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Selective herbivory by mammals on 19 species planted at two densities

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ABSTRACT

The impact of mammalian herbivory, particularly macropods, upon seedling establishment in a post-fire environment was studied experimentally at Whiteman Park Reserve, Perth, Western Australia. Nineteen plant species of contrasting morphology and chemistry were established at low and high densities in protective exclosures, and half of the plants later exposed to herbivores. After one year of exposure, 16 species showed evidence of greater mortality and/or reduced shoot mass due to mammal herbivory. Two species had reduced shoot mass at high density (competition) and two had the reverse (facilitation), both annulled in the presence of herbivores due to poor growth at both densities. There was no preference by herbivores for high over low density plots. A general preference (high percentage plants eaten, large difference between biomass inside and outside exclosures) for species high in K, N or P and leaf mass: area, and low in initial shoot mass, spinescence, moisture and height was evident from principal components and canonical variates analyses. Grass-like species were more vulnerable to herbivory than seedlings of shrubs.

1. Introduction

Herbivory can strongly influence the extent of seedling recruitment (Crawley, 1983; Hanley et al., 1998; Hanley and Lamont, 2001). Seedlings are typically tender and nutrient-rich (Clifford, 1999), with leaves high in nitrogen and water content, and having low levels of sclerophylly (Groom et al., 1997). Such characteristics have often been correlated with increased susceptibility to herbivores (Kudo, 1996; Lindlof et al., 1974; Palo and Robbins, 1991). The greatest effects of herbivores on plant survival is likely to be at the seedling stage (Maron, 2001; Watkinson et al., 2001), with seedling palatability, growth form and timing of herbivory crucial in controlling seedling survivorship (Hanley et al., 1996). It has been demonstrated that grazing, particularly after fire, has a profound effect on plant community species composition (Whelan and Main, 1979; Mills, 1986). For palatable species, grazing by native animals may have a greater effect on plant survival than the fire itself (Leigh and Holgate, 1979).

Our research investigated the role of selective mammalian herbivory upon experimentally planted species in post-fire *Banksia* woodland at Whiteman Park Reserve, Western Australia. Fire affected much of the conservation area at Whiteman Park on 14 February 2001, providing an ideal opportunity to observe post-fire herbivory activity by the primary native vertebrate herbivores in the area, the western grey

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kangaroo (*Macropus fuliginosus*) and black-gloved wallaby (*M. irma*), and the introduced rabbit (*Oryctolagus cuniculus*). Rippey and Hobbs (2003) showed that fire is an important factor in shaping the vegetation at Rottnest Island, in conjunction with quokka (*Setonix brachyurus*) grazing. Their work highlights the importance of understanding herbivore activity, in particular selective feeding behaviour, following large-scale disturbance.

Herbivores are typically selective feeders, only consuming a subset of the plants available to them (Hjalten and Palo, 1993). Selection may be measured as the proportional intake of a plant type relative to its proportional availability in the environment (McArthur et al., 2000). Defoliation intensity is therefore rarely proportional to availability, with certain species selected in preference to others, regardless of season or abundance. A number of factors may be involved in the determination of food selection. These include levels of protein, fibre, water and toxins, as well as morphological attributes (Halford et al., 1984; Kababya et al., 1998). Differences in diet preferences between and within species may also reflect herbivore behavioural patterns (Shepherd et al., 1997). Some animals may sample and continue to consume species that are tolerable, while animals of the same species may encounter, and subsequently utilize, a range of contrasting plant species in their diet (Augner, 1995).

