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Responses of plant populations to fire: fire season as an under-studied element of fire regime

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ABSTRACT

It is well known now that the responses of plant populations to fire depend on the fire regime. Different fire intensities and fire frequencies can both alter plant population dynamics, but other aspects of the fire regime have received less attention. We have set up a replicated study to examine how season of burning might affect plant populations by altering recruitment in Hawkesbury Sandstone vegetation. Time to germination and germination rates of sown seeds of *Banksia* and *Hakea* were measured after fires in two different springs and two different autumns. Recruitment varied markedly between fires in the same season but different years. Unlike studies in Mediterranean-climate regions, the timing of germination after fire was not predictable. We conclude that the vagaries of post-fire climate introduce a stochastic element into the plant population response to fire that should be incorporated into population models and fire management strategies.

INTRODUCTION

Many characteristics of plant species in fire-prone ecosystems are considered to have evolved in response to an historic fire regime - with fires of an intensity, frequency and season that are typical of a given region (Gill 1975). Gill's work (e.g. Gill 1975, 1981, 1989) has emphasized the importance of focussing on fire regime in interpreting and predicting the ecological impacts of fire.

Considerable experimental and modelling work has been done on the effects of several components of fire regime on plant populations and communities. This work has focussed on the effects of varying fire intensities and fire frequencies on mortality of plants and recruitment to plant populations (e.g. Bradstock and Myerscough 1981; Bradstock and O'Connell 1988; Auld 1986), perhaps because these aspects of fire regime are the most conspicuous ways in which fire regimes prescribed for some land-management objectives differ from natural fire regimes.

Prescribed fires also differ in the season in which they are applied, the cool-season being favoured because deliberate fires can be more readily controlled. In this paper, we explore the possible ecological effects of season of burning by presenting some preliminary data from a pilot study designed to examine time to germination and magnitude of germination in two Proteaceae species in the Wollongong area.

Empirical studies of the effects of fire season, mostly conducted in Mediterranean-climate ecosystems with predictable timing of wildfires and strong climatic seasonality, suggest that seedling densities are lower after fires in winter/spring than after summer/autumn fires (e.g. McMahon 1984; Bond *et al.* 1984; Midgley 1989). One mechanism that has been proposed to explain this pattern is that the post dispersal seed losses are greater after a spring fire (see Bond 1984; Cowling and Lamont 1987). It is argued here (i) that germination occurs because of the favourable conditions in winter/spring, and (ii) that seeds are at risk while they lie on the soil surface after dispersal and prior to germination. Hence seed losses would be minimized after autumn fires, because seed release is immediately followed by germination. After spring fires, seeds must see out summer and autumn before germination.

As Bradstock and Bedward (1992) pointed out, much of the information on the effects of season of fire (with some exceptions – see Bond *et al.* 1984) comes from single studies of fires that are unreplicated within years or seasons. Moreover, there is no reason to expect that the processes determining the patterns of recruitment are similar in other ecosystems.

In this study, we conducted an experiment with replicated fires in each of two springs (1990 and 1993) and two autumns (1992 and 1993). We measured the time from seed release until germination and also the proportion of seeds germinating after each fire.

METHODS

In 1990, an 8100 m^2 site of Hawkesbury Sandstone vegetation was selected near Picton, New South Wales. This woodland with a heath understorey is typical of many sites in the Sydney region and contained extensive populations of two woody shrub species that were the focus of the study: *Hakea sericea* (Harden 1992) and *Banksia spinulosa* (George 1984). The site was divided into 36 plots, each between 0.1 and 0.2 ha. This patch area is typical of hazard-reduction burning carried out by the Balmoral Bush Fire Brigade in the general area of the study (I. Tait, personal observation). The season-of-fire treatments (initially to be one each of spring, autumn, summer) were allocated randomly to plots. After the first spring (1990) and autumn (1992) fires, it was decided that replication of these seasons of burning was important, so the third group of 12 plots was divided into two sets of 6, randomly allocated to either spring 1993 or autumn 1993 burning.

Fires in the replicate plots for each year/season were held within a few days of each other, and all were burned in the mid to late afternoon in a manner typical of a routine hazard reduction fire. Fire intensity varied both between and within plots, with canopy scorch in some areas and only patchy burning of leaf litter in others. Seeds released from fruits heated over a fire outside the site were sown on the ground in each plot. In each plot, 20 seeds of each species were dropped from a height of about 30 cm into a 50 x 100 cm grid, and their precise locations in the grid recorded. Sowings were completed 2-3 weeks after the fires, which is when natural seedfall was occurring. The grids were visited regularly to record the appearance and survival of seedlings.

