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The effects of fire and quokkas (*Setonix brachyurus*) on the vegetation of Rottnest Island, Western Australia

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Abstract

Three different plant communities have dominated the vegetation of Rottnest Island over the past two centuries; low forest, *Acacia rostellifera* scrub, and sclerophyllous heath. In 1997 a fire burnt 90 ha of heathland and provided an opportunity to examine the relationships between dominant vegetation types, fire and grazing by quokkas (*Setonix brachyurus*). Our study and the literature indicated four major findings.

- Burnt heath recovered slowly if grazed. If not grazed, heath regenerated rapidly to become dense, tall and weed-free compared with the surrounding heathland, and the number of native species increased.
- Where there was no grazing, all three vegetation communities were able to become established immediately after the fire. Four and a half years after the fire, *Acacia* thickets dominated in some areas and reached 3-4 m in height, overshadowing a group of self-seeded *Melaleuca* seedlings and outcompeting heath species. It is anticipated that the *Melaleuca* will emerge and dominate when the shorter-lived *Acacia* declines, and that heath will continue to occupy open areas.
- The three dominant vegetation communities can be regarded as stable state alternatives. Heath will dominate if there is heavy grazing, as the young trees and *Acacia* are palatable and so cannot regenerate. Low forest dominates if there are only occasional widespread fires. Fire triggers the release of seed stored in tree canopies, and also temporarily reduces the local quokka population, giving seedlings a chance to become established. *Acacia* dominates if there are frequent fires and little grazing. Frequent fires stimulate *Acacia* to sucker from underground parts, while competition from tree species disappears, as trees are killed by fire, and if a second fire occurs before young trees set seed, they are eliminated locally.
- It appears that occasional widespread hot fires, presumably started by lightning, are likely to have occurred on Rottnest Island over the millennia before European settlement for *Melaleuca/Callitris* forest to have persisted.

Key words: Rottnest Island, vegetation, fire, quokkas, vegetation dynamics

Introduction

A row of islands lies off the coast of Perth, Western Australia, the largest of which are Rottnest Island (1900 ha) and Garden Island (1200 ha). These aeolianite limestone islands are remnants of Pleistocene dune ridges, left above sea level after the last post-glacial marine transgression. The vegetation of Rottnest and Garden Islands has strong similarities (Marchant & Abbott 1981). The majority of their native plant species are common to both islands, including the three tree species, *Melaleuca lanceolata*, *Callitris preissii* and *Pittosporum ligustrifolium*, as well as the tall shrub *Acacia rostellifera*. Small wallabies graze both islands, quokkas (*Setonix brachyurus*) on Rottnest Island and tammars (*Macropus eugenii*) on Garden Island. Over the past 200 years, the vegetation of Rottnest Island has been heavily exploited by humans to the point where the concept of 'natural' vegetation is almost irrelevant. However, fossil pollen data and historical reports over the last two centuries make it possible to trace changes in the vegetation types that have dominated the island, and the processes associated with the changes. The parallel with Garden Island, which has suffered less disturbance, serves as an additional check or reference point.

We attempt to find a conceptual framework for changes in the vegetation of Rottnest Island. The dynamics are studied from three aspects; the historical information is reviewed, the vital attributes of dominant species are assessed using criteria established by Noble & Slatyer (1980) with a view to predicting their response to a disturbance event, and the recovery of the vegetation after a fire in 1997 is examined.

Vegetation history

There have been significant changes in the vegetation of Rottnest Island since separation from the mainland

6500 years ago. Fossil pollen of native species dominant on the coastal plain today, such as fire tolerant *Eucalyptus, Casuarina, Banksia, Macrozamia* and *Xanthorrhoea*, have been found in the swamps on Rottnest Island, dating back to the early Holocene (Storr *et al.* 1959; Churchill 1960; Backhouse 1993). All of these genera became extinct on Rottnest after separation when a different set of influences came into operation.

There has been some uncertainty as to whether there were fires on Rottnest after the island was separated from the mainland and before European settlement. Abbott *et al.* (2000) suggested that the islands off Perth escaped anthropogenic disturbance, especially fire, for at least 5000 years, as the Aboriginal people did not use watercraft in this area (Abbott 1980). However occasional fires do appear to have occurred. Core samples taken from Barker Swamp reveal that layers of charcoal, which could only have resulted from fires, were deposited in the sediments. Backhouse (1993) discovered 14 charcoal bands laid down in the 1200 years between about 6850 and 5645 years before present indicating that fires occurred more than once per century. The frequency of the bands thereafter decreased to one per 350-400 years. The pollen record indicates that this decrease is because the fire-prone *Callitris* and *Eucalyptus* that had dominated the area disappeared from the catchment of the swamp and were replaced by a comparatively sparse low cover of *Pimelia* and Asteraceae. Other fires could have occurred elsewhere on Rottnest during this period. Groves (2001) separated large charcoal fragments (>1 mm) from small fragments (5-150 mm) in sediment cores from Barker Swamp, assuming that large fragments would indicate local fires on Rottnest Island while small fragments may have been transported on the wind from fires on the mainland. He concluded that major local fire events on Rottnest over the past 5300 years occurred about every 210 years while major regional fires (probably on the mainland) occurred about every 120 years. Unfortunately it is now difficult to resolve the question of the frequency of fires on Rottnest Island by studying cores from other catchments, because most of its swamps have been bulldozed to obtain marl for roadbuilding (Playford 1988; J Dodson, University of Western Australia, personal communication).

Today many of the native plant species on Rottnest and Garden Islands are killed by fire, including *Callitris* and *Melaleuca*, with regeneration only taking place through germination of seeds (Bell *et al.* 1987). In the absence of very frequent fires, the critical factors for vegetation are exposure to wind and salt, lower rainfall than the mainland with summer drought, and grazing by quokkas. Reports on the vegetation of Rottnest Island by visitors in the 17th and early 19th century mention the wooded nature of the island. In 1822 the botanist Cunningham reported that *Callitris* was abundant on the island 'to the point of monotony… occasionally relieved by … *Melaleuca* … and the more elegant *Pittosporum*' (quoted by Pen & Green 1983). Early reports of Garden Island described a similar picture. In 1827 Fraser reported areas 'thickly covered with cypress [*Callitris preissii*] and … extensive thickets of arborescent metrosiderous' [*Melaleuca lanceolata*], and in 1829 Fremantle noted that the vegetation was '… covered in a small kind of pine [*Callitris*] …. from the thickness of the trees and underwood it was impossible to move' (quoted by Wykes & McArthur 1995). However, Wilson described a very different landscape after a visit to the central southern part of Rottnest in 1829; '… miserably barren. The hummocks are sand hills, many of which are entirely destitute of any kind of herbage, in the valleys are some stunted trees and shrubs and very little grass' (quoted by Marchant & Abbott 1981). He had probably described the large blowout at Barnett's Gully, but his description also fits the desolation that follows fire on Rottnest Island.

