

Rabbit (*Oryctolagus cuniculus* L.) impacts on vegetation and soils, and implications for management of wooded rangelands

David J. Eldridge¹, Robyn Simpson^{2,*}

¹Department of Land and Water Conservation, c/o School of Geography, University of New South Wales, Sydney, NSW, Australia

²School of Geography, University of New South Wales, Sydney, NSW, 2052, Australia

Received December 8, 2000 · Accepted August 8, 2001

Abstract

Rabbit warrens are a distinctive landscape feature in the semi-arid woodlands of eastern Australia. We examined the surface morphology and vegetation composition of ten rabbit warrens in central-western NSW in order to assess their roles as a harbor for weedy plants. In general, mounds were characterised by a degraded soil surface dominated by bare soil and coarse gravel, whilst adjacent non-mound (control) surfaces were characterised by an extensive cover of cryptogams (lichens and mosses). Mounds supported significantly more exotic plants than non-mounds, and there was a clear separation between the two microsites in terms of the cover-abundances of vascular plants. Mound microsites contained significantly more tall (> 50 cm) species, and species with burrs compared with non-mound microsites. Germination studies indicated enhanced germination of two common, weedy, mound species (*Marrubium vulgare* and *Brassica tournefortii*) on the eroded mound surface, and greater germination of the perennial grass *Austrodanthonia caespitosa* on the cryptogam-dominated non-mound surface. The work suggests that the higher cover-abundance of weedy species is a result of alterations to the soil surface caused by rabbit disturbances, and that destruction of the warren complex, in order to prevent re-invasion and hence re-working of the mound, is required to enable native perennials to colonise.

Kaninchenbauten sind ein auffälliges Landschaftsmerkmal des semi-ariden Waldlandes Ostaustraliens. Wir untersuchten die Oberflächenmorphologie und Vegetationszusammensetzung von 10 Kaninchenbauten im zentralen Westen von New South Wales, um ihre Rolle als bevorzugte Standorte für Unkrautgewächse zu beurteilen. Im Allgemeinen waren die Bautenhügel durch eine degradierte Bodendecke und groben Kies gekennzeichnet, während angrenzende, von Bautenhügeln freie, (Kontroll-) Flächen durch ausgedehnten Kryptogamenbewuchs (Flechten und Moose) charakterisiert waren. Bautenhügel wiesen deutlich mehr exotische Pflanzen als die hügel-freien Flächen auf, und es zeigte sich ein ausgeprägter Unterschied zwischen beiden Mikrostandorten bezüglich des Flächenbewuchses durch Gefäßpflanzen. Mikrostandorte mit Bautenhügeln wiesen im Vergleich zu denen ohne Bauten deutlich mehr hochwüchsige (>50 cm) Arten und Klettenpflanzen auf. Keimungsstudien zeigten verbessertes Keimen zweier weitverbreiteter, auf Bautenhügeln wachsender Unkrautarten (*Marrubium vulgare* und *Brassica tournefortii*) auf der erodierten Oberfläche der Bauten und verstärktes Keimen des perennierenden Grases *Austrodanthonia caespitosa* auf der von Kryptogamen dominierten erdhügelfreien Fläche. Die Studie deutet darauf

*Present address: Robyn Simpson, 2 Casuarina Ave, Nhulunbuy NT 0881, Australia, Phone: ++61-8-8987-1797, E-Mail: robyn_simpson@bigpond.com

hin, dass der dichtere Flächenbewuchs mit Unkrautpflanzen von durch Kaninchenaktivität hervorgerufenen Veränderungen der Bodendecke verursacht wird. Dies erfordert die Zerstörung der Bautenkomplexe zur Verhinderung einer Neubesiedlung und damit Reaktivierung der Erdhügel durch Kaninchen, um eine Kolonisation durch einheimische perennierende Pflanzen zu ermöglichen.

Key words: Rabbit warrens – burrowing – soil processes – semi-arid woodland – germination – cryptogam

Introduction

In 1788 five European rabbits (*Oryctolagus cuniculus* L.) arrived in Australia aboard the First Fleet, and escapees quickly became established in the vicinity of the new colony around Sydney Harbour (Rolls 1984). Within 100 years of their release, rabbits had spread to all States and Territories, quickly becoming Australia's number one vertebrate pest (Coman 1999). Today the rabbit now occupies extensive areas of southern Australia, and a substantial industry has developed around its control.

Over much of their range in continental Australia rabbits live in large underground colonies or warrens. Warrens comprise a series of burrows or entrance holes, generally originating in the elevated section of the warren (mound) which, in semi-arid woodlands, is typically 0.3 to 0.5 m above the general level of the landscape (Eldridge & Myers 2001). This mound comprises soil excavated by the rabbits, with annual soil accumulation levels of up to 63 m³ ha⁻¹ being reported (Butler 1995). Warren excavation is an ongoing process, with the mound being replenished by a buildup of freshly excavated soil (Parer et al. 1987, Myers et al. 1994). This process of burrow excavation and warren replenishment leads to extensive and sustained soil disturbance in the vicinity of warrens.

Under conditions of severe rabbit infestation, warrens may occupy many hundreds of square metres per hectare. Circular grazing gradients radiate out from the warrens, with plants close to the warrens likely to be more heavily grazed than those at greater distances (Lange & Graham 1983). Rabbits are highly selective grazers (Foran 1986, Leigh et al. 1989, Myers et al. 1994), and palatable or desirable plants are likely to be less abundant close to the warrens than further away. Rabbits also damage woody vegetation, reducing seedling establishment and influencing the population structure of many species (Crisp & Lange 1976, Lange & Graham 1983, Leigh et al. 1989). Long-term, continuous grazing by rabbits results in increased total grazing pressure, reduced pastoral productivity (Williams et al. 1995) and eventually increased landscape degradation (Cooke 1991).

Since the release of the rabbit calicivirus disease (RCD) in Australia in 1998, land managers have been encouraged to adopt a strategic program of warren destruction, generally by ripping with a crawler tractor, in order to maximise the effectiveness of biological control of the extant rabbit population. Because most rabbits live in warrens, and rabbits stranded above ground are vulnerable to predation, ripping of warrens is generally seen as an effective method of increasing mortality following population decline.

In the semi-arid wooded rangelands of eastern Australia, little is known about the physical nature of rabbit warren surfaces and the vegetation communities they support. Anecdotal evidence and limited empirical data (Eldridge & Myers 2001) suggest dramatic and persistent effects of rabbit activity on both the warren surfaces and the surrounding vegetation community (Eldridge & Myers 1999). Land management agencies such as the New South Wales National Parks and Wildlife Service have undertaken regular control of rabbits at Yathong Nature Reserve in an attempt to reduce populations to manageable levels. The effect of ripping on warren plants is an issue of concern, as is the question of whether ripping is likely to lead to a more or less stable surface than existed had the warrens been left intact.

