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Influence of climate and community composition on the population demography of pasture species in semi-arid Australia

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Abstract

Substantial recruitment of *Callitris glaucophylla* in woodland, *Sclerolaena birchii* in cleared woodland, and *Astrebla lappacea* in grassland is related to catastrophic events of the past century in the form of interactions between climate, the impact of European land use (sheep, cattle, rabbits) and the rabbit myxoma epizootic. The direct effect of rainfall on the demography of these species and its indirect effect through competition via suites of accompanying plant species are examined. Major long-term changes in plant populations are generated by extreme sequential events rather than by random isolated events. One of the most potent climatic agents for change in eastern Australia is the El Niño/Southern Oscillation phenomenon.

Introduction

Vegetation dynamics are influenced by factors that operate either simultaneously or sequentially (Austin 1981). These factors include both the intrinsic properties of the component species populations as expressed in primary succession and regeneration cycles, and extrinsic forcing factors such as climate. In semi-arid environments the occurrence of extreme rainfall events in successive years is a potent extrinsic factor and the long-term dynamics of plant communities initiated by sequential extreme events may bear little resemblance to predicted communities offered by models based on random climatic events.

In this paper we select three Australian examples which illustrate the consequences of sequential climatic extremes. The first example describes the direct impact of climate on the dynamics of *Callitris glaucophylla* Thompson and Johnson, a conifer tree in grazed, semi-arid woodlands in Australia south of the Tropic of Capricorn (Thompson & Johnson 1986), and the two other examples describe the indirect effect of climate on the dynamics of *Sclerolaena birchii* (F. Muell.) Domin in former *Eucalyptus populnea* F. Muell. woodland and *Astrebla lappacea* (Lindl.) Domin in *Astrebla* tussock grassland through its impact on the establishment and survival of associated species.

Callitris glaucophylla

An area of 400000 ha known as the Pilliga scrub and now mostly a State Forest was open grazing country 120 years ago (Rolls 1981; Chiswell 1982). When the first Europeans moved into the area in the 1830s, they found an open grassy 'forest' with large trees of *Eucalyptus crebra* F. Muell. and *Callitris glaucophylla* at a density of about 8 trees/ha. This woodland had developed under an Aboriginal fire regime and grazing by indigenous marsupials. Figure 1 summarizes the events which then took place. Less

