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DEVELOPING AGE-SIZE RELATIONSHIPS FOR LONG LIVED TREE SPECIES

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Calculating the age of trees is often desirable in vegetation studies, but is sometimes difficult. In arid areas in particular, tree rings may not be annual, and growth may be related more to rainfall than annual cycles. A relationship between age and trunk circumference was developed for two species, *Acacia aneura* and *Myoporum platycarpum*, based on measurements of trees of known age (<80 years) growing on permanent quadrats on the Koonamore Reserve, in semi-arid South Australia. Extrapolation beyond the known ages was made by finding the maximum girth of mature trees in a larger population and using this to estimate an asymptote to which the curve is constrained to approach. We envisage that the techniques developed here could be applied to other species of a similar nature, those for which there is no relationship between number of tree rings and age.

Keywords: Tree Age; Mathematical Model; Arid Lands; Allometric Growth.

1. Introduction

For many years, a major concern of managers of arid and semi-arid areas has been the gradual disappearance of trees and tall shrubs from landscapes. This is a problem in many parts of the world, especially in areas where domestic stock herding and other human activities are applying increasing pressure to fragile ecosystems with low rainfall. Reductions in tree densities have been frequently reported.[1–9] In other cases encroachment has been observed.[10–13] In Australia, evidence for severely limited regeneration of trees under grazing pressure has been published for many species.

Demographic data on ages of trees is useful in determining past recruitment events and can provide important information on changes in abundance over time.

However, determining the age of a tree is not straightforward. A number of methods are possible.

Tree rings have been very widely used to age temperate forest trees, and dendrochronology is highly developed.[13,14] Dating by tree rings is less reliable in Mediterranean[15] or arid[16] climates, where plants may grow in response to rainfall events rather than annual seasons. Roughton[17] found that some shrubs in Colorado could be aged by tree rings, others not, while several but not all chaparral shrubs studied by Keeley[18] in California had annual growth rings. Flinn *et al.*[19] found one tree species in the SW of USA and Mexico which had reliable annual rings, while four other species had not. In the African savannah tree rings were not usually reliably related to age.[20] In the Australian arid-zone, Lange[21] showed that *Callitris columellaris* growing near Woomera, South Australia, produced about one ring per year, sometimes more, sometimes none. Westbrooke[22] found good correlation between number of tree rings, stem diameter and age in trees of known age, for *Myoporum platycarpum*; ring counts were more uncertain for *Casuarina pauper*, *Alectryon oleifolius* and *Geijera parviflora*, as the central heart wood was very dark or had disintegrated, making counts difficult or impossible.

For some species a series of "life history classes" may be set up (seedling, juvenile, mature, senescent, etc.), with the assumption that the stages follow one another chronologically, so that by assigning trees to classes a relative age structure may be derived. This will only give a broad estimate of age, and the length of time a tree spends in each class may be unknown. Life history classes have been widely used in forestry, and their use is reviewed by Harcombe.[23] They have been also used in the Australian arid zone.[24–28]

The size of a tree may be measured in various ways and used to estimate age, if some correlation between age and size can be determined.[19,26,29] All such methods of estimating tree age need to be calibrated by reference to trees of known age. However such trees are usually uncommon and old trees particularly can seldom be dated reliably. Ages can occasionally be determined from photographic records,[31] personal observation from people who have lived long in an area, or estimates from records of past unusual climatic events (high rainfall periods, floods, etc.), which are likely to have produced a crop of new seedlings.[32,33]

One source of trees of known age is to be found on the TGB Osborn Vegetation Reserve on Koonamore Station, South Australia. This reserve is a very long-running vegetation monitoring project, spanning over 80 years from 1926 to the present. Permanent quadrats and photopoints have been maintained over this period, so that the records contain a rare and extremely valuable set of data concerning the vegetation of the area. Quadrats were mapped annually between 1926 and 1931, except for 1929, when no recording was done. Since then they have been read less frequently, with some gaps of several years.[34] Since 1978 the number of plants has increased to the point that all quadrats cannot be read in any one year. Each one is now revisited every two to four years. There have been several establishment episodes for a number of trees and shrub species since the reserve was fenced[34] and consequently there is now a sizeable population of trees and shrubs whose ages are known reasonably accurately. The tree species *Acacia aneura* and *M. platycarpum* are particularly well represented and the records of their dimensions form the basis of this paper.

2. Approach

The aim of this research was to use measurements of trees of known age to generate relationships between age and tree girth.

Such relationships will later be used to generate age structure histograms for populations of trees, and to test whether these show evidence of germination events which can be related to past rainfall events.

The process of generating a relationship between age and tree girth is less than straightforward. The data we are using are limited in age to 80 years (even this represents the most comprehensive data set available). The tree species we are examining are conjectured to have a life span of some hundreds of years. We will be designing a model that will allow predictions of tree ages far beyond the range for the data we have available. How do we effectively construct mathematical models where the goal is to reliably employ extrapolation, an endeavor usually avoided?

