Dating Fires from Balga Stems: The Controversy over Fire Histories Based on South-western Australian *Xanthorrhoea*

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Abstract

Knowing the fire regimes of an area helps one derive an understanding of landscape dynamics and assists in management planning. Between-fire interval, one of the components of the fire regime, has been reported from analyses of stems of the widely occurring *Xanthorrhoea* of south-western Australia. However, in the most sample-rich use of the method to date, both 'false positive' and 'false negative' fire dates have been obtained. As a result, the Western Australian Department of Environment and Conservation, the managers of the south-western Australian conservation estate, established a forum to consider the merits of the results so far and to ascertain a constructive way forward for further assessment of the method; this paper provides background to the debate, summarises the present situation (July 2006). It is recommended that rigorous testing of the method using different field investigators sampling a large number of stems at multiple sites take place in both *Banksia* shrublands using *X. acanthostachya* and in eucalypt forests using *X. preissii*. Consistency between field investigators and between stems would be sought as well as the matching of stem histories with validated fire occurrences determined by remote sensing and from Departmental records. Other recommendations are also made.

Introduction

Conservation of biodiversity in south-western Australia has special importance at regional, national and international scales. The southwest has the "greatest native floral diversity in Australia" and is one of the few areas of the world with such diversity (Mummery and Hardy 1994, p. 35). Most of the flora is found nowhere else. Its management necessarily involves fire, whether prescribed or unplanned. Fires at too long or too short an interval could eliminate some species. Thus, knowing the fire intervals in which the species have evolved and persisted has particular interest. While between-fire intervals are important, other components of the fire regime – type of fire (peat or above-ground), seasonality of fire occurrence and fire intensity (Gill 1975, Gill 1981) – can also be important.

In July 2006, the Western Australian Department of Environment and Conservation established a forum to discuss and attempt to resolve a scientific puzzle centred on the fire history of south-western Australia. On the one hand were many years of work using the stems of *Xanthorrhoea preissii* – 'Balga', or 'Grasstree' - as the primary mode of ascertaining the fire history of the eucalypt forest and woodlands of south-western Australia (Ward *et al.* 2001, Lamont *et al.* 2004). On the other hand were recent observations in shrublands which suggested an incompatibility between fire histories derived from *X. acanthostachya* and the evidence of recent fire histories - from fire records and satellite imagery - and the studied responses of selected shrub species to fire regimes (see Enright *et al.* 2005). In short, it appeared that the current understanding of fire chronologies using *Xanthorrhoea* stems was imprecise. Thus, there was a serious question raised over the method and a forum was established to address the issue. Most of the concern was over the apparent occurrence of fires at short intervals, especially during the period before European settlement when most fires were presumed to be set by Aboriginal people (Enright *et al.* 2005); fires as discerned by the *Xanthorrhoea*-stem method were reported at mean intervals between four and five years in both shrublands (Enright *et al.* 2005) and eucalypt (Jarrah, *Eucalyptus marginata*) forest (Ward *et al.* 2001) in the late 19^{th} century.

In this report, the issue of the accuracy of determining fire chronologies from *Xanthorrhoea* stems in forests, woodlands and shrublands is addressed by providing a botanical and ecological backdrop to the matter and by drawing attention to ways that the issue might be resolved.

Annual Stem-diameter Fluctuations and Fire Markers in *Xanthorrhoea*: The Basis of a Fire History

Growth habit of Xanthorrhoea

Xanthorrhoea is a picturesque genus of 28 species of endemic monocotyledonous shrub-like plants or trees with thick stems and a bushy crown of long needle-like leaves atop each of its few thick branches or single stem (Borsboom 2005). The genus is found along the entire eastern coast of Australia, across southern south-eastern Australia (including Tasmania), in south-western Australia, and in more-scattered populations in inland locations (Staff and Waterhouse 1981, Borsboom 2005). All *Xanthorrhoea* locations may be considered to be fire prone and mature individuals to be generally tolerant of repeated fires. Flowering in the form of tall terminal spikes may be stimulated by fire occurrence (*e.g.* Adamson and Osborne 1924, Gill and Ingwersen 1976, Baird 1977, Lamont and Downes 1979, Lamont *et al.* 2000, Ward and Lamont 2000; see also the reviews by Lamont *et al.* 2004 and Borsboom 2005).

