The Influence of Fire, Herbivores and Rainfall on Vegetation Dynamics in the Mallee: a Long-term Experiment

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Fire regimes, grazing regimes and climatic variation potentially influence the distribution and abundance of plant species in the mallee over long time scales. For example, the timing of fires and rainfall events influences the establishment of many plant species, while herbivory and drought have selective effects on plant survival. Rainfall events influence short-term bushfire fuel dynamics and, with herbivores, determine landscape flammability. The frequency and spatial pattern of fire regimes have been identified as important management tools that may influence the persistence of mallee biota. A long term ecological experiment has been established in the Tarawi-Scotia-Danggali reserves to improve understanding of the mechanisms that influence vegetation change and the ability of the ecosystem to sustain its characteristic biota. Herbivore-specific grazing exclosures were established in tandem with planned management burning and some unplanned fires over a 12-year period. In this paper we outline the management issues and research questions that the study seeks to address, describe the design of the experiment and the data collected from the treated sites. We discuss the strengths and weaknesses of the experiment and the valuable insights that long term ecological studies of this type can produce.

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KEYWORDS: adaptive management, desert, experimental design, fire regimes, grazing, long term ecological research, management experiment, monitoring, rainfall variability, Scotia.

INTRODUCTION

Ecosystems change over time scales that vary from days to centuries. The pathways and rates of change are influenced by environmental conditions, biotic interactions, disturbance events and anthropogenic processes (Pickett and White 1985; Likens 1992; Hooper et al. 2005). Understanding how these processes operate is fundamental to informed management of ecosystems to conserve their biodiversity and maintain the services they provide to human industry and well being (Millenium Assessment 2005).

Arid and semi-arid ecosystems are notable for their relative stability punctuated by episodic boom/bust events that may leave long-lasting legacies (Bestelmeyer et al. 2009; Morton et al. 2011). Understanding the cause-effect relationships of dynamics in these systems is challenging because many changes play out over long time scales that extend beyond the span of human lives and practicable ecological observational studies. Furthermore, these systems exhibit highly stochastic dynamics, with high levels of variability making it difficult to draw generalisations about how ecosystems may respond to particular scenarios of environmental events and human activity.

Productive insights into the mechanisms that drive ecosystem dynamics require thoughtful design of ecological investigations that permit systematic probing of causal agents, preferably under a range of conditions and over appropriate time scales (Likens 1989; Walters and Holling 1990; Lindenmayer and Likens 2010a). A systematic comparison of ecosystem responses to experimental probing is central to adaptive management approaches that seek to learn by doing (Walters and Holling 1990; Keith et al. 2011). Long-term ecological studies with their experimental design focussed on processes relevant to ecosystem management are well suited to adaptive management approaches (Walters and Holling 1990; Lindenmayer and Likens 2010b) and there is renewed interest in the benefits that these studies can bring to environmental management in Australia (Likens and Lindenmayer 2011; Lindenmayer et al. in press).

In this paper, we describe a landscape scale experiment that seeks to produce insights into the dynamics of semi-arid mallee vegetation. The study is located on the extensive red sand dune landscapes in the Scotia district of far south-western New South Wales and adjacent areas of South Australia. We first briefly review the roles of fire regimes, herbivory and rainfall in mallee vegetation dynamics. We use this as context to outline some salient questions about mechanisms of change that led to the establishment of the experiment. We then describe the study area and the experimental design, with an appraisal of its strengths and weaknesses. We conclude by considering how this type of long term ecological research can contribute to informed management of mallee ecosystems, and to a broader research infrastructure that can help to discover fundamental principles about the behaviour of ecosystems.

AGENTS OF ECOSYSTEM CHANGE

Fire regimes

Mallee woodlands are fire prone (Noble et al. 1980; Bradstock and Cohn 2002). Fires vary in size up to several thousand hectares and may return at intervals that vary from decadal to centennial scales. They may consume most or all of the standing biomass, although spatial patterns may be complex, partly because flammable mallee vegetation is juxtaposed with non-flammable belah woodland (*Casuarina pauper*) and partly because mallee vegetation is less flammable in swales than on dunes (Bradstock and Cohn 2002).

Four main components of the vegetation produce biomass that varies in its flammability and its distribution in space and time. Throughout the landscape, the dominant eucalypts contribute aerial fuels and well-aerated ground fuels comprising leaves, twigs and branches. Hummock grasses, which are most abundant on dune slopes and crests, are highly flammable surface fuels. They are typically absent from the dune swales, which are generally dominated by less flammable shrubs at varying densities. Ephemeral grasses emerge periodically in abundance after substantial rains and, when cured, may contribute a substantial additional surface fuel throughout the system (Noble and Vines 1993).

A wide range of mallee shrubs and forbs are killed outright by fire, regenerating only from seed stored on site or dispersed from other areas (seeders), while others are equipped with vegetative recovery organs from which they may resprout new shoot biomass during the months after fire (sprouters). Many mallee plant species have seed banks that remain dormant and viable in the soil for varying lengths of time (Auld 1995a). A few species have serotinous seedbanks in which seed are retained in woody fruits for two or more years and released gradually thereafter or *en masse* when the stems are killed by fire (Wellington and Noble 1985; Bradstock and Cohn 2002b). Fires provide an important stimulus for seedling recruitment in many mallee plants, although the germination response varies greatly between different fire events. The timing of fires in relation to seed bank development is a crucial determinant of recruitment and population persistence (Keith 2011). The timing of fires also influences the suitability of habitat for a range of mallee animals. While interval and event characteristics of the fire regime affect the abundance of plants that provide particular resources such as nectar and shelter, time since fire also influences habitat suitability through the structural development of features such as loose bark and hollows associated with mallee stems and the development and degeneration of spinifex hummocks that provide shelter for various mammals, reptiles and macroinvertebrates (Haslem et al. 2011).

