Arid land vegetation dynamics after a rare flooding event: influence of fire and grazing

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1. Introduction

Arid vegetation community structure, function, patterns of species colonization and succession are largely determined by climatic factors (Johnson et al., 1976; Aguado-Santacruz and Garcia-Moya, 1998). On an annual scale, precipitation pattern and intensity affect the floristic composition and biomass of grassland (Sala et al., 1988; Silvertown et al., 1994; Oesterheld et al., 2001). Even rainfall events involving 5 mm or less can play a vital role in affecting the species composition (Sala and Lauenroth, 1982, 1985; Florentine, 1999). Australian arid environments face El Niño-Southern Oscillation (ENSO) and therefore drought, fire and flood may occur at varying intervals (Flannery, 1999). ENSO events may consequently influence the vegetation on longer time scales, over 10–100 s of years, emphasizing the importance of understanding what happened in the past and the need to monitor future changes over a long term (Lunt, 2002).

Vegetation in arid ecosystems is affected by grazing and fire (Florentine, 1999; Drewa and Havstad, 2001). It is also a general belief that Australian arid zone vegetation is modified by episodic or sporadic high rainfall events and subsequent flooding (Smith and Morton, 1990). Griffin and Freidel (1985) emphasized that such events are crucial in triggering recruitment of long-lived perennials. Understanding the effect of a rare flooding event, and how its effect is moulded by other important vegetation-shaping factors like fire and grazing, is essential for management of semi-arid vegetation.

In this study we evaluated the relative importance of fire, flooding and grazing on native vegetation by opportunistically placing pairs of permanent plots within vegetation that had experienced different combinations of fire and flooding. One plot in each pair was fenced to prevent grazing by vertebrate animals.

2. Materials and method

2.1. Study area

The study area is within the catchment of the ephemeral Olary Creek, where the vegetation is comprised of mallee open-scrub (Specht and Specht, 1999). Such vegetation has a sparse canopy of multi-stemmed eucalypts with lignotubers, so called mallee. Olary Creek arises in the Olary Ranges in northeast South Australia and flows south and east through Oakvale Station and across the New South Wales border into Loch Lilly Station (S33°01′00″, E141°08′10″). There, it splits into two channels, one of which flows due east to fill Woolcunda Lake and White Lake, and the other flows southeast into Nagaela Station (Fig. 1). The Creek flowed for the first time in many years in February 1989 (K. Weitch, Oakvale Station, pers. comm.) and again more extensively in February 1997 following up to 200 mm rainfall in 24 h (close to mean annual rainfall). This rare flooding event caused severe erosion and also formed an ephemeral lake within Nagaela Station after washing through mallee vegetation. The water level in the newly created lake was up to 2 m in the deepest

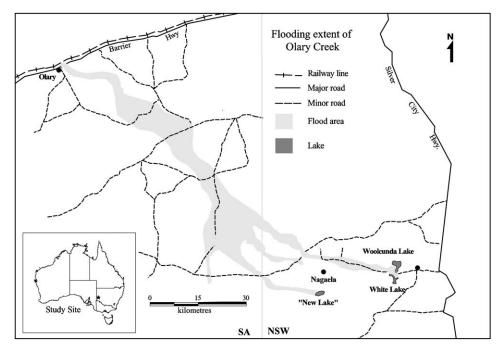


Fig. 1. Location of study site and extent of the 1997 Olary Creek flooding.

point. The floodwater-formed lake stayed for approximately a year and a half. Weston and Westbrooke (1999) suggested that the water flooded an original creek line that had not flowed to this extent for more than 100 years, allowing the drift of sand and establishment of mallee vegetation. Rainfall records and reports from Olary and Mannahill suggest four flooding events since the 1920s (Table 1). Prior to the February 1997 flooding event, part of the vegetation around Olary Creek had been burnt by natural fire. Major vertebrate herbivores in the Olary Creek catchment are kangaroo, goats and rabbits.