Responses of plant species to grazing are inevitably individualistic, with some species increasing in abundance while others decrease (Kirby, 2001). The key factors contributing to these individualistic grazing patterns were explored here. Legumes have been reported to be more susceptible to herbivory than grasses, exhibiting both lower survival and greater loss of biomass (Hulme, 1996), although increase in grass abundance is typical in the absence of herbivore activity (Hobbs et al., 1995; Pettit and Froend, 2001). Kangaroos often show a strong preference for grasses, switching to this food source whenever it is available. Positive selection for grasses has been attributed to greater nutritional content (Halford et al., 1984), especially high nitrate levels (Wann and Bell, 1997). For the bridled nailtail wallaby (*Onychogalea fraenata*) and black-striped wallaby (*Macropus dorsalis*), relative palatability, digestibility, levels of secondary metabolites and nutritional content all appear to contribute to the process of diet selection (Evans and Jarman, 1999). The effect of rabbits on native vegetation has been well documented (Ebenhard, 1988; Gill, 1992; Myers et al., 1994), with their broad dietary niche thought to impede plant regeneration to a greater extent than the kangaroo. Rabbit damage includes soil disturbance from digging activity.

Herbivory research has traditionally focused on the separate components involved in the interaction between plants and animals (Herrera et al., 2002). This approach ignores possible influences of other factors, and the role of multiple, correlated factors, commonly leading to an oversimplification of the mechanisms involved in the ecology of herbivore–plant relationships. Relative damage upon different plant species by herbivores in field trials is the net result of many factors, including physiological impacts of leaf chemistry, past experiences, predation risk, alternative food sources and foraging costs (Scott et al., 2002). Understanding why animals eat a particular diet may assist in controlling depredation of vegetation by livestock and wildlife.

The aim of our study was to demonstrate and explain selective browsing of seedlings that establish after a major environmental disturbance, fire, and identify key components driving selection by macropods in regenerating ecosystems. In addition to plant morphology, arrangement of plants within the herbivore habitat were also considered. Following disturbance, plants may perform better in close proximity due to facilitation, providing protection for one another from extreme conditions as well as herbivore feeding (Eccles et al., 2001). Alternatively, performance may decline with increased density due to the effects of competition (Lamont et al., 1993). The relative importance of planting density relative to herbivore impacts was considered in this study, particularly in regards to the plant resource hypothesis, which suggests specialist herbivores may aggregate in increased densities within favourable feeding areas (Root, 1973).

The design of this study was based on the use of exclosures, half of which were opened to herbivores after 5 months of seedling establishment. Exclosures have proven useful in understanding the impacts of mammalian herbivores in North America (Brookshire et al., 2002; Proulx and Mazumder, 1998), New Zealand (Fitzgerald and Gibb, 2001; Wardle, 2001), Europe (Hester et al., 2000), Japan (Nomiya et al., 2002) and southwestern Australia (Pettit and Froend, 2001), aiding in overcoming logistical difficulties often involved in large-scale studies. A number of hypotheses were tested via the use of exclosures in an effort to clarify the primary factor(s) driving diet selection of the primary herbivores, particularly the western grey kangaroo, at Whiteman Park Reserve. These were that:

1. Mammals preferentially select plant species relatively high in nutrients (Halford et al., 1984; Wann and Bell, 1997);
2. Mammals preferentially select grass-like species (Bell, 1994; Edwards, 1989; Jarman and Phillips, 1989; Pettit and Froend, 2001);
3. Mammals preferentially select relatively taller species (Kullberg and Bergstrom, 2001; Moss et al., 1972);
4. Mammals select against plant species with high tannin concentrations (Palo and Robbins, 1991; Provenza, 1995; Sagers and Coley, 1995) and essential-oil containing plant species (Jones et al., 2003);
5. Mammals select against highly spinescent species (Belovsky et al., 1991; Campbell, 1986; Myers and Bazely, 1991);
6. Mammals select against highly sclerophyllous (Howe and Westly, 1988; Sagers and Coley, 1995) and fibrous (Dawson, 1989; Evans and Jarman, 1999; McArthur et al., 2000) species;
7. Mammals select plant species growing at high-density arrangements (Horvitz and Schemske, 2002; Stephens and Krebs, 1986);
8. Mammalian herbivory affects survival and growth of plants to a greater extent than competition (Horvitz and Schemske, 2002).