CSIRO PUBLISHING
www.publish.csiro.au/journals/ajb *Australian Journal of Botany*, 2005, **53**, 101–108

Use of growth characteristics for predicting plant age of three obligate-seeder Proteaceae species

Meaghan E. Jenkins[A,D], *David A. Morrison*[A,B] *and Tony D. Auld*[C]

[A]Department of Environmental Sciences, University of Technology Sydney, Westbourne Street, Gore Hill, NSW 2065, Australia.
[B]Department of Parasitology (SWEPAR), National Veterinary Institute and Swedish University of Agricultural Sciences, Uppsala 751 89, Sweden.
[C]Biodiversity Conservation Science, Department of Environment and Conservation (NSW), PO Box 1967, Hurstville, NSW 2220, Australia.
[D]Corresponding author. Present address: Department of Earth Sciences, The Open University, Walton Hall, Milton Keynes, MK7 6AA England. Email: meaghanjenkins@hotmail.com

Abstract. We tested the ability to predict plant (and hence population) age for three fire-sensitive obligate-seeder Proteaceae species (*Banksia ericifolia*, *Banksia marginata* and *Petrophile pulchella*) in the heath and woodland vegetation of the Sydney region. To do this we sampled the number of growth whorls, as well as other growth characteristics (stem girth and height measurements, and canopy area and volume estimates), in areas of known time since last fire (TSLF). The average number of growth whorls was a very good predictor of plant age for both *Banksia* species ($R^2 = 98\%$, 99%), but this needed to be corrected for linear underestimation in *P. pulchella* ($R^2 = 92\%$). This technique could successfully be applied to these species in similar habitats across a large spatial scale, and so this information can be used to determine the age of a population in areas of unknown TSLF. A sample size of 15 plants was sufficient for accurate age estimates of all species; however, better estimates of TSLF for a particular plant community were obtained when estimates from two or more of the species were combined. We thus provide empirical evidence for the validity and accuracy of the growth-whorl technique for predicting plant age and hence TSLF. This information will assist in informing the development of appropriate management strategies for plants in relation to fire. Of the other growth characteristics studied, stem girth was the most reliable predictor; however, in general these other characteristics had wide confidence intervals on the predictions for sites greater than 10 years TSLF, owing to a non-linear relationship with age.

Introduction

Plant abundances in fire-prone environments are usually characterised by biological attributes that increase the probability of population survival and/or recruitment following disturbance by fire, including resprouting after fire, fire-stimulated flowering and seed production, and fire-triggered germination (Gill 1981; Enright *et al*. 1998). In this regard, the ability to accurately measure plant age in fire-prone vegetation is an important issue in fire management, because of the role that fire plays in the life cycles of plants, through its effects on survival of individuals of all life stages and the function of fire as a cue for transfers between life stages (Keith 1996).

Plant species are generally considered to fall into two main groups with regard to their response to fire: resprouters, characterised by vegetative regrowth after fire, where individuals resprout from buds protected from the fire (fire-tolerant species), and obligate seeders, which regenerate from seed either stored in the soil before the fire or held on the plant within woody fruits for release after the fire (fire-sensitive species). In the latter group, plant age will be related to fire frequency in the habitat if recruitment is linked to fire (Gill 1981; Benson 1985). Thus, for these species plant age will be directly related to time since last fire (TSLF). However, plant age will not be exactly the same as the TSLF because the seeds are unlikely to germinate until the first substantial rains after the fire. Fire frequency is the most critical aspect of fire regimes for such plants, because fire repeatedly interrupts processes such as fruit production and growth that maintain the capacity of the population to persist and regenerate (Keith 1994).

Ideally, the most accurate method for determining plant age, growth rate, survival and fecundity is to measure seedling growth regularly over time for a cohort of plants. However,

 10.1071/BT04067 0067-1924/05/020101

this requires repeated measurements over lengthy periods of time, possibly even decades for long-lived perennial plants. The development of a simple means to estimate plant age would aid the assessment of population structure and demographic attributes, as well as assisting interpretation of likely impacts of fire, especially issues such as fire frequency.

If plant age is directly related to TSLF, then there are several techniques that could be used to quantify TSLF and thus estimate age, including use of fire-history maps and records, aerial photography, methods based on counting tree rings or grass-tree banding patterns, and charcoal data from cores (Wills 2003). Alternatively, a simpler and/or less-destructive method is to count growth whorls of fire-sensitive Proteaceae species, as originally described by Lamont (1985). This technique has been widely adopted, primarily for predicting plant age and estimating cone age for Western Australian *Banksia* species (Abbott 1985; Cowling and Lamont 1985; Cowling *et al*. 1987; Lamont and Barker 1988; Witkowski *et al*. 1991, 1992; Enright *et al*. 1996), although some work has been conducted with several pine (*Pinus*) species in Spain (Tapias *et al*. 2001). This type of technique has been rarely applied in eastern Australia, usually to estimate TSLF (e.g. Specht *et al*. 1958; Rogers and Westman 1977; Brown and Podger 1982; Wills 2003).