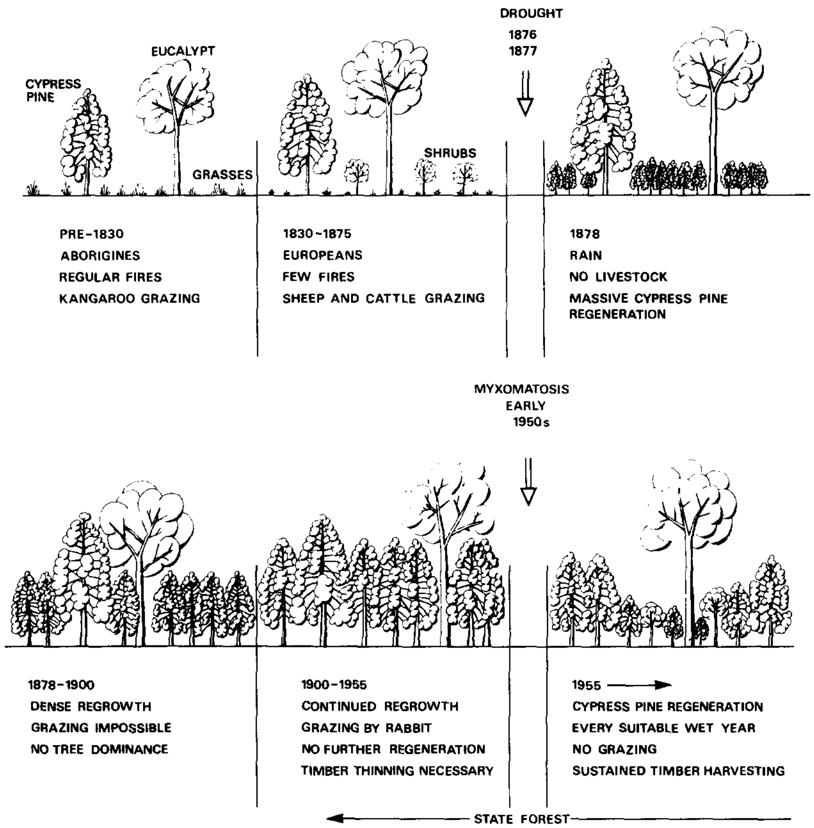

Fig. 1. Events leading to the transformation of forest under Aboriginal hunting and gathering followed by European pastoralism into the Pilliga Scrub and sustainable timber harvesting.

frequent fires and increased grazing by cattle and sheep quickly resulted in an increase in shrubs (the 'woody weed' problem which now plagues many of Australia's grazing lands). These shrubs and other associated species apparently had been, and still are, characteristic of the ridges but over a century ago they began to invade the broad valleys. The resumption of burning by the settlers to control these invaders was unsuccessful. Droughts in 1876 and 1877 forced destocking of the pastures, and when the drought broke in 1878 abundant regeneration of *Callitris, Eucalyptus* and other woody species occurred. *Callitris* does not self-thin very rapidly, and the dense thickets of slow-growing saplings that developed were so firmly entrenched by 1900 that grazing was nearly impossible (Chiswell 1982).

A second catastrophic event in the late 1880s occurred when the European rabbit (*Oryctolagus cuniculus*) invaded the area and stopped any further regeneration of the conifer. As a consequence, by 1950 ecologists had come to regard *C. glaucophylla* as a relict species under the current climate (Lacey 1972). The third catastrophic event was the myxoma epizootic which reached the area in the early 1950s and almost eliminated rabbits. This event, which was aided by abundant rainfall, high rivers and high insect vector populations allowed prolific regeneration of *C. glaucophylla*, completely altering its earlier ecological status under Aboriginal and European cultures. Over 2.5 million stems per ha were recorded locally. Recruitment is now a common phenomenon.

Different types of grazing by native marsupials, domestic livestock and rabbits have interacted with different fire regimes, disease and extreme climatic events to totally change the appearance, ecology and economics of a large area (Rolls 1981; Chiswell 1982). To quote Adamson & Fox (1982), 'The European invasion was a watershed beyond which Australian ecosystems are permanently changed. A revolution has occurred and no steady state is in sight'. It is this turbulent environment with which Australian ecologists have to contend.

Detailed demographic studies of such major events are rare; evidence is anecdotal and interpretations are often limited by confounding factors. Conversely long-term experiments on grazing effects may be confounded by climatic effects; e.g. Austin *et al.* (1981) found that successional trend, seasonal fluctuations in winter rainfall and soil type differences totally obscured any effect of the designed experimental treatment of grazing intensity in a 20 year grazing trial.

Scleroleana birchii in southern Queensland

In undisturbed *Eucalyptus populnea* woodland this species is a sparse stunted (to 10 cm) spiny shrub. Following tree clearing and sheep grazing *S. birchii* exhibits periodic abrupt increases in abundance (Fig. 2) and it has been proclaimed a noxious weed under state legislation (Menz & Auld 1977). It can develop into wide-spread and dense monospecific communities of plague proportions, with individual hemispherical plants to 1 m diameter. By three months of age *S. birchii* plants produce viable seed within spined woody monocarpic fruits even on heavily grazed plants; ultimately the plants decay and the fruits break-down in the soil over a period of years to produce a fluctuating pool of germinable seed (Auld 1981). R. Roe established an experiment near St George, Queensland (28°10′ 148°54′) using permanent quadrats under various grazing treatments over the period 1937 – 47 to examine the population dynamics of the species. The results reported here are quoted from a collaborative but unpublished re-analysis of the original data by Austin, Roe, Williams and Werner. The full results will be published shortly.