2.2. Placement of permanent plots and enclosures

To assess the relative impact of flood, fire and grazing, permanent 625 m^2 ($25 \times 25 \text{ m}^2$) plots were established in February 1999, after the flooding (February 1997) and fire (December 1996) events. The permanently marked plots were placed in pairs in areas that had one of the following histories: (i) not flooded, not burnt; (ii) flooded, not burnt; (iii) not flooded, burnt; and (iv) flooded, burnt. One of the plots in the pair was left unfenced while the other was fenced to prevent grazing by vertebrate animals. The fence was 1.7 m tall, with a 150 mm mesh size. There were, in total, eight pairs of plots, hence, with two replicates of the different combination of flooded and burnt.

Year	Olary		Mannahill		Effects	
	Feb	March	Feb	March	-	
70 year average	25	18	21	15		
1921	a	a	143	134	Flooding of Olary Creek. Woolcunda and White Lake filled (R. Seccombe, Woolcunda Station, pers. comm.)	
1950	152	107	74	87	Presumed flow in upper sections of Olary Creek	
1989	0	214	0	171	Extensive flooding along Olary Creek; Woolcunda lake filled (Weston and Westbrooke, 1999)	
1997	216	0	271	0	Extensive flooding along Olary Creek; Woolcunda and White Lake filled (Weston and Westbrooke, 1999)	

]	Monthly rainfall (mm) and events causing	flows over the	Olary Creek over	the past 100 years

^aData not available.

Table 1

2.3. Vegetation records

Detailed vegetation data were collected in September 1999 (2 years and 7 months after the flooding event started) and October 2002 (5 years and 8 months after the flooding event started). The objective was to monitor recovery of vegetation following different combinations of impact. In each survey, all individuals were counted and, if possible, identified to species level. Species unable to be identified in the field were collected and identified with the aid of herbarium specimens at the University of Ballarat. Data presented here did not include *Eucalyptus* species. During the sampling time, lack of flower buds or capsules prevented us for accurate species identification.

2.4. Statistical analyses

The data were analysed with both univariate and multivariate methods. It is important to note that as the plots were opportunistically allocated after the impact, *P*-values should only be used as indicators of relationships, and we put more emphasis on the relative differences between the four explanatory variables: (i) flooded vs. not flooded, (ii) burnt vs. not burnt, (iii) year (1999 and 2002), and (iv) fenced vs. not fenced vegetation.

The explanatory power of the four factors on number of species per plot was evaluated in repeated measurement split-plot ANOVAs with grazed vs. enclosed as the split-plot factor. Only those interactions involving the controlled factors (fencing and year) were considered. Multivariate analyses were conducted on $\log_{10} (x + 1)$ transformed vegetation data using the CANOCO 4.5 software and its default options (ter Braak and Smilauer, 2002). The purpose was to explore community level responses with direct gradient analyses (McCune and Grace, 2002; Leps and Smilauer, 2003). Initial partial Detrended Correspondence Analysis, with each one of the four factors as environmental variable and the three others as covaribles, revealed that gradients in data were relatively short (length of longest gradient between 3 and 4 SD). Without covariables, however, gradients were longer (maximum of 4.0 SD). Therefore, we used a model based on linear assumptions, partial redundancy analysis (pRDA), to decompose the explainable variation in the data, and a model based on unimodal assumptions, canonical correspondence analysis (CCA), for a joint illustration of all factors together. The strengths of the pRDAs were evaluated in permutation tests (9999 permutations) where appropriate permutation blocks were formed to reflect the repeated measurement and split-plot design.

3. Results

Table 2

3.1. Number of species

The number of species recorded in plots changed with time (Table 2): the average number per 625 m^2 dropped from 11.8 (SE 2.16) in 1999 to 5.7 (0.79) in 2002. Grazed and enclosed plots also differed (Table 2): ungrazed plots had 11.2 (1.87) and grazed 6.2 (1.06).

