Developing general allometric relationships for regional estimates of carbon sequestration—an example using *Eucalyptus pilularis* from seven contrasting sites

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Abstract

General non-site-specific allometric relationships are required for the conversion of forest inventory measurements to regional scale estimates of forest carbon sequestration. To determine the most appropriate predictor variables to produce a general allometric relationship, we examined *Eucalyptus pilularis* aboveground biomass data from seven contrasting sites. Predictor variables included diameter at breast height (dbh), stem volume, $dbh^2 \times H$, $dbh \times H$ and height (H). The data set contained 105 trees, ranging from 6 to over 20,000 kg tree^{-1}, with dbh ranging from 5 to 129 cm. We observed significant site differences in (1) partitioning of biomass between the stem, branch wood and foliage; (2) stem wood density and (3) relationship between dbh and height. For all predictor variables, site had a significant effect on the allometric relationships. Examination of the model residuals of the site-specific and general relationship indicated that using dbh alone as the predictor variable produced the most stable general relationship. Furthermore, the apparent site effect could be removed by the addition of a constant value to the measured diameter (dbh + 1), to account for the differing diameter distribution across the seven sites. Surprisingly, the inclusion of height as a second predictor variable decreased the performance of the general model. We have therefore demonstrated that for *E. pilularis* a general allometric relationship using dbh alone as the predictor variable can be as accurate as site-specific allometry, whilst being applicable to a wide range of environments, management regimes and ages. This simplifies regional estimates of aboveground biomass from inventory measurements, eliminating the need for site-specific allometric relationships or modifiers such as height, wood density or expansion factors.
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1. Introduction

Participation in international or domestic carbon trading schemes requires estimates of carbon sequestered by forests. Because of the monetary value being

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attached to carbon sequestration there is increased scrutiny of techniques for estimating aboveground biomass (e.g. de Jong, 2001; Coomes et al., 2002; Specht and West, 2003). Traditionally, allometric relationships, which relate an easily measured tree variable (e.g. stem diameter), to aboveground biomass, have been used at the experimental scale to estimate aboveground biomass. Applying allometric relationships to inventory data to estimate regional forest biomass provides an extension of this approach. The literature contains many allometric relationships (e.g. Ter-Mikaelian and Korzukhin, 1997), although typically these estimate tree components (i.e. foliage, branches, stemwood and bark). Allometric relationships for an individual component, particularly foliage and branches, are often site-specific (Feller, 1992). Furthermore, summing individual components to estimate total aboveground biomass requires forcing additivity to ensure the components sum to the predicted total for the tree (Parresol, 1999). Consequently, directly estimating total aboveground biomass using a single allometric equation is preferred.

For cost-effective estimation of aboveground biomass, at multiple sites across the geographical range of a species, general non-site-specific allometric relationships are required. Published allometric equations are typically site-specific, reflecting the original objective for which they were developed. Surprisingly, there are few studies that have combined data, across sites, to systematically examine the development of general aboveground biomass allometric relationships for a species. Where general allometric relationships have been developed these have been reliant on the combination of regression equations to produce either species-specific allometry (e.g. Schmitt and Grigal, 1981; Grigal and Kernik, 1984; Pastor et al., 1984) or allometry for groups of species (e.g. Keith et al., 1999; Jenkins et al., 2003). Such an approach has been hampered by the different mathematical forms of equations, use of different predictor variables, differences in measurement techniques and insufficient reporting of error terms for the published allometric relationships (Jenkins et al., 2003). As a result only limited examination of the sources of variation in allometric equations from different sites is possible from the published relationships. Furthermore, it is not possible to determine if the inclusion of other predictor variables into the

relationship would create more robust general relationships.

Inclusion of stand height and/or wood density as predictor variables in allometric equations has been suggested to allow for the influence of site factors (Crow, 1978; Ketterings et al., 2001) and differences between tree species (Brown et al., 1989). However, there is conflicting evidence regarding the value of including height in allometric equations. The addition of height, as an additional predictor variable, has been reported to add little to the predictive capacity of a diameter-based allometric equations at one site (Madgwick and Satoo, 1975). However, inclusion of tree height in allometric relationships may account for variations in the allometric relationship across contrasting sites (Schmitt and Grigal, 1981).

In this paper we examine the variation in allometric relationships within one species, *Eucalyptus pilularis*, across seven contrasting sites. The species occurs naturally along the coastal strip of eastern Australian (Fig. 1, Boland et al., 1984). Recently, plantations of *E. pilularis* have been established on previously cleared land within the natural range of the species. Specifically, we examined whether site factors might cause a change in the allometric relationship and how this could be accounted for in a general allometric equation for making regional estimates of aboveground biomass from inventory data.

2. Materials and methods

2.1. Study sites

Aboveground biomass data from seven sites were used in this study. Fig. 1 shows the location of the study sites and the natural range of *E. pilularis*. Four of these sites were planted forests and three were native forests. Stand and climate details of the seven sites are shown in Table 1. Temperature and rainfall data were obtained from interpolation of Bureau of Meteorology point data (Jeffrey et al., 2001).

