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Article

Modelling individual tree maximum basal area growth rates of five tall eucalypt species growing in even-aged forests

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Abstract: Inventory plot data were available providing over 87,000 individual tree basal area growth rates from even-aged native forests of three ash eucalypts (*Eucalyptus regnans*, *E. obliqua*, and *E. delegatensis*), from temperate regions, and two other species from more sub-tropical climes (*E. grandis* and *E. pilularis*). Models were developed relating maximum observed growth rates for these species in relation to tree size when, presumably, trees were under ideal environmental conditions and without competition from neighbours for site growth resources. These maximum growth rates increased with increasing tree size to a maximum of their own and then declined as tree size (hence age) increased further. The tree sizes, at which these maximum growth rates reached their maxima, were much greater for the ash eucalypts than for the other two species. It is hypothesised that the ash eucalypts may have evolved physiological characteristics that make them more efficient in compensating for the well-known physiological constraints imposed on growth rates as trees grow to great heights and ages.

Keywords: growth model; maximum growth; basal area; tree height; growth efficiency

1. Introduction

Many growth models have been developed to predict the growth rates of individual trees in forests [1,2]. One approach used commonly is to first develop a model that predicts the maximum possible growth rate (sometimes termed potential or optimum growth rate) that a tree might have in relation to its size at the time the growth is occurring [1,3]. Terms are then added to the model to predict the reductions from this maximum that are a consequence of both the particular environmental circumstances of the site on which the tree is growing, and the competitive pressures exerted on it by neighbouring trees.

The present work aimed to develop such individual tree maximum growth rate models in stem basal area for five eucalypt species growing in regions of their natural occurrence in Australia. Three of the species are part of a group commonly termed “ash” eucalypts, *Eucalyptus regnans* F. Muell., *E. obliqua* L’Hér. and *E. delegatensis* R. Baker; these grow principally in temperate regions of south-eastern Australia. The other two species, *E. grandis* W. Hill ex Maiden and *E. pilularis* Smith grow principally in sub-tropical regions along the east coast of Australia. All five species grow mainly in tall-open, even-aged forests and often in virtual monocultures. All have been of major commercial importance for timber production for many years and some have been grown in plantations both in Australia and overseas. Once the models were developed here, it was hoped they might offer useful comparisons be between the growth behaviours of the five species.

2. Methods

2.1. Data

The data used here had been collected during 1931−1989 from 280 forest plots by various Australian forestry agencies. The data for each species was obtained from regions that made up only part of the total area of natural occurrence of the species. Most plots (202) were established in regrowth forests whilst the remainder were in plantations. The plots in regrowth forest were located in even-aged stands that were essentially monospecific, with only rare inclusions of individuals of other species. Forest ages ranged over 2−118 yr at the time of measurement. Plots were rectangular or circular in shape and varied in area over the range 0.03−0.5 ha. Plots were measured 2−28 times at intervals of 0.4−5 yr. The data were collated by Mattay and West[4]. It should be appreciated that these data do not represent a formal sample of the forests concerned but were those data available immediately from the contributors over the period they were being collated (1983−1991).

At each measurement of a plot, the diameters at breast height (1.3 m) over bark of live trees were measured. For every tree that survived over a growth period between plot measurements, its basal area growth rate was determined as the change in basal area divided by the length of the growth period. This was recorded together with its basal area at the start of the period. Over all five species and all growth periods of all plots, a little over 87,000 individual tree growth rates were determined. **Table 1** summarises the data that were available for each species, together with the latitudinal and longitudinal ranges within which the plots of each species were located. Maps are available [4] showing both the regions of natural occurrence of each species and the regions from which the plots were selected. The data have been used previously to develop models relating stand stem wood volume growth to stand age and site productive capacity [5].