In order to answer some concerns relating to the management of warren-infested landscapes, we embarked upon a comprehensive study of warrens, their vegetation and soils, and the likely impacts of rabbit removal on landscape stability. Our study examined a number of hypotheses relating to the physical and biological features of rabbit warren surfaces. Firstly, we hypothesised that the warren surfaces are physically degraded compared with non-warren soils. Anecdotal and empirical evidence (Foran 1986, Leigh et al. 1989) suggest that rabbits preferentially remove certain species from the vicinity of their warrens, creating a distinct generally weedy community on the mound compared with that surrounding the mounds. Thus a second hypothesis we tested was that mounds on the warrens supported a distinct vegetation community dominated by weedy, exotic plants. Third, we wished to determine whether differences in germination rates

might account for differences in the abundance of species growing on and off mounds. Using two mound and two non-mound species, we hypothesised that mound species should have higher germination rates on the mounds and *visa-versa*. Finally, we wished to investigate whether vegetation assemblages on the mound and non-mound microsites differed in relation to a unique set of morphological, reproductive or dispersal attributes. We did this by looking at differences in the number of species on both microsites which were characterised by particular attributes.

Materials and methods

The study area

The study was undertaken at Yathong Nature Reserve which is located 130 km south of Cobar near Mount Hope, in central-western New South Wales, Australia (32° 35'S, 145° 35'E; altitude 200–425 m). Yathong Nature Reserve consists of former grazing leases acquired by the National Parks and Wildlife Service in the 1970s. The red earth soils support an open woodland with an upperstorey of *Eucalyptus intertexta* and *Eucalyptus populnea*, a midstorey of scattered shrubs of the genera *Dodonaea* and *Acacia*, and a groundstorey dominated by perennial grasses, and perennial and annual forbs. Slopes were generally less than 1% and the soils dominated by massive red earths (Gn 2.13; Northcote 1979), often with an extensive cryptogamic soil crust.

Experimental design

Rabbit warrens are a characteristic landscape feature of much of arid and semi-arid Australia (Myers et al. 1994), and at Yathong Nature Reserve, are common in grasslands and open woodlands (Leigh et al. 1989, Eldridge & Myers 1999). Warrens are readily identified by their slightly elevated, concave surface profile, and their apparently distinct assemblages of weedy vegetation.

Warren complexes comprise three main microsites: i) the mounds or elevated sections of the warren dominated by burrow entrances and characterised by extensive soil disturbance, ii) the non-mound surface around the perimeter of the mound showing no evidence of soil disturbance, and iii) intermediate disturbed areas showing attributes of both microsites, and characterised by scratchings, dung piles, small piles of disturbed soils and undisturbed cryptogamic crusts (Wood 1984, Eldridge & Myers 1999). These microsites are readily distinguished in the field.

Soil surface and vegetation attributes were measured at 10 warren complexes (defined as the central,

raised portion of the warren, as well as the surrounding non-warren "control" surface) within a 200 ha section of woodland on the eastern boundary of the nature reserve. The ten warrens were selected so that they were of similar size, not located around old trees, and separated from each other by more than 150 m. Given that rabbits generally forage close (i.e. 50–100 m) to their warrens, separation of warrens at distances of 150 m ensured that each warren could be regarded as independent in a statistical sense.

Soil surface characterisation

Previous work from a smaller number of warrens ($n = 5$) used for a more detailed soil chemistry study revealed some differences in soil surfaces between mound and non-mound microsites (Eldridge & Myers 2001). At five of the ten warrens (every second warren), soil surface morphology was assessed on both the mounds and adjacent control sites using the line intercept method. Two 1 m transects were randomly located on the surface of each of the five warrens, and the morphology of the surface described as either litter, bare soil, dung, lag gravel (deposits of coarse sand), vegetation or cryptogamic crust to the nearest millimetre. Two control locations adjacent to each mound were also assessed. The results were used to determine differences in the proportion of various surface morphologies between mounds and controls.

Cover-abundance of vascular plants

A 60 m transect was placed along the longest axis of each warren so that the middle of the transect was aligned with the centre of the warren, defined as the location with the highest elevation. A second 60 m transect was placed perpendicular to the first transect through the centre. Quadrats, measuring 0.5 by 0.5 m, were placed every 2 m along both transects, and each quadrat was recorded as either mound or non-mound. Quadrats falling on intermediate surfaces i.e. showing characteristics of both mounds and non-mounds, were rejected, and additional quadrats were examined until a total of 10 mound and 10 non-mound quadrats was measured on each warren, resulting in a total of 200 quadrats for the 10 warrens. In doing this the aim was to restrict our analyses to those microsites which were predominantly either mound or non-mound, though we realised that intermediate microsites are a common warren feature. Cover-abundance of all vascular plants in each quadrat was assessed using the following categories: 1 = <10% cover and <6 plants, 2 = <10% cover and 6–10 plants, 3 = <10% cover and >10 plants, 4 = 10–25% cover, 5 = 26–50% cover, 6 = 51–75% cover, 7 = >75% cover.

Classification of the vegetation community

We wished to test whether vegetation assemblages on the mound and non-mound microsites differed on the basis of a unique set of morphological, reproductive or dispersal attributes. Thirty ecological and morphological attributes from 10 characters (Tab. 1) were scored for the 25 species which occurred in 25% (50) or more of the 200 quadrats. The choice of attributes was a compromise between what could easily be assessed in the field and their ecological relevance (*sensu* McIntyre et al. 1999). Consequently, we used attributes which could easily be measured in the field and/or supplemented from the literature. Measurements of field specimens were complemented by information obtained from the literature (Harden 1990–1995, Cunningham et al. 1992) as some characters such as seed ornamentation were difficult to find in field specimens at the time of this study. Plant attributes were generally binary or continuous, and generally easily quantifiable in the field.

Table 1. Ecological and morphological characters and attributes used to assess species.

Character type	Attribute states
Growth form	ascending or prostrate
Cotyledon	monocotyledon or dicotyledon
Life form	annual or perennial
Origin	native or exotic
Dispersal mode	unassisted, wind assisted or animal assisted
Seed ornamentation	no ornament, hair/pappus, awn, barb, wing or burr
Fruit type	succulent indehiscent, dry indehiscent or dry dehiscent
Leaf height	0–10 cm, 10–20 cm, 20–30 cm, 30–50 cm or > 50 cm
Leaf arrangement	predominantly basal, basal and cauline or predominantly cauline
Root type	fibrous or tap root

Germination trials

To test for possible differences in germination rate between the mound and non-mound microsites, a laboratory-based reciprocal germination trial was undertaken using two species commonly found on mound surfaces (*Marrubium vulgare* and *Centaurea melitensis*) and two species common on non-mound surfaces (*Austrodanthonia caespitosa* and *Aristida jerichoensis*). Seeds of all species were collected from the vicinity of Yathong Nature Reserve between March 1998 and April 1999.