2.2. Sample tree selection

At each site between 7 and 25 trees were sampled (Table 1). Five diameter classes were established for each site, based on the stem diameter range, and
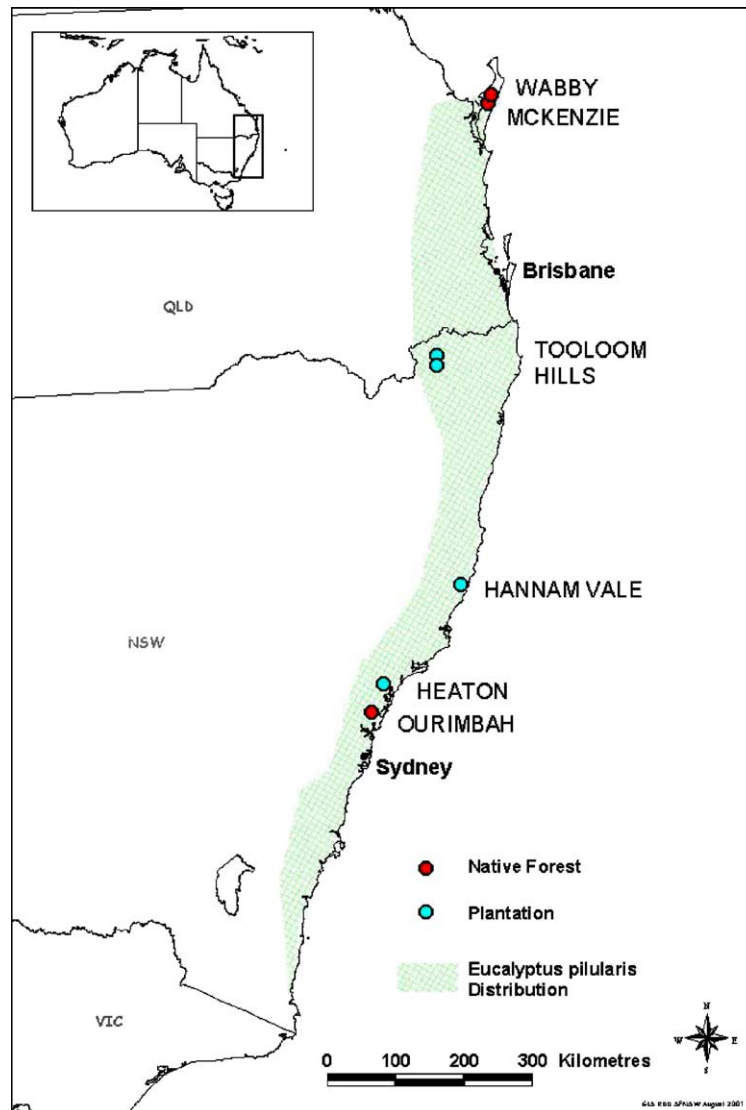
Fig. 1. Location of study sites, and natural distribution of *E. pilularis*.

sample trees randomly chosen within each diameter class.

2.3. Aboveground biomass estimation

Aboveground biomass of individual trees was estimated using two methods. The methods chosen reflected the equipment available and size of trees being measured. The direct measurement of fresh mass should be used to minimise errors in the primary data. Load cell technology now make it possible to measure the fresh mass of large trees and this approach is encouraged. However, even when fresh mass is measured, biomass can only ever be an estimate for large trees, as drying entire trees is not possible. At Ourimbah, Heaton, Tooloom, Hills and Hannam Vale sites, the aboveground biomass of individual trees was estimated from direct measurements of the fresh mass of the entire tree (stem, branches and foliage).

Table 1
Location, forest structure and climate of seven stands from which aboveground biomass of *E. pilularis* trees was measured

	Wabby	McKenzie	Ourimbah	Heaton	Tooloom	Hills	Hannam Vale
Latitude (S)	25°27'	25°27'	33°19'	33°00'	28°37'	28°33'	31°40'
Longitude (E)	153°08'	153°04'	151°20'	151°25'	152°22'	152°22'	152°34'
Forest type	Native	Native	Native	Plantation	Plantation	Plantation	Plantation
No. of trees sampled	7	10	10	10	22	21	25
Age	14	45	Mixed	33	3	3	3
Trees (ha^{-1})	940	920	799	886	800	800	800
Dbh range (cm)	13.1 (25.3)	17.8 (128.9)	10.8 (75.4)	10.3 (57.8)	5.5 (15.5)	5.2 (19.0)	5.1 (19.8)
Predominant height (m)	17	34	30	34	8	9	10
Stand basal area (m^2 ha^{-1})	17	35	40	37	6	8	10
Rainfall (mm year^{-1})	1523	1500	1228	1128	1058	982	1492
Mean temperature (°C)	21.4	21.0	17.4	15.9	15.8	16.3	17.1

We also included two data sets, Wabby and McKenzie (Applegate, 1982), which employed subsampling techniques to estimate the biomass of tree components. This approach can be more error prone due to the greater reliance on correct sampling for each tree component, with estimates for each component summed to estimate the entire tree biomass, i.e. the total tree biomass is not restrained by a measure of total tree fresh mass measurement, as used at Ourimbah, Heaton, Tooloom, Hills and Hannam Vale.

2.4. Biomass estimation—Ourimbah, Heaton, Tooloom, Hills and Hannam Vale

The sample trees were felled into an open area. The branches were removed and the total stem (i.e. from base to tip) and canopy (branches and foliage) fresh mass was measured. For large trees a digital load cell (2500 kg capacity, PCS Measurements, Newcastle, Australia) suspended from the arm of an excavator was used. For smaller trees, which could be handled manually, either a load cell suspended from a tripod or a balance was used to measure tree fresh mass. Immediately following fresh mass measurement, a minimum of three and five disks per stem and branches, respectively, were then taken to determine moisture content. All subsamples were dried at 70 °C until constant mass was reached.

The measured fresh mass of the canopy was partitioned into branch wood and foliage components by subtracting foliage estimates from the measured canopy fresh mass. Methods for estimating the foliage fresh mass varied across sites due to tree size. The inherently error prone estimates of foliage, from any estimation technique, would have had little impact on the total aboveground biomass estimate. This is due to the foliage estimates only being used to partition the measured canopy fresh mass into its components. Furthermore, the foliage component for most trees was below 25% of the tree biomass. Branch and foliage moisture contents were applied to the fresh mass of the components to estimate biomass.

A range of methods was used to estimate the foliage fresh mass (leaf lamina and petiole). For the large trees either randomised branch sampling (Ourimbah; Snowdon et al., 2002) or the "Adelaide"

technique (Heaton; Andrew et al., 1979) was used to estimate foliage fresh mass. Application of the randomised branch sampling involved the selection of five sample paths, using selection probabilities based on branch diameter[2.5] and terminating when branch diameter declined below 5 cm diameter. For each branch thus identified the foliage was stripped from the branch and fresh mass determined before a subsample taken and moisture content determined. Foliage mass per tree was then calculated using the unconditional probability for each path. At the Heaton site tree foliage mass was estimated by visual selection of a representative canopy sample unit for each tree prior to felling. The number of units per tree was then determined by eye. After harvesting, the foliage of the canopy sample unit was removed and weighed, and subsampled for moisture content. The tree foliage mass per tree was estimated from the product of the number and dry mass of the sample unit.