The detailed records enabled cohort life tables to be prepared. These showed germination occurring in all seasons, but with major recruitment usually in the cool season. Figure 3 shows the survival of the cohorts from the years 1936 to 1947 in a permanent quadrat within the light grazing treatment. The cohorts from August – December 1936, March 1937 and August 1942 were longer lived than all other cohorts, due to precipitation which briefly arrested mortality. From early 1940, severe drought was punctuated by a few small rainfall events which were adequate to initiate cohorts, but insufficient to prolong their existence. From 1937 to 1945 the density of all species on the permanent quadrat was

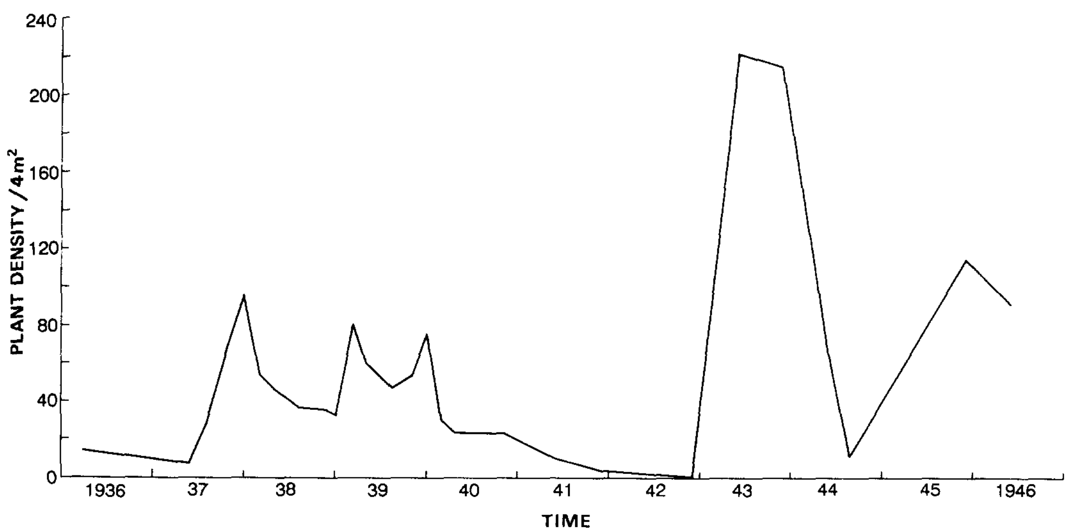

Fig. 2. Population dynamics of mature plants (>6 months age per 4 m^2) of *Sclerolaena birchii* 1936 – 1946 under light grazing by Merino sheep.

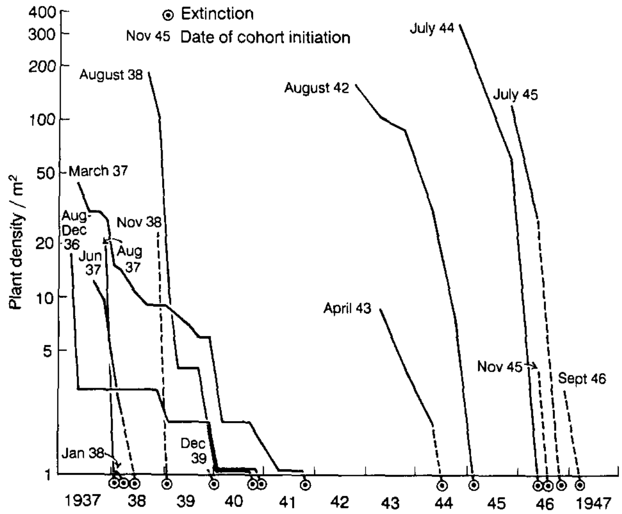

Fig. 3. Survivorship of cohorts of *Sclerolaena birchii* under light grazing by Merino sheep 1936–1947 (per 1 m²). Extinction o; Date of cohort initiation.