When employing the growth-whorl ageing technique, targeted species need to have distinct terminal growth patterns, and bark that does not obscure older node scars on the trunk (Cowling *et al*. 1987). Furthermore, this technique has several potential limitations, such as a tendency to underestimate stem age if all of the current season's terminal buds do not produce shoots (Lamont 1985). It is therefore important to quantitatively assess its reliability individually for each target species. Only Wills (2003) has previously provided an explicit quantitative assessment of the usefulness of this technique in one species (*Banksia marginata*) in eastern Australia.

Our study aimed to determine whether the growth characteristics of three fire-sensitive Proteaceae species could provide adequate predictors of plant age and hence TSLF of a population. We used a chronosequence analysis in order to quantify the growth characteristics of each of the three Proteaceae species (*Banksia marginata* Cav., *Banksia ericifolia* L.f., *Petrophile pulchella* (Schrad.) R.Br.) with canopy-stored seeds, to determine whether individual plants could be used to estimate population age and therefore the TSLF age of a community. We quantified several alternative growth characteristics as potential predictors of age, including growth whorls, stem girth, stem height, canopy area and canopy volume.

Materials and methods

Study species and area

Banksia marginata, *B. ericifolia* and *P. pulchella* (Proteaceae) are shrubs up to 5 m that are abundant in sclerophyll vegetation of the Sydney region. Several growth characteristics of these three fire-sensitive obligate-seeder species were measured at 19 sites during March–August 2001, covering a wide range of TSLF ages (Table 1). The sample sites were located on the southern edge of Sydney, in Royal and Heathcote National Parks, Garawarra and Dharawal State Recreational Areas, and within the Woronora Catchment area (Fig. 1). For *B. ericifolia* and *P. pulchella*, four additional sites were sampled in Ku-ring-gai Chase National Park to the north of Sydney, approximately 60 km from the previous sites (Fig. 1), thus allowing comparisons to be made regarding large spatial variation and differences within and among populations of the same species.

Table 1. Co-efficients of variation (%) for the growth-whorl ageing technique, with sample sizes of 15 and 30 individuals at varying sites of TSLF age for the three study species

A dash indicates that no sample was taken for that species at that site. Note that some ages have replicate sites

TSLF	*B. marginata*		*B. ericifolia*		*P. pulchella*	
(years)	$n = 15$	$n = 30$	$n = 15$	$n = 30$	$n = 15$	$n = 30$
1	–	–	6.58	5.84	–	–
3	–	–	8.69	5.68	4.08	2.58
5	–	–	4.40	3.48	6.87	5.21
7	3.24	2.39	5.43	3.23	5.41	4.00
7	3.37	3.34	4.80	3.16	9.28	5.57
8	3.48	2.59	8.60	5.36	4.80	3.16
8	4.73	2.81	4.75	3.23	6.31	4.69
10	3.26	2.10	5.35	3.64	6.93	4.49
10	3.91	2.51	4.47	3.69	4.76	3.89
15	2.65	2.80	4.70	3.05	6.70	3.92
16	–	–	3.77	2.54	4.47	3.69
19	3.27	1.97	4.30	2.92	4.27	3.15
21	3.06	2.01	4.04	3.24	–	–
21	2.99	2.10	3.10	2.29	4.44	4.11
24	2.06	1.55	3.38	2.20	5.08	3.51
24	2.76	1.57	4.22	2.87	6.46	4.12

Sites were selected to cover a representative range of those TSLF ages available, with the following selection criteria:

(1) time since last fire was known from fire history maps obtained from the New South Wales National Parks and Wildlife Service;
(2) the site contained at least one of the three study species;
(3) the population appeared to be even-aged, i.e. all previous individuals had been killed by the most recent fire, so that the current individuals were recruited at the same time;
(4) sites with more than 50% exposed rock were not used, because of the patchy nature of fires in these habitats; and
(5) care was taken to sample a reasonable distance (usually ~5–10 m) from roads, walking and maintenance trails, and any other disturbances, to avoid edge effects such as possibly higher growth rates of plants on roadsides and potential fire patchiness in these areas (Lamont *et al*. 1994).

Finally, an extra southern site of 15 individuals per species was included in the Woronorra Catchment area, and sampled in December 2001. This site had an unknown TSLF age, and was used to assess the reproducibility of the predicted TSLF age based on measurements of all three species.