For the smaller trees at the Tooloom, Hills and Hannam Vale sites a regression approach was used to estimate foliage mass. For each tree, the diameter of all branches (5 cm above the junction with the stem) was measured. Five branches per tree were chosen and the foliage mass measured. The relationship between branch diameter and foliage fresh mass was applied to all branch diameters to estimate foliage fresh mass for each tree. The foliage moisture content was used to convert fresh mass to an estimate of foliage biomass.

2.5. Biomass estimation—Wabby and McKenzie

Stem biomass was obtained using dendrometry to estimate volume of stem sections, and basic density applied from samples from each section to estimate biomass (Method 2.4.1, Snowdon et al., 2002). Regression equations relating branch diameter to the mass of branch, foliage and capsules were developed and applied to measurements of branch diameters. Full details of the tree sampling method are given in Applegate (1982).

2.6. Diameter and height measurement

Tree diameter at breast height (dbh; 1.3 m) and tree height (H) were measured prior to felling. Tree height data were not available for trees sampled at Wabby and McKenzie. For these sites height was estimated from dbh (Bi et al., 2000).

2.7. Stem volume

Stem volume was calculated for all trees using equations based on dbh and tree height. Two species-specific equations were used. For trees 5–20 cm dbh Eq. (1) was used (Huiquan Bi, personal communication):

$$V = 0.0034 + (0.2448 \times \mathrm{dbh}^2 H) \tag{1}$$

where V is total underbark stem volume from ground to tip (m^3); dbh is diameter at breast height over bark (m); and H is height (m).

For trees greater than 20 cm dbh Eq. (2) was used (Bi, 1998):

$$V = (0.118 \times \mathrm{dbh}^2 H) + (0.003 \times \mathrm{dbh}^3 H)$$
$$+ (0.002 \times H) \tag{2}$$

2.8. Wood density

Basic wood density was determined on stem disks taken at 1.3 m. Under-bark volume was determined prior to disks being dried at 103 °C to constant dry mass (Downes et al., 1997).

2.9. Statistical analysis

To test the effect of site on biomass partitioning, density and height analysis of covariance was used, with site the categorical factor and dbh the continuous predictor.

We restricted our analysis to the most common allometric form (Parresol, 1999) to examine the relationship between aboveground biomass (kg tree^{-1}) and a number of predictor variables. Predictor variable were chosen to range from dbh to height alone, with differing combinations of dbh and height used to examine if incorporating height improved the generality of relationships. Because a fixed reference height (1.3 m) is used for dbh measurement there is the potential to introduce curvilineanity into the relationship where data sets span a large dbh range. To correct for this we used a

simple weighting function (dbh + 1) (Madgwick, 1979).

The models used were:

$$\text{agb} = \beta_0 \text{dbh}^{\beta 1} \tag{3}$$

$$\text{agb} = \beta_0 (\text{dbh} + 1)^{\beta 1} \tag{4}$$

$$\text{agb} = \beta_0 \, \text{stem volume}^{\beta 1} \tag{5}$$

$$\text{agb} = \beta_0 (\text{dbh}^2 \times H)^{\beta 1} \tag{6}$$

$$\text{agb} = \beta_0 (\text{dbh} \times H)^{\beta 1} \tag{7}$$

$$\text{agb} = \beta_0 H^{\beta 1} \tag{8}$$

where agb is the aboveground biomass (kg tree^{-1}); dbh the diameter at breast height (1.3 m, dbh units for Eqs. (3) and (8) are cm, while for Eqs. (6) and (7) units are m); H the height (m); and β_0 and β_1 are parameter estimates.

Data exhibited heteroscedasticity (i.e. the error variance was not constant across all observations). Data were natural logarithm (ln) transformed to give the following models:

$$\ln (\text{agb}) = \ln (\beta_0) + \beta_1 \ln (\text{dbh}) \tag{9}$$

$$\ln (\text{agb}) = \ln (\beta_0) + \beta_1 \ln (\text{dbh} + 1) \tag{10}$$

$$\ln (\text{agb}) = \ln (\beta_0) + \beta_1 \ln (\text{stem volume}) \tag{11}$$

$$\ln (\text{agb}) = \ln (\beta_0) + \beta_1 \ln (\text{dbh}^2 \times H) \tag{12}$$

$$\ln (\text{agb}) = \ln (\beta_0) + \beta_1 \ln (\text{dbh} \times H) \tag{13}$$

$$\ln (\text{agb}) = \ln (\beta_0) + \beta_1 \ln (H) \tag{14}$$

Models were fitted to the transformed data using ordinary least-squares regression analysis. Statistical testing of the above models involved three distinct steps. Firstly, for each model (Eqs. (9)–(14) analysis of covariance was used to test for site effects (Statistica V5.0). This involved testing the seven site models for common slope, followed by common intercepts, if no significant difference in slopes was detected. Secondly, a comparison of the general equations was undertaken using Furnivals Index (Furnival, 1961). Finally, a comparison of the general equation with the seven site-specific equation was undertaken. Residuals of the site-specific equations were examined

using diagnostic plots and determined to be normally distributed allowing the residuals from the site-specific equations to be pooled. The pooled residual errors from the seven site-specific equations were compared to residual errors of a single general equation fitted to all data and differences in variances assessed by F-test.

Logarithmic regressions (Eqs. (9)–(14) produce inherently bias estimates of biomass. Bias correction can be achieve either using the methods of Baskerville (1972), using the regression error mean square, or Snowdon (1991) using the ratio of arithmetic sample mean and mean of the back-transformed predicted values from the regression. As the latter requires the raw data, these values were calculated for each site and equation.

3. Results

Across the seven sites tree biomass ranged from 6 to over 20,000 kg tree^{-1}.