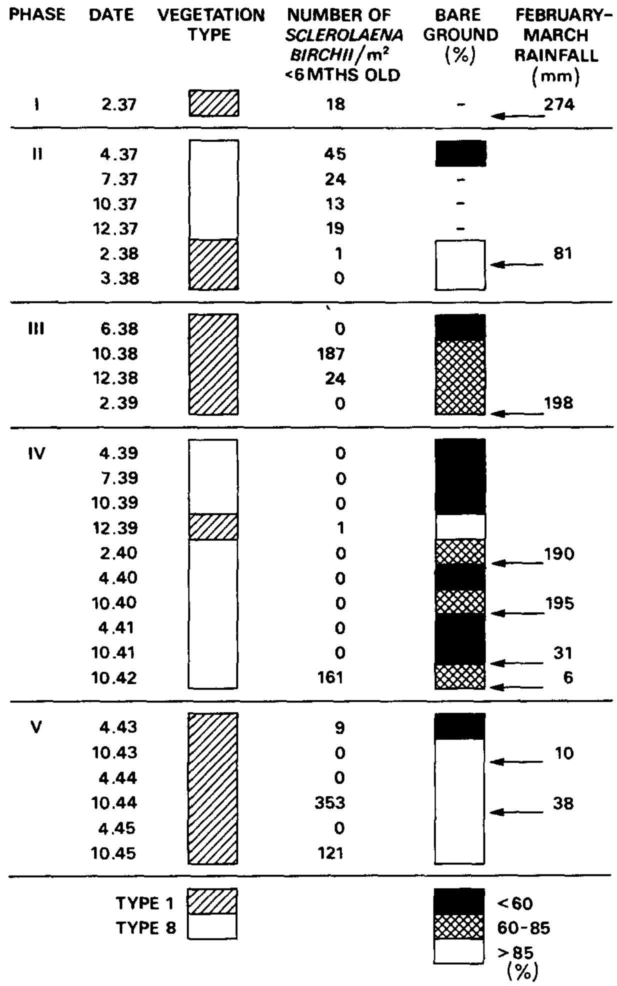

Fig. 4. Changes in vegetation type and numbers of *Sclerolaena birchii* juveniles (>6 months age) under light grazing by Merino sheep in relation to bare ground over the period February–March 1937–1945 (per 1 m²). Type 1 is erect, perennial, small shrub. Type 8 is prostrate, perennial and herbaceous.

recorded and this enabled us to complete a floristic analysis of changes in the total vegetation of the quadrats (cf. Austin *et al.* 1981); no pattern or sequence of relevant changes was detected. Grazed semi-arid pastures in Australia are a mixture of native grasses, herbs and small shrubs with many introduced species of annual weeds and grasses with similar habitat requirements. Because many of the species have similar phenological life histories and morphological growth patterns it was hypothesized that they might well substitute for each other in the open grazed community. The species were then classified into a number of groups with similar morphologies. The observations for each quadrat at each recording were then classified on the basis of the presence of these species groups.

Figure 4 shows the behaviour of the vegetation through time for the quadrat in the light grazed treatment. Abundant February–March rainfall triggers a change in vegetation type and a decrease in bare ground. There is relatively little change in *S. birchii* numbers. With insubstantial late summer rainfall the vegetation type switches – autumn germinating species are replaced by winter and spring germinators, bare ground increases, and there is a spring flush of *S. birchii* juveniles. Abundant late summer rain occurred in 1939 and 1941. Without a preceding spring flush these late summer rainfall events produce a massive growth of autumn annuals. Dense stands of small plants, e.g. *Tripogon loliiformis* (F. Muell.) C. E. Hubbard with mats of warm season species, e.g. *Portulaca oleracea,* L. suppress the *S. birchii* plants that germinate in the following cool season. Note that even though winter rains were generally satisfactory for recruitment in this period and a substantial population of adult plants of *S. birchii* persisted, no plague outbreak of *S. birchii* occurred. After 1941 a general drought occurred, characterized by a lack of late summer rains which increased the amount of bare ground. Sporadic rainfalls initiated 2 cohorts in 1943 (Fig. 3). The drought killed the perennial grass species of genera such as *Stipa* and *Aristida* that partially control *S. birchii* when there is abundant summer rainfall; although *S. birchii* recruitment occurred in the absence of this competition on ungrazed plots, the recruits were both fewer and smaller than with grazing.

