Estimating the accuracy of tree ageing methods in mature *Eucalyptus obliqua* forest, Tasmania

Amelia J. Koch[1,2,3], Don A. Driscoll[4] and J.B. Kirkpatrick[1]

[1]School of Geography and Environmental Science, University of Tasmania, Private Bag 78, Hobart, Tasmania, 7001, Australia
[2]Email: ajkoch@utas.edu.au
[3]Current address: Tasmanian Forest Practices Authority, 30 Patrick St, Hobart, Tasmania, 7000, Australia
[4]Centre for Resource and Environmental Studies, Australian National University, W.K. Hancock Building (43) Biology Place, Canberra, ACT 0200, Australia

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Summary

Estimates of tree age are important for making management decisions on the tree hollow resource because hollows suitable for fauna occur with greater frequency in older trees. The methods used to age trees vary with the practicalities of obtaining wood samples and the quality of the wood samples available. Ring counting is commonly used on smaller sample sizes when complete wood samples are available. When wood samples are incomplete, a combination of ring counting and extrapolation is often used. When no wood samples are obtained, growth models are generally used to estimate tree age. This paper uses all three methods, including three different growth models, to examine the accuracy of ageing trees. Simple regressions between tree age and diameter at breast height (over bark, dbh) provided the most accurate growth models at a site. Age estimates obtained from such models, however, had unacceptably large errors when few trees were used or when variable growth rates occurred. Under these circumstances, smaller errors margins were obtained from using a model based on tree dbh and site attributes than when averaging growth rates across sites. The estimated error in tree age estimates when using ring counting and extrapolation was about 10% of the tree age. The error of extrapolation increased with the amount of wood sample that was missing. Error margins were large for the oldest trees (average ±42.4 y for trees >350 y old) but less than ±15 y for most (73%) of the trees estimated to be 100–300 y of age. These middle-aged trees are often the most useful to study when examining the rate of hollow production in eucalypts. Therefore, age estimates acquired in this way are generally accurate enough to be useful for making management decisions regarding the tree-hollow resource in production forests.

Keywords: age; accuracy; habitats; growth rings; growth models; regression analysis; *Eucalyptus obliqua*

Introduction

Tree hollows provide important habitat for fauna (Gibbons and Lindenmayer 2002) and older trees are more likely to contain hollows (Mackowski 1987; Whitford 2002). The time required for a hollow suitable for faunal use to form (150 y: Mackowski 1987; 165 y: Wormington and Lamb 1999; 130 y: Whitford and Williams 2002) is substantially longer than the 60–120 y generally planned between harvesting operations in production forests (Whiteley 1999; Department of Natural Resources and Environment 2002a,b). Management of the hollow resource in production forest areas therefore requires an understanding of the age at which trees in different areas produce hollows suitable for use by animals.

Trees can be aged according to the disturbance history of a site (Bradshaw and Rayner 1997b), by radiocarbon dating (Turner 1984), by tree ring counting (Banks 1997) or by using tree ring counts or tree diameter increment data to produce growth models (Lloyd and Lau 1986; Wormington and Lamb 1999; Gibbons *et al.* 2000; Moloney *et al.* 2002). The accuracy of tree age estimates can potentially influence the effectiveness of management prescriptions. For example, if there are large error margins and the average values are adopted by managers, hollows may be thought to occur in trees retained in harvested areas when they do not. It is therefore important to select an appropriate method for estimating tree age and to assess the accuracy of the technique used.

Ring counting relies on the assumption that seasonal variation in growth conditions affects the density or size of the cells accumulated. Darker latewood bands can form when cold temperatures or moisture deficit cause seasonal periods of slower growth (Pilcher and Gray 1982; Leal *et al.* 2004), but can also result from defoliation by grazers and fire (Mazanec 1968; Mucha 1979). Consequently, their production is not always strictly annual, with some rings being locally absent, or 'false' rings being produced. The rate of false ring production can vary with the dominance status of the tree (Mucha 1979; Brookhouse 1997; Masiokas and Villaba 2004; Bar *et al.* 2006). Locally absent or 'missing' rings occur most frequently on trees that are old, suppressed, have poor crown development and in areas where environmental stresses are high (Brookhouse 1997; Lorimer *et al.* 1999; Jonsson *et al.* 2002; Bar *et al.* 2006; Waring and O'Hara 2006; Mayfield *et al.* 2007; but see Rozas 2003). The annualarity of tree rings is usually assessed by cross-dating patterns of tree ring width, distinct rings or markings either between trees or with known disturbance events (Yamaguchi 1991; Rayner 1992; Brookhouse 1997; Brookhouse and Brack 2006).

In eucalypts, the latewood bands often lack clear definition (Brookhouse 1997) and older trees frequently have a rotten or hollow middle. However, annual patterns in cell structure and therefore growth rings have been observed in a range of areas for a number of species (Mucha 1979; Akeroyd *et al.* 2002; Leal *et al.* 2004; Brookhouse and Brack 2006). The number of rings in the hollow middle is usually estimated using the size of the rings found in the solid wood (Rose 1993; Woodgate *et al.* 1994; Alcorn *et al.* 2001). Tasmanian old-growth *E. obliqua* with hollow centres were aged in this way and estimated to have an error of about 15%, although how this figure was obtained is not specified (Alcorn *et al.* 2001). Woodgate *et al.* (1994) used two mature trees with a solid centre to estimate the upper and lower age limits of the hollow middle in three other trees at the same site. The error margins ranged between 13 and 17 y for trees estimated to be 137–237 y old. Ageing eucalypts can also be complicated by swelling in the base of some old trees, or 'butt swell'. This swelling may occur asymmetrically to form 'buttresses'. Expansion of the growth rings can occur at the buttresses, with compression of the rings in the areas between (Koch, *pers. obs.*). Trees exhibiting butt swell will have a disproportionately large diameter at breast height (dbh) than trees of similar age without this feature, potentially biasing age estimates based on dbh. Estimating the age of the tree at a point above the swelling is one solution to this issue (Walshe 2001).

Growth models are a widely used tree-ageing technique. Known tree ages, growth rates or tree increment widths are used to make an estimate of tree age based on dbh (Bowman and Kirkpatrick 1984; Bradshaw and Rayner 1997a; Gibbons *et al*. 2000). Growth rates can vary with a number of factors, including tree age, dominance and species, environmental factors, site quality, tree density, management practices and insect attack (Mucha 1979; Rose 1993; Cherubini *et al.* 1998; Wormington and Lamb 1999; Leal *et al.* 2004; Bar *et al.* 2006; Mayfield *et al.* 2007). Therefore, while linear models can be used (e.g. Bradshaw and Rayner 1997a; Gibbons *et al*. 2000), non-linear models may be more appropriate in some areas (Abbott and Loneragan 1983, Walshe 2001). Caution is often advised when using growth models (Abbott and Loneragan 1983; Rose 1993), but few studies examine the error associated with their age estimates. Some papers using ring-width data to produce growth models indicate the error of these widths, but do not indicate the error of the resulting age estimate (Abbott and Loneragan 1983; Rose 1993). Lindenmayer *et al*. (1999) checked the accuracy of their age estimates against independent fire mapping, but did not report an error.