3.2. Decomposition of the variation in vegetation

Flooded plots differed in species composition from non-flooded plots (Table 3). Also, there was a significant change over time in vegetation composition (Table 3). In contrast,

Source	d.f.	MS	F	Р
A. Burnt vs. not burnt	1	9.03	0.16	0.7037
B: Flooded vs. not flooded	1	30.0	0.54	0.4955
Error	5	55.6		
C: Exclosed vs. grazed	1	205.0	25.69	0.0039
C*A	1	3.8	0.47	0.5219
C*B	1	0.03	0.004	0.9525
Error	5	8.0		
D: 1999 vs. 2002	1	294.0	20.10	0.0065
D*A	1	13.8	0.94	0.3764
D*B	1	42.8	2.92	0.1480
Error	5	14.6		

ANOVA (spilt plot repeated measures) of number of species per 25 m^2 in plots that had been subjected to different combinations of fire, flooding and grazing and surveyed on two occasions

Environmental variables	Co variables	Explained variance (%)	F	Р	Permutation blocks defined by: (samples per block)
A: Fire/no fire	B, C, D	1.7	0.775	0.4684	A, B & C (4)
B: Flooded/not flooded	A, C, D	14.7	6.789	0.0001	A, C & D (4)
C: 2000/2002	A, B, D	18.9	9.148	0.0001	D & plot id (2)
D: Fenced/not fenced	A, B, C	6.2	2.970	0.0080	C & plot id (2)

Table 3 Decomposition of the explainable variation according to four different pRDA:s

whether plots had been burnt or not seemed less important (Table 3). Plots left open to grazing by vertebrates differed significantly from fenced plots, but the amount of variation explained was small compared with flooding and time (Table 3). Hence, the dominating trends in the data were explained by flooding and a change over time (Fig. 2).

3.3. Flooding

Taxa that seemed to benefit most from flooding were *Eragrostis* spp., the exotic *Nicotiana glauca* (Solanaceae) and the perennial herb *Pseudognaphalium luteoalbum* (Asteraceae) (low ordination scores in Table 4). Species associated with non-flooded plots were *Ptilotus exaltatus, Duboisia hopwoodii, Sclerolaena diacantha* and *Triodia scariosa* ssp. *scariosa* (high ordination values in Table 4).

3.4. Change over time

The most pronounced increase over time was exhibited by the grasses *Triodia* scariosa ssp. scariosa and *Stipa* spp. (high ordination score in Table 4). Several short-lived herbs decreased, e.g. *P. luteoalbum*, *Ptilotus exaltatus*, *Calandrinia eremaea* and *Pimelea trichostachya* (low scores in Table 4).

3.5. Grazing

Fencing promoted most species, especially saltbush species (Chenopodiaceae) and *Stipa* spp. (high ordination scores in Table 4). The spinifex grass *Triodia scariosa* ssp. *scariosa* and the exotic *N. glauca* were associated with unfenced plots (low scores in Table 4).

4. Discussion

4.1. Relative importance of flood, fire and grazing

Water availability is a key factor for plant growth, regeneration and death in arid and semiarid systems. For example, recruitment of some long-lived species is

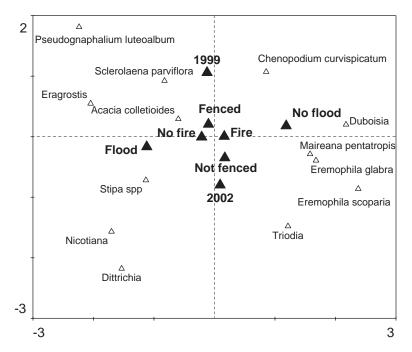


Fig. 2. Ordination graph (CCA) on vegetation in 16 plots in the Olary Creek area experiencing different combinations of flood, fire and grazing. Vegetation was sampled on two occasions (1999 and 2002). Only the most abundant of the 63 taxa recorded are illustrated; full species names in Table 4. Eigenvalues are 0.580 and 0.495 for axis 1 and 2, respectively. Bold text and symbols indicate the explanatory variables.