Sample technique

Thirty individuals of each species (when available) were randomly sampled at each site; however, where species were in low abundance, all

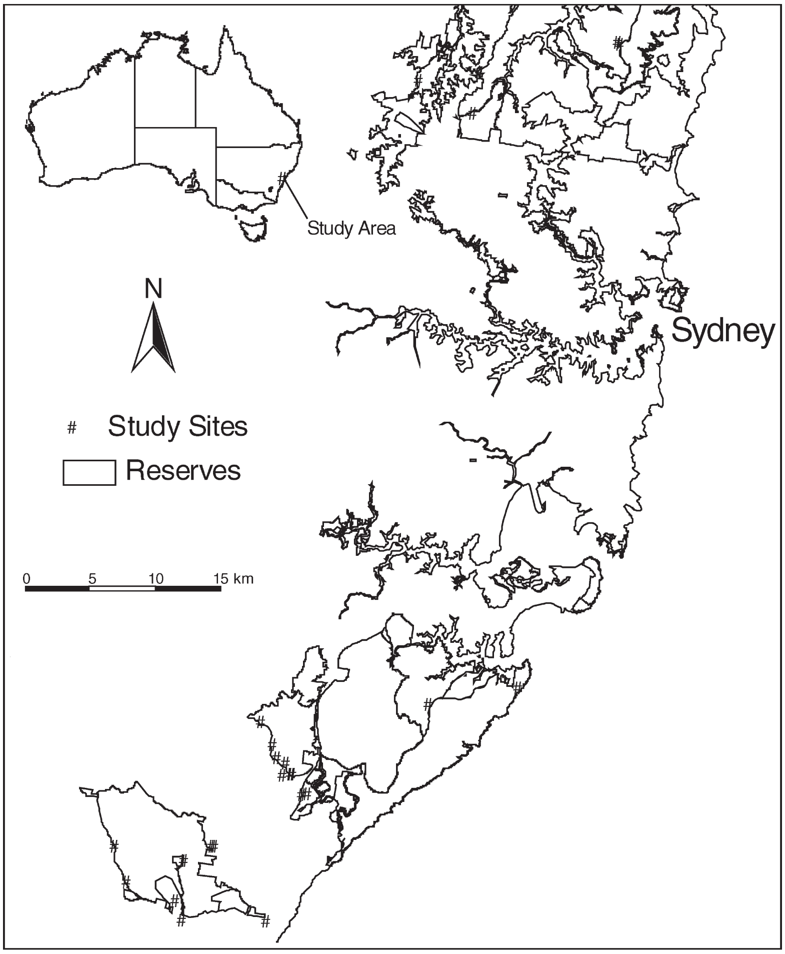

Fig. 1. Location of study sites.

available individuals were sampled. One site at 8 years TSLF showed a varied-age population for *B. ericifolia*, suggesting that the most recent fire was a patchy burn; so, a sample size of 25 individuals for this species was used and unusually large individuals (i.e. those apparently not burnt and killed in the last fire) were avoided. Replicate sites were sampled for TSLF (Table 1) if several fires occurred in the same year, or where the area burnt by the last fire was sufficiently large to allow separate populations to be sampled. For the samples taken in Ku-ring-gai Chase National Park, the sample size was reduced to 20–25 individuals, as this sample size had already given reliable results concerning the growth data for the southern sites.

During the annual growing season, all three Proteaceae species produce new shoots that are terminated by a resting bud, which may or may not produce a conflorescence in the next season. Thus, each annual growth increment is usually detectable either by a bud scar (if no conflorescence was produced) or by a whorl of lateral shoots (if a conflorescence was produced). For each individual, the growth whorls and bud scars were counted from the highest branch, treating the terminal bud as the current season's growth (i.e. one) then counting each annual growth whorl/scar downwards to the base of the plant, as described and illustrated by Lamont (1985). The maximum number of growth increments recorded per individual was then used as the estimate of that plant's age. Usually, the maximum was easy to determine by inspection, but for older individuals it was sometimes necessary to try several different starting locations on the outer edge of the canopy.

Several other growth characteristics were also measured for each plant, including

(1) stem girth (cm), measured at 10 cm from the base of the plant;
(2) stem height (m); and
(3) estimates of canopy size, calculated by taking the widest width of the canopy (w_1) and the width perpendicular to the widest width (w_2).

