of high (>500 mm yr^{-1}) and low (<500 mm yr^{-1}) rainfall, respectively. Further details about these sources and the datasets are provided by Paul *et al.* (2016). See text above for the definition of the various Plant Functional Types.

Plant Functional Type	High rainfall		Low rainfall	
	N	**Sites**	**N**	**Sites**
Wood:AGB				
F_{Euc}	930	39	84	24
F_{Multi}	43	6	73	18
$F_{Other-H}$	34	5	115	20
F_{Shrub}	NA	NA	107	26
Total	*1,007*	*50*	*379*	*88*
Bark:AGB				
F_{Euc}	856	34	28	4
F_{Multi}	39	4	27	9
$F_{Other-H}$	NA	NA	6	2
F_{Shrub}	NA	NA	NA	NA
Total	*895*	*38*	*64*	*15*
Branch:AGB				
F_{Euc}	404	35	69	23
F_{Multi}	18	3	52	15
$F_{Other-H}$	25	2	42	17
F_{Shrub}	NA	NA	99	26
Total	*447*	*40*	*262*	*81*
Foliage:AGB				
F_{Euc}	600	44	28	4
F_{Multi}	18	3	46	10
$F_{Other-H}$	47	4	6	2
F_{Shrub}	9	1	3	1
Total	*674*	*52*	*83*	*4*
Bole:AGB				
F_{Euc}	684	50	228	14
F_{Multi}	11	5	218	40
$F_{Other-H}$	70	8	128	23
F_{Shrub}	NA	NA	126	27
Total	*765*	*63*	*700*	*127*

Hardwood and Softwood plantations

Hardwood and softwood plantations are generally stands of a single species, and of a single age. Allocation of AGB at the individual-level was thereby assumed to be applicable to the stand-level. So AGB allocation data collated at the individual-level was directly used to develop empirical models applied at the stand-level.

Over 1,084 and 520 measurements of one or more components of AGB of an individual tree were collated from a hardwood and softwood plantations, respectively (Table 4). Most (70%) of these individuals sampled from hardwood plantations were either *Eucalyptus globulus* or *E. grandis,* but other species were also represented (e.g. *E. pilularis*, *C. maculata*, and some species of *Acacia*). Similarly, most (98%) of the individuals sampled from softwood plantations were *Pinus radiata*, but other species were also

represented (e.g. *P. elliottii*). For these plantations, individuals sampled were generally separated into stem wood, bark, branch and foliage (Fig. 1).

Auxiliary data on stand age, MAR, stand density and planting configuration were often unavailable from the studies from which the datasets were collated. Hence, using the individual tree datasets collated, empirical models of ratios of Wood:AGB, Bark:AGB, Branch:AGB and Foliage:AGB were developed using only AGB as the explanatory variable. Where AGB-based empirical models were not significant, the average (and SD) of the ratio was calculated.

Table 4. Number of datasets collated (N) on biomass derived from different numbers of trees sampled from hardwood and softwood plantations across Australia. Datasets were collected from 25 and 22 different sources for the hardwood and softwood plantation datasets, respectively. Further details about these sources and the datasets are provided by Paul *et al.* (2016).

Ratio	Hardwood		Softwood	
	N	Sites	N	Sites
Wood:AGB	1,008	37	421	60
Bark:AGB	1,012	48	320	55
Branch:AGB	981	37	520	61
Foliage:AGB	1,084	56	520	61

2.1.2 Below-ground biomass components

Here, data collated was predominately of coarse root biomass BGB_C; the roots of ≥ 2 mm diameter which comprise a majority of the BGB. Data on fine root biomass (BGB_F) was not collated given their negligible contribution to biomass C and the inconsistency in methodologies applied across various studies to obtain estimates of BGB_F. For all forest types, BGB_F was added to predict total BGB_T (=BGB_C+ BGB_F) mass for each stand studied. This was done using the relationship derived by Mokany & Raison (2004) following a global review of root biomass datasets: BGB_F: $BGB_T = -0.049.Ln(AGB) + 0.388$, where the AGB is that of the stand (Mg ha^{-1}) (R^2=0.4, N=31).

Environmental and mallee plantings

Measurements of BGB_C were available from 770 individuals sampled from environmental and mallee plantings (Table 5). These datasets were used to develop allometic equations of BGB_C based on plant functional type as reported by Paul *et al.* (2013a,b, 2014a); namely mallee tree, other trees and shrubs. For all trees and shrubs at each stand listed in Table 2, data on plant stem diameter measured at 10 cm height were collated (D10). For individuals where diameter was measured at 130 cm height, conversion to an equivalent D10 estimates were derived (Paul *et al.* 2014a). When the D10-based allometric models were applied to predict both AGB (Paul *et al.* 2013a,b) and BGB (of Paul *et al.* 2014a) at each site, estimates of stand-level BGB_C:AGB were calculated. Then as descried above for testing empirical stand-level AGB allocation models, GLM was applied to explore whether AGB, or any auxiliary factors, influenced stand-scale BGB_C:AGB. This analysis was done separately for environmental and mallee plantings.

Table 5. Number of datasets collated (N) on BGB_C:AGB derived from different numbers of planting sites (Sites) of varying ages. Data were collected from 14 different sources as described in detail by Paul *et al.* (2014a).

Type of individual sampled					
Mallee tree		Other tree		Shrub	
N	Sites	N	Sites	N	Sites
306	44	368	47	96	21

Given D10-based allometric models were applied to obtain estimates of stand-level BGB_C:AGB, some statistical analysis was also undertaken to explore factors influencing stand-level D10, and thereby partly explaining the variations in BGB_C:AGB between contrasting stands. Linear regression and ANOVA analysis were also used to assess which stand-level auxiliary factors significantly influenced the plant average D10 within the stands. This analysis was done separately for environmental and mallee plantings. Measurements of stand density were natural log-transformed. Datasets from stands with sph>5,000 in environmental plantings were excluded from the analysis. This was because a descriptive statistical analysis of sph data from these plantings showed this dataset not to be normally distributed, with a long tail of distribution of larger sph values.

Native forests, woodlands and shrublands

A total of only 346 different individuals of various plant functional types from various types of native ecosystems were sampled for BGB_C (Table 6); about half from regions of high rainfall (N=168), and about half from regions of low rainfall (N=178). Consistent with the AGB datasets from native systems, the paucity of auxiliary information on growth rates, stocking densities and species-mix in various types of native systems led to the approach of utilising the collated datasets to verify the adaption of stand-level empirical models developed for environmental plantings, with the same assumptions used as specified above (Section 2.1.1). As found for the collated datasets of AGB allocation ratios (Table 3), the datasets BGB_C:AGB ratio datasets (Table 6) also supported that assumption that PropEuc>0.75 was appropriate for native forests (i.e. 65% of the individuals sampled were of the F_{Euc} plant functional type), whereas PropEuc<0.75 was appropriate for a woodlands/shrublands (i.e. only 26% of the individuals sampled were of the F_{Euc} plant functional type).

Table 6. Number of datasets collated (N) on individual tree or shrub BGB_C:AGB derived from different locations (Sites) from native forests and woodlands across Australia. Datasets were collected from 46 and 7 different sources for high (>500 mm yr^{-1}) and low (<500 mm yr^{-1}) rainfall regions, respectively. Further details about these sources and the datasets are provided by Paul *et al.* (2016). See text in previous Section for the definition of the various Plant Functional Types.

Plant Functional Type	High rainfall native forests		Low rainfall woodlands & shrublands	
	N	Sites	N	Sites
F_{Euc}	102	17	46	5
F_{Multi}	1	1	22	3
$F_{Other-H}$	32	9	4	1
F_{Shrub}	33	3	106	2
Total	*168*	*30*	*178*	*11*

For both high and low rainfall regions, we compared the average (± SD) of all observed BGB_C:AGB ratios (Table 6) with that predicted under scenarios of a wide range of representative mature (100 year old) stands. Only such broad average comparisons could be made given there was insufficient data from the various plant functional types to quantifying the impact of these on BGB_C:AGB. There was also insufficient data from young individuals to have any confidence in quantifying the impact of age on BGB_C:AGB, with <5% of the dataset being from stands with a stand age of <20 years (data not shown). This paucity of datasets from younger native systems requires addressing given that when compared to allocation of components of AGB, the BGB_C:AGB ratio is anticipated to be relatively sensitive to stand age (Mokany *et al.* 2006).

Hardwood and softwood plantations

Given hardwood and softwood plantations are stands of a single species of a given age, as when exploring the AGB allocation, the simplifying assumption was made that BGB_C:AGB at the individual-level were also applicable to the stand-level. Therefore for plantation systems, the approach used was to use collated BGB_C:AGB estimates at the individual-level to develop empirical models of allocation that could be directly applied at the stand-level.

A total of 97 and 248 different individuals of from hardwood and softwood plantations were sampled for both AGB and BGB_C, respectively, thereby providing estimates of BGB_C:AGB (Table 7). In these datasets, hardwood plantations were predominantly (40%) *E. globulus* or (18%) *E. nitens*, but data were also collated from plantations of five other species (*E. citriodora*, *E. cladocalyx*, *C. maculata*, *E. microcorys*, and *E. saligna*). For softwood plantations, the dataset was divided into only two key species; *P. radiata* from regions of relatively high rainfall, and *P. pinaster* from regions of moderate-low rainfall (<620 mm yr^{-1}).

Table 7. Number of datasets collated (N) on BGB_C:AGB derived from different numbers of planting sites (Sites) of hardwood and softwood plantations. Hardwood plantations were predominantly (40%) *E. globulus* or (18%) *E. nitens*. Softwood plantations could be grouped according to the species planted. Data were collected from 5 different sources as described in detail by Paul *et al*. (2016).

Type of plantation	Species	N	Sites
Hardwood		97	15
Softwood	*P. radiata*	134	4
	P. pinaster	114	15

Because most (86-95%) were from stands of relatively young age (<20 years), it was not feasible to develop models of BGB_C:AGB using stand age as an explanatory variable. Hence, for each dataset shown in Table 7, empirical models of BGB_C:AGB were developed, using AGB as the single explanatory variable given there was a paucity of auxiliary data other stand factors (e.g. age, MAR, stand density and planting configuration). Where not significant, the average (± SD) of all observed BGB_C:AGB were calculated.

2.1.3 Biomass Allocation Calculator & Scenario Analysis

Biomass Allocation Calculator

The stand-scale empirical models developed were used to construct a Biomass Allocation Calculator in MS Excel (Fig. 2). The purpose of this Calculator was to utilise these data-informed models to derive recommended defaults for use in FullCAM's stand-age based allocation tables when simulating different types of forests. The key input required in the Calculator was the yield curve for the stands AGB. This was derived from TYF, and hence, required the TYF parameters (*M*, *G*, *y* and *r*). Other inputs to the Calculator included any of the statistically significant explanatory variables, which varied for the five different empirical models incorporated within this Calculator:

1. Environmental and mallee plantings, where in addition to the TYF parameters, other inputs required included:
   a. Type of planting, including whether the planting has PropEuc>0.75 or PropEuc<0.75 if an environmental planting, and the species planted if a mallee eucalypt;
   b. Planting established in temperate or tropical regions, and if temperate, whether the MAR>500 mm yr^{-1} or MAR<500 mm^{-1};
   c. Category of stand density (sparse, standard or dense), and;
   d. Category of planting configuration (block, wide belt or narrow belt.

2. Native forests, where MAR was assumed to be >500 mm yr^{-1}, PropEuc>0.75, <500 stems ha^{-1} and a block planting configuration. Only inputs required were the TYF parameters.

3. Woodlands/shrublands, where MAR was assumed to be <500 mm yr^{-1}, PropEuc<0.75, <500 stems ha^{-1} and a block planting configuration. Only inputs required were the TYF parameters.

4. Hardwood plantations, where the only inputs required were the TYF parameters.

5. Softwood plantations, where the only inputs required were the TYF parameters.

The output of this Calculator is a table of relative allocation to braches, bark, foliage, coarse roots and fine roots, each expressed relative to the allocation of the stem at each year of growth. As such, these outputs may be copied and pasted into the allocation input tables within FullCAM when configured to simulate the same TYF.
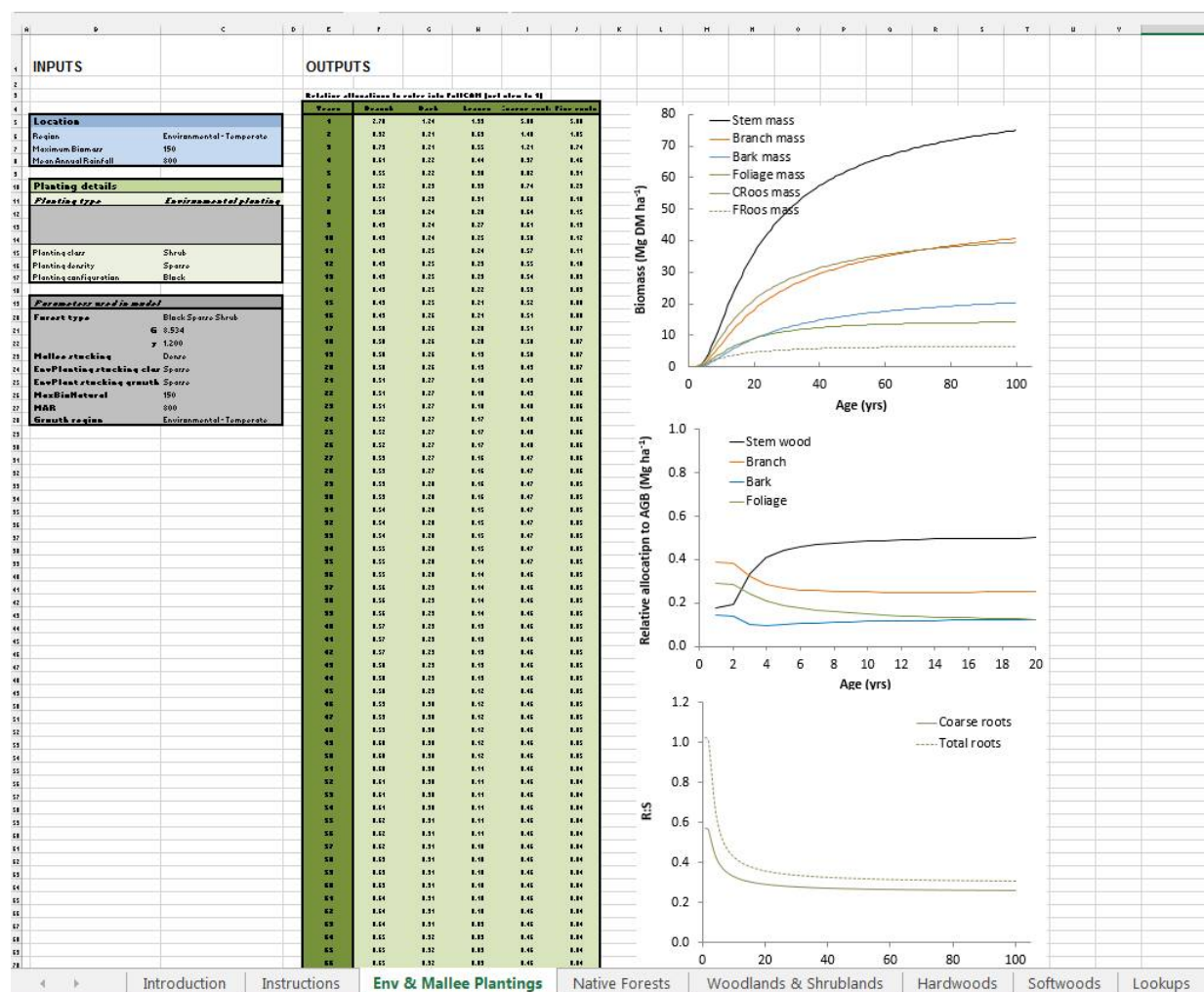
Figure 2: Example of a scenario of one type of environmental planting being simulated within the 'Allocation Calculator'. Outputs of this Calculator are estimates annual allocation of branches, bark, foliage, coarse and fine root components when expressed relative to that of the stem. These outputs can be used as inputs in the FullCAM allocation tables for this given forest type scenario, and hence, rates of accumulation of AGB.

Scenario Analysis

The Calculator was applied to generate 41 scenarios (Table 8) for exploring differences in predicted AGB and BGB allocation between contrasting forests types at stand age of 5, 10, 50 and 100 years. The TYF parameters of G, y, r applied were the default values for these types of plantings currently simulated in FullCAM v 4.1.6.19417 (2016). Although it is acknowledged that each of these forests types may grow across a wide range of climates, the simulations were run at hypothetical locations that had a site productivity (and typical climate) based on the average M observed across the represented domain of each forest type.

Table 8. Scenarios used to compare the revised Calculator-predicted biomass allocation with the original FullCAM-predicted biomass allocation. The different types of forest simulated are indicated: MR-LR and MP-HR, mallee plantings in low and high rainfall, respectively; EP-LR, EP-HR, EP-Trop, environmental planting in low rainfall, high rainfall and tropical regions, respectively; NF-HR, native forests in high rainfall regions; WS-LR, woodlands/shrublands in low rainfall regions; HW, hardwood plantations, and; SW, softwood plantations. Low and high rainfall are defined as <500 mm yr^{-1} and ≥500 mm yr^{-1}, respectively. For MP plantings, the stand density category is also provided as either sparse (<2300 sph) or dense (≥2300 sph). Similarly for EP plantings, the stand density category is also provided as either sparse (<500 sph), standard (<1500 sph) or dense (>1500 sph). For both MP and EP, the planting configuration category is provided as either narrow belt, wide belt or block. For NF and WS, the type of planting is based on the standard regimes used for the given National Plantation Inventory region.

Scenario	Species	Type	M (t DM ha^{-1})
Mallee planting	*E. loxophleba*	MP-LR; >2300; Narrow	47.6[++]
	E. loxophleba	MP-LR; <2300; Wide	38.4[++]
	E. loxophleba	MP-LR; <2300; Block	51.2[++]
	E. polybractea	MP-HR; <2300; Block	73.4[++]
Env. plantings	PropEuc < 0.75	EP-LR; PropEuc<0.75; >1500; Narrow	74.9[+]
		EP-LR; PropEuc<0.75; <1500; Wide	78.8[+]
		EP-LR; PropEuc<0.75; >1500; Block	66.3[+]
		EP-LR; PropEuc<0.75; <500; Block	67.3[+]
		EP-HR; PropEuc<0.75; >1500; Narrow	105.9[+]
		EP-HR; PropEuc<0.75; <1500; Wide	106.3[+]
		EP-HR; PropEuc<0.75; >1500; Block	117.8[+]
		EP-HR; PropEuc<0.75; <500; Block	127.5[+]
	PropEuc ≥ 0.75	EP-LR; PropEuc≥0.75; >1500; Narrow	67.0[+]
		EP-LR; PropEuc≥0.75; <1500; Wide	67.8[+]
		EP-LR; PropEuc≥0.75; >1500; Block	67.3[+]
		EP-LR; PropEuc≥0.75; <500; Block	53.7[+]
		EP-HR; PropEuc≥0.75; >1500; Narrow	114.7[+]
		EP-HR; PropEuc≥0.75; <1500; Wide	98.7[+]
		EP-HR; PropEuc≥0.75; >1500; Block	117.8[+]
		EP-HR; PropEuc≥0.75; <500; Block	135.2[+]
	PropEuc ≥ 0.75	EP-Trop; PropEuc≥0.75; <500; Block	366.1[+]
Native Forest	PropEuc ≥ 0.75	NF-HR; Rainforest and vine thickets	319.3[*]
		NF-HR; Eucalypt open forest	206.1[*]
		NF-HR; Eucalyptus tall open forest	326.8[*]
		NF-HR; Tropical euc. woodlands/grassland	39.4[*]
Woodland Shrublands	PropEuc < 0.75	WS-LR; Eucalypt open woodlands	19.8[*]
		WS-LR; Acacia open woodlands	13.3[*]
		WS-LR; Acacia forest and woodlands	16.2[*]
		WS-LR; Eucalypt woodland	48.1[*]
		WS-LR; Acacia Shrublands	14.7[*]
Hardwood	*Eucalypts globulus SR*	HW; Western Australia	105.4[^]
	Eucalypts globulus SR	HW; Green Triangle	129.7[^]
	Acacia	HW; Northern Territory	147.1[^]
	Eucalypts globulus LR	HW; Bombala- East Gippsland	175.2[^]
	North Coast eucalypts	HW; North Coast	209.2[^]
	Eucalypts nitens LR	HW; Central Gippsland	268.4

Softwood	*Pinus pinaster*	SW; Western Australia	77.5^
	Pinus radiata	SW; Green Triangle	122.3^
	Pinus radiata	SW; Central Gippsland	162.4^
	Pinus radiata	SW; Tasmania	188.2^
	Hoop pine	SW; Northern Queensland	235.9^

*Source: S. Karunaratne, pers com. (2017) ;++Source; Paul *et al.* (2014c); +Source; Paul *et al.* (2014b); ^Source; Waterworth *et al.* (2007).

