Vegetation responses to chaining in an isolated remnant in Western Australia's wheatbelt

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Abstract

This study examines secondary succession in an isolated remnant following disturbance by chaining, where a chain suspended by two tractors was drawn along the ground knocking over the vegetation. The disturbance resulted in distinct zones within the chained area (chained and mulched, chained and cleared, and chained with vegetation piles burnt). Two to three years after disturbance distinct assemblages occurred within each zone, with high diversity in all three zones in the chained area compared with the intact remnant, and a number of abundant taxa restricted to particular zones. 4–5 years after disturbance some early colonisers were absent, but the plant assemblages were still distinct. The distribution and abundance of the Declared Rare species *Boronia adamsiana* occurring in the chained area was surveyed. The value of this managed disturbance within remnants in an agricultural landscape for rare and seral species is discussed.

Keywords: Succession, *Boronia adamsiana*, chaining, diversity, rare species, fire, vegetation mosaics

Introduction

Clearance of native habitat for agriculture is a global issue threatening native biodiversity (Tilman 1999). Land clearing in some areas of the wheat-growing region of Western Australia, commonly known as the wheatbelt, has resulted in losses of up to 97% of the native vegetation (Dilworth *et al.* 2000). The wheatbelt (including upper catchment areas) retains only 7% of its native vegetated area (Beecham 2004). A common method used to clear the land, referred to as 'chaining', was developed during the Second World War and involved the use of a chain or cable suspended between two tractors which was drawn along the ground (Beresford 2001). The cable rides over small trees tearing off limbs and leaving a medium for a fire which was then used to remove the bulk of the plant debris prior to cultivation. Similar techniques with a roller are used to create fire breaks and although they maintain species richness, can alter species composition compared to neighbouring unrolled habitat, with species capable of resprouting being advantaged and obligate post-fire reseeders, such as *Hakea* and *Allocasuarina* being disadvantaged with the absence of fire (Pelton & Conran 2002). Seed from serotinous species may not be released by rolling or chaining in the absence of fire (Gill 1976), but if they are, can be destroyed by subsequent fire (McCaw & Smith 1992).

The vegetation fragments within the wheatbelt are islands of native vegetation (mostly less than 400 ha in size) surrounded by agricultural land (Hobbs & Atkins 1988), and this fragmentation has had devastating consequences for the native flora and fauna (Hobbs & Huenneke 1992) and has contributed to population extinctions (Hobbs & Mooney 1998). The long-term sustainability of these fragments is dependent on both processes within the fragment, such as its size and disturbance history, and on its location within the broader landscape (Norton *et al.* 1995) which together affect the composition of the extant community.

Landscape fragmentation can alter disturbances occurring within native vegetation, including changes to fire regimes (Gill 1999; Carlquist 1974), typically the most common natural disturbance in the Western Australian landscape (Gill *et al.* 1981). The flora of small remnants are highly susceptible to increases in the frequency of fire, as death of adults and exhaustion of the seed bank can occur (Enright *et al.* 1996; Auld *et al.* 2000), with diminished chance of recolonisation from outside the remnant should they go locally extinct. Conversely the incidence of fire in many remnants has declined significantly with clearing due to the surrounding land use (Beecham 2002), and a common management practice is to protect remnants from disturbance by fire, and thus promote maintenance of a "climax" plant community.

Changes to disturbance regimes have important implications for species that require disturbance to regenerate. In addition, long-term removal of disturbance from a habitat may eliminate those species reliant on disturbance for regeneration unless they have a persistent seed bank. Early seral species often exhibit greater longevity in the seed bank than late seral species

(Chambers & MacMahon 1994), although survival rates are highly variable between species (Auld *et al.* 2000).

Fencing and protection of fragments alone is insufficient in many fragments to ensure biodiversity enhancement (Spooner *et al.* 2002). The incorporation of disturbance into the management of native fragments is an important consideration to promote biodiversity and prevent domination of sites by a few long-lived species (Maher 2007). Can alternate disturbances be introduced if fire events continue to be excluded from small remnants? A fortuitous event, the chaining and subsequent land abandonment of part of a small bushland remnant, has allowed the effects of a human induced disturbance to be studied. Our aims were to compare species assemblages between recently disturbed and 'climax' (remnant) habitats to determine the value of this type of anthropogenic disturbance for promoting plant succession and to determine if the type of disturbance facilitates the development of different successional trajectories.

Methods

Study Site

The 16.1 ha remnant is located about 2 km south of Westonia in the eastern central Wheatbelt (31°19'14"S, 118°41'37"E). The area has a Mediterranean climate with an average annual rainfall of about 300 mm (327 mm at Merredin about 55 km west of Westonia, 294 mm at Southern Cross about 60 km east of Westonia; Commonwealth Bureau of Meteorology 2007). Although surrounded by wheat fields, the remnant is about 600 m from the edge of the Westonia commons, consisting of about 5000 ha of remnant thicket and woodland vegetation (Fulton & Majer 2006). The remnant is not fenced and signs of domestic stock (sheep and cattle), feral herbivores (rabbits), and foxes were evident within the remnant.

Within the site are two major habitats; the remnant *Allocasuarina/Acacia/Eucalyptus burracoppinensis* thicket and a 6 ha area in the south east corner that was chained between April 2003 and April 2004 (Figure 1; Fulton & Majer 2006). The chained area was to be cleared and then converted into a wheat field, however, only some sections were cleared, some vegetation piles burnt and any further steps to convert it to a wheat field abandoned. These actions left three distinct disturbed zones within the chained area: Cleared – chained vegetation was cleared; Burnt – piles of cleared plants were burnt leaving areas with ash on the ground; Mulched – vegetation was chained and the debris left as it fell.

Sampling methods

During April and July 2006 the vegetation was sampled in 50 4x4 m quadrats. The size of the quadrats used in this study were relatively small, thereby creating greater heterogeneity within zones, but larger quadrats would have resulted in sampling across zones and reduced the ability to compare the zones within the chained area.