3. Data

The TGB Osborn Reserve, formerly known as the Koonamore Vegetation Reserve (KVR), is a rectangle of 390ha, fenced in July 1925 in the corner of a heavily grazed and degraded paddock on Koonamore Station, a sheep-grazing lease 400 km north-east of Adelaide (32° 07'S, 139° 20'E). The area is predominantly chenopod shrubland, with mean annual rainfall of 214 mm. The reserve consists of a complex of low sand dunes alternating with sand plain and harder loamy soils, underlain by travertine limestone. Tree cover is a low open woodland formation, including *A. aneura* Benth. (mulga), *M. platycarpum* R.Br. (false sandalwood, sugarwood), *Alectryon oleifolius* (Desf). S.T. Reynolds (bullock bush, rosewood) and *Casuarina pauper* F. Muell ex L.A.S. Johnson (blackoak, belah). Historical background and a detailed description of the KVR may be found.[30,34]

The original intention was to exclude all domestic stock and feral rabbits, and record how the vegetation recovered from overgrazing, by means of permanent quadrats, photopoints and transects. However, rabbits were not completely excluded and after the first few years of control their numbers increased again. Effective rabbit control was recommenced in the mid 1970s.

Data used were derived from the permanent quadrats Q100, Q200, Q300 and Q400, each 100×100 m squares, Q6-80, a 60×80 m rectangle, and QFrA1, a small (8×25 m) rectangle enclosing a grove of *A. aneura* which germinated after a set fire in 1929. This quadrat had been previously used by Crisp[24] to derive an age-size relationship for the seven *A. aneura* trees which germinated there after the fire. The current analysis extends that work, using a larger data set and a longer time span. When records began the plants were simply mapped, but no measurements of size were recorded. Later, heights began to be measured and then canopy dimensions. Stem diameters were not usually recorded.

In December 2004, all trees of both species on all of these quadrats were measured. Measurements taken were height, canopy diameter north-south and east-west, and trunk circumference approximately 10 cm above ground level. The quadrat database was then searched to locate the date at which each tree was first recorded and its height at that date. From the date of first recording, a minimum age could be calculated for the tree. Unfortunately the quadrats have not been mapped regularly.[34] Consequently tree seedlings when first measured were often several years old, so that the age derived from the date of first recording was an underestimate. To correct for this, a preliminary relationship for current age versus height was derived, by selecting plants which were less than an arbitrary height at first recording. A similar method was used by Stewart.[35] Heights chosen were 20 cm for *A. aneura*, and 11 cm for *M. platycarpum*.

The relationship derived for *M. platycarpum* was further checked using a separate data set. Fifteen seedlings had been located outside quadrats, beginning in 1962, and their heights, canopy dimensions and stem diameters or circumferences recorded several times since. This information was not used in deriving the age/size relationship, but the fit of the predicted curve to these data points is shown below.

4. Mathematical Modeling

4.1. *A. aneura*

This *Acacia* species, mulga, can be described as an iconic Australian tree species. Mulga savannah and mulga co-dominant tussock grasslands cover roughly 20% of the Australian continent, or about 1.5 million square kilometres. Mulga scrub is distinctive and widespread, with the Mulga Lands of eastern Australia defined as a specific bioregion.

4.1.1. *Age–Height relationship for small plants*

Tree seedlings when first measured were often several years old, so that the age derived from the date of first recording was an underestimate. We assumed that trees below 20 cm at first reading for *A. aneura* would be only a few years old at first recording, hence their current ages would be accurate within a few years. The age versus height relationship derived for this subset of trees was then used to estimate the age at first recording of each seedling with height greater than 20 cm at first recording. This age was then added to their age from date of first recording to December 2004.

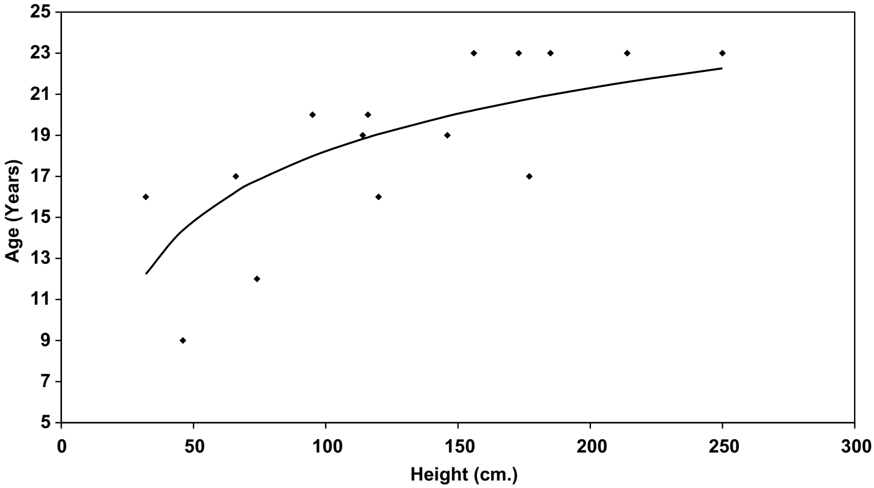

Fig. 1. *A. aneura* current age (years) versus height (cm) and logarithmic model (Eq. (4.1)) for seedlings which were less than 20 cm at first recording.

The scatterplot of current age versus height for seedlings <20 cm when first recorded is shown in Fig. 1. We determined through goodness of fit tests that a logarithmic relationship is the most appropriate. We used Solver in Excel to estimate the coefficients, as given in Eq. (4.1) and shown in Fig. 1. Solver is an optimization tool embedded in the Excel software. It is usual for small optimization problems and uses search techniques to find extrema of objective functions. We set up the problem as a minimization of the sum of squared deviations between model and data, finding the values of the parameters that give the minimum, in other words an ordinary least squares determination. For this fit, the coefficient of determination, $R^2 = 55.3\%$.

$$A = 4.07 \ln(h - 11.74), \tag{4.1}$$

where $A \equiv$ age, $h \equiv$ height.