A major rainfall event following the spring 1990 fire re-assorted seeds, litter and soil, such that continuing germination could potentially be confused with seed rain from surrounding plants. Seedlings from sowings in the other fires remained in their locations and were readily identified in consecutive censuses. The surrounds of each seedling grid were searched thoroughly for seedlings, confirming that 'background' germination levels were negligible.

RESULTS

Following the fires in spring 1990, the time to first germination was 10 months after sowing for both *Hakea* and *Banksia* (Fig. 1a). Thus seedlings first appeared in August 1991. Over 25 per cent of *Hakea* and 10 per cent of *Banksia* seeds germinated, but survival over the ensuing 1.5 years was low, with just over 5 per cent of the original seeds still remaining as seedlings.

Germination following the fires in autumn 1992 did not occur, as expected, in the following winter (Fig. 1b). Seedlings of both species first appeared 7 months after sowing: in January 1992. New seedings continued to appear for a further 7 months with very little mortality. In contrast to the spring 1990 fire, a very low proportion of seeds germinated: less than 5 per cent for *Hakea* and less than 2 per cent for *Banksia*.

After the autumn 1993 fires, germination had already started at 4 months: i.e. in September 1993 (Fig. 1c), though it is not yet possible to assess the magnitude of germination. The spring 1993 fires have just occurred.

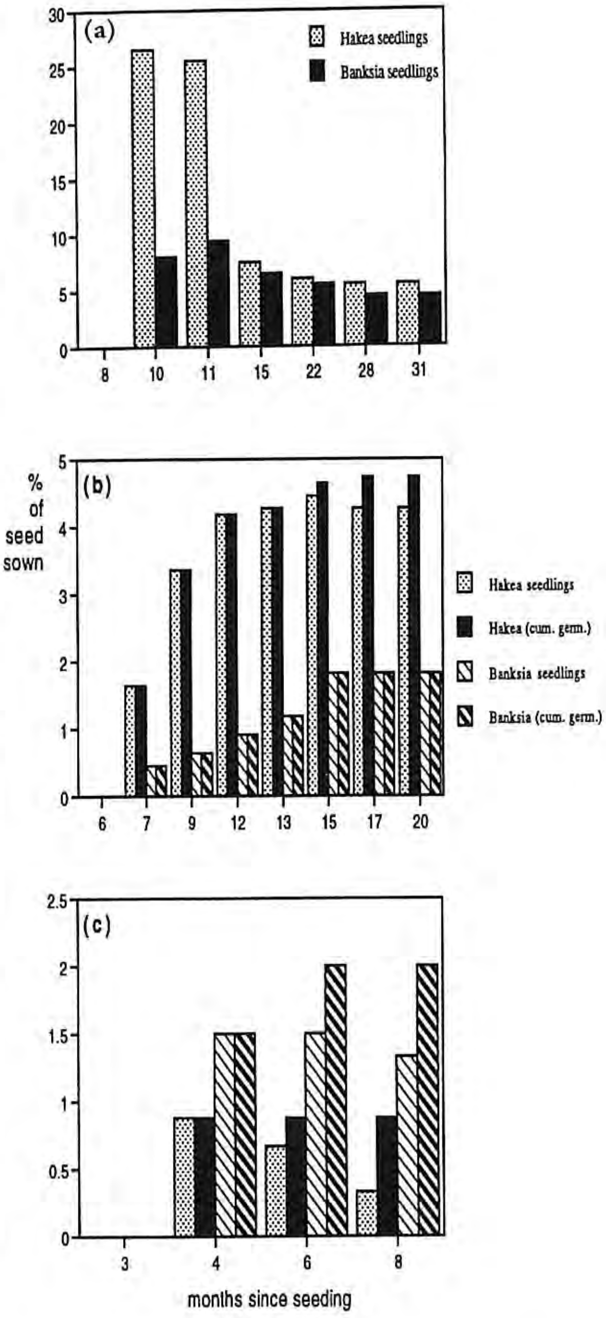

Figure 1. (a) Changes in numbers of Hakea sericea *and* Banksia spinulosa *seedlings with time after fires in spring 1990; (b) and (c) cumulative germination and numbers of seedlings alive with time after fires in autumn 1992 (b) and autumn 1993 (c).*