The aims of this paper are to develop an appropriate growth model for estimating the age of *Eucalyptus obliqua* L'Herit. trees in Tasmania and to develop methods for approximating the error of age estimates when using either ring counting and extrapolation or a growth model. Error estimates are measured using several techniques, but all are a measure or indication of the accuracy of the tree ageing process.

Methods

Site selection and data collection

Thirty-eight forestry coupes in mature wet or dry *E. obliqua* forest were examined between January 2004 and May 2005 (18 dry sites, 8 damp sites and 12 wet sites; Fig. 1, Table 1). Sites were selected on the basis of an impending logging operation and included previously harvested and unharvested areas. Site altitude ranged from 60 to 560 m above sea level. A wide range of aspects, topographies and soil types were included. The specific location examined at each site was determined by the forest contractor according to logistical constraints. The first tree encountered of a suitable size (at least 50 cm dbh over bark) was examined. The nearest neighbour with a dbh of at least 50 cm that was at least 20 m from all other trees was then selected until 11–13 trees had been examined. Tree and site variables were obtained on site and remotely (Table 1). The trees were felled as part of normal forestry operations and a slice of wood was cut from the stump of 329 trees (between four and twelve trees per site). The average stump height was 77 cm (±30 s.d.). Where possible, wood samples were cut from an area of the stump with clear rings and solid wood that was as close as possible to the centre. All samples were planed and sanded as required (using up to 1000 grit sandpaper) for clear identification of tree rings. Tree rings were identified by the denser and darker coloured 'reverse latewood' bands that have been shown to be roughly annual in *E. obliqua* in a similar climate in Victoria (Brookhouse and Brack 2006). The number of tree rings was counted on one radius for each sample. Additional counts were prohibited by the small size of the wood

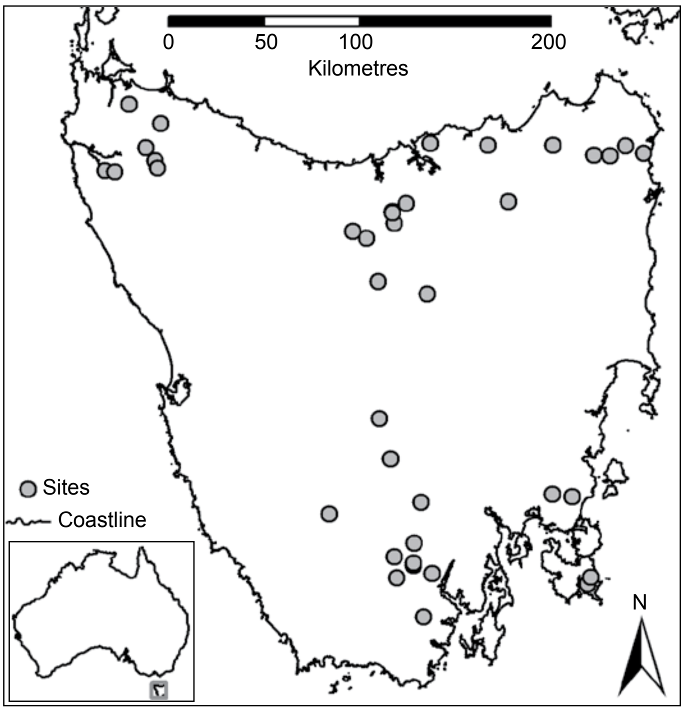

Figure 1. Location of study sites in Tasmania, Australia

Table 1. Tree and site attributes measured

Site and tree attributes	Description
Dbh	Tree diameter at breast height (1.3 m) over bark measured using a diameter tape (cm)
Tree shape	A classification of the shape of a tree, based on definitions by Smith and Lindenmayer (1988): (1) tree with full round crown; (2) mature tree with large branching; (3) mature tree with dead branches; (4) mature tree with dead top but big crown; (5) mature tree with dead top and small crown.
Crown class	The relative dominance of each tree was categorised as: (1) dominant; (2) co-dominant; (3) sub-dominant or suppressed.
Tree height	The height of the tree was measured after felling (m).
Burn damage	The burn damage of the tree was assessed as: (0) no evidence of fire; (1) bark damage; (2) wood exposed and damaged by fire; (3) severe fire damage where the base of the tree forms a bridge.
Tree species	Tree species was determined.
Forest type	The forest type was determined using the RFA classification available from the *Forest Botany Manual* (Forest Practices Authority 2005) and then reduced to the classes: Dry: (DRY hOB) understorey dominated by bracken or low shrubs; Damp (DRY shOB) understorey dominated by shrubs over 2 m, often including broad-leaved species; Wet: (WET all types) understorey dominated by broad-leaved species.
Eastings	A GPS was used to determine the eastings of the sites in GDA. Values were confirmed using a map of the area.
Northings	A GPS was used to determine northings of the sites in GDA. Values were confirmed using a map of the area.
Aspect	A compass was used to determine the direction directly downslope. The aspects were divided into four categories (N, S, E, W).
Altitude	A GPS was used to determine the altitude of the sites (m). Values were confirmed using a map of the area.
Topography	The average topography of the site was categorised as: (1) ridge; (2) upper slope; (3) mid-slope; (4) lower slope or gully.
Slope	A clinometer was used to determine the slope of the site in degrees.
Rock	Parent rock type of the substrate; this was obtained from the plans developed for the harvesting of the coupe (Forest Practices Plans) and was classified as: (1) granite; (2) dolerite; (3) sediment.
Soil type	Soil type as obtained from Forest Practices Plans; this was classified as: (1) loamy; (2) clayey; (3) sandy.
Soil pH	Four soil samples were collected from the top 10 cm. The samples were mixed and the pH was measured using a probe in a 1:5 soil: distilled water solution.
Soil nitrogen	Soil was air-dried, ground, sieved and measured for total nitrogen using the Kjeldahl method (Jackson 1964).
Soil phosphorus	As for soil nitrogen, but measured for extractable phosphorus using the Bray and Kurtz method (Jackson 1964).
Stand age	Categorised according to the information from the photographic interpretation (PI) of the vegetation age structure within each plot (obtained from Forestry Tasmania's concise PI type maps): (1) mature; (2) mature with regrowth; (3) regrowth with mature; (4) regrowth.
Stand height	Categorised according to the information from the photographic interpretation (PI) of the vegetation age structure within each plot into: (0) unknown; (1) 20 m; (2) 30 m (3) 37 m; and (4) 50 m.
Average temperature	Annual mean temperature values obtained from ESOCLIM (McMahon *et al.* 1995) using data on the latitude, longitude and altitude of the site.
Rain	Annual mean precipitation values obtained from ESOCLIM using data on the latitude, longitude and altitude of the site.
Radiation	Annual mean radiation values obtained from ESOCLIM using data on the latitude, longitude and altitude of the site.

sample generally obtained. Terminology used in this paper and specific to it is defined in Table 2.