4.1.2. *Age–circumference relationship*

We used the model in Eq. (4.1) to adjust the age for the underestimated plants in the original data set, and thus obtain the full data set for this species shown in Fig. 2. Our aim was to construct a relationship between age and circumference. Note that there are various models reported in the literature relating these two variables, or indeed age and some measure of size. Perhaps one of the most comprehensive forms is the Schnute model.[36] However, their goal was principally to infer size from knowledge of age. Our motive is exactly opposite that of inferring age from a knowledge of size. One might be tempted to simply invert the relationship, but the whole principle of regression analysis is based on the assumption that the

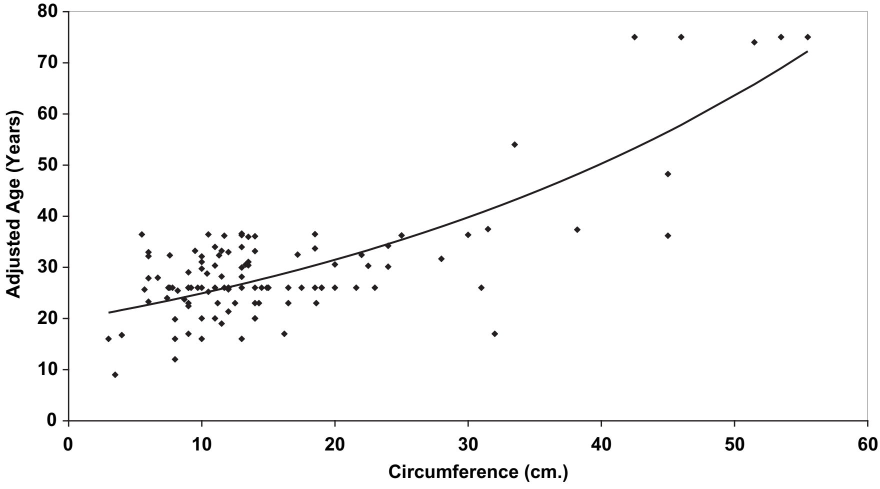

Fig. 2. *A. aneura* adjusted age (years) versus circumference (cm) and exponential model (Eq. (4.2)).

predictor variable is known with certainty and the response variable has distributional qualities, thus making a simple inversion not sensible. If one simply wants to best fit the data set available, an exponential relationship is most appropriate. Once again, we made use of Solver to perform the curve fitting, and obtained the relationship

$$A = 19.06e^{0.024C}, \tag{4.2}$$

where $A \equiv$ age, $C =$ circumference.

This is depicted in Fig. 2. For this relationship, $R^2 = 63.2\%$.

The data were all derived from young trees, less than 80 years old, as they had all established since the Reserve was fenced in 1925. To be useful, the relationship must be extrapolated to include older and larger trees. However, extrapolation of this relationship involved exponential growth in both variables, which becomes unrealistic. We propose a method of deriving an alternative model which makes use of information about the largest trees in the wider population to set an upper bound for the circumference. This is in line with the physical reality that a plant can continue aging (until death of course) but will approach a maximum circumference.

From physical considerations, a plant growth model should have age zero when the circumference is zero. As the tree reaches maturity and then senescence, the rate of expansion of the trunk should slow and eventually cease. The maximum circumference found in the remnant population gives an indication of the maximum circumference likely to be reached by a mature tree at this site. Hence we would expect the circumferences of the population measured to approach an asymptote at this value. For mulga, in a population of 318 trees measured inside and outside the Reserve, the largest circumference found was 400 cm. We decided to take this as an estimate of maximum circumference in the subsequent model building. We report, though, on whether the modeling is sensitive to this assumption.

We tried two particular forms that fit these criteria and found that one that has some synergies with allometric growth fits the data very well. Hendriks[37] gives evidence for allometric relationships for quantities as diverse as ingestion, mortality, age at maturity, maximum density, territory size of different species groups and trophic levels. In our case, it is not exactly allometric growth in that it is not simply circumference that is taken to a power, but a function of circumference. The data and fit are shown in Figs. 3 and 4, first with simply the data used for the fit and then extrapolated beyond the limits of that data. This type of function is more realistic than the exponential form in Fig. 2, which takes no account of the slowing of trunk growth as trees reach maturity and senescence. The fitted model is given in Eq. (4.3).

$$A = 144.0\left(\frac{C}{M - C}\right)^{0.460}, \tag{4.3}$$

where $A \equiv$ age, $C \equiv$ circumference, and $M \equiv$ maximum circumference.