Two estimates were calculated as previously described for *Banksia* species by Witkowski *et al*. (1994):

$$\text{Canopy area} = \pi \times (w_1/2) \times (w_2/2) = 0.7854 \times w_1 \times w_2\,(\text{m}^2);$$

$$\text{Canopy volume} = \pi \times (4/3) \times (w_1/2) \times (w_2/2) \times (h/2) = 0.5236 \times w_1 \times w_2 \times h\,(\text{m}^3).$$

Data analyses

Mean values per population were calculated for all five growth measurements. Modal values were also considered, as suggested by Wills (2003), but these were always almost identical to the means. Linear least-squares regression analyses were then conducted separately for all five growth measurements (as the dependent variable) and TSLF age (as the independent variable) for each species, with 99%

confidence intervals calculated for the equation of best fit (Minitab 2000). Logarithmic transformations were also used for the growth-characteristic data to determine which regression gave the best fit (i.e. had the greatest R^2).

Results

All study species showed a linear trend of increasing number of growth whorls with increasing plant age (Fig. 2). The growth whorls of the two *Banksia* species could be used to provide reliable direct estimates of plant age, with the greatest variation shown in younger populations. *B. marginata* (Fig. 2*a*) and *B. ericifolia* (Fig. 2*b*) clearly showed that the predicted linear regression and 99% confidence intervals deviated from the expected values ($x = y$) in individuals less than 8 years of age, where there was a slight (1–2 years) overestimate of plant age. However, overall, there was one whorl/scar produced per year on each branch.

In contrast, *P. pulchella* (Fig. 2*c*), although following a linear trend, appeared to produce fewer growth whorls than the two *Banksia* species. Younger plants (<5 years old) followed an annual pattern, whilst older individuals appeared to produce growth whorls at a lower rate, i.e. not every shoot produced a whorl/scar every year. This might, however, also be attributed to whorls not being clearly detected in older plants, resulting in an underestimate of age. Nevertheless, the regression equation obtained from the data will be a useful predictor of TSLF age of this species.

A sample size of 15 appeared to be sufficient to provide a reliable prediction of plant age in any one population for all three species, based on the small estimated co-efficient of variation for each site for both sample sizes of 15 or 30 individuals (Table 1).

The other growth characteristics measured in this study generally showed a geometric rather than a linear relationship, similar to the one illustrated for stem girth (Fig. 3), for the three sample species. Therefore, the 99% confidence intervals became increasingly wide for older individuals, making these other growth characteristics less reliable predictors of plant age.

To examine the effect of widely spatially separated samples on the effectiveness of the growth characteristics as age predictors for *B. ericifolia* and *P. pulchella*, the regression equation and 99% confidence intervals for the data obtained from south of Sydney were plotted against data collected from Ku-ring-gai Chase National Park. Although data were not as widely sampled with respect to TSLF age at the northern sites, those sites sampled were comparable to the southern sites (Figs 4, 5).

Finally, the extra southern site with unknown TSLF produced plant-age estimates (± standard error) of 8.1 ± 0.3 (*B. marginata*), 7.3 ± 0.3 (*B. ericifolia*) and 7.9 ± 0.5 (*P. pulchella*) years. Although the prediction based on *B. ericifolia* was slightly lower than for the other two species,