Table 1. Summary of data available here for each eucalypt species. Minimum−mean−maximum values are shown where appropriate

Variable	***E. regnans***	***E. obliqua***	***E. delegatensis***	***E. grandis***	***E. pilularis***
Number of plots	31	102	26	25	96
Latitudinal range (°S)	39−43	39−43	41−43	26−27	26−29
Longitudinal range (°E)	146−148	145−148	146−148	152−153	152−153
Ages of measurement (yr)	10−31−85	6−47−118	9−31−83	2−23−52	2−28−63
[1] Stand stocking density (stems ha^{-1}) $\times 10^2$	1.1−13.7−33.3	0.5−6.1−22.6	3.4−13.2−132.3	0.8−3.7−10.8	0.6−3.7−20.1
[1] Stand basal area (m^2 ha^{-1})	5−41−75	1−41−76	8−31−79	4−21−40	0.1−22−70
[1,2] Total number of individual trees	12,422	24,060	4,608	10,123	35,876
[1,2] Tree diameter at breast height (cm)	1−23−131	1−32−118	0.4−20−82	1−27−82	0.1−27−78
[1,2,3] Tree basal area growth rate (m^2 yr^{-1}) $\times 10^{-2}$	–0.19−0.15−2.96	–0.20−0.19−2.91	–0.19−0.12−1.59	–0.20−0.29−2.07	–0.20−0.31−2.00

[1] At the start of growth periods of each plot. [2] Trees that survived a growth period; many individual trees have results for numerous growth periods. [3] Some trees are measured as having smaller diameters at later measurements, hence show negative growth rates.

2.2. Model development

Given broad-scale plot data, such as those available here, it is impossible to know if the trees that show the fastest growth rates were actually growing under the optimal environmental circumstances for the species concerned and were free of competition from neighbours for the resources required from the site for growth (light, water and nutrients). However, perhaps it might be assumed that, amongst the many thousands of observed growth rates, there are at least a few that represent growth under those ideal circumstances. Thus, to achieve the objective here of developing models that related individual tree maximum possible growth rates to tree sizes, it was first necessary to reduce the available data to leave only those for trees which showed those maxima. This has been done in other studies with different species around the world [3,6−12] using quantile regression [13,14]. Other methods are available to achieve equivalent results [12,15−17]. For this study, the method of Bi and Turvey [15] was used, termed here the “class maxima” method. Note that, incorrectly, it has been termed quantile regression [18,19]. This method was considered appropriate for the present work because it uses data that include, unequivocally, the maximum growth rates observed for the tree sizes encountered in the data set. To obtain the data for any one species, its entire data set was split into 50 equal sized tree basal area classes and the observation with the highest growth rate in each class was selected. Scatter plots showing the stem basal area growth rates against stem basal area of the data selected by this process for each species are shown in **Figure 1**.