Our age-specific analysis of the reproductive status of *S. birchii* during 1937–48 on the south-western Queensland site suggest that depletion of the labile seed pool in the soil is unlikely (cf. Auld 1981 for a more southerly site). There is a 'window' for *S. birchii* outbreaks through the agency of suitable winter and spring rains, but *only* if there are no prior heavy rains in late summer. Indeed, the average rainfall in February–March for four consecutive years in this early experimental period when establishment did not occur was at least three times the long-term average. Drought opens this 'window' for *S. birchii* on all types of grazing management in this type of degraded plant community. Although rabbits do not have a formative role as with *Callitris glaucophylla* in the Pilliga example, their activities do maintain heavy fruiting populations of *S. birchii* around warrens in ungrazed treatments at the time of maximum *S. birchii* control through the summer rainfall – perennial grass phase described earlier.

In this degraded plant community with its short-lived herbaceous vegetation, the changes are transient but have important impacts and implications for pasture management and research. Climate overwhelms the effects of management practices imposed on a suite of plant species none of which are capable of exerting a long-term dominant role either singly or in combination. *S. birchii*, like *Callitris glaucophylla*, is playing a role that it did not have under Aboriginal management. Recruitment in both species depends on occasional rainfall events.

Astrebla grasslands

Grasslands dominated by *Astrebla lappacea*, *A. pectinata* (Lindl.) F. Muell. ex Benth, and *A. elymoides* F. Muell. ex Benth. occur on heavy clay soils in Queensland and the Northern Territory. Debate over the decline of these grazing lands and concern at

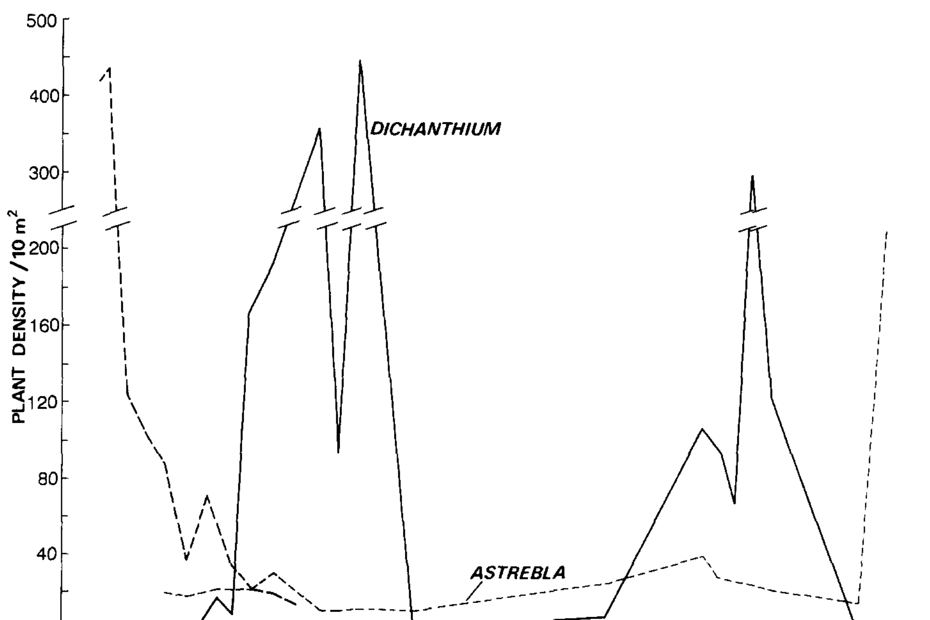

Fig. 5. Population dynamics of *Astrebla lappacea* and *Dichanthium sericeum* 1940–1984 (per 10 m²).