Method for estimating tree age

For each wood sample, the number of rings counted, the length of the sample and an estimate of the distance missing on that radius to the central ring of the tree was recorded. Often the middle of the tree could be seen when cutting the sample, but it was not possible to include it because of rot or because the distance was greater than the bar of the chainsaw. In such cases the missing distance of the radius could be measured accurately. When trees were hollow in the middle, the missing distance was estimated as best as possible based on the curvature of the rings that were visible. The 70 samples that contained the tree centre will be referred to as 'complete samples'. The other 259 samples with a section missing will be referred to as 'incomplete samples'. The distance between every ten rings was measured from the inside out to determine ring width or 'decadal increments' (Table 2). For each tree, the length of the radius was plotted against the number of 'decadal increments' and a regression line was fitted that passed through the origin. The slope of this relationship, from now referred to as the 'Increment Formula', ranged between 0.09 and 1.05. For incomplete samples, the increment formula was used to estimate the number of rings likely to have occurred in the missing section of wood. Tree ages estimated using this technique are referred to as ring count and extrapolation ages (RCAE ages) (Table 2). No account was taken of the time taken for the tree to reach the height at which the wood slice was cut or of the difference in age between stump height and breast height. Alcorn *et al.* (2001) estimated that *E. obliqua* trees grow to 0.3–0.5 m by age 1 y in wet forest in south-western Tasmania. We deemed this error to be sufficiently small for the purpose of this study to be disregarded.

We considered several sources of error when estimating the age of trees (Fig. 2). When a wood sample is available there is error from tree ring counting and from extrapolating the number of rings on the missing centre of a tree. When no wood sample is available for a tree, a growth model may be constructed from trees at the same site or from trees at another similar site. The accuracy of the age estimate will depend on the location of the trees from which the growth model is constructed.

Error in ring counts

Although tree rings are assumed to be annual in this study, false rings, missing rings or observer error can affect the accuracy of ring counts. Greater error is expected for workers unfamiliar with eucalypt growth rings (Mucha 1979). To assess the accuracy of the ring counter in this paper, the rings of 16 *E. obliqua* samples were counted by Koch and two other experienced counters. There was an average difference of 7% (4.5 s.d., maximum 17.8, minimum 1) between the number of rings counted by Koch and the first experienced ring counter and an average of 16% (16.2 s.d., maximum 55.6, minimum 1.2) with the second. Ring counts made by Koch were consistently higher than that of the first experienced ring counter but were evenly distributed above and below the counts of the second experienced ring counter (Fig. 3). However, the difference between the two experienced ring counters was an average of 16% (maximum 60), suggesting the senior author of this paper was as accurate as other experienced counters. Differences in counts did not appear to be related to tree age and are more likely to have been influenced by ring clarity (Fig. 3).

Ring count error can be estimated by comparing the estimated age with known disturbance events. It was not possible to accurately cross-date the tree ages in this study (see Appendix 1). We therefore adopt the error rates estimated by Brookhouse (1997), who used the same tree species growing in similar climatic conditions on mainland Australia. Brookhouse (1997) found that ring counts over-estimated tree age by 3% in co-dominant, 7% in dominant and 8% in suppressed trees.

Error in extrapolating

For incomplete wood samples, the number of rings on the missing distance of wood was estimated by fitting a straight line to the growth increment data and extrapolating it back to the origin. Extrapolation using a quadratic function was also examined but the difference in R^2 value between the two fits was on average 0.0129 (s.d. 0.0189, maximum 0.124) and was not significantly related to any tree variable examined. However, the increment formulas were significantly associated with tree age and shape ($P < 0.05$), suggesting a deceleration in dbh growth rates with increasing age and senescence. Some trees showed accelerating

Table 2. Definitions of terms used throughout the text

Term	Definition	Sampling details
RCAE method	The method for estimating tree age, where ring counts are done and the age of the missing stem centre is estimated using linear extrapolation.	
RCAE age	The age of the tree as estimated using the RCAE method.	RCAE ages were estimated for 329 samples. Between 4 and 12 samples were examined for each of 38 sites.
Decadal increments	The distance between every ten rings on a wood sample.	
Increment formulas	The slope of the fitted line between the radius and the number of rings for each tree, used to extrapolate the age of the missing stem centre.	Three hundred and twenty-nine increment formulas were constructed. Between 4 and 40 decadal increments were used to construct each formula.
Extrapolation error model	The model predicting the absolute percentage error in tree age based on the percentage of wood sample that was missing.	Six wood samples from dry forest that were not used in any other part of the current study were used to construct this model.
Site formulas	The models predicting tree age, produced from Bayesian regression analysis between the tree diameter and estimated age for all trees at a site.	Thirty-eight site formulas were constructed. Between 4 and 12 trees were used to construct the formula for each site.
Overall formula	The model predicting age of a tree produced from Bayesian regression analysis between the tree diameter and estimated age for all trees combined.	Three hundred and four samples were used to construct this model.
Predictive model	A growth model predicting the age of a tree produced by Bayesian regression model between the RCAE age of a tree and site and tree variables.	Three hundred and four samples were used to construct this model.

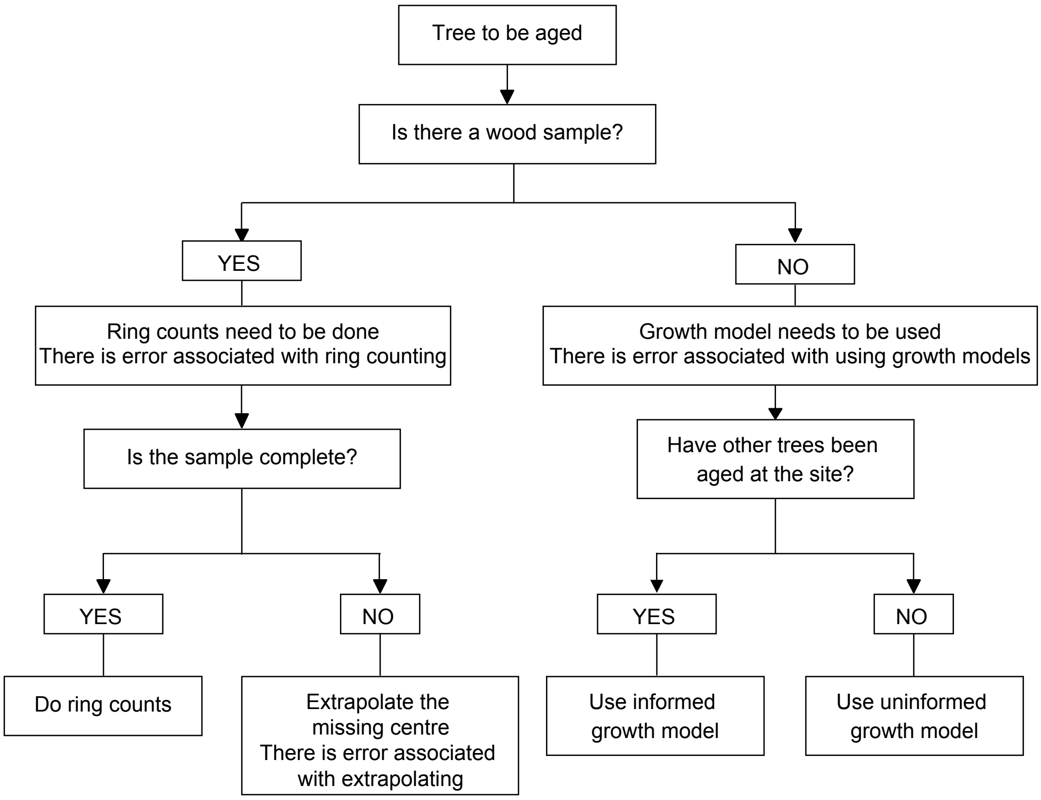

Figure 2. A schematic diagram illustrating how the age of a tree is determined and the associated error. The 'informed' growth model means that information is available on the growth rate of trees at the site and 'uninformed' means that no such information is available and the average growth rate across all sites is used.