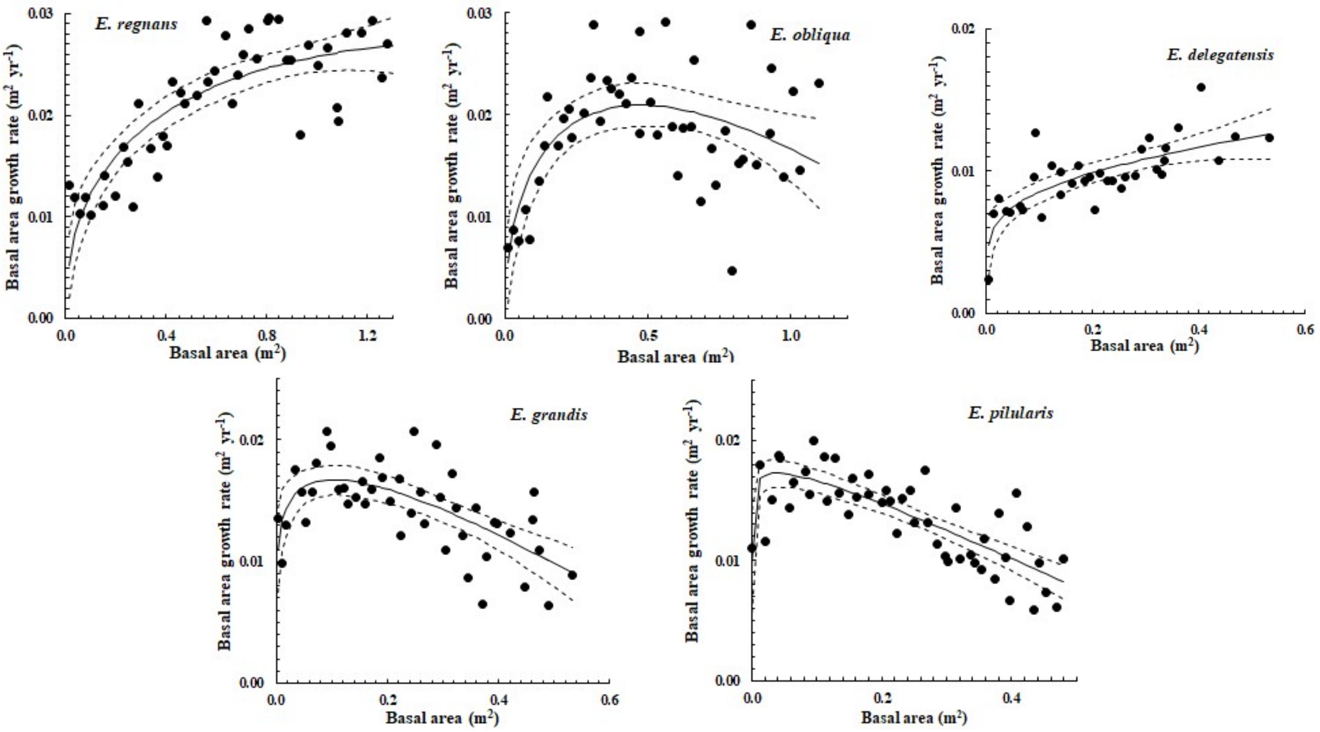

Figure 1. Scatter plots (●) of tree basal area growth rate against tree basal area of the data included in the class maxima data sets constructed here for each of the species (as indicated). The solid lines are the fit to the data of Model (1), with parameter estimates as shown in **Table 2**. The dashed lines are the 95% confidence limits about each fitted line of the true mean value of an estimated basal area growth rate for a tree of given basal area. Note that the scales of the diagrams are not the same.

The next step in model development was to choose a model function that would describe these selected data. West [18,20], and Smith et al. [21] have used the well-known Chapman-Richards function [22] for this purpose. Its form is:

$$\Delta B_m = aB^b - cB \qquad (1)$$

where ΔB_m (m^2 yr^{-1}) is the maximum basal area growth rate that an individual tree with basal area B (m^2) may have and a, b and c are parameters. This nonlinear model was fitted to the class maxima data selected for each species by least-squares regression using the NLIN procedure of the SAS statistical package[1].

3. Results

The parameter estimates, with their standard errors, obtained for the fit to the data of Model (1) for each species are listed in **Table 2**. The fit was very good in all cases, with all the coefficient of determination (r^2) values exceeding 0.92. Parameter values were generally significantly different from zero (as assessed from t tests with $p = 0.05$), except in the case of *E. delegatensis* for which only *a* was significantly different from zero. The fit to the data, together with the 95% confidence limits of estimates made using the model, are drawn on **Figure 1**. Note that the fit to the data for *E. pilularis* differs little from that determined earlier for that species [18] from a slightly smaller data set, that included many of the data used here but had rather more data from smaller trees.

Table 2. Parameter estimates, with standard errors in parentheses, obtained with the fit to the data of Model (1) for the class maxima data available for each of the species here. Also shown is the tree stem diameter at breast height that the model predicted has the fastest growth rate.