Previous studies indicated that mound surfaces were characterised by bare, eroded soils whilst cryptogamic crusts dominated the non-mound surfaces (Eldridge &

Myers 1999). Undisturbed samples of surface soil dominated by either bare soil (from active mounds) or cryptogams (from non-mound “control” microsites) were collected in 80 mm diameter plastic Petrie dishes and transported intact to the laboratory. The germination experiment consisted of a fully orthogonal design of two surface types (cryptogam and bare soil) by four species, each with five replicates, resulting in a total of 40 Petrie dishes. Fifty seeds of each of the four species were placed on each of the 10 Petrie dishes. On the cryptogamic surface, seeds were placed in the cracks between individual lichens and mosses, as previous studies indicated significant differences in germination between different niches (i.e. surface vs cracks) within the cryptogamic crust community (Eldridge unpublished data).

The 40 Petrie dishes were illuminated for 12 h photoperiods with a flux of 50 $\mu\text{mol m}^{-2} \text{s}^{-1}$ using an array of fluorescent lights. Petrie dishes were watered *ad libitum* with distilled water. Seeds were counted daily and removed once they had germinated, i.e. when the shoot had emerged. The species chosen are not known to have dormant seeds, and previous studies (Eldridge unpublished data) indicated that the majority of seeds germinated within 10 days. Consequently, germination was assessed up until day 10 only.

Statistical analyses

One-way ANOVA was used to test for differences in soil surface cover and cover-abundance of each species between the two microsites after checking for homogeneity of variance (Minitab 1997). The cover-abundance data matrix of 44 species by 20 sites (10 warrens by 2 microsites) contained many zero entries thereby precluding techniques for normalising the data. Where transformation failed to improve the distribution of the data, the non-parametric Mann-Whitney U Test was used.

A matrix comprising the cover-abundance of each of the 44 species according to microsite (mound vs non-mound) was converted to a similarity matrix using the Bray-Curtis similarity coefficients contained within the PRIMER (Version 4) statistical package (Clarke & Warwick 1994). This similarity matrix was subjected to non-metric Multi-Dimensional Scaling (MDS) using one of the PRIMER (Version 4) routines in order to determine whether microsites supported a unique assemblage of species. Hypothesis tests of differences between two groups of species i.e. those typical of mounds and those typical of non-mounds, defined *a priori*, were performed using ANOSIM, which is comparable to a distribution-free two-way ANOVA (Clarke 1993). Using a number of random permutations on the similarity matrix, ANOSIM produces a

test statistic (Global R) with a significance level which we used to determine whether cover-abundance of the species varied significantly between mound and non-mound microsites.

The mean number of species from the 10 mounds and 10 non-mounds possessing each attribute state were compared using the non-parametric two-sample Wilcoxon rank sum test (Minitab 1997) as the data were not normally distributed and could not adequately be transformed.

Differences in percentage germination at 10 days were analysed using two-way ANOVA (GENSTAT 1997). Diagnostic tests revealed that the raw data did not require transformation. To guard against inflating the experiment-wise Type 1 error rate, *a priori* orthogonal, single degree of freedom contrasts (GENSTAT 1997) between soil surface type within each plant species were used in the analysis of average germination at 10 days.

Results

Soil surface condition

Morphology of the mounds was significantly different from that on adjacent non-mound areas. Mounds were characterised by significantly more bare ground ($P < 0.01$), gravel ($P = 0.04$) and dung ($P = 0.02$), and significantly less cryptogam cover ($P < 0.01$). Greater cover of litter on the non-mound areas was however not significant ($P = 0.052$; Fig. 1). Pooled across the ten micro-transsects, the mounds averaged almost 60% bare ground and 20% lag gravel.

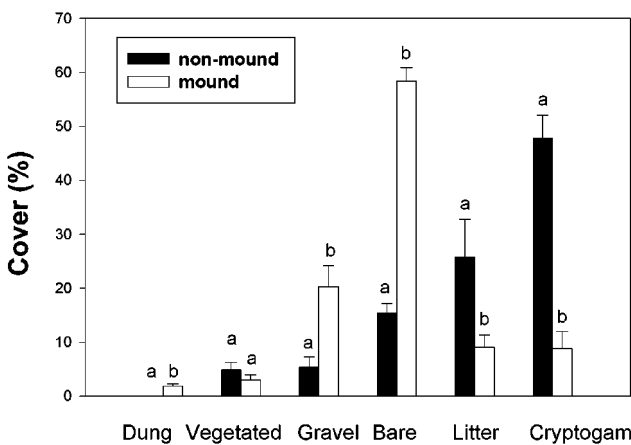


Fig. 1. Mean soil cover for various surface components on the mound and non-mound microsites. Bars indicate one standard error of the mean. Different letters within a component indicate a significant difference at $P < 0.05$.

Floristics of the warren complexes

Forty-four vascular plants comprising 33 forbs, 10 grasses and one shrub were recorded from the rabbit warren complexes (Tab. 2). Twelve species accounted for 80% of total cover-abundance, and of these, five species (*Medicago laciniata*, *Centaurea melitensis*, *Erodium crinitum*, *Sclerolaena diacantha* and *Sysimbrium irio*) accounted for half (50.1%) of total cover-abundance.

Some species were found primarily on mound microsites (*Sysimbrium irio*), some on both mound and non-mound (*Medicago laciniata*), and others primarily on non-mound microsites (*Aristida* spp). Ten species had significantly different cover-abundance levels between the microsites ($P < 0.05$; Tab. 3). For example, *Centaurea melitensis* had significantly higher cover-abundance on the mounds, accounted for 17.1% of total cover-abundance. On the non-mound microsites however it accounted for only 2.1% of cover-abundance. The first dimension of the MDS ordination indicated a clear and significant separation (Global R = 0.862, $P = 0.001$) between mound and non-mound microsites based on cover-abundance of the 44 species (Fig. 2).