The location of each quadrat was determined by constructing eight north/south transects 50 m apart spanning the remnant and chained areas (Figure 1). Quadrats were positioned systematically along the

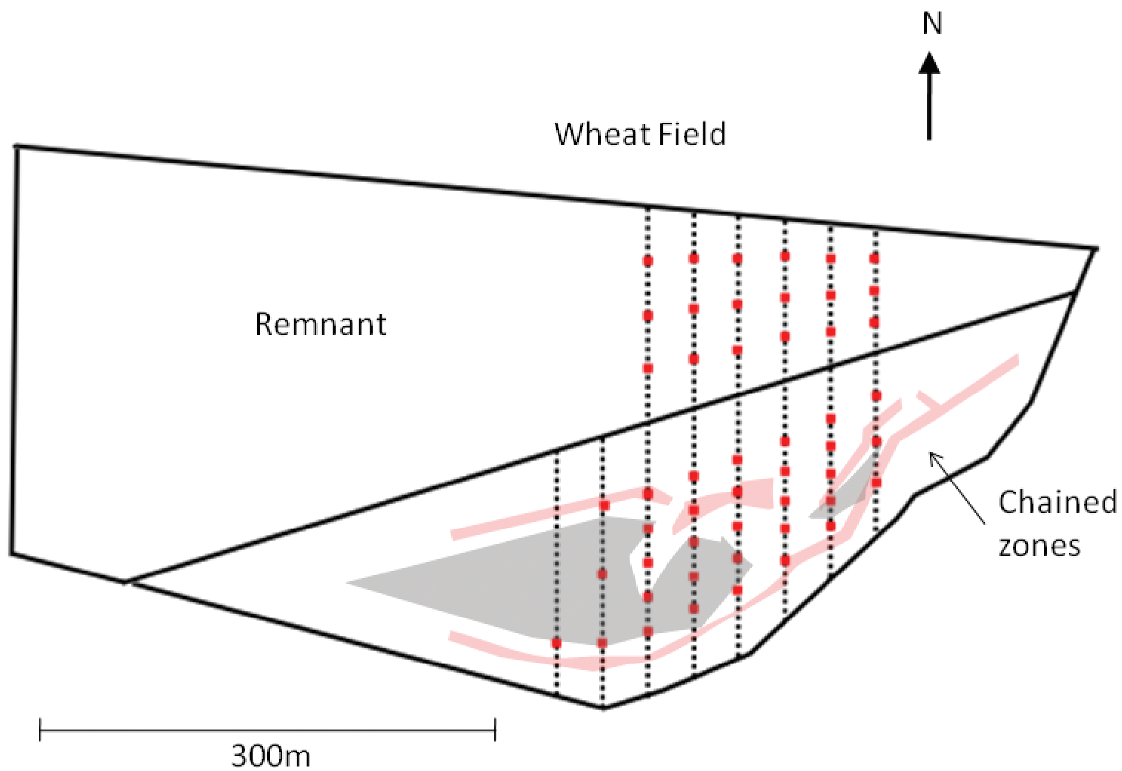

Figure 1. Sketch map of study site showing the extent of the chained zones. The approximate location of transects (dottled line) and sampling plots (squares) are indicated. Within the chained zones the approximate location of the mulched zone (dark central area) and areas where vegetation was burned (light shaded areas) is indicated with the remainder being cleared.

transect in the remnant and in the chained area and categorized by the type of disturbance in each quadrat (Undisturbed remnant, Cleared, Burnt, Mulched). For each species in a quadrat the total number of plants was counted and the percent cover estimated. For each quadrat the percent bare ground and litter cover was also estimated. In March 2008 a subset (20) of the quadrats were resurveyed. For all taxa a reference specimen was collected and where possible identified to species with the assistance of reference material at Curtin University and the Western Australian Herbarium. Due to the time of year of the study no annuals were recorded.

The distribution of *Boronia adamsiana* F.Muell (Barbalin boronia), a Declared Rare Flora (DRF) species found in the 2006 survey, was surveyed within the site in March 2008. All the chained area and 1.4 ha of the remnant were systematically searched. The height and width of each plant was measured and the presence/absence of seed set was recorded.

Data analysis

Repeated measures ANOVA was used to compare species richness between zones and years. One –way ANOVA was used to compare canopy height, ground cover percentages, and density of plants in each mode of regeneration between zones. Plant density data was log transformed prior to analysis. Post hoc LSD comparisons were performed where a significant ANOVA was obtained. The program SPSS (SPSS Inc. 2002) was used for these analyses. Two-sample t-tests assuming unequal variance were used to compare the height and crown diameter of *Boronia adamsiana* plants with and without seed.

Detrended correspondence analysis (DCA; Hill & Gauch 1980) was used to explore patterns of species association within the floristic data. DCA arranges quandrats along ordination axes, based on the taxon composition, and does not force association among groups. Relative to other ordination techniques, DCA has improved performance when data are heterogeneous (Hill & Gauch 1980). Cover data for each species was transformed to log (x + 1) before ordination, which reduced the impact of very abundant species on the result. Blocked multi-response permutation procedure (MRPP; Mielke 1984) was used to test for differences between the quadrats from the 4 zones in 2006. For MRPP A = 1 – (observed delta/expected delta). A = 1 when all items are identical within groups (delta = 0); A = 0 when heterogeneity within groups equals expectation by chance; A < 0 when there is more heterogeneity within groups than expected by chance. P = probability of smaller or equal delta. The program PC-ORD (McCune & Mefford 1999) was used for these analyses.

Results

Vegetation patterns

A total of 94 vascular plant taxa were sampled from the 50 quadrats. The MRPP analysis indicated the *a-priori* groupings were distinct (MRBP; A = 0.09, P < 0.001). Ordination indicates general separation of the quadrats into three relatively distinct groupings (Figure 2). Quadrats from the burnt zone and the remnant were the most distinct with those from the other two zones intermediate. There was one major outlier from the remnant that plotted with the burnt quadrats. This quadrat was across an old fence line within the northern edge of the remnant and had minimal vegetation. An outlier from the chained and cleared zone stood alone on axis two in an initial ordination. It had 5 taxa (all less than 1% cover) unique to that plot and was located at the south eastern corner of the sampled quadrates. It was removed and the analysis rerun.

Species richness in 2006 differed significantly between habitats (MS = 135.9, d.f. = 3, p < 0.001) with the remnant having the lowest richness (5.9 taxa/quadrat). The chained and mulched zone (13.0 taxa/quadrat) had the highest species richness (Table 1).

Only *Baeckea elderiana*, *Drummondita hassellii* and *Allocasuarina* spp. had a high cover and/or abundance across all zones (Table 2). The canopy species *Allocasuarina* spp., *Acacia acuminata*, *Eucalyptus burracoppinensis* and the midstorey shrub *Baeckea elderiana* were the dominant cover in the remnant quadrats. In addition *Drummondita hassellii* and *Euryomyrtus maidenii* were abundant. Five taxa were recorded only in the remnant. Of the common taxa none was unique to the remnant, although *A. acuminata* was rare within the chained zones (Table 2). In general *Acacia* species were relatively abundant in the remnant, but rare within the chained area.

The chained and mulched zone had a high proportion of litter on the ground, and less bare ground than all other chained zones and similar to the remnant (Table 1). There was a high density of *Allocasuarina* seedlings resulting from the seeds shed from the cones of the chained vegetation. Equally abundant was the small

Table 1

Summary of canopy height, ground cover and taxon richness within each zone in 2006 (mean ± SE). For each parameter, zones with different letters are significantly different (LSD, p = < 0.05).