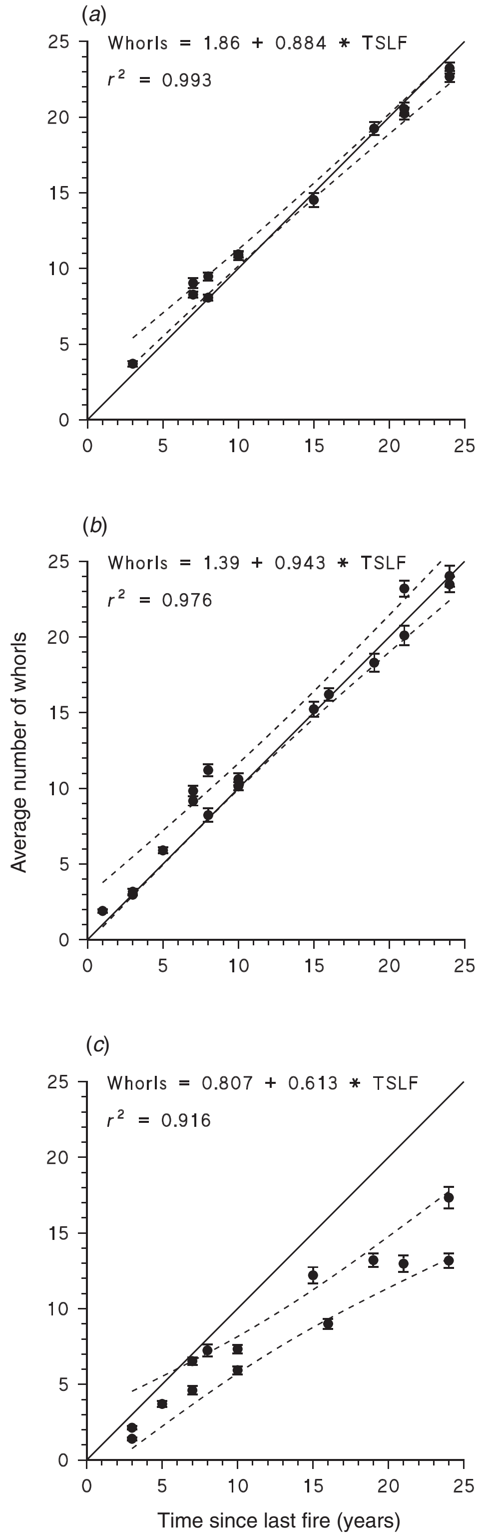

Fig. 2. Relationship between average number of whorls and time since last fire (TSLF) for (*a*) *Banksia marginata*, (*b*) *B. ericifolia* and (*c*) *Petrophile pulchella*. Each symbol represents a population average with standard errors. Expected values ($x = y$, solid line) and the 99% confidence intervals of the linear regression (dashed lines) are plotted.

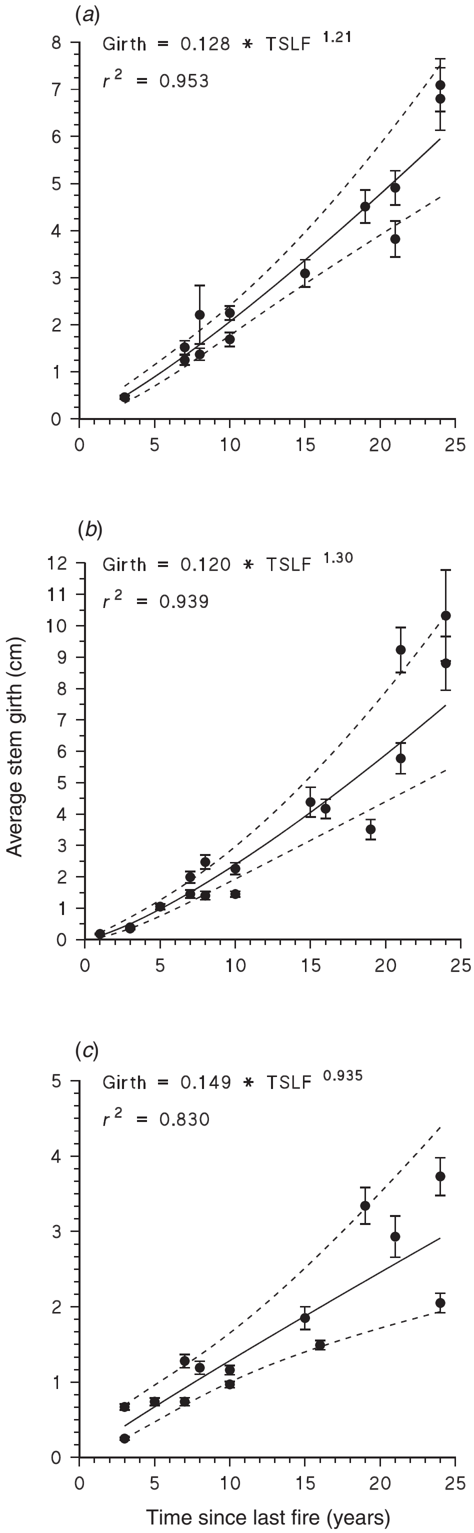

Fig. 3. Relationship between average girth and time since last fire (TSLF) for (*a*) *Banksia marginata*, (*b*) *B. ericifolia* and (*c*) *Petrophile pulchella*. Each symbol represents a population average with standard errors. Predicted values (solid line) and 99% confidence intervals (dashed lines) of the best-fit regression are plotted.

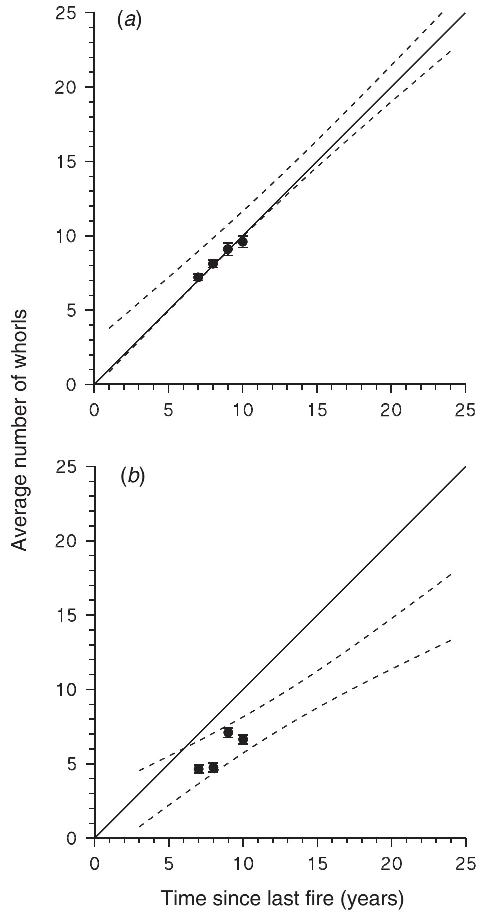

Fig. 4. Relationship between average number of whorls and time since last fire (TSLF) for (*a*) *Banksia ericifolia* and (*b*) *Petrophile pulchella* in Ku-ring-gai Chase National Park, compared with the summary data obtained from south of Sydney (cf. Fig. 2).