In 1831 settlers started farming on Rottnest Island. In 1838 the prison was established and farming was intensified, with the introduction of pigs, horses, rabbits, sheep and cattle, and crops of wheat, barley, rye, stock fodder, fruit and vegetables, even tobacco and castor oil at times (Somerville 1976; Ferguson 1986). Wood was taken for fuel, and buildings and roads were constructed. Quokkas became scarce. The Aboriginal prisoners used fire to hunt them for food, and vice-regal parties hunted them for sport towards the end of the 19th century, as did tourists in the early 20th century (Storr 1963). The vegetation changed under the new regime of frequent fires, low wallaby numbers and removal of trees. In 1855, Jewell reported areas of dense scrub, *Acacia rostellifera* (quoted by Marchant 1977). In 1905, Lawson wrote that the interior of the island was covered with very dense *Acacia* scrub, quite impenetrable apart from the 'rides' that had been cut through it, and that trees were absent except in the settlement at the eastern end of the island and most of these were introduced (Lawson 1905). By 1919, Weir estimated that two thirds of the island (1200 hectares) was covered by *Acacia* scrub (Storr 1963), and in 1929 Glauert wrote that 'much of the island is clothed in dense wattle [*Acacia*] scrub' (quoted by Pen & Green 1983).

In 1917, legislation was passed prohibiting shooting on the island (Anon 1917), but shooting apparently persisted because in 1926 J B Stark was appointed Honorary Guardian under the Game Act 1912-13 (Storr 1963). New laws were promulgated in 1933 prohibiting firearms on the island altogether (Anon 1933). The quokka population recovered during this period, with an abundant food supply of nutritious *Acacia rostellifera* and palatable introduced plants associated with crops and improved pastures. By 1932 it was reported that quokkas were more numerous than before and were damaging crops (Storr 1963).

Overgrazing by quokkas prevented the regeneration of *Acacia* scrub, which by 1941 was fragmented and covered only 400 ha (Pen & Green 1983), one third of the area it had occupied 22 years earlier. In the mid-1950s, *Acacia* was even more restricted, to sheltered valleys and slopes (Storr *et al.* 1959). Here it was 3-6 m high, and often associated with the climber *Clematis linearifolia*. *Callitris* had apparently become so rare that it was not mentioned at all. The scrub was replaced by grassy heath consisting mainly of *Acanthocarpus preissii* and tussock grass *Austrostipa flavescens.*

In 1955 a major fire burnt two thirds of Rottnest Island, and a year later there was a widespread fire on Garden Island. The recovery of the vegetation on both islands was documented (Storr 1963; Baird 1958) and the effects of fire on the vegetation of the islands have been widely discussed since this time (White & Edmiston 1974; O'Connor *et al.* 1977; Hesp *et al.* 1983; Osborne *et al.* 1985; McArthur 1996a, b; 1998; Abbott *et al.* 2000).

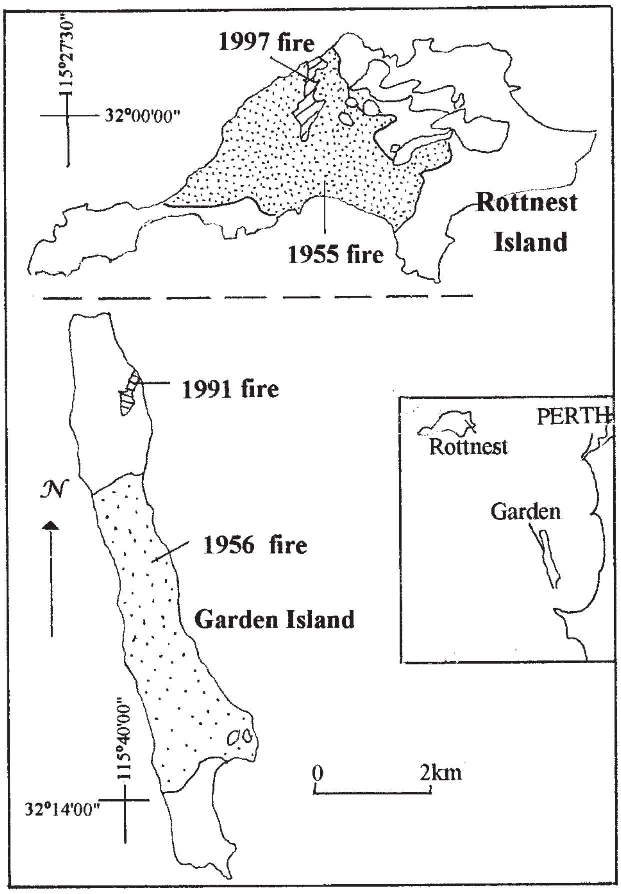


Figure 1. Location of major fires on Rottnest and Garden Islands since 1955.

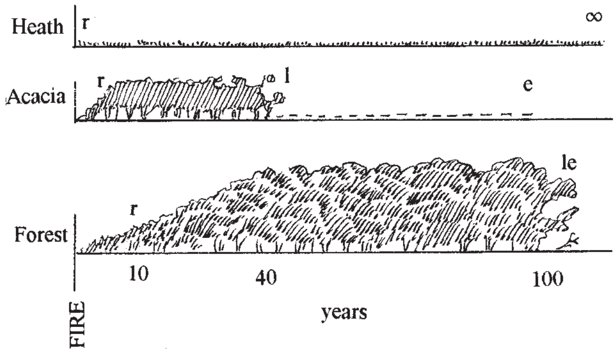


Figure 2. Vital attributes of the three dominant communities (r representing the time at which the species reaches reproductive maturity, l the end of the lifespan, and e the time at which all propagules, plants and seeds become extinct). After Noble & Slatyer 1980.

During the latter half of the 20th century, the cover by forest and woodland was further reduced, to 7% by 1974 (White & Edmiston 1974), while heath became increasingly widespread. The primary management objective over this period was the provision of tourist amenities, as the island was an A Class reserve with the gazetted purpose of public recreation, with about 500 000 visitors per annum by the end of the century. Maintenance of the quokka population was another concern, as quokkas were endearing to tourists and also a declared threatened species. Fires were rapidly controlled if they occurred. A small fire on Garden Island in 1991 was studied in some detail (McArthur 1996a,b; McArthur 1998). A restricted fire on Rottnest Island in 1997 and the subsequent response of the vegetation is discussed in this paper. Fig 1 shows the positions of the four major fires on Rottnest and Garden Islands over the past fifty years; all fires occurred at the height of summer (end of January or during February).

Attributes of dominant plant species on Rottnest Island

Melaleuca lanceolata/Callitris preissii low forest, *Acacia rostellifera* scrub and *Acanthocarpus* heath have dominated the Rottnest Island flora at various times. Noble & Slatyer (1980) suggested that successional changes in plant communities subject to recurrent disturbances can be predicted by examining the vital attributes of the dominant component species. Applying their criteria, *Melaleuca/Callitris* would be classified as CI (seeds are stored in the tree canopy not the soil, and germinants are intolerant of competition). Reproduction of *Melaleuca/Callitris* is solely propagule-based. These are bradysporous species with seeds stored in the capsules or cones in the canopy. The seeds are short-lived and there is no seedbank in the soil (McArthur 1996a). The trees are killed by fire, but dense germination in the vicinity of burnt parent trees can follow burning (Baird 1958; McArthur 1998; White & Edmiston 1974). They regenerate in open conditions, being unable to compete with conspecific adults. The trees take up to 10 years to reach sexual maturity (C Hansen, environmental officer, Rottnest Island Authority, personal communication), and their life span is about 110 years (McArthur 1998), although one *Callitris preissii* of about 140 years has been recorded (Powell & Emberson 1981). Fig 2 gives these vital attributes in diagrammatic form.