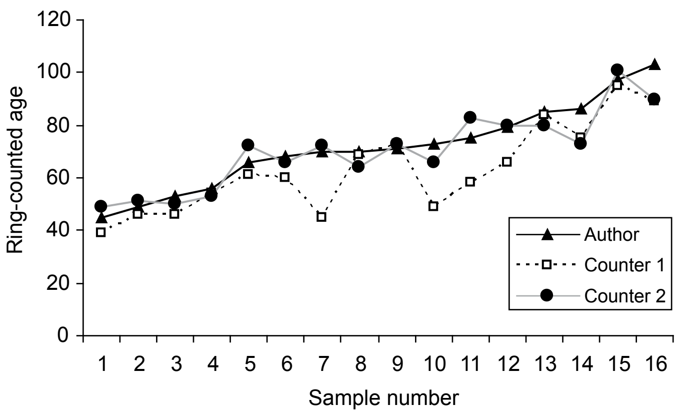

Figure 3. Comparing the results of ring counting by the senior author of this paper to those of two other experienced ring counters on 16 samples of *E. obliqua.*

growth rates, some decelerating and others a combination of the two, which made the uniform application of a decelerating function inappropriate. Visual examination of the growth rates revealed no consistent trend within sites. In the vast majority of cases a straight line was an adequate (and often more appropriate) fit for the data than a quadratic curve. No significant association was found between the increment formulas and tree dominance ($P > 0.05$).

The data collected for the present study could not be used to establish the error of extrapolation because the complete samples collected were not from older trees. Consequently, data collected from another source in dry forest in eastern Tasmania was used (von Platen, unpublished). The sites were similar to dry forest sites we examined in eastern Tasmania. The relevance this information has to wet forest is uncertain, but no similar information was available for wetter forests. Six slabs were cut from large, complete *E. obliqua* tree stumps (Table 3). A high-resolution photograph was taken of each sanded slab and a computer program used to identify growth rings, which were verified either by Koch or von Platen. Von Platen (University of Tasmania, *pers. comm.*, 2008) examined these slabs in more detail and found that ring counting resulted in an error of plus or minus six rings over an entire radius which was not cumulative. We recorded the age of each tree (number of growth rings) and the distance between every ten rings. We then 'removed' ten rings at a time and the number of rings in the 'absent' area was estimated using linear extrapolation, as outlined above, to give a series of new RCAE ages. Linear regression analysis was done using SPSS (2005). The dependent variable was the absolute percentage difference between the original ring counted age and the new RCAE age. The independent variable was the percentage of sample removed. The resulting regression model will be referred to as the extrapolation error model (Table 2). This model predicts the percentage error in age estimation associated with extrapolation according to the percentage of the wood sample that was missing. We multiplied the RCAE age by the percentage error predicted to obtain an estimate of extrapolation error in years for each tree we studied. The extrapolation error was added to the ring count error (see above) to estimate total error for the RCAE Method.

Growth models and associated error

Modelling the influence of site and tree variables on growth rates

To identify the most important variables influencing the growth rate of individual trees, Bayesian linear modelling with uninformative priors was done in WinBUGS 1.4 (Spiegelhalter *et al*. 2003). The 25 trees with an RCAE age greater than 400 y were not included as the ages of these trees may have been erroneous (see discussion), leaving a sample size of 304 trees. The dependent variable was the RCAE age of the tree, square-root transformed. The independent variables considered are outlined in Table 1. All continuous variables were standardised to reduce autocorrelation between successive samples (i.e. the mean was subtracted from the data, which was then divided by the standard deviation). Variables were entered into the model in a forward stepwise manner. The initial 1000 samples were discarded as a 'burn in' and the following 10 000 samples were used to calculate the Deviance Information Criterion (DIC). A difference in DIC value of less than two indicates a lack of difference in the models, while a difference of three or more indicates that the model with the smaller DIC value is increasingly superior (McCarthy 2007). Bayesian methods were used because they allow complex correlation structures (such as hierarchical models) to be easily modelled. The variable 'site number' was added as a random factor to determine the unexplained variation between sites. For the final model (excluding site number), 100 000 samples were used to calculate the mean, standard deviation, 2.5th and 97.5th percentiles of the coefficients. The percentiles represent a 95% Bayesian credible interval. The residuals (observed value minus predicted value) were examined to assess the fit of the model. The results of this model were used to produce the 'predictive model', which predicts the age of a tree based on site and tree characteristics.

Tree growth rates vary between sites of different quality (Abbott and Loneragan 1983) as does the floristic composition and, therefore, the forest type category assigned to an area (Ashton 1981). To determine if a difference in growth rate was observed between the broad forest types considered here, ANOVA analysis was done using R (R Development Core Team 2006) between the slope of the increment formula and forest type. The increment formula was calculated using trees only 400 y old or less. One site was removed due to poor correspondence, leaving 18 dry sites, 8 damp and 11 wet sites in the analysis.

Table 3. Details of the trees examined for establishing error in linear extrapolation

Tree number	Ring count	Sample radius (cm)	Tree dbh (cm)
1	220	62.6	140
2	270	57.4	125
3	230	55.9	165
4	221	64.3	130
5	155	46.0	120
6	146	32.6	100

Examining alternative growth models

The predictive model is one way of estimating tree age. Many growth models, however, use only dbh to predict tree age (e.g. Bradshaw and Rayner 1997a; Gibbons *et al.* 2000). Consequently, Bayesian regression analysis was done between tree age and dbh for all trees with an RCAE age of 400 y or less, to produce the 'overall formula', and for the trees within a site, to produce a series of 'site formulas' (Table 2). The three growth models (predictive, overall and site models) were used to predict the age of all trees. The accuracy of the models was examined in three ways. Firstly the percentage of trees where the RCAE age fell within one standard deviation of the predicted age was determined. Then the RCAE age was regressed against the predicted age for each model and the slope coefficient and adjusted R^2 values of the relationship were examined. Finally the error of the predictions was inspected by visually examining the relationship between the standard deviation and predicted age of each tree. The same data were used to produce and test the growth models to maximise the data available for model construction. Ideally, a new data set should have been used to verify the accuracy of these models.

Results

Ring counts and linear extrapolation

When extrapolation methods were used to account for a 'missing' length of wood, the error of the age estimate increased with the percentage of wood sample removed. The age estimated from the modified wood sample was not consistently greater than or less than the age as determined by ring counting alone until about 70% of the sample was removed. When more than 70% of the sample was removed there appeared to be greater inaccuracy in the age estimate for most trees, with ages being overestimated more than underestimated. The relationship between the absolute percentage change in age estimate and the percentage of sample missing was roughly linear (Fig. 4). The model showed a reasonable fit (average difference between predicted and ring counted age was 3.15 y), but the 95% confidence intervals showed a lack of precision in the results.

The error of the RCAE method was determined for each tree and was, on average, about 10% of the estimated tree age (Fig. 5). The maximum error rate for the trees examined was ± 80 y but for most trees (88%) the error was ± 30 y or less.