Ten of the 44 species recorded on the warren complexes were exotics. As expected, exotics had significantly higher cover-abundance on the mounds (64.1% of total cover-abundance) compared with the non-mounds (21.7%, $P < 0.01$). Cover-abundance of the naturalised

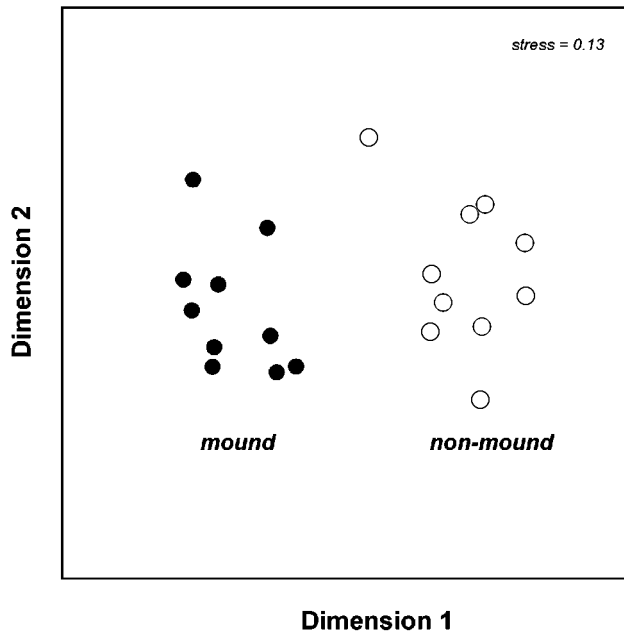


Fig. 2. The first two dimensions of the non-metric MDS biplot based on cover-abundance of the 44 vascular plants, showing the relative positions of mounds and non-mound microsites.

legume *Medicago laciniata* was very high on both microsites (Tab. 2), and accounted for 86% of total exotic cover-abundance on the non-mound microsites.

Species attributes and germination

Mound microsites contained significantly more exotic and tall (> 50 cm) species, and species with burrs compared with non-mound microsites (Tab. 4). In general,

non-mound species were erect or prostrate, low growing (< 30 cm tall), native perennials, with awns barbs or wings, and with fibrous or tap roots (Tab. 4).

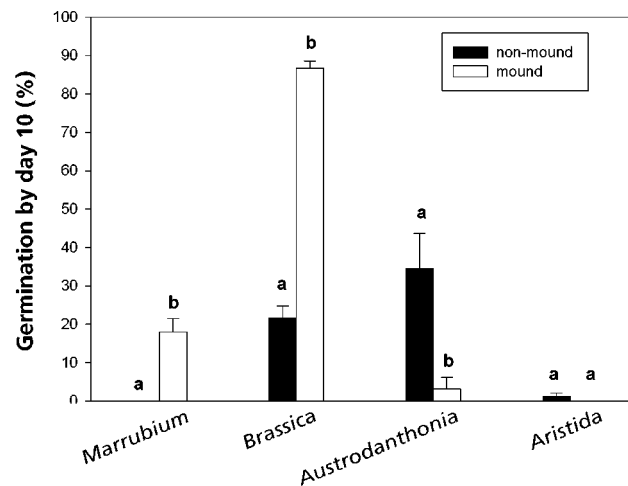
Germination of *Marrubium vulgare* and *Brassica tournefortii* at 10 days was significantly greater on the bare mound surfaces compared with the cryptogamic non-mound surfaces ($F_{1,32} = 24.82$ and 20.62 , $P < 0.001$ for *Marrubium* and *Brassica* respectively; Fig. 3). Germination of *Austroanthonia caespitosa* was signifi-

Table 2. Mean cover-abundance of each of the 44 species recorded at the study site. Species are arranged in order of decreasing cover-abundance averaged across the mound and non-mound microsites. Ranking refers to the relative importance of a particular species to total cover-abundance within a particular microsite; F = forb, G = grass, S = shrub; - insufficient data to allow significance testing (see Methods); # cover-abundance < 1%, *exotic species. Nomenclature follows Harden (1990–95).

Species	Life form	Ranking		P value	Proportion of total cover-abundance (%)
		Mound	Non-mound		
<i>Medicago laciniata</i> *	F	2	1	> 0.05	16.92
<i>Centaurea melitensis</i> *	F	1	13	< 0.01	9.85
<i>Erodium cicutarium</i>	F	6	3	0.02	8.71
<i>Sclerolaena diacantha</i>	F	6	4	> 0.05	7.39
<i>Sisymbrium irio</i> *	F	3	21	0.02	7.26
<i>Aristida jerichoensis</i>	G	13	2	< 0.01	6.69
<i>Tetragonia tetragonioides</i>	F	4	36	-	5.74
<i>Marrubium vulgare</i> *	F	5	26	> 0.05	3.66
<i>Stipa scabra</i>	G	19	5	0.03	3.60
<i>Rhodanthe corymbiflora</i>	F	21	6	> 0.05	2.97
<i>Paspalidium constrictum</i>	G	14	7	> 0.05	2.65
<i>Salsola kali</i> *	F	8	26	0.01	2.65
<i>Chamaesyce drummondii</i>	F	14	9	> 0.05	1.77
<i>Convolvulus erubescens</i>	F	12	19	> 0.05	1.70
<i>Maireana humillima</i>	F	17	11	> 0.05	1.52
<i>Vittadinia cuneata</i>	F	35	8	< 0.01	1.52
<i>Schismus barbatus</i> *	G	10	36	-	1.45
<i>Goodenia hederacea</i>	F	23	9	> 0.05	1.39
<i>Chenopodium melanocarpum</i>	F	11	36	-	1.33
<i>Ptilotus obovatus</i> var. <i>obovatus</i>	F	23	12	0.04	1.20
<i>Hordeum leporinum</i> *	G	9	36	-	1.18
<i>Chenopodium curvispicatum</i>	F	14	20	> 0.05	1.14
<i>Austroanthonia caespitosa</i>	G	36	13	-	1.01
<i>Sida cunninghamia</i>	F	21	17	0.03	1.01
<i>Abutilon otocarpum</i>	F	28	15	< 0.01	#
<i>Actinobole uliginosum</i>	F	36	15	-	#
<i>Wahlenbergia</i> sp.	F	28	17	> 0.05	#
<i>Sclerolaena divaricata</i>	F	19	26	> 0.05	#
<i>Sonchus oleraceus</i> *	F	18	36	-	#
<i>Boerhavia dominii</i>	F	23	26	> 0.05	#
<i>Monachather paradoxa</i>	G	23	23	> 0.05	#
<i>Solanum esuriale</i>	F	36	22	-	#
<i>Carthamus lanatus</i> *	F	28	26	> 0.05	#
<i>Chloris truncata</i>	G	36	23	-	#
<i>Nicotiana velutina</i>	F	23	36	-	#
<i>Scaevola aemula</i>	F	36	23	-	#
<i>Alternanthera denticulata</i>	F	36	26	-	#
<i>Aristida behriana</i>	G	36	26	-	#
<i>Cheilanthes sieberi</i> subsp. <i>sieberi</i>	F	36	26	-	#
<i>Eremophila longifolia</i>	S	28	36	-	#
<i>Lomandra effusa</i>	F	36	26	-	#
<i>Oxalis perennans</i>	F	28	36	-	#
<i>Solanum ferrocissimum</i>	F	28	36	-	#
<i>Thyridolepis mitchelliana</i>	G	36	26	-	#

Table 3. Mean cover-abundance of species differing significantly between microsites. M = mound, C = control (non-mound).