Acacia rostellifera falls into Noble & Slatyer's category of SVI (seeds are stored in the soil, but the species also reproduces vegetatively; germinants are comparatively intolerant of competition). The species germinates from seed and also resprouts after fire from underground parts up to 50 m distant from the parent plant (Storr 1963). *Acacia rostellifera* seeds are hard-coated and have a prolonged dormancy, in common with the great majority of *Acacias* (Simmons 1981). Successful regeneration requires open conditions such as follow disturbance, especially fire. The shrubs have a lifespan of about 40 years (Powell & Emberson 1981; McArthur 1996a), but become senescent on the islands after about 20 years (White & Edmiston 1974; McArthur 1996b).

The heath species *Acanthocarpus preissii* and *Austrostipa flavescens*, which together with the introduced *Trachyandra divaricata* make up two thirds of the vegetation cover in the heathland surrounding the burnt zone, are capable of regenerating vegetatively or from seed. *Trachyandra* is a rhizomatous herb, growing to 0.35 m, with ribbon-like leaves. These three dominant species are widespread on Rottnest Island and for the purposes of this analysis we assume that there is a constant supply of propagules from the surrounding heathland. *Acanthocarpus*, *Austrostipa* and *Trachyandra* are considered tolerant of competition as they continue to

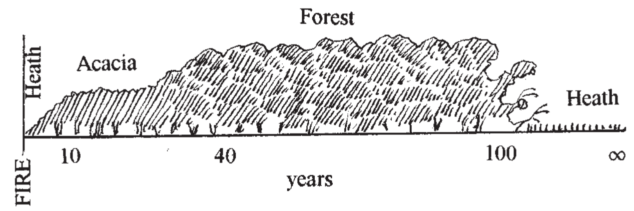


Figure 3. Vegetation replacement sequence for Rottnest Island forest-woodland-heath system following a fire, in the absence of further disturbance. After Noble & Slatyer (1980).

regenerate and are self-maintaining within an established heath environment, although they occur only occasionally as understorey species in dense *Melaleuca/ Callitris* or *Acacia*. The fourth major component of the heath, *Thomasia cognata* (providing some 17% of vegetation cover) reproduces from seed alone. For this analysis, we classify the species of the heath as DT (seeds are dispersed widely so are available at any time, and seedlings are tolerant of competition).

A sequence can be predicted for the development of the three vegetation communities following a fire and in the absence of further disturbance except perhaps for light grazing (Fig 3). All species germinate or resprout immediately after fire. Most heath species regenerate from seed and rootstock, and reach maturity rapidly. The *Acacia* forms dense scrub 3-4 metres high within 5 years. Senescence starts at about 20 years (McArthur 1996b) with deterioration from the centre, and the plants die out by 40 years, leaving a seedbank in the soil for about 60 years or more. *Melaleuca* and *Callitris* are more slow-growing, but as the *Acacia* declines the forest species grow through and dominate until the last survivors die off at about 110 years. Thus, immediately following a fire and in the absence of further fire or grazing thereafter, all species would regenerate in the presence of seed and/or rootstock. The heath would dominate briefly before being overwhelmed by *Acacia* (Fig 3). The tree species would only grow through the *Acacia* as the latter thinned out and then died by 40 years of age. By about 110 years the *Melaleuca/Callitris* would have died leaving no seedbank, the *Acacia* seeds left in the soil would also have died by this time, and only the heath species would persist.

Materials and methods

Plant nomenclature is based on Pacskowska & Chapman (2000) and information from the Western Australian Herbarium.

Field survey

On 17th February 1997 a fire (started by a power pole) burnt through about 90 ha on Rottnest Island between the centre of the island and the north coast (Fig 4). The vegetation consisted of *Acanthocarpus* heath, apart from a small zone of coastal heath at the northern extremity (which is not considered in this survey). Several plantations adjoining the burnt area were protected from the fire by firebreaks, and the only trees burnt were two *Melaleuca lanceolata*. The burnt area and the immediately surrounding *Acanthocarpus* heath that was not burnt will be referred to as the Research Site. Within five months the Rottnest Island Authority had fenced 70% of the burnt area into six separate plots, using 1 m high fencing reputed to be quokka-proof for at least 8 years (C Hansen, Environmental Officer, Rottnest Island Authority, personal communication). Some quokkas were able to jump the fence but were removed periodically (C Wright, Environmental Manager, Rottnest Island Authority, personal communication). The entire fenced area was planted with *Melaleuca lanceolata* and *Callitris preissii* seedlings, of local provenance, over the ensuing four years at a density of about one plant per 20 m^2; a few *Pittosporum ligustrifolium* were planted but none survived (C Hansen, Environmental Officer, Rottnest Island Authority, personal communication).

In August 2001, four sites were selected where the surrounding unburnt vegetation was in close proximity, and had a similar aspect to the area that had been burnt, within and outside the fenced plots. Further sampling was not possible because much of the burnt unfenced area surrounding the plots was taken up by fire breaks and vehicle access tracks. Three 25 m x 2 m transects were established at each site to compare the surrounding heathland that had not been burnt with the vegetation that had been burnt, both fenced and not fenced (Fig 4). Each of the 12 transects consisted of five 5 m x 2 m

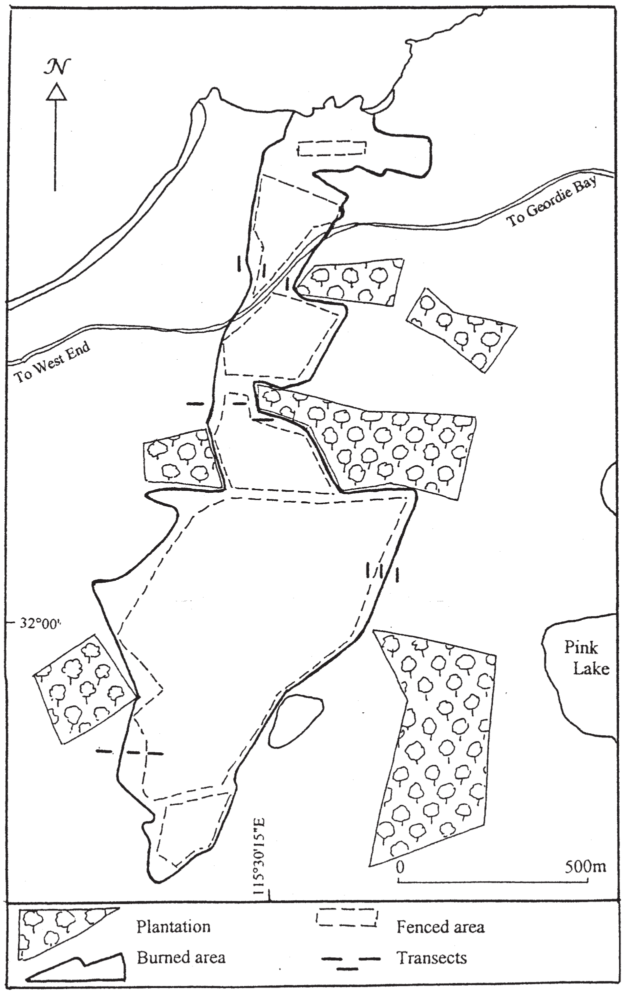


Figure 4. Rottnest Island: area burnt in 1997 showing fenced plots, adjacent plantations and positions of transects.

quadrats, for which the percentage cover and average height of each species present was recorded. The proportion of bare earth was also noted.