3.1. Variations in stem, branch and foliage partitioning

There was considerable variation in aboveground biomass partitioning between stem, branches and foliage across the seven sites (Fig. 2a–c, respectively). The stem accounted for 40–95% of the aboveground biomass. The proportion of aboveground biomass in the stem initially increased with tree size. However, at any diameter the variation in the proportion of aboveground biomass in the stem was large. For example, at a dbh of 20 cm the proportion of aboveground biomass in the stem ranged from 54 to 95%. For trees over 50 cm dbh there appeared to be a decline in the proportion of aboveground biomass in the stem. Site differences in the proportion of stems as aboveground biomass were evident ($P < 0.01$). Trees from Wabby and McKenzie sites had the greatest proportion of aboveground biomass in the stem (80 and 86%, respectively) with the lowest stem % observed at the Tooloom, Hannam vale and Hills sites (48, 55 and 58%, respectively). Branches wood accounted for 5–45% of the aboveground biomass. Changes in biomass partitioned to the branches were the inverse of that observed in the stem.
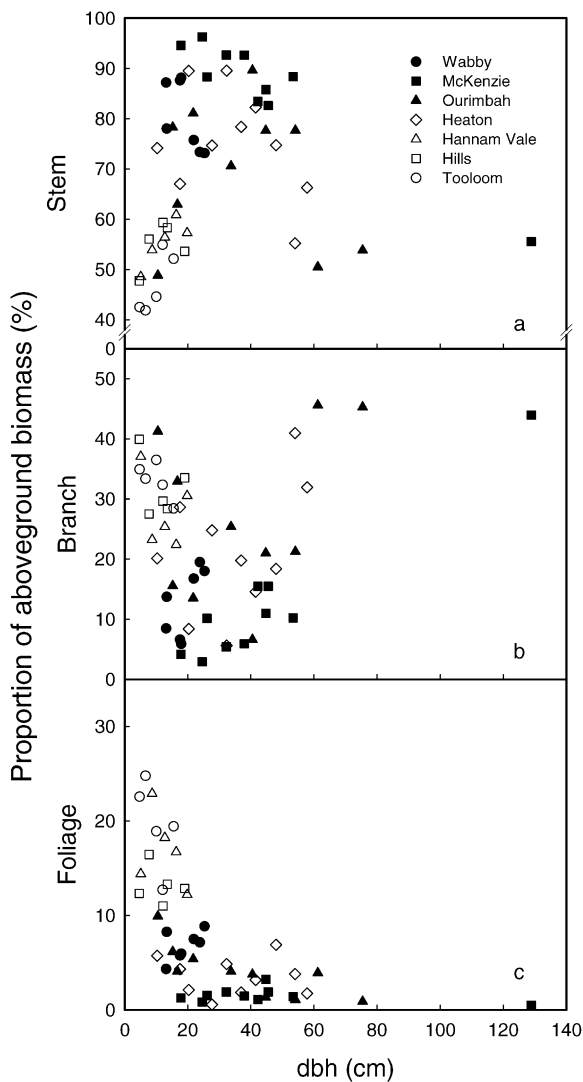
Fig. 2. Partitioning of aboveground biomass between the stem (a), branches (b), and foliage (c), of *E. pilularis* from seven sites. Hollow and filled symbol indicate trees sampled from plantation and native forests, respectively.

The proportion of aboveground biomass as foliage declined from 25% in small trees to less than 5% in trees greater than 30 cm dbh. Again, differences between sites were evident ($P = 0.03$). Trees from the young plantation sites had a greater proportion of aboveground biomass as foliage, compared with the other four sites.

3.2. Stem wood density variation

Stem wood density varied by 74% (Fig. 3). The stem wood density of trees from Tooloom, Hills and Hannam Vale sites were lower than that of trees from Ourimbah and Heaton sites ($P < 0.01$).

3.3. Variations in tree height

The relationship between height and dbh differed across sites ($P < 0.01$) (Fig. 4). The trees from the young plantation sites had a lower height, for a given dbh, than those from Ourimbah and Heaton sites. Furthermore, between the young plantation sites, trees from the Hannam Vale site were taller, for a given dbh, than trees from Hills and Tooloom sites.

3.4. Relationship between aboveground biomass and predictor variables

At each site dbh was strongly related to aboveground biomass, with dbh accounting for 89–99% of the variation in aboveground biomass (Fig. 5a; Table 2). Between the seven sites differences in the slope of the relationship between dbh and aboveground biomass were observed ($P < 0.01$), with lower slopes in the young plantation sites (Tooloom, Hills and Hannam vale) compared to those of the other four sites (McKenzie, Wabby, Ourimbah and Heaton). However, within each of the two groups, no difference in the relationship between dbh and aboveground biomass was observed ($P = 0.74$ and 0.69, respectively). To determine if the differing diameter distributions (Table 1) was causing the differences in slopes between the two groups, a constant was added to dbh (dbh + 1; Madgwick, 1979). This resulted in all sites having the same slope and intercept ($P = 0.24$ and 0.12, respectively) (Fig. 5b). The addition of the constant did not affect the proportion of aboveground biomass variation accounted for by dbh at each of the seven sites (c.f. Tables 2 and 3).

Calculated stem volume accounted for 87–99% of aboveground biomass variation at each site (Table 4). Differences between sites were also observed ($P < 0.01$). The relationships varied both within the three young planted forests sites ($P < 0.01$), and between the young planted forest sites and the remaining four sites (Fig. 5c).
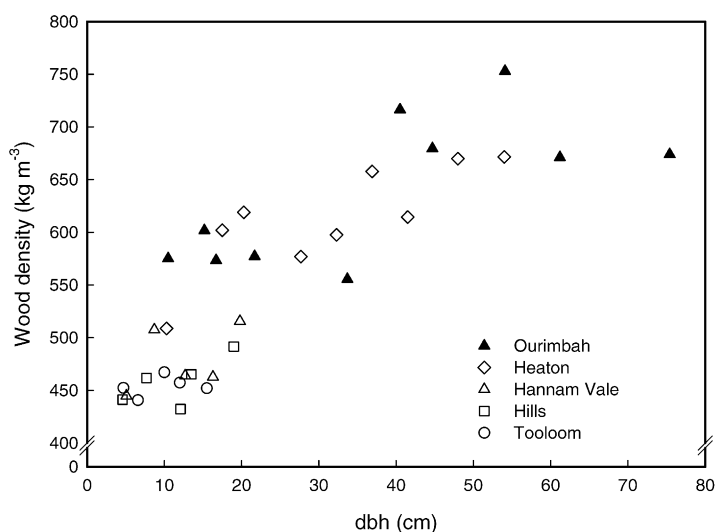
Fig. 3. Woody density of *E. pilularis* from five sites. Hollow and filled symbol indicate trees sampled from plantation and native forests, respectively.