Xanthorrhoea does not have the conventional woody growth rings of many Northern hemisphere tree and shrub species, in which each ring of the stem's cross section faithfully marks off the passage of another year of winter dormancy and summer growth. Rather, *Xanthorrhoea* is like many other 'arborescent' monocotyledons such as palms in having a plethora of vascular bundles – like the 'dots' on a transverse-cut banana skin - arranged across the cut stem with no sign of annual rings unless secondary thickening occurs in the form of discontinuous rings of secondary vascular bundles, perhaps annual (Staff and Waterhouse 1981). Such secondary thickening is often distinguished as "anomalous" (*e.g.* Lamont and Downes 1979).

X. preissii in southwestern Australia can be ascribed a visible annual-growth pattern in the form of wider and narrower widths of the true stem (Lamont and Downes 1979) – a succession of alternating bulges and troughs - found beneath a layer of persistent, dead, and tightly packed leaf bases. To see all the growth bulges of a *Xanthorrhoea* stem, a longitudinal section or a stem exposure is needed. The latter is achieved by removing all the leaf bases from the stem after freeing them from a resinous glue which has been softened by heating in an oven (Lamont and Downes 1979) – a sampling method which destroys the stem.

As the stems age ".. anomalous secondary thickening ... obliterates the annual increments in the lower parts of the stem" (Lamont and Downes 1979). Because of this, extrapolation from upper sections to lower may be necessary to estimate plant ages and fire frequency (Ward *et al.* 2001). Lamont and Downes (1979) found individual 25-cm stem segments to vary in growth rate from 1.1 to 2.4cm yr^{-1} so there may be considerable uncertainty in such extrapolation even though average lifetime growth rates of the plants seem remarkably constant at a site – at least in forest (Lamont and Downes 1979, Lamont *et al.* 2003).

Fire markers in stems

In addition to annual time markers like the growth bulges and troughs in *Xanthorrhoea*, a fire marker is necessary to determine fire history. In the case of fire-surviving trees with annual growth rings, fire scarring followed by renewed cambial growth adjacent to the wound allows the establishment of the time of a fire in relation to the present. Multiple scars tend to form in the same place on the tree so multiple episodes of scarring and regrowth can provide a convenient fire history of that 'point' in the landscape. Tree-ring methods have been used to date fire scars in south-western Australia but bias may occur from such methods due to the resistance of trees to scarring by low intensity fires, thereby giving lower frequency, longer intervals, than actual (Burrows *et al.* 1995). For some species of shrubs, annual growth is indicated by node formation on stems (Specht *et al.* 1958) so this method can provide an estimate of time since the last fire but not information about fire interval directly. The same time-since-fire information can be derived for other fire-killed plant populations if they have conventional annual growth rings. Because of the limitations of these methods, a method in which both years and fires are marked on stems, as perceived for *Xanthorrhoea*, has considerable appeal.

For *Xanthorrhoea preissii*, Lamont and Downes (1979) pointed out that given an association between flowering and fire and an ability to date stems by successive annual bulges and troughs: "information could be obtained on fire frequencies at particular sites, even prior to European settlement". However, subsequent work has shown that the proportion of plants flowering increases asymptotically with height to about 85-95% of 2-3 m height populations (Ward and Lamont 2000) and that season of burn is important (Lamont *et al.* 2000). The analyses of stems using fire-based flowering would therefore miss numbers of fires according to the height of the specimen; this flowering-based method has since been succeeded by a non-destructive technique using fire-marks on smoothed *Xanthorrhoea* stems in south-western Australia (Ward 1998; Ward *et al.* 2001). This non-destructive method is the one under particular scrutiny here.