overstocking is a periodic phenomenon. In addition, early rather limited ecological studies (Blake 1939) had suggested that major community changes could take place on these heavy clay soils from an *Astrebla* dominated grassland to one dominated by *Dichantheum sericeum* (R. Br.) A. Camus (the so-called 'shifting climax'). However, observations by R. Roe and O. B. Williams on the long-term dynamics and demography of *Astrebla lappacea*, using permanent plots and careful recording within a simple experimental design provide clear evidence of what has occurred (Fig. 5). Grazing has been shown to have little impact on recruitment and survival of *A. lappacea* plants. Although seedlings establish in small numbers every few years when it rains, few plants persist. Records from 1941–1983 (Fig. 5) show only two major seedling establishment events. For *A. lappacea* to establish in any numbers requires either (a) at least 100 mm of rain on one occasion in spring followed by consistent summer rains or (b) a similar autumn rainfall with suitable rain in the following winter.

When populations of *Astrebla* spp. fall to a hundred plants or less per ha, exceptional rainfall sequences are required in order to produce a seed-bearing cohort which in turn can generate a substantial cohort in the following year (Roe 1941). The community in south-western Queensland appears to get this rainfall sequence once in every fifteen to twenty years, with anecdotal evidence suggesting previous events around 1916 and 1934. The long gap from 1941 to 1984 may be attributed to competition from *S. sericeum* cohorts in the wet 1950s, drought in the middle 1960s and infrequent cool-season rainfall in the 1970s (see also Roe & Davies 1985). Both *D. sericeum* and, to a lesser extent, the annual grass *Isielema membranacea*, will germinate and establish in dense populations under warm-season rainfall conditions to out-compete *A. lappacea* spp. seedlings. Further, the large suite of cool-season species that grow when the occasional winter rainfalls occur can also outcompete *A. lappacea*, hence the significance of the late spring and autumn rains in providing the limited 'window' for *Astrebla* recruitment.

Records of other associated species suggest (Fig. 5) that the observations in the literature about *D. sericeum* dominance were probably made during visits in years when there had been a pulse of establishment and growth by this species which behaves as a short-lived perennial in semi-arid Queensland.

Conclusion

Knowledge of Australian environment and the changes which have taken place since the invasion of Europeans and their animals and plants is still poorly documented and poorly understood (Williams 1985). Mechanisms determining community structure and their relative importance are much discussed and speculated upon at present. Without observations and understanding of what actually happens in a series of communities from different parts of the Australian environment such theoretical debate is unfruitful. Conclusions based on single locations and for short time periods would be risky in the light of the examples discussed here and the current knowledge of north-south demographic clines in eastern Australia for species such as *Enteropogon* (Williams 1970; Michalk & Herbert 1978) and *Astrebla* spp. (D. M. Orr pers. comm.).

Knowledge of climate, global weather systems and local weather can aid demographic analysis. Central to this knowledge is the operation of the El Niño/Southern Oscillation (ENSO) phenomenon (Nichols 1987), formerly studied as two separate entities, but now recognised as linked parts of the same atmosphere-ocean climate system. A strong occurrence of ENSO affects weather on the west coast of South and North America, Australia, New Zealand and Indonesia (World Climate Data Programme 1987). Each of the examples given can be placed in the context of ENSO climatic events.

We can now appreciate that the Pilliga scrub developed in the rainy aftermath of the severe ENSO event of 1876–78, and the myxoma virus epizootic recruitment of *Callitris glaucophylla* and *Eucalyptus crebra* occurred in the rainy aftermath of the 1951 ENSO. The converse appears to operate with *Sclerolaena birchii* with the warm-season rainy phase of ENSO discriminating against *S. birchii* recruitment in the following cool season. Significant *Astrebla lappacea* recruitment can be shown to be the result of either the rainy phase of an ENSO event, or substantial warm-season precipitation in an off-ENSO year. Further establishment events occurred when a 'window' was opened briefly following the ENSO events of 1957–58, 1965–66, 1972–73 and 1982–83.

We suggest that vegetation responses at both coarse and fine scale, whether under the full power of a strong ENSO event, a mild event, or a substantial rainfall event in a non-ENSO year, are capable of prediction to an extent not appreciated hitherto. Such prediction could have a substantial impact on how we model plant demography in semi-arid regions and conduct future pasture research and management.

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