Simple combinations of $dbh^2 \times$ height and $dbh \times$ height accounted for 98–88% of variation in aboveground biomass at an individual site (Tables 5 and 6, respectively). However, the relationships differed across the seven site ($P < 0.01$), with the exception of Ourimbah and Heaton sites where the relationship was the same for both $dbh^2 \times$ height

height and $dbh \times$ height ($P = 0.75$ and 0.83, respectively) (Fig. 5d and e).

Tree height alone was the worst predictor variable, accounting for 74–93% of the variation in aboveground biomass at each site (Table 7). The relationship between aboveground biomass and height differed between sites (Fig. 5f) ($P < 0.01$). For each site a
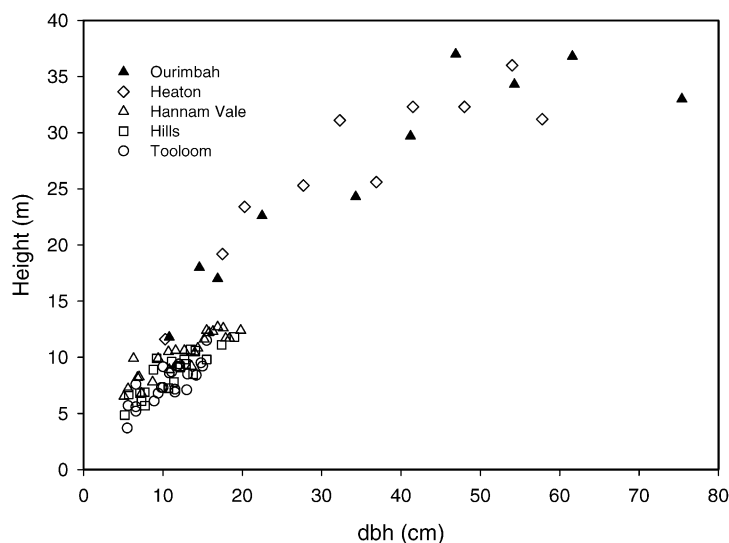

Fig. 4. Tree diameter–height relationships for *E. pilularis* from five sites. Hollow and filled symbol indicate trees sampled from plantation and native forests, respectively.
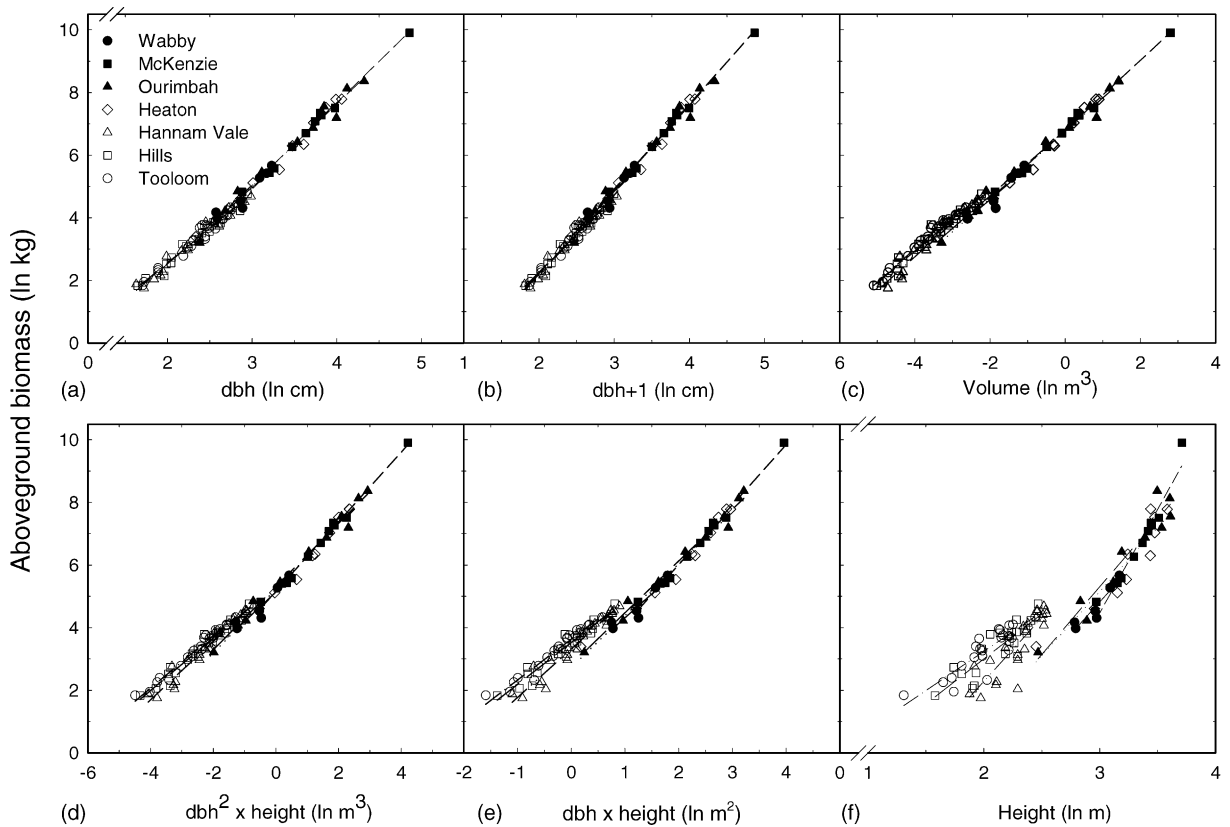
Fig. 5. Site-specific relationships between natural log-transformed aboveground biomass and dbh (a), dbh + 1 (b), stem volume (c), $dbh^2 \times height$ (d), $dbh \times height$ (e), and height (f). Lines are site-specific regressions. See Tables 2–7 for details of the relationships. Hollow and filled symbol indicate trees sampled from plantation and native forests, respectively.

