

Fire and grazing influence food resources of an endangered rock-wallaby

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Abstract

Context. Fire and grazing have complex and interacting impacts on food resources available to endangered herbivores and can potentially be manipulated as part of conservation strategies.

Aims. We examined the interacting impacts of fire and grazing on the food resources available to a colony of endangered brush-tailed rock-wallabies (*Petrogale penicillata*) to test fire as a potential management tool.

Methods. We conducted two manipulative experiments using a repeated-measures split-block design. We measured the effects of grazing and strategic burning on total vegetation biomass and on particular plants selected by rock-wallabies. In the first experiment we measured the impact of rock-wallaby grazing alone. In the second experiment we measured grazing impacts by both rock-wallabies and potentially competitive sympatric macropods. Grazing was manipulated with three treatments: grazed (open), ungrazed (fenced) and procedural control (half fence).

Key results. In both experiments, burning resulted in greater above-ground biomass of plants selected by rock-wallabies. The response of different plant functional groups to fire was staggered, with forb biomass peaking early and browse biomass increasing above unburnt levels a year after burning.

Conclusions. Despite the limited grazing pressure exerted by the small colony of rock-wallabies in Experiment 1 we detected a negative grazing effect on forbs growing after fire in burnt plots. In Experiment 2, grazing pressure was much more marked due to the high densities of sympatric macropods. In this case, while burning resulted in greater biomass of plants selected by rock-wallabies, grazing (predominantly by sympatric macropods) negated this effect.

Implications. Small patchwork burning can be a useful tool to improve food resources for brush-tailed rock-wallabies, with effects sustained over more than two years. However, when rock-wallabies are sympatric with possible competitor species, the grazing impacts of sympatric macropods may cancel out any benefits to rock-wallabies.

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Introduction

The processes of fire and grazing can have dramatic and complex impacts on the food resources available to herbivores. Both act as consumers by exerting control over biomass and species composition in ecosystems (Bond and Keeley 2005). A detailed understanding of how fire and grazing affect the food resources of a threatened species may inform the development of conservation management strategies.

Fire initially causes a sudden reduction in resources, followed by a staggered succession of pulses of higher resource availability (Fox 1982). Fire also changes the nature of available resources by restructuring plant assemblages at different stages of the succession (Gill 1981). As well as altering the state of vegetation, fire can have secondary and tertiary impacts on consumer assemblages. For example, low-intensity burning in the early dry season in Australian tropical savannas leads to an initial pulse of arthropod prey for skinks (Nicholson *et al.* 2006). Consumers exhibit a range of strategies for taking advantage of resource pulses, ranging from mobile specialists to opportunistic residents (Yang *et al.* 2008). The latter can alter their diet in response to ephemeral pulses of resource availability.

Grazing has a sustained effect on a specific assemblage of palatable plant species (Brown and Stuth 1993). The effects of grazing on plants can be altered and increased with the introduction of novel herbivores, either domestic or feral (Lunt *et al.* 2007). On a tertiary level, predators can alter grazing effects by causing changes in the dynamics of herbivore communities (Bakker *et al.* 2005).

We examined the impact of fire and grazing on the food resources available to a colony of endangered herbivores, brush-tailed rock-wallabies (*Petrogale penicillata*). Rock-wallabies are medium-sized macropods that require high-quality food because of their small size (average mass: males 7.9 kg, females 6.3 kg: Van Dyck and Strahan 2008; Dawson 1989). They are intermediate grazer-browsers that consume a diverse diet of grasses, shrubs and herbs (Short 1989), and use complex rocky habitat as a refuge from predation (Laws and Goldizen 2003).

Little is known about the impact of fire on rock-wallabies. There are anecdotal reports of rock-wallaby colonies disappearing (Burrowa-Pine Mountain, upper Murray River), relocating (Kangaroo Valley) and disappearing then recolonising (Mount Wallerawang in eastern New South

Wales) as a result of fire (NPWS 2003). Other reports suggest that numerous small fires appear not to affect rock-wallabies (Kangaroo Valley and the Watagan State Forest, New South Wales) (NPWS 2003), while the extensive fires in 2002–03 that passed through rock-wallaby habitat at Little River Gorge in Victoria did not affect the population size or body condition of rock-wallabies (Prober and Theile 2005).

In contrast to fire, we have a better understanding of grazing impacts from both native and introduced mammalian herbivores on rock-wallabies. Brush-tailed rock-wallabies often coexist with larger macropods such as eastern grey kangaroos (*Macropus giganteus*), common wallaroos (*M. robustus*) and red-necked wallabies (*M. rufogriseus*). These species are predominantly grazers and, because of their size (range: 30–70 kg, 20–55 kg, 14–20 kg respectively: Van Dyck and Strahan 2008) they can process large quantities of poor-quality plant material (Dawson 1989). Larger macropods can also roam further in search of better food, as they are not restricted by refuge use. There is the potential for competition for certain shared plant species between rock-wallabies and *M. robustus* (Dawson and Ellis 1979; Tuft 2010). Concerns over excessive exploitation of rock-wallaby food resources by large macropods have heightened in areas, particularly national parks, where removal of livestock, the addition of artificial water sources and altered predator densities have led to increases in large macropod populations.

Our aim was to examine the interacting impacts of fire and grazing on rock-wallaby food resources and to test fire as a potential management tool. Strategic burning has been used by Australian indigenous people to manipulate the food resources of prey species, usually large macropods, for thousands of years (Yibarbuk *et al.* 2001). Using two experiments we investigated the potential for small patchwork burning to improve food available to rock-wallabies while taking into account the interacting effects of grazing by rock-wallabies themselves and by large macropods. Natural variation in the landscape gave us the opportunity to compare the impacts of different herbivores without manipulating population densities.

Our first aim was to determine the effects of fire and rock-wallaby grazing on vegetation in terms of total vegetation biomass and biomass of food plants that are selected by rock-wallabies. For this, we ran Experiment 1 near a rock-wallaby refuge, in an area grazed exclusively by rock-wallabies, as it was inaccessible to sympatric macropods. Our second aim was to determine the effects of fire and grazing – this time predominantly by sympatric macropods rather than rock-wallabies – on total vegetation biomass and biomass of food plants selected by rock-wallabies. For this, we ran Experiment 2 in an area that rock-wallabies shared with sympatric macropods.

Methods

Study area

The study was undertaken around a rock-wallaby colony on Chalkers Mountain in the Warrumbungles National Park (31°15'S, 148°56'E) in New South Wales, Australia. Macropods are the predominant mammalian herbivores in the park and include *M. giganteus*, *M. robustus*, *M. rufogriseus* and the swamp wallaby (*Wallabia bicolor*). The site for Experiment 1 was located above cliffs that exclude large mammalian

herbivores, with the exception of rock-wallabies. The site for Experiment 2 was located 400 m below the cliffs and thus accessible to all herbivores. Counts of faecal pellets indicated that sympatric macropods were approximately 10 times more abundant than rock-wallabies in this area (Tuft *et al.* 2011a).