To assess the goodness of fit, we use the three measures: coefficient of determination, mean absolute percentage error (MAPE) and mean bias error (MBE). These are given in Table 1. As we can see from the measures, there is a reasonable fit to the data, with the most encouraging feature being the quite small MBE value, indicating very little bias. As inferred above, it is important however, to provide some check on the sensitivity of the model to the one fixed parameter, the maximum circumference. To do this, the model was fitted with maximum circumference set at 350, 375, 425 and 450. Table 2 gives results for MAPE and MBE for these

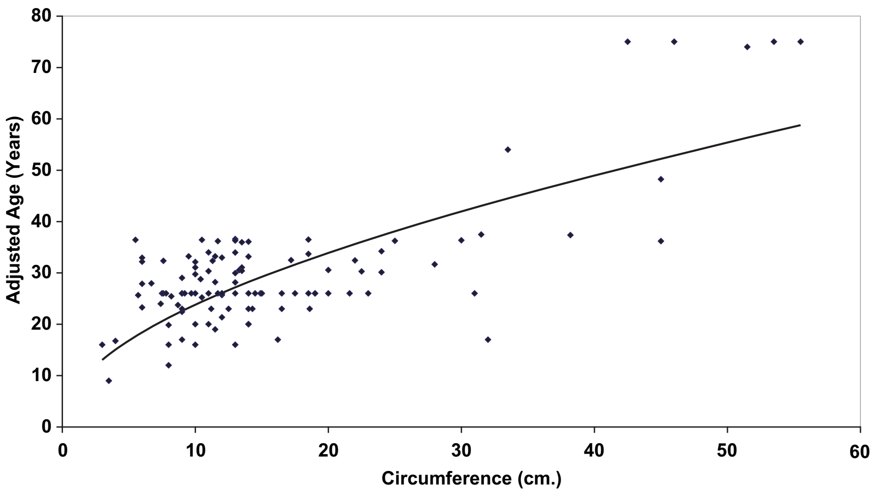

Fig. 3. *A. aneura* adjusted age (years) versus circumference (cm) and asymptotic model (Eq. (4.3)) within the limits of the raw values.

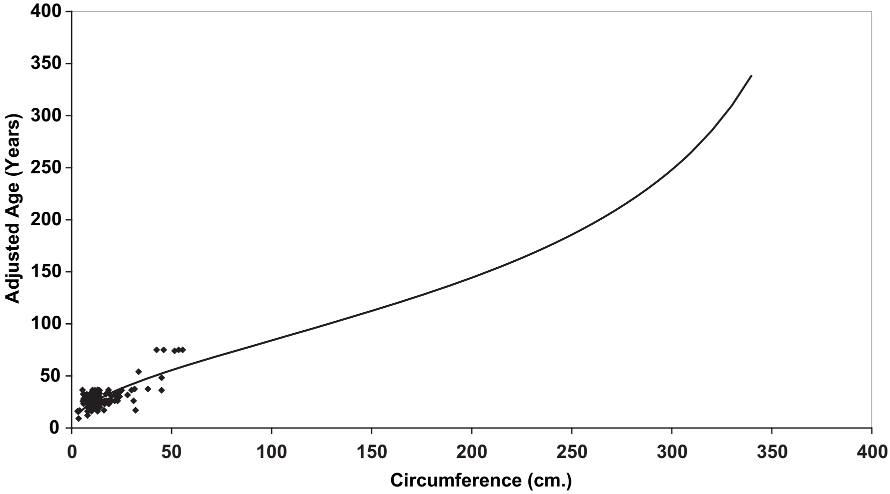

Fig. 4. *A. aneura* adjusted age (years) versus circumference (cm) and asymptotic model (Eq. (4.3)) extrapolated beyond the limits of the raw values.

Table 1. Error measures for the *A. aneura* model.

R^2	MAPE	MBE
50.4%	23.9%	−0.45

Table 2. Results of sensitivity testing for *A. aneura*, with varying maximum circumference.

350		375		400		425		450	
MAPE	MBE	MAPE	MBE	MAPE	MBE	MAPE	MBE	MAPE	MBE
0.232	0.513	0.237	−0.42	0.239	−0.45	0.242	−1	0.242	−1

determinations. As can be seen, there is not much difference in the goodness of fit measures as the maximum circumference is altered. All one could possibly say is that there is a slight trend upward in MAPE, and the MBE becomes negative unity for sizes 425 and 450. Perhaps one could say that the size should be set at 375–400 for best fit.

4.1.3. *Out of sample testing*

Finally for *A. aneura*, we used our model to compare estimated ages versus real ages for data from a number of trees of known age measured by Jodie Reseigh on Roxby Downs station, in northern South Australia, 580 km north of Adelaide.[26] The results are of interest as the site is far to the north and west of Koonamore, which is toward the southern extremity of *A. aneura* distribution. Note that here

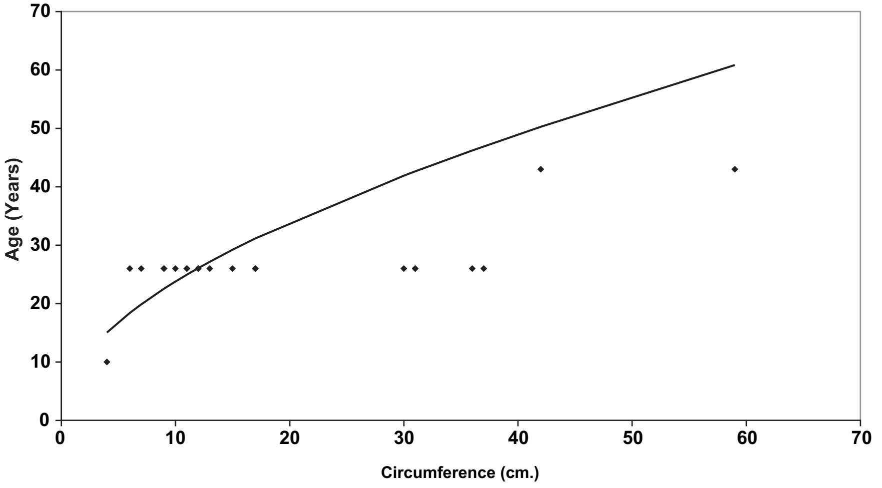

Fig. 5. *A. aneura* age (years) versus circumference (cm) data from Roxby Downs, with asymptotic model (Eq. (4.3)) from KVR data.