Table 2
Tree biomass regression equations[a] relating dbh to aboveground biomass of E. pilularis from seven contrasting sites and a general equation fitted to all data (refer to Table 1 for site details)

Site	β_0	β_1	EMS[b]	r^2	Bias c.f.[c]	n
Wabby	−2.322 (0.099)	2.432 (0.338)	0.048	0.894	1.028	7
McKenzie	−2.897 (0.279)	2.643 (0.075)	0.015	0.993	0.976	10
Ourimbah	−2.683 (0.419)	2.579 (0.119)	0.057	0.981	0.992	10
Heaton	−2.930 (0.395)	2.649 (0.114)	0.036	0.984	1.047	10
Hannam vale	−2.061 (0.172)	2.293 (0.070)	0.020	0.978	1.000	25
Hills	−1.845 (0.208)	2.208 (0.087)	0.019	0.970	1.004	21
Tooloom	−1.944 (0.219)	2.248 (0.094)	0.019	0.965	1.008	22
General	−2.642 (0.074)	2.551 (0.026)	0.032	0.989	1.109	105

Values in parenthesis are standard errors.

[a] ln (agb) = ln (β_0) + β_1 ln dbh; where: agb is the aboveground biomass (kg); ln the natural log; dbh the diameter at 1.3 m (cm).

[b] Error mean squared in natural log units.

[c] Calculated bias correction factor (Snowdon, 1991).

Table 3
Tree biomass regression equations[a] relating dbh + 1 to aboveground biomass of *Eucalyptus pilularis* from seven contrasting sites and a general equation fitted to all data (refer to Table 1 for site details)

Site	β_0	β_1	EMS[b]	r^2	Bias c.f.[c]	n
Wabby	−2.870 (1.050)	2.572 (0.353)	0.047	0.897	0.973	7
McKenzie	−3.201 (0.290)	2.705 (0.078)	0.015	0.993	1.036	10
Ourimbah	−3.122 (0.453)	2.677 (0.128)	0.060	0.980	1.014	10
Heaton	−3.425 (0.399)	2.763 (0.114)	0.033	0.985	0.960	10
Hannam Vale	−2.849 (0.199)	2.523 (0.078)	0.020	0.978	1.002	25
Hills	−2.623 (0.242)	2.438 (0.098)	0.020	0.969	0.998	21
Tooloom	−2.767 (0.254)	2.498 (0.105)	0.019	0.964	0.993	22
General	−3.270 (0.074)	2.707 (0.026)	0.027	0.991	0.971	105

Values in parenthesis are standard errors.
  [a] ln aboveground biomass = $\beta_0 + \beta_1$ ln (dbh + 1) (see Table 2 for details).
  [b] Error mean squared in natural log units.
  [c] Calculated bias correction factor (Snowdon, 1991).

Table 4
Tree biomass regression equations[a] relating calculated stem volume to aboveground biomass of *E. pilularis* from seven contrasting sites and a general equation fitted to all data (refer to Table 1 for site details)

Site	β_0	β_1	EMS[b]	r^2	Bias c.f.[c]	n
Wabby	6.636 (0.307)	1.027 (0.161)	0.060	0.869	1.034	7
McKenzie	6.809 (0.033)	1.110 (0.027)	0.011	0.995	0.994	10
Ourimbah	6.785 (0.072)	1.041 (0.044)	0.046	0.984	1.013	10
Heaton	6.763 (0.065)	1.072 (0.046)	0.036	0.984	1.068	10
Hannam vale	7.088 (0.148)	1.083 (0.044)	0.034	0.962	0.994	25
Hills	7.006 (0.184)	1.017 (0.050)	0.029	0.954	0.998	21
Tooloom	7.281 (0.137)	1.069 (0.036)	0.012	0.977	0.995	22
General	6.802 (0.036)	0.979 (0.012)	0.044	0.985	1.161	105

Values in parenthesis are standard errors.
  [a] ln (agb) = ln (β_0) + β_1 ln volume; volume = stem volume (m^3).
  [b] Error mean squared in natural log units.
  [c] Calculated bias correction factor (Snowdon, 1991).

Table 5
Tree biomass regression equations[a] relating $dbh^2 \times$ height to aboveground biomass of *E. pilularis* from seven contrasting sites and a general equation fitted to all data (refer to Table 1 for site details)

Site	β_0	β_1	EMS[b]	r^2	Bias c.f.[c]	n
Wabby	5.135 (0.099)	0.938 (0.132)	0.049	0.892	1.029	7
McKenzie	5.156 (0.063)	1.111 (0.033)	0.016	0.992	1.040	10
Ourimbah	5.306 (0.077)	1.010 (0.041)	0.045	0.985	1.029	10
Heaton	5.238 (0.084)	1.023 (0.052)	0.049	0.977	1.086	10
Hannam vale	5.416 (0.083)	0.930 (0.037)	0.032	0.964	1.005	25
Hills	5.349 (0.101)	0.840 (0.040)	0.027	0.957	1.011	21
Tooloom	5.419 (0.079)	0.839 (0.029)	0.013	0.975	1.008	22
General	5.427 (0.027)	0.899 (0.012)	0.053	0.982	1.325	105

Values in parenthesis are standard errors.
  [a] ln (agb) = ln (β_0) + β_1 ln ($dbh^2 \times H$) (see Table 2 for details, note dbh in m).
  [b] Error mean squared in natural log units.
  [c] Calculated bias correction factor (Snowdon, 1991).

Table 6
Tree biomass regression equations[a] relating dbh × height to aboveground biomass of *E. pilularis* from seven contrasting sites and a general equation fitted to all data (refer to Table 1 for site details)

Site	β_0	β_1	EMS[b]	r^2	Bias c.f.[c]	n
Wabby	2.784 (0.307)	1.421 (0.211)	0.054	0.881	1.029	7
McKenzie	1.903 (0.191)	1.941 (0.073)	0.026	0.987	1.091	10
Ourimbah	2.820 (0.169)	1.651 (0.074)	0.053	0.982	1.051	10
Heaton	2.724 (0.230)	1.656 (0.104)	0.074	0.966	1.112	10
Hannam vale	3.314 (0.046)	1.549 (0.077)	0.050	0.944	1.012	25
Hills	3.522 (0.046)	1.334 (0.080)	0.042	0.933	1.019	21
Tooloom	3.629 (0.037)	1.304 (0.062)	0.024	0.955	1.012	22
General	3.425 (0.036)	1.351 (0.026)	0.107	0.963	1.462	105

Values in parenthesis are standard errors.