all three predictions were quite consistent with the suggestion that the site was burnt approximately 8 years previously, this being the level of accuracy of the technique. Furthermore, it appears that measurements on several species are needed in order to provide a reliable estimate for a particular site (i.e. TSLF).

Discussion

The ability to accurately predict the age of populations in fire-prone habitats, such as those observed in this study, may be vital to the development of bushfire management plans, in particular in areas where the most recent fire history remains largely unknown. This might include areas where fire-history records are unavailable, where the tree canopy remains unscorched so that satellite imagery cannot detect a fire or near fire boundaries where maps and images are imprecise. Under these circumstances, ground truthing of remotely sensed fires or incomplete records is essential. Therefore, from the observation of

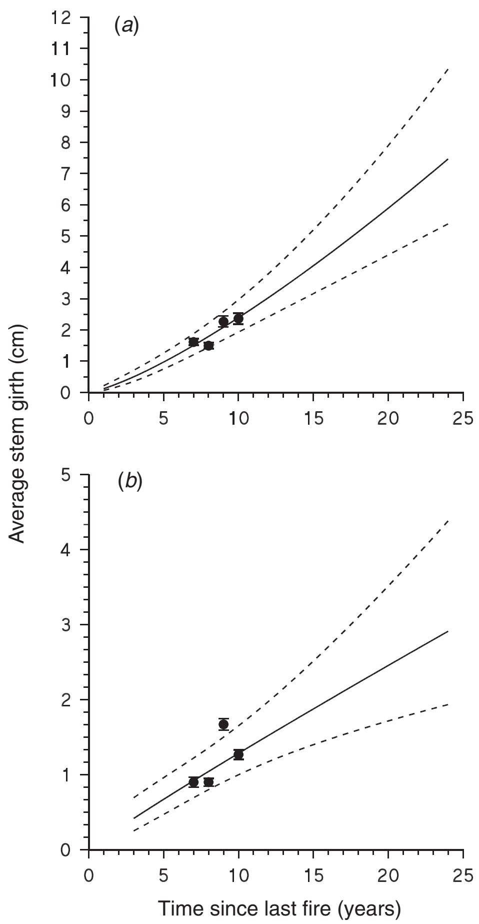

Fig. 5. Relationship between average girth and time since last fire (TSLF) for (*a*) *Banksia ericifolia* and (*b*) *Petrophile pulchella* in Ku-ring-gai Chase National Park, compared with the summary data obtained from south of Sydney (cf. Fig. 3).

three fire-sensitive species, *B. marginata*, *B. ericifolia* and *P. pulchella*, in areas of known time since last fire (TSLF), the growth-whorl ageing technique proved to be a simple, accurate and time-efficient predictor of population age and hence TSLF.

The three study species varied in the usefulness of their growth characteristics as predictors of plant age. Individuals of the two *Banksia* species provided very good direct indicators of population age, with respect to the growth-whorl ageing technique, deviating only in younger populations (less than 8 years old). However, this deviation from the expected value may prove inconsequential, because in terms of management these species should be given a minimum fire-free period of at least 8 years in order to replenish their canopy-stored seed banks (M. Jenkins, pers. obs.). The use of growth whorls for both *Banksia* species seems to provide the most accurate predictions for populations between the ages of 10 and 20 years TSLF. In terms of management, this is important, as between these ages a substantial seed bank will have accumulated to allow for regeneration to occur after death of the adult population caused by a fire.

The data for *P. pulchella* clearly followed a linear trend, providing an equation that can be applied to accurately predict plant age. However, in contrast to the *Banksia* species, it produced results that indicate either that production of growth whorls in this species does not occur on every shoot in each year, or that an underestimate of growth whorls results from difficulties associated with distinguishing between leaf scars and growth-whorl scars in older individuals. Either explanation could account for the underestimate in predicted TSLF age, but the production of whorls less than annually was more evident, and probably accounts for the majority of the underestimation observed. We found no evidence of multiple growth increments per annum in any of the species.