	Remnant	Chained & mulched	Chained & cleared	Chained & burnt
Quadrats	18	11	11	10
Canopy height	2.9 ± 0.2^{a}	1.4 ± 0.2^{b}	1.1 ± 0.2^{b}	1.0 ± 0.2^{b}
% bare ground	51.8 ± 7.1^{a}	34.5 ± 3.9^{a}	75.6 ± 5.0^{b}	75.1 ± 3.7^{b}
% litter cover	35.9 ± 7.5^{a}	46.4 ± 4.4^{a}	10.5 ± 2.1^{b}	10.7 ± 2.5^{b}
% vegetation cover	19.8 ± 5.3^{a}	19.1 ± 3.2^{a}	13.1 ± 2.8^{a}	14.2 ± 2.0^{a}
Species richness	5.9 ± 0.4^{a}	13.0 ± 1.0^{c}	9.5 ± 0.9^{b}	11.2 ± 1.0^{bc}

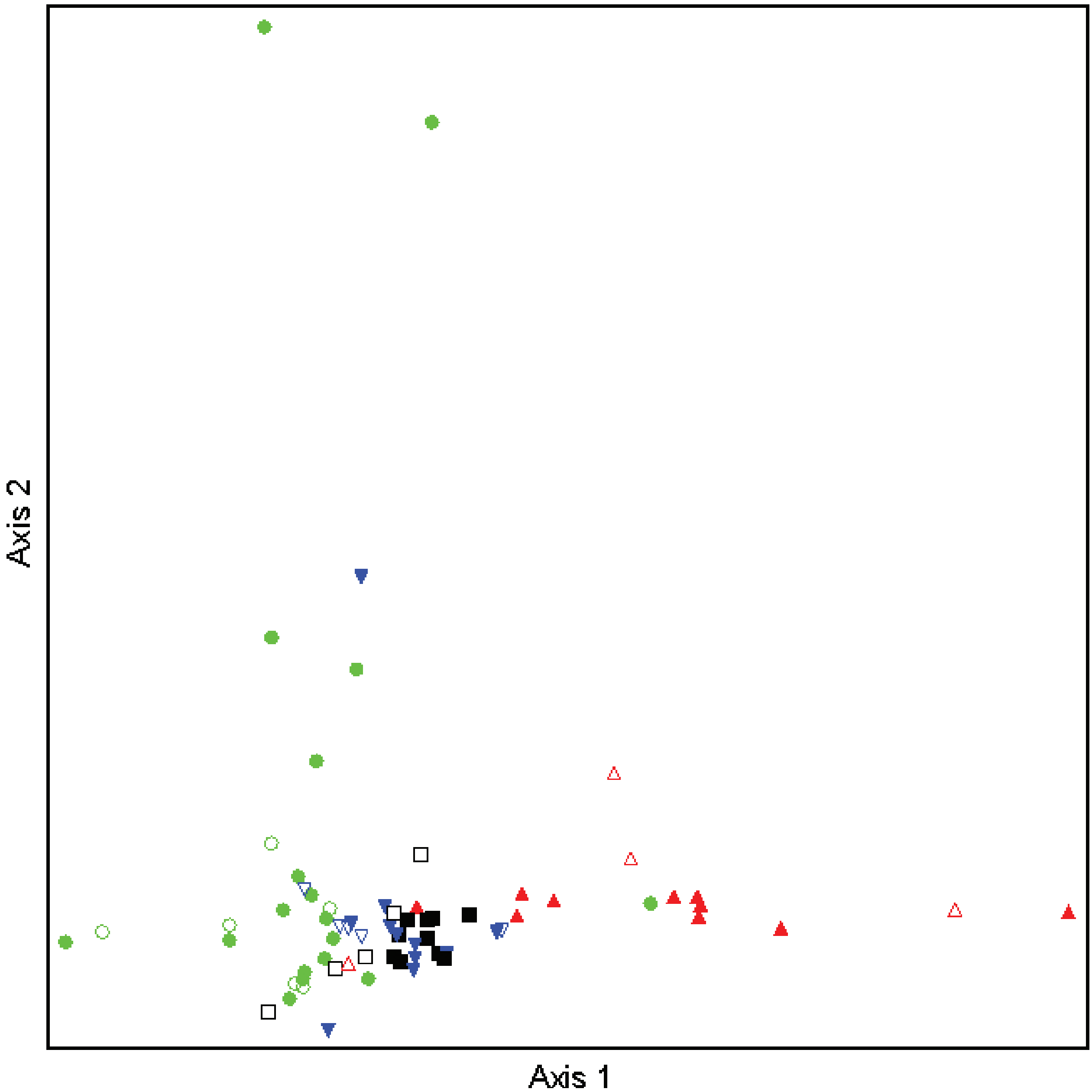

Figure 2. Ordination of vegetation cover in chained remnant across different zones. Zones: ● = remnant, ■ = chained & cleared, ▼ = chained & mulched ▲ = chained & burnt. Filled symbols are from 2006, open symbols from 2008. R^2 axis-1 = 0.15; R^2 axis-2 = 0.16. One chained and cleared plot which was an outlier on axis 2 was removed and the analysis rerun.

prickly shrub *Comesperma spinosum,* not sampled in the remnant and absent from quadrats in the burnt zone. Resprouting *Euryomyrtus maidenii, D. hassellii* and *E. burracoppinensis* were also abundant. 13 taxa were unique to the chained habitat and 33 other taxa not sampled in the remnant quadrats. Of the common taxa *E. maidenii* was predominant in this zone and a further 4 taxa present in this zone were not found in the remnant (Table 2).

In the chained and cleared zone *Gonocarpus confertifolius* var. *helmsii* was the most abundant taxon present and had the second highest cover after *Baeckea elderiana. Allocasuarina* spp. were also abundant. Thirteen taxa were unique to the cleared habitat and 26 of the species in the cleared zone were not found in the remnant quadrats. Of the common taxa *Grevillea paradoxa* was predominant in this zone and a further 4 taxa present were not sampled in the remnant.

In the chained and burnt zone *G. confertifolius* var. *helmsii, Keraudrenia integrifolia* and *Dampiera luteiflora* all from the soil seed bank were the most abundant taxa and had the greatest cover. 12 taxa were unique to the burnt habitat (but 8 of these were represented by a single specimen) and 33 species found in this zone did not occur in the remnant quadrats. Of the common taxa *K. integrifolia, D. luteiflora* and *Neurachne alopecuroidea* were predominant in this zone.

Those taxa identified to at least generic level were classified according to their mode of regeneration:

Table 2

Summary of important taxa (classified as having mean density > 2 plants per quadrat or average cover > 2% in any zone) within each zone from the 2006 survey of quadrats across a chained remnant. # indicates not found in quadrats sampled in 2008. Mode of regeneration: R = respouter; C = serotonous seeder; S = soil seedbank.