Herbivory

Native, feral and domestic herbivores inhabit mallee landscapes. The primary native species are large macropods including *Macropus fulignosus* (Western Grey Kangaroo), *M. robustus* (Euro) and *M. rufus* (Red Kangaroo). In addition, the regionally extinct *Onychogalea fraenata* (Bridled Nail-tail Wallaby) has been re-introduced within large enclosures in Scotia Sanctuary. Feral herbivores include *Oryctolagus cuniculus* (Rabbit) and *Capra hircus* (Goat), while *Ovus aries* (Sheep), *Bos primigenius* (Cattle) and *C. hircus* are the main domestic livestock in the Scotia region. While the diets of these herbivores differ, consumption of plant biomass by herbivores can limit rates of survival, growth, reproduction and recruitment in palatable species (Crisp and Lange 1976, Auld 1995b) and shift the composition of communities towards dominance by unpalatable species (Landsberg et al. 2003). Herbivore activity may also involve substantial soil disturbance which, combined with the effects of reduced vegetation cover, may expose unconsolidated soils to erosion by wind (Beadle 1948). Severe episodes and symptoms of erosion associated with overgrazing are well documented in western New South Wales. The Scotia district may have been less affected than most areas due to the relatively late arrival of domestic livestock and relatively low stocking rates (Westbrooke this issue).

Important interactions are postulated between herbivory and fire (Noble et al. 2007; Keith 2011). Young post-fire plant growth may be more palatable to herbivores than older biomass due to reduced chemical and physical defences and higher nutritional content (Keith 2011). Plants exposed to elevated rates of herbivory in the post-fire environment are more prone to mortality (Walker et al. 1981; Hodgkinson and Cook 1995). Herbivores may move into recently burnt areas, increasing the impact on prey populations (e.g. Isaac et al. 2008). Consequently, vegetation within small burnt areas or around the margins of large burnt areas may suffer greater impacts than vegetation within the interior of large burnt areas (Keith 2011).

Rainfall variability

Arid climates are noted not only for low average rainfall, but high variability in rainfall between years (van Etten 2009). Extended drought periods punctuated by rainfall events of varying magnitude regulate cyclic transitions of a large ephemeral flora from dormant seedbanks to standing plant phases (Morton et al. 2011). Large infrequent rainfall events also provide cues for the recruitment of long-lived perennial plants (Watson et al. 1997; Lopez et al. 2008). Rainfall events of varying sizes also produce flushes of biomass, fruits and seeds which, together with enhanced supply of moisture, support population growth in higher trophic levels (Morton et al. 2011).

Three-way interactions are likely to exist between rainfall variability, herbivore populations and fire activity (Noble and Vines 1993; Morton et al. 2011). Large rainfall events may be antecedent to extensive fires, as growth of ephemeral vegetation enhances fuel connectivity permitting fire spread over a wider range of fire weather conditions than is normally possible (Noble and Vines 1993; Bradstock and Cohn 2002a). Increased availability of forage promotes higher densities of herbivores either through opportunistic breeding to generate population growth or nomadism that enables immigration into transient resource-rich patches (Caughley et al. 1987; Morton et al. 2011). As water availability declines, herbivores exploit plant forage more heavily and their populations decline as the resource becomes scarce.

Research questions

The synopsis above poses a number of questions about mallee ecosystem dynamics, for which answers are needed to inform management strategies that seek to conserve mallee biodiversity. Ecological experiments provide a powerful means of developing such a knowledge base to support biodiversity management. In Table 1 we summarise some of the salient management issues and research questions about mallee vegetation dynamics as a prelude to describing the experimental design of our study.

Management concern about the effects of long fire intervals was an early motivation for our study. Parts of the district have gone without fire for almost a century (see below) and plant species richness of the standing vegetation in those areas is conspicuously lower than that of vegetation that had been burnt during the past 30 years. It seems likely that many of the plant species present in more recently burnt areas had disappeared above ground from long-unburnt areas as their standing plants senesced. These species may persist in the soil seed bank, but how long would the seed remain viable and able to re-establish standing plant populations? If soil seed banks were decaying appreciably over these long intervals and seed dispersal is limited, management fires may be required to avoid local extinctions of the affected plant species. To provide advice on this management problem, we compared the species composition of early post-fire vegetation after a number of prescribed fires carried out for protection purposes in areas that had last been burnt 20-30 years ago and >80 years ago. While preliminary results suggested that regeneration capacity was similar across this range of fire histories, the investigation illuminated a complex suite of management issues that require long-term ecological research to resolve (Table 1).

EXPERIMENTAL DESIGN

Study area and landscape

The study is located in the red aeolian sand dunefield landscape of the Scotia district within Tarawi Nature Reserve (33.44ºS 141.16ºE), Scotia Wildlife Sanctuary (33°17′S 141°05’E) and Danggali Nature Reserve (33° 22’ S 140° 45’ E) in south-western New South Wales and adjacent area of South Australia (Fig. 1). The study area sits on the south-eastern edge of the Australian arid zone. This location is close to

Table 1. Management issues and research questions related to mallee vegetation dynamics.