In the *Xanthorrhoea spp.* concerned, the passage of fire is marked by the trapping of a dark chemical compound into the vasculature of the leaf bases at the base of the crown thereby causing an annulus of black stain which contrasts with the lighter background of annual cream and brown bands on the stem (Ward *et al.* 2001). The lighter-coloured bands are revealed after grinding back the rough, often charred, outer parts of the tightly packed dead leaf bases (Ward *et al.* 2001). Each pair of brown and cream bands revealed on the smoothed surface represents one year (Ward *et al.* 2001). By examining the annual markers and the fire markers a fire chronology can be established (Ward *et al.* 2001).

The pattern of annual colour banding "is difficult to explain" but may be based on tannin differences in leaf bases reflecting levels of environmental stress during the growing season (Lamont *et al.* 2003). Another possibility is that if leaf bases had the same length across the true stem's bulges and troughs, the partial grinding down of the dead leaf bases externally to give a smooth surface would differentially-truncate leaf-base lengths; if leaf bases were weathered to equal depths from the outside, the different extents of truncation by grinding would reveal coloured annual bands reflecting a constant depth of weathering and leaching of the water soluble tannins noted by Colangelo *et al.* (2002).

Consistency in Fire History Reconstructions using *Xanthorrhoea*

Consistency is expected in the ideal method. It may be expected to be so between different observers, between results from adjacent stems, and from the evidence of shrub dynamics, fire behaviour and oral histories, for example. These topics are considered briefly below.

1. *Consistency between observers*. One person only has processed *Xanthorrhoea* stems and published the results as yet (David Ward) so all reports of fire dates in this paper are the result of his work. However, in an unpublished report on stem analyses in woodland, Williams (2001) reported difficulty in identifying annual bands, interpreting partial black bands and dealing with stem segments which had rotting leaf bases. Scientifically, there is a need for repeatability of results between field investigators. G. Van Didden has also processed stems (D.Ward, personal communication) but has not published the results.
2. *Consistency of results between closely-spaced stems of the same* Xanthorrhoea *species ('internal' comparison) at the same site*. Enright *et al.* (2005) reported 'false positives' and 'false negatives' for fire occurrence discerned from *Xanthorrhoea acanthostachya* stems in their 50ha *Banksia*-kwongan (shrubland, heathland) study area. Ward (in press) asserts, however, that there were "only two" stems of the 15 examined (13.3%) with anomalies in their fire history. In response to this, Enright *et al.* (in press) note that there were many more anomalies present than those of the two pairs of plants highlighted in their original paper (Enright *et al.* 2005): "even for two recent and extensive fires (in 1984 and 1991) only 11 and 8 (respectively) of 15 grasstrees recorded these fires, only 5 recorded both, while another indicated fires in both 1979 and 1981 when there were none" identified (Enright *et al.* in press). It would be interesting to know the full extent of 'false positives' and 'false negatives' in the study: what bias do they introduce to the mean interval? The evidence of Enright *et al.* (2005) that the method is imprecise in shrublands using *X. acanthostachya* appears convincing and forthcoming unpublished data appears to reinforce this view (commentary-point 3 in Enright *et al.* in press,).

However, the method using another grasstree, *X. preissii*, in moister areas supporting forests, has not had the same level of published scrutiny. In each forest site, "three or four single-stemmed grasstrees of contrasting heights (ages) were chosen" for analysis (Ward *et al.* 2001), the results for fires agreeing with records kept by the management authority for the past 20-40 years in the 50 sites examined and, as a highlight, in an area where there had been fire exclusion for 66 years - thereby "supporting both the ageing and fire history technique" (Ward *et al.* 2001). Listing of fire dates obtained from the agency record and from the stems would allow independent assessments to be made of the results.