2.2 Litter fall

Data on litter fall were collated from 156 estimates of annual litter fall obtained from litter trap studies reviewed by Paul and Polglase (2004a), and updated by England *et al.* (2017) and Paul *et al.* (2017b). These comprise a range of forest types (Table 9), including: environmental plantings (N=4); hardwood plantations (N=15); softwood plantations (N=29); native forests (N=83), and; woodlands (N=24). All of these datasets were sources from Australian studies. The only exception was for 10 datasets from the softwood plantations (South Africa, Versfield, 1981; New Zealand, Baker *et al.* 1986, and; Greece, Kavvadiaas *et al.* 2001).

Where required, average %Foliage, %Twig and %Bark observed in litter fall for the different forest types was used to 'fill-gaps' for studies where the total litter fall was not partitioned into these components. Similarly, where the stand-based mass of foliage, twigs and bark were not measured, these were predicted using FullCAM and the revised biomass allocation input tables (Section 2.1). Average 'observed' rates of turnover were thereby calculated for each forest type.

Table 9. Datasets collated from field studies with litter fall traps monitored under environmental planitngs, native forests, woodlands, hardwood plantations and softwood plantations. All forest types had observations of total litter fall mass (N varying from 4 to 83, depending on the forest type), with a percentage of these further sub-sampled to attained observations of the relative contribution of foliage, twig and bark components to this total litter fall.

Forest type	Total N	Foliage % of N	Twig % of N	Bark % of N	Source
Env. plantings	4	100	0	0	Paul *et al.* (2017b)
Native forests	83	70	52	36	England *et al.* (2017)
Woodland	24	33	25	21	England *et al.* (2017)
Hardwood	16	50	44	44	England *et al.* (2017)
Softwood	29*	100	0	0	Paul & Polglase (2004a)
Total	156	69	36	27	Paul & Polglase (2004a)

*Source: Total litter fall was attributed to pine needles.

Using all datasets, three ANOVA analyses were applied to determine whether forest type had a significant influence on litter fall of foliage, litter fall of twigs, or litter fall of bark. These results were then used to inform average rates of litter fall that were appropriate for each forest type, or groups of forests types.

2.3 Decomposition of litter

As outlined in Table 10, a total of 123 litter bags studies of decomposition were reviewed from a range of forest types, inluding: deadwood, bark litter and foliage litter from under eucalypt-dominant stands (N=23, 13 and 59, respectively), and; pine needle litter under softwood plantations (N=28). Data were only used from studies where the litter in the bags was collected from litter fall (i.e. data from collection of green leaves etc. were excluded).

Table 10. Datasets collated from field studies with litter bag monitored under eucalypt-dominant stands, or under softwood plantations.

Forest type	Litter type	N	Source
Eucalypt-dominant	Deadwood	23	England *et al.* (2017)
	Bark litter	13	
	Foliage litter	59	
Softwood	Pine needle litter	28	Paul & Polglase (2004a)
Total		123	

Although some workers have also calcualted long-term rates of decomposition from the ratio of litter fall to the mass of litter, such estimates are only reliable when both of these processes are accurately measured, and are in a steady-state equilibrium (Olson, 1963). Hence, when compared to litter bag studies, estimates of decomposition derived using this approach were inferior, and so such estimates were not used here to inform rates of decomposition.

In litterbag studies, mass loss is described by exponential decay functions. Although the single exponential decay model is the most widely used, the double exponential decay model often provides a better description of decomposition of leaf and some bark material (e.g. O'Connell 1988). The single exponential decay model (e.g. Olson, 1963) assumes that substrate is of constant quality and that a constant fraction is lost at each time step:

$$W_t = W_0 e^{-kt} \hspace{4cm} \text{(Equation 1)}$$

where W_0 is the initial litter dry weight, W_t is the dry weight at time t, and k the instantaneous decay constant. By comparison, the double exponential decay model assumes that there is an early rapid loss of labile compounds (e.g. soluble matter and non-lignified organic carbon), and that resistant compounds are slowly decomposed later in the decomposition process (e.g. Minderman, 1968):

$$W_t = W_l e^{-k't} + (W_0 - W_l) e^{-kt} \hspace{3cm} \text{(Equation 2)}$$

where W_l is the amount of labile component present in a litter fraction, $(W_0 - W_l)$ represents the resistant component, and k' and k are the decay constants of the labile and resistant components, respectively.

As found previously by Paul and Polglase (2004a), in general, double exponential decay models best described the leaf decomposition, while single exponential decay models were adequate to describe decomposition of bark and wood. Hence for all forest types, FullCAM inputs for the fraction of debris that was resistant were set to 100% for deadwood and bark, while for foliage it was set to the average values observed from the fitting of the double-pool decay function to litterbag studies of foliage litter.

Rates of decomposition in FullCAM are influenced by temperature and rainfall either using the 'Mulch-style' or 'Soil-style' sensitivity. Decomposition was particularly sensivite to climate when applying the 'Soil-style' approach. Given the lack of data on how climate impacts rates of decomposition, the more conservative approach of using 'Mulch-style' sensitivity was applied; with sensitivitie values of 1 being used as per DoEE (2016). Using the scenarios listed in Table 8, it was tested whether the predictions of decomposition using this 'Mulch-style' sensitivity of decomposition to climate were within the bounds of that expected; namely the 20th and 80th percale values of the empirical decay models fitted to observations attained from litterbag studies.

FullCAM predicts C stocks of debris pools, and yet measurements are often made of the dry matter within two separate components of debris; (i) litter, and; (ii) coarse woody debris (CWD, deadwood with diameters generally >1.0-2.5 cm). To be able to reconcile FullCAM predictions against measurements, assumptions made were that debris was 45% carbon (DoEE 2016), and that 70% of deadwood debris is CWD, with only 30% of deadwood debris being dead twigs as part of the litter component. It was assumed that all of foliage and bark debris are measured within the litter component.

As indicated in Table 11, data on mass of litter and CWD under Australian forests were previously collated. These datasets were used to calculate estimates of the average (and standard deviation) of observed litter

and CWD under the various forest types. These estimates provided verification of the revised parameters for litter fall and litter decomposition as testing using the 41 scenarios given in Table 8. The upper bounds of litter and CWD expected were simulated post harvesting events. Hence, for the mature woodlands and native forest scenarios, two simulations were run; the first being under uncleared mature vegetation, and second being a year after clearing a mature stand. Similarly, for plantation scenarios two estimates were made over a 100 year simulation that included multiple rotations; first being under the mature stand of the final rotation within this period, and the second being after harvesting in the final harvest cycle within this 100 year period.

Table 11. Datasets collated from field studies with litter bag monitored under eucalypt-dominant stands, or under softwood plantations. Studies in eucalypt-dominant stands included assessments of decomposition of deadwood, bark litter and foliage litter. But under softwood plantations, only pine needle litter was assessed.

Forest type	Litter (Mg DM ha^{-1})	CWD (Mg DM ha^{-1})	Source
Environmental plantings	115	NA	Paul *et al.* (2017b)
Hardwood plantations	24	14	Woldendorp and Keenan (2005)
	12	NA	England *et al.* (2017)
	7	NA	Snowdon *et al.* (2005)
Softwood plantations	17	11	Woldendorp and Keenan (2005)
	10	NA	Snowdon *et al.* (2005)
	1	NA	Bubb *et al.* (1998)
Native forests	71	60	Woldendorp and Keenan (2005)
	51	NA	England *et al.* (2017)
	46	NA	Snowdon *et al.* (2005)
	2	NA	O'Connell (1997)
	1	1	Hingston *et al.* (1981)
Woodlands	27	NA	Harms *et al.* 2005
	13	5	Woldendorp and Keenan (2005)
	10	NA	Murphy *et al.* (2002)
	5	NA	England *et al.* (2017)
	NA	19	Prior *et al.* (2016)
Total	*412*	*110*	

2.4 Parameters influencing soil C

Previous work by Chappell and Baldock (2013) provided recommendations and justification for soil C turnover parameters applied in the RothC sub-model. This included an RPM pool turnover rate of 0.17 % yr^{-1}, and a HUM pool turnover rate of 0.02 % yr^{-1}. All other RothC parameters were as per the original model calibration (e.g. Jenkinson *et al.* 1991).

A recent national study of soil C changes following reforestation with environmental plantings (Paul *et al.* 2017b) greatly expanded the datasets available from long-term irrigation and fertiliser trials in temperate plantations (Paul *et al.* 2004; Paul and Polgase 2004a). In all of these studies, measurements of pools of soil C (i.e. IOM, RPM and HUM) were made together with measurements of stand biomass, litter fall and litter mass. In each of these field studies, measurement were also made for assessment of biomass, litter fall and litter mass. The collation of datasets from across these studies provided 158 sites (and/or treatment plots) where predictions of pools of soil C could be 'tuned' to that observed (Table 12).

Due to being relatively resource-intensive to measure, there is a paucity of data for FullCAM input parameters for root turnover and decomposition, and the fraction of C lost as CO_2 on decomposition of debris. The approach used here was to calibrate rates of root turnover and decomposition, and the fraction of CO_2-C loss on decomposition, to ensure that predicted pools of soil C match that observed,

while at the same time: (i) constraining predictions of biomass to that observed at these sites (Paul and Polglase 2004b; Paul *et al.* 2017b), and; (ii) applying the revised parameters for allocation of biomass, litter fall and decomposition of litter. This was done using the RothC parameters as per Chappell and Baldock (2013). In the absence of any justification to assume otherwise, parameters for root turnover and decomposition, and the fraction of CO_2-C loss on decomposition of resistant and decomposable debris pools, were each assumed to be constant across the different forest types.

Given these assumptions, and uncertainties in measurements of pools of soil C and biomass, and given the application of generic rates of allocation of biomass, litter fall and decomposition of litter, prediction of soil C pools is unlikely to be highly accurate at the site-level. The aim was to achieve the best overall model fit for parameters influencing soil C for which there is a paucity of information. To provide an assessment of the success of this model fit, efficiencies of model prediction across the 158 sites listed in Table 12 were calculated for total soil C, as well as the two large pools of soil C measured; RPM and HUM.

Table 12. Details of the soil C study sites (or treatments within a site) under environmental plantings (Env. plantings), hardwood plantations (*E. grandis*) and softwood plantations (*P. radiata*). Included here is the region of Australia from which sites were located (SE= south east; S= central south; NE= north-east, and; SW= south-west of Australia), number of sites (N), stand age, and previous land use (PLU: G = grazing; C = cropping or rotational cropping/grazing; P = *Pinus radiata* plantation).

Forest type	Region	N	Age (yrs)	PLU	MAR (mm yr^{-1})	Source
Env. plantings	SE	36	5-46	G	448-794	Cunningham *et al.* (2015)
Env. plantings	SE	20	1-19	G	550-884	Read (2016)
Env. plantings	SE	7	8-16	G, C	352-1112	Baker, T., unpublished data
Env. plantings	SE, Intensive	3	5	G	427-965	Paul *et al.* (2017b)
Env. plantings	SE, Repeat#	21	5-20	G, C	509-696	Paul *et al.* (2017b)
Env. plantings	SE, Riparian	10	9-23	G, C	407-774	Paul *et al.* (2017b)
Env. plantings	SE	19	9-20	G, C	365-1423	Paul *et al.* (2017b)
Env. plantings	S	4	6-29	C	372-652	Paul *et al.* (2017b)
Env. plantings	NE	3	5-19	G	852-1474	Paul *et al.* (2017b)
Env. plantings	SW	2	15-16	C	370-422	Paul *et al.* (2017b)
Softwood	SE^	18	10-20	P	791	Paul & Polglase (2004b)
Hardwood	SE+	8	1-10	G	570	Paul & Polglase (2004b)
Softwood	SE+	8	1-10	G	570	Paul & Polglase (2004b)
Total		158				

#Sites were measured two or three times.
^The BFG experiment, including treatment plots of: (i) control; (ii) once-only solid fertiliser applied; (iii) irrigation only; (iv) irrigation and once-only solid fertiliser applied; (v) irrigation and liquid fertiliser applied weekly; (vi) once-only solid fertiliser applied, but left unthinned.
+The WEPP experiment, including treatment plots of: (i) irrigation at low rates, and; (ii) irrigation at medium-high rates.

2.5 Initialising pools of biomass and debris

Each of the 51 different forest types in FullCAMs database has a default initial age at the start of simulation; Environmental and mallee plantings with various regimes, 0 years; Hardwood plantations, between 10 and 35 years, depending on the species, and; Softwood plantations, 35 years, and; Native systems, 50 years.

For each of the 51 forest types, the Allocation Calculator was applied to generate outputs of the percentage contribution of each biomass pool to total biomass at the nominated initial stand age. It was again ensured that the simulations were undertaken for a region (and hence climatic conditions and growth rates) typical of that forest type.

Using the revised parameters outlined in Sections 2.1-2.4, a plot file was generated for each of the 51 different forest types, again ensuring that the simulation was for a typical region. The predicted

decomposable and resistant pools of deadwood, bark litter, foliage litter, and dead coarse and fine roots were then recorded at the nominated stand ages at initialisation. These debris pools where then used as the revised initial pools of debris for each of these 51 forest types. Note for plantations, the debris pool at the nominated stand age was taken from the last rotation simulated with a 100 year period, and thus, included the legacy impacts of harvesting residues from previous rotations.

3 Results and Discussion

3.1 Allocation of biomass

3.1.1 Empirical models of allocation of AGB

Environmental and mallee plantings

Allocation models for environmental and mallee plantings were obtained for prediction of Bole:AGB, Bough:Bole, Bark:Bole and Twigs:Canopy at both the individual- and stand-scale (Table 13). These models demonstrated that allocation of biomass was influenced by not just biomass and stand age, but also by rainfall, stand density, and PropEuc.

Table 13. Models derived for prediction of Bole:AGB, Bough:Bole, Bark:Bole and, Twig:Crown at the individual- and stand-scale for environmental plantings (EP) and mallee plantings (MP). Statistically significant variables, and whether they have a positive or negative influence on the ratio, are listed. The model's statistical significance (P-value), R^2 and sample number (N) are also provided. Resulting models are provided in detail by Paul & Waterworth (2015).

Model	Type	Significant variables	P	R^2	N
		Individual-scale			
Bole:AGB	Tree	+Ln(AGB); +MAR; +PropEuc	<0.01	0.36	693
	Shrub	+Ln(AGB)	<0.01	0.05	123
	Mallee	+Ln(AGB)	<0.01	0.26	518
Bough:Bole		+Ln(Bole)	<0.01	0.13	73
Bark:Bole		None, constant of 0.17	NA	NA	183
Twig:Crown		Growth habit; +Mallee tree, and +Shrub	<0.01	0.07	498
		Stand-scale			
Bole:AGB	EP	+ Ln(AGB)[1]; +Ln(Age)[2]; − Dense$_{[1,0]}$[3]; − PropEuc<0.75$_{[1,0]}$[4]; +MAR>500$_{[1,0]}$[5]	<0.01	0.91	736
	MP	+Ln(AGB)[6]; +Ln(Age)[7]; − Dense$_{[1,0]}$	<0.01	0.94	391
Bough:Bole	EP	+Ln(Bole); +Ln(Age)[8]; PropEuc>0.75$_{[1,0]}$	<0.01	0.54	736
	MP	+Ln(Bole); +Ln(Age)	<0.01	0.88	391
Bark:Bole		None, constant of 0.170	NA	NA	1,127
Twig:Crown	EP	− PropEuc>0.75$_{[1,0]}$; − Ln(Crown)[9]	<0.01	0.22	736
	MP	None, constant of 0.554	NA	NA	391

[1] Particularly with increased Age, and/or particularly Tropical forests, and/or less so when Sparse
[2] Less so for tropical forests.
[3] Particularly for tropical forests.
[4] Particularly when sparse or very sparse, and/or MAR<500$_{[1,0]}$.
[5] Particularly when tropical forest, and/or PropT>0.75.
[6] Less so when Sparse.
[7] Particularly when Sparse.
[8] Particlarly when high Bole and/or PropT>0.75$_{[1,0]}$
[9] Particlarly when PropT<0.75$_{[1,0]}$.

As indicated by results shown in Fig. 3, all individual-scale models obtained were highly significant (P<0.01) and un-biased, and when applied explained some (>47%) of the variation in component biomass. At the stand-scale, 'observed' biomass of components were actually calculated values based on the application of the individual-scale models. Therefore as expected, stand-scale model performance was very high (EF>0.97), and the residuals were relatively low (<12 % variation in AGB) (data not shown).
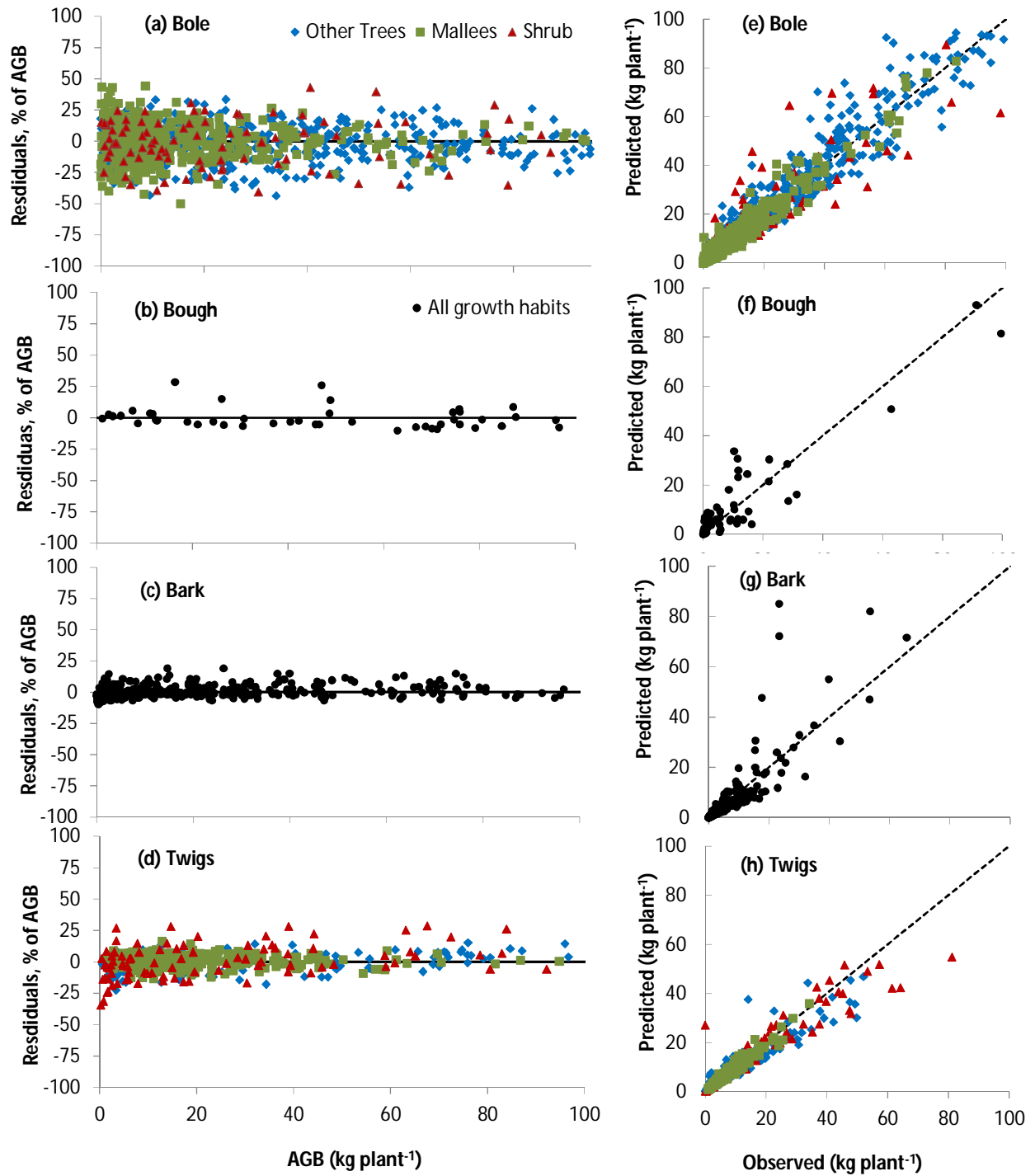
Figure 3: Plots of residuals in predicted biomass, expressed as a percentage of AGB, for predictions of the components of; (a) Bole, (b) Bough, (c) Bark, and (d) Twig, and the corresponding relationships between observed and predicted biomass of these components of; (e) Bole (Overall EF=0.99, N=1401; Tree EF=0.99, N=693; Shrub EF=0.77, N=190; Mallee EF=0.95, N=518), (f) Bough (Overall EF=0.74, N=145), (g) Bark (Overall EF=0.47, N=434, or for trees <100 kg, EF=0.98, N=383), and (h) Twig (Overall EF=0.97, N=498; Tree EF=0.98, N=142; Shrub EF=0.77, N=190; Mallee EF=0.90, N=94).