the circumference was measured at 50 cm height, which may not be exactly the same methodology as was used for the present data. The comparison is given in Fig. 5. Despite the difference in location and methodology, the fit is reasonable ($R^2 = 46.9\%$). Obviously one cannot get carried away with the results as most of the plants in this study were the same age. It is difficult finding exhaustive measurements of *A. aneura* at other locations to test the method.

4.2. *M. platycarpum*

This tree grows to over 6 m in height. Its wood is quite soft and sometimes powdery in the center. It is similar to the sandalwood and produces a pleasant sandalwood smell when burnt. It is resident in the semi-arid to arid lands of Australia.

4.2.1. *Age–Height relationship for small plants*

The scatter-plot of age versus height for seedlings <11 cm when first recorded is shown in Fig. 6. The large number of plants of age 14 years is due to a major germination event after the heavy rains of 1973–1975. These plants were first recorded in 1990.[34]

As for *A. aneura* a logarithmic relationship was found, Eq. (4.4).

$$A = 6.28 \ln(0.099h). \tag{4.4}$$

This relationship was used as before to adjust the ages of the plants whose ages were underestimated in the data set, by predicting the age at first recording and adding that to the estimated age. Then we could model the age as a function of

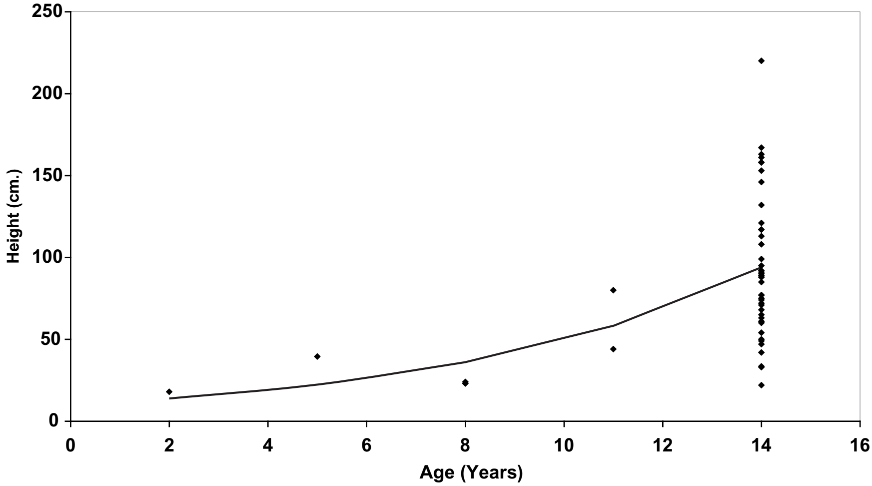

Fig. 6. *M. platycarpum* current height (cm) versus age (years) and logarithmic model (Eq. (4.4)) for seedlings which were less than 11 cm when first recorded.

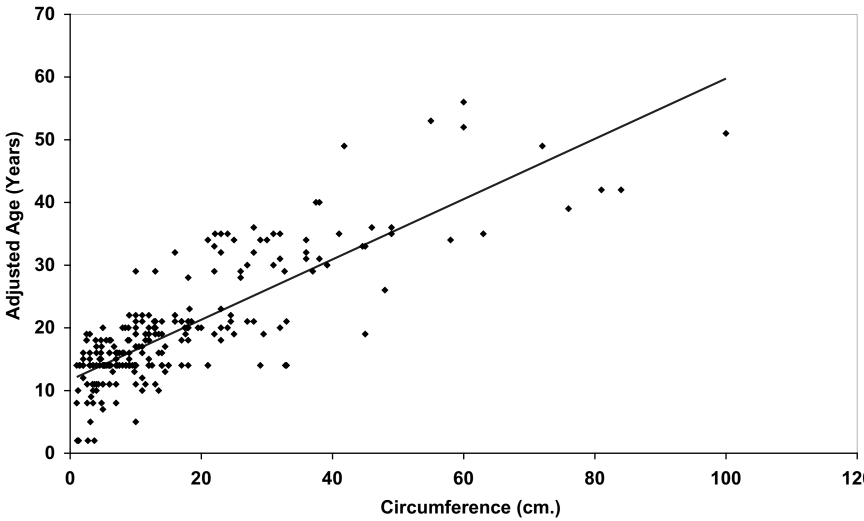

Fig. 7. *M. platycarpum* adjusted age (years) versus circumference (cm) and linear model (Eq. (4.5)).

the circumference of the trees (Fig. 7). In this case a linear function fitted the data well ($R^2 = 67.0\%$), as given in Eq. (4.5).

$$A = 0.48C + 11.66. \tag{4.5}$$

A similar technique to that used for *A. aneura* was used to find an asymptotic model for age versus circumference. The largest *M. platycarpum* tree found in a sample size of 478 had a circumference of 195 cm. However, Chesterfield and Parsons[32] reported one tree with a girth in the range 260–270 cm in a survey of about 1100 trees, and Westbrooke[33] reported one of girth 250 cm and two at 235 cm in a sample of about 350 trees. These surveys were done in arid South-eastern Australia, an area which includes Koonamore. Consequently the maximum circumference for the model was taken as 300 cm to be conservative.