[a] $\ln (\text{agb}) = \ln (\beta_0) + \beta_1 \ln (\text{dbh} \times H)$ (see Table 2 for details, note dbh in m).

[b] Error mean squared in natural log units.

[c] Calculated bias correction factor (Snowdon, 1991).

different relationship was observed, except the Ourimbah and Heaton sites, which were similar ($P = 0.64$).

A clear improvement in the performance of the general model was observed as the relative weighting of dbh increased. Graphically, this can be observed in the behaviour of the residuals (Fig. 6). The Furnival Index confirmed the observed trend, with values of 47.4, 25.0, 17.6, 16.0, 13.7 and 12.6 for predictor variables of height, dbh × height, dbh^2 × height, volume, dbh and dbh + 1, respectively.

The application of a single model to the data increased the model residuals for all predictor variables, compared to the seven site-specific relationships (Fig. 6). The exception being dbh + 1, where the pooled residuals of the seven site-specific models was the same as the residuals from the general

model ($P = 0.17$). The least increase in residual distribution was observed where dbh was the predictor variable ($P = 0.04$). For all other predictor variables the increase in residuals was larger and increased in significance as the relative weighting for dbh decreased (volume > dbh^2 × height > dbh × height > height; $P = 0.002$, 0.0001, 1×10^{-6} and 9×10^{-6}, respectively), indicating increasing sensitivity of the predictor variable to site factors.

4. Discussion

The principal aim of this study was to determine the most suitable predictor variables for producing general non-site-specific aboveground biomass relationships applicable to diverse stands across a region,

Table 7
Tree biomass regression equations[a] relating height to aboveground biomass of *E. pilularis* from seven contrasting sites and a general equation fitted to all data (refer to Table 1 for site details)

Site	β_0	β_1	EMS[b]	r^2	Bias c.f.[d]	n
Wabby[c]	−7.504 (1.802)	4.107 (0.603)	0.053	0.883	1.031	7
McKenzie[c]	−15.394 (2.012)	6.620 (0.600)	0.141	0.930	1.465	10
Ourimbah	−7.662 (1.360)	4.321 (0.422)	0.239	0.920	1.133	10
Heaton	−7.100 (1.808)	4.082 (0.555)	0.313	0.855	1.230	10
Hannam vale	−5.858 (1.135)	4.070 (0.491)	0.234	0.738	1.086	25
Hills	−2.762 (0.805)	2.878 (0.377)	0.163	0.742	1.073	21
Tooloom	−1.777 (0.632)	2.510 (0.312)	0.130	0.751	1.006	22
General	−2.612 (0.272)	2.749 (0.105)	0.385	0.869	1.976	105

Values in parenthesis are standard errors.

[a] $\ln (\text{agb}) = \ln (\beta_0) + \beta_1 \ln H$ (see Table 2 for details). H: tree height (m).

[b] Error mean squared in natural log units.

[c] Tree heights estimated from dbh–height relationship (Bi et al., 2000).

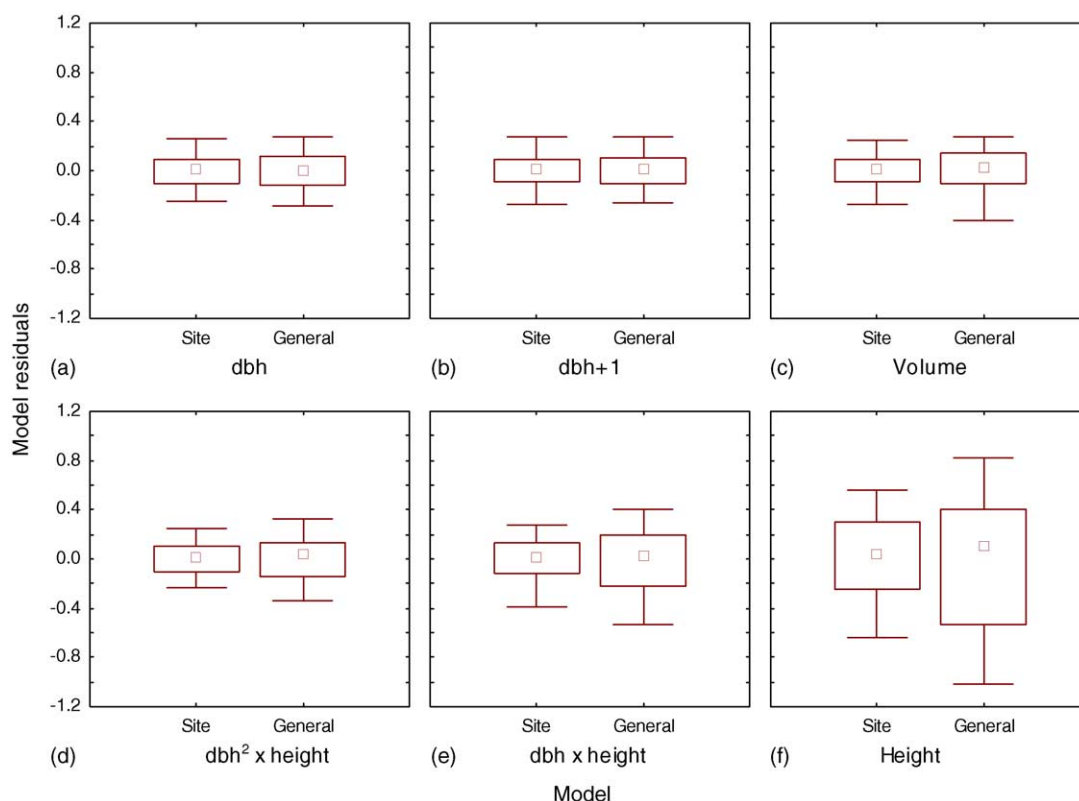[d] Calculated bias correction factor (Snowdon, 1991).