Native forests, woodlands and shrublands

Results in Table 14 show comparison between the average (±SD) observed Wood:AGB, Bark:AGB, Branch:AGB, Foliage:AGB and Bole:AGB for native forests (or woodlands/ shrublands) and that predicted from a range of relevant scenarios when applying the stand-level allocation models derived for low density

environmental plantings with PropEuc>0.75 (or PropEuc<0.75). Predictions were generally within ± 1SD of the average observed. The only exception was the over-prediction of Branch:AGB in high rainfall regions. Conversely, there was a slight under-prediction of Branch:AGB in low rainfall regions.

These results indicate that although there is an increased bole mass in areas of relatively high rainfall, in native systems, this increase is mainly attributable to an increase in stem wood, and not attributable to an increase in the biomass of branches. If verified, the empirical model for Bough:Bole calibrated to environmental plantings may require refinement for native ecosystems to reflect this. But otherwise, current results suggest that stand-level allocation models derived for low density environmental plantings with PropEuc>0.75 (or PropEuc<0.75) were largely appropriate for the application to native forests (or woodlands/ shrublands).

Table 14. Average (±SD) observed and predicted range of biomass allocation ratios. Datasets were collected from 46 and 7 different sources for high (≥500 mm yr^{-1}, native forests) and low (<500 mm yr^{-1}, woodlands and shrubland)rainfall regions, respectively. Further details about these sources and the datasets are provided by Paul *et al.* (2016) and Paul *et al.* (2017a).

Ratio	High rainfall native forests		Low rainfall woodlands & shurblands	
	Observed	Predicted	Observed	Predicted
Wood:AGB	0.65 ± 0.12	0.52-0.54	0.41 ± 0.21	0.43-0.46
Bark:AGB	0.12 ± 0.06	0.14-0.15	0.12 ± 0.04	0.11-0.12
Branch:AGB	0.14 ± 0.09	0.25-0.26	0.32 ± 0.18	0.28-0.29
Foliage:AGB	0.05 ± 0.06	0.06-0.09	0.11 ± 0.07	0.13-0.17
Bole:AGB	0.84 ± 0.10	0.82-0.88	0.61 ± 0.18	0.62-0.71

Hardwood and softwood plantations

For both hardwood and softwood plantations, allocation of AGB to stem wood increased with AGB. This came at the expense of allocation of AGB to foliage, which declined with increased AGB (Table 15). The other AGB components of branches and bark were relatively constant over a range of tree sizes. As outlined below (Section 3.1.2), the increased proportion of stem wood with increased AGB is well documented for commercial forests (Schroeder *et al.*, 1997; Snowdon *et al.*, 2000; Kantola & Mäkelä, 2006), as is the finding that this increased stem wood production comes at the expense of foliage production (Dewar & McMurtrie, 1996; Albaugh *et al.*, 1998; Lehtonen, 2005).

Table 15. Models derived for prediction of Wood:AGB, Branch:Bole, Bark:Bole and, Foliage:AGB at the individual-scale for hardwood and softwood plantations. These models were also assumed to apply at the stand-scale given these plantings have a single species of a specific stand age and hence, specific size range. Statistically significant variables, and whether they have a positive or negative influence on the ratio, are listed. The model's statistical significance (P-value), R^2 and sample number (N) are also provided.

Model	Type	Significant variables	P	R^2	N
Wood:AGB	Hardwood	+Ln(AGB)	<0.01	0.53	1,008
	Softwood	+Ln(AGB)	<0.01	0.31	421
Branch:AGB	Hardwood	None, constant of 0.25±0.09	NA	NA	981
	Softwood	None, constant of 0.19±0.09	NA	NA	520
Bark:AGB	Hardwood	None, constant of 0.09±0.04	NA	NA	1,012
	Softwood	None, constant of 0.09±0.03	NA	NA	320
Foliage:AGB	Hardwood	– AGB	<0.01	0.72	1,084
	Softwood	– AGB	<0.01	0.29	520

3.1.2 Key factors influencing allocation of AGB

For each forest type, variations in partitioning of AGB biomass were originally predicted based only on stand age. In contrast, when the new empirical models predicting partitioning of AGB biomass are applied via generating revised allocation inputs tables using the Allocation Calculator, numerous factors are also accounted for. These are outlined below.

Forest type

As expected, empirical modelling indicated that allocation of AGB to stem is relatively high (and allocation to branches relatively low) in hardwood and softwood plantations given these are managed for wood production (Fig. 4c,d). In contrast, allocation of AGB to stem was relatively low (and allocation to branches relatively high) in low rainfall systems such as many woodland systems (Fig. 4f). The increased allocation to structural components as the stands mature was offset by a decreased allocation to foliage, such that in mature stands, foliage biomass was predicted to be relatively small.

The observed differences in allocation of AGB between forest types is consistent with the understanding that biomass partitioning is partly genetically controlled (e.g. Cannell *et al.* 1983; Berninger & Nikinmass 1997), with differences in partitioning partly explained by photosynthetic efficiency related to plant architecture (e.g. Gower *et al.* 1994). A specific example of this was found in the differences between the portion of the canopy that was twigs between mallee eucalypts and other trees (Table 13). At the individual-scale, mean twig proportion to the total crown ratio (Twig:Crown values) of 0.62 was observed for mallee eucalypts, whereas Twigs:Crown was only 0.52 for other trees. For a given canopy size, mallees (which generally grow in hash low rainfall environments) tend to have a relatively high proportion of twigs in order to support their relatively larger umbrella-like leaf canopy (ANBG 2004), and have relatively high ratio of photosynthesic mass to body mass as a consequence of thicker leaves and relatively smaller body size (e.g. Xu *et al.* 2014).
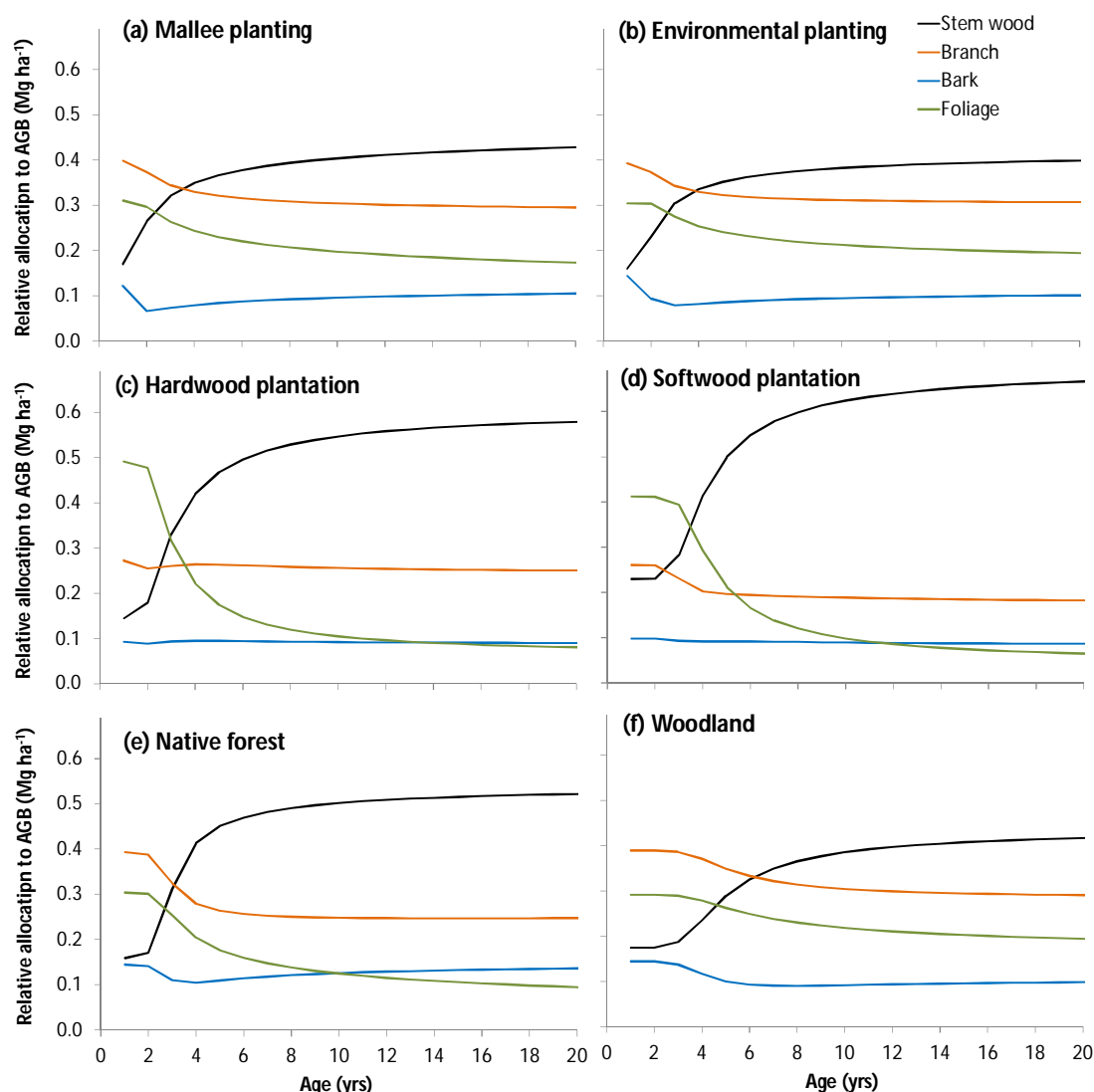
Figure 4: Examples of differences in allocation of AGB between the key categories of forest types. In (a), the mallee plantings were *E. loxophleba lissophloia* established as wide belts in a low rainfall region. In (b), the environmental planting was established in a region of low rainfall in a block configuration with a tree-dominant species mix using standard densities. In (c), the hardwood plantation was *E. globulus* established in the south-west of Western Australia. In (d), the softwood plantation was *P. radiata* established in the East Gippsland region of Victoria. In (e) and (f) the native systems were Eucalyptus Tall Open Forest in regions of high rainfall, and Eucalyptus Open Woodland in regions of low rainfall, respectively.

Growth habits of mixed-species plantings, forests, woodlands or shrublands

Although there are broad differences in allocation of AGB between key forest types, within stands of mixed-species, some additional variability in the allocation of AGB can be attributable to the relative mix of trees to shrubs. Results given in Table 13 and Fig. 5a show that when compared to stands that had a good mix of trees and shrubs (PropEuc<0.75), Bole:AGB was higher in mixed-species stands that were predominately trees (PropEuc≥0.75).
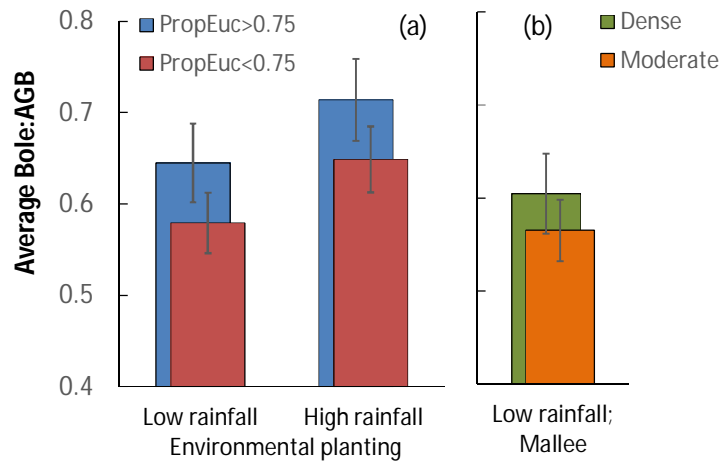
Figure 5: Average Bole:AGB in: (a) low and high rainfall environmental plantings that were either tree dominant (PropEuc≥0.75), or had a good mix of trees and shrubs (PropEuc<0.75), and; (b) low rainfall mallee plantings established in wide belts of either high density (≥2,300 sph) or moderate-low density (<2,300 sph). In (a), averages were obtained from across plantings of various configurations and stand densities. In (b), averages were obtained from across plantings of various species.

There was also evidence that when compared to low rainfall woodland/shrublands, the average Bole:AGB was observed higher in higher rainfall native forests (Table 14). These results were consistent with the review of Poorter *et al.* (2011). They showed that temperate forests had a higher stem mass fraction and lower leaf mass fraction than those of woodlands and shrublands. They also showed vegetation type accounted for 66% of the variation across observations of stem mass fraction. Stands dominated by trees have a relatively high allocation to stems (and thus bole) given trees have more bole than shrubs (e.g. Stewart *et al.* 1979; Birk *et al.* 1995), and because in woody species, allometric constraints cause plants to increasingly invest in stems when size increase, and trees are larger than shrubs (e.g. Poorter *et al.* 2011).

Biomass and age

Statistical analysis of the large environmental and mallee plantings dataset demonstrated that AGB or age were not able to explain variations in allocation to non-structural components of twigs, and particularly bark (Table 13). Hence, allocation of AGB to branches (which comprise twigs as well as some larger branches) and bark were less responsive to changes in stand age than stem wood and foliage (Fig. 4).

The constant Bark:Bole of 0.17 was just as efficient at predicting bark biomass as more complicated models. Confidence in the use of a constant ratio between bark and bole (dominated by stem) is provided by previous findings that bark varies proportionally to stem wood, particularly in stands >3 years (Madgwick *et al.*, 1977; Paul & Polglase *et al.*, 2004b).

In contrast, given structural components such as the bole and bough grow cumulatively with AGB, the AGB was a key determinant of allocation to these components (Table 13). Most of the accumulation of AGB as stands mature may be attributable to an increase in stem biomass and, with the exception of some plantation species, a corresponding increase in branch biomass (Fig. 4). As discussed above, allometric constraints cause woody plants to increasingly invest in stems when size increases (Schroeder *et al.*, 1997; Snowdon *et al.*, 2000; Kantola & Mäkelä, 2006; Poorter *et al.* 2011).

Another interesting observation in the analysis of the large environmental and mallee plantings datasets was that the importance of stand age on allocation of was only important only at the stand-scale, not the individual-scale (Table 13). Individuals sampled for biomass were selected from a range of stands; a small tree for example could have been harvested from a young stand, or alternatively, from an older stand of with relatively poor growth rates. This made AGB of individual trees and shrubs, and hence allocation of biomass, poorly correlated with age. In contrast, at the stand-scale the total sum biomass of all plants within the stand were more likely to be related to age. However, stand age is often difficult to accurately

ascertain in many forests types, particularly those of individuals of mixed-age. Hence, the revised empirical models that take into account AGB as well as estimate of stand age are preferable over the original input tables that are based on age alone.

Climate

Environmental plantings and native systems are distributed across a wide range of climates. Hence, for these systems, there was a significant positive impact of MAR on Bole:AGB (Tables 13 and 14, Fig. 5a). These findings may be explained by increased MAR, and hence productivity, resulting in an increased allocation to stem wood (e.g. Campoe *et al.* 2012), as demonstrated when productivity was influenced by water manipulation (Giardina *et al.* 2003; Stape *et al.* 2008; Ryan *et al.* 2010). Consequently, Bole:AGB was higher in tropical than temperate regions (Table 13), consistent with the findings of others (e.g. Poorter *et al.* 2011).

For both environmental plantings and native systems, allocation of AGB to foliage was found to increase with decreased MAR, and this was at the expense of a decreased allocation of AGB to stem wood. For example, results from native systems across Australia showed that in regions of relatively low MAR, there was a relatively small Bole:AGB (and Wood:AGB), while Foliage:AGB was relatively high, when compared to that observed in regions of relatively high MAR (Table 14). This may be because trees in hash environments have relatively high ratio of photosynthesic mass to body mass as a consequence of thicker leaves and relatively smaller body size (e.g. Xu *et al.* 2014). Indeed Bole:AGB was particularly low in mallee plantings given these tree species are well adapted to drought conditions (ANBG 2004), and so tend to be established in regions of relatively low MAR. However, given the branch pool in FullCAM includes the twig component of the crown, the relatively low Bole:AGB of mallee plantings is not obvious from Fig. 4-5. Further work is required to refine FullCAM biomass allocation inputs to separate twigs from the branch pool, particularly given these will have differing rates of turnover.

Stand density

The statistical analysis of the large environmental and mallee planting dataset suggested that an increase in stand density was associated with an increase in allocation to the stem at the expense of allocation to foliage and twigs (Table 13). This is demonstrated in Fig. 5b, where Bole:AGB, which is dominated by the stem, is relatively high in stands of relatively high density. This observation was consistent with the fact that many of the highest density stands in the database were from narrow belt plantings where edge trees seeking additional light resources branch-out into the area between belts. This would explain why these results were inconsistent with those obtained from competition studies. Such previous studies indicated that as competition between trees increases, allocation to the stem increases at the expense of foliage. This was thought to be as a result of these species responding to closed canopies by positioning foliage at the top of the canopy via increasing their length per unit stem mass (e.g. Schmitt *et al.* 1999; Poorter *et al.* 2011). Further work is required to ascertain the impact of stand density of allocation of AGB for other combinations of plantations species and planting configurations.

3.1.3 Empirical models of BGB$_C$:AGB

The changes in allocation of AGB discussed above do not affect the total biomass C per se (as AGB is determined by the TYF), and therefore only influence the C budget in terms of input of C into the debris pools via turnover or disturbance events. In contrast, the allocation to BGB$_C$:AGB directly affects total biomass C. Changes in BGB$_C$:AGB ratios are therefore of particular interest, and hence, discussed separately here.

As discussed previously, BGB$_F$ are typically the smaller pool of BGB$_T$ (e.g. Keyes & Grier 1981; Snowdon *et al.* 2000; Mokany *et al.* 2006) and is therefore of less concern for biomass carbon accounting. This was confirmed by our results; BGB$_T$ being only marginally greater than BGB$_C$. Fine roots are nonetheless one of the most dynamic pools of biomass (Vogt *et al.* 1996), and thereby a major driver of soil nutrient and

carbon dynamics following reforestation. Here we have related BGB_F to AGB, although there is some evidence suggesting that BGB_F reaches a max at canopy closure, after which it stabilises or slowly decreases (Jackson *et al.* 1996; Snowdon *et al.* 2000). Further work is required to explore whether BGB_F predictions may be improved by BGB_F to foliage rather than the total AGB (Shackleton *et al.* 1988; Litton *et al.* 2003).