Species	Mean cover-abundance		P	Trend in cover-abundance
	Control	Mound		
<i>Centaurea melitensis</i>	0.16	1.40	< 0.001	M > C
<i>Sisymbrium irio</i>	0.04	1.11	0.019	M > C
<i>Salsola kali</i>	0.01	0.41	0.014	M > C
<i>Erodium crinitum</i>	0.94	0.44	0.019	C > M
<i>Aristida jerichoensis</i>	0.95	0.11	0.002	C > M
<i>Stipa scabra</i>	0.53	0.04	0.034	C > M
<i>Vittadinia cuneata</i>	0.23	0.01	0.006	C > M
<i>Ptilotus obovatus</i>	0.17	0.02	0.049	C > M
<i>Sida cunninghamia</i>	0.13	0.03	0.049	C > M
<i>Abutilon otocarpum</i>	0.14	0.01	0.006	C > M

**Fig. 3.** Percentage germination of the four plant species after 10 days on mound and non-mound microsites. Bars indicate one standard error of the mean (sem); different letters indicate a significant difference for a particular species at $P < 0.05$.**Table 4.** Mean numbers of species of a given attribute in each of the five mounds and five non-mounds. M = mound, C = control (non-mound), n.s. = not significant ($P > 0.05$). Attributes are described in Table 1.

Attribute	Non-mound	Mound	P value	Trend
Ascending	10.5	7.3	0.0132	C > M
Prostrate	3.0	2.2	0.0082	C > M
Monocotyledonous	3.2	1.6	0.0203	C > M
Dicotyledonous	10.7	8.0	0.0163	C > M
Annual	4.2	4.7	0.4330	n.s.
Perennial	9.7	4.9	0.0010	C > M
Native	11.5	5.3	0.0005	C > M
Exotic	2.4	4.3	0.0011	M > C
Unassisted	3.3	3.1	0.6677	n.s.
Wind assisted	3.6	2.5	0.1429	n.s.
Animal assisted	6.0	3.1	0.0004	C > M
No ornament	4.3	3.7	0.3898	n.s.
Hair/pappus	2.7	2.1	0.3907	n.s.
Awn	3.2	1.4	0.0006	C > M
Barb	1.7	0.3	0.0003	C > M
Wing	0.9	0.4	0.0252	C > M
Burr	1.1	1.7	0.0087	M > C
Succulent indehiscent	1.2	1.0	0.4276	n.s.
Dry indehiscent	9.5	5.1	0.0027	C > M
Dry dehiscent	3.2	3.5	0.3365	n.s.
0–10 cm	3.4	3.0	0.4387	n.s.
11–20 cm	4.5	2.1	0.0027	C > M
21–30 cm	4.2	1.7	0.0013	C > M
31–50 cm	1.7	2.1	0.2656	n.s.
> 50 cm	0.1	0.7	0.0087	M > C
Basal	1.7	0.4	0.0005	C > M
Basal and cauline	2.8	2.9	0.9070	n.s.
Cauline	9.4	6.3	0.0073	C > M
Fibrous root	5.0	2.8	0.0187	C > M
Tap root	8.9	6.8	0.0091	C > M

cantly greater on the cryptogamic surface ($F_{1,32} = 22.82$, $P < 0.001$). *Aristida* failed to germinate substantially on either the mound or non-mound surface ($< 2\%$), and was not significantly different between the two surfaces (Fig. 3).

Discussion

The present study focussed on warren systems in a wooded rangeland, and indicates that marked differences in the surface morphology between mounds and non-mounds are reflected in differences in cover-abundance, morphology and germination of some common woodland plants. Disturbed warren surfaces tended to be dominated by exotic plants whilst undisturbed non-mound microsites were dominated by native species. Previous research on the impact of rabbits has highlighted their impact on shrub recruitment (Lange & Graham 1983, Auld 1990), and vegetation cover and composition at varying distances from the warrens (Wood 1984, Myers et al. 1994). The present results reinforce the notion that rabbits are important agents of disturbance in arid and semi-arid landscapes, with warren excavation resulting in local, small-scale but persistent changes to the soils and vegetation within the environment of the warrens (Meadows & Meadows 1991, Kinlaw 1999).

Plant species associated with the warrens

Analyses of plant attributes on mounds and non-mounds indicated a high degree of overlap in individual species across both microsites. Despite this, however,

mounds supported more exotics, more tall (> 50 cm) species and more species with burrs compared with non-mound microsites (Tab. 4). In our study the dominance of taller plants was due predominantly to the erect annual forbs *Centaurea*, *Sisymbrium*, *Marrubium* and *Salsola* on the mounds. The dominance of these tall exotic forbs is consistent with observations from other disturbed sites such as sheep camps, stock yards and roadsides where domestic animals are concentrated, or where the soils are regularly disturbed (Campbell 1978, Cunningham et al. 1992). We also found about half as many species in the intermediate height range (12–30 cm) on the mounds compared with the non-mounds (Tab. 4). In contrast to the tall, annual forbs on the mounds, short (< 30 cm tall), erect, perennial grasses such as *Aristida jerichoensis*, *Stipa scabra* and to a lesser extent *Austrodanthonia caespitosa* characterised the non-mound sites (Tab. 2). The greater number of tall forbs on the disturbed mound surfaces compared with non-mounds is, however, inconsistent with the general trend in many temperate grasslands of decreasing plant size with increasing disturbance (Noy-Meir et al. 1989, Trémont 1994, McIntyre et al. 1995).

There are abundant data to demonstrate that prolonged, small-scale disturbance created by mammals in a range of vegetation communities results in a decline in the relative abundance of perennial grasses at the expense of annual forbs (Friedel et al. 1988, Noy-Meir et al. 1989, Dean et al. 1994, Boeken et al. 1995, Gómez-García et al. 1995, Milton et al. 1997). Research results from other landscapes suggest that, given the extirpation of rabbits, it is unlikely that the original perennial grasses would return to the mounds due to the abundant seedbank of annual forbs in the mound soils (Lunt & Morgan 1999), and the fact that many perennial grasses are unable to reestablish in disturbed, unstable sites (Walker et al. 1995). Suppression of germination of perennial grasses such as *Austrodanthonia caespitosa* on the mound surfaces (Figure 3) may explain some of the observed difference in cover between mounds and non-mounds. Compared with the non-mounds, there were more mound species dispersed by burrs (Tab. 4). Inter-warren dispersal of *Centaurea melitensis* (the capsules of which have small barb-like hooks) and *Marrubium vulgare* was probably enhanced by rabbits through attachment of both seeds or capsules to their fur.

