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Variation in age to first flowering and fruiting of *Banksia baxteri* and *Banksia coccinea* at the Stirling Range, south-western Australia

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Abstract

Age of first flowering (juvenile period) and fruiting were compared between cohorts of *Banksia baxteri* and *Banksia coccinea* established following fires in autumn 1989 and spring 1990 at a uniform site in the Stirling Range, south-western Australia. Following the 1989 fire both species commenced flowering by the time that plants were 59 months old, and more than 90% of individuals had flowered by the age of 97 months. By the age of 130 months 95% of plants of both species bore fertile cones. Both species took longer to reach reproductive maturity following the spring 1990 fire and only 35% of the *B. coccinea* cohort survived at the end of the 157 month study period. Very much below average rainfall in 1994 may have delayed flowering and cone production amongst the spring 1990 cohort which were still in the juvenile stage at the onset of the dry conditions. Intra-species variation in juvenile period has been documented for a range of plants in south-western Australia and warrants consideration in models of plant population dynamics.

Keywords: *Banksia*, mallee-heath, juvenile period, fire, south-western Australia

Introduction

Life history attributes provide important information about the ability of plants to persist under different fire regimes (Whelan *et al*. 2002; Burrows *et al*. 2008). Juvenile period, which is the period between plant establishment and first flowering, is commonly used as an indicator of the minimum inter-fire period required for persistence of fire sensitive plants that rely for regeneration on seeds held in serotinous fruits. Mature plants killed by fire release stored seeds, providing opportunity for recruitment of a cohort of seedlings. Seedling recruitment may be affected by a variety of factors in the post-fire environment including seedbed receptivity, seed predation, and climatic conditions. Replenishment of seed stores following fire may take considerably longer than the juvenile period. Minimum inter-fire periods of at least twice the juvenile period have been suggested for fire-sensitive shrub species in south-western Australian forests and heathlands (Gill & Nicholls 1989; Cowling *et al*. 1990; Witkowski *et al*. 1991; Burrows & Wardell-Johnson 2003; Burrows *et al*. 2008).

This paper reports observations of age of first flowering and fruiting for cohorts of *Banksia baxteri* (R. Br.) and *Banksia coccinea* (R. Br.) established following two fire events at adjacent sites in the Stirling Range, south-western Australia.

Study area

The study area was located near Two Mile Lake (34° 28.7'S, 118° 15.7'E) at an elevation of 180 m above sea level in the Stirling Range National Park, about 90 km north of Albany. This region of Western Australia experiences a moderate Mediterranean-type climate with cool moist winters and warm dry summers (Beard 1984). General features of the climate in the Stirling Range and surrounding areas are described by Courtney (1992). The nearest climate observation station is at Mettler (Bureau of Meteorology) which is located 25 km south-east of the study area and closer to the Southern Ocean. At Mettler the mean maximum temperature in the hottest month (January) is 25.1°C and mean minimum temperature in the coldest month (August) is 6.1°C. Annual rainfall at Mettler in the period 1966–2007 averaged 606 mm with a median of 611 mm. Until 1991 rainfall observations were also taken at Kojaneerup which is equi-distant between the study site and Mettler. Annual average rainfall at Kojaneerup (1961–1991) was 130 mm less than at Mettler. Descriptive rainfall categories and decile ranges referred to in this paper are as defined by the Bureau of Meteorology: very much below average (decile 1), below average (deciles 2–3), average (deciles 4–7), above average (deciles 8–9), very much above average (decile 10).

Soils at the study area are predominantly brown sandy-gravels with lateritic pisoliths (small ironstone nodules) interspersed in a mosaic of white sand sheets overlying laterite (Churchward *et al.* 1988). The dominant vegetation is *Eucalyptus tetragona* mallee-heath (Keighery and Beard 1993) with a diverse layer of low shrubs including Proteaceae (*Banksia, Hakea, Isopogon, Petrophile*), Myrtaceae (*Beaufortia, Calothamnus, Calytrix*) and Fabaceae (*Chorizema, Daviesia, Jacksonia*). Thickets of *B. baxteri* and *B. coccinea* occur on white sand substrates.