The three 'groups', burnt and fenced, burnt and unfenced, and unburned and unfenced were compared with regard to the number of native species, percentage cover of native species, and percentage cover of the introduced *Trachyandra divaricata*. Analysis of variance was used to test for significant differences amongst groups and transects. Logarithmic transformation was employed to stabilise the variance for species count data. The Kruskal-Wallis rank sum test was applied to the percentage cover data of both native species and *Trachyandra divaricata* because standard assumptions for ANOVA (in particular normality and homogeneity of variance) were violated.

Aerial photographs

Photocopies of the following aerial photographs were obtained from the Western Australian Department of Land Administration to assess vegetation changes on Rottnest Island, particularly at the Research Site.

- aerial photographs of Rottnest Island, 1942: black and white 29/9/42, Run 1 YX4140, YX4142; Run 3 YX 4155, YX4157, YX4159, YX4160, YX4162; Run 4 YX4136, and a copy of a map derived from these photographs: Australian Section Imperial General Staff 1943, Rottnest Island, 4th Australian Survey Co, RAE, scale approx: 1:16,000 (4 inches to 1 mile).
- aerial photographs of Rottnest a few days after the 1955 fire: black and white Run 1. WA 158. Scale 1:7920 taken 25/02/1955. These photographs were used to assess changes between 1942 and 1955. Subsequent vegetation changes were identified by comparing these images with aerial photographs taken in later years, by superimposing images which had been reduced to the same scale by photocopying. Photographs were: 8/4/1964 5114, WA 854, Rottnest Island (5112-5116) from 12,500', Project D60; 18/3/1967 5067 WA 1016, Rottnest Road Guide Revision Run 1 (5062-5069) 7920; 14/2/1972 5063 WA 1378 (C) Rottnest Island Run 1 (5059-5067) 7920 152.56; 1/2/1980 5018, WA 1857(C), Rottnest Island Run I (5014-5020) scale 1:10000, Job no 800001; 11/3/1990 WA 2851 (C), Rottnest Island Run 1 (50001-5010) Scale 1:15000, 900890.
- further series of aerial photographs was used to examine changes brought about by the 1997 fire; these comprised Rottnest Island, 6/2/1997 Metro regional area Run 41, 5002, 5004 and 5006, 1:20,000; an enlarged colour photocopy of aerial photograph 10/01/1998 WA 4044C; Perth regional area Metro photography project no 970000, Run 41:5003, Scale 1:25,000. Computer generated, enlarged images of aerial photographs were also obtained: Perth regional area Metro Photography 17/02/2000 Project no 990000, WA 4422C Run 41:5003, 1:25,000; 14/12/2000 Project no 000001, WA 4544C, Run 41:5139, Scale 1:25,000. Vegetation distribution was related to topography in the Research Site with the use of a photocopy of a contour map of Rottnest Island produced by the Department of Lands and Surveys, Job no 800001, 1m contours, from photography taken February 1980 and October 1981.

Results

Field survey

The vegetation of the surrounding *Acanthocarpus* heath that had not been burnt consisted almost entirely of three native species, *Acanthocarpus preissi*, *Austrostipa flavescens*, and *Thomasia cognata*, and the introduced *Trachyandra divaricata* (Table 1). Burning of *Acanthocarpus* heath

Table 1

% cover and frequency of plant species in burnt and fenced, burnt and unfenced, and unburnt areas.

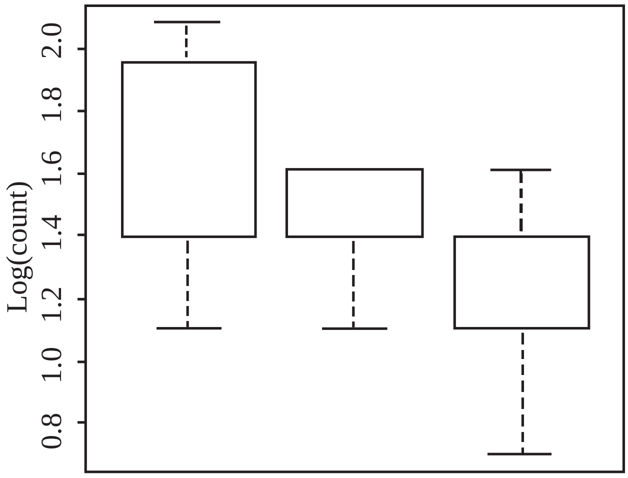
	Burnt and fenced		**Burnt and unfenced**		**Unburnt**	
	% cover	**% Freq**	**% cover**	**% Freq**	**% cover**	**% Freq**
Acanthocarpus preissii	7	70	21	100	32	100
Austrostipa flavescens	26	100	19	100	14	95
Thomasia cognata	15	80	8	60	15	75
Olearia axillaris	8	60	0		0	
Acacia rostellifera	29	60	0		0	
Solanum symonii	1	25	1	25	0	
Lepidosperma gladiatum	4	15	1	20	0	
Lepidosperma pubisquameum	3	20	0		0	
Carex preissii	0.2	5	0.2	30	0	
Conostylis candicans	3	40	5	55	3	50
Rhagodia baccata	4	15	0		0	
Guichenotia ledifolia	0.05	5	2	20	3	15
Trachyandra divaricata	1	45	11	95	14	80
Planted *Melaleuca* and *Callitris*	7	35	N/A		N/A	
Seedlings of ephemerals	3	100	9	100	8	100
Bare	8		23		11	
TOTAL	**>100[a]**		**100**		**100**	

[a] *Acacia rostellifera* formed a canopy with an understorey, so that the total coverage shown for burnt and fenced sites is greater than 100%. The understorey consisted almost entirely of native species, so the understorey was disregarded when calculating percentage cover of native species for the statistical analysis.

Table 2

Number of native species and percentage cover of various types, with 95% confidence intervals (n = 20 quadrats, over 4 transects).