Growth models and associated error

Modelling the influence of site and tree variables on growth rates

When using site and tree variables, the best model predicting tree age included tree dbh, soil phosphorus, average temperature

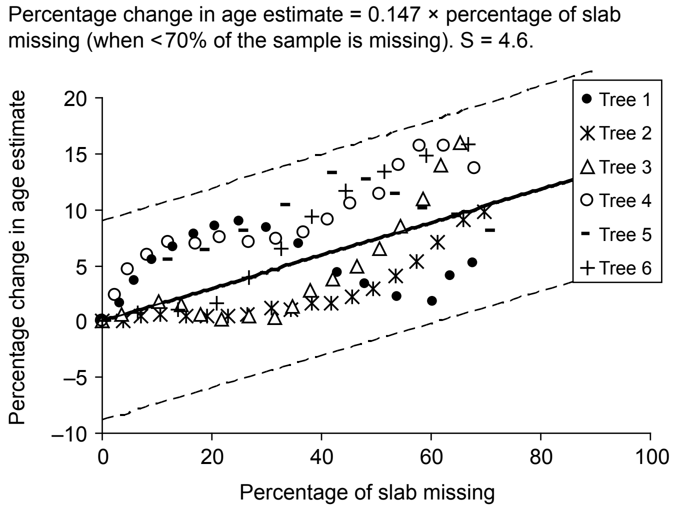

Figure 4. The absolute difference in age estimate, expressed as a percentage of the age of the tree, in relation to the percentage of the sample that was removed. The points are the data used to create the model and the lines are the mean and 95% confidence interval of the predictive model. S is the standard deviation of the model. A maximum of 70% of the sample was removed because beyond this point there was a marked change in error.

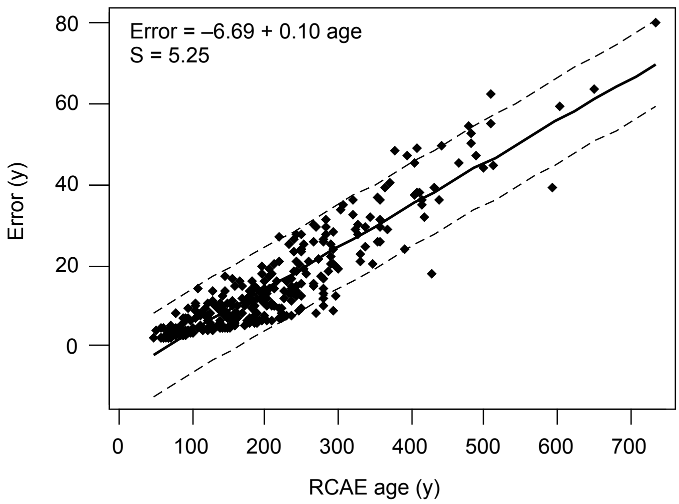

Figure 5. The error (in years) of each estimate of tree age in relation to the RCAE (ring count and extrapolation) age of the tree ($n = 329$). The line is the result of the regression between the RCAE age and error in the estimate. The dashed lines are the 95% confidence intervals of the data. The equation for the solid line is displayed above. S is the standard deviation in the data.

and stand age classification (Table 4). The stand age categories 'regrowth' and 'regrowth with mature' were combined into one category which will be referred to as simply 'regrowth'. The negative relationships with the variables other than dbh mean that trees have faster growth rates and so are younger for the same size. If the random factor 'site' was included, there was a decrease in DIC value of 36 units, indicating there was unexplained variation between sites. However, as the model is to be used for predictive purposes, the coefficients are indicated for a model excluding the random factor. The WinBUGS code for this model is provided in Appendix 2 or can be obtained from the authors. Examination of the residuals indicated that trees younger than 120 y were likely to be over-estimated and trees older than 250 y to be underestimated in age when using the predictive model. The average absolute residual was 45.3 ± 35.4 s.d., indicating low levels of accuracy.

After removal of the site with extremely poor fit, there was a significant difference in growth rate between the different forest types ($F = 3.42$, $P = 0.045$, df = 2). The difference was significant only between dry forest and the others, but there was a large amount of overlap (Fig. 6). The mean and standard deviation of the Increment Formulas was 0.453 ± 0.09 for dry forest, 0.354 ± 0.13 for damp forest and 0.383 ± 0.09 for wet forest. If these values are used to estimate the age of a tree about 100 cm

Table 4. Coefficients (mean, standard deviation, 2.5th and 97.5th percentile) of the explanatory variables included in the best Bayesian linear model for predicting tree age using only trees with an RCAE age of 400 y or less ($n = 299$)

Variable	Mean	s.d.	2.5%	97.5%	DIC[A]
Intercept	14.470	0.204	14.070	14.870	1538
Dbh	2.635	0.170	2.309	2.966	1379
Mature	0				1344
Mature with regrowth	–1.069	0.327	–1.705	–0.436	
Regrowth[B]	–1.983	0.294	–2.565	–1.403	
Soil phosphorus	–0.762	0.142	–1.043	–0.493	1332
Average temperature	–0.602	0.142	–0.877	–0.324	1316

[A]DIC values are the Bayesian equivalent of an AIC value to indicate progressive model improvement by addition of each new variable
[B]Regrowth includes the stand age categories 'regrowth with mature trees', and 'regrowth'

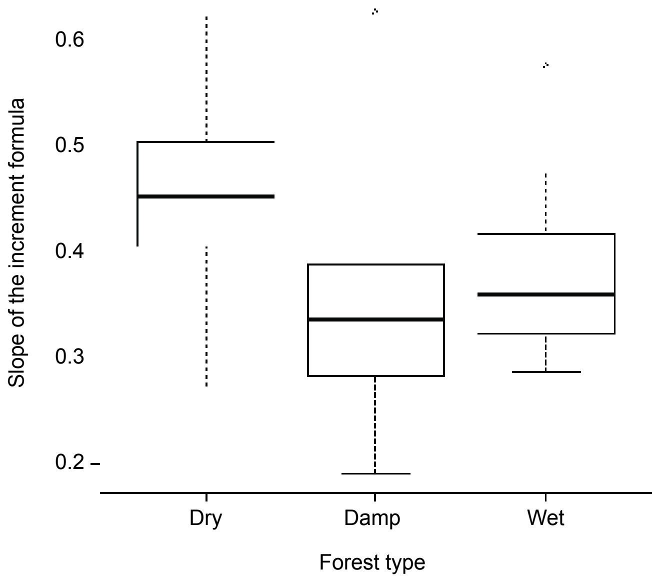

Figure 6. The relationship between tree growth rates (the slope of the increment formula) and forest type. The box length is the interquartile range. The circles are outliers with values between 1.5 and 3 box lengths from the upper edge of the box.

in dbh (i.e. around 500 mm in radius), the ages produced are: 226.5 ± 45 y for dry forest, 177 ± 64 y for damp forest and 192 ± 43 y for wet forest.

Examining alternative growth models

A higher percentage of trees had the RCAE age within one standard deviation of the predicted age when using the predictive model and overall formula than for the site formulas (Table 5). However, the regression of predicted age against RCAE age had a greater R^2 value for the site formulas. The slopes of the site formulas ranged from 0.99 to 2.83. The relationship between the RCAE and predicted age had a slope coefficient closer to one for the site formulas than for either the predictive model or overall formula (Fig. 7), but the error of the predictions varied greatly between sites (Fig. 8b). The variability in error magnitude was related to the number of samples obtained and the strength and linearity of the relationship between tree dbh and age at a site. Therefore, the site formulas provided accurate and precise estimates of tree age, but only when sufficient samples were used to construct the formula. The number of samples required depended on the strength of the linear association between tree age and dbh at the site.