Methods

Flowering, fruiting and height growth were observed for cohorts of *B. baxteri* and *B. coccinea* regenerating following experimental fires conducted in March 1989 and November 1990 which consumed all leaf litter on the ground and the foliage on live shrubs. Prior to the experimental fires, the site had been unburnt since 1969. Areas burnt in 1989 and 1990 were separated by a track but were otherwise uniform in aspect, slope, surface soil characteristics and vegetation. In August 1994 20 plants of each species were selected at random within the areas burnt in 1989 and 1990. Individual plants were identified with a numbered tag, the number of flowers and fertile cones on each plant was recorded and the height of the growing tip was measured. Plants were re-measured in September 1995 and 1996, October 1997, May 1999, June 2000 and September 2004. The number of plants of each species that had flowered or produced fertile cones at each measurement date was expressed as a proportion of the number of individuals tagged at the commencement of the study without adjustment for mortality.

Results

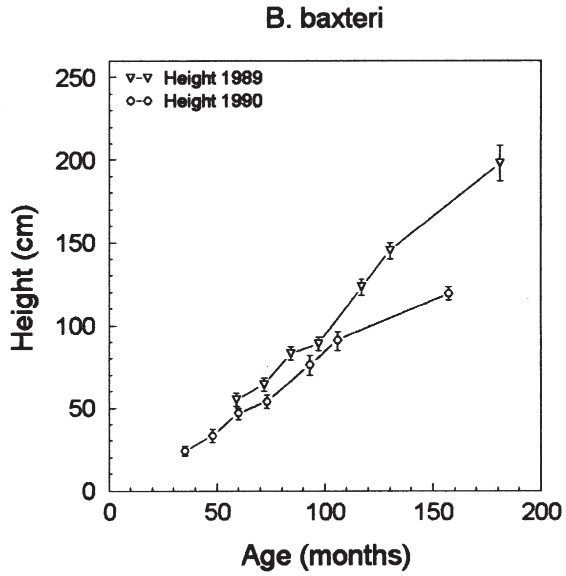
Observations of post-fire regeneration made at the site indicate that seedlings of *B. baxteri* and *B. coccinea* emerge in late winter and early spring (August–September), regardless of whether the area was burnt in autumn or the previous spring. Nominal plant ages were assigned that assumed a delay between burning and seedling emergence of 6 months for the autumn cohort and 10 months for the spring cohort. Thus, at the commencement of the study the ages of seedling cohorts regenerated following the autumn 1989 and spring 1990 fires were respectively 59 and 35 months.

Autumn 1989 cohort

Most (90%) of the autumn 1989 cohort of *B. baxteri* tagged at the beginning of the study remained alive in September 2004 and attained an age of at least 181 months. Survival of B. *coccinea* was somewhat poorer and declined from 90% at 117 months to 75% at 181 months. The rate of height growth of *B. baxteri* was relatively consistent throughout the period of the study and surviving plants had an average height of 200 cm at an age of 181 months, while *B. coccinea* grew slightly faster and attained an average height of 245 cm at 181 months (Fig. 1). Both species had already begun to flower when the study commenced and 60% of *B. baxteri* and 65% of *B. coccinea* had at least one inflorescence by the age of 59 months (Fig. 2). By the age of 97 months 90% or more of plants of both species had flowered. Fertile cones with fully developed follicles were observed on 50% of *B. baxteri* plants by the age of 84 months, and 95% of plants bore fertile cones by the age of 97 months. Fertile cones were first observed on *B. coccinea* at the age of 84 months, but the proportion of plants bearing cones did not reach 95% until the age of 130 months.

Spring 1990 cohort

The spring 1990 cohort of *B. baxteri* exhibited good survival for the duration of the study with 90% of tagged individuals attaining an age of 157 months. Plants from the spring 1990 cohort exhibited a similar rate of height growth to the autumn 1989 cohort up until the age of 106 months but the rate of growth declined thereafter such that the average height was 119 cm by the end of the study (Fig. 1). Survival of the spring 1990 cohort of *B. coccinea* remained at 85% or greater up to the age of 86 months but had declined to 35% by the end of the study (157 months). Height growth of the spring 1990 cohort was slower than that of autumn 1989 cohort particularly up to the age of 73 months, and there was substantial variability in height of surviving plants at the end of the study as reflected by the large standard error (Fig. 1).