DISCUSSION

The timing of first germination after the 1990 spring fires was indeed delayed until the following winter. This is the pattern that would be expected from Bond (1984) and Cowling and Lamont (1987). The long-term results of the 1993 spring fire remain to be seen, but there had clearly not been substantial germination by summer 1993-94. The time to germination differed between the two autumn fires. There was a delay of over 7 months before germination occurred after the autumn 1992 fires. Thus seedlings started to appear in summer. In contrast, germination had started just 4 months following the 1993 autumn fires. Even with these three sets of fires, it is apparent that the timing of germination is not strongly seasonal. It is likely that the less predictable season bringing substantial rainfall in the Sydney region, in contrast to Mediterranean-climate regions, is the major factor controlling the season of germination. The coincidence of germination with the first period of substantial rainfall after the first two sets of fires (spring 1990, autumn 1992) lends support to this hypothesis (Fig. 2).

Although the time to germination was greatest after the spring 1990 fires, the proportion of seeds germinating was not substantially greater than after the other fires (Fig. 1a; nearly 30 per cent of seeds for *Hakea* and 10 per cent for *Banksia*). Poor germination was expected to result from the long period during which seeds were at risk from predation, fungal attack and other hazards. Poor germination did occur following the 1993 autumn fire (less than 5 per cent for *Hakea* and less than 2 per cent for *Banksia*), where there was also a substantial delay between the fire and germination. It is not yet possible to assess the timing or magnitude of germination following the autumn 1993 fires.

The main conclusion of these preliminary studies is that germination is not strongly tied to the winter/spring season. Nor does there appear to be a strong inverse relationship between the proportion of seeds germinating and the length of time between a fire and germination. In this environment, therefore, the pattern of post-fire rainfall, irrespective of season, appears the most likely determinant of the timing of germination. The factors determining the magnitude of germination are still unclear. One possibility is suggested by the observation of reassortment of seeds and litter into soil depressions, following the major rains after the 1990 fires. This process may have deposited seeds in microsites that were especially suitable for germination (see Whelan 1986; Enright and Lamont 1989; Lamont *et al.* 1991; Battaglia and Reid 1993).

The building of realistic models of population dynamics under various fire regimes will clearly require careful inclusion of the impact of factors such as post-fire rainfall (Bradstock and Bedward 1992), and other factors that might affect timing and amount of germination, such as spatial heterogeneity of safe sites, and post-dispersal seed removal.

CHALLENGES FOR MANAGERS

Understanding the effects of different fire seasons on plant demography and then incorporating this information in management offer enormous challenges for land managers, especially in situations where conservation of plant species and communities is a significant management objective (see Whelan and Muston 1991).

If the timing of prescription burning does influence recruitment to populations of some plant species, then wide-spread hazard reduction burning, especially in winter/spring, may be expected to have detrimental effects. However, the preliminary results of our study indicate that reduced recruitment after spring fires may not be a general effect. The differences between this study and previous work in Mediterranean-climate systems reinforce the view (Williams *et al.* 1994) that management *prescriptions* are not likely to be 'portable', depending on the characteristics of a particular site. It is therefore crucial that research and monitoring is built into prescription burning programs in each area (Christensen and Maisey 1987; Gill 1989; Whelan and Muston 1991).

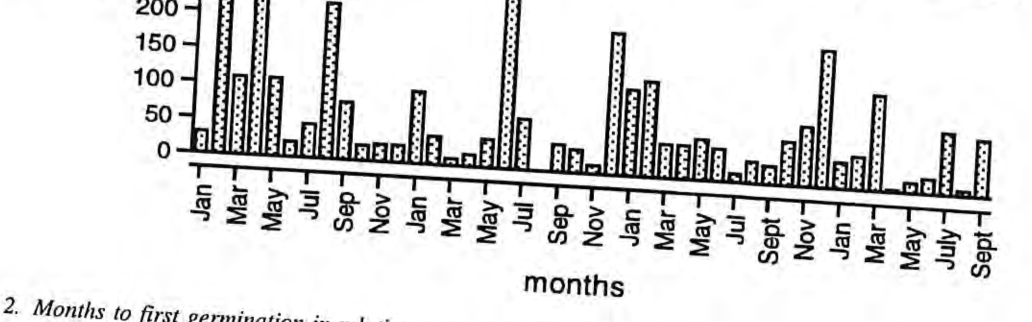

Figure 2. Months to first germination in relation to rainfall. The solid lines above the rainfall bars represent the time between seed sowing and first germination after the three fires.

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