When no information on growth rates is available at a site, a choice between the predictive model and the overall formula needs to be made. The two alternatives had a similar percentage of trees whose RCAE age lay within one standard deviation of the predicted age. However, the R^2 value of the association between RCAE age and predicted age was higher for the predictive model (Table 5). In addition, the slope coefficient of the relationship between RCAE and predicted age was slightly lower for the overall model than for the predictive model (Fig. 7), indicating slightly inferior accuracy. The overall formula was calculated by regressing RCAE age against tree dbh for all trees combined, so a constant error rate of about 76 y was predicted across all tree ages (Fig. 8c). This error margin is larger than that of the predictive model until trees reach about 300 y. Larger error margins means the RCAE age has a greater likelihood of lying within one standard deviation of the predicted age, but results are less precise. It therefore seems that when no site specific information on growth rate is available, the predictive model is the superior choice. The predictions made by the predictive model were relatively well correlated with RCAE age (Table 5, Fig. 7a) and the error margins were flexible, increasing with estimated tree age (Fig. 8a). The relationship between tree age and error for the predictive model was: error = 0.153age + 30.4.

Table 5. Comparing the accuracy of the growth models

Method	Fraction of trees within one standard deviation[A] (%)	Adjusted R^2 of regression with RCAE age[B]
Predictive model	67.8	0.642
Site formulas	84.2	0.699
Overall formula	74.5	0.426

[A]The percentage of trees whose RCAE (ring count and extrapolation) age was found to lie within one standard deviation of the predicted age for the three growth models considered (n = 329)

[B]The adjusted R^2 value of the regression analysis between the predicted results from the growth models and the RCAE age

Discussion

Two main methods for ageing trees were examined in this study, ring counting with extrapolation and growth models. For the first method, error can be associated with both the ring counting and the extrapolation. Only the second source of error could be examined in this study due to a lack of precise information on disturbance history which prevented cross-dating. Ring counting

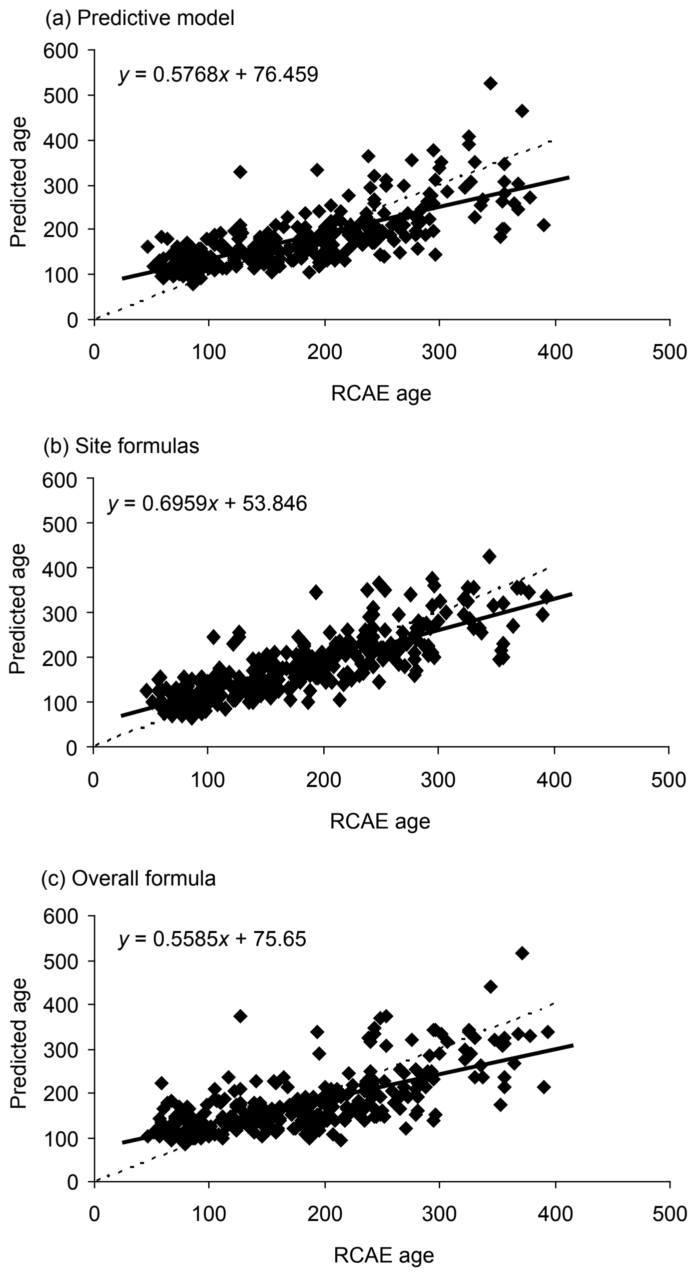

Figure 7. The predicted age of each tree plotted against the RCAE (ring count and extrapolation) age of that tree using (a) the predictive model; (b) the site formulas; and (c) the overall formula. The solid line is the result of the regression between the RCAE age and predicted age. The dashed line indicates perfect correspondence between predicted and RCAE age, where the slope of the line is equal to one.

error was estimated using work by Brookhouse (1997). The error resulting from extrapolating was estimated at about 15% of the proportion of the wood sample that was missing. This held true until about 70% of the wood sample was removed, when the error rates showed a less consistent pattern. The extrapolation error was added to the ring counting error and the total error was estimated to increase linearly with estimated tree age at a rate of roughly 10%.