	Management issue	Research question
1	Long fire intervals	Does plant diversity decline with long intervals between successive fires?
2	Short fire intervals	How long does it take mallee trees and shrub species to build up seed banks after fire?
3	Diversity relationships between standing vegetation and soil seed banks	How closely does species composition of soil seedbanks resemble that of standing vegetation? Do sites with similar standing vegetation also have compositionally similar seedbanks?
4	Plant persistence	How does survivorship and fecundity of different plant species vary with time since fire?
5	Generalising plant responses to fire	How are differential responses to fire between plant species related to their life history traits?
6	Differential effects of herbivore species	Do different herbivore species have contrasting effects on standing vegetation?
7	Interaction between fire and hebivores	How does herbivore activity vary with time since fire?
8	Spatial pattern of fires	How does fire size affect post-fire herbivory by vertebrates?
9	Interactive effects of fire and rainfall on vegetation	Can varied vegetation responses to different fires be explained by inter-annual variation in rainfall?
10	Recruitment of woody plants	How does variability in fire events and climate affect seedling recruitment?
11	Drought	How does soil moisture vary with temperature and antecedent rainfall?

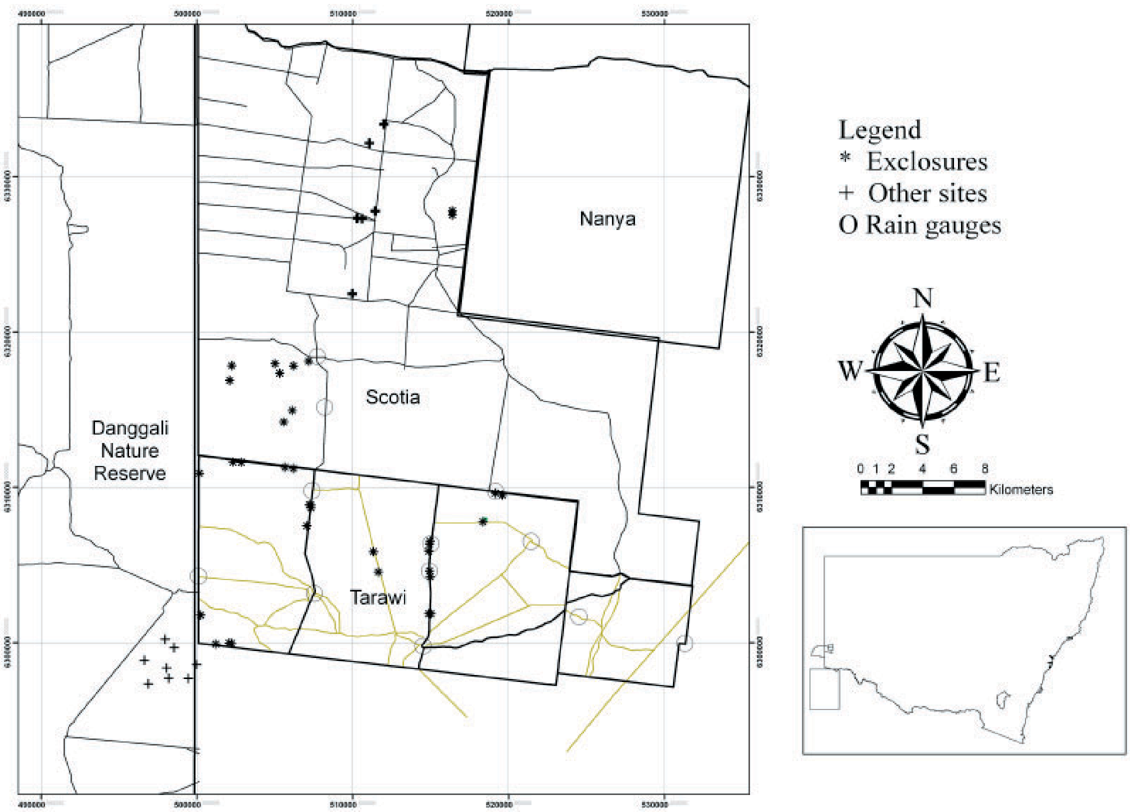

Figure 1. Location of experimental sites within Tarawi Nature Reserve, Scotia Wildlife Sanctuary and Danggali Nature Reserve study area

the arid limits of distribution of the mallee woodland biome, which stretches across the temperate semi-arid belt of southern Australia (Noble 1984). Mallee woodlands typically occur within regions receiving 200-500 mm rainfall per year. During 1940-2010, mean annual rainfall at Tarawi Homestead was approximately 240 mm, with an average of 209 mm in the last decade (data summary courtesy of John Warren, Tarawi NR).

In the Scotia district and its surrounding region, mallee woodlands occur within a landscape mosaic that includes patches of woodland dominated by *Casuarina pauper* (Belah) and shrublands dominated by *Maireana sedifolia* and *M. pyramidata* (bluebush) (Westbrooke et al. 1998). These latter vegetation types occur on gently undulating sandplains with a calcareous crust not far below the soil surface. In contrast, mallee woodlands dominate transverse east-west oriented dunefields. The dunes are characterised by deep red sandy loams dominated by *Eucalyptus socialis* (Pointed mallee), *E. dumosa* and *E. costata*, occasionally with *Callitris verrucosa*, with a mixed understorey of hummock grasses and shrubs and a largely ephemeral ground layer of tussock grasses and forbs. The intervening swales have finer textured red loams and generally support a wider range of eucalypts including *E. oleosa* and *E. gracilis*, but *C. verrucosa* is absent. Their understoreys typically include a higher density and diversity of shrubs but lack hummock grasses and the ground layer is typically sparse. Detailed descriptions of vegetation and landscapes are included in Westbrooke et al. (1998).