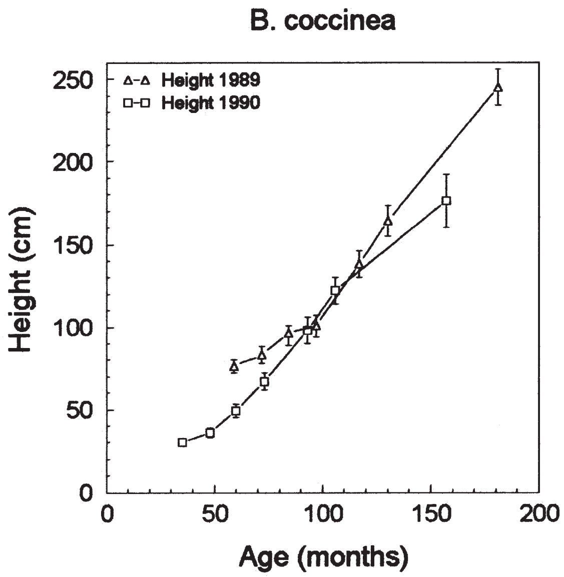


Figure 1. Height growth of *B. baxteri* (top) and *B. coccinea* (bottom) seedling cohorts regenerated following fires in autumn 1989 and spring 1990. Bars represent standard errors.

No plants of either species in the spring cohort had flowered by the age of 35 months when the study

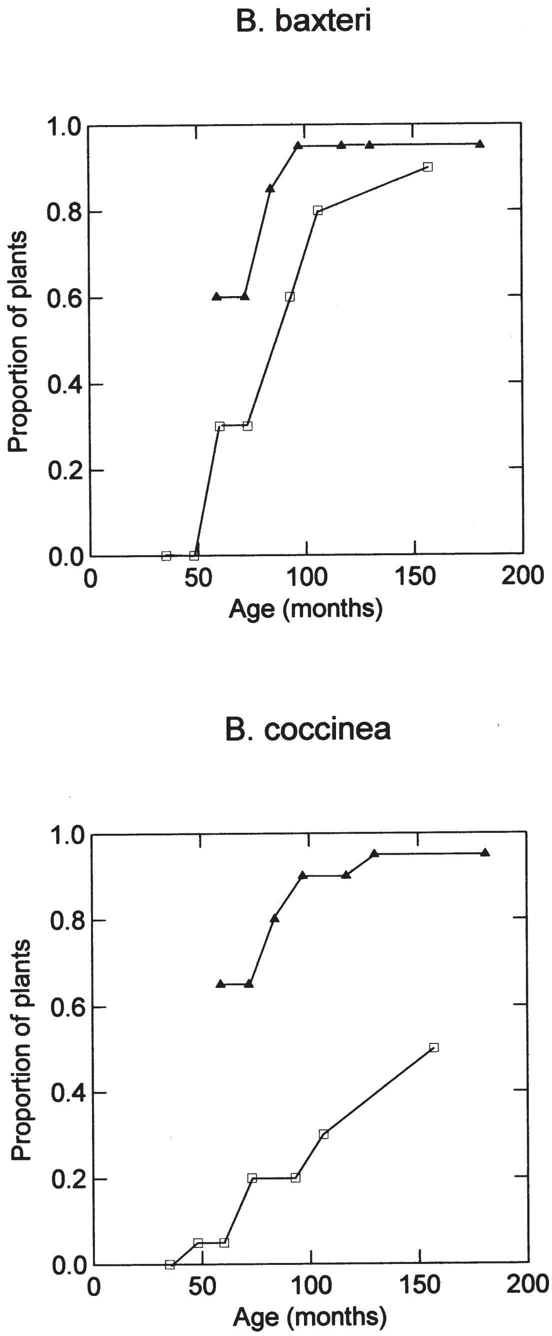


Figure 2. Proportion of plants of *B. baxteri* and *B. coccinea* flowering with increasing time since fire. Symbols represent cohorts regenerated following fires in autumn 1989 (triangles) and spring 1990 (squares).