Fig. 6. Aboveground biomass model residuals of site-specific equations or a general equation fitted to all the data for dbh (a), dbh + 1 (b), stem volume (c), dbh^2 × height (d), dbh × height (e), and height (f). Residuals for the seven site-specific equations have been pooled. Point, box and bars represent the median, 25–75% and 5–95%, respectively.

using *E. pilularis* as an example. Generalised relationships are required to simplify the conversion of forest inventory measurements to regional estimates of carbon sequestration. Previous examinations of general allometric equations, either for multiple species (Jenkins et al., 2003; Keith et al., 1999) or the same species (Pastor et al., 1984; Grigal and Kernik, 1984), have been constrained by the absence of primary data. Thus, while such approaches appear promising, it has not been possible to assess if general allometric relations are as accurate as site-specific relationships or if additional predictor variables are required.

For *E. pilularis* the general allometric relationship, with dbh alone as a predictor variable, was found to be the most stable relationship across the seven contrasting sites. This indicates that robust estimates of aboveground biomass for this species can be made across sites using a general allometric relationship and standard inventory measurements, without the need for site-specific relationships or modifiers, such as proposed by Ketterings et al. (2001). The stable nature of the general allometric relationship was despite significant variations across the sites in tree size, partitioning, wood density and dbh–height relationships. However, apparent site differences were observed. The relationship differed between the young plantation sites (Hills, Tooloom and Hannam Vale), compared with that observed at the other four sites. On closer inspection this ''site'' difference appeared to arise from the differing size distribution, rather than a fundamental change in the allometric relationship between dbh and aboveground biomass. A fixed reference height (1.3 m) for diameter measurement was used in this study, as is common in forest inventories. Thus, for shorter trees, diameter is

measured at a higher position relative to the total tree height, compared with taller trees. This fixed height for diameter measurement gives a poor representation of stem "size" in small trees (Snowdon et al., 2000), introducing curvilinearity into the log-transformed plot of the allometric relationship when small trees are included in a large diameter range. As small trees were only present in the young plantation sites, the curvilinear trend resulted in the three plantation sites appearing to have a different relationship. However, addition of a constant value to the diameter measurement (Madgwick, 1979), removed the apparent "site" effect. This is clearly shown in Fig. 6, where the pooled residuals from the seven site-specific dbh + 1 equations are the same as the residuals from the general equation. By contrast, for the other predictor variables, fitting of a general equation increased the residuals.

In this study incorporating height into the equation decreased the performance of the general allometric equation, compared to the relationship based on dbh alone (Fig. 6) For example, even across the three young plantation sites different relationships between aboveground biomass and all predictor variables, except dbh, were observed (Tables 2–7). Therefore, while the inclusion of height as a second predictor variable improves stem biomass estimates (Schmitt and Grigal, 1981) and produces volume estimates which are more general (Husch et al., 1982), it does not appear to make aboveground biomass allometric relationships more stable. This is due to the apparent inverse and compensatory relationship between stem and canopy mass, resulting in similar aboveground biomass for trees of the same diameter, but different partitioning (Bickelhaupt et al., 1973). This compensatory relationship is also observed in this study and is illustrated by comparing two trees of similar dbh and aboveground biomass from the contrasting Ourimbah and Hannam Vale sites (Table 8). Despite being 40% taller and having stem wood density 25% greater, the tree from the Ourimbah site has a similar aboveground biomass to that of the Hannam vale tree. This is due to the changes in partitioning between the canopy and stem.

The constant nature of the dbh-aboveground biomass allometric model for this eucalypt species is consistent with the biomechanical requirements of the stem. As tree mass increases the stem must have greater mechanical strength to support the increasing weight. For a tree, increased mechanical strength can be achieved through increases in either wood density (Niklas, 1994) or stem diameter (King, 1986). However, diameter growth is principally responsible for the increase in strength, as variation in elasticity and strength due to changes in density are relatively limited (Niklas, 1993). This is consistent with the common scaling laws proposed for trees (Enquist, 2002). However, Enquist (2002) also proposed that incorporation of wood density would be likely to explain a significant degree of residual variation. In this study, where there was considerable variation in wood density between trees (Fig. 3; Table 8), wood density did not appear to affect the allometric relationship between dbh and aboveground biomass.

There are practical reasons for using dbh alone as the predictor variable when making estimates of aboveground biomass from inventory measurements. Firstly, it is statistically more appropriate as it is the parameter with the least measurement error. Errors associated with dbh measurement are typically less than 3% (Gregoire et al., 1989). By contrast, measurement of tree heights in mature stands are within 10–15% of the true height (Brown et al., 1995) and time-consuming, and thus costly. As a consequence routine tree height measurements are not commonly undertaken in forest inventories. Thus, biomass allometric relationships which require tree height measurements may be limited in their application.

Table 8
Contrasting aboveground biomass (AGB) partitioning, height and wood density of two trees from different sites

Site	Dbh (cm)	AGB (kg)	Height (m)	Wood density (kg m^{-3})	Proportion of AGB (%)		
					Stem	Branch	Foliage
Ourimbah	14.8	68.3	18.0	602	78	16	6
Hannam Vale	14.2	62.0	10.8	462	52	28	19

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The "expansion" of volume estimates, using wood density values and canopy expansion factors, is a method commonly used for estimating aboveground biomass. While this study does not attempt to compare the volume expansion and biomass allometric approaches some observations on the stability of the expansion method across sites are possible using this data set. The performance of site-specific stem volume allometric equations is comparable to those of dbh equations in accounting for variations in aboveground biomass (Tables 2 and 4). Consequently, where site-specific information on wood properties and expansion factors are available, accurate estimates from either approach will be obtained for those sites. However, expansion factors and wood density vary across sites (Figs. 2 and 3). As a consequence site-specific expansion factors and wood density would be required to obtain estimates of aboveground biomass across a range of sites with a similar accuracy as those given by a general dbh allometric relationship. Given the resources required to gather additional site-specific information across multiple sites it is desirable to avoid this where possible.

We have demonstrated for *E. pilularis*, that a general allometric relationship can be developed which is as accurate as site-specific allometry, whilst being applicable to a wide range of environments, management regimes and stand ages. This simplifies regional estimates of aboveground biomass from inventory measurements of dbh, eliminating the need for site-specific allometric relationships or modifiers such as height, wood density or expansion factors.

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