This study focussed on vegetation dynamics on dune crests and upper slopes, primarily because resources were insufficient to sample across the full catenary sequence of dunes and swales. Study of swale landforms was problematic because these are rarely flammable under prescribed fire conditions due to the absence of hummock grasses, which augment lateral fuel connectivity and thus promote fire spread on the dune crests and slopes.

Experimental sites and treatments

Fifty-three experimental sites were established on dune crests and upper slopes during 1996 - 2011 (Appendix 1), of which 29 are located within Tarawi NR, with 16 in Scotia and eight in Danggali NR (Figure 1). In Tarawi NR, each is marked with a steel sign on an adjacent access track. These include four pilot sites established during 1996-1998, during which the design of herbivore exclosures were developed.

All but one of the 53 sites (1998/CON1) were burnt, either in prescribed fires (33 sites) or wildfires (19 sites). Prescribed fires varied in area from 1 - 70 ha, whereas wildfires varied in area from 70 ha to 3000 ha (Appendix 1). Prescribed fires were implemented in 2000, 2001, 2003, 2005, 2006, 2009, 2010 and 2011. The 33 sites were stratified across this chronosequence, with 4 sites sampled in each burn year except 2005 (5 sites), 2009 and 2010 (2 sites each) and 2011 (8 sites). For each burn year, the sites were stratified between locations with different prior fire histories; half had previously been long unburnt (1917 or earlier) and half had been unburnt for 20-30 years (1979-1984). However, the four sites sampling prescribed burns in Scotia in 2010 only sampled a single fire history (Appendix 1).

Three surveys were undertaken in successive years at the time of treatment for all sites burnt in prescribed fires except the four sites burnt in 2010 within Scotia Sanctuary. These sites to be burnt in prescribed fires were initially marked out and surveyed one to three months prior to burning treatment (pre-fire survey). Within one to three months of burning treatment, they were fenced to exclude all vertebrate herbivores. A second survey (post-fire survey) was carried out approximately one year after the first survey. Within one to two months of the second survey, fences were modified to allow access to selected hebivores into compartments of the exclosures (see details below). During the second survey, additional plots were recorded outside the exclosures where herbivores had continual access to the vegetation prior to and after burning. A third survey (post-grazing survey) was carried out within and outside the exclosures approximately one year after the second survey. Pre-fire surveys could not be carried out at any sites burnt in wildfires. The eight sites in Danggali NR were not fenced to exclude herbivores and consequently only one post-fire post-grazing survey was carried out, equivalent to the external plots carried out on the third annual visit to the other sites.

Grazing exclosures were constructed at all sites except those in Dangalli NP and the Scotia Sanctuary sites burnt in 2009 and 2010. The latter site was within the Scotia Stage 1 fenced area from which goats and rabbits had been eliminated, kangaroos were at low densities and in which Bilbies, Numbats and Burrowing Bettongs had been introduced (Tony Cathcart, Australian Wildlife Conservancy, pers. comm.). The design of all exclosures constructed since year 2000 (inclusive) followed the layout in Fig. 2. Each comprised five contiguous fenced cells 15 m square. Initially all five cells were closed to all vertebrate herbivores for approximately a year after their construction. The basic fence design

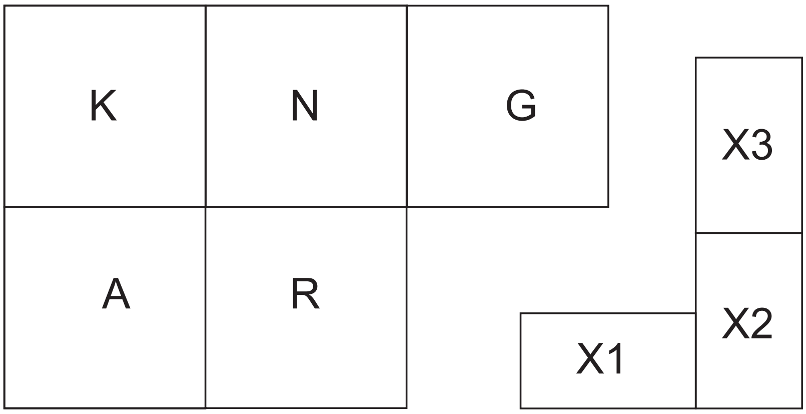

Figure 2. Standard layout of grazing exclosures at each site (K: Kangaroo entry only, A: All in, unrestricted access, N: None in, total exclusion, R: Rabbit entry only, G: Goat entry, X1 – X3: unrestricted access). Goat entry was facilitated using wooden ramps but this has proven ineffective and no goats entered these cells, which therefore replicate the total exclusion treatment. Each of the cells K, A, N, R, G, were closed to all herbivores for one year after fire, and then opened to all entry to respective herbivores. Plots X1-X3 remained unfenced throughout, allowing continuous access to all herbivores.

comprised treated pine posts at each corner, four star pickets along each side with two droppers per panel between pickets supporting a 1.8 m tall sheep mesh wire fencing with chicken mesh covering the lower 0.6 m of vertical fall and turned outward at ground level to a further 0.6 m lateral apron. After being surveyed at the end of this period total, the fences of respective cells were modified to allow selective access to different combinations of vertebrate herbivores as shown in Fig. 3. One cell was retained in an unmodified state as a total exclusion treatment (None plot). In a second cell, the chicken wire mesh was removed from two sides, leaving a gap of 0.6 m beneath the sheep wire mesh and allowing access to macropods, goats and rabbits (All plot). In a third cell, the sheep mesh was removed from two sides leaving a 0.6 m tall chicken mesh fence, allowing access to macropods but not goats or rabbits (Kangaroo plot). In a fourth cell, the mesh apron was lifted and pinned to the fence, leaving a 10 cm gap at the base of the 1.8 m tall fence, allowing access to rabbits, but not macropods or goats (Rabbit plot). The fifth cell was designed to allow access to goats, but not macropods or rabbits (Goat plot). A wooden ramp 30cm wide was constructed on the outside of the exclosure leading to a gap in the upper part of the fence 1.2 m above ground level in one corner of the plot. A similar ramp was constructed on the opposite corner of the cell, but with the ramp installed on the inside allowing exit from the cell. Subsequent scat counts indicated that neither goats, macropods or rabbits gained access to this cell, so that in practice Goat plots functioned as a second total exclusion treatment (cf. None plot). In addition, three external plots 13 m x 7.5 m were established outside and 7.5 m from the exclosure fence, where all vertebrate herbivores had continual access to the vegetation before and after burning treatment.