	Burnt fenced	Burnt unfenced	Unburned unfenced
Number of native species	5.6 (4.9-6.3)	4.3 (4-4.6)	3.6 (3.3-3.9)
% cover of native species	91 (89-93) %	57 (51-63) %	68 (61-75) %
% cover of *Trachyandra*	1 (0-2) %	11 (7-15) %	13.7 (11.7-15.7 %)
% cover of introduced species (including *Trachyandra*)	4.5 (3-6) %	20 (15-25) %	22 (15-29) %
% Bare earth	4.5 (2.5-7) %	23 (19-27) %	10.5 (7.5-13.5) %



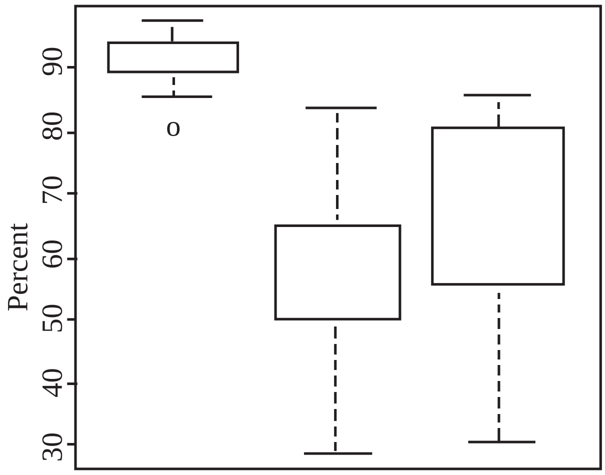


Figure 5. A: Number of native species in the three areas (burnt fenced, burnt unfenced and unburnt unfenced). **B:** % cover by native species in the three areas (burnt fenced, burnt unfenced and unburnt unfenced).

increased the number of native species present, particularly if the area was fenced against quokkas (Table 2; Fig 5A). The ANOVA for log of species count was highly significant for different groups ($P < 0.001$). The percentage cover of native species in the three areas also showed significant differences ($P < 0.001$; Table 2). In unfenced and unburned heath, percentage cover of native plants was variable (Fig 5B). Where the heath had been burnt but not fenced, cover was low indicating that where quokkas could graze the new growth the vegetation had not recovered even after 4.5 years. By contrast the cover of native species in burnt areas fenced against grazing was high.

Melaleuca/Callitris

Melaleuca lanceolata and *Callitris preissii* trees growing in plantations adjacent to the burnt area were not burnt but two isolated *Melaleuca* trees and one *Pittosporum ligustrifolium* were burnt. One of the *Melaleucas* was included in the quokka-proof fencing subsequently erected, and numerous *Melaleuca* seedlings germinated to the west side of this tree after the fire (although not within the sampled quadrats). These self-seeded *Melaleucas* grew much more rapidly than the planted *Melaleuca* seedlings. The second burnt *Melaleuca* tree was not fenced and no seedlings were observed growing in its vicinity. The *Pittosporum* tree that was burnt was just outside one of the fenced plots. This species is capable of sprouting from damaged roots after fire (McArthur 1996a) but in this case did not do so. No seedlings were observed outside the fence, but 76 young *Pittosporum* 30-40 cm high were growing within the fence to the west of the burnt tree in August 2001 (C Hansen, Environmental Officer, Rottnest Island, personal communication). *Melaleuca lanceolata* and *Callitris preissi* planted in the four years following the fire were noted in all transects within fenced areas, and formed some 7% of cover in those transects (Table 1).

Acacia rostellifera

The most striking contrast between the vegetation of the three areas was the dense germination and growth of the native *Acacia rostellifera* within enclosures, reaching 5 m height on sheltered slopes. It had not grown in the research site for over 40 years prior to the 1997 fire. However, patches of acacia scrub had grown there between 1942 and 1955, decreasing in extent until eliminated after the 1955 fire (Figs 6A,B). The distribution of *Acacia rostellifera* in 2000 (Fig 6C) corresponded with that 60 years earlier, in 1942. Comparison of the distribution of acacia after the 1997 fire with a contour map showed that the species had germinated in swales and on east-facing slopes (Fig 7).

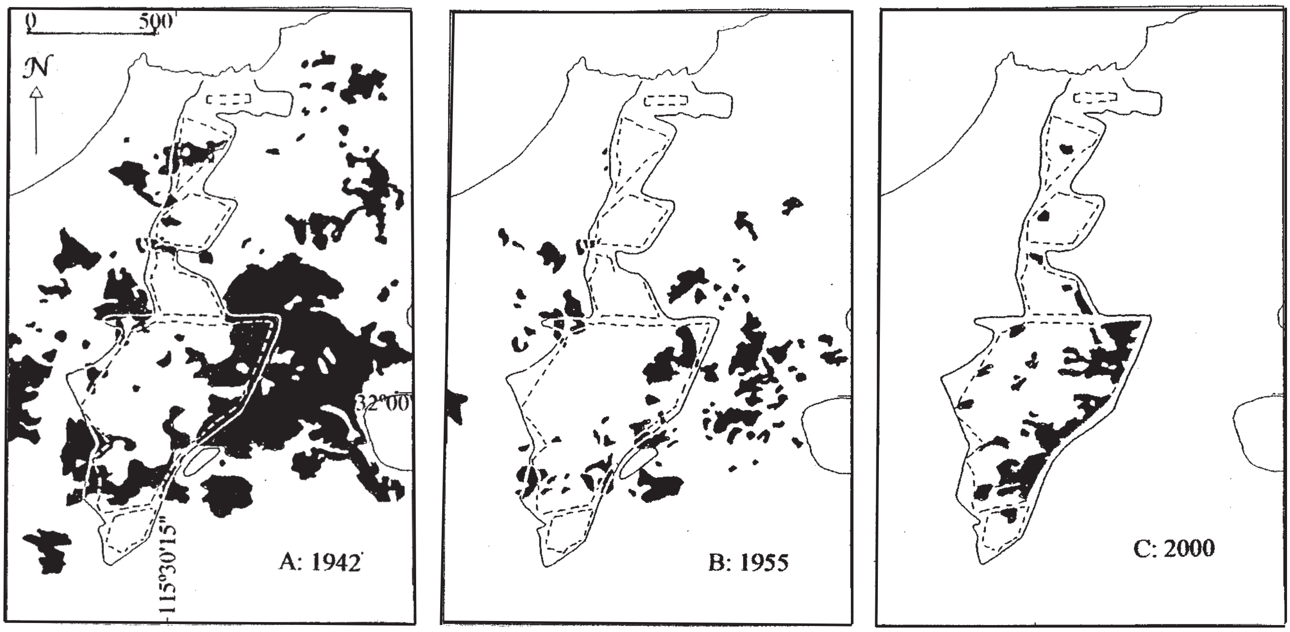


Figure 6. A: Distribution of *Acacia rostellifera* in 1942. **B:** Distribution of *Acacia rostellifera* in 1955. **C:** Young growth of *Acacia rostellifera* in the enclosures. The only acacia in the area between 1956 and 1997 was in plantations.