Experiment 1: Fire and rock-wallaby grazing

We used a repeated-measures split-block design to test the effects of low-intensity burning and grazing by rock-wallabies on vegetation. Fire treatments (burnt and unburnt) were randomly assigned to pairs of plots (each plot 25 × 25 m) within five randomly located blocks (Fig. 1). Low-intensity burning was conducted in May 2007, followed by construction of fences for the grazing treatments. Burning was conducted on a day with minimal wind after the edges of plots were cleared of combustible material. Fires were lit on the low edge of each plot and allowed to burn upwards slowly.

Within each burn treatment plot, there were three replicates of each of three grazing treatments (grazed, ungrazed, procedural control) randomly assigned to a grid of nine 2 × 2 m subplots within each plot. The ungrazed treatment consisted of fences 3 × 3 m in area, 2 m high, and constructed of wire netting around aluminium frames. We minimised possible fence effects such as reduced wind and increased condensation by using a low density of wire with 20 × 10 cm spacings on the upper section and more impenetrable 50-mm-diameter netting on the lower, and by using a 50-cm buffer between the fence and the survey subplot. We formally tested fence effects by including a procedural control treatment of a single fence panel (3 m wide by 2 m high), which was erected with guy ropes and allowed free access to all herbivores. Subplots for the grazed treatment were marked with small steel pegs at each corner. The use of enclosures rather than enclosures ensured that all but the ungrazed treatments were available for grazing so that there was no exacerbated grazing effect from concentrating animals in an area. We measured the vegetation 5, 9, 12, 17 and 29 months after burning (i.e. October 2007, February 2008, May 2008, October 2008 and October 2009). Fences were built after burning, for logistical reasons, and no measurements were made of the vegetation before treatments were applied.

We conducted vegetation surveys in each 2-m² subplot to quantify dry weight of each plant species below 1.5 m in height (the height limit available to rock-wallabies). Plant species were classified into functional groups: grass, browse, forb, orchid/lily, fern and sedge (these groups are described in Tuft *et al.* 2011b). Dry weight (gDM) was calculated using a variation on the Adelaide method (Andrew *et al.* 1976). The contribution of each species to the total biomass was estimated and compared with a 'unit' (branch or clump) of the most abundant species, which was then collected and dried. We also measured the dry weight responses to fire and grazing of plant species selected by rock-wallabies at Chalkers Mountain. Selected species were defined by calculating selection indices (Manly *et al.* 2002) for plant species detected in rock-wallaby scats along with concurrent measures of field availability (Tuft *et al.* 2011b). Selection indices for each plant species were standardised across eight sampling periods over two years and selected species were defined as those that had a positive mean selection index in one or more sampling

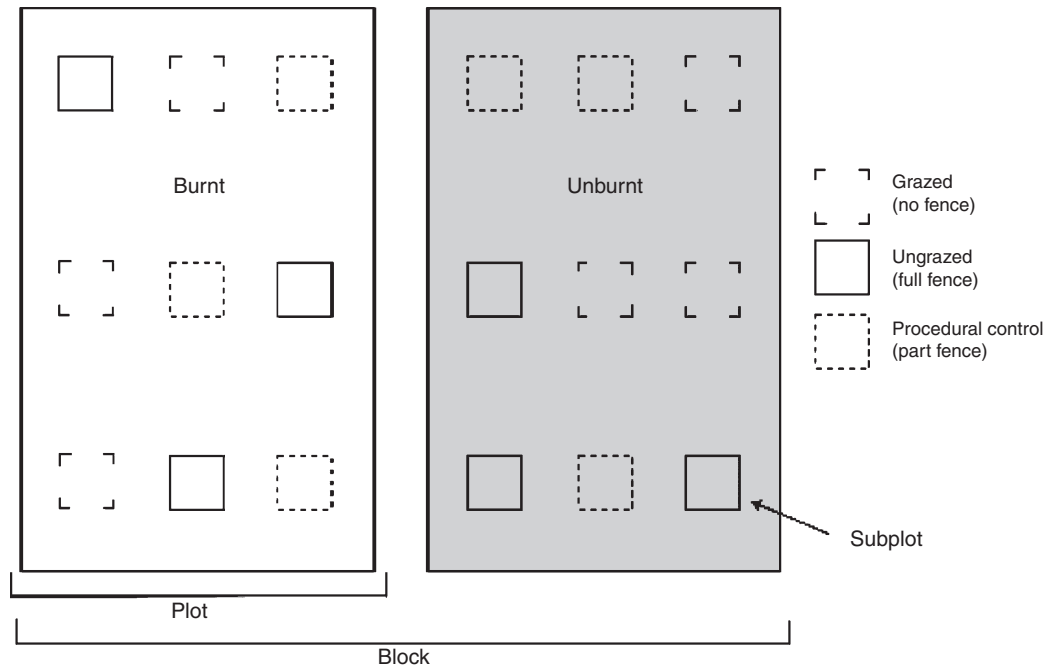


Fig. 1. Schematic representation of the experimental design of Experiments 1 and 2 with fire and grazing treatments illustrated within one block.

periods. All ferns and orchid/lilies present in both experiments were selected for by rock-wallabies, while sedges were not selected at all.

Experiment 2: Fire and sympatric macropod grazing

The design for Experiment 2 was identical to the above, except that the fire treatment plots were 50 × 100 m in area and two vegetation assessments were made before burning. Three of the six planned blocks did not burn successfully and hence could not be used as treatment plots. The three corresponding paired unburned plots were also discarded from the analysis. Fences for grazing treatments were established in January 2007 and low-intensity burning was conducted in May 2007. Fences in burnt plots were removed one week before the burn and replaced one week after the burn. We measured vegetation 5, 9, 12, 17 and 29 months after burning, as for Experiment 1.

Statistical analysis

We analysed the effects of fire, grazing and sampling period on vegetation biomass (gDM) using generalised linear modelling with repeated-measures using PROC MIXED in SAS 9.1 (SAS Institute, Gary, NC) (Littell *et al.* 2008) according to the models:

$$\text{Experiment 1: gDM} = \mu + \text{fire} + \text{grazing} + \text{period} \\ + \text{interactions} + e$$

$$\text{Experiment 2: gDM} = \mu + \text{startgDM} + \text{fire} + \text{grazing} \\ + \text{period} + \text{interactions} + e$$

The interactions were fire × grazing, fire × period and grazing × period. Fire, grazing and period were analysed as fixed factors, while block was random and period was a

repeated-measure. Data were drawn from six blocks (pairs of burnt and unburnt plots) for Experiment 1, and from three blocks for Experiment 2. For Experiment 1, sampling at time zero (startgDM), before treatments were imposed, was included as a covariate in order to account for pre-existing differences between plots. We square-root transformed the data to meet normality and homogeneity of variance assumptions. Up to nine pairwise comparisons were made between levels of grazing treatment within fire treatments and between fire treatments within each level of grazing treatment, and the α level was reduced accordingly ($\alpha = 0.006$). The dry weight biomass of plant species selected by rock-wallabies was pooled by functional group and analysed using generalised linear modelling as above.