Environmental and mallee plantings

In environmental and mallee plantings, BGB_C:AGB of individual trees or shrubs tended to be much higher than the typically-applied default of 0.25 (Mokany & Raison 2004), but varied greatly depending on the size of the individual and its life-form (Fig. 6). On average, mallee eucalypts trees had exceptionally high BGB_C:AGB (Fig. 6b). There were also differences between life-forms in the sensitivity of BGB_C:AGB to plant size. Trees, particularly mallee eucalypt trees, had a relatively high sensitivity of BGB_C:AGB to plant size (Fig. 6). In contrast, shrub life-forms had BGB_C:AGB that varied very little with plant size.
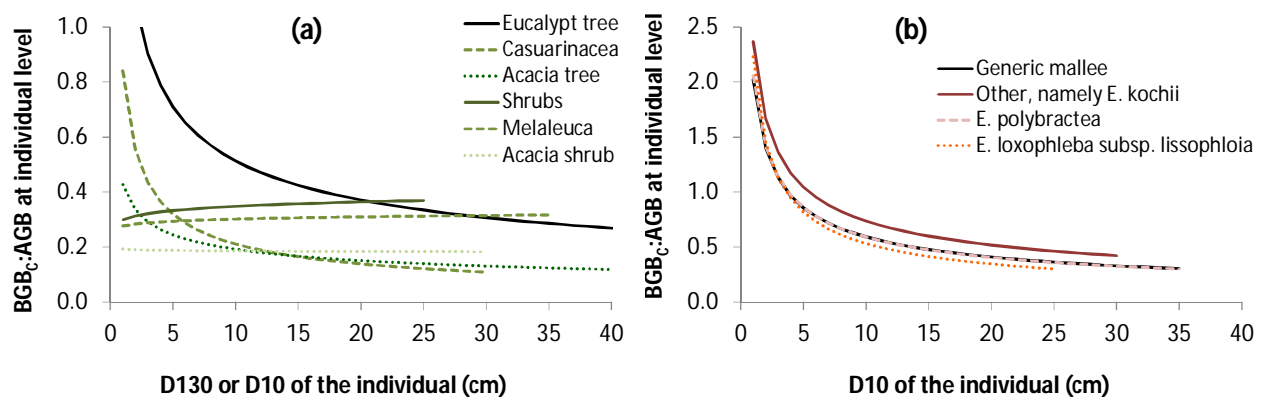

Figure 6: Relationship between BGB_C:AGB and stem diameter for different groups of species or life-forms in; (a) environmental plantings, and (b) mallee plantings. These relationships were derived from the application of allometric equations as described by Paul *et al.* 2014a,b,c.

When the individual-scale BGB_C:AGB estimates were applied to the stand-scale, it was found that the efficiency of prediction of stand-level BGB_C:AGB was only 43% across the wide diversity of environmental plantings, but was much higher (73%) for the more uniform mallee plantings (Table 16, Fig. 7). This empirical modelling of BGB_C:AGB at the stand-scale demonstrated that an increase in stand density resulted in a decrease in BGB_C:AGB for both environmental and mallee plantings (Table 16). This may be at least partly explained by the observation that across the stands of environmental and mallee plantings studied, average D10 of live plants within the stands decreased with increased density of the stand, or plants per hectare (Fig. 8).

Table 16. Models derived for prediction of BGB_C:AGB at the stand-scale. Statistically significant variables, and whether they have a positive or negative influence, are listed. Statistical significance (P-value), R^2 and sample number (N) are provided. Resulting models are provided in detail by Paul & Waterworth (2015).

Type	Significant variables	P	R^2	N
Mixed	– Ln(AGB)[1]; + PropEuc>0.75$_{[0,1]}$[2]; – Sparse or very sparse$_{[0,1]}$[3]	<0.01	0.43	736
Mono	– Ln(AGB)[4]; – Ln(Age)[7]; – Sparse$_{[0,1]}$; + Dense$_{[0,1]}$	<0.01	0.73	369

[1] When PropEuc<0.75.

[2] Less so when relatively high Ln(AGB).

[3] Particularly with relatively high Ln(AGB), and/or when PropEuc<0.75.

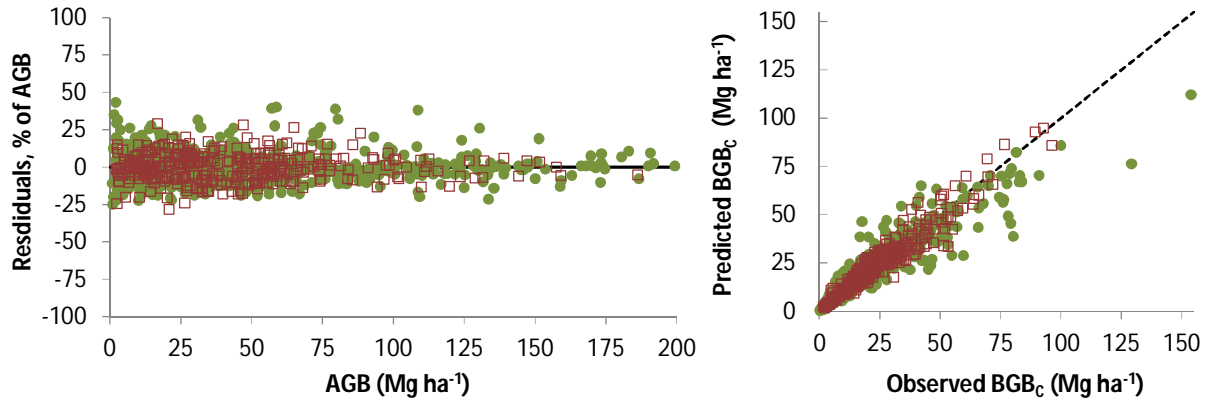[4] Less so when relatively high Age.

Figure 7: Plots of residuals in predicted stand-level BGB_C, expressed as a percentage of stand-level AGB, and the corresponding relationships between observed and predicted BGB_C for: environmental plantings (green circles), EF=0.43, N=736; mallee plantations (red squares) EF=0.73, N=369.
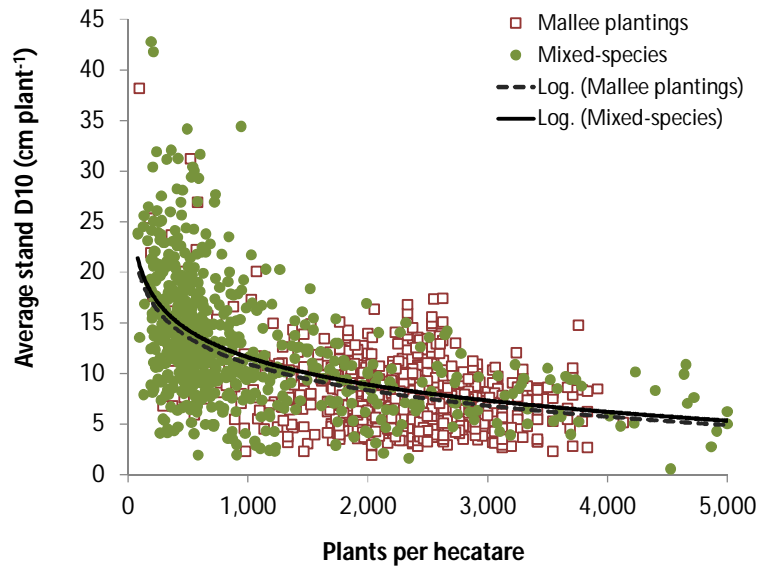

Figure 8: Relationship between average diameter of stems (at 10 cm height above the ground; D10 cm) of live plants within a stand, and the density of that stand (number of live plants per hectare measured).

In addition to stand density, AGB was also a key factor determining BGB_C:AGB, with this ratio declining in stands of both environmental and mallee plantings as AGB increases (Table 16). For environmental plantings, the PropEuc was also a statistically significant explanatory variable (BGB_C:AGB being higher in stands with PropEuc≤0.75 when compared to those with PropEuc>0.75), while for mallee plantations, stand age was important (BGB_C:AGB being relatively high in young stands).

Other explanatory variables considered (planting configuration, MAR during the years of growth, FPI and the AGB-growth category of planting) were either statistically insignificant, or increased the amount of explained variation in BGB_C:AGB by <2%. Although there was some evidence that different species of mallee eucalypts had differing BGB_C:AGB, the impact was weak, with species only explaining 12% of the variation in BGB_C:AGB for mallees (data not shown). Moreover, the explanatory variable of species of mallee eucalypt lost its statistical significant once other factors were also considered, thereby suggesting that any impact of species on BGB_C:AGB may have only been an artefact of other confounding factors.

Native forests, woodlands and shrublands

As expected, the BGB_C:AGB observed in native systems was found to be higher woodlands and shrublands in regions of relatively low rainfall, and which were found to have more observations of F_{Mulit} and F_{Shrubs} than found in stands of native forests from regions of relatively high rainfall (Table 17). The empirical modelling of BGB_C:AGB discussed above suggests that this was probably attributable to the combination of both the lower MAR, and the increased proportion of plant functional types known to have relatively high BGB_C:AGB ratios, e.g. shrubs and multi-stemmed trees such as mallee eucalypts. Indeed results obtained indicated that the application of the stand-level model for low (< 500 sph) density environmental plantings with PropEuc>0.75 (or PropEuc<0.75) was appropriate for a wide range of native forests (or woodlands/ shrublands) from high (or low) rainfall regions. The predicted BGB_C:AGB ratios for a wide range of scenario of stands (Table 8) of between 20 and 100 years of age were within ±1 SD of that averaged observed (Table 17).

Table 17. Mean (± SD) observed BGB_C:AGB at the individual-scale for various species of within high rainfall native forests and low rainfall woodlands/shrublands, and the comparison of these observations to that predicted in relevant 20-100 year old stands.

Native ecosystem	Observed	Predicted
Native forests	0.33 ± 0.14 (N=168)	0.19-0.39
Woodlands/shrublands	0.41 ± 0.19 (N=178)	0.29-0.40

Although previous work (Westman & Rogers 1977; Ash & Helman 1990; Gonzalez *et al.* 2013) and results from the environmental planting datasets showed that allocation to BGB in shrubs is relatively small when compared to trees, results obtained here confirm that this does not necessarily imply that shrublands have relatively low BGB_C:AGB. The finding that BGB_C:AGB was higher in the relatively F_{Shrub}-dominant woodland/shrublands than in the F_{Euc}-dominant native forests (Table 17) was consistent with the findings from the global review of Mokany *et al.* (2006). They showed shrublands had much higher BGB_C:AGB than temperate eucalypt forests/plantations (i.e. BGB_C:AGB average of 1.84 compared to 0.20-0.44). Caution is therefore needed when considering BGB_C:AGB of shrubs; these ratios may depend on whether the shrubs are integrated with trees in mixed-species plantings, or whether they are shrublands that may be comprised of a quite different cohort of species of shrubs, and which tends to be in regions of relatively low MAR.

Hardwood and softwood plantations

The average BGB_C:AGB observed was moderate (0.24 ± 0.13) for hardwood plantations, relatively low for plantations of *Pinus radiata* (0.20 ± 0.06), and relatively high for plantations of *P. pinaster* (Table 18). These results were consistent with the global review of Mokany and Raison (2004, Fig. 20). They showed that the mean BGB_C:AGB of temperate conifer plantations were generally less than that of temperate eucalypt plantations, but that these differences were less pronounced for conifer plantations that had relatively low biomass (<50 Mg ha^{-1}, e.g. many stands of *P. pinaster*).

Table 18. Mean (± SD) observed BGB_C:AGB at the individual-scale for various species of Australian hardwood and softwood plantations.

Type of plantation	Species	Observed
Hardwood		0.24 ± 0.13 (N=97)
Softwood	*P. radiata*	0.20 ± 0.06 (N=134)
	P. pinaster	0.54 ± 0.23 (N=114)

3.1.4 Key factors influencing BGB$_C$:AGB

For each planting type, variations in BGB$_C$:AGB predicted by FullCAM were originally based on stand age only. When the new empirical models predicting BGB$_C$:AGB are applied via the Allocation Calculator, numerous factors are also accounted for. These are outlined below.

Forest type

The highest BGB$_C$:AGB was predicted to be in the stands growing in relatively harsh low rainfall environments; mallee planting and *Pinus pinaster* softwood plantations (Fig. 9a, and insert in Fig. 9d). The BGB$_C$:AGB was also predicted to be relatively high for low rainfall environmental plantings and woodlands/shrublands (Fig. 9b, f). In contrast, BGB$_C$:AGB tended to be relatively low for high rainfall environmental plantings and native forests (Fig. 9e). The lowest BGB$_C$:AGB predicted were those from hardwood plantings (average 0.30 at age 10 years), and particularly softwood plantations grown in regions of relatively high rainfall (average 0.25 at age 10 years) (Fig. 9c,d).

These wide range in BGB$_C$:AGB between different forests types is expected based on previous findings. For example, many workers (e.g. Cuevas *et al.* 1991; Vogt *et al.* 1996; Mokany *et al.* 2006) have found that forest plantations have lower BGB$_C$:AGB than natural forests. Furthermore, Paul *et al.* (2014a) found differences in allometry for BGB$_C$ between different groupings of genera. They reported that for a given stem diameter, BGB$_C$ of an individual was highest for mallee trees and lowest for shrubs. This finding was consistent with other reports (Jonson & Freudenberger 2011). Such differences in allometry between growth habits explained why BGB$_C$:AGB was highest in stands of mallee eucalypt, and lowest in mixed-species forests that had PropEuc<0.75, e.g. woodlands/shrublands.

Differences in BGB$_C$:AGB between forest types of differing tree species, and PropEuc, may be attributable to three evolutionary-based factors. Firstly, shrubs have shallower rooting systems than trees as they tend to be smaller, and thereby did not have the same evolutionary pressure as trees to develop the large structural roots that contain large quantities of biomass (e.g. Ludwig 1977; Wilson 1993; Mokany *et al.* 2006). Secondly, BGB$_C$:AGB tend to be larger in species that re-sprout from root stock following disturbance compared to those that regenerate by seed (Higgins *et al.* 1987; Low & Lamont 1990). Most eucalypt trees, and particularly mallee eucalypts, are prolific re-sprouting species whereas most of the shrubs in environmental plantings regenerate from seed (e.g. ANBG 2004). Third, BGB$_C$:AGB may be particularly high for mallee eucalypts as these species have evolved to survive hash environments and prolonged drought by storing water in larger structural storage organs in their rooting systems (lignotubers) (ANBG 2004; Hilbert & Canadell 1995). These lignotubers would be anticipated to add additional biomass to the rooting systems above that required for structural purposes.
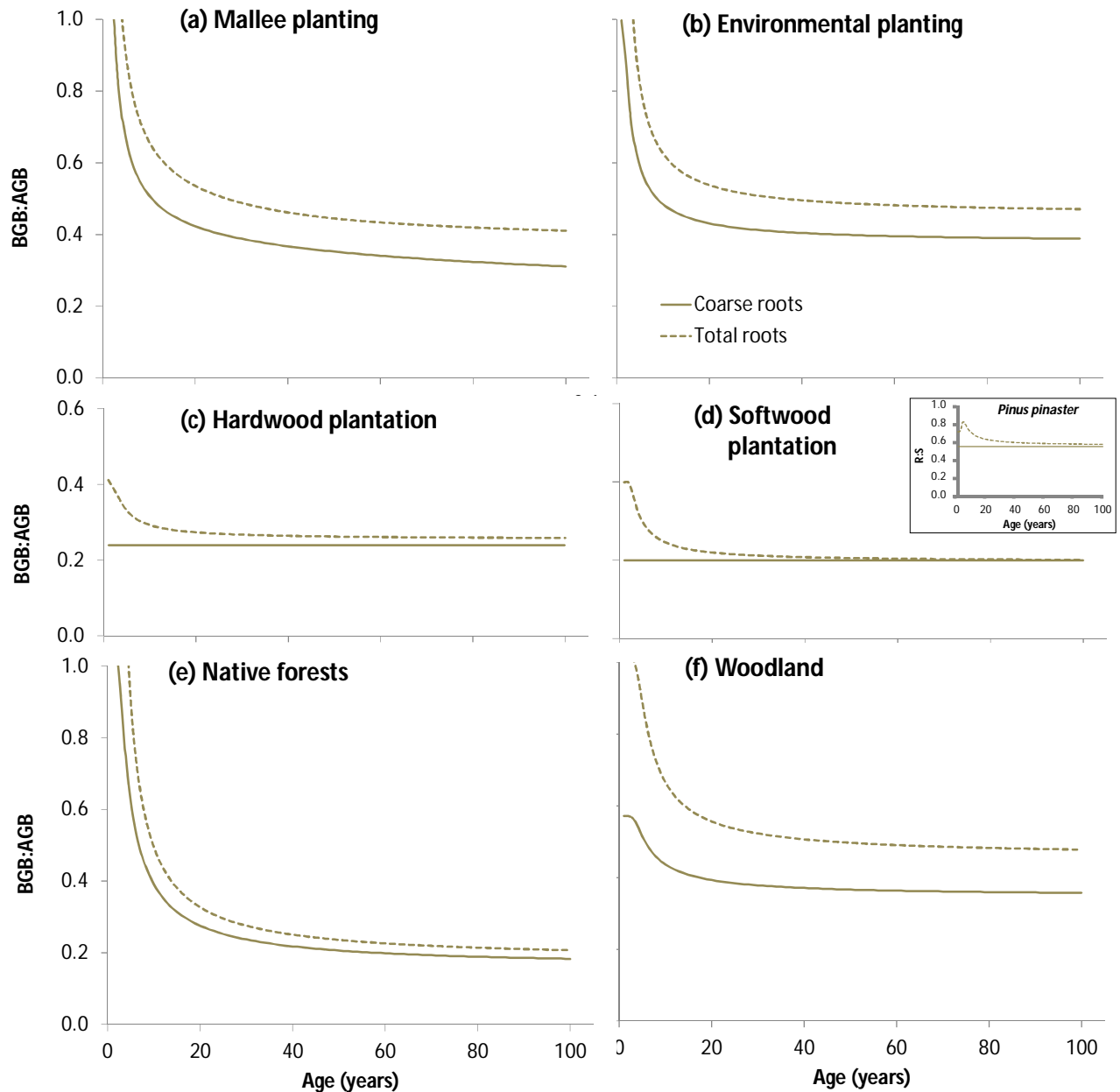
Figure 9: Examples of differences in BGB$_C$:AGB between the key categories of forest types. In (a), the mallee plantings were *E. loxophleba lissophloia* established as wide belts in a low rainfall region. In (b), the environmental planting was established in a region of low rainfall in a block configuration with a tree-dominant species mix using standard densities. In (c), the hardwood plantation was *E. globulus* established in the south-west of Western Australia. In (d), the softwood plantation was *P. radiata* established in the East Gippsland region of Victoria, with output in the box showing the *P. pinaster* established in south-west of Western Australia. In (e) and (f) the native systems were Eucalyptus Tall Open Forest in regions of high rainfall, and Eucalyptus Open Woodland in regions of low rainfall, respectively.

Growth habits of mixed-species plantings, forests, woodlands or shrublands

Although there are broad differences in BGB$_C$:AGB between key forest types, within stands of mixed-species, some additional variability in BGB$_C$:AGB can be attributable to the relative mix of trees to shrubs. Results indicate that for environmental plantings, BGB$_C$:AGB was higher in stands dominated by trees (PropEuc≥0.75) relative to that found in stands with a good mix of trees and shrubs (PropEuc<0.75), especially in regions of low rainfall (Table 16; Fig. 10a).

These results were consistent with previous work showing that at the stand-scale, allocation to BGB in shrubs or under-story species is relatively small compared to over-story species (Westman & Rogers 1977; Ash & Helman 1990; Gonzalez *et al.* 2013). As discussed above, shrubs have shallower rooting systems than trees as they tend to be smaller, thereby they do not have the same evolutionary pressure as trees to develop the large structural roots that contain large quantities of biomass (e.g. Ludwig 1977; Wilson 1993b; Keith *et al.* 2000).
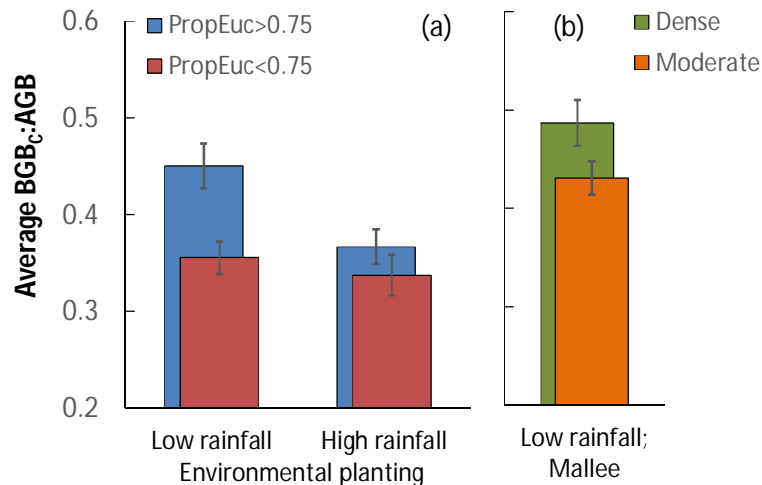

Figure 10: Average BGB_C:AGB in: (a) low and high rainfall environmental plantings that were either tree dominant (PropEuc≥0.75), or had a good mix of trees and shrubs (PropEuc<0.75), and; (b) low rainfall mallee plantings established in wide belts of either high density (≥2,300 sph) or moderate-low density (<2,300 sph). In (a), averages were obtained from across plantings of various configurations and stand densities. In (b), averages were obtained from across plantings of various species.