Species	**Parameters**			**Diameter with fastest growth rate (cm)**
	a	***b***	***c***	
E. regnans	0.0381 (0.0131)	0.450 (0.135)	0.0123 (0.0132)	153
E. obliqua	0.0624 (0.0291)	0.511 (0.159)	0.0457 (0.0300)	78
E. delegatensis	0.0121 (0.0034)	0.166 (0.086)	–0.0032 (0.0059)	–
E. grandis	0.0297 (0.0053)	0.171 (0.056)	0.0330 (0.0087)	37
E. pilularis	0.0220 (0.0016)	0.057 (0.020)	0.0268 (0.0037)	22

Model (1) has a form that reaches a maximum at a particular stem basal area. Using straightforward calculus, that basal area may be estimated as $[c/(ab)]^{[1/(b-1)]}$ (m^2). Estimates of the corresponding stem diameters, where those maxima occurred, are listed in the last column of **Table 2**. The estimate for *E. regnans* was based on an extrapolation of the model beyond the range of the data. In the case of *E. delegatensis*, no such estimate could be reasonably made, reflecting the negative (and statistically non-significant) estimate of the parameter *c* in that case (**Table 2**). Its result suggest that its data did not include stem basal areas large enough to reasonably predict a maximum. Simple extrapolation by eye of the trend of its model suggests its maximum might occur at a diameter somewhere near that of *E. regnans*.

The results for the various species shown in **Figure 1** have been drawn at scales that suited the data of each species. Direct comparison between the fitted models, all drawn at the same scale, is shown in **Figure 2**. This suggests that the maximum growth rates ever encountered for a single tree of any particular size are greater for the three ash eucalypt species than for the other two; the maximum growth rates observed in the data, and listed in **Table 1**, are consistent with that contention. It is apparent also that

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[1] Documentation for the SAS statistical package is available at https://support.sas.com/en/documentation.html (accessed September 2023).

the maximum growth rates occur in much larger trees in the case of the ash eucalypts than for the other two species.

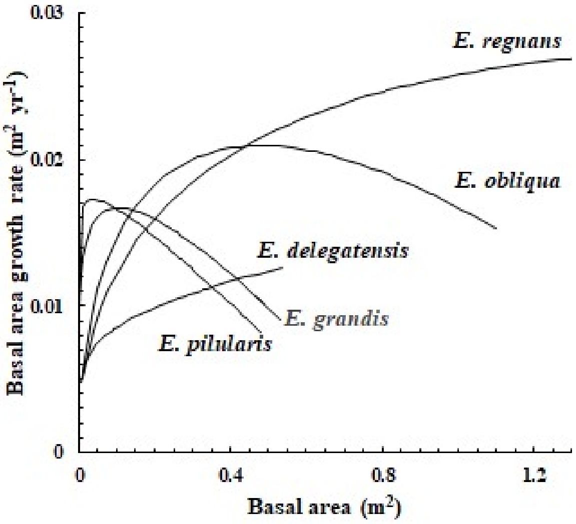

Figure 2. The lines fitted with Model (1) for the class maxima data of each of the five species here. They are the same as the solid lines drawn on each section of **Figure 1** but are all drawn here at the same scale. Each line extends over the range of data that was available for each species.

4. Discussion and conclusions

A number of authors have attempted to develop models predicting maximum individual tree growth rates in stem basal area (or diameter) in relation to tree size for a species when growing under ideal circumstances over its region of occurrence [3,6,21,23−25]. These have included both soft- and hardwood species from various parts of the world and from various forest types. Assorted models have been used to describe the relationship, but these have consistently displayed trends with the same form as shown in **Figures 1** and **2**. Other studies have found similar forms applying when using smaller data sets or somewhat different approaches to modelling their data [8,10,26−29].

It is well known that stand growth rates of even-aged forests tend to increase during the early life of the forest, but, after a few decades or so, reach a maximum and decline progressively thereafter. Various reviews and texts describe this phenomenon [30−34]. These trends are evident in whatever measures of tree size are used, measures such as biomass or stem wood volume or characteristics correlated with these, such as stem basal area. The trends shown in **Figure 2** and in the works mentioned in the previous paragraph are entirely consistent with this. During early stages of stand development, when trees are relatively small, their individual growth rates increase with their sizes, hence ages. Stand growth is the sum of individual tree growths, so as individual trees get bigger, stand growth rate will get correspondingly bigger. However, after some years, some trees will reach a size beyond which their growth rate declines. As time passes, more and more trees will reach that size and so stand growth rates will continue to decline, the decline increasing steadily with increasing tree size, that is, with increasing stand age.