Results

Experiment 1: Fire and rock-wallaby grazing

Total vegetation biomass

In Experiment 1, significant effects of fire on plant biomass were always accompanied by a significant effect of fire*period, which applied to all plant functional groups (Table 1). However, each plant functional group responded differently to fire over time. Grass biomass was near zero after fire in burnt plots and then increased until it was similar to grass biomass in unburnt plots 29 months after fire (Fig. 2a). Browse biomass in burnt plots was much lower than in unburnt plots until 17 months after fire, then reached twice the biomass of unburnt plots by 29 months after fire (Fig. 2b). Forb biomass increased rapidly from zero in burnt plots, reaching double the unburnt quantity within 5 months of fire, and then remained slightly higher than in unburnt plots (Fig. 2c). Sedge biomass was initially lower after burning but

Table 1. Results of generalised linear modelling for Experiment 1

F-values and significance values for all plant species in functional groups and those groups of species selected by rock-wallabies (indicated by the RW prefix) in fire and grazing treatments in Experiment 1 are shown. Significant ($P < 0.05$) values are indicated in bold

Functional group	Fire		Grazing		Period		Fire × Grazing		Fire × Period		Grazing × Period	
	$F_{1,4}$	<i>P</i>	$F_{1,4}$	<i>P</i>	$F_{4,412}$	<i>P</i>	$F_{2,412}$	<i>P</i>	$F_{2,412}$	<i>P</i>	$F_{8,412}$	<i>P</i>
Grasses	6.7	0.06	8.6	<0.01	14.5	<0.01	2.1	0.12	7.64	<0.01	0.3	0.96
Browse	10.7	0.03	7.8	<0.01	6.6	<0.01	13.9	<0.01	9.77	<0.01	0.3	0.96
Forbs	3.2	0.15	1.8	0.17	7.9	<0.01	1.3	0.26	10.7	<0.01	0.3	0.96
Sedges	3.7	0.13	5.6	0.01	9.1	<0.01	4.0	0.02	6.54	<0.01	0.4	0.94
RW Grasses	6.1	0.07	2.5	0.09	2.1	0.08	0.8	0.44	0.65	0.63	1.1	0.39
RW Browse	1.0	0.37	3.8	0.02	2.0	0.10	2.6	0.08	2.19	0.07	0.8	0.65
RW Forbs	53.3	<0.01	5.0	<0.01	37.9	<0.01	1.0	0.38	43.6	<0.01	0.8	0.59
RW Ferns	8.0	0.05	1.0	0.37	9.0	<0.01	0.2	0.83	3.95	<0.01	0.9	0.54
RW Orchid/lily	9.0	0.04	0.8	0.47	65.3	<0.01	1.8	0.17	8.6	<0.01	1.6	0.12

subsequently increased, and remained higher than in unburnt plots (Fig. 2d).

Grazing had a significant effect on grasses, browse and sedges but only on grass as a main effect alone (Table 1). Grass biomass was higher in ungrazed than in both grazed ($t = 3.0$, $P < 0.006$) and control treatments ($t = 4.0$, $P < 0.006$) (Fig. 3a). Fire*grazing had a significant effect on browse and sedges (Table 1).

Impacts on plants selected by rock-wallabies

For grasses selected by rock-wallabies, fire tended to reduce biomass (Fig. 2e). Fire also tended to affect selected browse over time, initially reducing browse below levels in unburnt plots, then increasing it between 17 and 29 months after fire (Fig. 2f). Fire*period had a significant effect on forbs, orchid/lilies and ferns selected by rock-wallabies (Table 1). There was a dramatic pulse in selected forb biomass in burnt plots during the first year after fire (Fig. 2g).

Grazing had a significant main effect on browse and forbs selected by rock-wallabies (Table 1). Selected forb biomass was higher in ungrazed plots than it was in both control plots ($t = 3.0$, $P < 0.006$) and in grazed plots ($t = 2.4$, $P = 0.02$), although this second effect was not significant (Fig. 3g).

Experiment 2: Fire and sympatric macropod grazing

Total vegetation biomass

Fire*period had a significant effect on forbs but on no other functional group in Experiment 2 (Table 2). After fire, forbs increased more in burnt than unburnt plots for each spring/summer sampling (9 and 17 months after fire: Fig. 4c). Period had a significant main effect on grass, browse and ferns (Table 2). Both grass and browse biomass decreased in burnt plots and continued to be lower than in unburnt plots in all post-fire periods (Fig. 4a, b).

Fire*grazing had a significant effect on grasses, browse and forbs, while grazing alone had a significant effect on sedges (Table 2). When burnt, grass biomass was lower in grazed plots than in ungrazed plots ($t = -7.5$, $P < 0.006$) (Fig. 5a). For browse within the unburnt treatments, biomass in grazed plots was lower than in ungrazed ($t = -3.4$, $P < 0.006$) and greater than in control plots ($t = -4.2$, $P < 0.006$) (Fig. 5b). For forbs within the burnt treatment, grazed plots had lower biomass than ungrazed plots ($t = 3.0$, $P < 0.006$) (Fig. 5c).

Impacts on plants selected by rock-wallabies

Fire*period had a significant effect on forbs selected by rock-wallabies (Table 2), where forb biomass was greater in unburnt than in burnt plots both years after fire (Fig. 4g). Grazing had a significant effect on browse and ferns selected by rock-wallabies (Table 2). Browse biomass was greater in ungrazed than in control plots ($t = -3.71$, $P = 0.0003$). There was a trend for more fern biomass in ungrazed plots than both grazed ($t = 2.1$, $P = 0.03$) and control ($t = -2.1$, $P = 0.03$) plots (Fig. 5h). Fire*grazing had a significant effect on forbs and grasses selected by rock-wallabies (Table 2). Biomass of forbs selected by rock-wallabies was greater in ungrazed plots than grazed plots in the burnt treatment ($t = 3.4$, $P = 0.008$) (Fig. 5g). Within the unburnt treatment, grazed plots had higher grass biomass than ungrazed plots ($t = -2.6$, $P = 0.01$), while in the burnt treatment, ungrazed plots tended to have higher biomass than control plots ($t = -2.4$, $P = 0.02$) (Fig. 5e).