Heath species

Additional native species recorded in burnt areas but not in the unburnt heath were *Rhagodia baccata, Olearia axillaris* and *Lepidosperma pubisquameum* only within enclosures, and *Solanum symonii* (a fire ephemeral, mostly dead by the time of the survey), *Lepidosperma gladiatum* and *Carex preissii* within and outside enclosures (Table 1).

The increased coverage by native species in enclosures was at the expense of *Acanthocarpus preissii*, the introduced *Trachyandra divaricata* and (to a lesser extent) small introduced annuals, notably *Euphorbia peplus* and the grass *Lagurus ovatus. Trachyandra* was an important component of the vegetation in unburned and unfenced heath (Table 2; Fig 8) but little *Trachyandra* persisted within enclosures (Kruskal-Wallis test, P<0.001).

Discussion

The vegetation recovery sequence proposed by Noble & Slatyer (1980) seems applicable to the dominant communities on Rottnest Island. The 1997 fire was followed by germination or regeneration of all dominant communities within fenced areas.

Melaleuca/Callitris.

The only germination observed of these species was beside a burnt *Melaleuca* within an enclosure, despite the fact that *Melaleuca* and *Callitris* trees were growing in plantations, which had not been burned, within 50 m of the fenced plots. Four and a half years after the fire the slender saplings reached 2 m high but were far outstripped by young *Acacia rostellifera.* It was anticipated that *Acacia* would overshadow these trees for another twenty or thirty years. At Woodman Point thirty years after a fire, a stand of senescent 5 m *Acacia rostellifera* was still taller than *Callitris preissii* trees but the *Callitris* were young at 30 years of age, and would shortly displace the *Acacia* (Powell & Emberson 1981). On Garden Island, progress of the forest trees could be traced over their life span as the ages of various stands of *Callitris/Melaleuca* trees were known from the dates of fires that stimulated their germination. It was found that forty year old trees numbered approximately 16 per 25 sq m, 75 year old trees numbered 6, and hundred year old trees only 1 per 25 sq m. As the decline progressed the forest was replaced by *Acanthocarpus preissii* heath (McArthur 1998).

Acacia rostellifera

This dominated parts of the Research Site enclosures, reaching 3-4 m. The changing distribution patterns of this species since 1942 have been mentioned. The decrease in *Acacia rostellifera* between 1942 and 1955 (Figs 6A,B) accords with Storr's report of major and continuing fragmentation of *Acacia rostellifera* scrub from the 1930s onwards (Storr 1963). The disappearance of *Acacia* from around Barker Swamp after the fire of 1955 was explained by Storr (1963) who recorded that there had been an abnormally high number of quokkas in this area after the fire. Small pockets of scrub had escaped the fire here, and within two years the quokkas surviving in these nodes had eaten all regenerating *Acacia,* and the scrub had been completely replaced with *Acanthocarpus* heath. The only *Acacia* in the area at the time of 1997 fire was in surrounding plantations, established between 1964 and 1972. The resemblance between the distribution patterns of *Acacia rostellifera* in 1942 and 2001 suggests that after the fire *Acacia* had grown from seed in the soil,

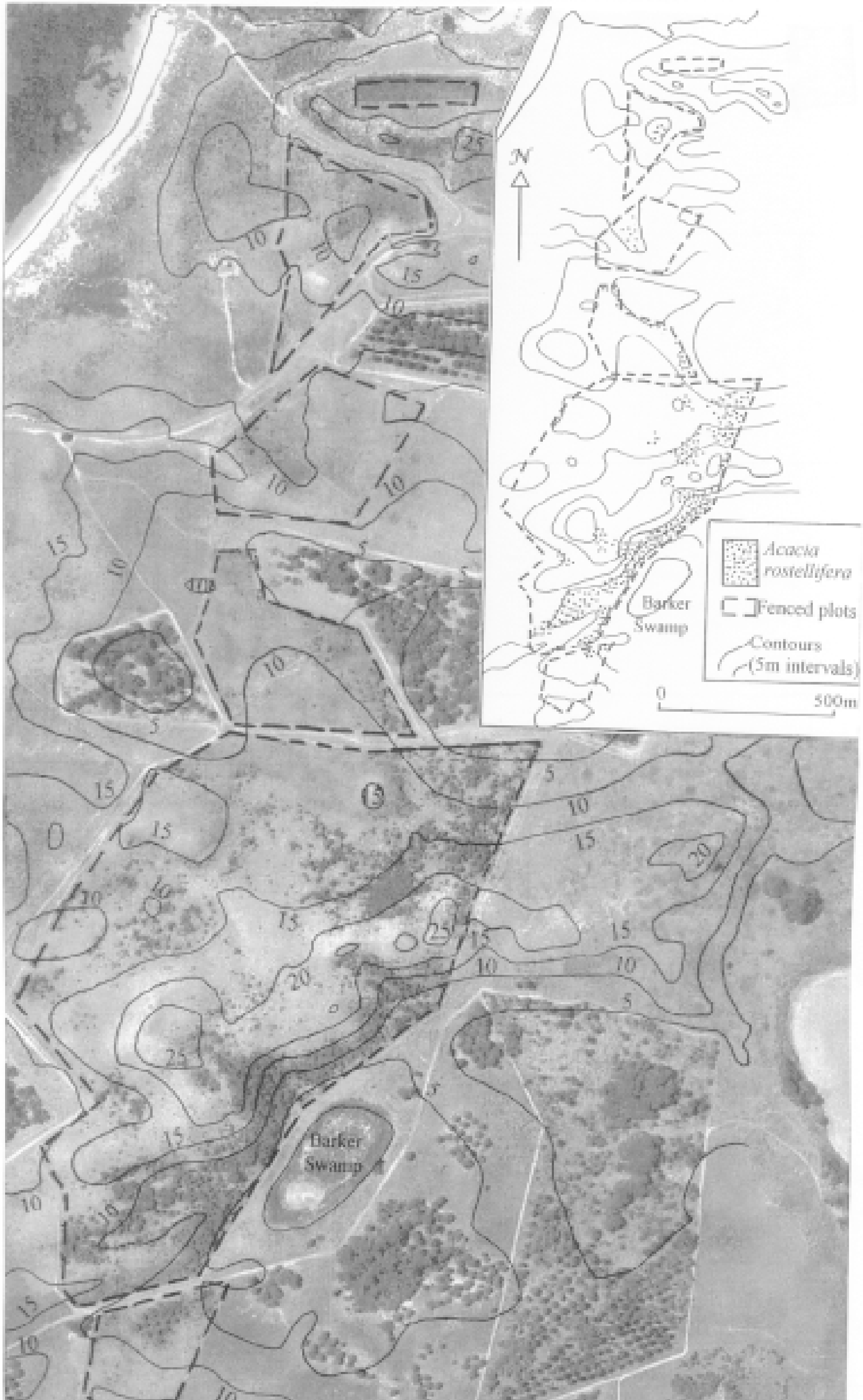


Figure 7. Growth of *Acacia rostellifera* in February 2000 in relation to topography.