Our field observations suggest that warren complexes are both spatially and temporally highly variable depending on the type of rabbit activity i.e. burrowing, scratching or digging when marking their territories or searching for food (Sneddon 1991, Eldridge & Myers 1999). The type and degree of disturbance (i.e. superficial scratching vs subsoil exposure) and the

spatial variability of disturbance on the warren complexes at scales of less than a metre, may explain the high degree of overlap in species recorded within a particular microsite. Small patches of rabbit scratching occur alongside areas of cryptogamic crust, re-stabilised areas of the mound and piles of subsoil both on the mound and on the non-mound surfaces. This results in a patchwork of micro-niches favouring plants with a range of regenerative strategies (Grubb 1977). Superficial scratching and digging are known to favour wind and mammal-dispersed seeds, whereas more substantial disturbances, which expose the soil to sunlight, favour self-dispersed small therophytes and agricultural weeds (Milton et al. 1997). The annual Brassica *Sisymbrium irio* produces abundant seeds which germinate readily in rabbit scratchings and pits dug by kangaroos as well as along eroded tracks and gullies (Eldridge personal observation). Similar disturbances by boars (*Sus scrofa*) resulted in a significantly higher proportion of species classified as weeds, therophytes and obligate reseeder (Milton et al. 1997). Where the soil disturbance is extreme, and subsoil material is deposited on the surface, the soil is likely to be colonised by either a dormant seed bank or from growth of vegetation from the sides, respectively.

Disturbance, soil morphology and germination

The long-term effect of disturbance by rabbits is to create a surface with a discontinuous matrix of vegetated, bare or eroded soils, often with exposed coarse lag gravel. This surface contrasted greatly whilst the moderately stable soil matrix surrounding the warrens which were dominated by cryptogams, perennial grasses and forbs (Eldridge & Greene 1994). Material excavated during warren construction is deposited near the burrow entrances (Myers et al. 1994, Eldridge & Myers 1999), and this not only covers the microphytic crust and extant vegetation, but is richer in silts and clays (Eldridge & Myers 1999). Given their high clay content, mounds are highly susceptible to physical crusting, hardsetting and even wind and water erosion when unvegetated, largely through the re-organisation of silts and clays under the action of raindrops (Eldridge & Greene 1994, Walker & Koen 1995). Continued rabbit activity will maintain a surface with a degraded morphology.

Unlike the concave pits, holes and depressions constructed by many animals during foraging or habitat modification (Gutterman et al. 1990, Meadows 1991, Gutterman 1997, Whitford & Kay 1999), rabbit warrens tend to be convex-shaped due to excavation of subsoil (Myers et al. 1994, Eldridge & Myers 2001). Concave structures tend to act as landscape “sinks” (Reader & Buck 1986, Boeken et al. 1995, Whitford

1998), trapping water, nutrients and seeds, and producing favourable sites for plant growth. Warren surfaces however tend to shed resources, due to their shape and smooth, eroded surfaces. The lower levels of favourable soil nutrients such as nitrogen and carbon on the mounds compared with the non-mounds (Eldridge & Myers 1999) suggest to us that either these nutrients are being eroded from the mounds, or that the rabbits are depositing less fertile soils at the surface.

A significant impact of rabbits was to destroy the cryptogamic crust either directly by disturbance, or indirectly by smothering it with excavated soil. The marked differences in morphology between the microsites was reflected in noticeable differences in germination in three of the four species tested (Fig. 3). Germination of the weedy *Marrubium vulgare* and *Brassica tournefortii* was significantly greater on the disturbed, mound surface compared with the non-mound, cryptogamic surface, and conversely germination of the grass *Austrodanthonia caespitosa* was significantly greater on the cryptogamic crust (Fig.3).

Cryptogamic crusts are known to both inhibit and promote germination, and their effects may be biological or physical in nature, and often species-specific (Johansen 1993, Zaady et al. 1997). Typically, cryptogamic surfaces provide an array of "safe sites" for some species; cracks between lichen thalli and moss clumps into which seeds become trapped (Harper & Marble 1988). Lichen and mosses shed small amounts of water into these micro-cracks, leading to enhanced water relations and thus higher germination rates for some species (Johansen 1993). However, some crust organisms (fungi and cyanobacteria) suppress germination for certain plant species. In our study, the biological surface dominated by lichens and mosses clearly favoured the grass *Austrodanthonia caespitosa*, though the mechanism for this is unknown. During the germination trials, the awns of *Austrodanthonia* were frequently observed trapped within the cracks between individual lichens, ensuring a moderate degree of soil seed contact. In the case of *Brassica*, we believe that the combination of a relatively small seed size and perhaps allelopathic effects from cyanobacteria in the crust (Zaady et al. 1997) may have accounted for the low levels of germination on the cryptogamic surfaces. At the scale of individual seeds, we observed that *Brassica* seeds falling on bare soil between lichens germinated readily. However, those which failed to make direct contact with the soil surface by being either falling directly onto a lichen thallus or becoming stranded on coarse sandy material, generally desiccated under the watering regime used, despite the fact that the seeds possess a mucilaginous sheath (Guterman 1986).

Compared with the cryptogamic surface however, the mound soils were typically dispersed (eroded), smooth, and contained large amounts of embedded gravel and coarse sand, but sparse litter. In general, reduced germination on these surfaces is likely to have resulted from poor soil-seed contact, high solar radiation, rapid moisture depletion and therefore poor soil moisture storage and a lack of suitable niches for seed entrapment (Peart & Clifford 1987). These barbed diaspores of both *Medicago laciniata* (dominant on mounds and non-mounds) and *Centaurea melitensis* readily trap soil particles, eventually becoming embedded in the soil matrix. The close soil seed contact probably account for the ability of these species to readily germinate on degraded mound surfaces. Further, in the case of *Marrubium vulgare*, the mucilaginous sheath around the seed may also have assisted in water retention (Guterman 1986).