Discussion

Effects of fire

In both experiments, plant functional groups exhibited staggered responses to fire in a classic pulse disturbance response. Some plant groups responded rapidly with a flush of post-fire growth (forbs), while others responded slowly through growth of new seedlings (browse). Burning had a dramatic effect on vegetation on the outcrop, much more so than it did on the surrounding slopes. This was largely due to the different ecosystems in these locations. Rocky outcrop vegetation communities tend to have a high proportion of species with seeder life-history strategies (killed by fire and regenerate from seed) and few resprouters (regenerate vegetatively) (Hunter and Clarke 1998; Clarke and Knox 2002). The short-term pulse response of forbs and of grasses selected by rock-wallabies to fire, combined with the immediate loss of edible plants and cover, suggests that strategic burning to improve food resources for rock-wallabies should be small-scale and in patches, creating a matrix of vegetation in different stages of succession.

Effects of grazing

In contrast to fire, the patterns for grazing were more sustained over time. In Experiment 1, grazing impacts were small, because

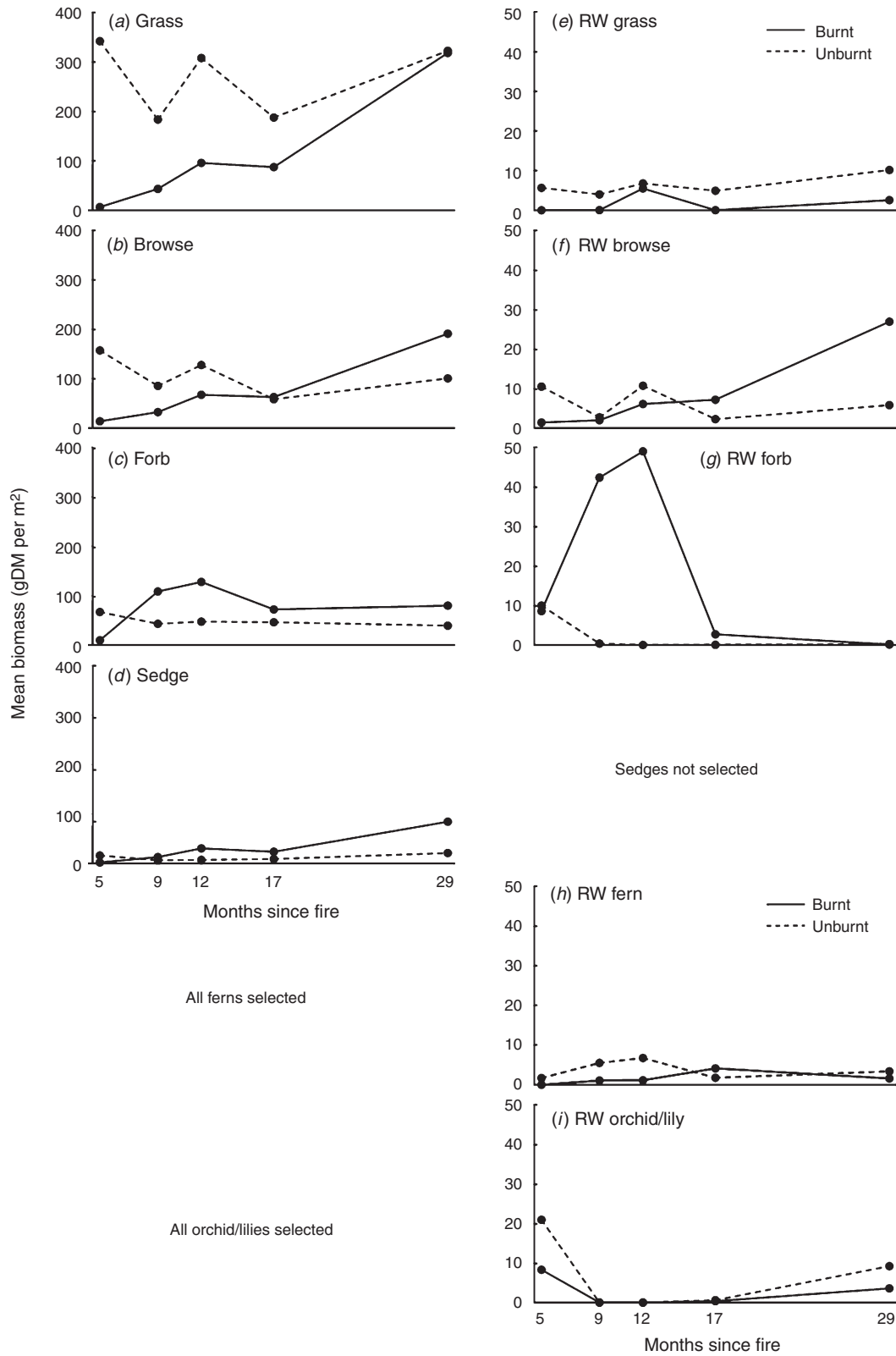


Fig. 2. Biomass (least-squares means) of each functional group by fire treatment over time in Experiment 1 for all plant species (a, b, c, d), and for species selected by rock-wallabies (RW) (e, f, g, h, i). Data are pooled across grazing treatments. Note change of y-axis scale in graphs in the right column.