Westbrooke[22] made a detailed study of *Myoporum* trunk girth compared with tree ring counts. He found a very good linear relationship between tree ring number and girth in cut and polished sections of trunks of 26 *Myoporum* trees from two sites. The sites were part of his larger survey area[33] and the ages of the trees were inferred from known rainfall events in the area which would have been expected to give rise to the trees. The tree ring counts agreed well with these ages. We incorporated these data from Westbrooke[22] into our data set.

The resulting form is given in Eq. (4.6) and the model fit is shown in Figs. 8 and 9 for the extent of the data and extrapolated outside that range.

$$A = 93.02 \left(\frac{C}{M - C} \right)^{0.514} . \tag{4.6}$$

Once again, we calculated error measures to test the goodness of fit — see Table 3. Interestingly, as can be seen from Fig. 8, there is increasing spread as the circumferences increase. So, this means that the APE is highly skewed with some quite high values. In this case, the median APE is a more appropriate measure of the fit. We

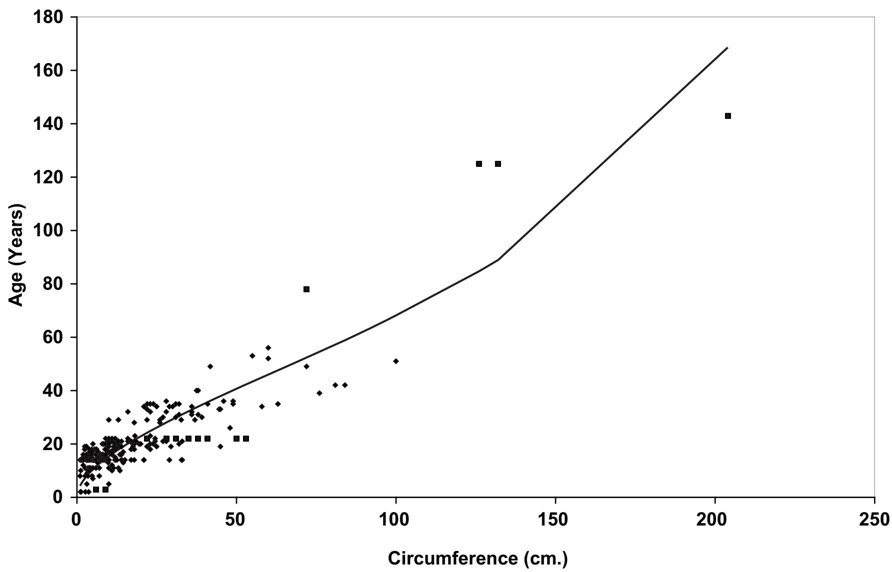

Fig. 8. *M. platycarpum*. Adjusted age (years) versus circumference (cm) and asymptotic model (Eq. (4.6)) within the limits of the raw values. ♦ KVR data; ■ Westbrooke data.

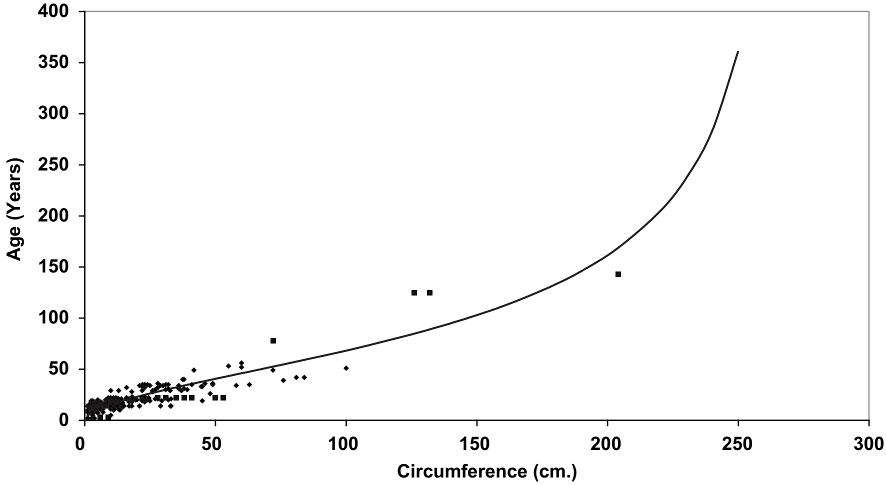

Fig. 9. *M. platycarpum* adjusted age (years) versus circumference (cm) and asymptotic model (Eq. (4.6)) extrapolated beyond the limits of the raw values. ♦ KVR data; ■ Westbrooke data.

Table 3. Error measures for *M. platycarpum*.

R^2	MeAPE	MBE
76.2%	19.8%	−0.139

denote this as MeAPE. It is interesting to note from the diagram and other analysis that the bias is not affected by the increasing spread, so the mean bias error is still the appropriate measure. Sensitivity analysis for the maximum circumference was also carried out, but it was done in conjunction with the checks done against the seedling data set. This was possible in this case, unlike with *A. aneura*, as the seedling set is a more comprehensive data set.