Implications for management of semi-arid woodlands

This study indicated that warrens generally support a vegetation community characterised by weedy exotic species, and with physically degraded surfaces maintained by rabbits. Furthermore, we believe that removal of the extant population is necessary for the restoration of warren-infested landscapes. Various methods have been proposed for control of rabbits in arid rangelands, many of which involve an integrated program of poisoning and biological control (Myers et al. 1994, Cooke 1999) supported by destruction of their harbour (Parker et al. 1976, Martin & Eveleigh 1979, Wood 1985, Parer & Parker 1986, Cooke & Hunt 1987, Mutze 1991).

Reinvasion by rabbits is imminent in the absence of physical destruction of warrens. Vine (1999) showed that approximately 30% of rabbit warren entrances were active on intact but previously abandoned warrens only 12 months after the release of RCD, compared with 4% for adjacent areas where warrens had been destroyed. Intact warrens tend to act as "refugia" for recovering rabbit populations, and in the absence of refuge warrens, a large proportion of rabbits remaining above-ground are likely to perish through predation.

Destruction of the warrens has two effects. Firstly, ripping is likely to change the morphology of the warren from one which is convex in cross-section to one which is concave. Field observations and limited empirical evidence (Vine 1999) indicate that ripped warrens are typically concave, particularly if the soil is dry when ripping is carried out. Concave, ripped warrens act as sinks for water, litter and soil, gradually accret-

ing organic matter, seeds and nutrients. Ripping is also likely to increase surface heterogeneity, reinstating micro-catchments for trapping of water. Secondly, in the short-term, ripping will likely promote the growth of annual weeds around the warrens. However, given the cessation of disturbance by rabbits, and reductions in preferential removal of the more palatable native species, these areas are likely to regenerate over time. The speed of regeneration is however unknown, and will depend on available seed source, soil type and post-treatment rainfall. In areas currently grazed by sheep and cattle, removal of stock for a limited period may be preferential. Studies are currently underway to monitor recovery of plant species on ripped and unripped warrens on areas from which rabbits have been removed.

Acknowledgements. We thank Adam Vine, Flynn Elton and Patrick Burke-Marcoo for assistance in the field, Terry Koen for statistical advice, Ray Thompson, Steve Lewer and Ross Anderson for providing seed used in the germination trials, and Dr. Ian Lunt and an anonymous referee for helpful suggestions on improving the manuscript. The germination trials were undertaken by Valerie Marsden and Joanne Roe under the CSIRO Student Research Scholarship Scheme. The research was undertaken under a permit from the NSW National Parks and Wildlife Service (Permit No. A2069). This is publication no CNR2000.047 of the Centre for Natural Resources.

References

- Auld TD (1990) Regeneration in populations of the arid zone plants *Acacia carnei* and *A. oswaldii*. *Proceedings of the Ecological Society of Australia* 16: 167–272.
- Boeken B, Shachak M, Gutterman Y, Brand S (1995) Patchiness and disturbance in plant community responses to porcupine diggings in the Central Negev. *Ecography* 18: 410–422.
- Butler DR (1995) *Zoogeomorphology: animals as geomorphic agents*. Cambridge University Press, London.
- Campbell DA (1978) Pasture species zonation associated with rabbit dunghills on the northern tablelands of NSW. Dip. Science thesis, University of New England, Armidale.
- Clark KR (1993) Non-parametric analyses of changes in community structure. *Australian Journal of Ecology* 18: 117–143.
- Clarke KR, Warwick RM (1994) *Change in marine communities: an approach to statistical analysis and interpretation*. Natural Environment Research Council, Plymouth, UK.
- Coman BJ (1999) *Tooth and nail: the story of the rabbit in Australia*. Text Publishing, Melbourne.
- Cooke BD (1991) Rabbits: indefensible on any grounds. *Search* 22: 193–194.
- Cooke BD (1999) Rabbit arrest: life after death. *Nature Australia* 26: 42–49.
- Cooke BD, Hunt LP (1987) Practical and economic aspects of rabbit control in hilly semiarid South Australia. *Australian Journal Wildlife Research* 14: 219–223.
- Crisp MD, Lange RT (1976) Age-structure distribution and survival under grazing of the arid zone shrub *Acacia burkittii*. *Oikos* 27: 86–92.
- Cunningham GM, Mulham WE, Milthorpe PL, Leigh JH (1992) *Plants of Western New South Wales*. Inkata Press, Sydney.
- Dean WRJ, Milton SJ, Ryan PG, Maloney CL (1994) The role of disturbance in the establishment of indigenous and alien plants at Inaccessible and Nightingale Islands in the South Atlantic Ocean. *Vegetatio* 113: 13–23.
- Eldridge DJ, Greene RSB (1994) Microbiotic soil crusts: a review of their roles in soil and ecological processes in the rangelands of Australia. *Australian Journal of Soil Research*. 32: 389–415.
- Eldridge DJ, Myers C (1999) Rabbit warrens: nutrient-deprived mosaics in a semi-arid woodland. In: Eldridge D, Freudenberger D (eds) *People and Rangelands: Building the Future*, Proceedings of the VIth International Rangelands Congress, Townsville, July 19–23, International Rangelands Congress Inc, Townsville, Australia. Vol. 1, pp 133–135.
- Eldridge DJ, Myers CN (2001) The impact of warrens of the European rabbit (*Oryctolagus cuniculus* L.) on soil and ecological processes in a semi-arid Australian woodland. *Journal of Arid Environments* 47: 325–337.
- Foran BD (1986) The impact of rabbits and cattle on an arid calcareous shrubby grassland in central Australia. *Vegetatio* 66: 49–59.
- Friedel MH, Bastin GN, Griffin GF (1988) Range assessment and monitoring in arid lands: the derivation of functional groups to simplify vegetation data. *Journal Environmental Management* 27: 85–97.
- GENSTAT (1997) *GENSTAT 5 Reference Manual*. Clarendon Press, Oxford.
- Gómez-García D, Borghi CE, Giannoni SM (1995) Vegetation differences caused by pine vole mound building in subalpine plant communities in the Spanish Pyrenees. *Vegetatio* 117: 61–67.
- Grubb PJ (1977) The maintenance of species richness in plant communities: the importance of the regeneration niche. *Biological Revue* 52: 107–145.
- Gutterman Y (1986) Influences of environmental factors on germination and plant establishment in the Negev Desert Highlands of Israel. In: Joss PJ, Lynch PW, Williams OB (eds) *Rangelands – A Resource Under Siege* Proceedings of the Second International Rangeland Conference, pp 441–443.
- Gutterman Y (1997) Ibex diggings in the Negev Desert highlands of Israel as microhabitats for annual plants. Soil salinity, location and digging depth affecting variety and density of plant species. *Journal of Arid Environments* 37: 665–681.
- Gutterman Y, Golan T, Garsani M (1990) Porcupine diggings as a unique ecological system in a desert environment. *Oecologia* 85: 122–127.
- Harden GJ (1990–1995) *Flora of New South Wales*, University New South Wales Press, Kensington.