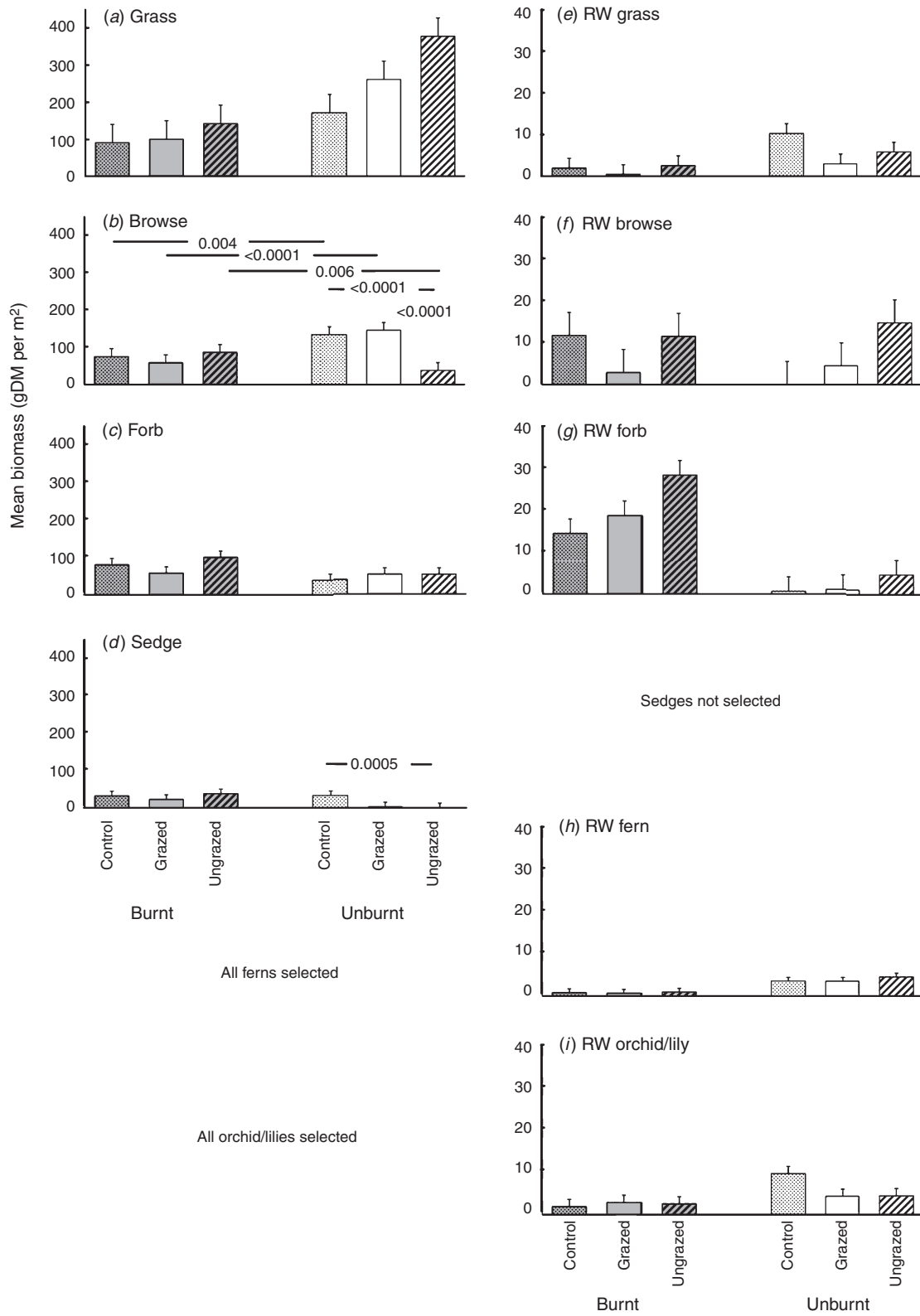


Fig. 3. Biomass (means + standard error) of each functional group for all plant species (*a, b, c, d*), and for species selected by rock-wallabies (RW) (*e, f, g, h, i*), by fire and grazing treatments in Experiment 1 over the 29-month post-fire period. Data are pooled across post-fire sampling periods. Note change of y-axis scale in graphs in the right column. *P*-values are marked for significant pairwise tests.

Table 2. Results of generalised linear modelling for Experiment 2

F-values and significance values for all plant species in functional groups and those groups of species selected by rock-wallabies (indicated by the RW prefix) in fire and grazing treatments in Experiment 2 are shown. Significant ($P < 0.05$) values are indicated in bold

Functional group	Fire		Grazing		Period		Fire × Grazing		Fire × Period		Grazing × Period	
	<i>F</i> _{1,2}	<i>P</i>	<i>F</i> _{2,235}	<i>P</i>	<i>F</i> _{4,235}	<i>P</i>	<i>F</i> _{2,235}	<i>P</i>	<i>F</i> _{2,235}	<i>P</i>	<i>F</i> _{8,235}	<i>P</i>
Grasses	1.8	0.31	25.0	<0.01	25.5	<0.01	6.1	<0.01	0.9	0.48	1.7	0.09
Browse	4.2	0.18	7.3	0.01	6.8	<0.01	3.7	0.03	0.7	0.58	0.6	0.75
Forbs	0.1	0.75	5.1	0.01	22.0	<0.01	3.6	0.03	2.5	0.04	0.2	0.99
Sedges	27.3	0.05	4.8	0.01	1.2	0.30	1.8	0.17	0.5	0.75	0.4	0.94
RW Grasses	0.1	0.80	6.9	<0.01	4.7	0.01	6.0	<0.01	0.1	0.99	0.3	0.98
RW Browse	0.2	0.69	4.9	0.01	3.1	0.02	0.1	0.97	0.8	0.50	0.4	0.92
RW Forbs	1.8	0.31	25.0	<0.01	9.1	<0.01	4.1	0.02	3.0	0.02	0.9	0.54
RW Ferns	0.2	0.73	3.1	<0.05	16.3	<0.01	1.1	0.35	0.4	0.83	0.6	0.78
RW Orchid/lily	0.4	0.57	2.1	0.12	1.0	0.34	0.1	0.95	1.0	0.40	1.3	0.25

the colony was small (fewer than five animals, which is substantially less than what the mountain was known to support in the past), but we did detect a significant negative grazing impact on forbs selected by rock-wallabies in burnt plots. This indicated that rock-wallabies were eating forbs more in burnt than unburnt areas and therefore that burning enhanced an important food resource. In Experiment 2, grazing by rock wallabies and sympatric macropods, together, was rarely significant as a main effect alone but was most often dependent on fire. For example, grasses and forbs selected by rock-wallabies were sensitive to fire, but only when combined with grazing.

In most cases, the measurements from procedural control plots were statistically indistinguishable from grazed plots, indicating that the fence did not have an effect on vegetation either through microclimatic effects or by influencing the behaviour of grazers or other animals. There were only three exceptions out of the 17 comparisons between control and grazed plots for each functional group in each experiment. These were sedge and rock-wallaby-selected browse in Experiment 1 and grass in Experiment 2.

Implications for rock-wallabies

The pulse of forbs within the first year after burning in Experiment 1 should benefit rock-wallabies, given that rock wallabies clearly consumed them (detected by a negative effect of rock-wallaby grazing) in burnt plots and that many of them were known to be positively selected. The rejuvenation of the dominant grass from senescent tussocks to new shoots was also positive for rock-wallabies, given that new shoots are usually favourable to herbivores for their higher nutrient and lower fibre contents (Villalba and Provenza 1999). The recruitment of new dominant trees may be helpful to rock-wallabies in the long term by renewing the late-climax canopy trees and possibly by providing nitrogen-rich foliage at an accessible level (Adams and Attivill 1984). Furthermore, increased nutrients in the soil after fire may lead to more nutrient-rich foliage that is more palatable to herbivores (Radho-Toly *et al.* 2001). Thus, the response of food plants to fire ultimately resulted in rock-wallabies having more abundant, and possibly more nutritious, resources available.