Since the mid-twentieth century, forest science has sought to explain this growth phenomenon. Consideration of various alternatives led Binkley [34] to conclude that the most likely cause was a reduction with age (hence size) of the "resource use efficiency" of tree growth, that is, the amount of growth per unit of light, water and nutrients that a tree obtains from the environment. A theory consistent with this and which has received much support in times past is the "hydraulic limitation theory". This proposed that water stress in leaves increased as taller trees had to transport water from roots to leaves to greater heights; this reduced their photosynthetic capability [31,35,36]. More recently, it has been suggested that the decline in growth rate is due to respiratory costs increasing progressively with increasing tree size [37]. In that theory, it is argued that greater respiratory costs are incurred in processes such as construction of more complex anatomy of newly developing leaves, changes that ameliorate photosynthetic limitations.

In the present work, the results of **Table 2** and **Figure 2** suggest that the tree sizes at which growth rates start to decline are much greater in the three ash eucalypts than in the two coastal, sub-tropical species. Trees of all five of these species commonly achieve heights of 70 m or more in native forests [38]. *E. regnans* is well known as the tallest hardwood tree species in the world, sometimes reaching heights in excess of 100 m, second only to the Californian redwoods (*Sequoia sempervirens* (D. Don) Endl.). The three ash eucalypts are closely related. *E. regnans* tends to occur on favourable sites, with desirable rainfall and soil properties. *E. obliqua* may occur on slightly less favourable sites and *E. delegatensis* is often found on steeper slopes in more mountainous areas [38,39]; the three species sometimes occur in mixture. *E. regnans* and *E. obliqua* may interbreed; studies of their growth rates when in mixture showed no differences between them [40]. Detailed study of tall trees of *E. regnans*, some with diameters at breast height in excess of 300 cm, suggested that growth rates of even the largest tended to increase with increasing diameter, perhaps as a consequence of larger trees developing greater leaf biomasses to compensate for hydraulic restrictions to photosynthetic rates [41−43]. Both *E. grandis* and *E. pilularis* occur in warmer sub-tropical climates than the ash species [38]. Both may grow in monoculture and sometimes co-occur. The distribution of *E. pilularis* may extend to somewhat drier sites than *E. grandis*, although the present data for both species were collated from sites close to the coast [4], where rainfall would be sufficient to favour rapid growth.

In understanding the apparently different growth behaviour observed here of the ash eucalypts and the two sub-tropical species, it is important to appreciate that the data used here were selected from individual trees showing the maximum growth rates being observed in their data sets; it was then assumed that these trees were suffering little competition for growth resources from their neighbours (Section 2.2). Thus, the species differences observed here may reflect the overall availability of those resources in the region of occurrence of each species. Certainly, the ash species occur in more southerly regions that are likely to have an overall cooler temperature regime than the sub- tropical regimes. However, the discussion above has suggested that physiological characteristics that reflect the resource use efficiency of these competition free individuals may be the important growth determinant here. At present, there are no studies available of the growth behaviour in relation to physiological characteristics of particularly tall trees of the species considered here, other than those mentioned above for *E. regnans* [41–43]. However, given that the three ash species appear to maximise growth rates in trees much larger than either *E. grandis* or *E. pilularis*, it is inviting to hypothesise that the ash eucalypts have evolved physiological characteristics that make them more efficient in compensating for the physiological constraints imposed on growth rates of tall trees than is the case for the two sub-tropical species. It would require detailed and substantial research to explore this hypothesis in detail.

The results here suggest that, for the five species considered, it would be practical to develop individual tree growth models that are based on functions that relate maximum growth rates to tree sizes, that is, the functions described in **Table 2**. The next stage in the development of such models would be to determine the effects on those maxima of changes in site productive capacity and then the effects of inter-tree competition [3,24,44−47]; this has been attempted for *E. Pilularis* [19,20]. Further work would then be required to extend the model to predict variables of interest to forest management, such as tree height, biomass or stem wood volume; this would often use allometric relationships between those characteristics and stem basal area [33,48−50].

Conflict of interest: The author declares that he has no conflict of interests.

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