# Modelling the growth of young rainforest trees for biomass estimates and carbon sequestration accounting

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## ABSTRACT

Few measurements for carbon sequestration, ratio of above-ground to below-ground biomass and wood density exist for young trees. Current allometric models are mostly for mature trees, and few consider trees at the sapling stage. Over four years we monitored the growth rates, from seedling to the sapling stage, of 490 trees (five native species) in environmental plantings, in the Wet Tropics of north-eastern Australia. Our biomass estimates were greater by several orders of magnitude in the first year ($6 \times 10^{-3}$ Mg ha$^{-1}$ cf. $4 \times 10^{-6}$ Mg ha$^{-1}$), and two orders of magnitude less at four years than those derived from the national carbon accounting model ($5 \times 10^{-1}$ Mg ha$^{-1}$ cf. 13 Mg ha$^{-1}$). We destructively sampled 37 young trees to accurately estimate the variation in below-ground and above-ground biomass (AGB) with stem size, and to derive a best fit model for predicting sapling biomass: $\ln \mathrm{AGB} = -5.092 + 0.786 \ln(\mathrm{Diam._{base}})^2\mathrm{Height}$. Biomass expansion factors for young tree species ranged from 1.71 to 2.44, higher than average for tropical forests. Root:shoot ratios are consistent with mean estimates for mature rainforest. Stem wood densities ranged from 0.444 to 0.683 Mg m$^{-3}$ for the five species measured, which was 6.5% lower than published estimates for three of the species, and 12% and 27% higher for two species. Relative growth rates were faster for species with lower wood density in the first four years, but these species also had the lowest survival over the same period. The findings are significant for a number of reasons. Ecologically, they indicate that young rainforest trees invest more in leaves and branches than in stem growth. From a survival perspective, in the context of rainforest restoration, it is best to invest in species with higher wood densities. From a carbon accounting point of view, refinements to the models used for national carbon accounting are required that include the contribution of the sapling stage. Sapling growth rates were significantly different from those assumed in the national model, requiring growth rates to be increased after four years (as opposed to after 2 years in the national model) before reaching an asymptote at some time in the future. This adjustment is essential to enable carbon farmers to judge the time it takes to receive returns from investment. Policies that encourage carbon plantings should take into account that young plantings grow slower than predicted by current national carbon accounting models.

## 1. Introduction

Sinking atmospheric carbon dioxide into planted forests is an important component of climate change mitigation, and around the world 26.5 million hectares of forestry projects were financed in 2012, valued at $216 million (Peters-Stanley et al., 2013). Despite the appeal of forestry projects, the costs of establishing forests can be prohibitively high (van Oosterzee, 2012; Matzek et al.,

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2014); therefore, it is important that carbon accounting models reflect carbon sequestered.

Estimates of carbon sequestered in forest stands are modelled using allometric relationships of tree dimensions that rely on several key parameters: diameter at set heights (e.g. breast height), wood density, an expansion factor to account for branches, foliage and below-ground mass, and total height (West, 2009). Difficulty measuring wood density and height in the field has promoted the use of tree diameter over density and height to estimate above ground biomass (Chave et al., 2005, 2014). However, the relationships between diameter, wood density and height can vary considerably among species, sites and tree age (Brown et al., 1989; Brown, 1997; Baker et al., 2004; Chave et al., 2005, 2014; Alvarez et al., 2012; Preece et al., 2012). While site- and species-specific allometrics have been investigated for some locations (e.g. Henry et al., 2010; Chaturvedi and Raghubanshi, 2013; Fayolle et al., 2013; Mugasha et al., 2013), tree age remains largely unaccounted for.

Historically, foresters and ecologists have not measured the early stages of growth, so established allometrics account only for sub-mature to mature trees. In the absence of information on young trees, the only available method to estimate biomass is to extrapolate allometric equations back to the origin. Although allometrics are assumed to be robust for a range of ages and sizes (e.g. Chave et al., 2005), they probably do not hold for seedlings and saplings because the architecture of trees changes with age (Claussen and Maycock, 1995).

In Australia, the government-approved method for estimating carbon stored in permanent environmental plantings is FullCAM (Department of Climate Change and Energy Efficiency, 2012). Young trees are excluded from FullCAM and other carbon models because the allometric equations used to derive tree volume and mass ignore stems below breast height (1.3 m above ground surface) and below 2.5, 5 or 10 cm diameter at breast height (dbh) (Brown, 1997; Baker et al., 2004; Chave et al., 2005, 2014; Alvarez et al., 2012; Preece et al., 2012).

Another poorly-studied measurement of young trees is the ratio of above-ground to below-ground biomass, because it requires destructive and intensive sampling (e.g. Mugasha et al., 2013). Data of root:shoot ratios are rare for Australian wet tropical species. The two studies we found (Osunkoya et al., 1994; Deines et al., 2011) investigated seedlings grown in pots in greenhouses for less than 100 days for the first and at 15 months for the second experiment, so they are not considered further in our analyses. Snowdon et al. (2000) were unable at the time to find any estimates of root biomass for Australian rainforests, but global literature suggests tropical trees world-wide have a mean of 24% of below-ground to above-ground biomass (Cairns et al., 1997). Likewise, the ratios of stems to leaves and branches, expressed as 'biomass expansion factors' (BEF) (West, 2009), are unavailable for both young trees and the Australian Wet Tropics in general. Young trees usually have an architecture different from older trees (Claussen and Maycock, 1995) and age provides important explanatory power for root:shoot (R:S) ratios (Cairns et al., 1997; Kenzo et al., 2010).

Wood density of juvenile trees has also been poorly studied (Chaturvedi et al., 2012b, 2012a). Nearly all published wood density data, such as the report on the state of knowledge of wood density in Australia (Ilic et al., 2000), report on mature trees only (we use the term 'wood density' ($\rho$; Mg m$^{-3}$) but Chave et al. (2005) and others use the dimensionless wood specific gravity, the density of wood relative to the density of water (Williamson and Wiemann, 2010)). In allometric equations for young trees, it is assumed that their wood density is the same as mature trees, but this may be an erroneous assumption. Models such as those developed by Chave et al. (2014) are likely to be unreliable for young planted forests.