Family	Taxa	Mode of regeneration	Zone: Remnant Density	Remnant Cover	Chained & mulched Density	Chained & mulched Cover	Chained & cleared Density	Chained & cleared Cover	Chained & burnt Density	Chained & burnt Cover
Casuarinaceae	*Allocasuarina corniculata* & *campestris*	C	2.6 ± 1.0	8.4 ± 2.9	12.1 ± 2.1	2.3 ± 0.3	6.8 ± 3.0	1.8 ± 0.6	1.0 ± 0.4	0.5 ± 0.2
Goodeniaceae	*Dampiera luteiflora*	S	0	0	0.5 ± 0.4	0.2 ± 0.1	0.1 ± 0.1	0.0 ± 0.0	6.6 ± 4.0	1.2 ± 0.5
Haloragaceae	*Gonocarpus confertifolius* var. *helmsii* #	S	0	0	0.4 ± 0.2	0.2 ± 0.1	14.4 ± 5.9	1.9 ± 0.9	9.0 ± 2.7	2.3 ± 0.9
Mimosaceae	*Acacia acuminata*	S	0.5 ± 0.3	6.1 ± 4.4	0	0	0.1 ± 0.1	0.0 ± 0.0	0	0
	Acacia sp.	S	0.5 ± 0.2	2.4 ± 1.3	0	0	0	0	0.7 ± 0.7	0.5 ± 0.5
Myrtaceae	*Baeckea* sp.	R	0.2 ± 0.2	0.3 ± 0.3	3.8 ± 1.5	0.9 ± 0.2	0	0	0	0
	Baeckea ?behrii	R	2.7 ± 1.3	1.6 ± 1.0	1.0 ± 1.0	0.4 ± 0.4	0	0	0	0
	Baeckea elderiana	R	16.3 ± 5.3	8.1 ± 2.9	3.7 ± 1.9	1.0 ± 0.3	4.7 ± 1.5	2.5 ± 0.9	2.1 ± 1.3	1.1 ± 0.7
	Eucalyptus burracoppinensis	R	1.2 ± 0.5	3.6 ± 2.8	0.9 ± 0.4	3.2 ± 2.8	0.9 ± 0.3	0.7 ± 0.3	1.2 ±0.5	0.5 ± 0.2
	Euryomyrtus maidenii	R	4.1 ± 1.7	0.8 ± 0.3	8.3 ± 2.5	1.2 ± 0.4	0.3 ± 0.3	0.1 ± 0.1	1.3 ± 0.7	0.4 ± 0.2
	Melaleuca conothamnoides	R	0.8 ± 0.4	0.4 ± 0.2	3.4 ± 1.3	1.7 ± 0.9	0.5 ± 0.3	0.4 ± 0.2	0.8 ± 0.6	0.5 ± 0.3
Poaceae	*Amphipogon* sp.	R	1.5 ± 0.7	0.2 ± 0.1	2.4 ± 1.9	0.9 ± 0.4	0.3 ± 0.1	0.2 ± 0.1	0	0
	Neurachne alopecuroidea	R	0	0	1.3 ± 0.7	2.9 ± 1.3	0.5 ± 0.4	1.1 ± 0.9	5.3 ± 5.0	0.6 ± 0.2
Polygalaceae	*Comesperma spinosum*	R	0	0	16.2 ± 4.8	2.8 ± 0.9	1.5 ± 1.2	0.4 ± 0.3	0	0
Proteaceae	*Grevillea paradoxa*	S	0.4 ± 0.4	0.0 ± 0.0	0	0	2.9 ± 2.1	0.2 ± 0.1	0	0
Rutaceae	*Drummondita hassellii*	R	4.4 ± 1.9	1.0 ± 0.3	8.6 ± 2.4	2.3 ± 0.9	3.7 ± 2.4	0.3 ± 0.1	1.8 ± 0.5	0.8 ± 0.1
Sterculiaceae	*Keraudrenia integrifolia*	S	0.2 ± 0.1	0.3 ± 0.2	0.2 ± 0.2	0.0 ± 0.0	0.6 ± 0.2	0.2 ± 0.1	8.2 ± 2.5	2.3 ± 0.5

resprouter, serotinous seeder, and from the soil seed bank (Appendix 1). Serotinous seeder density varied significantly among zones with the burnt zone having the lowest density compared with their density in the other zones (MS = 1.999, d.f. = 2, $p < 0.001$; Figure 3). Resprouter density differed between zone with the cleared area having the highest density (MS = 1.952, d.f. = 2, $p < 0.001$; Figure 3). The density of species from the seed bank also differed between zone with the mulched zone having the lowest density (MS = 1.498, d.f. = 2, $p < 0.001$; Figure 3).

Changes between 2006 and 2008

There was significant variation in species richness among zones and this effect was consistent between years (Figure 3; MS = 144.9, d.f. = 1, $p < 0.001$ (year); MS = 64.4, d.f. = 3, $p = 0.012$ (zone) and MS = 3.69, d.f. = 3, $p = 0.58$ (time × zone). The remnant and the chained and cleared zone had the lowest species richness, the chained and mulched the highest, and the chained and burnt zone had species richness that was intermediate between these two extremes (Figure 4). Notable changes in species composition between the two sampling periods were the disappearance of *Gonocarpus confertifolius* var *helmsii* which was very abundant in 2006, an increase from very low levels in the abundance of 3 *Acacia* species in the chained zones, and an increasing cover of *Allocasuarina* spp. and *Eucalyptus burracoppinensis.* Generally quadrats still fell within the same grouping as 2006 although they were generally closer to the remnant quadrats in 2008 than in 2006 (Figure 2).

***Boronia* survey**

Eighty seven *B. adamsiana* individuals were located in the chained region, while none was found in the 1.4 ha of remnant searched. Plants of this species were recorded in all 3 chained zones in the quadrat survey in low densities (0.1, 0.5, and 0.1 plants per quadrat for the burnt, cleared, and mulched zones respectively). Only 5 of the 88 plants found across the site were in a burnt zone, the rest spread equally between the chained and mulched zones. About 36% of the plants had evidence of having produced seed and these were significantly taller (t = 3.5, d.f. = 82, $p < 0.001$) and had a larger mean crown diameter (t = 6.4, d.f. = 75, $p < 0.001$) than underproductive plants (Table 3; Figure 5).

Discussion

Disturbance of this remnant through chaining has had a beneficial response in terms of above ground plant species richness. It has allowed numerous species to establish in the disturbed area. The fortuitous creation of different zones within the chained areas due to the incomplete land conversion has likely promoted different species within each zone.