3. *Consistency with the dynamics of shrubs or other associated plants or organisms.* If the fire intervals discerned from the *Xanthorrhoea* stems implied that there would be extinction of co-occurring shrubs or other organisms on the site, then the method – or the knowledge of population dynamics of the plants in question - may be called into question. The argument against short intervals and the persistence of certain shrubs may be stated briefly as follows. Shrub species may be classified as 'seeders' or 'sprouters' with or without regeneration from seedlings concentrated in the period soon after fire (after Noble and Slatyer 1980). In shrubland fires all plants may be expected to experience top-kill because the plants are relatively short and the fires fully scorch them or consume their crowns. With two fires within a suitably short interval – less than the time for seedlings to develop seeds - 'seeder' species without soil-stored seed may be eliminated because potential sources of seed are undeveloped locally. For the 'seeder' *Banksia hookeriana* in the study site of Enright *et al.* (2005), 5 years has been given as the time to first flowering; for *B. prionotes* the period was 8 years (see Groenveld *et al.* 2002). Important exceptions to this simple consideration of local-extinction theory occur if:

(i) mixed mature and immature stands are burnt in the same fire and seed shed by mature plants disperses across all burnt sites (after Hammill *et al.* 1998);

(ii) seeds are shed from partially-serotinous fruits (*i.e.* some open up without fire-stimulation), or non-serotinous fruits along unburnt edges which disperse into the burned area and allow establishment in regrowth. This would be expected to have special applicability after patchy fires. Establishment may fail if the recovering vegetation does not provide suitable habitat for seedling establishment; Bradstock (1991) found that predation of newly germinated seedlings – even those in cages – may have been the factor limiting establishment in 'intact' vegetation.

These exceptions require that not all sites will be burnt at short intervals. How quickly a site may be replenished with 'seeders' after their fire-induced elimination is unknown but will be expected to be a function of the distance of dispersal from a mature source – Groenveld *et al.* (2002) considered that 95% seeds spread up to 15m after fire but the extreme distance may be the most important. Mature sources of 'seeders' may exist as small patches within a shrubby matrix of 'sprouters' rather than be completely intermixed; are the seeder *Banksia* species intimately mixed with *Xanthorrhoea* and has this always been the case?

Enright *et al.* (2005), referring to a number of sources, suggest that a fire interval "compatible with coexistence of many fire-killed, woody species ...of south-western Australia is 12-16 years". The extent of occurrence of patches of 'seeders' with fire intervals longer, or shorter, than this would depend on the extent and skewness of variance about the mean fire interval (see McCarthy *et al.* 2001 for various Australian-based models); the study of Groenveld *et al.* (2002) assumes the frequency distribution of intervals is Gaussian but a skewed distribution would be expected to influence outcomes, particularly at short mean intervals. The means and standard deviations of intervals have been published but shapes of frequency distributions of intervals, assumed Gaussian, have not. However, unpublished data of "fires per decade" collated from many sites in the Jarrah forest showed more-or-less Gaussian distributions at the end of the 19^{th} century and increasingly skewed distributions subsequently (Ward and Van Didden 1997).

The research backing the shrub-dynamic models has been extensive and thorough (see Groenveld *et al.* 2002), but like all models various assumptions such as minimum intervals for fire spread (see below) and distances of seed dispersal (see above) are necessary. Models can be changed readily as more information comes to hand. Consideration needs to be given to the levels of fire-regime components – interval, intensity and perhaps seasonality – that define the <u>extinction</u> limits of the 'seeder' species rather than using modelling to determine persistence of a contemporary or maximum abundance. Is the assumption of canopy death in all fires valid? Like *Xanthorrhoea* in Jarrah forest, could some individuals be burned beneath while canopies survive?