probably confined to very rare occasions when soil water reservoirs are substantial enough to allow the growing taproot of seedlings to reach soil depths with reliable ground water (Henschel and Seely, 2000). Furthermore, the mortality of perennials is affected by periods of limited water availability (Herbel et al., 1972; Milton and Dean, 2000). Finally, the abundance of annuals is, to a large extent, determined by the amount of rainfall (O'Connor and Roux, 1995; Guo and Brown, 1996; Ward et al., 2000; Milton and Dean, 2000). In addition to these ways in which variation in precipitation can affect plant population dynamics, there is in some arid areas the effect of inundation. When desert soil is under water for extended time, we expect a possible wash-way effect of salt in topsoil (Zamora-Arroyo et al., 2001), additions to groundwater, as well as the death of many plants. When water eventually recedes, soil water is at a maximum, providing ample opportunity for germination and establishment of plants, especially the perennials relying on rare, large rainfall events.

Short-term dynamics in arid/semi-arid systems has been relatively well studied. As mentioned above it is well known that annuals respond strongly to interannual variation in rainfall (Bowers, 1987; Gutierrez and Whitford, 1987; Aronson and Shmida, 1992; Hobbs and Mooney, 1995; Guo and Brown, 1996; Milton and Dean,

Table 4

Responses of the more abundant species to flooding and grazing and their change over time according to the three significant pRDAs (see Table 3)

Species	Family			Frequency (max 32)	Total abundance	Ordination score flooded ^a	Ordination score fenced ^b	Ordination score year ^c
Acacia colletioides Benth.	Mimosaceae	Shrub	Perennial	9	13	0.154	0.365	0.048
Calandrinia eremaea Ewart	Portulacaceae	Herb	Annual	7	12	0.125	0.022	0.497
Chenopodium curvispicatum Paul G. Wilson	Chenopodiaceae	Shrub	Perennial	8	33	0.202	0.273	0.079
Chenopodium desertorum (J.M. Black) J.M. Black	Chenopodiaceae	Shrub	Perennial	6	14	0.046	0.325	0.139
<i>Duboisia hopwoodii</i> (F. Muell.) F. Muell.	Solanaceae	Shrub	Perennial	7	20	0.464	0.012	0.050
Eragrostis spp.	Poaceae	Grass	Annual	11	56	0.646	0.063	0.205
<i>Eremophila glabra</i> (R.Br.) Ostenf.	Myoporaceae	Shrub	Perennial	8	40	0.355	0.167	0.236
Maireana pentatropis (Tate) Paul G. Wilson	Chenopodiaceae	Shrub	Perennial	7	31	0.336	0.336	0.243
Nicotiana glauca Graham ^d	Solanaceae	Shrub	Perennial	9	111	0.539	0.112	0.344
Pimelea trichostachya Lindl.	Thymelaeaceae	Herb	Annual	7	7	0.227	0.076	0.529
Pseudognaphalium luteoalbum (L.) Hilliard & B.L. Burtt	Asteraceae	Herb	Perennial	8	17	0.529	0.007	0.529
Ptilotus exaltatus Nees	Amaranthaceae	Herb	Annual	7	9	0.500	0.000	0.500
Sclerolaena parviflora (R.H. Anderson) A.J. Scott	Chenopodiaceae	Herb	Perennial	14	99	0.207	0.207	0.189
Sclerolaena diacantha (Nees) Benth.	Chenopodiaceae	Shrub	Perennial	7	16	0.429	0.248	0.024
Stipa spp.	Poaceae	Grass	Perennial	22	12110	0.433	0.380	0.372
Triodia scariosa N.T. Burb. ssp. Scariosa	Poaceae	Grass	Perennial	23	2583	0.388	0.156	0.723

^aHigh ordination score: most abundant in non flooded plots. ^bHigh ordination score: most abundant in fenced plots. ^cHigh ordination score: most abundant on the second survey.