Wood density also affects growth and survival rates of trees (Falster, 2006), and must be considered for young trees in planted forests (Larjavaara and Muller-Landau, 2010, 2012; Niklas and Spatz, 2010). In addition, mean stand-level wood density across forest regions can vary significantly, affecting estimates of biomass (Baker et al., 2004) for both mature and young trees. Consideration of the variation in wood density among species is important, and the default wood density values (Ilic et al., 2000) may be wrong for mature trees in different bioclimatic regions, and for young trees, for which there are virtually no data.

We examine the contribution of small stems to carbon stocks. Small stems are ignored in current carbon accounting models because of the complex nature of growth at this stage caused by changes in wood density with ontogeny, and the difficulty of measuring various growth parameters other than stem diameter. We demonstrate that sapling growth and survival are influenced by wood density and sapling physiognomy.

We explore the contribution of young trees to carbon sequestration in the Wet Tropics of north-eastern Australia. We sampled established experimental plots and monitored the growth of planted tree seedlings over their first four years. We determined the biomass of saplings in each plot on several occasions and from destructively sampled young trees from nearby forest, including the biomass of excavated roots. We assessed the effects of species (and consequently wood density) on species survival and growth. We derived a best-fit allometric model of growth using height, diameter at three heights, and stem biomass.

## 2. Methods

### 2.1. Study site

The study site is at 1000 m.a.s.l. on the southern Atherton tablelands in the wet tropical region of far north Queensland (17.43°S, 145.51°E). Mean annual rainfall at the nearest weather station (Evelyn SF, 12 km south of our site) is 1442 mm (range 792–2442 mm) and mean monthly temperatures range from 14 °C to 26 °C at Atherton (18 km N) (Bureau of Meteorology, http://www.bom.gov.au; accessed 26 February 2015). Seedlings were planted in pastures that, until a few months prior to planting, had been grazed by cattle for approximately 70 years. The pastures comprised tropical pasture grass species, dominated by *Melinis minutiflora*, *Urochloa decumbens* and *Setaria sphacelata* (Poaceae), none of which are native to Australia. Native vegetation adjacent to the planting area is described as remnant and regrowth, simple to complex notophyll vine forest of cloudy wet highlands on basalt (Regional Ecosystem 7.8.4) (Environmental Protection Agency, 2007).

### 2.2. Experimental design

The experimental design was described by Preece et al. (2013). We planted ten replicated plots in February 2010 along a ridge-line. The plots were each 24 m × 24 m and marked at spacings of 3 m × 3 m, giving a total of 49 trees per plot. Plots varied in their history, with plots 3 and 10 on an old road surface, the upper half of plot 4 located on a rehabilitating former farm track, and the remainder being on moderate to steep grassy slopes (10–30°). Plots were treated with the herbicide glyphosate to remove grass at least two weeks prior to planting. Spraying was limited initially to a one metre radius circle where each seedling was to be planted. Post-planting spraying was conducted in May and September 2010, and January 2011 using glyphosate and again in

January, April and December 2012 using fluazifop-p (a grass-specific herbicide) to prevent sapling damage from glyphosate and to reduce glyphosate resistance of weeds. Post-planting spraying was done in parallel lines one metre wide along the contour. An annual exotic weed, blue top *Ageratum* sp. (Asteraceae), and the native bracken fern *Pteridium esculentum* (Dennstaedtiaceae) established around many seedlings, but we left these to grow during the dry season as they provided protective cover. Woody weeds were removed and poisoned periodically as they were found.

Seedlings were grown from local provenance seed at a local commercial nursery and sun-hardened for several months prior to planting. Species used were *Cardwellia sublimis* F. Muell. (Northern Silky Oak) and *Stenocarpus sinuatus* Endl. (Wheel-of-fire) (Proteaceae), *Syzygium luehmannii* (F. Muell.) L.A.S. Johnson (Cherry Satinash) (Myrtaceae), *Guioa lasioneura* Radlk. (Silky Tamarind) (Sapindaceae) and *Flindersia brayleyana* F. Muell. (Queensland Maple) (Rutaceae). One hundred of each of the first four species and 90 of *F. brayleyana* were planted in equal numbers in the ten plots (only 9 of *F. brayleyana* to make up 49 plants per plot). Mean height at planting was 31.0 cm (±0.5 SE). All seedlings were grown in 'forestry' tubes and planted randomly in each plot.

Saplings were measured in March 2010, April 2011, and February 2012, 2013 and 2014. Except for the first measurement period, height, diameter at base, 30 cm, and 130 cm, and survival (number dead as proportion of number planted) were measured at each period.

As we did not measure stem diameter in the first period (one month after planting), we used data from a later experiment (March 2013) at the same site for the same species within one month of planting, except for measurements of 4-month old planted *C. sublimis*, which we measured separately in July 2013. Comparison with other measurements has shown that growth in this cool period of the year (April–July) is very slow, so we consider the *Cardwellia* measurements to be adequate substitutes for March measurements.

Many individuals of *S. luehmannii*, *C. sublimis*, and *G. lasioneura* had multiple stems or large, low branches. We measured the largest stem, and the height of the tallest apical meristem for the multi-stemmed individuals. We did not calculate AGB for the combined stems of multi-stemmed individuals.

Existing data on tree mass for the study region rely on measurements from mature trees, and these are limited to few data points. From sites within one kilometre of the plots, we felled and dug up four young trees within the size range of the saplings in the planted plots to obtain mass estimates for stems (shoots), roots and leaves and branches. Each plant was divided into roots (where excavated), all shoots as main stems, and branches with leaves.

We also harvested 37 young trees to measure the ratios of leaves and branches to stems, the biomass expansion factor (BEF) (Fonseca et al., 2012). The BEF is the ratio of the foliage and branches to the shoots or main stem (West, 2009). The root and shoot samples were then weighed, dried at 105 °C for 72 h and re-weighed (Ilic et al., 2000). Roots were measured from the root collar, and all roots (>0.05 mm wide) were washed to remove clinging soil particles, air dried and weighed. They were then dried as for shoots and stems, and the whole root mass re-weighed. The volumes of each component were estimated using Archimedes' volumetric principle by water displacement (Ilic et al., 2000). Wood density was determined for whole stems and for roots as a function of mass to volume (Mg m$^{-3}$) with bark retained. A mean multiplier factor to account for the root portion of young trees was derived from the ratio of roots to shoots.