4. *Consistency with fire behaviour knowledge.* If the results of fire history demand intervals that are too short for enough fuel to accumulate and fire to carry, then doubt would be cast on the method, or on our knowledge of fuel accumulation and fire behaviour. Abbott (2003), reviewing the south-western Australian literature, notes that minimum fire-free periods after a previous fire event may be as short as three years under severe weather conditions in shrub lands of the northern sandplains while in eucalypt forest (Jarrah) minimum intervals may be anything from 3 to 12 years across a spectrum of sites from generally wetter to drier conditions. Minimum intervals are difficult to define and are a function of extreme weather conditions. If extreme weather is necessary for short intervals to be feasible, do these occur extensively each year?

5. *Consistency with oral history, changes of management policy.* These topics are elaborated in Lamont *et al.* (2003) and lend support to the fire history derived for eucalypt (Jarrah) forest. Wallace (1966) for example, considered that Aboriginal people in south-western forests burned the forest every 2 to 4 years. Correlations are broad with this type of evidence. Fires could be common in the area but it does not necessarily follow that the mean fire interval at a point is short. On the other hand, the intervals could be short; critical examination of quotes in the historical literature is necessary.

The value of evidence used to establish consistency is varied and consistency in itself does not ensure accuracy. All the evidence may be wrong; it may all be correct; or it all may be probabilistic. The last of these is often true so it becomes a matter of degree as to which evidence is better than another. One would expect that consistency between field investigators and between closely neighbouring stems was critical. With shrub and fire models, quality can be evaluated. With oral evidence, accuracy of memory is involved and estimates of intervals may be based on regions – 'there were fires at two year intervals somewhere in the region' – rather than at a point – 'there were fires at two-year intervals here'; discrimination of these differences by local observers appears to be rare. Perhaps the historical data most likely to be unequivocal and consistent between observers would be categorical data – such as 'all fires occurred in summer'. However, local histories may represent all the supporting evidence that is available in the most contentious periods of the *Xanthorrhoea* record; fire-behaviour information under current conditions may be sought but do these represent the fuel conditions of the past? What was the proportion of 'seeders' and 'sprouters' in shrublands on the sandplains at the end of the 19th century or earlier?

If data from all grasstree stems from a range of vegetation types, climates and likelihoods of past Aboriginal presence all show similar mean intervals throughout the same periods of time then a search for explanations other than fire occurrence, or mixed with fire occurrence, may be tempting (N. Burrows, personal communication). The data so far show a more-or-less consistent 3-4 yr mean interval for the 120 years after 1750 in eucalypt forest (Ward *et al.* 2001), to slightly increased mean intervals of about 4 years by the end of the 19th century in both forest (Ward *et al.* 2001) and shrubland (Enright *et al.* 2005), and then a divergence most evident in the late 20th century when mean intervals of around 10 years in shrubland (Enright *et al.* 2005) and about 20 years in forest (Ward *et al.* 2001) were found. A comparison of data from the 50 forest and woodland sites of Ward *et al.* (2001) against rainfall, and thus against correlated changes of fuel dynamics, could be instructive in relation to minimum intervals recorded. Unpublished material (Ward and Van Didden 2003) indicates a "likely traditional burning cycle of 8-10 years" at the turn of the 19th century in the Coolgardie District.

Consistency, along with accurate cross dating with other methods, would give greater confidence in the method. The cross dating conducted so far – see above - has been with known occurrences of fires (from fire records, maps, anecdotal accounts of fires, images from remote sensing, all of which have their own limits). The evidence for accuracy appears to be stronger for data from *X. preissii* in forests (Ward *et al.* 2001) than for *X. acanthostachya* in shrubland (Enright *et al.* 2005). The obvious hypothesis to test, albeit a broad one, is that the dating techniques for fire presence (and thus intervals) are more accurate in forest (with higher rainfall) than shrubland (lower rainfall).

Dating Fires from *Xanthorrhoea* Stems: Issues

There are a number of points that require further examination with respect to the preparation of stems of *Xanthorrhoea* spp. for the assessment of fire-interval distributions.