Diversity and disturbance

Fragmentation of vegetation communities alters disturbance regimes within them (Saunders *et al.* 1991). Maintaining such remnants in a climax state through a "lock and key" approach, through attempting to remove disturbances such as fire from the landscape can lead to a dominance of relatively few canopy and midstorey shrubs, and a relatively sparse ground cover (Maher 2007). Some areas within the remnant zone are very species poor with mature vegetation senescing, and no evidence of replacement. Continued maintenance of remnants in this state may eventually simplify the

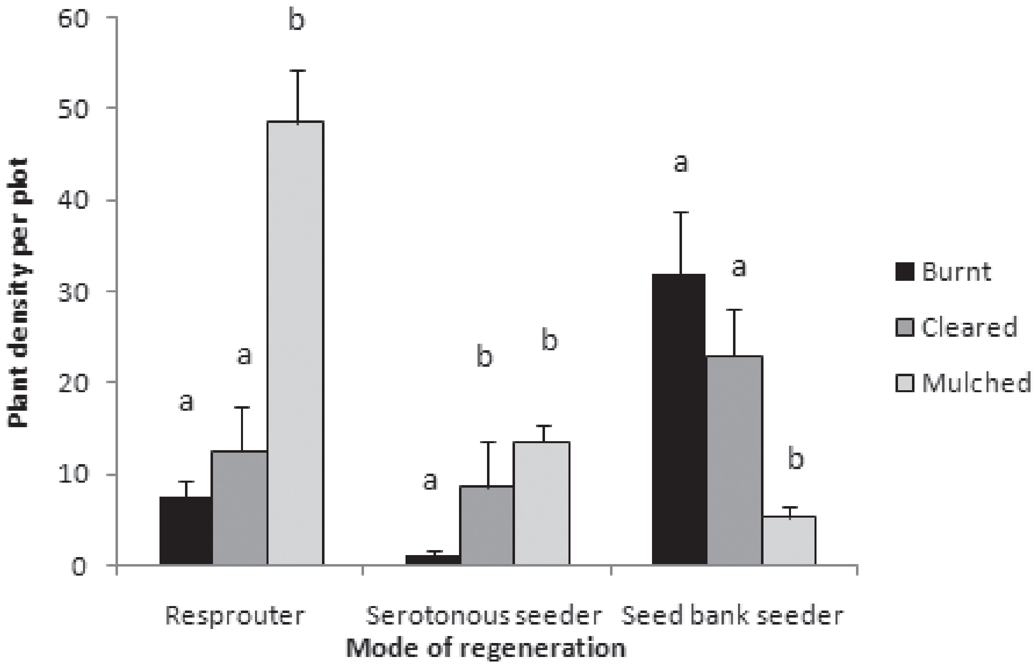

Figure 3. Density of resprouters and seeders (serotinous and seed bank storage) within each of the zones within the chained area. Data are means ± SE. Within each mode of regeneration zones with different letters have significantly different densities (LSD, p = < 0.05).

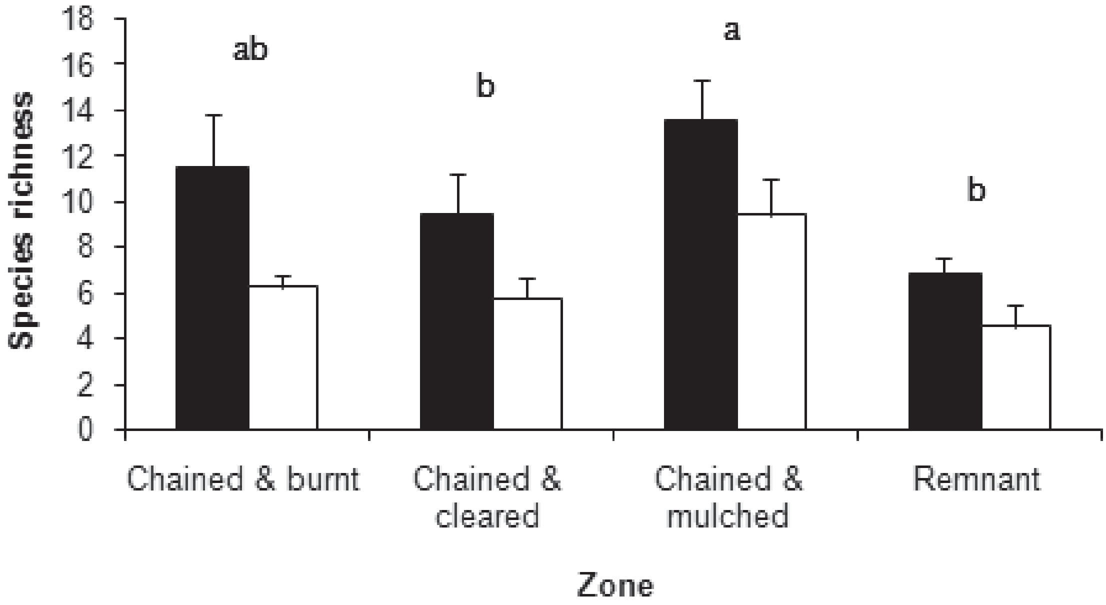

Figure 4. Species richness sampled within quadrats in each zone in 2006 (black) and 2008 (white). Zones with different letters have significantly different species richness (LSD, p = < 0.05).

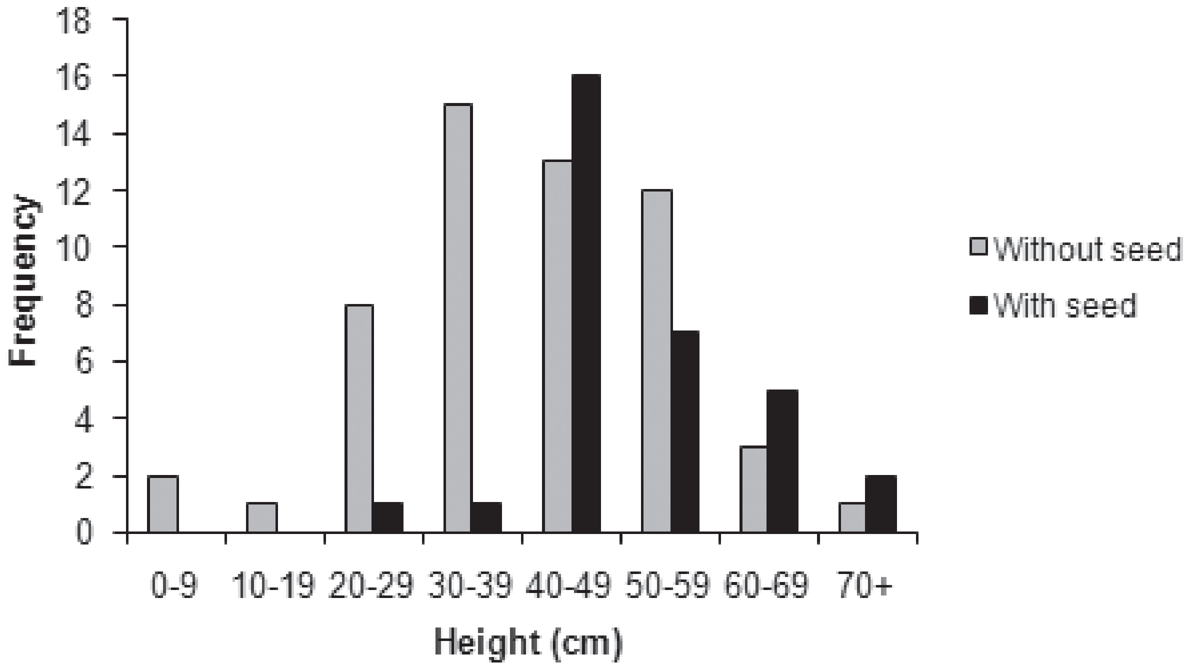

Figure 5. Size distribution of *Boronia* plants with and without evidence of seeding.