Opportunistic generalists have the capacity to capitalise on resource pulses (Yang *et al.* 2008). Since rock-wallabies are

versatile feeders (Short 1989), they should be able to adapt rapidly and switch to a diet with less of the species negatively affected by fire, and more of the species positively affected by fire just as generalist rodents persist in post-fire environments by utilising a range of food types as they become available (Luo and Fox 1996; Sutherland and Dickman 1999).

Despite the benefits of fire-driven resource pulses, animals may initially face resource shortages immediately after fire. When eastern pygmy possums (*Cercartetus nanus*) in recently burnt areas were supplemented with food, their body condition increased, compared with no increase for possums in more resource-rich unburnt areas (Tulloch and Dickman 2007). If burning had covered a large proportion of the site in this study, then food shortage may have been a short-term problem for rock-wallabies. However, the maintenance of forage in unburnt areas through the mosaic design ensured that rock-wallabies were not severely resource limited for that period.

Grazing, predominantly by sympatric macropods rather than rock-wallabies, had a negative effect on plants selected by rock-wallabies in Experiment 2. Grazing had a negative long-term effect on rock-wallaby browse and ferns regardless of burning, and on rock-wallaby grasses and forbs in burnt areas only. The interaction of grazing and fire on selected browse and fern species is most likely due to increased rates of herbivory on the fresh plant growth after fire (Klop *et al.* 2007). It appears, then, that the potential benefits to rock-wallabies from increased food resources from burning were negated (or even made worse, as in grasses selected by rock-wallabies) by the more abundant sympatric macropods. These impacts are particularly concerning given the potential for competition between rock-wallabies and at least one of these sympatric macropods (the common wallaroo), as indicated by dietary overlap between them (Tuft 2010). The dynamics of this herbivore community have been altered by changes in the predator guild with the introduction of foxes and the decline of dingoes (Johnson *et al.* 2007; Letnic *et al.* 2009), whereby rock-wallabies have greatly reduced in density (Lunney *et al.* 1997) and larger macropods have increased (Calaby and Grigg 1989; Pople *et al.* 2000). This shift in balance may place rock-wallabies at a competitive disadvantage and mean that the impact of sympatric species on food resources is an important consideration in using burning to improve forage value for threatened herbivores.

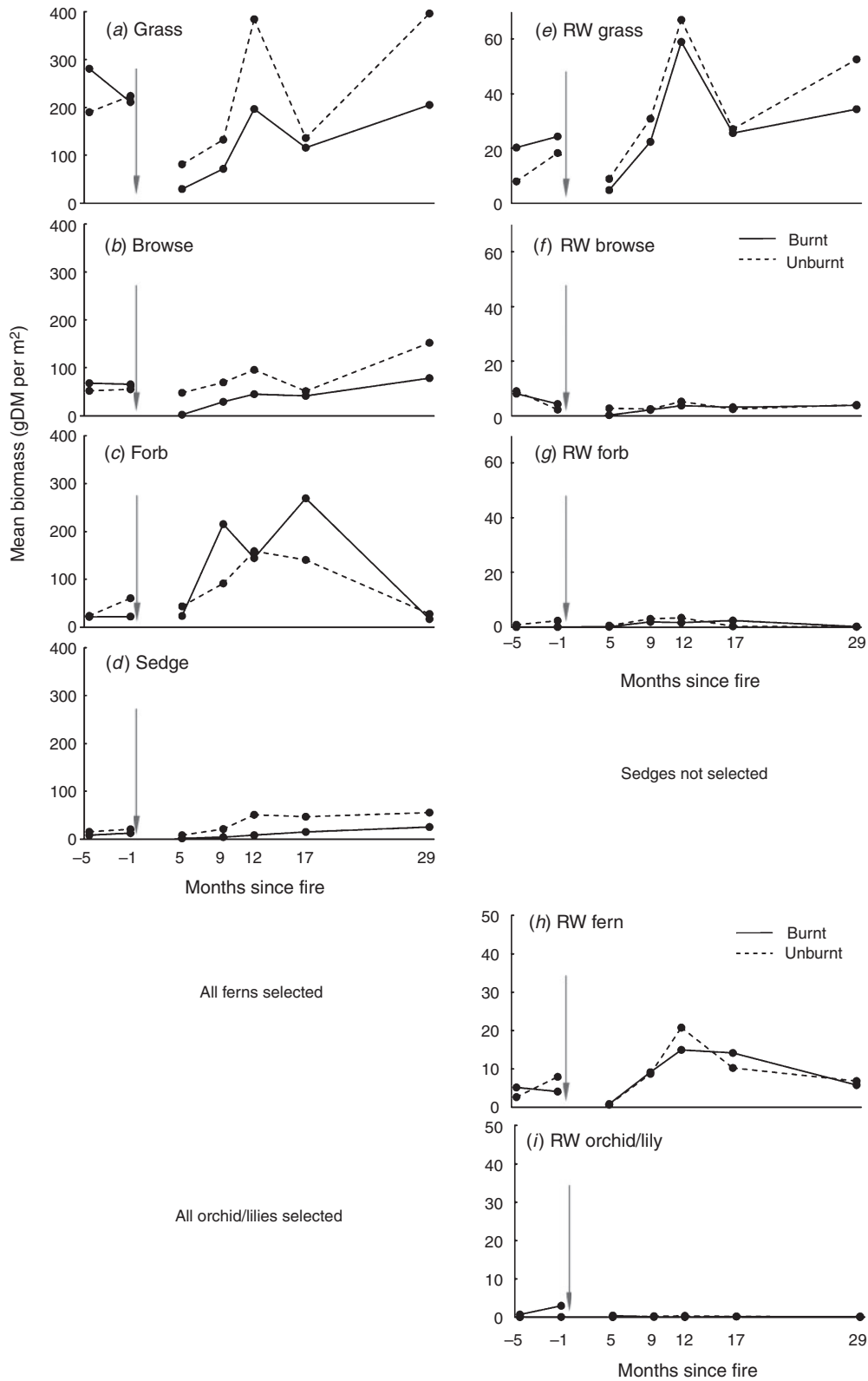


Fig. 4. Biomass (means) of each functional group by fire treatment over time in Experiment 2 for all plant species (a, b, c, d), and for species selected by rock-wallabies (RW) (e, f, g, h, i). Data are pooled across grazing treatments. Time of fire is indicated with arrow. Note change of y-axis scale in graphs in the right column.