^d Exotic.

2000). Furthermore, the effect of grazing and fire has been studied (Waser and Price, 1981; Kelt and Valone, 1995; Valone and Kelt, 1999; Ward et al., 2000; Drewa and Havstad, 2001). However, the effects of very rare events, are difficult to observe and most often have to be inferred from indirect evidence (Henschel and Seely, 2000). Therefore, to evaluate the relative importance of the major factors involved in shaping vegetation in arid/semiarid environments is a difficult task. In the present study, we retrieved data after a partly burnt area had been partly flooded. Our interpretation of the data is that flooding was the most important factor for vegetation composition while fire and grazing were of much smaller importance (Table 3). It is important to note that there are potential confounding factors that might have inflated the explanatory power of "flooding". For example, although the study area is a flat landscape, flooded plots were inevitably at lower altitude. It is also worth noting that our design meant a higher power in detecting grazing effects than that of fire or flooding (paired grazed and ungrazed plots contain substantially less spatial variation than that of opportunistically placed plots spaced over a much larger area).

To put the present study into the appropriate context within the theories of water availability effect on vegetation, we need to consider that the rainfall in 1997 in itself would have meant much more water than received in a normal year. Hence, considering the interannual variation in rainfall, 1997 and the following year are likely to have been unusually good for both plant growth and regeneration and with low mortality. The flooding therefore is likely to have added an extra effect. The species that seemed to benefit most from flooding were *Erogrostis* spp., *P. luteoalbum* and the exotic *N. glauca* while those species associated with non-flooded plots were most notably *Ptilotus exaltatus, Sclerolaena diacantha* and *Triodia scariosa*.

4.2. Change over time

With only two points in time it is, of course, not possible to separate fluctuations from directional trends. Despite this, we would like to infer the following sequence of events. The 1997 rainfall, and the flooding, is likely to have caused a flush in regeneration from seed and surviving root parts, once the water receded. As annual rain inputs went back to normal, we would expect to encounter drought-caused mortality among the large number of recruits. As we have no assessment of vegetation before the impact, we could not monitor the expected "flush-effect" of the 1997 rain. But we did observe a decrease in species richness, most likely caused by such mortality. Similar effects have been observed in other fire prone vegetation communities (Auld and O'Connell, 1991; Friedel et al., 1993; Pickup et al., 2003).

4.3. Grazing

Grazing explained parts of the variation in vegetation data (Table 3). Only two species, the exotic *N. glauca* and *Triodia scariosa* clearly benefited from grazing while the majority were negatively affected. *Trioida* is a genus of so called spinifex grasses that dominate in arid parts of Australia and which are prickly and avoided by

herbivores (Griffin, 1990). *N. glauca* has deterring chemicals and can be highly toxic to humans (Mizrachi et al., 2000) and animals (Panter et al., 2000).

A detailed study of *N. glauca* in the area confirms that the invasion of this species was greatly facilitated by flooding, especially in combination with grazing (Florentine and Westbrooke, submitted). Moreover, this study showed the legacy of the flooding event by the presence of *N. glauca* in the seed bank of flooded areas only. Another flooding may help *N. glauca* spread further with seeds along the catchment and extend its distribution. Thus flooding can contribute to expanding the distribution of environmental weeds (Cellot et al., 1998).

5. Conclusions

Although much has been published on the effects of fire and grazing on native vegetation and species composition, our study highlights the effects of episodic flooding events on arid landscape vegetation. Our study clearly showed that (i) the unusual flooding event affected post-flood vegetation, (ii) plots left open to grazing by vertebrates differed from fenced plots, but the amount of variation explained was small compared with flooding and the change over time, (iii) species that seemed to benefit most from flooding were *P. luteoalbum, Eragrostis* spp. and the exotic *N. glauca.*

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