Therefore, the growth-whorl ageing technique provides a simple, accurate and time-efficient method that could probably be applied to populations of unknown TSLF age of other obligate-seeding *Banksia* or *Petrophile* species that show terminal growth similar to the species studied here (not all species do so). Quantification of the technique in other Proteaceae genera with obligate-seeder species that display a similar growth-whorl pattern (e.g. *Persoonia* species) would potentially allow individuals to be used to age populations. Furthermore, the ability to cross-reference among several species within one community would provide an accurate resource for the prediction of TSLF of a community as a whole.

Abbott (1985), Cowling *et al*. (1987) and Wills (2003) all encountered limitations similar to those we experienced in this study. For example, beyond certain ages, remnant growth whorls were obscured by leaf scars and bark thickness. This technique thus becomes limiting as individuals age, with greater variation becoming evident within populations of same-aged individuals; and the interpretation of growth whorls on older individuals as nodal scars becomes increasingly difficult, especially for *P. pulchella*. Similarly, in the oldest individuals (24 years TSLF) the swollen base of the stem of individuals of *B. ericifolia* often made it difficult to distinguish nodal scars. However, given the age of these individuals, the standard error of approximately 1 year encountered in the current study may prove insignificant.

Furthermore, this technique is reliable only if the plants sampled are even-aged. The 8-year Woronora TSLF site contained several larger individuals of *B. ericifolia*, which clearly had survived the last fire; these were not included in our study. However, if the nature of the recent fires is very patchy, then this technique would not be reliable for predicting the overall population age, because a mixture of two or more different-aged populations would appear in the number of growth whorls observed (cf. Wills 2003). However, this then allows a quantitative assessment of fire patchiness, or even inter-fire recruitment events (e.g. Witkowski *et al*. 1991), as multimodal frequency distributions will result. Growth whorls can thus be used to quantify the size and distribution of fire patches, thus measuring fine-scale variation in fire ages that may arise from heterogeneous burning patterns.

The additional growth characteristics examined here (stem girth and height, and canopy area and volume) lacked the directness and accuracy of the growth-whorl ageing technique for predicting plant age, and all showed larger variation within populations greater than 20 years old. Although stem girth was a reasonable predictor of plant age, girth and the other size characteristics may be influenced greatly by climatic and other environmental factors that are site-specific. However, if the purpose of predicting age is to implement prescribed burning practices, which only require a rough age estimate to within a few years, then girth and other growth characteristic may be suitable, as they will give a crude estimate of which life-history stage the individuals are presently in, and therefore the capability of these populations to regenerate after a fire. If an accurate estimation of population age is required, then the growth-whorl ageing technique would be more suitable.

The development of techniques that enable the prediction of TSLF age of a community is important for the maintenance of biodiversity. However, if these techniques can be applied irrespective of spatial variation then they could prove invaluable. We studied populations to the north and south of the Sydney region, results indicating that large-scale spatial variation had no major influence on the growth characteristics examined for all three study species. Therefore, the use of a chronosequence technique in this study was not limiting.

A sample size of 15 plants was adequate for accurate predictions of population age for all three species. This conclusion contrasts with that of Wills (2003) for *B. marginata* in Victoria, where sampling 50 individuals was considered to be more appropriate. This difference may be due simply to the use of the mode by Wills (2003) rather than the mean, as accurately estimating a population mode from a sample always requires a larger sample size than does estimating the population mean (Zar 1999). If this is so, then it will be more efficient to exclude outlying or unusual plants from the sample and then calculate the mean (as we did), rather than to include all plants and calculate the mode. An alternative explanation is that there may be different growth patterns in this particular species in the two study areas, even though the same age range of sites was used for both studies.

We also demonstrated that the age predictions produced by all three species are broadly compatible, although not identical, when applied to the different populations within the same site, at least for a relatively young site (~8 years TSLF). This result does, however, suggest that producing predictions from two or more species will improve the accuracy of the predicted time of the most recent fire. Nevertheless, prediction from a single species will be accurate to within a year and is thus still a reliable predictor of plant age.

Our study thus provides empirical evidence of the accuracy of the use of growth whorls for ageing populations of *B. ericifolia* and *P. pulchella*, as well as generalising the results of Wills (2003) for *B. marginata*. We expect that the technique will turn out to be valid for many other fire-sensitive Proteaceae species as well.

Acknowledgments

Thanks go to the New South Wales National Parks and Wildlife Service for the use of facilities, and especially to Mark Ooi for his help. Kate Langdon and Simon Rowe helped with the fieldwork, and the referees provided helpful comments on the manuscript. The sampling was carried out under licences from the New South Wales National Parks and Wildlife Service and the Sydney Catchment Authority.

References

Abbott I (1985) Rate of growth of *Banksia grandis* Willd. (Proteaceae) in Western Australian forest. *Australian Journal of Botany* **33**, 381–391.