Relative height growth rate (RGR) was calculated by dividing the difference in height between two subsequent measurements by the number of months separating the measurements. We calculated RGR using the standard formula (Hoffmann and Poorter, 2002):

RGR = (ln[final size] − ln[initial size])/(final date − initial date)

The currently accepted value for the proportion of carbon in plant biomass is 0.47 (Intergovernmental Panel on Climate Change, 2006; Martin and Thomas, 2011), although it should be noted that this varies among species (West, 2009).

The wood density of most Australian rainforest trees is poorly known. We used the published wood density for the tree species (Ilic et al., 2000) with some adjustments from sampled trees (Table 1). These values have low confidence. For the calculations of mass of stems, branches and leaves, and roots, we used the higher density values to compare with our empirical data.

Mass per unit volume of the stems, leaves and branches, and roots of the five rainforest species were used to model early growth of saplings. We were unable to cleanly remove the bark from the young saplings, so the measured wood density is for the wood and bark of the stems, and is probably a slight underestimate of wood density. Measurements of bark thickness of four of these species in the size range of the saplings shows that bark is never more than 3 mm thick (Preece, unpublished data).

### 2.3. Statistical analysis

We examined the relationship between stem mass and stem size by exponential ($Y = ae^{bx}$) non-linear regression with data pooled for all species, as the data best fit this model. Stem mass was regressed against stem diameter at three heights separately (base, 30 cm and 130 cm above the ground). We used the $R^2$ to identify the best fit among the three height measurement models.

We calculated mean relative height growth rates for all surviving saplings of all five species. The species height growth rates were modelled using a power function ($y = ax^c$) because the power function fits the asymptotic growth curve described by the data. The height growth rate was modelled against the number of months since the seedling was planted. Height growth was calculated for each time interval. Data were blocked by species.

Whether an individual sapling was alive or dead (binary variable) was recorded at each sampling period. Accordingly, the survival probability of each species over the 48 month monitoring period was modelled using logistic regression with a logit link function. Logistic regression is commonly used to model survival probabilities. Months since a seedling was planted was the explanatory variable and species identity and the planting method were initially included as fixed effects, but planting method was dropped from the model as this effect was not significant.

We modelled the increase in above ground biomass over 48 months using the basic power function. The functional form used most commonly predicts oven-dry aboveground biomass (AGB; tonne) of an individual tree from its diameter ($D$, cm) at breast height (usually) over bark and is given as (West, 2009):

$$AGB = \alpha D^{\beta} \tag{1}$$

where $\alpha$ and $\beta$ are estimated parameters. Chaturvedi and Raghubanshi (2013) used this model in their analyses but linearized it by ln-ln transformation:

$$\ln AGB = \alpha + \beta \ln D^2 \tag{2}$$

and $\alpha$ and $\beta$ are the estimated parameters after transformation. To preserve the quadratic relationship between AGB and $D$, we squared $D$. This is important particularly when including height ($H$; m) and wood density ($\rho$; Mg m$^{-3}$) in the model (Chaturvedi and Raghubanshi, 2013). This is not applied by some, for example see

**Table 1**
Published and unpublished wood density values (from Ilic et al., 2000; D. Metcalfe, unpubl. 2009) (converted to Mg m$^{-3}$).

| Species | Group | Density (Mg m$^{-3}$) | 95% prob. range for mean | $n$ | Confidence (H, M. L) |
|---|---|---|---|---|---|
| *Cardwellia sublimis* | Low | 0.436 (0.461[b]) | 0.413–0.459 | 12 | L |
| *Flindersia brayleyana* | Low | 0.442 (0.477[b]) | 0.428–0.456 | 20 | L |
| *Syzygium luehmannii* | High | 0.570[a] | | n.s.[c] | L |
| *Stenocarpus sinuatus* | High | 0.589 | | 4 | L |
| *Guioa lasioneura* | High | (0.536[b]) | | n.s. | L |

[a] Estimated basic density from air-dry (12%) moisture content.
[b] D. Metcalfe, unpubl. data, 2009.
[c] n.s. – not stated.

Chave et al. (2005) and Basuki et al. (2009), but is recommended by Segura and Kanninen (2005a) for moist forests. We adopted the form of the full ln–ln model that is applied by Chaturvedi and Raghubanshi (2013), as follows:

$$\ln AGB = \alpha + \beta \ln(\rho D^2 H)$$

We modelled estimates of total aboveground biomass (AGB; kg), which is the sum of foliar and stem biomass; total foliage biomass (TFB) and total stem biomass (TSB) separately, as a function of stem wood density ($\rho$), stem diameter ($D$) (at three different heights: base, 30 cm and 130 cm) and stem height ($H$). Model fit was examined using the $F$-test and $R^2$.

Model selection was based on *a priori* hypotheses defined as competing models containing different combinations of $\rho$, $D$ and $H$. Model selection and ranking was conducted using Akaike's Information Criterion (AIC$_c$), a second order form of AIC appropriate for both large and small sample sizes (Burnham and Anderson, 2001), which favours both model fit and model simplicity based on the principle of parsimony (fewer parameters in the model). Lower values of the AIC indicate greater support for a model, relative to other models in the same candidate set.

The measured wood density estimates include the wood and bark densities of the stems, so are slight underestimates of wood densities for the species. As we examine the carbon balance of young trees, actual wood density of sap and heart wood is not as important as the whole stem biomass.

Statistical analyses and modelling were performed in R (The R Foundation for Statistical Computing, 2014, Ver. 3.1.0, http://www.R-project.org) and in Genstat v. 16 (VSN International, 2013).

Biomass for forest stands is based usually on extrapolating from individual trees measured in sample plots to hectares. We extrapolated from the number of surviving trees in all plots to the number of trees per hectare, based on the tree spacings (3 m by 3 m apart), which is 1100 trees per hectare. As survival rates varied, we estimated trees per hectare from the surviving number of trees, which declined slightly over time. This method enables calculations of biomass for other densities of plantings. Although tree spacing affects growth rates (Chave et al., 2005), especially as trees mature, it is not so important at the early stages of growth.