The standard exclosure layout was not followed at the four pilot sites established prior to year 2000 (Appendix 1). T1996/1 had a single-celled exclosure comprising a 1.8 m fence with 0.6 m ground apron to exclude all vertebrate herbivores (None plot). T1997/1, T1997/2 and T1998/CON1 comprised four cells as described above for the None, All, Kangaroo and Rabbit plots, except that all vertebrates were initially excluded using an electric fence constructed 2 m outside the perimeter of the exclosure fence and powered by 12-Volt batteries. The electric perimeter fences were dismantled 1.5 - 2.5 years after construction to allow access to respective herbivores.

Collectively, the experiment established a set of sites that sampled a chronosequence of fire ages crossed with different grazing treatments and sampled sequentially before and after implementation of the treatments (Table 2). In addition to the sequence of three surveys carried out during establishment of the plots, an additional contemporaneous survey was carried out in spring 2011 at a random selection of 15 sites stratified by year of establishment and burn history.

Response variables and sampling protocol

The density (number of individuals per unit area) of each vascular plant species was recorded in every plot. Counts of each species were partitioned into: live reproductive plants; live non-reproductive established plants; fire-killed established plants; plants that had emerged as seedlings or resprouted after fire and subsequently died; live seedlings less than 2 years of age; and dead seedlings.

The density of macropod, goat and rabbit scats

Figure 3. Example of cellular exclosure fencing allowing selective access to different mammalian herbivores. Site T2005/5 at third census, two years after burn treatment and one year after exclosures opened to allow selective herbivore access. Note A plot (foreground right) with negligible cover of tussock grasses and soil disturbance from numerous footprints of goats and kangaroos; K plot (foreground left) with open cover of tussock grasses; R plot (background right) with very sparse cover of tussock grasses; and N plot (background left) with abundant tussock grasses and other ground layer plants. G plot is obscured from view (far background left).

was recorded in all plots as an approximate measure of herbivore activity.

In the contemporaneous survey carried out in spring 2011, several parameters estimating vegetation structure were visually estimated in each exclosure cell and external plot. These included: tree cover and height range (single estimate per plot); shrub height (single estimate of median and range per plot); shrub cover (5 5×3 m subplots per plot); hummock grass cover (5 subplots per plot); hummock grass height (10 randomly selected individuals per plot); ephemeral grass cover (5 subplots per plot); leaf and twig litter cover (5 subplots per plot); and bare ground cover (5 subplots per plot).

Seedling cohorts of *Eucalyptus* and *Callitris* that emerged after fires in 1996, 1997, 2005 and 2006 were marked with uniquely numbered metal tags and monitored for survival, growth and reproduction in subsequent years.

Environmental monitoring

Automatic weather stations were established at Tarawi Homestead and Scotia Sanctuary homestead in 1994. They record precipitation, temperature, relative humidity and wind speed and direction. Prior to that time, rainfall records had been maintained since 1941 by visually monitored rain gauge (Fig. 4). Four additional visually monitored rain gauges were established in Tarawi NR in January 1997, a further five were established in May 2001, and two were established in Scotia Sanctuary in September 2007.

In May 2011, monitoring tubes for soil moisture probes were installed at intervals along two transects extending across the catenary sequence from swale to swale across a dune crest. Tubes were installed in each swale, on the dune crest and on the upper and lower flanks on each side of the dune. Soil moisture is currently monitored at monthly intervals at depths

Site	Grazing treatments	98	99	00	01	02	03	04	05	06	07	08	09	10	11
T1998/ CON1	N														
T1996/1	A,N								4						4
T1997/1	K,A,R,N			3											4
T1997/2	K,A,R,N			3											
T2000/1	K,A,R,N,G				2	3									
T2000/2	K,A,R,N,G				2	3									
T2000/3	K,A,R,N,G				2	3									
T2000/4	K,A,R,N,G				2	3									
T2001/1	K,A,R,N,G				1	2		3							4
T2001/2	K,A,R,N,G				1	2		3							
T2001/3	K,A,R,N,G				1	2		3							
T2001/4	K,A,R,N,G				1	2		3							
T2003/1	K,A,R,N,G						1	2	3						4
T2003/2	K,A,R,N,G						1	2	3						
T2003/3	K,A,R,N,G						1	2	3						
T2003/4	K,A,R,N,G						1	2	3						
T2005/1	K,A,R,N,G								1	2	3				4
T2005/2	K,A,R,N,G								1	2	3				
T2005/3	K,A,R,N,G								1	2	3				4
T2005/4	K,A,R,N,G								1	2	3				
T2005/5	K,A,R,N,G								1	2	3				
T2006/1	K,A,R,N,G									1	2	3			4
T2006/2	K,A,R,N,G									1	2	3			
T2006/3	K,A,R,N,G									1	2	3			
T2006/4	K,A,R,N,G									1	2	3			
S2007/1	K,A,R,N,G											2	3		
S2007/2	K,A,R,N,G											2	3		
S2007/3	K,A,R,N,G											2	3		
S2007/4	K,A,R,N,G											2	3		
S2007/5	K,A,R,N,G											2	3		4
S2007/6	K,A,R,N,G											2	3		
S2007/7	K,A,R,N,G											2	3		
S2007/8	K,A,R,N,G											2	3		
D2010/1	A													3	
D2010/2	A													3	
D2010/3	A													3	
D2010/4	A													3	
D2010/5	A													3	
D2010/6	A													3	
D2010/7	A													3	
D2010/8	A													3	
S2010/1	N														2
S2010/2	N														2
S2010/3	A														2
S2010/4	A														2
T2011/1	K,A,R,N,G														1
T2011/2	K,A,R,N,G														1
T2011/3	K,A,R,N,G														1
T2011/4	K,A,R,N,G														1
S2011/1	A														1
S2011/2	A														1
S2011/3	A														1
S2011/4	A														1