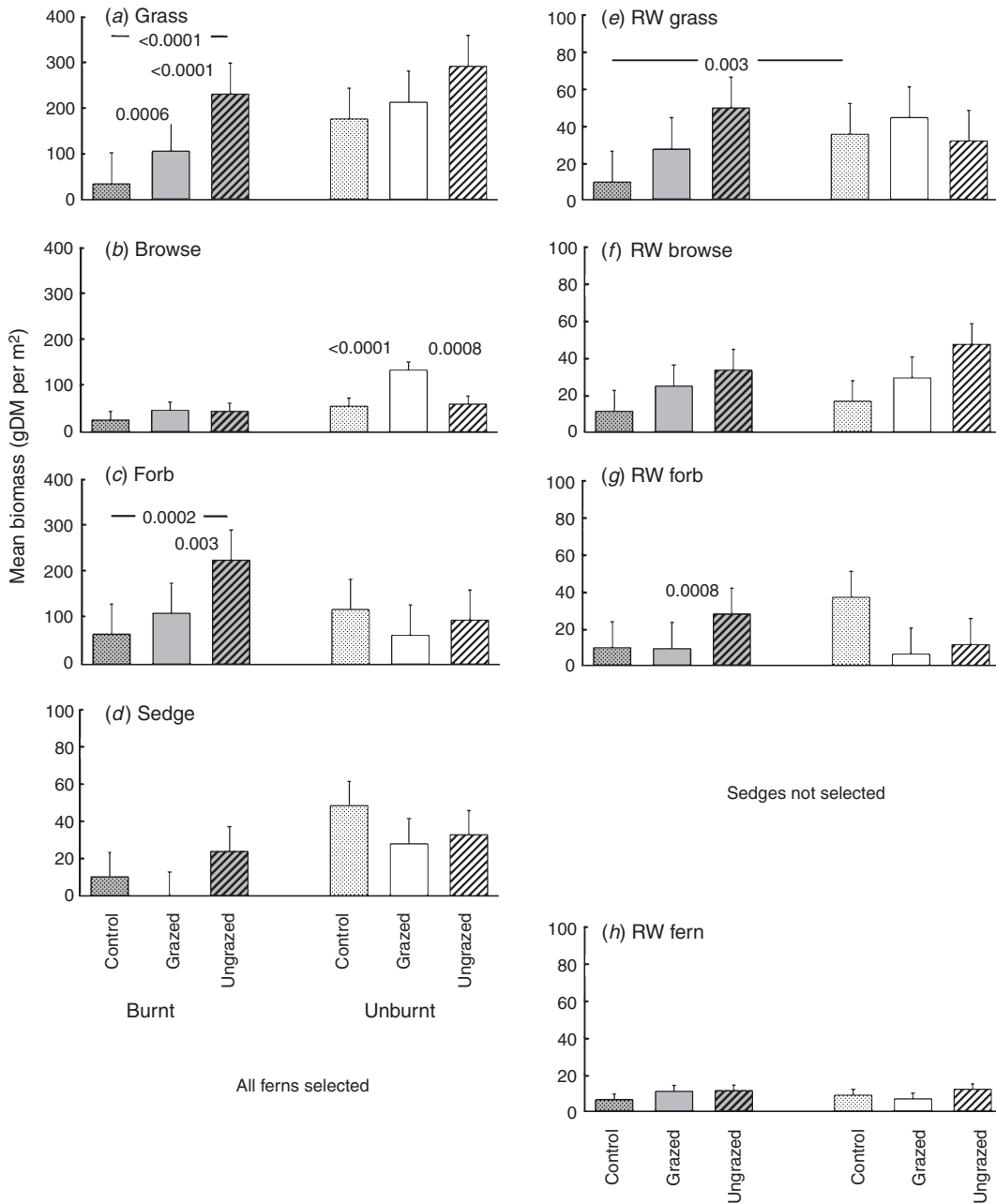


Fig. 5. Biomass (means + standard error) of each functional group for all plant species (a, b, c, d), and for species selected by rock-wallabies (RW) (e, f, g, h), by fire and grazing treatments in Experiment 2 over the 29-month post-fire period. Data are pooled across sampling periods. Note change of y-axis scale in graphs in the right column and for (d). P-values are marked for significant pairwise tests.

Recommendations

We found that fire can be beneficial to rock-wallabies by improving the food resources available to them, but not when combined with a high population density of sympatric grazers. We recommend small-scale, low-intensity burning using a mosaic pattern in order to retain patches of unburnt vegetation to sustain rock-wallabies in the weeks immediately following the burn before the first flush of forbs and new grasses, and to retain palatable browse plants as new ones are recruited and grow to

maturity. Care should be taken to assess the density of potential competitor herbivores before burning and, where possible, burning should be conducted where other herbivores have restricted access.