Benson DH (1985) Maturation periods for fire-sensitive shrub species in Hawkesbury Sandstone vegetation. *Cunninghamia* **1**, 339–349.

Brown MJ, Podger FD (1982) Floristics and fire regimes of a vegetation sequence from sedgeland-heath to rainforest at Bathurst Harbour, Tasmania. *Australian Journal of Botany* **30**, 659–676.

Cowling RM, Lamont BB (1985) Variation in serotiny of three *Banksia* species along a climatic gradient. *Australian Journal of Ecology* **10**, 345–350.

Cowling RM, Lamont BB, Pierce SM (1987) Seed bank dynamics of four co-occurring *Banksia* species. *Journal of Ecology* **75**, 289–302.

Enright NJ, Lamont BB, Marsula R (1996) Canopy seed bank dynamics and optimum fire regime for the highly serotinous shrub, *Banksia hookeriana*. *Journal of Ecology* **84**, 9–17.

Enright NJ, Marsula R, Lamont BB, Wissel C (1998) The ecological significance of canopy seed storage in fire-prone environments: a model for non-sprouting shrubs. *Journal of Ecology* **86**, 946–959. doi: 10.1046/j.1365-2745.1998.00312.x

Gill AM (1981) Adaptive responses of Australian vascular plant species to fire. In 'Fire and the Australian biota'. (Eds AM Gill, RH Groves, IR Noble) pp. 243–272. (Australian Academy of Science: Canberra)

Keith DA (1994) Ecological and environmental impacts of natural fire regimes. In 'Bushfire! Looking to the future'. (Eds C. Brown, L. Tohver) pp. 33–39. (Nature Conservation Council of New South Wales: Sydney)

Keith DA (1996) Fire-driven extinction of plant populations: a synthesis of theory and review of evidence from Australian vegetation. *Proceedings of the Linnean Society of New South Wales* **116**, 37–78.

Lamont BB (1985) Fire responses of sclerophyll shrublands—a population ecology approach, with particular reference to the genus *Banksia*. In 'Fire ecology and management in Western Australian ecosystems'. (Ed. JR Ford) pp. 41–46. Curtin Environmental Studies Group Report No. 14 (Curtin University: Perth)

Lamont BB, Barker MJ (1988) Seed bank dynamics of a serotinous, fire-sensitive *Banksia* species. *Australian Journal of Botany* **36**, 193–203.

Lamont BB, Rees RG, Witkowski ETF, Whitten VA (1994) Comparative size, fecundity and ecophysiology of roadside plants of *Banksia hookeriana*. *Journal of Applied Ecology* **31**, 137–144.

Minitab (2000) 'MINITAB user's guide, MINITAB release 13.' (MINITAB Inc.: State College, PA)

Rogers RW, Westman WE (1977) Seasonal nutrient dynamics of litter in a subtropical eucalypt forest, North Stradbroke Island. *Australian Journal of Botany* **25**, 47–58.

Specht RL, Rayson P, Jackman ME (1958) Dark Island Heath (Ninety-Mile Plain, South Australia). VI. Pyric succession: changes in composition, coverage, dry weight and mineral nutrient status. *Australian Journal of Botany* **6**, 59–88.

Tapias R, Gil L, Fuentes-Utrilla P, Pardos JA (2001) Canopy seed banks in Mediterranean pines of south-eastern Spain: a comparison between *Pinus halepensis* Mill., *P. pinaster* Ait., *P. nigra* Arn. and *P. pinea* L. *Journal of Ecology* **89**, 629–638. doi: 10.1046/j.1365-2745.2001.00575.x

Wills TJ (2003) Using *Banksia* (Proteaceae) node counts to estimate time since fire. *Australian Journal of Botany* **51**, 239–242. doi: 10.1071/BT01074

Witkowski ETF, Lamont BB, Connell SJ (1991) Seed bank dynamics of three co-occurring banksias in south coastal Western Australia: the role of plant age, cockatoos, senescence and interfire establishment. *Australian Journal of Botany* **39**, 385–397.

Witkowski ETF, Lamont BB, Walton CS, Radford S (1992) Leaf demography, sclerophylly and ecophysiology of two *Banksia*s with contrasting leaf life spans. *Australian Journal of Botany* **40**, 849–862.

Witkowski ETF, Lamont BB, Obbens FJ (1994) Commercial picking of *Banksia hookeriana* in the wild reduces subsequent shoot, flower and seed production. *Journal of Applied Ecology* **31**, 508–520.

Zar JH (1999) 'Biostatistical analysis'. 4th edn. (Prentice-Hall: Upper Saddle River, NJ)

Manuscript received 12 May 2004, accepted 21 October 2004