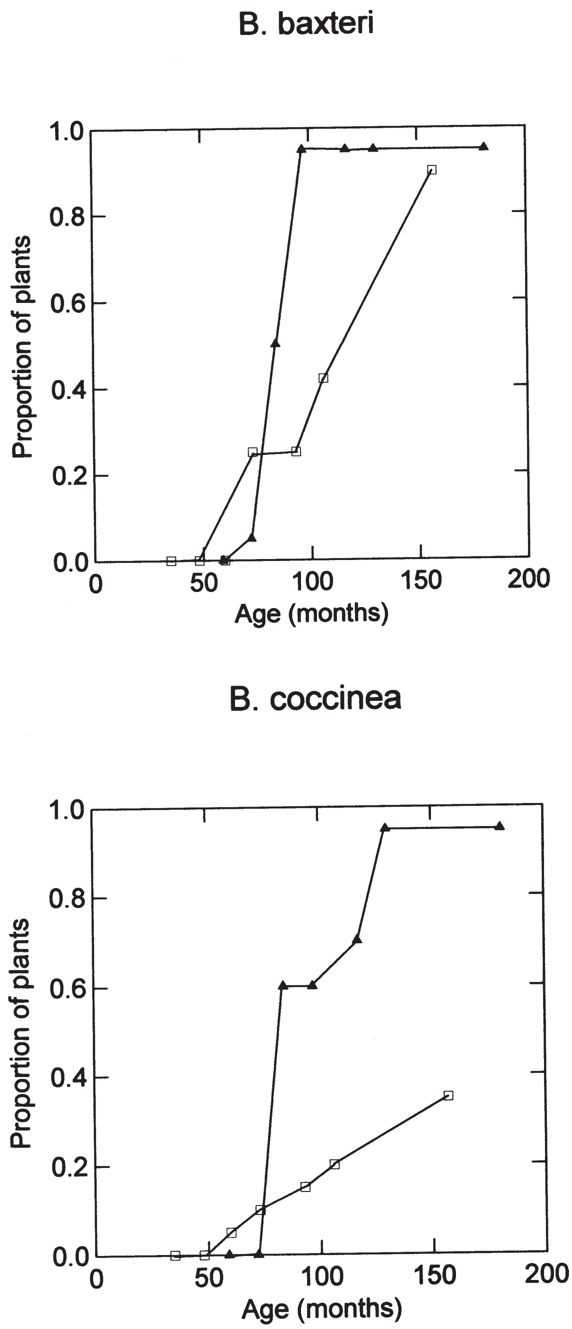


Figure 3. Proportion of plants of *B. baxteri* and *B. coccinea* bearing fertile cones with increasing time since fire. Symbols represent cohorts regenerated following fires in autumn 1989 (triangles) and spring 1990 (squares).

commenced. First flowers appeared on *B. baxteri* by the age of 54 months but it took 93 months for at least 50% of plants to flower and 157 months for >90% of plants to flower (Fig. 2). A small proportion of *B. baxteri* from the spring 1990 cohort developed fertile cones at first flowering but overall the spring cohort developed fertile cones at a slower rate than the autumn 1989 cohort (Fig. 3). Flowers first appeared on a small number of *B. coccinea* by the age of 48 months but only 50% of plants managed to flower during the 157 month period of the study (Fig. 2), some of which later died. Only (40%) of *B. coccinea* from the spring 1990 cohort developed fertile cones during the study and this took place more slowly than for the autumn 1989 cohort.

Rainfall during the period of the study

Rainfall at Mettler was average to above average from 1989 to 1993 during the period when seedlings emerged and commenced the juvenile growth phase (Fig. 4). Rainfall in 1994 was the lowest on record with only 379 mm recorded for the year and four consecutive months of very much below average rainfall between January