In some cases, there may however be a confounding influence of MAR on BGB_C:AGB in stands with relatively high proportions of shrubs. For example, woodland/shrublands appeared to have relatively high proportions of shrubs than native forests (Tables 3 & 6). Despite this, woodland/shrublands had significantly higher BGB_C:AGB than native forests (Table 17). As discussed below, this was presumably due to the fact that woodland/shrublands are generally from regions of relatively low rainfall when compared to native forests.

Stand biomass and age

The relatively large BGB_C:AGB dataset for environmental and mallee plantings enables the assessment of the impacts of stand biomass and age on partitioning to BGB. The observed influence of AGB on BGB_C:AGB was consistent with previous reviews of collated datasets for forests and woodlands showing that BGB_C:AGB decreases significantly as the AGB increases (e.g. Ovington 1957; Applegate 1982; Negi & Sharm 1985; Ruark & Bockeim 1987; Gerhardt and Fredriksson 1995). For example, Mokany *et al.* (2006) found temperate eucalypt forests/plantations of AGB <50, 50-150 or >150 Mg ha^{-1} had BGB_C:AGB of 0.44, 0.28 and 0.20, respectively (N=10, 11 and 6).

The influence of AGB on BGB_C:AGB has been attributable to the 'functional equilibrium' theory; BGB_C:AGB will be determined by the equilibrium between AGB and BGB to ensure that the assimilation of C by the AGB is kept in balance with the uptake of water and nutrients by the BGB (e.g. Brouwer 1963). This theory may explain why factors resulting in an increase AGB will have a negative influence on BGB_C:AGB (e.g. Nihlgård & Lindgren 1977; Keyes & Grier 1981; Brown & Lugo 1982; Nadelhoffer *et al.* 1985; Murphy & Lugo 1986; Roa-Fuentes *et al.* 2012; Gower *et al.* 1992; Brand 1999; Cairn *et al.* 1997).

Accumulation of AGB can be related to stand age for monoculture plantings established within a constrained range of climates. This may explain why for mallee eucalypt plantings, stand age was also a significant factor explaining variations in BGB_C:AGB. In contrast, for mixed-species forests established across a much greater diversity of climates and mix of species, stand age had little impact on BGB_C:AGB.

Hence, the observed decline in BGB_C:AGB with increased stand age in Fig. 9 is largely attributable to the fact that AGB is increasing with stand age, and is perhaps often not directly related to stand age per se.

A caveat on the results obtained was that the most of the environmental and mallee plantings studied (Table 5) were relatively young, with the 95th percentile of stand age in study sites being only 24 and 14 years for the mixed-species forests and mallee eucalypt plantations, respectively (Paul *et al.* 2013a,b; 2014a). This fact may partly contribute to the relatively high BGB_C:AGB observed. To improve our understanding of the impacts of stand age and AGB on BGB_C:AGB, further work is required to expand the BGB_C:AGB datasets for more mature stands of a wider range of forest types.

Climate

Results obtained suggest that the only impact of MAR on BGB_C:AGB of stands studied here was an indirect via AGB. Our results indicated that BGB_C:AGB was not statistically influenced by MAR per se. This was consistent with the fact that BGB_C allometry was not significantly influenced by MAR (Paul *et al.* 2014a). This may be partly explained by the fact that most (87%) of the datasets collated were from MARs of only 250-850 mm yr^{-1}, with relatively few (<10%) from regions where MAR>1,500 mm yr^{-1}. Differences in the range of MARs considered may explain why some workers have found MAR influences BGB_C:AGB (e.g. Nihlgård & Lindgren 1977; Keyes & Grier 1981; Brown & Lugo 1982; Nadelhoffer *et al.* 1985; Murphy & Lugo 1986; Roa-Fuentes *et al.* 2012; Gower *et al.* 1992; Brand 1999; Comeau & Kimmins 1989), while others have found the opposite (Cairns *et al.* 1997; Compton *et al.* 1999; Joslin *et al.* 2000). For example, Mokany *et al.* (2006) found a trend of decreased BGB_C:AGB with increased MAR, but that this trend was only apparent when including BGB_C:AGB datasets from sites with MARs>1000 mm yr^{-1}. There was no effect in lower MAR regions. Further work is required to verify these findings for Australian forest types.

Stand density

Evidence was obtained from this study that the BGB_C:AGB of individual trees (but not shrubs) increases inversely with stand-average stem diameter (Fig. 6b), which in turn increases inversely with stand density (Fig. 8). Therefore, consistent with the findings of others others (Pearson *et al.* 1984; Litton *et al.* 2003; Luo *et al.* 2014), stands with higher density had higher BGB_C:AGB (e.g. Fig. 10b). Indeed in a global review, Mokany *et al.* (2006) reported that BGB_C:AGB of forests and woodlands tended to increase with stand density.

In contrast, other studies have found smaller BGB_C:AGB with increased stand density (Puri *et al.* 1994; Ritson & Sochacki 2003), presumably because these trees were competing for light. The 'functional equilibrium' theory might be used to infer either an increase or decrease in BGB_C:AGB with stand density, depending on whether trees were predominately competing for water (which results in a relative increased BGB allocation) or light (which results in a relative increased AGB allocation) (van Wijk *et al.* 2003; Comeau & Kimmins 1989; Wilson 1993; Litton *et al.* 2003). As most of the stands of environmental and mallee plantings studied were in regions of low-moderate average MAR (87% of the dataset from regions with MAR of only 250-850 mm yr^{-1}), it is anticipated that they were predominately competing for water, particularly for older stands in block planting configurations.

Given these conflicting results, it is recommended that additional datasets be collated in order to ascertain the impact of stand density on BGB_C:AGB for different forest types, climatic conditions and planting configurations.

3.2 Litter fall

The sample numbers (N) were relatively high for measurement of foliage litter fall, but relatively low for the twig and bark litter fall (Table 19). As a result, there was evidence to justify differing rates of foliage litter fall for the five different forest types (Table 20). Results suggested that average rates of foliage litter fall tended to increase with decreasing aridity of climates in which the forest generally grows; woodlands

< environmental and mallee plantings < native forests < softwood plantations < hardwood plantations. In contrast, given the lack of statistical differences between forest types, an overall average rates of litter fall were applied across all forests for twigs (8.5 % yr⁻¹) and bark (4.8% yr⁻¹) (Table 20).

Table 19. Mean (as well as standard deviation, SD; and range, Min and Max) observed rates of litter fall under five contrasting forest types, and the mean (as well as standard deviation, SD; and range, Min and Max) observed percentage contribution of this litter fall from foliage, twigs and bark litter. The sample numbers (N) were relatively high for measurement of total litter fall and foliage litter fall, but relatively low for the twig and bark litter fall.

Forest type	Annual litter fall (Mg DM ha⁻¹ yr⁻¹)	Mean	SD	Min	Max	N
Env. plantings	Total	3.26	0.47	2.49	3.65	4
	%Foliage	40	14	17	55	4
	%Twig	NA	NA	NA	NA	NA
	%Bark	NA	NA	NA	NA	NA
Native forests	Total	5.11	2.06	1.13	10.4	83
	%Foliage	58	12	28	89	58
	%Twig	19	7	1	32	43
	%Bark	16	10	2	46	30
Woodland	Total	1.92	0.97	0.72	5.14	24
	%Foliage	49	16	22	73	8
	%Twig	28	8	20	39	6
	%Bark	6	3	20	10	5
Hardwood plantation	Total	5.58	2.54	1.72	9.60	16
	%Foliage	78	20	51	98	3
	%Twig	5	4	0	9	2
	%Bark	4	2	1	6	2
Softwood plantation	Total*	2.83	1.05	1.30	6.00	29
	%Foliage	68	15	51	98	8
	%Twig	14	7	0	21	7
	%Bark	8	4	1	13	7

*Total litter fall was attributable to pine needles.

Table 20. Calculated average rates of litter fall for the foliage, twigs and bark under contrasting forest types. Within each column, estimates with differing letters represent significant (P<0.05) differences were found between forest types.

Forest type	Foliage (% yr⁻¹)	Twigs (% yr⁻¹)	Bark (% yr⁻¹)
Env. plantings	15.7 [b,c]	NA	NA
Native forests	30.3 [b]	9.6 [a]	5.6 [a]
Woodland	14.3 [c]	7.2 [a,b]	4.3 [a,b]
Hardwood	40.4 [a]	4.7 [b]	2.5 [b]
Softwood	31.2 [a,b]	NA	NA
Total	28.7	8.5	4.8

3.3 Decomposition of litter

Table 21 provides the parameters for the emprical exponential decay models (Section 2.3) that were calibrated to the datasets collated from litter bag studies. For deadwood and bark, there was clear evidence that a sinlge exponential decay model is suffice (Eq. 1, Section 2.3), while for foliage litter, a double exponential decay model is required (Eq. 2, Section 2.3). Therefore, deadwood and bark litter were

both be assumed to be 100% resistant, and thereby the W_l parameter was not required (Table 21). The collated datasets for eucalypt-dominant stands indicated that typical resistant fractions for foliage litter was 77%, with the remaining 23% therefore being decomposable (Table 21). Pine needles were more recalcitrant, with the collated datasets for softwood plantations indicating that typical resistant fractions are 85%, with the remaining 15% therefore being decomposable. Based on these findings, revised FullCAM parameter for resistant fraction of foliage debris was set to 85% for softwood plantaitons, and 77% for all other forest types.

Decomposition rates for deadwood and bark indicated that on average, 14% of deadwood would be lost after 1 year, while 16% of bark litter would be lost after 1 year (Table 21). In the absence of data to justify otherwise, it was assumed that all forest types had the same decomposition rates for deadwood and bark litter. Rates of deadwood decomposition decline exponentially as the diameter of the wood increases (Mackensen and Bauhus 1999).

The decomposition rates of 14% yr^{-1} for deadwood (k of 0.14) was consistent with twigs and small branches (<10 cm diameter). Much slower rates of decomposition (i.e. k of 0.07 to 0.01 as diameter decreases from 10 cm to 100 cm diameter) are anticipated for larger branches and logs in coarse woody debris (CWD, Mackensen and Bauhus 1999). Further work may therefore be required to further refine rates of decomposition under FullCAM scenarios where significant amounts of CWD remains on-site as 'slash' post disturbance events such as fire or thinning/clearing. One options currently being explore is to effectively slow the decomposition of slash via the simulation of a 'standing dead' pool of debris, with C from this pool only slowly becoming available for decomposition.

For foliage litter, rates of decomposition for decomposable components exceeded the allowable maximum in FullCAM of 100% yr^{-1}; avering 1,316% yr^{-1} under eucalypt-dominant stands, and 327% yr^{-1} under softwood plantations (Table 21). Therefore, for all forest types, the revised parameter for decomposable pools of foliage litter was set to the maximum rate of decomposition; 100% yr^{-1}. The more reclcitrant resistant pool of folliage litter decomposed an an average rate of 32% yr^{-1} under eucalypt-dominant stands, and 22% yr^{-1} under softwood plantations. However as indicated in Table 21 through the 20th and 80th percentiles observed, there was much variation in these estimates between studies. Indeed this variation was between 18-27% yr^{-1} under eucalypt-dominant stands, and between 15-27% yr^{-1} under softwood plantations. Given the larger variation in observed rates of decomposition of foliage litter, and because it is anticipated that decomposition in litter bags may be faster than undisturbed foliage litter, the conservative approach of using a slightly lower rate than the average observed was applied. Hence, revised parameter values in FullCAM for decomposition of resistant pools of foliage litter were assumed to be about 10% less than the average observed; or 28% yr^{-1} under eucalypt-dominant stands, and 20% yr^{-1} under softwood plantations.

Table 21. Average (and range, based on the 20th and 80th percentiles) labile component present in a litter fraction (W_l, or the fraction of debris that is decomposable, with the rest being resistant), instantaneous decay constant of resistant debris (k, or % debris lost after 1 year), and the instantaneous decay constant for the decomposable debris (k', or % debris lost after 1 year).

Forest type	Litter type	N	W_l	k	k'
Eucalypt-dominant	Deadwood	23	NA	14 (9-21)	NA
Eucalypt-dominant	Bark litter	13	NA	16 (13-22)	NA
Eucalypt-dominant	Foliage litter	59	23 (18-27)	32 (14-47)	1316 (234-1570)
Softwood	Pine needle litter	28	15 (8-19)	22 (15-27)	327 (20-500)

When applying these revised parameter values for decomposition, the predicted rates of loss of pools of deadwood, bark litter and foliage litter were reflective of that expected based on the observed typical decay functions for these pools (Fig. 11). The slight variation between FullCAM-predicted rates of decomposition of a given component of debris (e.g. for deadwood, as shown in box inserted in Fig. 11a)

was attributable to the differing temperature and rainfall among the various locations simulated, with these affecting decomposition rates in accordance with the 'Mulch-style' sensitivity (Section 2.3).
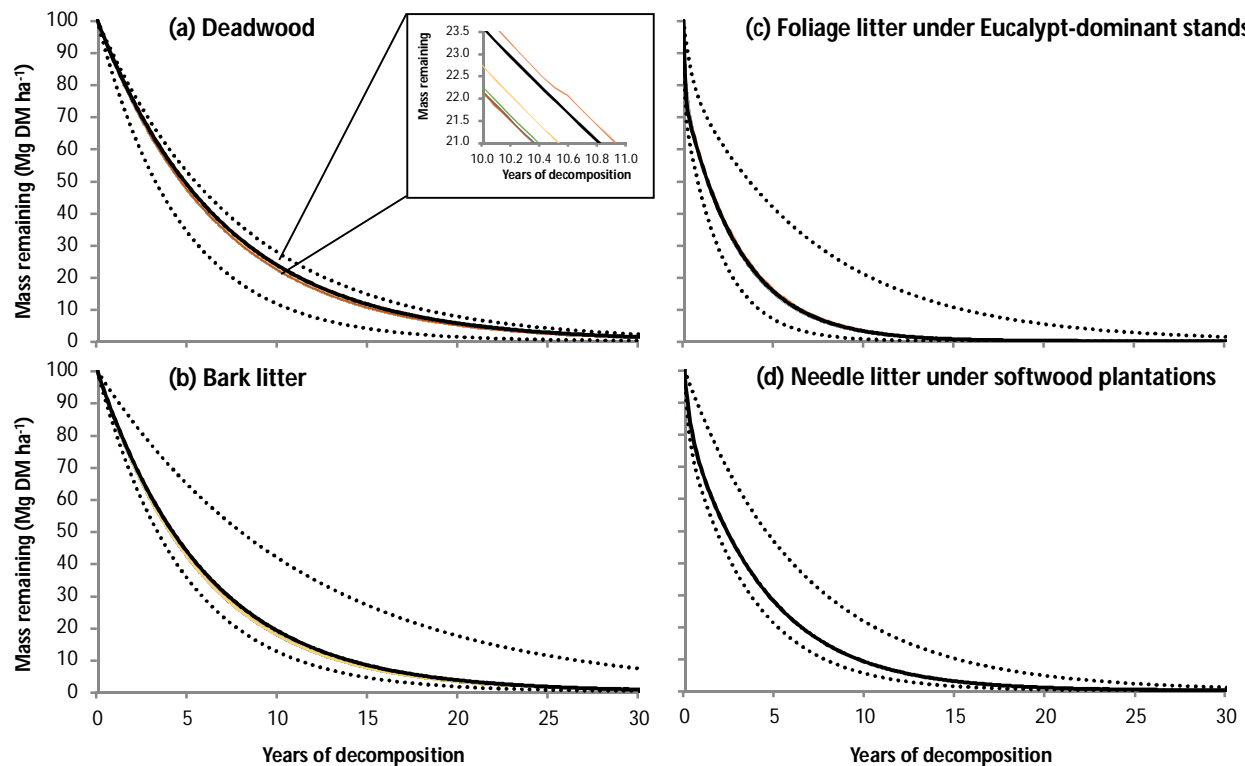

Figure 11. Simulated decomposition of 100 Mg DM ha^{-1} of deadwood and various types of litter when applying the revised litter decomposition parameters together with the 'Mulch style' sensitivity to temperature and rainfall. Simulations were for the 41 example plot files outlined in Table 8, but which were configured such that there was no forest growth, and the initial pools of debris were 100 Mg DM ha^{-1}. Although outputs from all 41 plot files are included, as indicated in the box in (a), these are difficult to distinguish given there was little variation in outputs between plots; especially those from similar climates. Solid black line represent the average observed decay functions as outlined by parameters provided in Table 21. Dashed black lines represent the observed decay functions when the 20th and 80th values were applied for the decay functions parameter (Table 21).

Figure 12 summarises predicted litter and CWD in the 41 representative plots files (Table 8), and that observed across different Australian forest types (Table 11). The average predicted litter and CWD across multiple rotations of the hardwood and softwood plantations were in general agreement with the averages observed, particualrly given the relatively large SD in the average observed, and the fact that observations of litter and CWD were made under stands of varying ages and management regimes. Similalry, for relatively young (20 year old) environmental and mallee plantings, and for mature (100 year old) native systems, predictions of litter and CWD were in broad agreement with the averages observed. The upper bounds of litter and CWD expected were represented by that predicted to be on-site as residue or slash following a harvesting event (stripped bars, Fig. 12). As expected, observed averages of litter and CWD were well below this predicted 'upper limit'. The only exception was for under softwood plantations where CWD in harvest residues appears to be under-predicted on average. However, in these stands the variation in observed CWD was relatively high, as indicated by the relative high SDs for softwood plantations (Fig. 12b).
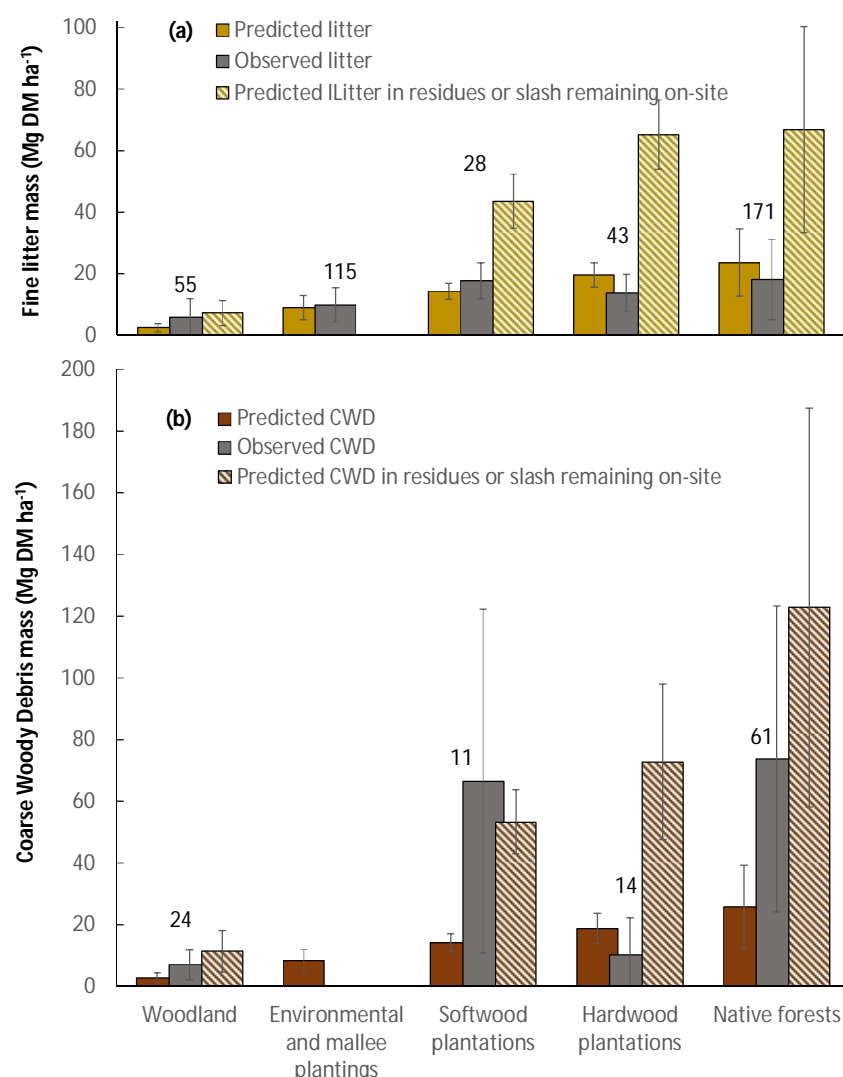
Figure 12. Predicted and observed (a) litter mass, and (b) coarse woody debris (CWD) under various forest types, including: mature (100 year) woodlands; relatively young (20 year) environmental and mallee plantings; softwood plantations of multiple rotations; hardwood plantations of multiple rotations, and; mature (100 year) native forests. For woodlands and native forests, predictions are at 100 years when left uncleared, and when assumed to be cleared the year 99 of simulation. For plantations, predictions the average observed across multiple rotations simulated over a 100 year period, or that predicted in the year post the final clearing event. Number labels represent the number of observations that were used to calculated the average observed litter or CWD. Error bars represent the standard deviations of the means. Predicted means were based on the simulation of 5 woodlands, 21 environmental or mallee plantings, 5 softwood plantations, 6 hardwood plantations, and 4 native forests (Table 8).