Table 3

Size (mean +/- SE (range)) and reproductive status of *Boronia adamsiana* occurring in chained vegetation.

	With Seed	Without Seed	Total
Height (cm)	49.5 +/- 1.9 (22–72)	40.2+/- 2 (8.9–95)	43.9 +/- 1.5 (8.9–95)
Crown Diameter (cm)	34.6 +/- 1.5 (16–53)	27.3 +/- 1.4 (5–56.5)	30.2+/- 1.1 (5–56.5)
n	32	55	87

community, even if there is subsequent disturbance, if the length of time between disturbances exceeds the seed bank life span (Whelan 1995; Bond & van Wilgen 1996). Furthermore there are limited dispersal opportunities for many of the seral species across the surrounding agricultural landscape if they are no longer represented in the seed bank.

Clearly many species have survived in the seedbank in this remnant despite what is probably a long period since disturbance by fire. Persistence in the seed back is unknown for many native species. It is likely to be highly variable between taxa (*e.g*., Weston 1985; Auld *et al.* 2000; Ooi *et al.* 2007), appears at best weakly related to seed size (Leishman & Westoby 1998; Moles & Westoby 2004), and varies with different temperature and rainfall conditions and burial depths (Owens *et al.* 1995; Hill & Vandeer Kloet 2005).

Disturbance caused by the chaining and associated clearing and fire, clearly promotes above ground diversity within this forest remnant from the soil seed bank, as has been shown elsewhere (Denslow 1980; but see Hubbell *et al.* 1999). However, there may have been an overestimate of the increase in diversity as some of the rarer specimens in quadrats were very small and so difficult to identify and may be represented as mature plants in other quadrats. Presumably if further disturbance involved in conversion of the land for agriculture proceeded, this promotion of above ground diversity would be lost. Many of the canopy species have a relative short seed bank life span and rely on regular seed production (Auld 1995) and therefore would not likely re-establish if there was a prolonged period of disturbance before the site was left to recover.

It appears likely that the different zones have different successional pathways and will lead to different species compositions in the climax assemblage. Areas that are chained and then burnt will likely have an under-representation of serotinous seeders in the canopy (in this case *Allocasuarina* and *Hakea*) compared to the other zones, and a greater representation of soil seed bank species such as *Acacia* that are dependant of fire for germination. A short period between chaining and burning, before seed is released from pods may minimise losses of serotinous taxa from the burnt zone (McCaw & Smith 1992). Resprouters appear in greatest abundance in the mulched zone and least abundance in the burnt, which may be due to the increased protection offered by the mulch and/or minimal disturbance compared to the burning and clearing that occurred post chaining in the other zones. The increased competition from resprouters and serotinous seeders may account for the reduced density of soil seed bank taxa in the mulched zone relative to the other zones.

Some of the observed differences in plant taxa between zones could be explained by pre-existing spatial differences in extant taxa and differences in the seral species in the soil seed bank prior to chaining. The vegetation was not surveyed prior to disturbance, and changes in vegetation over small spatial scales are common in WA (*e.g*., Craig *et al.* 2008). However there was no obvious differences in the sandy soil across the chained area, nor between the southern margin of the remnant and the chained area (the northern margin of the remnant is slightly stonier). However, this seems unlikely to explain all the difference as the burnt zone is a relatively narrow strip that runs across the site in close proximity to both the other zones, and patterns of presence or absence of some taxa can be explained by known response to presence or absence of fire.

Somewhat surprising was the relatively low abundance of weed species in the chained area, 3 taxa all in low abundance, despite the small size of the remnant and the surrounding fellow wheat fields containing various weed species. This indicates the site has a relatively high resistance to weed invasion, and that the chaining has not significantly reduced this resistance. This may reflect the limited grazing disturbance that this predominantly cropping landscape has had compared to other areas of the wheatbelt, and the possible resilience of parts of this ancient landscape to fragmentation (Yates & Hobbs 1997; Hobbs 2001; Hopper 2009 but see Standish & Hobbs 2009).

The lower diversity of species in all zones in 2008 probably reflects differences in the search efficiency of the surveyors for the rare taxa, as the remnant site is unlikely to have changed significantly over 2 years. However, there were clear changes in some dominant species within the communities in the chained zones consistent with vegetation succession; seral species becoming less abundant and species dominant in the remnant area increasing in density and cover within the chained zones.

Value of chaining and maintaining a mosaic of habitats in remnant management

Although fire is a common form of disturbance and promoter of diversity in the Australian landscape (Penman *et al.* 2008) only a small proportion of the species colonising the chained area were largely restricted to the burnt zone and appeared to require direct contact with fire. Physical disturbance caused by the chaining appeared adequate for many species, such as the DRF *B. adamsiana* to establish within the chained area and greatly increased the overall diversity of species growing within this remnant. Therefore chaining could be a useful management tool to promote diversity and maintenance of seral species in areas where fire is unwanted or needs to be limited so as not to affect an entire remnant or adjacent infrastructure. The chained vegetation does not necessarily need to be cleared, although its remaining *in situ* would increase the fuel load and subsequent risk of fire. Chaining with subsequent fire would alter community structure compared to a fire alone, with serotonous seeders particularly venerable (McCaw & Smith 1992; Pelton & Conran 2002; Gosper *et al.* 2010). Plants that rely on fire for recruitment (many *Acacia* for example) may also have fewer opportunities for regeneration if fires were eliminated altogether (Buist *et al.* 2002).

Although not directly affected by fire, some of the species may have been stimulated to germinate from the soil seed bank by the smoke or heat generated from the nearby burnt vegetation piles as has been demonstrated in the laboratory (Dixon *et al.* 1995; Enright *et al.* 1997; Baker *et al.* 2005). If this is the case then incorporation of fire into parts of the chained area would be needed to aid persistence of more species than just those we recorded unique to the burnt zone.

Disturbance does promote above ground diversity, but promoting chaining at a site should only be necessary if other disturbances are so infrequent that the soil-stored seedbank has become diminished, which may take decades or even centuries for some taxa (Weston 1985), so its application would need to be carefully considered. The use of chaining will also result in a different successional trajectory compared to burning (Gosper *et al.* in press).

Rare species

The population of the DRF *Boronia adamsiana* is outside its previously recorded range, with the nearest record about 70 km NW of this site (Mollemans *et al.* 1993; Davis 2005). This is not altogether unexpected as other plants thought to be extinct or rare have had significant range extensions recorded from sites surveyed after fire (Yates *et al.* 2003). It is also suspected to have occurred in an area revegetated after quarrying on the edge of Sandford Rock Nature Reserve, about 13 km NE of this study site (PM pers. obs.), although brief searches for specimens in 2008 did not locate any remaining plants.