Using the allometric (Eq. (2)) developed above, we estimated the biomass and carbon for young planted forests under two different planting densities, 1100 and 3300 trees per hectare, over the first four years of growth and compared our results with those estimated by the FullCAM model Version 3.55 (Richards and Evans, 2008).

## 3. Results

We destructively sampled a number of saplings of various sizes to determine ratios of roots:shoots and of leaves and branches to stems of saplings (Table 2).

Destructive sampling yielded a range of proportions of stems to foliage and branches from 0.41 to 0.58, which produced a range of BEFs from 1.71 to 2.44 (Table 3).

The average root:shoot ratios for the sampled saplings was 0.24 (Table 4). Although the sample size is small, it represents the only empirical observations of root:shoot ratios of young trees of these species.

The relationship between height and diameter of saplings and their dry stem mass followed an exponential increase with stem size ($R^2$ from 0.78 to 0.85; only diameter at 30 cm shown; Fig. 1).

The mean stem-wood density of the saplings ranged from 0.444 to 0.683 Mg m$^{-3}$ across the five species (Table 5). Stem densities differed by 5–27% from published wood density for mature stems. In general, the stem density of saplings was 6.5% lower than the wood density of mature stems, but *C. sublimis* and *G. lasioneura*, had much higher sapling wood density, by 12% and 27% respectively, than the density of their mature stems.

Species with lower wood density grew faster and taller than species with high wood density (Fig. 2). Species with higher wood density appear to reach their maximum rate of height growth within two to three years of establishment.

Survival differed significantly among species ($F_{10,3419} = 32.3$, $P < 0.001$) over the 48 month long monitoring period (Fig. 3). Although the species with the lowest wood density (*C. sublimis*, *F. brayleyana*; Table 5) grew fastest, they had the lowest survival over the monitoring period and their survival decreased significantly over time ($P < 0.001$). The survival of the remaining three species with higher wood density declined only slightly over the monitoring period. This slight decline in survival was not significant for *G. lasioneura* ($t = 0.06$, $P = 0.55$) but was for *S. sinuatus* and *S. luehmannii* ($P = 0.002$).

Sapling biomass was best predicted by the model including the diameter and sapling height in all instances, except foliar biomass predicted by stem diameter at 30 cm height ($D_{30}$) (Fig. 4). This model was a much better fit than using just the diameter ($D$) measure (Table 6). Including wood density ($\rho$) in the model did not improve the model fit. In addition, diameter measured at the stem base was the better diameter measure for predicting both the stem and the total aboveground biomass. Diameter measured at 30 cm height on the stem was a better measure for predicting total foliage biomass.

### 3.1. Comparison of empirical model with the national carbon accounting model for early growth

Calculating the carbon sequestered in carbon sink forests requires use of standard tools so that all estimates from all plantings are comparable. In Australia, the tool is the FullCAM model. At 1100 trees per hectare, our empirical model estimates were greater by several orders of magnitude in the first year ($6 \times 10^{-3}$ Mg ha$^{-1}$ cf. $4 \times 10^{-6}$ Mg ha$^{-1}$), and two orders of magnitude less at four years than those derived from FullCAM ($5 \times 10^{-1}$ Mg ha$^{-1}$ cf. 13 Mg ha$^{-1}$) (Fig. 5) (Supplementary table).

We also modelled the fast growing trees (those with lowest wood density), to determine if these more closely fit the FullCAM model. Although the fit was better, our models still predicted 17% less carbon sequestered by young trees at 14 months than

**Table 2**
Range of sizes of sampled saplings.

| Species | Height range (mm)[a] | Diam. at base range (mm)[a] | Diam. at 30 cm range (mm)[a] | Diam. at 130 cm range (mm)[a] |
|---|---|---|---|---|
| *Cardwellia sublimis* | 450–1270 (7) | 10–23 (7) | 5–18 (7) | – |
| *Flindersia brayleyana* | 312–1394 (12) | 8–39 (12) | 4–26 (12) | 10 (1) |
| *Guioa lasioneura* | 498–2164 (10) | 7–26 (10) | 4–21 (10) | 2–15 (6) |
| *Stenocarpus sinuatus* | 1110–1630 (4) | 16–23 (4) | 11–19 (4) | 4–9 (3) |
| *Syzygium luehmannii* | 1110–1570 (4) | 13–25 (4) | 9–17 (4) | 3–5 (2) |

[a] Number of samples within height and diameter ranges shown in brackets.

**Table 3**
Proportions of stems to total above-ground biomass.

| Species | Mean | SD | SE | n | BEF |
|---|---|---|---|---|---|
| *Cardwellia sublimis* | 0.41 | 0.07 | 0.03 | 7 | 2.44 |
| *Flindersia brayleyana* | 0.44 | 0.09 | 0.03 | 12 | 2.29 |
| *Guioa lasioneura* | 0.58 | 0.11 | 0.03 | 10 | 1.71 |
| *Stenocarpus sinuatus* | 0.55 | 0.01 | 0.01 | 4 | 1.81 |
| *Syzygium luehmannii* | 0.48 | 0.07 | 0.04 | 4 | 2.09 |

the FullCAM model. Increasing the density of planted trees to 3300 trees per hectare, using only the two fast-growing species, improved the fit of the models up to 48 months, but thereafter the FullCAM estimates were unrealistically greater than estimates derived from our data.

## 4. Discussion

We developed an allometric for young trees in planted forest in the Wet Tropics region of Australia to enable estimates of biomass and carbon sequestered at the early stages of a new forest's growth. This is one of the very few allometrics suitable for young plantations in humid tropical forests (e.g. Chaturvedi and Raghubanshi, 2013 model Indian tropical dry forests). New estimates of root:shoot ratios for young trees, wood density of young stems, and biomass of total shoots with leaves and branches enable more accurate estimates of total biomass in young planted forests. We discuss these findings in relation to survival and growth rates.