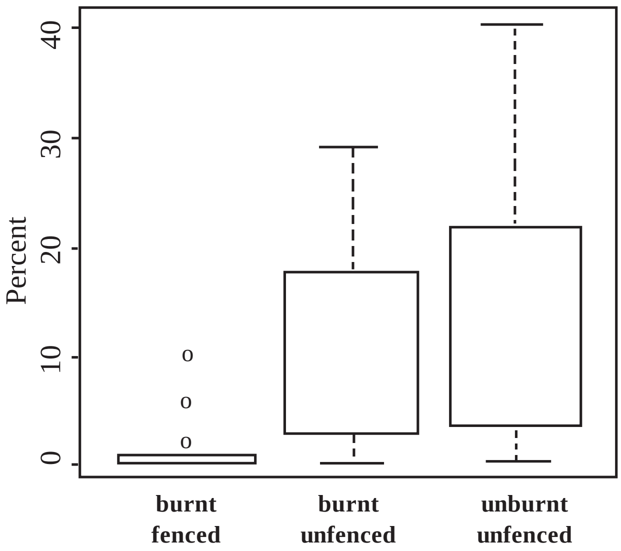


Figure 8. % cover by the introduced *Trachyandra divaricata* in the three areas (burnt fenced, burnt unfenced and unburned unfenced).

deposited some 60 years previously. Germination triggered by the 1997 fire in areas outside enclosures presumably succumbed to grazing.

The relationship between the distribution of *Acacia* within the enclosures and topography, with growth restricted to swales and east-facing slopes could be associated with the fact that the senescent parent *Acacias* of the 1940s and 1950s are likely to have survived longest in favourable sites.

Acanthocarpus heath

This was the most widespread vegetation community throughout the burnt area at the time of the survey, dominating except in areas of *Acacia rostellifera*.

Fire and marsupial grazing/browsing

The basic model of Noble & Slatyer (1980) illustrates the development of the vegetation communities of Rottnest Island after a single disturbance event. However if the vegetation dynamics are considered in terms of two major factors, fire and marsupial grazing, then a second model of alternative stable states becomes useful.

Charcoal deposits indicate that infrequent fires have occurred on Rottnest Island over the 6500 years since separation from the mainland (Backhouse 1993; Groves 2001). Presumably these would have been initiated by lightning, concurring with summer and drought years. Fires occurred about every 200 years in the vicinity of Barker Swamp alone (Groves 2001). Hopkins *et al.* (1985) suggested that infrequent major conflagrations take place on islands where there is no Aboriginal presence. Fires are known to be started by lightning on islands in the Recherche Archipelago (Weston 1985; A Hopkins, Department of Conservation & Land Management, Woodvale Research Centre, personal communication; M Fitzgerald, Department of Conservation & Land Management, Esperance, personal communication). Fires caused by lightning strikes are not uncommon on the Perth coastal plain, and it is likely that these could have occurred more than once per century on the islands (R Smith, Wildfire Prevention, Fire and Emergency Services Authority of Western Australia**,** personal communication).

These fires could have been fierce and widespread in woodland areas, as a considerable amount of flammable material presumably had accumulated. Total available fuel in mature *Melaleuca* forest has been estimated at 15-25 tonnes ha^{-1}, and in *Acacia rostellifera* scrub 30 t ha^{-1} (McArthur 1996a). This is a heavy fuel load in view of the fact that the maximum loading that can be handled by a bush fire fighting brigade on a normal summer day is 8 t ha^{-1} (M Cronstedt, Fire and Emergency Services Authority, personal communication).

There is also doubt as to whether communities of *Callitris/Melaleuca* or *Acacia rostellifera* could have persisted indefinitely in the absence of fire. McArthur (1996b) suggested that *Callitris* and *Melaleuca* very rarely regenerate other than in the vicinity of burnt parent trees. In the Research Site, germination of *Melaleuca* was restricted to the vicinity of a burnt *Melaleuca* within a fenced plot. Seed-bearing cones of *Callitris preissii* were scattered in one fenced plot but failed to produce any seedlings (C Hansen, Environmental Officer, Rottnest Island Authority, personal communication). However, *Callitris* and *Melaleuca* can sometimes reproduce without fire; in 2000 they germinated on Rottnest Island at Oliver Hill, where seed-bearing branches of the two species had been laid down to stabilize a small blow-out. Some *Callitris preissii* also germinated in the absence of fire on the mainland coast at Woodman Point (Powell & Emberson 1981).

McArthur (1998) reported that *Acacia* may regenerate without fire, mainly from root suckers, and can even be rejuvenated if seasonal conditions and the insect load permit. *Acacia rostellifera* can regenerate from rootstock after damage to the above ground parts along footpaths or after destruction by nesting cormorants, but there is not the massive germination and regeneration that follows fire. Fire appears to trigger germination and possibly reduces insect numbers.

Melaleuca, Callitris and *Acacia* are palatable to quokkas, and in the presence of a large quokka population regeneration rarely occurs (Storr 1962). Planted specimens do not survive unless fenced. Palatable species can become established however after a widespread fire as macropod grazing can be reduced for a time (Whelan & Main 1979). Baird (1958) found virtually no signs of grazing for two years along the southern margin of the huge 1956 fire on Garden Island. After the 1955 fire on Rottnest Island, some sites were almost completely deserted by quokkas (Storr 1963). This may be because resident quokkas are killed by fire (McArthur 1996a) or because there is no shelter for too great a distance (Storr 1963). The influence of grazing by macropods on the survival of seedlings is not fully understood. The occurrence of highly palatable plant species in an area or strong territorial instincts on the part of the animals can affect the ranges of grazing animals after fire (Whelan & Main 1979).

Acanthocarpus heath is self-maintaining under a regime of heavy grazing, although at a suppressed level. In those areas burnt in the 1997 fire but not enclosed against grazing, almost a quarter of the area was still denuded after 4½ years. The heath within enclosures after the 1997 fire appeared rejuvenated, and resembled the more diverse heath described in the 1950s (Storr 1959), while that surrounding the burnt area resembled the more degraded heath described in the 1980s (Hesp *et al.* 1983). In the 1950s there were *Acanthocarpus preissii* with *Austrostipa flavescens*, and two less common tussock grasses *Poa caespitosa* (probably *Poa poiformis*) and *Danthonia caespitosa* (probably a misidentification of *Austrodanthonia occidentalis* - M Hislop, WA Herbarium, personal communication), *Acacia rostellifera*, the sedges *Lepidosperma gladiatum, L. pubisquameum* and *Carex preissii* and *Conostylis candicans*. Dicotyledons were uncommon, with *Thomasia cognata, Guichenotia ledifolia* and *Trachymene coerulea* in disturbed areas. By the 1980s heath was described as the most widespread community on the island, covering about one-third of the island's area and the species list was reduced to *Austrostipa, Acanthocarpus, Thomasia, Guichenotia* and *Conostylis* but with the notable addition of the introduced *Trachyandra divaricata* (Hesp *et al.* 1983). In 2001 these were the species found in the heath surrounding the burnt site.