Boronia adamsiana was once thought to be extinct (Hopper *et al.* 1990), but is now known from a number of populations (Mollemans *et al.* 1993; Davis 2005) including those on roadsides (Beecham 2002). Of the nine populations reported by Mollemans *et al.* (1993) four were on private properties within areas cleared with chains and left to regenerate. In 1993, three populations had senescing plants and appeared to be in decline (Mollemans *et al.* 1993). It is likely that ongoing disturbance would be required to maintain a population of this species at a site as it occurs in early succession stages after disturbance. However, seed of this species is clearly persistent in the seed bank, with no source populations nearby, an absence of plants within the unchained remnant, and the suspected absence of fire within this remnant for many years.

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References

Auld T D 1995 Soil seedbank patterns of four trees and shrubs from arid Australia. Journal of Arid Environments 29: 33–45.

Auld T D, Keith D A & Bradstock R A 2000 Patterns in longevity of soil seedbanks in fire-prone communities of south-eastern Australia. Australian Journal of Botany 48: 539–548.

Baker K S, Steadman K J, Plummer J A, Merritt D J & Dixon K W 2005 Dormancy release in Australian fire ephemeral seeds during burial increases germination response to smoke water or heat. Seed Science Research 15: 339–348

Beecham B C 2002 Avon Wheatbelt 2 IBRA Sub-Region Biodiversity Strategy Case Study. Unpublished report for National Land & Water Resources Audit, National Heritage Trust. <http://audit.deh.gov.au/anra/vegetation/docs/case_studies/AW2_casestudy.pdf> 25/July/2007.

Beecham B C 2004 A Conservation Case Study Of Western Australia's Rejuvenated Drainage Subregion. Department of Conservation & Land Management, Perth.

Beresford Q 2001 Development and its environmental legacy: The Western Australian wheatbelt, 1900 – 1990s. Australian Journal of Politics & History 47: 403–414.

Bond W J & van Wilgen B W 1996 Fire and Plants. Chapman & Hall, London.

Buist M L, Coates D J & Yates C J 2002 Rarity and threat in relation to the conservation of *Acaci*a in Western Australia. Conservation Science Western Australia 4: 36–53.

Carlquist S 1974 Island Biology. Columbia University Press, New York.

Chambers J C & MacMahon J A 1994 A day in the life of a seed: movements and fates of seeds and their implications for natural and managed systems. Annual Review of Ecology & Systematics 25: 263–292.

Commonwealth Bureau of Meteorology 2007 < http://www.bom.gov.au > 25/July/2007.

Craig G F, Hickman E J, McQuoid N, Newell J, Rick A M & Sandiford E M 2008 Vegetation of the Ravensthorpe Range, Western Australia: Mt Short to Kundip, 1:10 000 scale. Department of Environment & Conservation and South Coast Natural Resource Management Inc, Albany, Western Australia.

Davis M 2005 Moningarin BioBlitz Report 2003. WWF-Australia, Sydney. <http://wwf.com.au/publications/BioBlitz2003_Moningarin.pdf> 25/July/2007.

Denslow J S 1980 Patterns of plant species diversity during succession under different disturbance regimes. Oecologia 46: 18–21.

Dixon K W, Roche S & Pate J S 1995 The promotive effect of smoke derived from burnt native vegetation on seed germination of Western Australia plants. Oecologia 101: 185–192.

Dilworth R, Gowdie T & Rowley T 2000 Living landscapes: the future landscapes of the Western Australian wheatbelt? Ecological Management & Restoration 1: 165–174.

Enright N J, Byron B L & 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 N I, Goldblum D, Ata P & Ashton D H 1997 The independent effects of heat, smoke and ash on emergence of seedlings from the soil seed bank of a healthy *Eucalyptus* woodland in Grampians (Gariwerd) National Park, western Victoria. Australian Journal of Ecology 22: 81–88.

Fulton G R & Majer J D 2006 The effect of recent chaining on birds in the eastern wheatbelt of Western Australia. Pacific Conservation Biology 12: 168–174.

Gill A 1976 Fire and the opening of *Banksia ornata* F. Muell. follicles. Australian Journal of Botany 24: 329–335.

Gill A M 1999 Biodiversity and bushfires: an Australia-wide perspective on plant-species changes after a fire event. *In*: Australia's Biodiveristy – Responses to Fire (eds A M Gill, J Woinarski & A York). Biodiversity Technical Paper, No.1. Department of Environment & Heritage, Canberra. 9–54.

Gill A M, Groves R H & Noble I R (eds) 1981 Fire and the Australian Biota. Australian Academy of Science, Canberra.

Gosper C R, Prober S M & Yates C J 2010. Repeated disturbance through chaining and burning differentially affects recruitment among plant functional types in fire-prone heathlands. International Journal of Wildland Fire 19: 52–62.

Hill M O & Gauch H G Jr 1980 Detrended correspondence analysis: an improved ordination technique. Vegetatio 42: 47–58.

Hill N M & Vander Kloet S P 2005 Longevity of experimentally buried seed in *Vaccinium*: relationship to climate, reproductive factors and natural seed banks. Journal of Ecology 93: 1167–1176.

Hobbs R J 2001 Synergisms among habitat fragmentation, livestock grazing, and biotic invasions in southwestern Australia. Conservation Biology 15: 1522–1528.

Hobbs R J & Atkins I 1988 The effect of disturbance and nutrient addition on native and introduced annuals in the Western Australian wheatbelt. Australian Journal of Ecology 13: 171–179.

Hobbs R J & Huenneke L F 1992 Disturbance, diversity and invasion: implications for conservation. Conservation Biology 6: 324–356.

Hobbs R J & Mooney H A 1998 Broadening the extinction debate: population deletions and additions in California and Western Australia. Conservation Biology 12: 271–283.

Hopper S D 2009 OCBIL theory: towards an integrated understanding of the evolution, ecology and conservation of biodiversity on old, climatically buffered, infertile landscapes. Plant & Soil 322: 49–86.

Hopper S D, van Leeuwen S, Brown A P & Patrick S J 1990 Western Australia's Endangered Flora and Other Plants Under Consideration for Declaration. Department of Conservation & Land Management, Perth.

Hubbell S P, Foster R B, O'Brien S T, Harms K E, Condit R, Wechsler B, Wright S J & Loo de Lao S 1999 Light-gap disturbances, recruitment limitation, and tree diversity in a neotropical forest. Science 283: 554–557.

Leishman M R & Westoby M 1998 Seed size and shape are not related to persistence in soil in Australia in the same way as in Britain. Functional Ecology 12: 480–485.

Maher K 2007 Encroachment of sandplain heathland (kwongan) by *Allocasuarina huegeliana* in the Western Australian wheatbelt: the role of herbivores, fire and other factors. PhD Thesis, Environmental Science, Murdoch University.

McCaw W & Smith R 1992 Seed release from *Banksia baxteri* and *Hakea crassifolia* follow in scrub-rolling and burning. Journal of the Royal Society of Western Australia 75: 47–50.

McCune B & Mefford M J 1999 PC_ORD. Multivariate Analysis of Ecological Data, Version 4. MjM Software Design, Gleneden Beach, Oregon, USA.