### 4.1. Biomass expansion factors

Current functions to estimate tree leaf biomass may not provide accurate results (West, 2009) and are usually not included in traditional forestry practices (Levy et al., 2004). Ratios of the biomass of stems to branches and leaves change over time as forests mature (Montagu et al., 2005; Petersson et al., 2012). They range between 1.1 and 2.5 across a number of forest inventories, but site-specific factors are recommended for accuracy and precision (Qureshi et al., 2012). For international inventories, the default BEF value of 1.74 is recommended for moist broadleaf forests (Brown et al., 1989; Brown, 1997). In Costa Rica, the mean BEF for mature tropical humid forest was 1.6 ± 0.2 (mean ± SE), but ranged from 1.4 to 1.8 (Segura and Kanninen, 2005b) and was 1.56 ± 0.72 and 1.57 ± 0.42 for two of the dominant tree species in Costa Rica
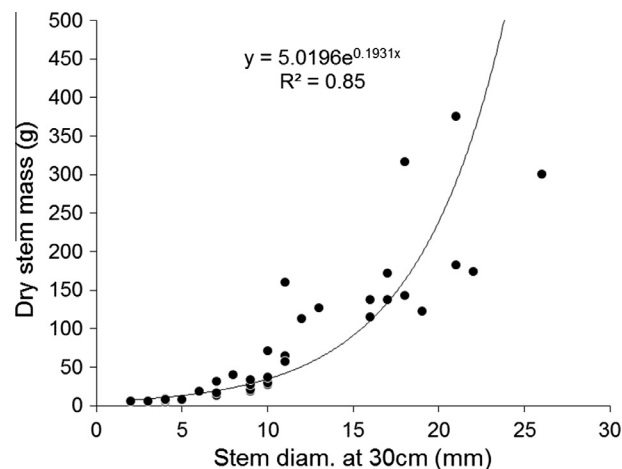


**Fig. 1.** Relationship of dry stem mass to stem diameter at 30 cm (all species pooled for analysis).

(Fonseca et al., 2012). Mean stand-level aboveground BEF for 30 samples of mature rainforest and monsoon rainforest types in China was 1.35 ± 0.17 (SD) (Luo et al., 2013), and for mature dense tropical forest in central Amazonia was 1.621 ± 0.415 (SD); normalized by diameter distribution per hectare, their estimate was 1.635 ± 0.441 (SD) at the stand level (Nogueira et al., 2008). BEF in our study ranged from 1.72 ± 0.03 (SE) to 2.44 ± 0.03 for *G. lasioneura* and *C. sublimis* respectively, suggesting that these young rainforest trees invest more in foliage and branches than do mature trees.

### 4.2. Root:shoot ratios

The root to shoot ratios of the young trees we sampled were within the range of published values for tropical trees. For our young trees, 81% of biomass was above ground. In a study of root to shoot ratios of forest trees in Sulawesi, the above-ground biomass represented 86% of the total biomass (Hertel et al., 2009); in Kenyan forests, the R:S ratio was 0.26 (74% above-ground) (Kuyah et al., 2012); a study in southern China found that 77–79% of biomass was in the above-ground component of tropical and subtropical trees (Luo et al., 2012); tropical trees world-wide
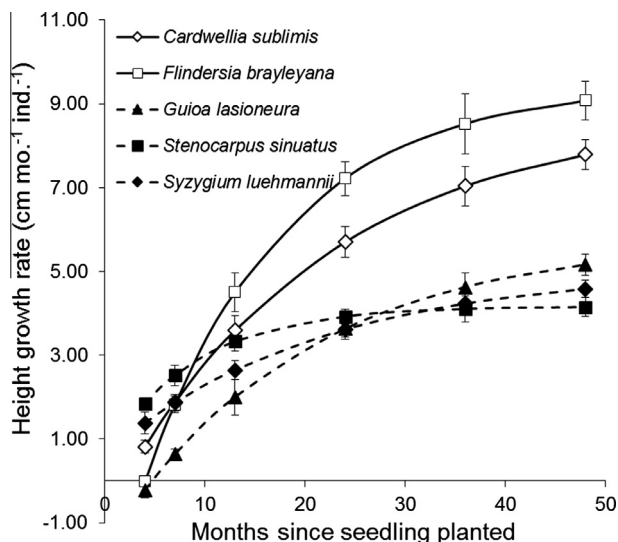
**Table 4**
Ratios of roots to shoots (including stems, branches and leaves) where the multiplier accounts for below-ground biomass in the absence of excavated roots.

| Species | AGB dry mass (g) | Dry root mass (g) | Total | Shoot:root | Root:shoot | Shoot ppn total (x) | Multiplier (1/x) |
|---|---|---|---|---|---|---|---|
| *Cardwellia sublimis* | 81 | 26 | 107 | 3.1 | 0.32 | 0.7570 | 1.32 |
| *Flindersia brayleyana* | 73 | 13 | 86 | 5.6 | 0.18 | 0.8488 | 1.18 |
| *Stenocarpus sinuatus* | 229 | 51 | 280 | 4.5 | 0.22 | 0.8179 | 1.22 |
| *Syzygium luehmannii* | 70 | 17 | 87 | 4.1 | 0.24 | 0.8046 | 1.24 |
| | | | | **Mean** | 0.24 | 0.81 | 1.24 |
| | | | | **SE** | 0.03 | 0.02 | |

**Table 5**
Measured wood density of stems with bark of five species of rainforest saplings.

| Species | Mean stem-wood density (Mg m$^{-3}$) | SE | n | Published wood density (Mg m$^{-3}$) |
|---|---|---|---|---|
| *Cardwellia sublimis* | 0.517 | 0.020 | 7 | 0.461 |
| *Flindersia brayleyana* | 0.444 | 0.018 | 12 | 0.477 |
| *Guioa lasioneura* | 0.683 | 0.024 | 10 | 0.536 |
| *Stenocarpus sinuatus* | 0.532 | 0.013 | 4 | 0.589 |
| *Syzygium luehmannii* | 0.540 | 0.022 | 4 | 0.570 |