3.4 Parameters influencing soil C

Figure 13 shows the efficiency of prediction of pools of soil C across the 158 forest sites where pools of soil C were measured (Table 12), and where parameters calibrated to achieve these efficiencies included root turnover and decomposition, and CO_2-C loss on decomposition of debris. Overall, the efficiency of prediction of total soil C was 46%. For the two largest pools of this soil C, the efficiencies of prediction were 36% for RPM, and 73% for HUM. These efficiencies of prediction of pools of soil C were relatively high given: (i) the RothC parameters recommended by Chappell and Baldock (2013) for agricultural soils was assumed to apply here for forest soils, (ii) large uncertainties in measurement of pools of soil C, mainly due to sampling errors (Cunningham *et al.* 2017); (iii) large uncertainties in the measured biomass that were used to constrain the predictions (Paul and Polglase 2004b; Paul *et al.* 2017b), and; (iv) the

application of the revised generic default parameters for allocation of biomass, litter fall and decomposition of litter across all 158 calibration sites, despite observations of these pools and fluxes at these sites suggested significant site-to-site variability.
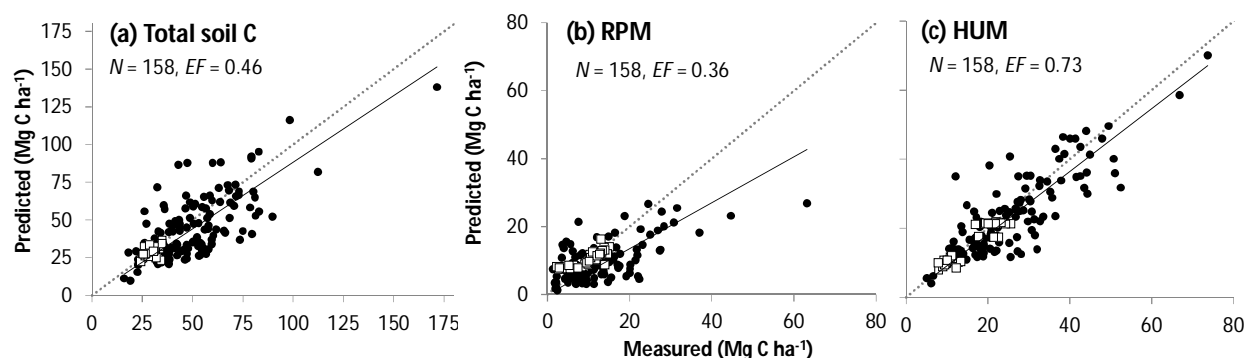

Figure 13. Relationship between observed and predicted carbon stocks (Mg C ha⁻¹) in surface soil (0-30 cm) for: (a) total soil organic carbon; (b) RPM pool of soil C; and (c) HUM pool of soil C. Datasets used are listed in Table 12. Black circles represent the paired-site environmental plantings (Paul *et al.* 2017b). White squares represent the hardwood and softwood repeated-measured forestry trials (Paul and Polglase 2014b).

The calibrated rates of root turnover were 10% yr⁻¹ for coarse roots and 80% yr⁻¹ for fine roots. Decomposition rates were calibrated to be 30% yr⁻¹ for coarse roots and 100% yr⁻¹ for fine roots. These values were applied across all forest types.

In contrast, when calibrating the parameters for CO_2-C loss on decomposition of debris across the 158 sites, it was found that as stands matured and a litter layer developed, inputs of C into the soil from debris decomposition needed to be decreased. In the absence of any clear justification for a relationship between CO_2-C loss and the development of a litter layer, it was simply assumed here than stands <10 years old had higher rates of C entering the soil (i.e. lower CO_2-C loss) from debris decomposition than did older stands. Highest model efficiencies were attained when CO_2-C loss on decomposition of decomposable and resistant pools of debris were 77⁻¹ and 40 % yr⁻¹ for stands <10 years old. For stands older than this, CO_2-C loss on decomposition of decomposable and resistant pools of debris were set to 90⁻¹ and 80 % yr⁻¹.

Given the evidence of a decrease in the rates of C input into the soil (as currently simulated by increased CO_2-C loss on decomposition of debris) as stands mature, further research is required to verify this, and ascertain the cause of this decline. Currently in FullCAM, the parameters for CO_2-C loss on decomposition of debris are not able to be varied with stand age; they are set constant for the entire simulation period. Hence, until research has been completed to inform any re-coding of FullCAM, it is recommended that simulations of afforestation of young stands use CO_2-C loss on decomposition of decomposable and resistant pools of debris were 77⁻¹ and 40 % yr⁻¹, respectively. But when simulating older stands, such as in deforestation events, the CO_2-C loss on decomposition of decomposable and resistant pools of debris should be set to 90⁻¹ and 80 % yr⁻¹, respectively.

3.5 Initialising pools of biomass and debris

At the nominated initial stand age, the revised initial relative allocation of total biomass to the various pools (stem, branches, bark, foliage and coarse and fine roots), were based on the changes to biomass allocation described in Section 3.1 (data not shown). They therefore differed for each of the 51 forest types given their different initial age and/or climatic conditions and growth rates typical of that forest type. The initial debris pool also greatly varied between the 51 forest types, depending on the different initial age and/or climatic conditions and typical growth rates (data not shown).

4 Impacts of the revised parameters

4.1 Approach used

Plot file simulations were used to assess the impact of the revised parameters (Section 3) on C stocks (Section 4.2), and the NIR (Section 4.3). For each parameter revised, @Risk was applied to assess the sensitivities of the change on total on-site C stocks. This was done by applying a uniform probability distribution to each parameter that was revised; with the minimum and maximum range determined by the original and new parameter values. A Monte Carlo analysis was then run (over 10,000 iterations) to observe the impact of this variation in parameter value on the on-site C stocks at a given time step. Due to interactions being important, all parameters were assess during the same Monte Carlo simulation. The only exception were the allocation of biomass input tables. The impact of these parameters had to be analysed separately. This was done by using 40 demonstrative plot files, representing key forests types and their typical management regimes, to indicate the extent of impact on predicted pools of biomass because of the changes to the allocation input tables.

4.2 Impact of changes in parameters on stocks of C

4.2.1 Allocation of biomass

Using collated biomass datasets, the time-series inputs of allocation of biomass to tree components were changed (Section 3.1). The most significant change was a general decrease in allocation to stem wood (Fig. 14), and a general increase in allocation to branch wood (Fig. 15). There was also an increase to foliage allocation for woodlands and shrublands (Fig. 17).

The changes in allocation of AGB discussed above do not affect the total biomass C per se (as AGB is determined by the TYF), and therefore only influence the C budget when there are disturbance or management events, or in terms of input of C into the debris pools via turnover. In contrast, the allocation to BGB_C directly affects total biomass C. Changes in BGB_C:AGB ratios are therefore of particular interest. For planted systems, the BGB_C:AGB increased, with this being particularly pronounced for mallee plantings, environmental plantings, and *Pinus pinaster* plantations (Fig. 20). In contrast, for native systems the allocation to roots was previously set relatively high, particularly for many woodlands and shrublands where there was generally a decrease in the BGB_C:AGB.
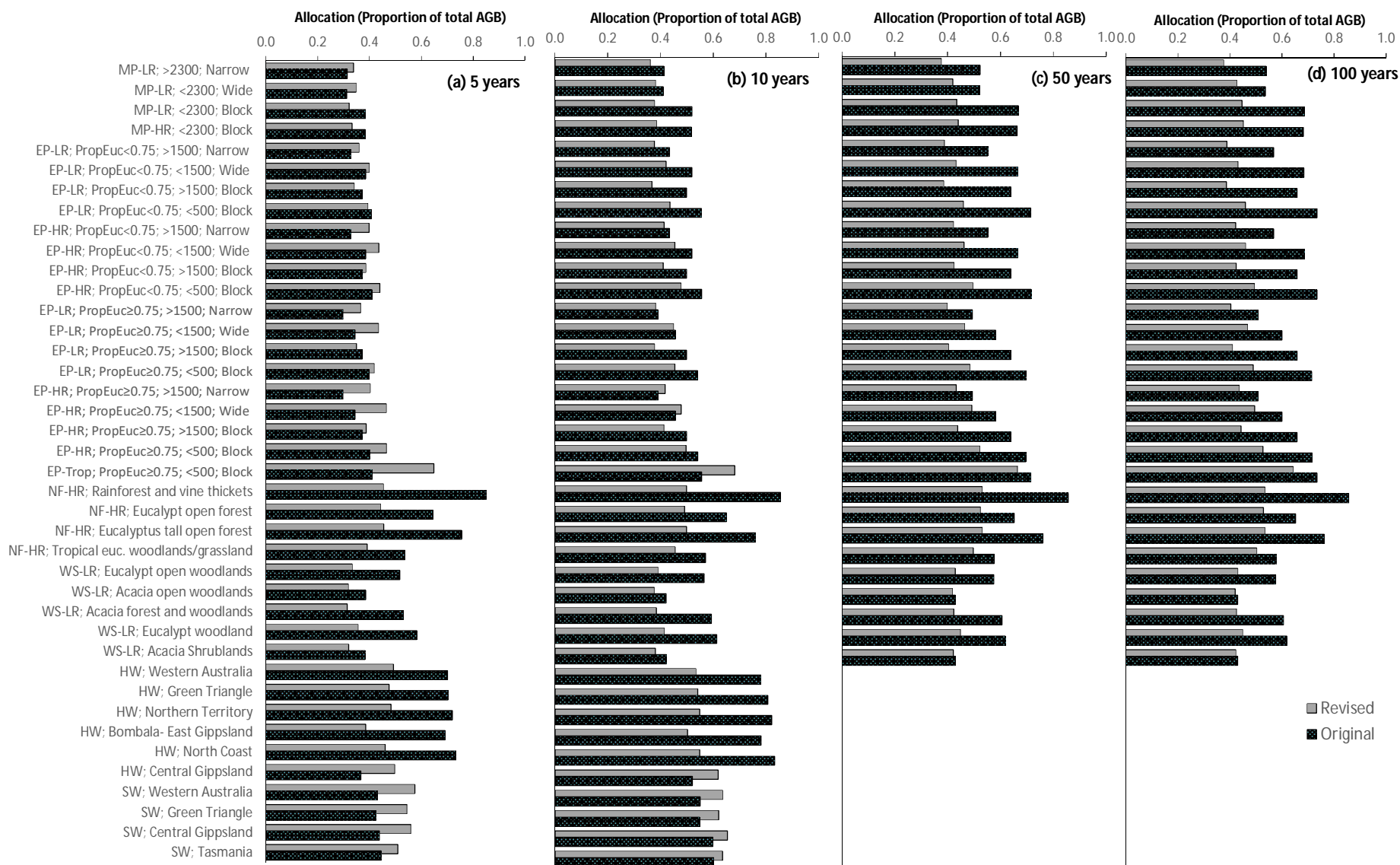
Figure 14: Comparison of revised Calculator-predicted proportion of AGB that is **stem wood** biomass and that predicted using the original FullCAM defaults at stand age of: (a) 5 years; (b) 10 years; (c) 50 years, and; (d) 100 years. Abbreviations of the different scenarios of forest types are provided in Table 8, with each being simulated under average values of M for the specific domain of that forest type.
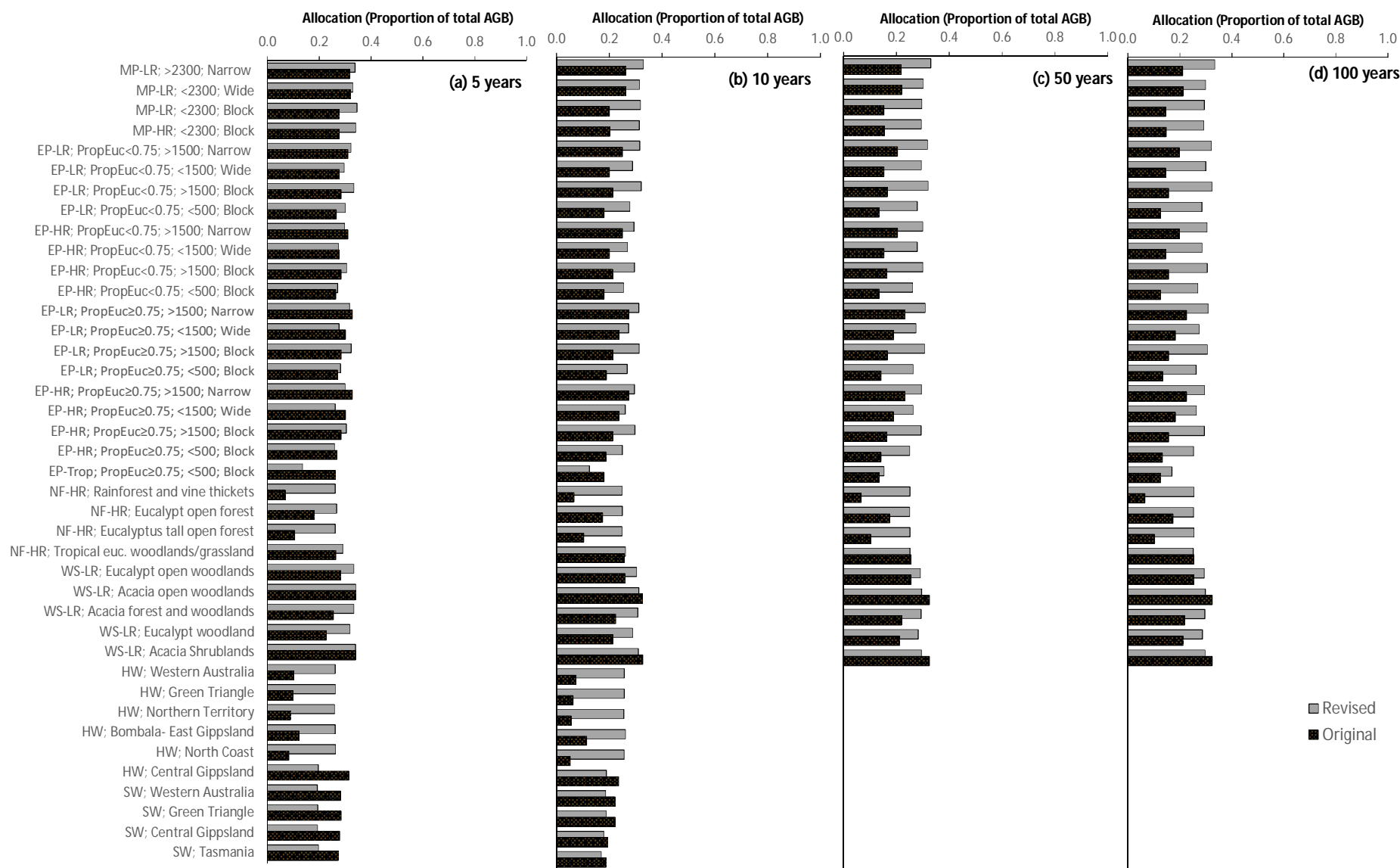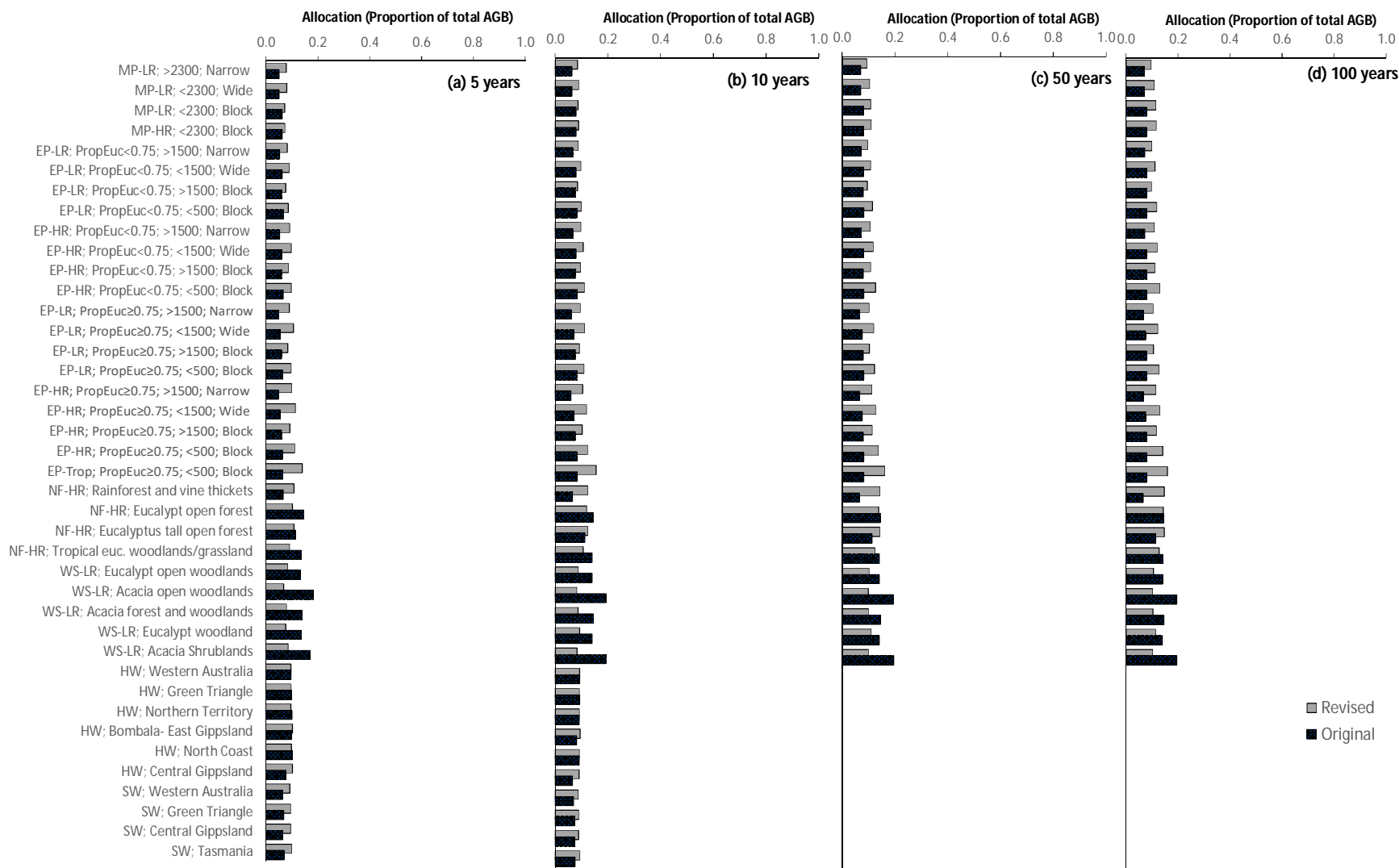
Figure 15: Comparison of revised Calculator-predicted proportion of AGB that is **branch** biomass and that predicted using the original FullCAM defaults at stand age of: (a) 5 years; (b) 10 years; (c) 50 years, and; (d) 100 years. Abbreviations of the different scenarios of forest types are provided in Table 8, with each being simulated under average values of M for the specific domain of that forest type.