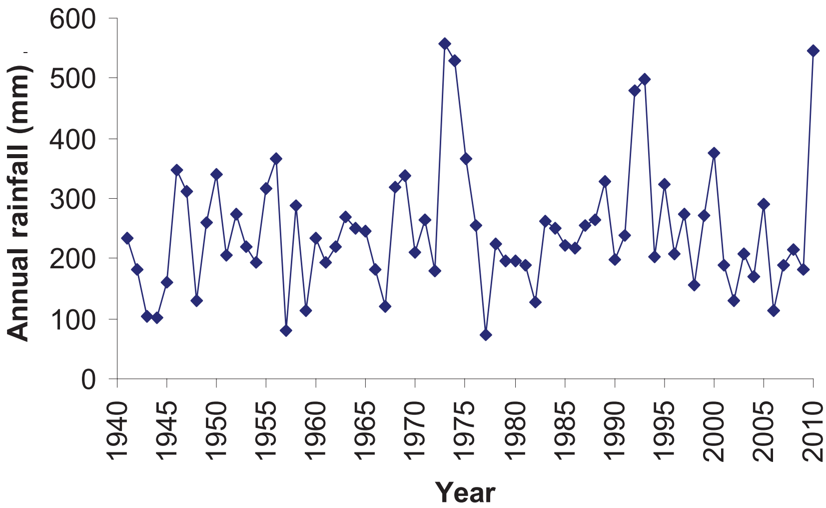

Figure 4. Annual rainfall statistics for Tarawi homestead.

of 100, 200, 300, 400, 600 and 1000 cm below the soil surface at monthly intervals using a PR2/6 Profile Probe manufactured by Delta-T Devices Ltd.

DISCUSSION

Long-term ecological studies are critical for providing insights into ecology, environmental change, natural resource management and biodiversity conservation (Lindenmayer et al. in press). The primary goal of this study is to improve understanding of how mallee vegetation responds to interacting fire regimes, herbivore activity and climatic variability. Its factorial design should enable the relative influence multiple ecosystem drivers to be evaluated under a range of environmental scenarios. In addition, the research infrastructure can contribute understanding to processes beyond the initial experimental treatments. For example, ecological baselines established in the experiment can be useful for surveillence monitoring and detection of surprise responses to rare events or ‘unknown unknowns’ - unforeseen phenomena that can have profound and long-lasting effects on the ecosystem, but are yet to emerge as management issues (Krebs et al. 2001; Keith 2002; Wintle et al. 2010). Important collateral benefits of long term research also emerge through contributions to ecological theory, which ultimately improve research and management efforts across a broad domain of ecosystems (Lindenmayer et al. in press). These important value-added benefits make long-term ecological research an extremely cost-effective means of developing cause-effect understanding of ecosystem change (Likens and Lindemayer 2011), provided the experiment is designed and maintained to avoid risks of failure (Lindenmayer and Likens 2010a).

The modular design of the mallee experiment enables it to be extended to examine additional permutations of the core factors (fire, grazing, climate) as opportunities arise and as understanding of salient processes develops. For example, the design of herbivore exclosures evolved from an early prototype established in 1997 that excluded all vertebrate mammalian herbivores to a cellular design that enables comparison of combined and individual effects of the major herbivore species. The original treatment was incorporated into the new design, allowing comparison of total exclusion with controls throughout the full chronosequence of sites. Other extensions to the sampling protocol include the addition of external plots in 2001 to assess the effects of immediate vs delayed post-fire access of herbivores, and addition of further sites in 2007 and 2008 to sample large unplanned fires for comparison of vegetation and herbivore responses to smaller planned cool-season fires that had been sampled in earlier treatments. Further sites were added in 2010 and 2011 to sample responses in rare high-rainfall years. Future elaborations could examine the influence of a regionally extinct assemblage of ground mammals and responses of other groups of biota such as various functional groups of invertebrates, lower plants and reptiles. These adjustments illustrate how the design of long-term ecological studies can be adapted to developing knowledge and evolving management needs without compromising the ability to address questions that were originally posed (Lindenmayer and Likens 2010b).

The current weaknesses of the mallee experiment stem primarily from logistic constraints and limitations

Table 2 (preceding page). Schedule of sampling of sites. 1- pre-fire census; 2- 1st year post-fire census; 3- 2nd year post-fire census; 4- census at multiple years post fire. Grazing treatments as per Figure 2.

on scope. The unpredictability of wildlife occurrence make it difficult or impossible to obtain pre-fire census data except by fortuitous means. Yet these data could be important to intrepretation of outcomes and strauctured comparisons with the effects of planned fires carried out under milder fire weather conditions and in smaller areas. The current scope of the mallee experiment is limited to dune crests and upper slopes. The intervening dune swales that support florstically different mallee woodlands and large tracts of sand plains that support non-flammable belah (*Casuarina pauper*) woodlands remain largely uninvestigated, but are potentially important in understanding landscape-wide processes of change, as well as contextual understanding for more localised changes on the dunes.