**Fig. 2.** Species relative height growth rates (cm mo$^{-1}$ ind$^{-1}$) to 4 years after planting ($F_{14,2647}$ = 102.2, $P < 0.001$; whiskers are 1 SE).
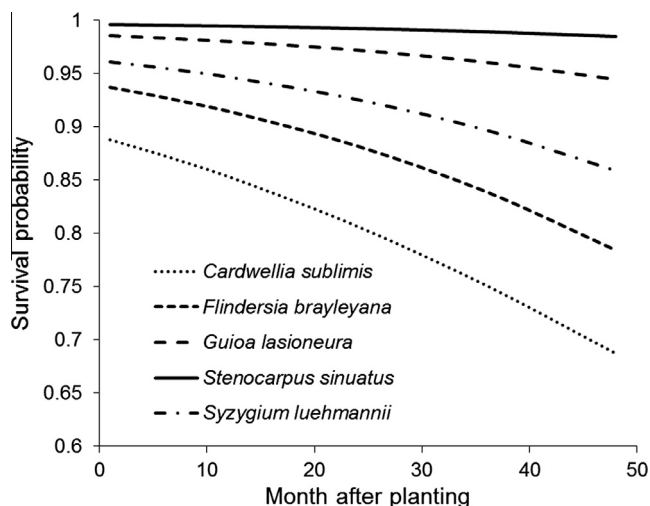


**Fig. 3.** Probability of survival of species over 48 months after planting showing that species with lower wood density (cf. Table 5) had lower survival.

had a mean of 75% above-ground biomass and a general mean for all forests between 70% and 80% (Cairns et al., 1997).

A review of root:shoot ratios for tropical forest types similar to our study site (with shoot biomass of >125 Mg ha$^{-1}$) (Mokany et al., 2006) reported median values of roots:shoots of 0.235, or 76.5% above-ground biomass. While the Mokany et al. study differed in approach to this one, as they calculated root:shoot ratios per unit area (i.e. in Mg ha$^{-1}$; whereas we reported the ratio per
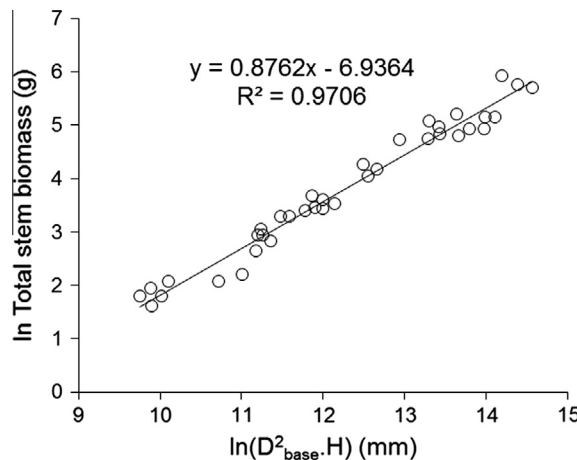


**Fig. 4.** Best fit model for predicting sapling biomass: $\ln AGB = -5.092 + 0.786$ $\ln(D_{base})^2 H$.

tree), the ratios we found are nevertheless well within the range of those found by Mokany et al. (2006). For forests of the type investigated in this study, ours and the Mokany et al. (2006) values are probably more accurate than the values used and published by the Intergovernmental Panel on Climate Change (Intergovernmental Panel on Climate Change, 2006), which provides root:shoot ratio values for montane moist tropical forests of 0.11–0.33, with an average of 0.22 (i.e. 67–89% range, 78% mean AGB).

A major difference between our root:shoot results (0.24 ± 0.03, mean ± SE) and those of other studies is that ours are based on young trees at the sapling stage, whereas the others are derived from mature trees. Age is known to affect root:shoot ratios across a range of forest types (Cairns et al., 1997; Werner and Murphy, 2001; Ritson and Sochacki, 2003; Mokany et al., 2006), with the ratio decreasing with age, probably because young plants send roots into the soil, seeking nutrients and moisture during the establishment phase, and as trees grow and become established, more energy is invested in above-ground biomass for greater net primary production.

A report on the re-calibration of the Australian FullCAM system for estimating biomass (Paul et al., 2013) observed that root:shoot ratios assumed in the National Inventory System (NIS) database (DIICCSRTE, 2011) are 0.55 at planting and decrease exponentially to 0.40 at age 8 years, before stabilising at 0.30 at ~50 years (they suggest that improvements could be made to these current default values). They suggest that for tree-dominated plantings, root:shoot ratios are more likely to be around 0.5 for young planted forests, decreasing to 0.30 after 15 years (Paul et al., 2013). However, they recommended that the default root:shoot ratios not be changed due to limited data, high variability and uncertainty, and suggested that root:shoot ratios can be better explained by stand productivity and AGB than by age (Paul et al., 2013). In contrast, Australia's National Inventory System (DIICCSRTE, 2011), which is informed by FullCAM and also provides FullCAM inputs (Paul et al., 2013), provides a range of values for below-ground proportions of biomass for trees from different forest types (Snowdon et al., 2000), but not rainforest. Thus, our results provide important empirical estimates of root:shoot ratios for young Australian tropical planted trees.

### 4.3. Effects of wood density on survival and growth

Wood density appears to affect both growth and survival in our planted forest sites. Growth rates of species with high wood

**Table 6**

Regression models for estimating total foliage biomass (TFB, g), total stem biomass (TSB, g), and total aboveground biomass (AGB, g) of saplings for stem diameter measured at the base ($D_{base}$) and at 30 cm above the ground ($D_{30}$). $R^2$, adjusted two-sided correlation between variables; SEE, standard error of estimate; $\rho$, wood density (g cm$^{-3}$); $D$, stem diameter (mm); $H$, sapling height (mm); AIC$_c$, modified Akaike's information criterion for small sample sizes.