Figure 16: Comparison of revised Calculator-predicted proportion of AGB that is **bark** biomass and that predicted using the original FullCAM defaults at stand age of: (a) 5 years; (b) 10 years; (c) 50 years, and; (d) 100 years. Abbreviations of the different scenarios of forest types are provided in Table 8, with each being simulated under average values of *M* for the specific domain of that forest type.
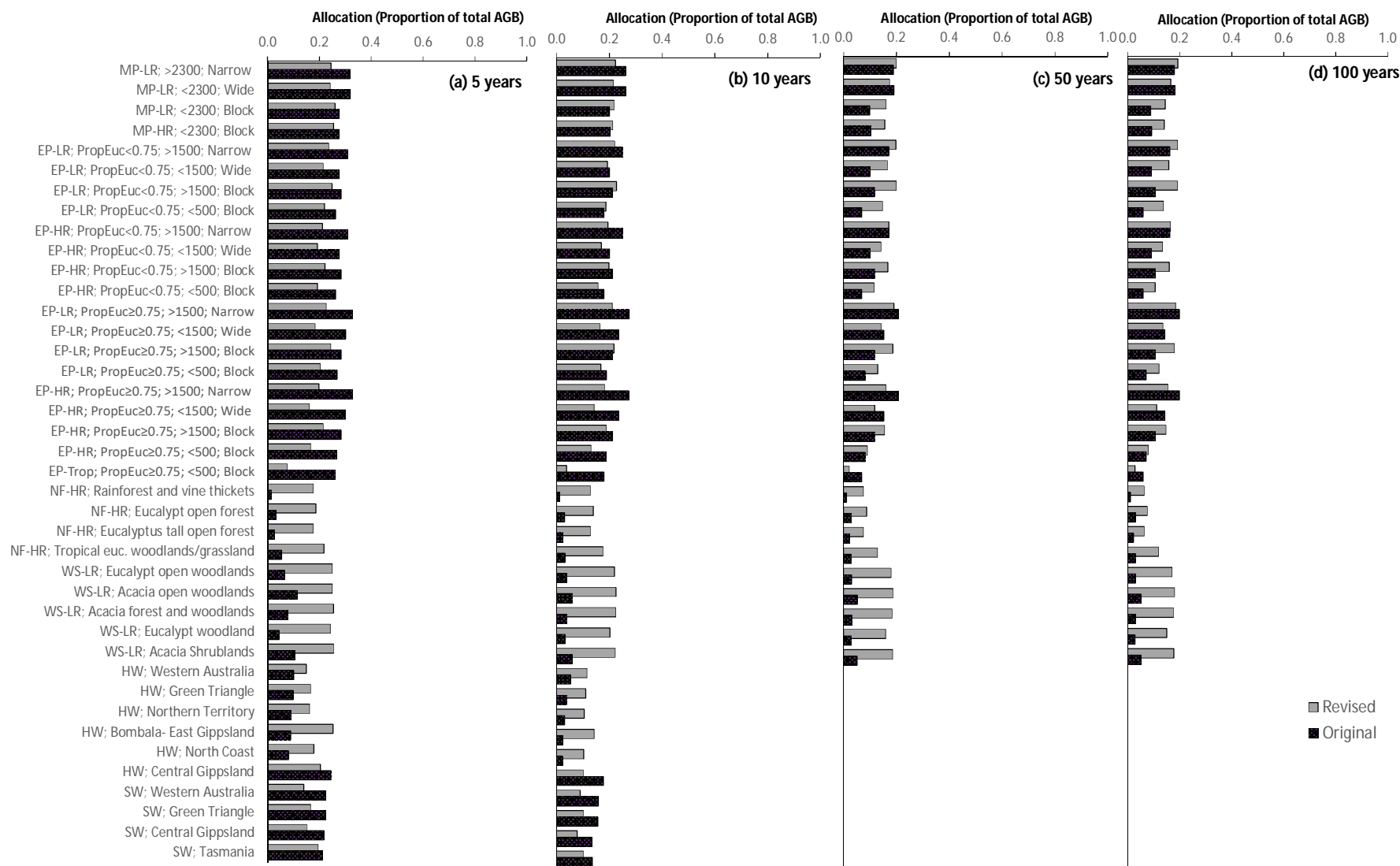
Figure 17: Comparison of revised Calculator-predicted proportion of AGB that is **foliage** biomass and that predicted using the original FullCAM defaults at stand age of: (a) 5 years; (b) 10 years; (c) 50 years, and; (d) 100 years. Abbreviations of the different scenarios of forest types are provided in Table 8, with each being simulated under average values of M for the specific domain of that forest type.
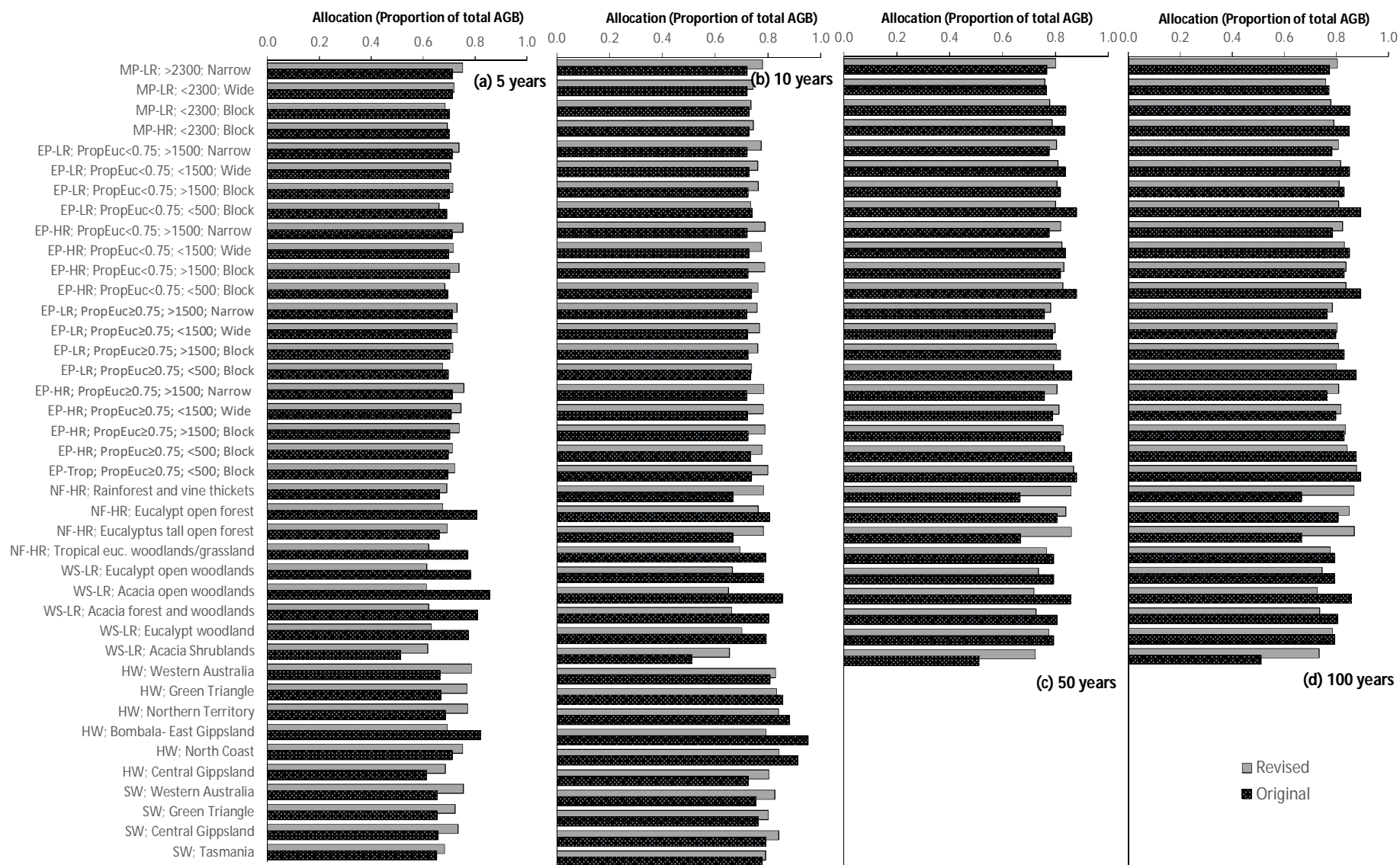
Figure 18: Comparison of revised Calculator-predicted proportion of BGB that is **coarse root** biomass and that predicted using the original FullCAM defaults at stand age of: (a) 5 years; (b) 10 years; (c) 50 years, and; (d) 100 years. Abbreviations of the different scenarios of forest types are provided in Table 8, with each being simulated under average values of *M* for the specific domain of that forest type.
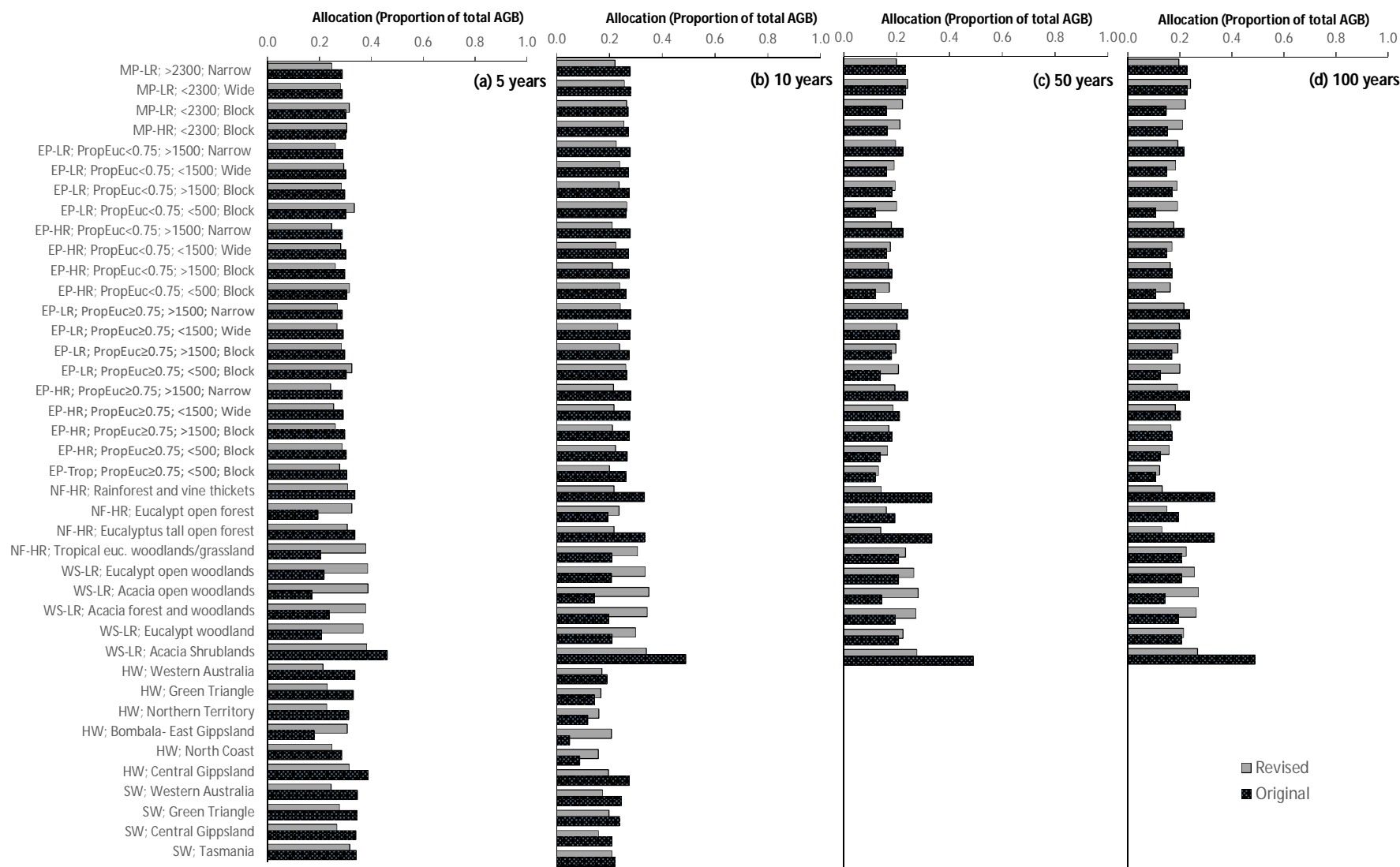
Figure 19: Comparison of revised Calculator-predicted proportion of BGB that is **fine root** biomass and that predicted using the original FullCAM defaults at stand age of: (a) 5 years; (b) 10 years; (c) 50 years, and; (d) 100 years. Abbreviations of the different scenarios of forest types are provided in Table 8, with each being simulated under average values of *M* for the specific domain of that forest type.

Figure 20: Comparison of revised Calculator-predicted proportion of BGB_C:AGB and that predicted using the original FullCAM defaults at stand age of: (a) 5 years; (b) 10 years; (c) 50 years, and; (d) 100 years. Abbreviations of the different scenarios of forest types are provided in Table 8, with each being simulated under average values of *M* for the specific domain of that forest type.
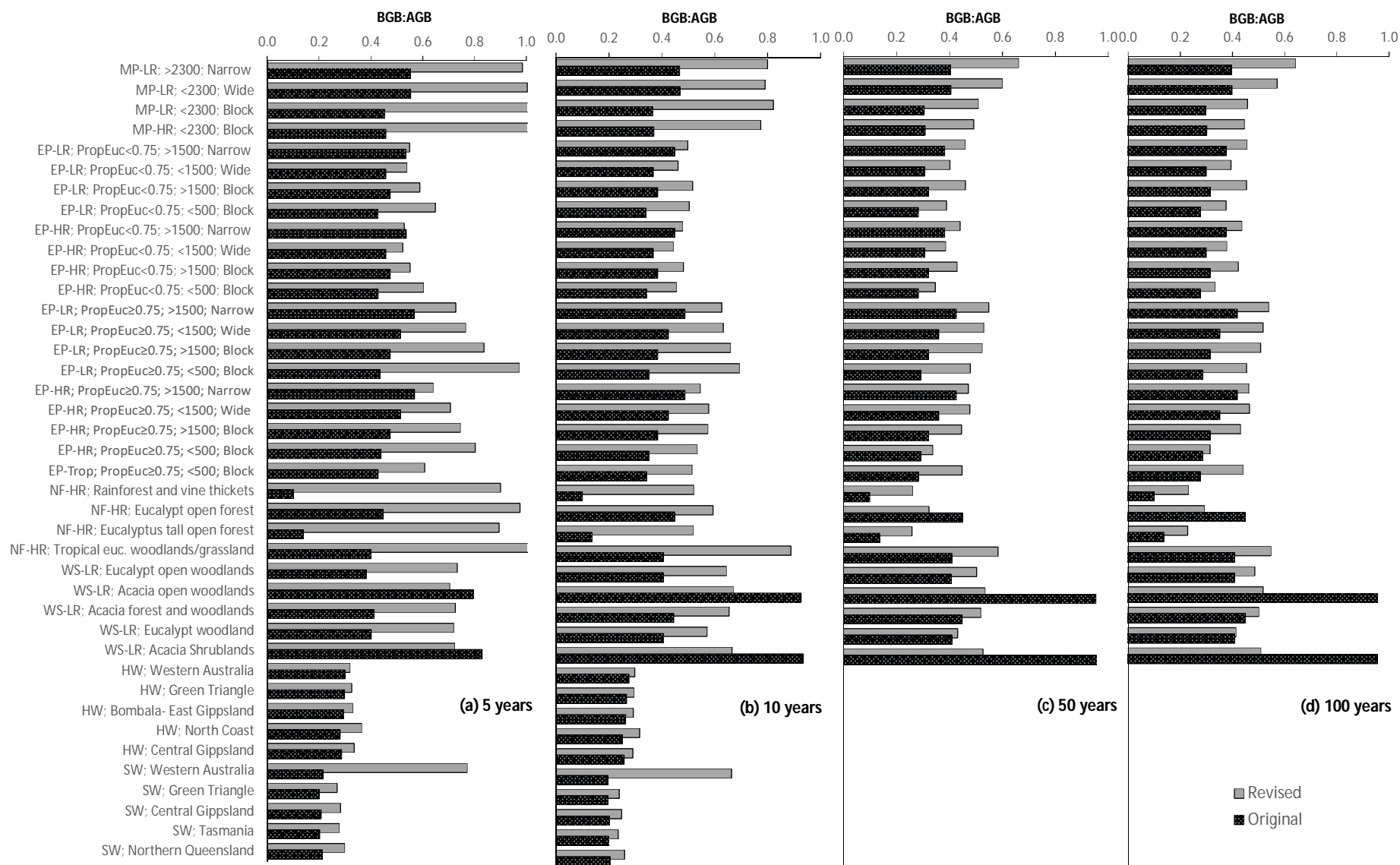
4.2.2 Turnover (litter fall)

Using collated datasets from litter trap studies, the inputs of turnover of tree components were changed (Fig. 21). Due to the error in data entry of turnover inputs for native systems, turnover of all pools significantly increased with the revised inputs. For the planted forests, in general, branch turnover increased (with the exception of environmental and mallee plantings), and bark turnover decreased (with the exception of softwood plantations). When compared to the original defaults, turnover rates of foliage changed little for softwoods, but decreased slightly for other planting types, especially environmental and mallee plantings, and for hardwood plantations.
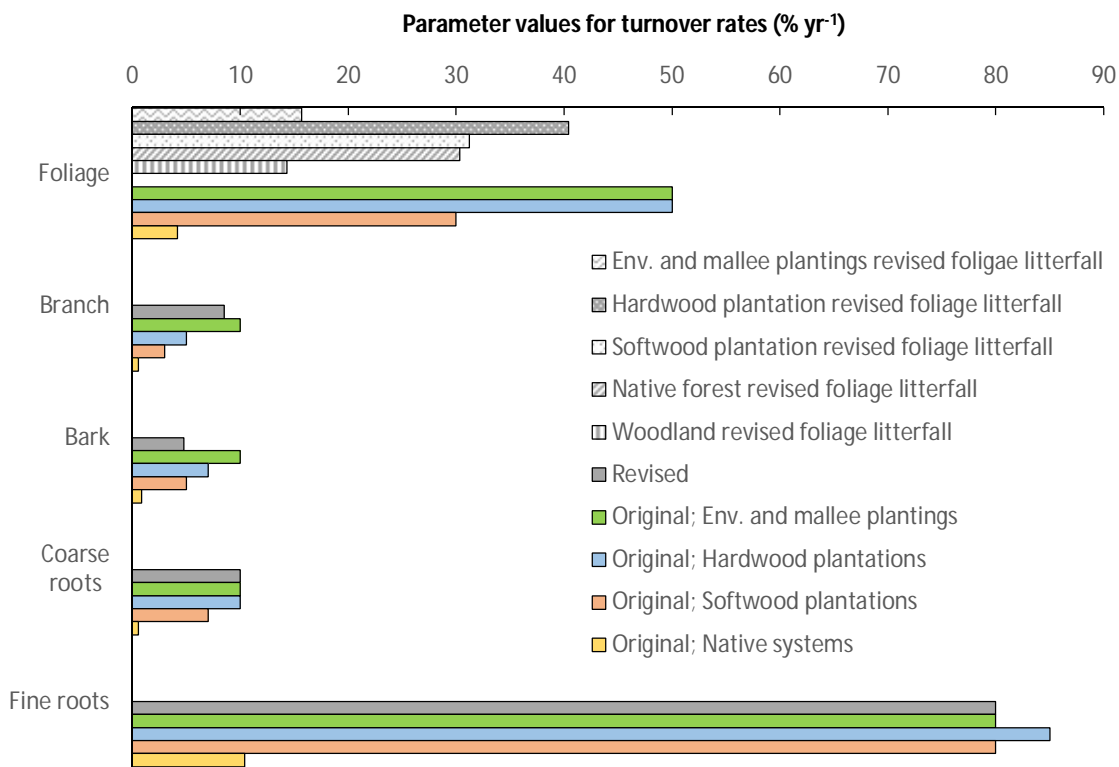

Parameter values for turnover rates (% yr⁻¹)

Legend:
- ▨ Env. and mallee plantings revised foligae litterfall
- ▦ Hardwood plantation revised foliage litterfall
- ▢ Softwood plantation revised foliage litterfall
- ▨ Native forest revised foliage litterfall
- ▥ Woodland revised foliage litterfall
- ■ Revised
- ■ Original; Env. and mallee plantings
- ■ Original; Hardwood plantations
- ■ Original; Softwood plantations
- ■ Original; Native systems

Figure 21: Revised and original parameter values for turnover of the various pools of biomass simulated by FullCAM.