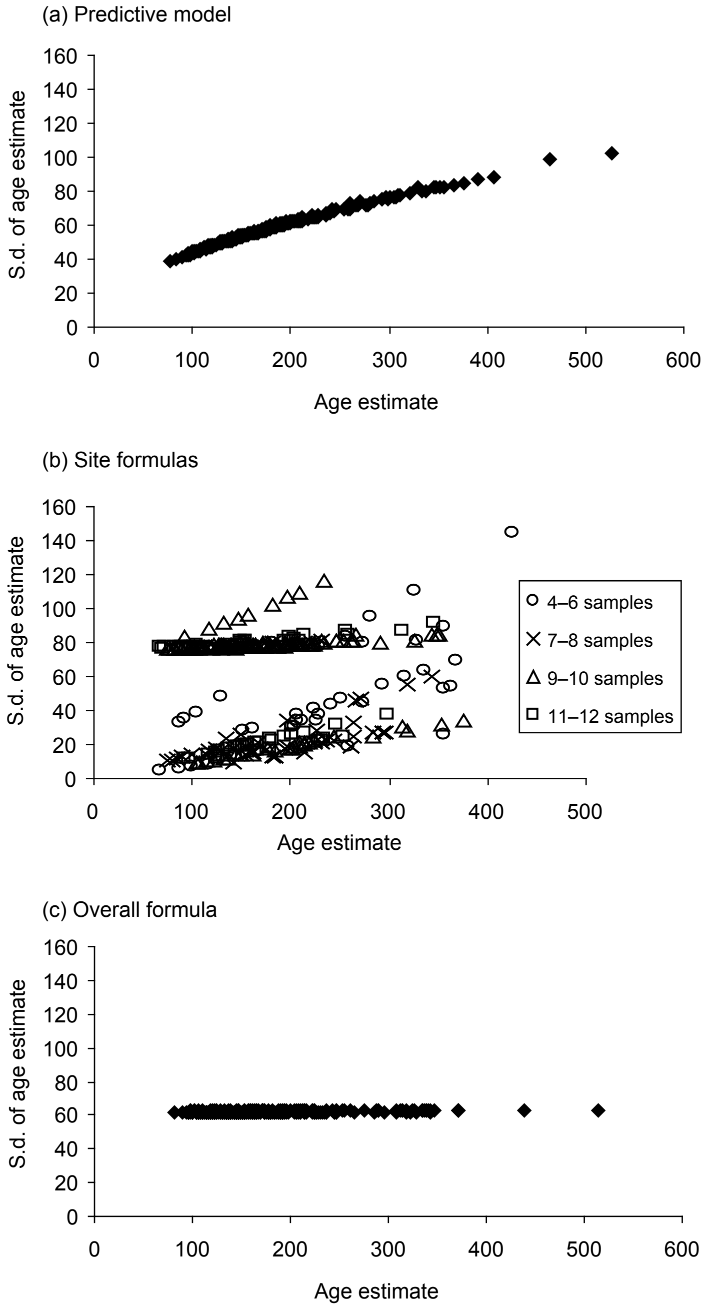

Figure 8. The standard deviation of the age estimate in relation to estimated age for all trees when using (a) the predictive model (b) the site formulas and (c) the overall formula. The different symbols in (b) indicate the number of wood samples that were used to establish the site formula.

Other studies have found that accurate age estimates can be obtained for most trees, but substantial error can occur. Banks (1990) cross-dated several eucalypt species and found that the greatest inaccuracy of ring counting was only a few years. Banks (1993) cross-dated radii and estimated the error of ring counting in *Eucalyptus regnans* F.Muell. from the Central Highlands of Victoria to be 2%. Banks (1982) examined the rings of *E. pauciflora* Sieb. ex Spreng. in alpine NSW and found most ages were accurate, although some large discrepancies occurred. For example, ring counts ranged between 24 and 50 on one tree due to some compression in the wood. Banks (1997) also found variable accuracy when using radiocarbon dating to check ring counts. Two trees estimated by ring counting to be 170 and 130 y old showed reasonable accuracy, with radiocarbon dating estimating the trees to be between 116 and 176 y old. However, for one tree the radiocarbon dated age was double the estimated ring count age due to indistinct outer rings (ring count age: 160; radiocarbon dated age 354 ± 30). Because radiocarbon dating and cross-dating were not available in the present study, a different technique was used to assess the accuracy of tree age estimates. The error rates estimated were relatively high. The trees we used were not selected for ring clarity or soundness of wood and the frequent use of extrapolation to cater for incomplete samples may have influenced ring count accuracy. The length of the missing section and the accuracy with which this length is measured has been shown to have a large influence on tree age estimation accuracy (Rozas 2003).

The estimates of tree age and associated error in the current study are believed to be appropriate for most trees, but the error may be underestimated for the older and larger trees for several reasons. Firstly, the error rate of ring counting was obtained for trees less than 100 cm in dbh (Brookhouse 1997). Many of the trees we examined were larger than 100 cm and ring counting can become more difficult in older trees (Banks 1982). Secondly, a linear extrapolation was used to estimate the age of the missing wood sample, despite the knowledge that trees often decrease in growth rate and produce narrower rings as they age (Rayner 1992; Banks 1993; but see Bradshaw and Rayner 1997b). Thirdly, when just a small amount of wood was available for ring counting, which occurred most often in older trees, only the outer rings could be used to determine the extrapolation slope (increment formula). The accuracy of the tree age estimate was found to decrease as the proportion of wood sample available diminished, and was extremely inaccurate if more than 70% of the wood sample was missing. As these outer rings were formed during a period of reduced growth, the process of linear extrapolation is likely to overestimate the age of the older and larger trees. Fourthly, the model estimating the extrapolation error was produced from only six trees. While they were relatively large trees (maximum dbh 165 cm), they were smaller than the biggest trees used in this study. It is uncertain if this model provides accurate error estimates for larger trees. Finally, excessive error is likely to have occurred in trees exhibiting butt swell (which occurs mostly in older stands), and the magnitude of the butt swell increases with stem size (Walshe 2001). Therefore, while the ages and associated errors are assumed to be reasonable for most trees, there is reason to suspect that this study underestimates the error in age estimates for the largest and oldest trees. Twenty-five trees were estimated to be between 400 and 735 y old with an average dbh of 188 cm

±67 s.d. Fourteen of these older trees did not include 400 y within the error margins. Butt swell and or buttressing was noted in 13 of these 25 trees which would have increased the error of the age estimates. Excessive error in these trees may also have occurred when a very small proportion of the radius was examined (four trees) or the rings were especially difficult to count (three trees). For three trees no reason for excessive error could be found and for the other two trees the size and condition of the stump suggested that the ages were appropriate (415 ± 35 y and 438 ± 36 y). These 25 trees were removed from growth model construction due to the potentially greater error in the estimation of tree age.

Tree growth rates were related to tree dbh and a number of site-level variables: soil phosphorus, average temperature of the site and stand age. Trees were found to grow faster on soils with high phosphorus concentrations, on warmer sites and in younger stands. Although the broad classification of forest type was not included in the predictive model, it was found that the trees in dry forest grew significantly more slowly than trees in either damp or wet forest. This effect was expressed in the model by the inclusion of soil phosphorus levels. Higher soil phosphorus levels corresponded to an increase in forest wetness for the sites examined (Koch, unpublished data). This effect means that trees found in dry forest will be, on average, older for the same size than trees found in either damp or wet forest (for a tree 100 cm in dbh a mean difference of 36.5 y is expected with damp forest and 28.5 y with wet forest). However, there was a large degree of overlap in tree growth rates (increment formulas) between the forest types. Therefore forest type alone is not an accurate predictor of growth rate.

The variables conspicuous by their absence from the predictive model were tree shape and crown class. Other studies have shown that more senescent trees have slower growth than younger, healthier trees (Banks 1993; but see Bradshaw and Rayner 1997b). In addition, subdominant trees are less able to compete for sunlight and so are likely to have slow growth. The lack of a relationship with tree dominance may be because the data contained few suppressed trees or because some of those classified as suppressed were merely young and had not reached the canopy. However, up to 50% of annual rings can be 'missing' in suppressed trees (e.g. regrowth *E. diversicolor* F.Muell: Rayner 1992), which means that these trees may have been older than they appeared. Therefore, the age of subdominant trees may have been less accurate than estimated despite the lack of a significant influence found in the current work. In relation to tree senescence, the relationship between tree senescence and stand age was not straightforward (33.1% of trees examined had dead tops in mature forest, 20.0% in mature forest with regrowth, 10.9% in regrowth with mature forest and 36.8% in regrowth forest) meaning that stand age is not an obvious surrogate for tree senescence in the current study. Although tree shape did not contribute significantly to the growth model, it was significantly related to the slope of the increment formula. This suggests that linear extrapolation may not be appropriate for these older trees (although no single other transformation was appropriate either), and there may be an undetected decrease in growth rate with increasing senescence. While this rationale is plausible, confirmation of tree ages by cross-dating would be required to verify it.