Experimental probing of ecosystem dynamics is a crucial element of adaptive management for biodiversity conservation (Keith et al. 2011). Current management of the mallee reserves involves i) manipulating fire regimes by controlling unplanned fires and burning to strategically manage bushfire fuels along accessible lineaments bounding landscape blocks; and ii) actively controlling and excluding feral herbivores to limit their impacts on vegetation composition and structure. These activities are carried out in a highly stochastic and unpredictable climate and in the face of highly uncertain, albeit the best available, knowledge about cause-effect relationships within the ecosystem. The experiment described above is integrated with these management activities to achieve structured learning by doing that progressively improves the knowledge base for future management (Walters and Holling 1990, Duncan and Wintle 2008). A key feature of the experiment is that it establishes a rigorous comparative experimental framework to assess the outcomes of real management actions while addressing the major ecosystem drivers: fire regimes, mammalian herbivores and climate variability. A second key feature is that it incorporates multiple alternative management options in the frequency, season, severity and size of fires, and the control or exclusion of different herbivore species across a number of years that span a range of environmental conditions. This enables risks to biodiversity associated with alternative management strategies to be evaluated under different environmental scenarios, informing the choice of management options to achieve conservation objectives with minimum risks of failure.

Detailed prior observations from precisely located points with a well-documented fine-scale environmental history provide valuable contextual evidence for distinguishing alternative causal mechanisms of ecosystem dynamics. Well maintained field research infrastructure and accessible data management systems can be attractive hubs for multi-disciplinary collaborations (Brown et al. 2001; http://www.warra.com/warra/about.html) that are capable of producing insights that are unlikely to be realised from a collection of smaller independent studies. Incorporation of the mallee ecosystem dynamics project into Australia's Terrestrial Ecosystem Research Network (http://www.tern.org.au/) will help develop collective knowledge of the processes that drive and sustain this important ecosystem.

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Appendix 1. Location and treatment of sample sites. [Co-ordinates are in Australian Geodetic Datum 66, Zone 54]

Site Label	Easting	Northing	Location	Date Burnt	Burn Type	Previous fire	Area burnt (ha)	Date Fenced	Notes
T1996/1	506741	6309952	W of west firetrail	Jan 1996	wildfire	1918	70	May 1996	permanent total exclusion (single exclosure only)
T1997/1	511943	6308381	E of spring Track	Nov 1997	wildfire	1918	436	Jul 1998	perimeter electric fence erected Nov-98 / added foot netting Feb-01 / electric fence dismantled Jul-01 and access allowed
T1997/2	512358	6308764	E of spring Track	Nov 1997	wildfire	1918	436	Jul 1998	perimeter electric fence erected Nov-98 / added foot netting Feb-01 / electric fence dismantled Jul-01 and access allowed
T1998/CON1	511466	6306052	E of spring Track control site	not burnt	not burnt	1918	-	Aug 1998	Perimeter electric fence erected Nov-99 / added foot netting Feb-01 / electric fence dismantled Jul-01 and access allowed
T2000/4	514985	6306528	W of centre firetrail	Apr 2000	prescribed	1918	40	Jul 2000	access allowed April-01 / wings on goat ramps Jul-02
T2000/3	514944	6306359	W of centre firetrail	Apr 2000	prescribed	1979	40	Jul 2000	access allowed April-01 / wings on goat ramps Jul-02
T2000/2	514898	6305897	W of centre firetrail	Apr 2000	prescribed	1979	40	Jul 2000	access allowed April-01 / wings on goat ramps Jul-02
T2000/1	514889	6301865	W of centre firetrail	Apr 2000	prescribed	1918	40	Jul 2000	access allowed April-01 / wings on goat ramps Jul-02
T2001/1	519608	6309485	S of north boundary firetrail	Apr 2001	prescribed	1918	74	May 2001	access allowed March-02 / goat ramps installed Jul-02
T2001/2	519173	6309618	S of north boundary firetrail	Apr 2001	prescribed	1984	74	May 2001	access allowed March-02 / goat ramps installed Jul-02
T2001/3	514940	6304626	E of centre firetrail	Apr 2001	prescribed	1918	74	May 2001	access allowed March-02 / goat ramps installed Jul-02
T2001/4	514981	6304238	E of centre firetrail	Apr 2001	prescribed	1984	74	May 2001	access allowed March-02 / goat ramps installed Jul-02
T2003/1	511348	6305853	W of spring track	May	prescribed	1979	4	June	access allowed May-04 / goat ramps installed