4.2.3 Decomposition of debris

Using collated datasets from litter bag studies, changes were made to the inputs of resistant fractions of debris, breakdown rates and the influence of climate on these rates. It was assumed that all forest types have the same parameters for decomposition until there was evidence to prove otherwise (Fig. 22). As a result, decomposition of pools of debris under native systems were generally slower (particularly for foliage litter, Fig. 23), the only exception being for deadwood and dead fine roots. In contrast, in planted systems, the changes generally resulted in faster rates of decomposition, with the exception of bark litter and dead coarse roots under environmental and mallee plantings.
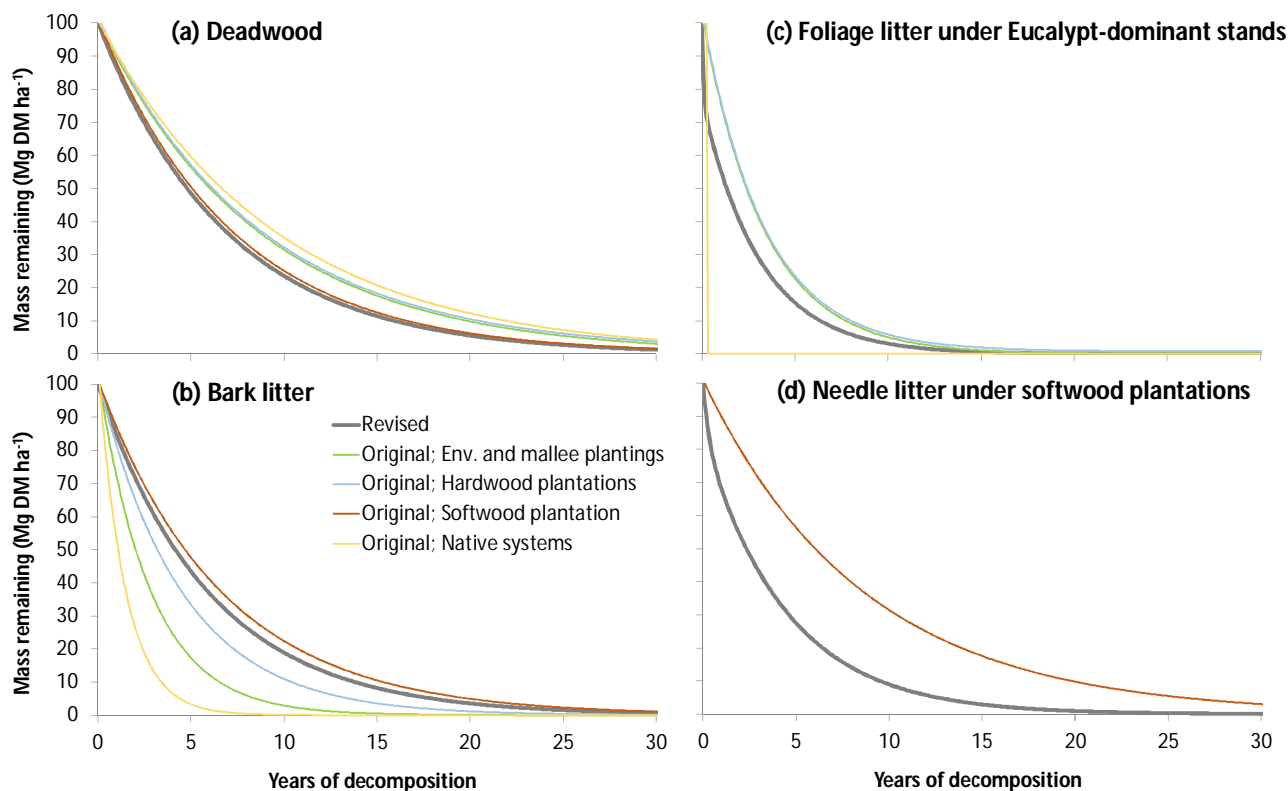
Figure 22: Demonstration of predicted rates of breakdown in of various litter pools of litter when using the revised and original parameters for decomposition.
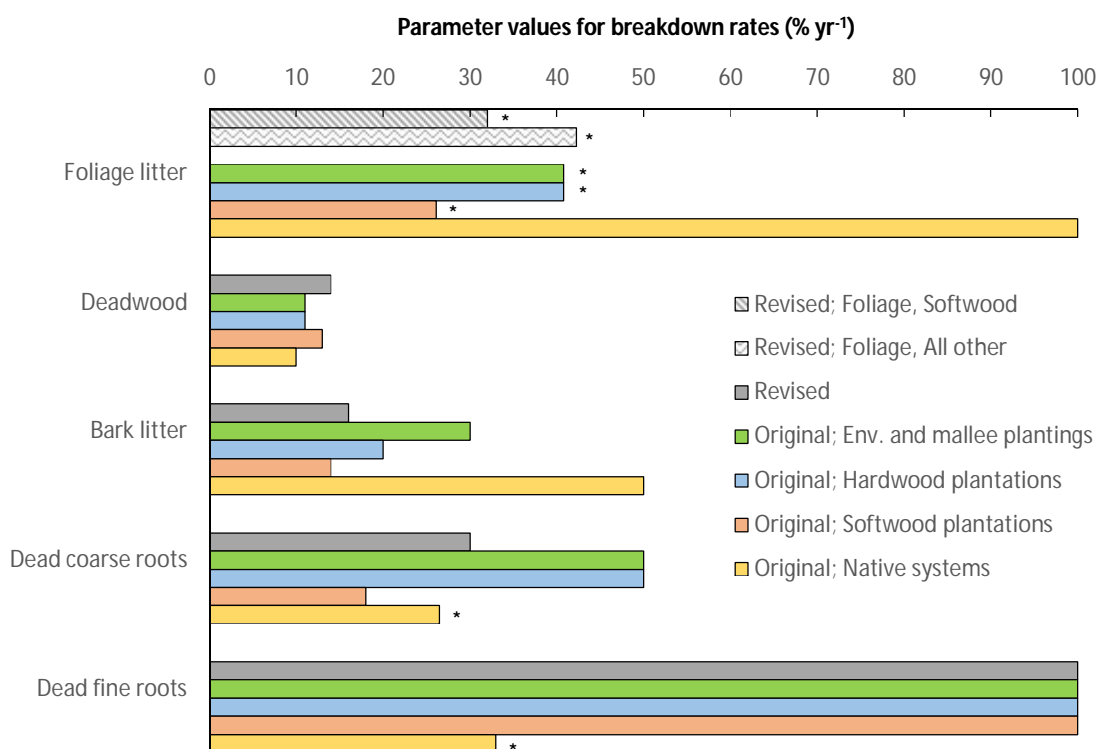

Figure 23: Revised and original parameter values for breakdown rates of the various pools of debris simulated by FullCAM. Some pools of debris were assumed to have decomposable and resistant components. * indicates breakdown rates shown were the weighted average of the decomposable and resistant components of the given pool of debris.

4.2.4 Parameters influencing soil C

It was assumed that all forest types have the same parameters for root turnover until there was evidence to prove otherwise. This generally resulted in a significant increase in total root turnover (Fig. 21). The only exception was for environmental and mallee plantings, where root turnover parameters were maintained.

Again, it was also assumed that all forest types have the same parameters for decomposition of dead roots until there was evidence to prove otherwise. This generally resulted in an increased decomposition of dead roots in native systems and softwood plantings, but a decrease in decomposition rates of dead roots (namely dead coarse roots) under all other forest types (Fig. 22).
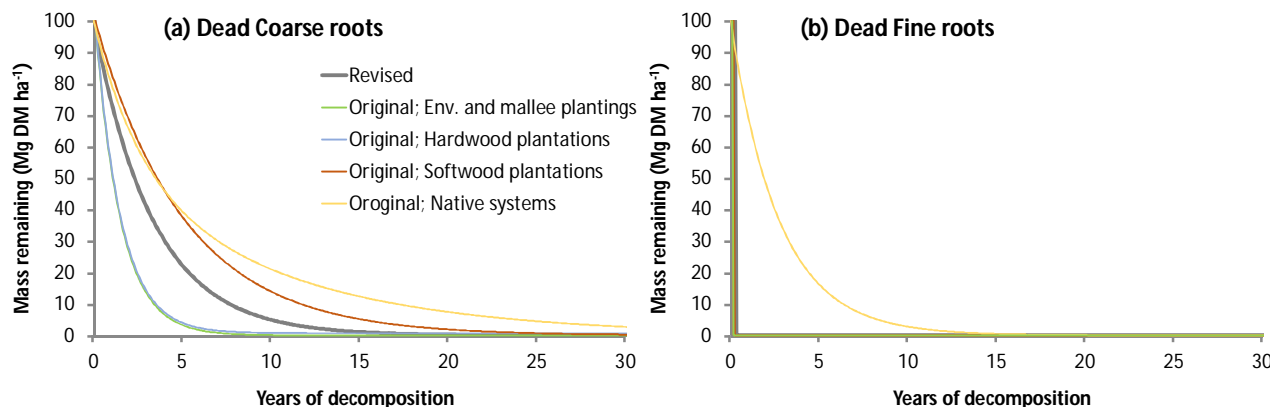

Figure 24: Demonstration of predicted rates of breakdown in of pools of dead roots when using the revised and original parameters for decomposition.

The original parameters for CO_2-C loss on decomposition were 87.5% for native systems, and 77% for all other forest types. The parameters defining the CO_2-C loss on decomposition were changed in three ways:

1. Vary there parameters between the resistant and decomposable pools given there was some evidence to suggest that more of the C lost on decomposition of debris reaches the soil on decomposition of resistant pools when compared to decomposable pools (Paul and Polglase 2004b).

2. Make these parameters for native systems consistent with those from planted systems.

3. Vary these parameters based on stand age. Until research has been completed to inform any re-coding of FullCAM, it is recommended that simulations of afforestation of young stands use CO_2-C loss on decomposition of decomposable and resistant pools of debris were 77^{-1} and 40% yr^{-1}, respectively. But when simulating older stands, such as in deforestation events, the CO_2-C loss on decomposition of decomposable and resistant pools of debris should be set to 90^{-1} and 80% yr^{-1}, respectively.

These changes resulted in significant decreases in rates of C entering the soil pools in planted systems, and a slight increase for native systems.

4.2.5 Initial pools of biomass and debris

The revised initial pools of biomass are based on the changes to allocation of biomass. Given the default initial age for environmental and mallee plantings was taken as zero, the initial pools of biomass were also assumed to be zero in both the original and revised settings. For all other forest types (with the exception of woodlands), there was a decline in the proportion of total biomass that was assumed to be stem wood, and an increase in the proportion of total biomass that was in other AGB components and in the BGB (Fig. 25). For woodlands, the allocation to stem wood and BGB was originally relatively low and high, respectively. Therefore, for these forest types, the there was only a slight decrease in allocation to stem wood and BGB, and a resulting increase in allocation to non-stem components of the AGB.
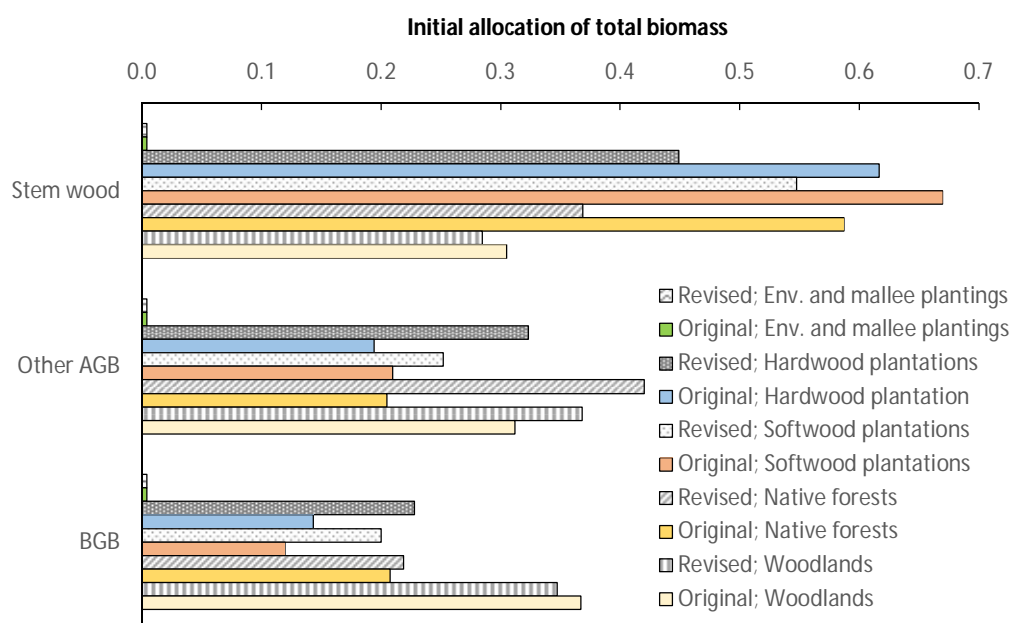
Initial allocation of total biomass

Figure 25: Revised and original parameter values for initial allocation of biomass to stem wood, other pools of AGB (or bark, branches and foliage), or to the BGB (coarse and fine roots).

For hardwood and softwood plantations, there was generally an increase in the initial debris pool, particularly for deadwood, but also for litter under hardwood plantations (Fig. 26). For native systems, there was substantial decline in initial deadwood and dead roots for native forests, but for woodlands, there was only a slight decline in all initial pools of debris. Given the default initial age for environmental and mallee plantings was taken as zero, the initial pools of debris were also assumed to be zero in both the original and revised settings.

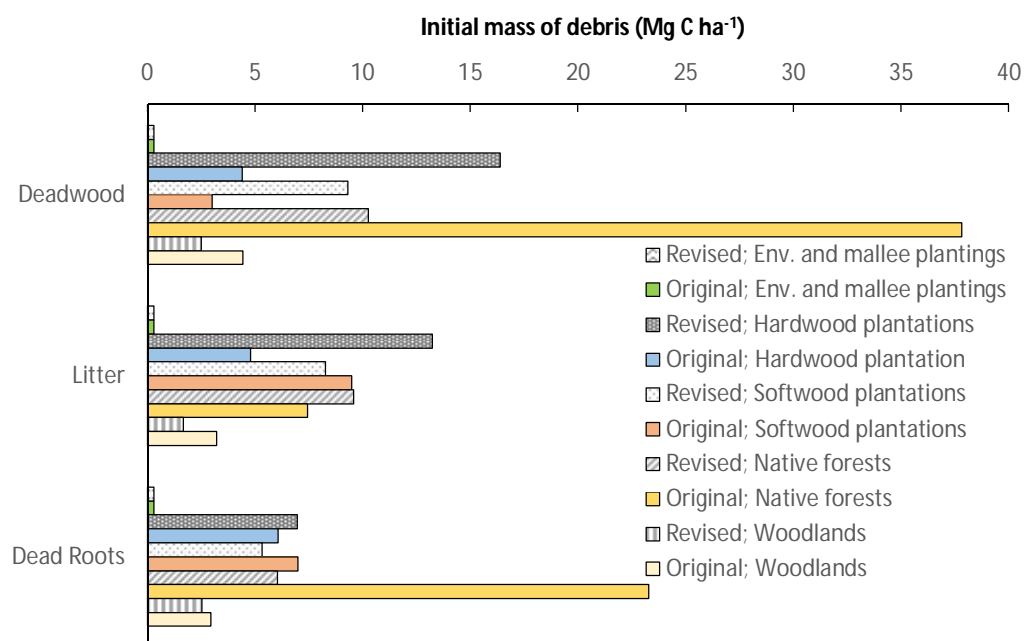**Initial mass of debris (Mg C ha⁻¹)**

Figure 26: Revised and original parameter values for initial mass of debris. Values of litter are the sum of the decomposable and resistant pools of bark litter and foliage litter, while the dead roots are the sum of the decomposable and resistant pools of dead coarse roots and dead fine roots.

5 Conclusions

5.1 Overall impacts on predictions of C sequestration by forests

In preparation for the update of DoEE (2016), various FullCAM simulations were generated to determine the impact of the revised parameters on predicted sequestration of C following land use change. These revealed that the overall impact of these changes was an increase in C sequestration following afforestation and reforestation. The largest increases were found in natural regeneration, e.g. of woodlands post clearing events. This was mainly attributable to increased rates of turnover assumed in native systems. Indeed, in all forest types, the greatest increases in sequestration of C was simulation in debris and soil pools. There was generally little change in sequestration of C in biomass. The only exception was an increase in biomass C sequestration for systems where BGB_C:AGB increased (Fig. 20).

5.2 Recommendations for further work

5.2.1 Allocation of biomass

This study utilised available data and information on allocation of AGB, and BGB_C:AGB, to develop and verify empirical models predicting allocation of biomass under a range of different forest types. There were a number of important caveats to this work which are summarised below, and which provide the recommendations for further work:

1. The environmental and mallee plantings datasets had age-limitations, being mostly derived from relatively young stands. Confidence in predictions of biomass allocation in older stands (greater than 24 and 14 years for the mixed-species forests and mallee eucalypt plantations, respectively) is therefore relatively uncertain. As these stands mature, monitoring of AGB and its components is required to verify, and perhaps refine, these models. This is particularly important for BGB_C:AGB given: (i) the young nature of the stands assessed may have partly contribute to the relatively high BGB_C:AGB observed, and (ii) although AGB is determine in FullCAM via the TYF, accurate inputs of assumed allocation of biomass to coarse roots will be important in ensuring accurate FullCAM-predictions of BGB, and hence, total biomass.

2. There was a paucity of biomass allocation data at the stand-scale for native forests, woodlands and shrublands. This necessitated an approach of using the individual-scale data available to verify predictions resulting from the adaption of empirical models developed for environmental plantings. Additional datasets of biomass allocation are required from these systems in order to provide specific empirical models.

3. There was some evidence that for plantations, different species have differing allocation of AGB, e.g. *Pinus pinaster cf.* other softwood species. Further work is required to verify predictions of allocation for hardwood and softwood plantations across a wider ranges of species from a diversity of locations. Further work is also required to explore allocation of biomass in plantations systems given thinning events may influence the relationships between allocation of biomass and the stand age and total biomass.

4. There was some evidence that the split of AGB into crown and bole differed between stands in high and low rainfall regions, e.g. Bole:AGB ratio being low for mallee plantations relative to plantings established in regions of higher rainfall. This is difficult to simulate in FullCAM given the branch pool contains the twig components of the crown. It is therefore recommended that further work be undertaken to refine FullCAM biomass allocation inputs to separate twigs from the branch pool, particularly given these will have differing rates of turnover.

5. Results obtains from this study conflict with those observed by other with respect to the impact of stand density on allocation of biomass, namely the BGB_C:AGB. Additional datasets are required to be collated in order to ascertain the impact of stand density of allocation of AGB for different forest types, climatic conditions and planting configurations.

6. There was some evidence that climate (MAR) had a direct impact on allocation of AGB in some forests types, but that the impact of climate on BGB_C:AGB was via an indirect influence on AGB per se. Further work is required to improved confidence of the direct and indirect influences of climate of allocation of biomass for different Australian forest types.

7. We made the naïve assumption that BGB_F may be predicted from stand AGB based on a generic global relationship. Although this may be suffice for quantification of biomass C given the negligible size of BGB_F, given their relatively high rate of turnover, allocation to BGB_F will be important in accurate prediction of C entering the debris, and hence soil, pools.

5.2.2 Litter fall and decomposition of litter

The main limitation to both parameters of litter fall and rates of decomposition of litter are that they are not comprehensive enough (i.e. insufficient sample sizes, N) to ascertain whether there are statistical differences between the different forest types. To provide justification for having differing parameters for litter fall and litter decomposition across contrasting forest types or locations, further litter trap and litter bag studies are required in strategically placed forests and climates.

5.2.3 Parameters influencing soil C

The calibration of root turnover and decomposition, and the CO_2-C loss on decomposition were based on only two long term repeat-measured planation field trials (of differing treatments of fertiliser and irrigation) located in temperate regions, and one national project on paired-site environmental plantings. So these parameter values are probably most relevant to planted systems. Further field work is required across contrasting native systems to provide verification that these calibrations are indeed widely applicable.

The prediction of soil C accumulation under forests is highly sensitive to parameters of CO_2-C loss on decomposition (Paul *et al.* 2003). Given the evidence of a decrease in the rates of C input into the soil (as currently simulated by increased CO_2-C loss on decomposition of debris) as stands mature, further research is required to verify this, and ascertain the processes involved so that these may be more accurately inherently modelled. This might entail undertaking laboratory studies designed to specifically monitor $^{14}CO_2$-C loss from incubated ^{14}C labelled forest litter.

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