Upon examining the predictive ability and the error rates of the three growth models, the site formulas proved to be the best for predictive purposes. The main concern with using the site formulas was that sufficient trees need to be used to create the formula, and greater error in predictions occurred when a non-linear association between tree age and dbh was present. While the predictive model proved superior to the overall model, the predictions made by all three growth models had relatively large error bounds, indicating a lack of precision in predictions. It is therefore recommended that such growth models should only be used as a rough guide when a more accurate alternative is unavailable. It should also be noted that these models need to be tested against new data in order to make a true assessment of their utility and accuracy. Gibbons *et al*. (2000) tested the accuracy of their growth model by ring counting additional trees and found that in all but three of the nineteen cases there was congruence between the age estimates.

Implications for management of tree hollows

While some studies have shown that eucalypts can form hollows at a very young age, most agree that more than 100 y is required (Ambrose 1982; Gibbons *et al.* 2000; Whitford 2002). Eucalypts, however, are unlikely to have hollows suitable for use by fauna if they are less than 120–180 y old, with large hollows being rare in eucalypts less than 220 y old (Gibbons and Lindenmayer 2002). Ambrose (1982) estimated that *E. obliqua* in Victoria commenced hollow formation at 110 y and the maximum number of cavities occurred at 430 y. In south-eastern Australia, Gibbons *et al.* (2000) found that less than 50% of *E. obliqua* and *E. fastigata* Deane and Maiden trees younger than 180 y old had hollows. Using the material documented in the present paper, Koch *et al.* (in press) found that trees needed to be at least 100 y old before forming hollows and 140 y before they were likely to contain larger hollows more suited for use by vertebrate fauna.

Although the rate of hollow occurrence increases with tree age (Mackowski 1987; Whitford 2002), we found the error of ring count and extrapolation age estimates also increased with tree age. (The error was less than ± 15 y for 73% of trees estimated to be 100–300 y of age compared to an average of ±42 y for trees >350 y). However, the higher probability of having a hollow suitable for fauna in the older trees means that making management decisions is possible despite imprecision in tree age estimates. Greater accuracy is achieved for the age at which eucalypts generally begin to produce hollows (100–200 y: Mackowski 1987; Whitford 2002). The imprecision in age estimates is likely to be small enough for the younger trees to mean that age estimates are useful when making management decisions.

Greater error is expected when using growth models compared with ring counting and extrapolation, but growth models will often be more useful because they are easily applied and non-destructive. Quantifying the error in these estimated tree ages can increase the certainty in achieving management objectives. For example, if the objective is to retain a certain number of trees with hollows, based on tree age, then the lower confidence limits of the age at which trees contain hollows can be used to select the trees. Alternatively, the rate of tree retention could be adjusted to cater for inaccuracies in tree age estimation. Taking into account the uncertainty in tree-age estimation will help ensure that most of the retained trees are above the hollow-bearing age, rather than only half of them as would result from using the mean age estimate.

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Appendix 1. Comparing tree age to disturbance history

One method for estimating the error in ring counts is to cross-date the estimated age with known disturbance events. Trees in Australia, particularly in wet forest, often regenerate after fire. Consequently, in Tasmanian wet forest there are often cohorts of trees of the same age but which vary in size (Alcorn *et al.* 2001). The trees we sampled from wet forest sites were subjectively divided into cohorts according to their RCAE ages. The ages of the trees within each cohort were averaged and, for those 100 y old or less, compared to the known disturbance in the area. The difference between the average age and the time of disturbance was estimated and we calculated the average difference as an indication of ring count accuracy. Exact dates of disturbance were unavailable so this examination is not conclusive. Four of five wet forest sites with trees less than 100 y old showed rough association with known disturbance in the area, indicating relative accuracy in tree ring counts (Table A1). The average error of all the sites was almost 10.5 y. Excluding the first site (because samples may not have been collected from all disturbance events), it is 5.3 y.

Because accurate information on disturbance events was not available, results from a study by Brookhouse (1997) were used to estimate the error in ring counting. Brookhouse (1997) examined *E. obliqua* and *E. cypellocarpa* L.Johnson trees of known age in Central Gippsland, Australia, and used cross-dated ring widths to examine error in ring counts. The results of Brookhouse (1997) were considered to be appropriate for use in the current study because the same tree species was examined, the understorey species were similar to those found in the wet forest sites considered in the present study and samples were taken from high-altitude sites (680–700 m asl) with climatic conditions similar to those of Tasmania (average minimum temperature of the coldest period 2.2 ± 1.6°C in the current study and below 5°C in Brookhouse (1997); annual rainfall 1170 ± 278 mm in the current study and averaging 1174 mm in Brookhouse (1997)).

Table A1. Examining the correspondence between the age estimated for cohorts in wet forest (where the age is below 100 y) and the approximate time of disturbance

Mean and s.d. of tree ages in cohort (y)	Number of trees in cohort	Estimated time of corresponding disturbance	Approximate error in age count
86	1	Logged in 1950s	31[A]
64.9 ± 4.5	4	Fire 1936 (69 y ago)	4.1
64.2 ± 5.2	4	Logged in 1940s (approx. 65 y ago)	0.8
78.2 ± 7.2	5	Fire about 80 y ago	1.8
84.5 ± 6.6	4	Fire 60–80 y ago	14.5

[A]Indicates poor correspondence. This may be a true indication of inaccuracy in the data or may be because no trees from that regeneration event were examined.

Appendix 2. Predictive growth model code for WinBUGS

```
Inits
list(sdtau=1,base=0, a=c(NA,0), b=c(NA,0.001),d=c(NA,
0.001,0.001,0.001,0.001), g=0.001, h=0.001)

model
{
for(i in 1:**) # replace "**" with the number of data points to
be examined
{
X[i,1] <- (dbh[i]-avdbh) / sddbh
X[i,2] <- (soilp[i]-avsoilp) / sdsoilp
X[i,3] <- (avtemp[i]-avavtemp) / sdavtemp

predage[i] <- pred[i] * pred[i]
pred[i] ~ dnorm(mean[i], tau)
mean[i] <- base + g*X[i,1] + a[stand[i]] + m*X[i,2] + n*X[i,3]
}

avdbh <- 101.39
avsoilp <- 255.55
avavtemp <- 10.41
sddbh <- 46.08
sdsoilp <- 134.54
sdavtemp <- 0.988
base ~ dnorm(14.47, sdbase)
sdbase <- 1/(0.204*0.204)
tau<-1/(sdtau*sdtau)
sdtau ~ dnorm(2.167,sdsdtau)
sdsdtau<- 1/(0.01772*0.01772)

a[1] <- 0
a[2] ~ dnorm(-1.069, sda2)
sda2 <- 1/(0.327*0.327)
a[3] ~ dnorm(-1.983, sda3)
sda3 <- 1/(0.294*0.294)

g ~ dnorm(2.635, sdg)
sdg <- 1/(0.170*0.170)
m ~ dnorm(-0.762, sdm)
sdm <- 1/(0.142*0.142)
n ~ dnorm(-0.602, sdn)
sdn <- 1/(0.142*0.142)
}
```

Data format:
Dbh [ ] soilp[ ] avtemp[ ] asp[ ] stand[ ]

Dbh, soil phosphorus and average temperature are continuous variables and aspect and stand are binary variables (Stand: 1 = mature forest; 2 = mature with regrowth, 3 = regrowth with mature or regrowth).