| Rank | Model | $R^2$ | SEE | $F_{1,35}$ | $P$ | AIC$_c$ |
|---|---|---|---|---|---|---|
| 1 | $\ln TFB = 0.144 + 0.8156 \ln(D_{30})^2$ | 0.862 | 0.0542 | 226.09 | <0.001 | 41.0 |
| 2 | $\ln TFB = -2.721 + 0.578 \ln(D_{30})^2 H$ | 0.853 | 0.039 | 209.4 | <0.001 | 43.4 |
| 3 | $\ln TFB = 0.912 + 0.751 \ln(D_{30})^2 \rho$ | 0.84 | 0.054 | 190.2 | <0.001 | 46.5 |
| 4 | $\ln TFB = -1.881 + 0.534 \ln(D_{30})^2 \rho H$ | 0.819 | 0.042 | 164.9 | <0.001 | 50.9 |
| 1 | $\ln TFB = -4.712 + 0.698 \ln(D_{base})^2 H$ | 0.857 | 0.048 | 215.8 | <0.001 | 42.5 |
| 2 | $\ln TFB = -0.774 + 0.961 \ln(D_{base})^2 \rho$ | 0.837 | 0.071 | 185.9 | <0.001 | 47.2 |
| 3 | $\ln TFB = -1.759 + 1.0306 \ln(D_{base})^2$ | 0.832 | 0.0769 | 179.7 | <0.001 | 48.2 |
| 4 | $\ln TFB = -3.602 + 0.640 \ln(D_{base})^2 \rho H$ | 0.825 | 0.049 | 171 | <0.001 | 49.8 |
| 1 | $\ln TSB = -4.318 + 0.715 \ln(D_{30})^2 H$ | 0.937 | 0.031 | 535 | <0.001 | 24.5 |
| 2 | $\ln TSB = -3.412 + 0.672 \ln(D_{30})^2 \rho H$ | 0.936 | 0.029 | 529.2 | <0.001 | 24.9 |
| 3 | $\ln TSB = 0.209 + 0.920 \ln(D_{30})^2 \rho$ | 0.906 | 0.049 | 348.2 | <0.001 | 39.2 |
| 4 | $\ln TSB = -0.605 + 0.9717 \ln(D_{30})^2$ | 0.876 | 0.0607 | 256.3 | <0.001 | 49.3 |
| 1 | $\ln TSB = -6.936 + 0.876 \ln(D_{base})^2 H$ | 0.969 | 0.026 | 1156 | <0.001 | 3.5 |
| 2 | $\ln TSB = -5.743 + 0.821 \ln(D_{base})^2 \rho H$ | 0.976 | 0.021 | 1477 | <0.001 | 12.3 |
| 3 | $\ln TSB = -1.962 + 1.199 \ln(D_{base})^2 \rho$ | 0.937 | 0.052 | 538.3 | <0.001 | 24.3 |
| 4 | $\ln TSB = -2.949 + 1.242 \ln(D_{base})^2$ | 0.866 | 0.0811 | 234.33 | <0.001 | 52.2 |
| 1 | $\ln AGB = -2.787 + 0.645 \ln(D_{30})^2 H$ | 0.925 | 0.031 | 444 | <0.001 | 23.8 |
| 2 | $\ln AGB = -1.918 + 0.602 \ln(D_{30})^2 H \rho$ | 0.909 | 0.032 | 363.2 | <0.001 | 30.6 |
| 3 | $\ln AGB = 1.285 + 0.834 \ln(D_{30})^2 \rho$ | 0.902 | 0.046 | 332.6 | <0.001 | 33.6 |
| 4 | $\ln AGB = 0.499 + 0.8911 \ln(D_{30})^2$ | 0.895 | 0.0509 | 306.73 | <0.001 | 36.3 |
| 1 | $\ln AGB = -5.092 + 0.786 \ln(D_{base})^2 H$ | 0.946 | 0.031 | 628.6 | <0.001 | 11.7 |
| 2 | $\ln AGB = -3.947 + 0.730 \ln(D_{base})^2 \rho H$ | 0.935 | 0.032 | 519.4 | <0.001 | 18.4 |
| 3 | $\ln AGB = -0.644 + 1.079 \ln(D_{base})^2 \rho$ | 0.919 | 0.053 | 410.4 | <0.001 | 26.5 |
| 4 | $\ln AGB = -1.622 + 1.1339 \ln(D_{base})^2$ | 0.876 | 0.0709 | 255.82 | <0.001 | 42.2 |
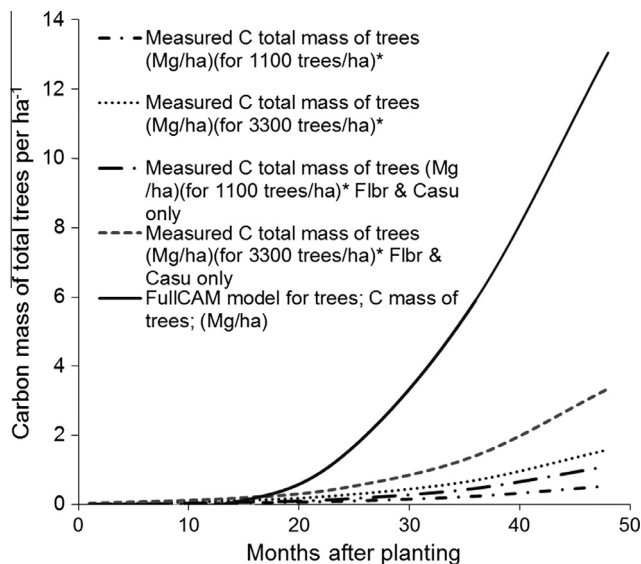


**Fig. 5.** Comparison of FullCAM model with models of carbon biomass of whole young trees (this study) (Flbr = *Flindersia brayleyana*; Casu = *Cardwellia sublimis*).

density were slower, but their survival was higher. Wood density, stem slenderness and leaf economics are traded-off against growth rate and survival (Falster, 2006; Van Gelder et al., 2006). In addition, plant damage and recovery rates have been shown to be affected by wood density (e.g. Curran et al., 2008). The strong correlation between species' wood density and their growth rates has been observed in many species (Wright et al., 2010). Species in our experimental plots that exhibited significantly higher growth rates had lower wood densities. These faster growth rates were, however, countered by higher mortality rates; a result that accords with other studies (King et al., 2006; Van Gelder et al., 2006). However, there was greater variation in wood density among our five study species than is accounted for in the available datasets (Ilic et al., 2000). Our data differed from published values in that they ranged from 5% lower to 27% higher for the five species

studied, even though bark was included in our measures. Clearly, the wood density of juvenile trees warrants more attention if young trees are to be included in carbon accounting schemes in the future.