1. *Choice of plant*. Plants chosen for analysis are likely to be the tallest, oldest and the least branched. Choosing such plants minimises processing time and gives the greatest return in terms of fire history. Is there bias associated with such choices? There is a decreasing opportunity for plants to catch alight and thus record a fire with increasing height (Vines 1968; Lamont *et al.* 2003), thereby causing inaccurate records of ever longer between-fire intervals in taller plants.
2. *Expression of bands and bulges*. (a) Annual bands are discerned by "subtle colour variations" which are "sometimes difficult to see" (Enright *et al.* 2005); "they are not always visible throughout the length of the plant" (Lamont *et al.* 2003). How

large is the margin of error due to difficulties in the discernment of bands? Could it be much more than 1-year in shrubland (Enright *et al.* 2005)? Annual-band distinctiveness declines with age because some pigments are water soluble (Colangelo *et al.* 2002, Lamont *et al.* 2004). (b) The "mantle splits and collapses and the bands darken and merge ... at the base of old plants" (Lamont *et al.* 2004), perhaps because of secondary thickening there which "obliterates the annual increments in the lower parts of the stem" (Lamont and Downes 1979). Furthermore, resin accumulation and cumulative fire damage can affect the "lower portion of stems" (Enright *et al.* 2005). Leaf bases close to the stem may be internally black just like fire bands (D. Ward, personal communication) and these are likely to be close to the outer surface of the stem near its base. The stem base also has the maximum extent of secondary thickening and potential stem distortion, the maximum weathering of leaf bases and the maximum likelihood of leaf-base loss from burning and, therefore, perhaps the maximum likelihood of error. If basal sections are taken out of the record or ignored then fire histories are truncated; how much of the stem can be considered to be unsuitable?

3. *Suitable sample size.* (a) In the data of Enright *et al.* (2005) there is a negative trend in the proportion of stems showing fire marks with time (data of Figure 1 in Enright *et al.* 2005); this has been attributed to patchiness of fires (Enright *et al.* 2005). In a response to the Editor of *Austral Ecology* regarding Enright *et al.* (2005), Ward (in press) suggests that 15 plants was an inadequate sample to determine fire patchiness. What is an adequate sample size and what is an appropriate scattering of sample plants to determine patchiness in various circumstances? Patchiness of fire within a study area can be considered to be that due to: the heterogeneity of burning within a fire perimeter –with a vertical dimension as well as a horizontal one; and the partial impingement of a fire into the study area. Patchiness in the fire, all else being equal, would be evident in the lack of a fire mark in some plants but not others; without fine-scale evidence of fire presence, it would be hard to tell if the record was a 'false positive' or a reflection of the patchiness of the fire. (b) Standard deviations for fire intervals in different eras are quite large, about half the mean (Enright *et al.* 2005); a larger sample could be expected to reduce them. (c) The number of specimens available for sampling declines with age of the plant: in Enright *et al.* (2005) there were only 3 old plants among the 15 plants sampled.
4. *Site, vegetation and species*. Two species of *Xanthorrhoea* have been used – *X. preissii*, typical of forests, and *X. acanthostachya*, found in heathlands (Lamont *et al.* 2003). To date, it has been the shrubland results that have been found to be at variance with the results of cross-checks (Enright *et al.* 2005). Is there a species effect? Is it possible that 'false positives' are due to black resin created in live leaf bases due to stresses such as drought in the drier shrubland site, and not just due to fire? If the latter is true, why would just one year's leaves, making a black annulus on the stem, be affected? Or, are the growth rates and seasonality of growth in shrubland sites such that growth bands are not annual? The latter could explain some of the 'false negatives'. It is presently unreported how the apparent discrepancies between plants (Enright *et al.* 2005, Figure 2) are distributed across the sampled landscape - on dunes but not in swales of the study area, for example.