Mielke P W Jr 1984 Meteorological applications of permutation techniques based on distance functions. *In*: Handbook of Statistics, Vol. 4 (eds P R Krishnaiah & P K Sen). Elsevier Science Publishers, New York, USA. 813–830.

Moles A T & Westoby M 2004 Seedling survival and seed size: a synthesis of the literature. Journal of Ecology 92: 372–383.

Mollemans F H, Brown P H & Coates D J 1993 Declared Rare Flora and Other Plants in Need of Special Protection in the Merredin District (excluding the Wongan-Ballidu Shire). Western Australian Wildlife Management Program No. 9. Australian National Parks & Wildlife Service, Canberra, ACT and Department of Conservation & Land Management, Como, WA.

Norton D A, Hobbs R J & Atkins L 1995 Fragmentation, disturbance and plant distribution: mistletoes in the woodland remnants in the Western Australian wheatbelt. Conservation Biology 9: 426–438.

Ooi M K J, Auld T D & Whelan R J 2007 Distinguishing between persistence and dormancy in soil seed banks of three shrub species from fire-prone southeastern Australia. Journal of Vegetation Science 18:405–412.

Owens M K, Wallacet R B & Archer S 1995 Seed dormancy and persistence of *Acacia berlandieri* and *Leucaena pulverulenta* in a semi-arid environment. Journal of Arid Environments 29: 15–23.

Pelton G A & Conran J G 2002 Comparison of two rolled sandy heath communities within a single fire patch in Ngarkat Conservation Park, South Australia. Austral Ecology 27: 85–93.

Penman T D, Binns D L & Kavanagh R P 2008 Quantifying successional changes in response to forest disturbances. Applied Vegetation Science 11: 261–268.

Saunders D A, Hobbs R J & Margules C R 1991 Biological consequences of ecosystem fragmentation: A review. Conservation Biology 1: 18–32.

Spooner P, Lunt I & Robinson W 2002 Is fencing enough? The short-term effects of stock exclusion in remnant grassy woodlands in southern NSW. Ecological Management & Restoration 3: 117–126.

SPSS Inc. 2002 SPSS for Windows. Release 11.5.0. SPSS Inc., Chicago.

Standish R J & Hobbs R J 2009 Restoration of OCBILS in south-western Australia: Response to Hopper. Plant & Soil D01 10.1007/S11104-009-0182-Z.

Tilman D 1999 Global environmental impacts of agricultural expansion: The need for sustainable and efficient practices. Proceedings of the National Academy of Science 96: 5995–6000.

Weston A S 1985 Fire – and persistence of the flora on Middle Island, a south-western Australian offshore island. *In*: Fire Ecology & Management in Western Australian Ecosystems (ed J Ford). WAIT Environmental Studies Group Report 14. Western Australian Institute of Technology, Perth, 111–118.

Whelan R J 1995 The Ecology of Fire. Cambridge University Press, Cambridge.

Yates C J, Abbott I, Hopper S D & Coates D J 2003 Fire as a determinant of rarity in the south-west Western Australian global biodiversity hotspot. *In*: Fire in Ecosystems of South-West Western Australia: Impacts and Management (eds I Abbott & N Burrows). Backhuys Publishing, Amsterdam. 395–420.

Yates C J & Hobbs R J 1997 Temperate eucalypt woodlands: a review of their status, processes threatening their persistence and techniques for restoration. Australian Journal of Botany 45: 949–973.

Appendix 1

List of taxa identified to at least generic level and likely mode of regeneration. * denotes introduced species.

Family	Taxa	Mode of regeneration
Asteraceae	*Conyza* sp.*	Soil seed bank
Aizoaceae	*Mesembryanthemum crystallinum**	Soil seed bank
Boryaceae	*Borya* sp.	Soil seed bank
Casuarinaceae	*Allocasuarina corniculata* & *campestris*	Canopy stored seed
Celastraceae	*Stackhousia monogyna*	Soil seed bank
Cucurbitaceae	*Cucumis myriocarpus**	Soil seed bank
Cyperaceae	*Lepidosperma gracile*	Resprouter
Dilleniaceae	*Hibbertia ?racemosa*	Soil seed bank
Euphorbiaceae	*Beyeria sp.*	Soil seed bank
Goodeniaceae	*Dampiera luteiflora*	Soil seed bank
	Dampiera stenostachya	Soil seed bank
	Dampiera wellsiana	Soil seed bank
	Goodenia pinifolia	Soil seed bank
	Velleia connata	Soil seed bank
	Verreauxia villosa	Soil seed bank
Gyrostemonaceae	*Gyrostemon racemiger*	Soil seed bank
	Gyrostemon sp.	Soil seed bank
Haloragaceae	*Glischrocaryon* spp.	Soil seed bank
	Gonocarpus confertifolius var *helmsii*	Soil seed bank
Lamiaceae	*Cyanostegia microphylla*	Soil seed bank
	Cyanostegia sp.	Soil seed bank
	Pityrodia lepidota	Soil seed bank
	Pityrodia terminalis	Soil seed bank
Mimosaceae	*Acacia acuminata*	Soil seed bank
	Acacia sp.	Soil seed bank
	Acacia longispinea	Soil seed bank
	Acacia ?neurophylla	Soil seed bank
Myrtaceae	*Baeckea* sp.	Resprouter
	Baeckea ?behrii	Resprouter
	Baeckea elderiana	Resprouter
	Calothamnus longissimus	Resprouter
	Chamelaucium sp.	Soil seed bank
	Eucalyptus burracoppinensis	Resprouter
	Eucalyptus leptopoda	Resprouter
	Euryomyrtus maidenii	Resprouter
	Melaleuca conothamnoides	Resprouter
	Micromyrtus sp.	Resprouter
	Regelia sp.	Resprouter
Myoporaceae	*Eremophila* sp.	Soil seed bank
Papilionaceae	*Daviesia nematophylla*	Soil seed bank
	Mirbelia rhagodioides	Soil seed bank
Poaceae	*Amphipogon* sp.	Resprouter
	Neurachne alopecuroidea	Resprouter
Polygalaceae	*Comesperma spinosum*	Resprouter
Proteaceae	*Grevillea eriostachya*	Soil seed bank
	Grevillea hookeriana subsp. *apiciloba*	Soil seed bank
	Grevillea paradoxa	Soil seed bank
	Hakea francisiana	Canopy stored seed
Rutaceae	*Boronia adamsiana*	Soil seed bank
	Drummondita hassellii	Resprouter
	Phebalium tuberculosum	Soil seed bank
	Philotheca tomentella	Soil seed bank
Santalaceae	*Exocarpos aphyllus*	Soil seed bank
	Leptomeria sp.	Soil seed bank
Sterculiaceae	*Keraudrenia integrifolia*	Soil seed bank
Stylidiaceae	*Stylidium* sp.	Soil seed bank
Thymelaeaceae	*Pimelea aeruginosa*	Soil seed bank
	Pimelea angustifolia	Soil seed bank
Xanthorrhoeaceae	*Xanthorrhoea* sp.	Resprouter