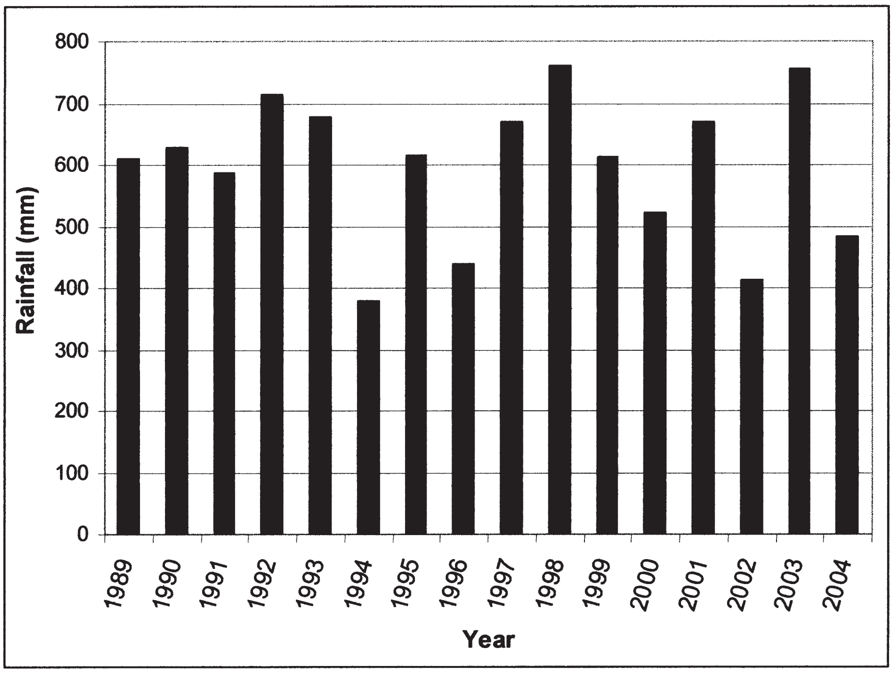


Figure 4. Annual rainfall at Mettler during the period 1989–2004.

and April. Further years of very much below average rainfall occurred in 1996, 2002 and 2004. Rainfall was very much above average in 1998 and 2003.

Discussion

Juvenile period length and timing of fertile cone production on *B. baxteri* and *B. coccinea* varied substantially between the two cohorts established following different fire events at the Stirling Range, even though both cohorts grew on an apparently uniform site. Wooller *et al*. (2002) reported that *B. baxteri* in the Fitzgerald River National Park flowered for the first time 60–72 months after fire which is similar to observations for the autumn 1989 cohort at the Stirling Range. They also observed that the proportion of plants flowering in any one year rose rapidly, peaking at close to 100 per cent after 180 months and gradually declining thereafter. Witkowski *et al*. (1991) reported that coastal populations of *B. baxteri* and *B. coccinea* at Hopetoun flowered for the first time 36 months after fire and produced fertile cones after 60 and 36 months respectively. The shorter juvenile periods at Hopetoun may reflect more favourable growing conditions due to coastal proximity compared with the sites examined by Wooller *et al*. (2002) and at the Stirling Range in this study. Post-fire juvenile periods of 639 plant species from the jarrah (*Eucalyptus marginata*) forest were examined by Burrows *et al*. (2008) who found that all species in their study flowered within 60 months of fire, and most flowered within 36 months. Burrows *et al*. (2008) noted that a number of widely distributed species had longer juvenile periods in drier eastern forest where annual rainfall is 750 mm or less.

Differences in environmental conditions during the post-fire juvenile period are a possible reason why the spring 1990 cohort took longer to flower and produce fertile cones. Seedlings established following the autumn 1989 fire experienced average to above average rainfall during four of the five years up to August 1994 when plants were first examined. In contrast, seedlings established following the spring 1990 fire experienced only two years of average or above average rainfall (1991–1993) before encountering very much below average rainfall in 1994. Dry conditions in 1994 and again in 1996 may have delayed flowering and cone production amongst this cohort.

Summer lightning storms are common in the Stirling Range and experience has shown that it is unlikely that fire can be excluded for more than a decade or two from the extensive tracts of mallee-heath that adjoin the range (McCaw & Gillen 1993). The rate of fuel accumulation in mallee-heath is such that fire can re-burn the same area after about 8 years (Keith *et al*. 2002). Data from this study indicate that provided growing conditions are favourable, *B. baxteri* and *B. coccinea* can produce fertile cones within 8 years (96 months) of establishment although maximum seed production is unlikely to occur until plants are about twice this age (Wooller *et al*. 2002). However, achievement of reproductive maturity may be delayed by adverse conditions in the post-fire environment. Land managers may choose to delay introducing planned fire to areas where seed stores are known to be limited, but must recognise that unplanned fires also pose a risk to plant communities in a post-fire recovery phase. For *B. baxteri* and *B. coccinea*, and similar taxa with on-plant seed storage, the risk of regeneration failure following fires at less than 10 years intervals will be reduced when some mature plants survive fire to provide a continuing supply of seed. Risk of localised extinction is greatest when all mature plants are killed by fire and the population is reduced to an even-aged cohort of juvenile plants that may be vulnerable to grazing or extremes of temperature (O'Brien 1989; Groom *et al*. 2004).

Models of plant population dynamics based on juvenile period and other life history attributes can provide important insights into the mechanisms by which populations persist in fire-prone environments (Enright *et al*. 1998). Some models have sought to incorporate the effects of seasonal weather conditions on seedling recruitment (Enright *et al*. 1998). Intra-species variation in juvenile period has been documented for a range of plants in south-western Australia and warrants consideration in models of plant population dynamics.

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