The native heath appears to be resilient, as *Trachyandra divaricata* was the only introduced perennial species noted in the Research Site after 180 years of settlement and the introduction of many other alien species. It is a primary coloniser of disturbed and unvegetated areas, and is known to be toxic to horses and unpalatable to quokkas (J Dodd, Department of Agriculture, WA, personal communication). *Trachyandra* was present on Rottnest in the 1960s but seldom occurred away from coastal dunes (Storr 1962); White & Edmiston (1974) expressed concern that the heath was being replaced by *Trachyandra*, and by 2001 it was an important component of the surrounding unburned heath in the Research Site. The species appears to persist with continued disturbance but to give way to competition from native species if disturbance ceases.

Alternative stable states

Vegetation dynamics may be usefully represented in terms of alternative stable states (Sutherland 1974; May 1977; Laycock 1991; Law & Morton, 1993; Hobbs 1994; Noble 1997). Transitions between states occur if there are specific changes in prevailing conditions. *Melaleuca/ Callitris* forest, or *Acacia rostellifera* scrub or *Acanthocarpus* heath, can dominate on Rottnest Island depending on the circumstances (Fig 9).

If there were occasional hot fires, then low *Melaleuca/ Callitris* forest would dominate. The dense shade of this forest has little understorey, so the quokka population would remain comparatively small. Fires would tend to be intense and infrequent but widespread, fuelled by accumulated litter so that parts of the island would be free of quokkas for a time after burning, and palatable tree species would escape grazing until they were large enough to withstand it.

Under conditions of frequent fires and little grazing, *Acacia* scrub would dominate; no shrub on Rottnest recovers as well after fire as *Acacia rostellifera* (Storr 1963). Frequent fires eliminate *Melaleuca/Callitris* locally, as two fires within about 10 years could kill mature trees and then their offspring before they reached reproductive age, leaving no propagules to germinate.

With heavy grazing, *Acanthocarpus* heath would

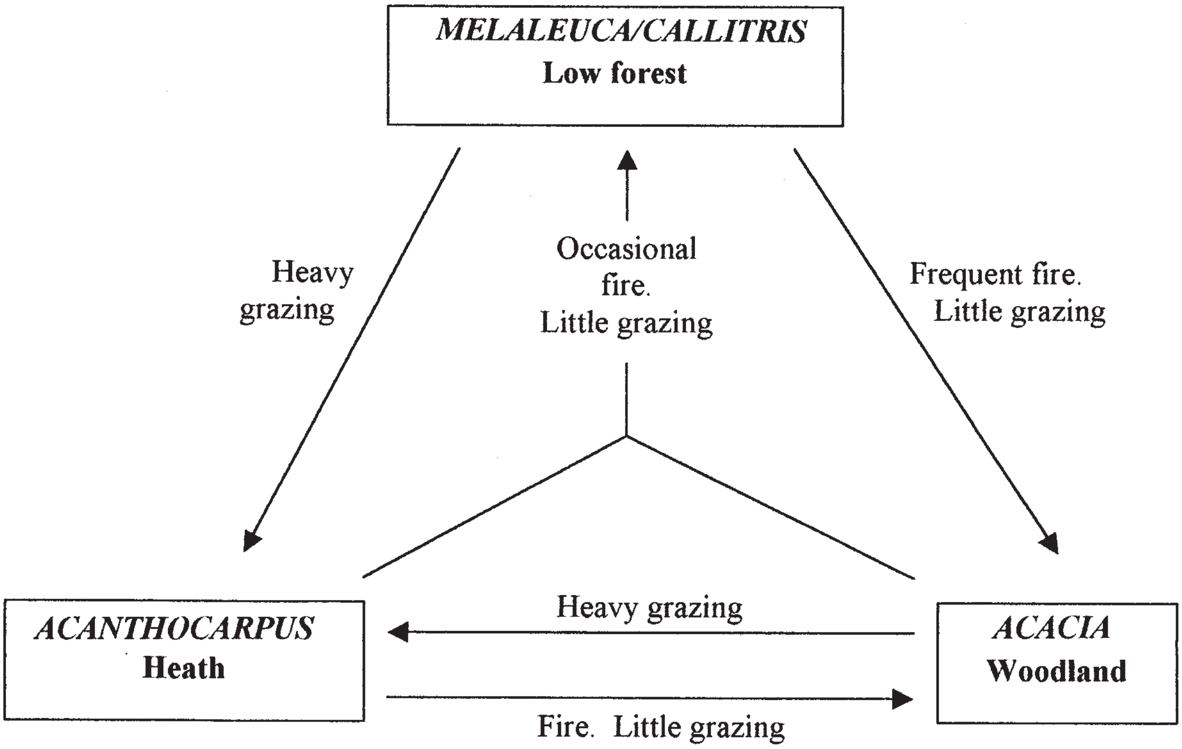


Figure 9. Alternative stable states model for Rottnest Island.

dominate. *Acacia rostellifera* is a favoured food for quokkas, and *Callitris* and *Melaleuca* are very palatable, and a large quokka population would destroy shoots and seedlings as they appeared so that these species would die out with the death of the mature plants.

The transitions from one stable state to another have been precipitate over the past 200 years, brought about by human intervention. It is postulated that there were occasional large fires before human occupation in 1838, and that these were associated with *Melaleuca/Callitris* forests. These gave way to *Acacia rostellifera* scrub between 1840 and the 1920s / 1930s, when frequent fires took place and the quokka population was kept low by hunting. After this the quokka population was protected and burgeoned; the population probably reached saturation point by the mid twentieth century. Heathland predominated with this heavy grazing, and the prevention or control of fires after 1955.

It is possible that the *Acanthocarpus/Austrostipa* heath is not stable, but is becoming increasingly degraded by invasion by *Trachyandra divaricata* and by overgrazing and damage by quokkas. The stable state concept does not preclude the possibility that future changes might occur to the vegetation, associated with changes in the island environment or invasion by other species.

It would seem that virtually all of the natural old growth trees on Rottnest must be drawing towards the end of their life span. Quokkas were protected from 1917 and there had been some limitations on quokka hunting prior to this (CSO File 2047 / 1900 in Joske *et al.* 1995), with the result that presumably little regeneration of trees could have taken place for 80 years. *Melaleuca/Callitris* forest thins out rapidly from 80 years of age and the trees disappear within about thirty years. Similarly, if quokka grazing prevents regeneration of *Acacia rostellifera*, then *Acacia* scrub senesces and dies in 20-40 years.

The exploitation of the vegetation of Rottnest Island for two centuries releases environmental managers to some extent of expectations that they should restore the vegetation to any ‘original’ state. This gives considerable freedom of action, but in practice severe constraints are imposed by the island’s gazetted purpose of ‘public recreation’, and by the threatened status of quokkas, which are a Western Australian icon. Both of these factors restrict the use of fire as a management tool, and it is interesting to note that the Draft Management Plan for the island for 2002-2007 states that ‘fire is a threat to all habitats … particularly … to woodland communities’. However from our study, it is clear that fire remains an important factor shaping the vegetation and that its occurrence (or that of a suitable alternative disturbance), in conjunction with local control of quokka grazing may be essential for the maintenance of some of the major vegetation types (outside plantations) on the island.

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