### 4.4. Effects of leaf and stem architecture on survival

Proportions of stems to total above-ground biomass differed significantly among species (Table 3). *C. sublimis* and *F. brayleyana* had the highest ratio of foliage to stem biomass and *S. luehmannii* had the next highest. The first two species have large compound leaves (*F. brayleyana* rachis + petiole 50–200 mm; *C. sublimis* leaflets 60–210 × 28–80 mm; 7–6 50 mm, 70–210 × 40–85 mm; Cooper and Cooper, 2004) and carry their leaves high on the stems, and the leaves and leaf branches comprise 59% and 56% respectively of the total above-ground biomass. In comparison, *S. luehmannii* has small simple leaves (30–70 × 7–28 mm) and carries them along and close to the stems, and the leaves and leaf branches comprise 52% of the total AGB. From our observations of *C. sublimis* and *F. brayleyana*, their large leaves high on the stems catch the wind, causing the motion of the stem bases to create a cone in the soil that breaks the lateral roots. In contrast, the smaller leaves of *S. luehmannii*, carried closer to the stems, do not cause the stem to move nearly as much, apparently deflecting the wind, rather than catching it.

The other two species included in our study have different leaf characteristics and architecture, which probably serve to reduce wind-shear. *G. lasioneura* may have either simple or compound leaves which range from 35–190 mm long and 15–70 mm wide (most are short and narrow), but are held close to the stems, and constitute only 42% of the above-ground biomass, and *S. sinuatus*, with 45% of AGB in leaves and branches, has large simple leaves 50–480 mm long and 20–250 mm wide, but these leaves tend to align vertically along the stem, and twist with the wind, rather than move the stems.

Wind can be an important mechanical stress on woody plants, especially those in exposed conditions. Although they studied open forest species, Butler et al. (2012) showed that the 'shoot frontal projected area' of stems (consisting of leaves, branches and stems),

coupled with other shoot factors affected the safety or breakage resilience of species. They confirmed that most woody shoots are streamlined objects in wind (Butler et al., 2012), which we consider may not apply to rainforest plants planted in the open. They found that species with larger shoot area tended to be taller plants and to have larger leaves, and a weak tendency towards lower wood density, which is consistent with our findings. They also had thicker stems, also consistent with our findings.

Tree architecture is known to be an important factor in mechanical stability and safety of trees (Poorter et al., 2006; Van Gelder et al., 2006), and in the species we studied, some of the factors identified by Butler et al. (2012) appear to predict survival (such as smaller projected area at rest for *S. luehmannii*), but larger leaf area and thicker stems at the base appear to increase the risk of death in both *F. brayleyana* and *C. sublimis*. This may be due to the effect that the larger leaf projected area has on the base of the stems and a lack of streamlining which open forest saplings adopt, and is worth further investigation in rainforest plants planted in exposed conditions at windy sites.

Deeper roots, with more biomass underground in the early stages, are very important for survival during the dry periods of the year. Investing more in below-ground biomass (roots) is important for young plants to establish. The large leaves of several species, which are an advantage in rainforest trees competing for light under a closed forest canopy, become a disadvantage in open environments where wind damage is likely, and where evapotranspiration is much higher than under the closed canopy. These factors become apparent when the climate in the forests and paddocks are compared. The mean monthly temperature at the study site in the grassland was 1.2 °C higher than in the adjacent rainforest, and maximum temperatures were as much as 7 °C higher. The mean monthly relative humidity in the grassland was 4–6% lower than in the rainforest, and monthly and diurnal fluctuations of both temperature and relative humidity were much greater in the grassed paddocks (Noel Preece, unpublished data).

### 4.5. The use of allometric models

The empirical model for our study site produced biomass estimates which differed by two to four orders of magnitude when compared with the FullCAM model. We argue that the FullCAM model, which is the national tool required by the Australian Government to be used for carbon accounting in the carbon credits trading system, should be revised. Our results indicate that the maximum growth rate of saplings is lower than projected in the FullCAM model and an exponential increase in growth rate occurs only after four years.

There are problems with using complex models at the full range of scales from millions of square kilometres to hectares. The accuracy of estimates of carbon stocks by pan-tropical allometry models has been questioned by several authors, with Alvarez et al. (2012) showing that the type II model of Chave et al. (2005) grossly over-estimated values in Colombia (Brown et al., 1989; Brown, 1997; Baker et al., 2004; Chave et al., 2005). We have previously demonstrated, for the Wet Tropics (Preece et al., 2012), that the FullCAM model consistently underestimated above-ground carbon by 17.8–54.9%, depending on which model was used. When small stems were excluded, FullCAM estimates were on average 9.0% (Keith et al., 2000), 25.3% (Chave et al., 2005) and 31.9%, (Brown, 1997) lower than estimates from tested models.

It is, however, impractical to develop site-level models, so it will be important to continuously refine existing models such as FullCAM. Recently in the Wet Tropics of Australia, using much larger datasets than used previously (Paul et al., 2013), AGB estimates were closer to those estimated by Brown et al. (1989).

The allometric model we developed is one of the few which addresses young trees. Our most parsimonious model allows sampling of a few simple measures to obtain reliable estimates of biomass and carbon in young forests.

## 5. Implications

We have provided new data and better models of early growth in tropical wet forest plantations in order to improve understanding of this critical stage in carbon sequestration forests.

Since the FullCAM model is the national tool required by the Australian Government under the *Permanent Environmental Plantings Methodology* (Department of Climate Change and Energy Efficiency, 2012) we recommend that it undergoes continuous refinement so that carbon farmers are better able to plan their investment strategies.

For farmers who are considering planting a forest for carbon sequestration, there are also other critical considerations, particularly survival. We have shown that slower growing species with higher wood densities have better survival rates. The dilemma for carbon farmers is whether to plant fast-growing species with lower survival or slow-growing species with higher survival rates.

Together with other serious cost and procedural impediments to carbon farming forests (van Oosterzee et al., 2010, 2012, 2014; van Oosterzee, 2012; Matzek et al., 2014), establishing forests on farmland will not be economically viable until the price of carbon is sufficiently high and stable to provide confidence in an investment strategy that may take years to produce a reasonable return. Underpinning this is the need for an established and stable policy environment.

## Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2015.05.003.

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