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References

- Adams, M. H., and Attivill, P. M. (1984). The role of *Acacia* species in nutrient balance and cycling in regenerating *Eucalyptus regnans* F. Meull. forests. I. Temporal changes in biomass and nutrient content. *Australian Journal of Botany* **32**, 205–215. doi:10.1071/BT9840205
- Andrew, M. H., Noble, I. R., and Lange, R. T. (1976). A non-destructive method for estimating the weight of forage on shrubs. *Australian Rangeland Journal* **1**, 225–231. doi:10.1071/RJ9790225
- Bakker, E. S., Reiffers, R. C., Olf, H., and Gleichman, J. M. (2005). Experimental manipulation of predation risk and food quality: effect on grazing behaviour in a central Texas foraging herbivore. *Oecologia* **146**, 157–167. doi:10.1007/s00442-005-0180-7
- Bond, W. J., and Keeley, J. E. (2005). Fire as a global 'herbivore': the ecology and evolution of flammable ecosystems. *Trends in Ecology & Evolution* **20**, 387–394. doi:10.1016/j.tree.2005.04.025
- Brown, J. R., and Stuth, J. W. (1993). How herbivory affects grazing tolerant and sensitive grasses in a central Texas grassland – integrating plant response across hierarchical levels. *Oikos* **67**, 291–298. doi:10.2307/3545474
- Calaby, J. H., and Grigg, G. C. (1989). Changes in macropodoid communities and populations in the past 200 years, and the future. In 'Kangaroos, Wallabies, and Rat-kangaroos'. (Eds G. C. Grigg, P. J. Jarman and I. Hume.) pp. 813–820. (Surrey Beatty: Sydney.)
- Clarke, P. J., and Knox, K. J. E. (2002). Post-fire response of shrubs in the tablelands of eastern Australia: do existing models explain habitat differences? *Australian Journal of Botany* **50**, 53–62. doi:10.1071/BT01055
- Dawson, T. J. (1989). Diets of macropodid marsupials: General patterns and environmental influences. In 'Kangaroos, Wallabies, and Rat-kangaroos'. (Eds G. C. Grigg, P. J. Jarman and I. Hume.) pp. 129–142. (Surrey Beatty: Sydney.)
- Dawson, T. J., and Ellis, B. A. (1979). Comparison of the diets of yellow-footed rock-wallabies and sympatric herbivores in western New South Wales. *Australian Wildlife Research* **6**, 245–254. doi:10.1071/WR9790245
- Fox, B. J. (1982). Fire and mammalian succession in an Australian coastal heath. *Ecology* **63**, 1332–1341. doi:10.2307/1938861
- Gill, A. M. (1981). Adaptive response of Australian vascular plant species to fires. In 'Fire and the Australian Biota'. (Eds A. M. Gill, R. H. Groves and I. R. Noble.) pp. 243–272. (Australian Academy of Science: Canberra.)
- Hunter, J. T., and Clarke, P. J. (1998). The vegetation of granitic outcrop communities of the New England batholith of eastern Australia. *Cunninghamia* **5**, 547–618.
- Johnson, C. N., Isaac, J. L., and Fisher, D. O. (2007). Rarity of a top predator triggers continent-wide collapse of mammal prey: dingoes and marsupials in Australia. *Proceedings of the Royal Society Biological Sciences Series B* **274**, 341–346. doi:10.1098/rspb.2006.3711
- Klop, E., van Goethem, J., and de longh, H. H. (2007). Resource selection by grazing herbivores on post-fire regrowth in a West African woodland savanna. *Wildlife Research* **34**, 77–83. doi:10.1071/WR06052
- Laws, R. J., and Goldizen, A. W. (2003). Nocturnal home ranges and social interactions of the brush-tailed rock-wallaby *Petrogale penicillata* at Hurdle Creek, Queensland. *Australian Mammalogy* **25**, 169–176.
- Letnic, M., Crowther, M. S., and Koch, F. (2009). Does a top-predator provide an endangered rodent with refuge from an invasive mesopredator? *Animal Conservation* **12**, 302–312. doi:10.1111/j.1469-1795.2009.00250.x
- Littell, R. C., Miliken, G. A., Stroup, W. W., Wolfinger, R. D., and Schabenberger, O. (2008). 'SAS for Mixed Models.' 2nd edn. (SAS Institute Inc.: Cary, NC.)
- Lunney, D., Law, B., and Rummery, C. (1997). An ecological interpretation of the historical decline of the brush-tailed rock-wallaby (*Petrogale penicillata*) in New South Wales. *Australian Mammalogy* **19**, 281–296.
- Lunt, I. D., Eldridge, D. J., Morgan, J. W., and Witt, G. B. (2007). A framework to predict the effects of livestock grazing and grazing exclusion on conservation values in natural ecosystems in Australia. *Australian Journal of Botany* **55**, 401–415. doi:10.1071/BT06178
- Luo, J., and Fox, B. J. (1996). Seasonal and successional dietary shifts of two sympatric rodents in coastal heathland: a possible mechanism for coexistence. *Australian Journal of Ecology* **21**, 121–132. doi:10.1111/j.1442-9993.1996.tb00593.x
- Manly, B. F. J., McDonald, L. L., Thomas, D. L., McDonald, T. L., and Erickson, P. (2002). 'Resource Selection by Animals: Statistical Design and Analysis for Field Studies.' 2nd edn. (Kluwer Academic Publishers: Dordrecht.)
- Nicholson, E., Lill, A., and Andersen, A. (2006). Do tropical savanna skink assemblages show a short-term response to low-intensity fire? *Wildlife Research* **33**, 331–338. doi:10.1071/WR05067
- NPWS (2003). Warrumbungle brush-tailed rock-wallaby endangered population recovery plan. NSW National Parks and Wildlife Service, Hurstville, NSW.
- Pople, A. R., Grigg, G. C., Cairns, S. C., Beard, L. A., and Alexander, P. (2000). Trends in the numbers of red kangaroos and emus on either side of the South Australian dingo fence: evidence for predator regulation? *Wildlife Research* **27**, 269–276. doi:10.1071/WR99030
- Prober, S. M., and Theile, K. R. (2005). Effects of the 2003 Bogong Complex fires on brush-tailed rock-wallaby habitat and *Acacia doratoxylon* scrubs in Little River Gorge, East Gippsland. Ecological Interactions report, Victoria.
- Radho-Toly, S., Majer, J. D., and Yates, C. (2001). Impact of fire on leaf nutrients, arthropod fauna and herbivory of native and exotic eucalypts in Kings Park, Perth, Western Australia. *Austral Ecology* **26**, 500–506. doi:10.1046/j.1442-9993.2001.01133.x
- Short, J. C. (1989). The diet of the brush-tailed rock-wallaby in New South Wales. *Australian Wildlife Research* **16**, 11–18. doi:10.1071/WR9890011
- Sutherland, E. F., and Dickman, C. R. (1999). Mechanisms of recovery after fire by rodents in the Australian environment: a review. *Wildlife Research* **26**, 405–419. doi:10.1071/WR97045
- Tuft, K. D. (2010). The foraging ecology of the brush-tailed rock-wallaby. Ph.D. Thesis, University of Sydney.
- Tuft, K. D., Crowther, M. S., Connell, K., Muller, S., and McArthur, C. (2011a). Predation risk and competitive interactions affect foraging of an endangered refuge-dependent herbivore. *Animal Conservation* **14**, 447–457.
- Tuft, K. D., Crowther, M. S., and McArthur, C. (2011b). Multiple scales of diet selection by brush-tailed rock-wallabies (*Petrogale penicillata*). *Australian Mammalogy* **33**, 169–180. doi:10.1071/AM10041
- Tulloch, A. I., and Dickman, C. R. (2007). Effects of food and fire on the demography of a nectar-feeding marsupial: a field experiment. *Journal of Zoology* **273**, 382–388. doi:10.1111/j.1469-7998.2007.00339.x
- Van Dyck, S. M., and Strahan, R. (2008). 'The Mammals of Australia.' 3rd edn. (New Holland: Sydney.)
- Villalba, J. J., and Provenza, F. D. (1999). Effects of food structure and nutritional quality and animal nutritional state on intake behaviour and food preferences of sheep. *Applied Animal Behaviour Science* **63**, 145–163. doi:10.1016/S0168-1591(98)00238-X
- Yang, L. H., Bastow, J. L., Spence, K. A., and Wright, A. N. (2008). What can we learn from resource pulses? *Ecology* **89**, 621–634. doi:10.1890/07-0175.1
- Yibarbuk, D., Whitehead, P. J., Russell-Smith, J., Jackson, D., Godjuwa, C., Fisher, A., Cooke, P., Choquenot, D., and Bowman, D. M. J. S. (2001). Fire ecology and Aboriginal land management in central Arnhem land, northern Australia: a tradition of ecosystem management. *Journal of Biogeography* **28**, 325–343. doi:10.1046/j.1365-2699.2001.00555.x