4.2.2. *Out of sample testing using the seedling set*

The seedlings located outside quadrats, that had been measured beginning in 1962 were used to validate the model. In earlier readings, diameters rather than circumferences were measured. These were converted, assuming a circular cross section. Also, the plants were not tracked since first emergence so once again we re-adjusted the age using Eq. (4.4). When we made these adjustments and plotted the adjusted age versus circumference and overlaid the model equation (4.6), the model fitted this new data set well ($R^2 = 76.6\%$), although with age somewhat overestimated (Fig. 10). This is the point at which we can make good use of a form of sensitivity analysis. We begin to alter the maximum circumference. We did try a number of values of maximum circumference but found that 350 cm was the most suitable. Let us explain why. If we take 350 cm as maximum circumference and find the values

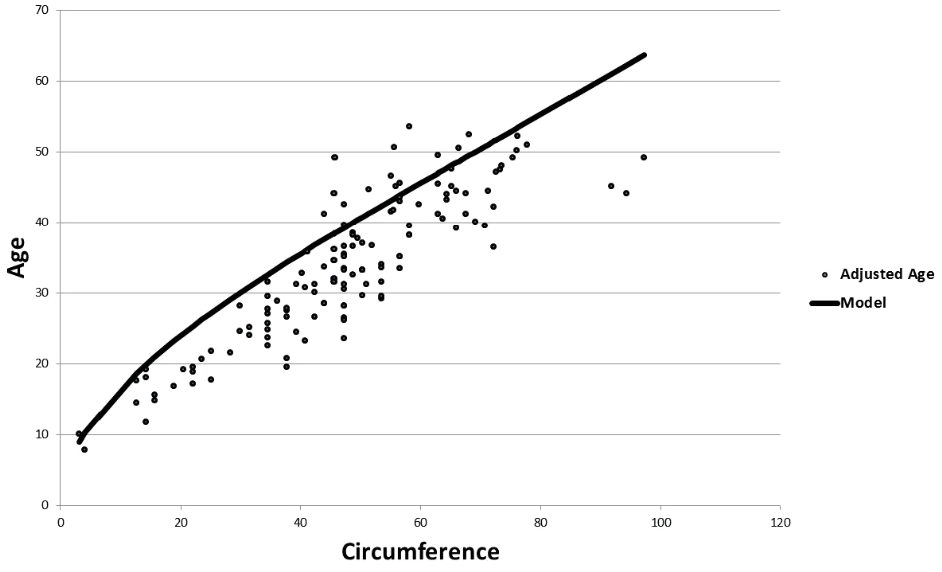

Fig. 10. *M. platycarpum* age (years) versus circumference (cm) for seedling cohort.

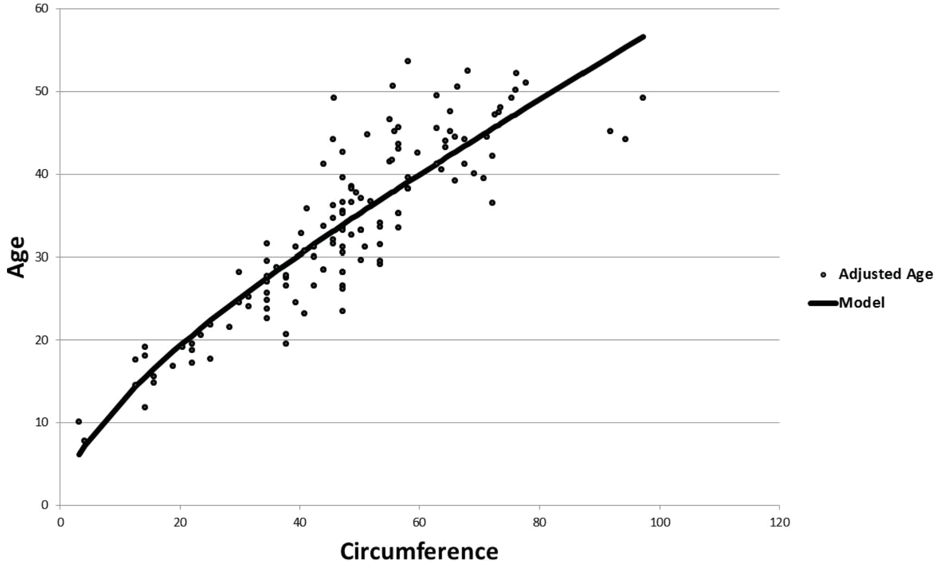

Fig. 11. The best fit for the seedling cohort.

of the two parameters to best fit the seedling data, we get an extremely good fit, as exemplified in Fig. 11. The error measures for this fit are

$$\text{MeAPE} = 9.29\%,$$

$$\text{MBE} = -9.0 \times 10^{-9}.$$

The parameter estimates are not significantly different from the previous fitting exercise, as shown in Eq. (4.7).