A comparison between dates of perceived fires on large numbers of *Xanthorrhoea* stems of different height, age and distance from nearest other sample stem in forests and in shrublands with well-known fire histories seems worthwhile; fire histories derived from the *Xanthorrhoea* stems could be compared with the nearby proportion of shrubby 'seeders with canopy-stored seed'. A test of the stress theory for black bands could be considered.

5. *Geographic applicability*. (a) At a local to regional scale, Burrows and Wardell-Johnson (2003) caution against the use of histories derived from *Xanthorrhoea* for areas without *Xanthorrhoea* occurrences. As Lamont *et al.* (2004) observe: "[populations of] grasstrees are not randomly distributed across the landscape". Thus, any history derived from grasstrees cannot be assumed to represent areas between locations of sample populations. (b) In a broader geographic sense, Lamont *et al.* (2004) have noted that "band development requires high levels of seasonality" in the climate for its expression. It may also be necessary for stem growth rates to be high enough to express seasonal change. Where the method would be predicted to work could be ascertained using a suitable environmental analysis perhaps. (c) At a national scale the use of *Xanthorrhoea* spp. for fire dating has not been successful outside south-western Western Australia as yet (Borsboom 2005, Enright *et al.* 2005).

Conclusions and Recommendations

Given the difficulties of applying traditional tree-ring and fire-scar methods in Australian ecosystems to determine fire intervals, using commonly occurring *Xanthorrhoea* stems of south-western Australia has considerable appeal. However, difficulties with the method have been encountered and, given the published evidence of Enright *et al.* (2005), further research on the method is warranted. There are many recommendations that could be made; some are made below but there are others embedded in the text above.

Recommendation 1. It is recommended that: a series of *Xanthorrhoea* stem analyses for fire history be conducted as part of a rigorous statistical examination of the technique. Devised by a professional statistician, the examination of the technique would include stems of different *Xanthorrhoea* species processed and examined by different field investigators in contrasting vegetation types (including Jarrah forest and northern shrub lands) in sites with long, validated, and agreed, fire histories using an adequate sample population. The effect of stem height, and perhaps branching, could be considered. A re-plotting of data for the 50 forest sites of Ward *et al.* (2001) against the known rainfall gradient across Jarrah forest - where there are corresponding changes in fuel dynamics - could be instructive as a preliminary exercise; the expectation would be that a difference in minimum intervals between fires, at least, would be evident.

Recommendation 2. It is recommended that: accumulation rates of live and dead materials in defined, structural, fuel arrays of northern shrublands be examined in relation to the probability of fire carriage and consequent fire properties under different weather conditions in the few years after a previous fire. Arrays across dune sequences would be examined. Experiments would be helpful but safety considerations may preclude them.

The situation for forests is better known and there is the promise of better understanding arising from Project Vesta of the CSIRO and the Western Australian Department of Environment and Conservation.

Recommendation 3. It is recommended that: shrub modellers explicitly determine the probabilities for the marginal persistence of a small population of 'seeders with canopy-stored seed' that could expand across the northern sandplain shrublands if longer intervals between fires followed in the manner suggested by the *Xanthorrhoea* stem histories. As part of this exercise, the sensitivity of the model to the time of first fire from a previous occurrence could be examined as well as the sensitivity to relatively long-distance dispersal of seed and fire patchiness (related to time-since-fire and weather?). Perhaps the results could be expressed in terms of the proportion of dunes, swales and slopes occupied by 'seeder species' (with canopy-stored seed) or other species.

Recommendation 4. It is recommended that: the oral and recorded fire history of the region in and around the study site of Enright *et al.* (2005) be examined and published if extensive enough. Such a history would critically examine knowledge of what is, and is not, known for the period of human occupation, especially that where the *Xanthorrhoea* record suggests short-interval fires. Topics would include: seasons of fires; sources of ignitions; techniques of ignition; areas of fires; types of shrub responses to fire; heights of shrubs across dunes and swales; fuel types (especially grasses) and fire properties in swales and dunes; dispersal distances of seeds by animals and wind; and intervals between fires at a point or in the region.

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