Site Label	Easting	Northing	Location	Date Burnt	Burn Type	Previous fire	Area burnt (ha)	Date Fenced	Notes
				2003				2003	Feb-05
T2003/2	511664	6304552	W of spring track	May 2003	prescribed	1918	3	June 2003	access allowed May-04 / goat ramps installed Feb-05
T2003/3	507352	6308660	E of west firetrail	May 2003	prescribed	1979	39	June 2003	access allowed May-04 / goat ramps installed Feb-05
T2003/4	507361	6308830	E of west firetrail	May 2003	prescribed	1918	39	June 2003	access allowed May-04 / goat ramps installed Feb-05
T2005/1	506211	6311210	S of north boundary firetrail	Apr 2005	prescribed	1918	20	May 2005	access allowed May-06
T2005/2	505664	6311286	S of north boundary firetrail	Apr 2005	prescribed	1918	20	May 2005	access allowed May-06
T2005/3	502088	6299969	N of south boundary firetrail	Apr 2005	prescribed	1983	59	May 2005	access allowed May-06
T2005/4	501215	6299904	N of south boundary firetrail	Apr 2005	prescribed	1983	59	May 2005	access allowed May-06
T2005/5	502239	6299934	N of south boundary firetrail	Apr 2005	prescribed	1918	59	May 2005	access allowed May-06
T2006/1	502325	6311648	S of north boundary firetrail	Apr 2006	prescribed	1918	26	Jul 2006	access allowed April-07
T2006/2	502846	6311634	S of north boundary firetrail	Apr 2006	prescribed	1918	26	Jul 2006	access allowed April-07
T2006/3	507241	6308859	W of west firetrail	Apr 2006	prescribed	1918	2.5	Jul 2006	access allowed April-07
T2006/4	507089	6307510	W of west firetrail	Apr 2006	prescribed	1918	2.5	Jul 2006	access allowed April-07
S2007/1	505352	6317356	West of Elliots Bore	Nov 2006	wildfire	1918	2455	June 2007	access allowed March-08
S2007/2	505047	6317966	West of Elliots Bore	Nov 2006	wildfire	1918	2455	June 2007	access allowed March-08
S2007/3	502124	6316984	West of Elliots Bore	Nov	wildfire	1918	2455	June	access allowed March-08

Site Label	Easting	Northing	Location	Date Burnt	Burn Type	Previous fire	Area burnt (ha)	Date Fenced	Notes
				2006				2007	
S2007/4	502260	6317844	West of Elliots Bore	Nov 2006	wildfire	1918	2455	June 2007	access allowed March-08
S2007/5	505611	6314199	South of Robinsons Dam firetrail	Nov 2006	wildfire	1918	2455	June 2007	access allowed March-08
S2007/6	506129	6314956	South of Robinsons Dam firetrail	Nov 2006	wildfire	1918	2455	June 2007	access allowed March-08
S2007/7	506196	6317912	West of Elliots Bore	Nov 2006	wildfire	1918	2455	June 2007	access allowed March-08
S2007/8	507176	6318110	West of Elliots Bore	Nov 2006	wildfire	1918	2455	June 2007	access allowed March-08
D2008/1	497965	6300213	South-east corner	Dec 2008	wildfire	1986	1297	Not fenced	Near fire boundary
D2008/2	498056	6298354	South-east corner	Dec 2008	wildfire	1918	1297	Not fenced	Remote from fire boundary
D2008/3	498546	6299680	South-east corner	Dec 2008	wildfire	1918	1297	Not fenced	Near fire boundary
D2008/4	496643	6298859	South-east corner	Dec 2008	wildfire	1986	1297	Not fenced	Remote from fire boundary
D2008/5	498203	6297708	South-east corner	Dec 2008	wildfire	1918	1297	Not fenced	Remote from fire boundary
D2008/6	496892	6297337	South-east corner	Dec 2008	wildfire	1986	1297	Not fenced	Near fire boundary
D2008/7	499463	6297689	South-east corner	Dec 2008	wildfire	1986	1297	Not fenced	Remote from fire boundary
D2008/8	500012	6298590	South-east corner	Dec 2008	wildfire	1918	1297	Not fenced	Near fire boundary

Site Label	Easting	Northing	Location	Date Burnt	Burn Type	Previous fire	Area burnt (ha)	Date Fenced	Notes
S2010/1	516401	6327780	Stage 1 Scotia Sanctuary, outside NW corner of Mala enclosure	Apr 2010	prescribed	pre-1980	5	1995	Within Stage 1 fence constructed pre-fire to exclude goats, rabbits, foxes and cats. Low density of kangaroos maintained
S2010/2	516400	6327522	Stage 1 Scotia Sanctuary, outside west boundary of Mala enclosure	Apr 2010	prescribed	pre-1980	5	1995	Within Stage 1 fence constructed pre-fire to exclude goats, rabbits, foxes and cats. Low density of kangaroos maintained
S2010/3	510298	6327321	Stage 3 Scotia Sanctuary, Sunset Boulevard	Apr 2010	prescribed	c.1980	5	Not fenced	Patchy strip burn along north side of track
S2010/4	510616	6327286	Stage 3 Scotia Sanctuary, Sunset Boulevard	Apr 2010	prescribed	c.1980	5	Not fenced	Patchy strip burn along north side of track
T2011/1	518362	6307774	North Elephant firetrail	Sep 2011	prescribed	1984	2	Dec 2011	
T2011/2	500180	6310892	Western boundary firetrail (north)	Sep 2011	prescribed	1918	1.5	Dec 2011	
T2011/3	500246	6301778	Western boundary firetrail (south)	Sep 2011	prescribed	1918	1.5	Dec 2011	
T2011/4	515025	6301859	Centre firetrail (south)	Sep 2011	prescribed	1984	1.5	Dec 2011	
S2011/1	511447	6327790	Stage 3 Scotia Sanctuary, outside Stage 1 fence line	Sep 2011	prescribed				
S2011/2	512003	6333384	Stage 3 Scotia Sanctuary, outside Stage 1 fence line	Sep 2011	prescribed				
S2011/3	511098	6332160	Stage 3 Scotia Sanctuary, outside Stage 1 fence line	Sep 2011	prescribed	1918			
S2011/4	509968	6322457	Stage 3 Scotia Sanctuary, outside Stage 1 fence line	Sep 2011	prescribed				