- Harper KT, Marble JR (1988) A role for nonvascular plants in management of arid and semiarid rangelands. In: Tueller PT (ed) Application of Plant Sciences to Rangeland Management and Inventory. Martinus Nijhoff/W. Junk, Amsterdam, pp 135–169.
- Johansen JR (1993) Cryptogamic crusts of semiarid and arid lands of North America. *Journal of Phycology* 29: 140–147.
- Kinlaw A (1999) A review of burrowing by semi-fossorial vertebrates in arid environments. *Journal of Arid Environments* 41: 127–145.
- Lange RT, Graham CR (1983) Rabbits and the failure of regeneration in Australian arid zone Acacia. *Australian Journal of Ecology* 8: 377–381.
- Leigh JH, Wood DH, Holgate MD, Slee A, Stanger MD (1989) Effect of rabbit and kangaroo grazing on two semi-arid grassland communities in central-western New South Wales. *Australian Journal of Botany* 37: 375–396.
- Lunt ID, Morgan JW (1999) Vegetation changes after 10 years of grazing exclusion and intermittent burning in a *Themeda triandra* (Poaceae) grassland reserve in south-eastern Australia. *Australian Journal of Botany* 47: 537–552.
- Martin JT, Eveleigh JN (1979) Observations on the effectiveness of warren destruction as a method of rabbit control in an semi-arid environment. *Australian Rangeland Journal* 3: 232–238.
- McIntyre S, Lavoural S, Trémont RM (1995) Plant life-history attributes: their relationship to disturbance response in herbaceous vegetation. *Journal of Ecology* 83: 31–44.
- McIntyre S, Lavoural S, Landsberg J, Forbes TDA (1999) Disturbance response to vegetation – towards a global perspective on functional traits. *Journal of Vegetation Science* 10: 621–630.
- Meadows A (1991) Burrows and burrowing animals: an overview. In: A Meadows, P Meadows (eds) *The Environmental Impact of Burrowing Animals and Animal Burrows: Symposia of the Zoological Society of London* 63: 327–338.
- Meadows A, Meadows P (1991) *The Environmental Impact of Burrowing Animals and Animal Burrows: Symposia of the Zoological Society of London*.
- Milton SJ, Dean WRJ, Klotz S (1997) Effects of small-scale animal disturbances on plant assemblages of set-aside land in Central Germany. *Journal of Vegetation Science* 8: 45–54.
- Minitab (1997) *References Manual, Release 10.1*, Minitab Inc State College Pennsylvania.
- Mutze GT (1991) Long-term effects of warren ripping for rabbit control. *Australian Rangeland Journal* 13: 96–106.
- Myers K, Parer I, Wood D, Cooke BD (1994) The Rabbit in Australia. In: Thompson HV, King CM (eds) *The European Rabbit: The History and Biology of a Successful Colonizer*, Oxford Science Publications, London, pp 108–157.
- Northcote KH (1979) *A Factual Key for the Recognition of Australian Soils*. Rellim Technical Publications, Glenside, South Australia.
- Noy-Meir I, Gutman M, Kaplan Y (1989) Responses of Mediterranean grassland plants to grazing protection. *Journal of Ecology* 77: 290–310.
- Parer I, Parker BS (1986) Recolonisation by rabbits (*Oryctolagus cuniculus*) after warren destruction in western New South Wales. *Australian Rangeland Journal* 8: 150–152.
- Parer I, Fullager PJ, Malafant KW (1987) The history and structure of a large warren of the rabbit, *Oryctolagus cuniculus* L. at Canberra, A.C.T. *Australian Journal of Wildlife Research* 14: 505–513.
- Parker BS, Myers K, Caskey RL (1976) An attempt at rabbit control by warren ripping in semi-arid western New South Wales. *Journal of Applied Ecology* 13: 353–367.
- Peart MH, Clifford HT (1987) The influence of diaspore morphology and soil-surface properties on the distribution of grasses. *Journal of Ecology* 75: 569–576.
- Reader RJ, Buck J (1986) Topographic variation in the abundance of *Hieracum floribundum*: Relative importance of differential seed dispersal, seedling establishment, plant survival and reproduction. *Journal of Ecology* 74: 815–822.
- Rolls EC (1984) *They all ran wild*. Angus and Robertson, Sydney.
- Sneddon I (1991) Latrine use by the European rabbit (*Oryctolagus cuniculus*). *Journal of Mammalogy* 72: 769–775.
- Trémont R (1994) Life history attributes of plants in grazed and ungrazed grasslands on the Northern Tablelands of New South Wales. *Australian Journal of Botany* 42: 511–530.
- Vine A (1999) Busting the bunnies – an assessment of integrated rabbit control techniques in semi-arid central New South Wales. BSc (Hons) thesis, University of NSW.
- Walker PJ, Koen TB (1995) Natural regeneration of ground-storey vegetation in a semi-arid woodland following mechanical disturbance and burning. 1. Ground cover levels and composition. *The Rangeland Journal* 17: 46–58.
- Walker PJ, Koen TB, Gittins R (1995) Natural regeneration of ground-storey vegetation in a semi-arid woodland following mechanical disturbance and burning. 2. Response of individual species. *The Rangeland Journal* 17: 59–68.
- Whitford WG (1998) Contribution of pits dug by goannas (*Varanus gouldii*) to the dynamics of banded mulga landscapes in eastern Australia. *Journal of Arid Environments* 40: 453–457.
- Whitford WG, Kay FR (1999) Bioperturbation by mammals in deserts: a review. *Journal of Arid Environments* 41: 203–230.
- Williams CJ, Parer I, Coman B, Burley J, Braysher ML (1995) *Managing Vertebrate Pests: Rabbits*. Bureau of Resource Sciences/CSIRO Division of Wildlife and Ecology. Australian Government Publishing Service, Canberra.
- Wood DH (1984) The rabbit (*Oryctolagus cuniculus* L.) as an element in the arid biome of Australia. In: Cogger HG, Cameron EE (eds) *Arid Australia: proceedings of a symposium on the origins, biota and ecology of Australia's arid regions*. Australian Museum, Sydney, pp 273–287.
- Wood DH (1985) Effectiveness and economics of destruction of rabbit warrens in sandy soils by ripping. *Australian Rangeland Journal* 7: 122–129.
- Zaady E, Gutterman Y, Boeken B (1997) The germination of mucilaginous seeds of *Plantago coronopus*, *Reboudia pinnata* and *Carrichtera annua* on cyanobacterial soil crust from the Negev Desert. *Plant and Soil* 190: 247–252.