$$A = 92.03\left(\frac{C}{M-C}\right)^{0.537}. \tag{4.7}$$

When this model is compared to the original data set, the MeAPE is 24.07% and the MBE is 3.10. On the other hand, if we simply use the estimated parameters of Eq. (4.6) with a maximum circumference of 350 cm, the error measures for the seeding set are

$$\text{MeAPE} = 12.36\%,$$

$$\text{MBE} = -1.84.$$

These are not substantially different from the best estimates, and Fig. 12 shows a much better fit to the seedling data than Fig. 10, and not much different from Fig. 11. As a result, it is best from many different viewpoints, to simply use the parameter estimates from the original estimation with a maximum circumference of 350 cm. Statistically, it makes sense since the comprehensive data set was essentially the training set, with the seedling set acting as a vehicle for tuning the maximum circumference. When checking how having $M = 350$ in Eq. (4.6) vis-à-vis the comprehensive data set, we find that we get

$$\text{MeAPE} = 21.35\%,$$

$$\text{MBE} = 1.73.$$

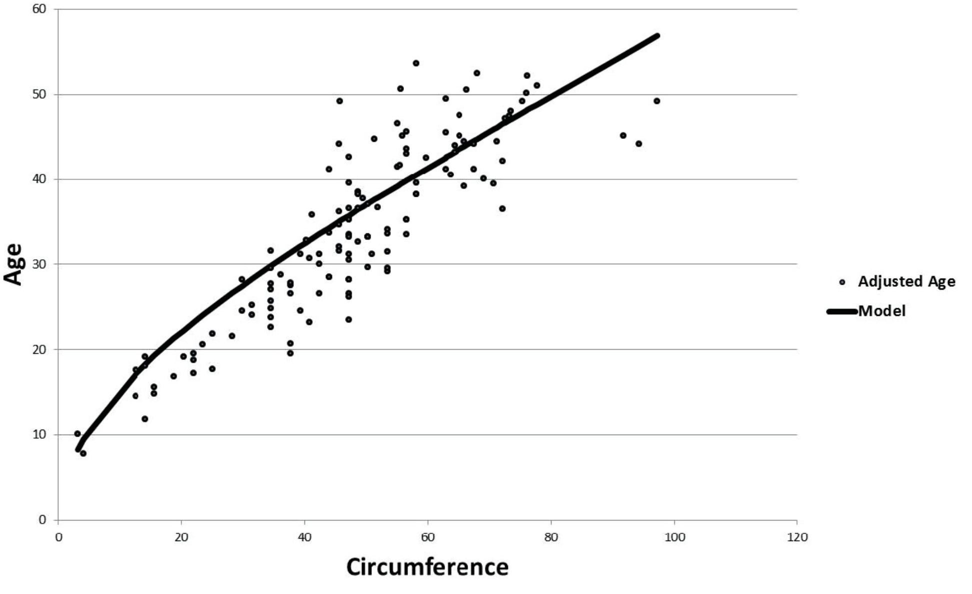

Fig. 12. Fitted model for the seedling set with original parameter estimates, but with 350 cm maximum circumference.

These error measures are not substantially different from the results with $M =$ 300 cm. Thus, we conclude that this procedure seems to have given us a sensible approach — use the comprehensive data set to fit the two parameters and use the seedling set to help firm up the maximum circumference value.

5. Conclusion

In the literature, when age and physical measurements of plants are related, the usual motivation is to use age to predict the expected size of the plant. A common use for this is in the case of plantation timbers, when one desires to schedule cropping of various tranches. In our case, there are two significant differences from the standard case. One is that our goal is precisely the opposite of the usual one, we wish to use a physical characteristic, specifically the circumference of our focus species, to infer the age. This can give us vital information as to the age distribution in a local sub-population, providing us with, for instance, knowledge as to whether that sub-population is viable in terms of being able to reproduce sufficiently in the long-term to survive. The other difference from the usual situation is that we are dealing with long-lived species, for which we have data for model building for only a short span of their projected life. Thus, a robust method of extrapolation has had to be devised.

The use of the maximum girth measurement from a large sample to set an upper bound to the size measurement in the model does not appear to have been previously used, but it is biologically reasonable. It appears to allow reasonable extrapolations beyond the measurements of trees of known age, which are always difficult to find, and should be useful in ecosystems where tree rings are not reliable indicators of age.

We have applied the method to two species for which we have reasonable sets of data. These are for important species in the semi-arid rangelands, *A. aneura* and *M. platycarpum*. We would hope that they may be applied, albeit with caution, to these species for other sub-populations throughout the Australian rangelands. The general method can also be applied if a similar model is to be devised for other long-lived species — thus it can be a valuable tool in the drier areas of the globe.

There are three requirements for our method to be successfully applied to other species:

(1) A number of trees of known age, spanning as long a time period as possible.
(2) A large enough sample from the tree population to obtain a reliable measure of the maximum girth for the oldest tree.
(3) An independent means of estimating ages of some trees, for example by using known recruitment events, as a means of testing the reliability of calculated ages.

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A very large number of staff, student and other volunteers have contributed to the collection of data on the Reserve over its life. As Osborn left Adelaide a few years after the Reserve was set up, JG Wood and Miss CM Eardley continued the monitoring work for many years. One of the authors (RS) has continued it since 1975. Messrs Hamilton and Wilcox held the Koonamore station lease in 1925 and gave generous support to establishing the Reserve, and donated the adjacent cottage. The lease passed to the McLachlan family in 1944, who continued to support the project. In 1992, the lease was sold to the Rasheed family, who have continued the tradition of interest and support for the work of the Reserve. The Reserve remains under the control of the University of Adelaide. We acknowledge the use of data from Jodie Reseigh's honours thesis and Martin Westbrooke's Ph.D. thesis. Thanks go to José Facelli for comments and suggestions on an early draft of this manuscript and to David Ladd for years of assistance with fieldwork.

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