

Fire season effects on the recruitment of non-sprouting serotinous Proteaceae in the eastern (bimodal rainfall) fynbos biome, South Africa

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Abstract Research in Mediterranean-climate shrublands in both South Africa and Australia shows that recruitment of proteoid shrubs (non-sprouting, serotinous Proteaceae) is best after warm-season (summer and autumn) fires and worst after cool-season (winter and spring) ones. This pattern has been attributed to post-dispersal seed attrition as well as size of pre-dispersal seed reserves. Here we investigate patterns of post-fire recruitment for four proteoid species in the eastern part of South Africa's fynbos biome, which has a bimodal (spring and autumn) rainfall regime. Despite the lack of significant differences in recruitment between cool- and warm-season burns, we find some evidence for favourable recruitment periods following fires in spring and autumn, immediately before, and coinciding with, the bimodal rainfall peaks. This suggests that enhanced recruitment is associated with conditions of high soil moisture immediately after the fire, and that rapid germination may minimize post-dispersal seed attrition. In two of the species, we also find a shift from peak flowering in winter and spring in the Mediterranean-climate part of the fynbos biome, to summer and autumn flowering in the eastern part. Because these two species are only weakly serotinous, warm-season flowering would result in maximal seed banks in spring, which could explain the spring recruitment peak, but not the autumn one. We conclude that eastern recruitment patterns differ significantly from those observed in the western and central parts of the biome, and that fire management protocols for the east, which are currently based on data and experience from the winter-rainfall fynbos biome, need to be adjusted accordingly. Fire managers in the eastern fynbos biome should be less constrained by requirements to burn within a narrow seasonal range, and should therefore be in a better position to apply the required management burns.

Key words: fire season, fynbos, Proteaceae, seedling recruitment, serotiny.

INTRODUCTION

Fire season is known to have an important effect on the recruitment of non-sprouting woody plants in Mediterranean-climate ecosystems. Although warm-season fires result in enhanced recruitment, population growth after cool-season burns is invariably much lower, with less than replacement levels recorded after some events (e.g. Bond *et al.* 1984; Cowling & Lamont 1987; Bradstock & O'Connell 1988; Parker & Kelly 1989; Lamont *et al.* 1991). For example, Bond *et al.* (1984) showed that in the central, weakly winter-

rainfall fynbos biome of South Africa, recruitment of non-sprouting, serotinous Proteaceae (hereafter referred to as proteoids) was highest after autumn burns, lower after summer burns, and poor to zero after winter and spring burns. Similar patterns were reported for the western, strongly winter-rainfall fynbos biome (van Wilgen & Viviers 1985).

Fire seasonal effects on the recruitment of proteoids in fynbos and analogous Australian scrub heath have been attributed to post-dispersal attrition (Bond 1984; Cowling & Lamont 1987). Seeds released from serotinous cones after cool-season burns are exposed to seed loss (from predation or heat exposure) for longer periods than after warm-season ones. After autumn burns, the period of exposure is shortest, because germination occurs in the early winter months, after the passage of the first rain-bearing cold fronts; hence, highest recruitment is recorded after fires in this

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season (Bond 1984; Cowling & Lamont 1987; Midgley 1989; Lamont *et al.* 1991; Bradstock & Bedward 1992).

An alternative hypothesis relates to pre-burn seed reserves (Jordaan 1949; Bond & van Wilgen 1996). This hypothesis predicts that recruitment will be maximized after burns that coincide with peak seed reserves. Important issues here are the degree of retention of seeds in serotinous cones (Bond 1985; Mustart & Cowling 1992), the rate of decay or predation of seeds in cones (Cowling *et al.* 1987; Le Maitre 1990, 1992; Mustart *et al.* 1995) and the phenology of seed ripening (Jordaan 1949, 1965; Midgley & Vlok 1986). Jordaan (1949, 1965) argued that poor recruitment of some fynbos proteoids after cool-season burns was a consequence of low pre-burn seed reserves, owing to winter flowering phenology of these species. Implicitly, he discounted the contribution to recruitment of seeds stored in serotinous cones. Many fynbos proteoids, especially in the genus *Protea*, are weakly serotinous, with seed reserves declining rapidly in cones older than 1–2 years (van Staden 1978; Bond 1985; Le Maitre 1990, 1992; Lamont *et al.* 1991; Mustart & Cowling 1992). Nevertheless, viable seed reserves can be found in older cones, depending on plant age, predation levels, location and species (Bond 1985).

No research has been conducted on the post-fire recruitment of proteoids in the eastern reaches of the fynbos biome. This part of the biome, occurring roughly east of 22°30'E (Fig. 1), differs from the central and western parts (roughly west of 20°E) in a number of ways. First, this region does not experience a Mediterranean-type climate. The most predictable rainy seasons are autumn and spring, and both the summer and the winter seasons might experience long, dry spells (Deacon *et al.* 1992). The implications of a bimodal rainfall pattern on germination cues and recruitment of fynbos proteoids have not been investigated. Conceivably, this pattern could produce two favourable periods for recruitment, namely one associated with the autumn rainfall peak, and the other with the spring peak. In eastern Australian scrub heath, which experiences a non-seasonal rainfall

regime, Whelan and York (1998) showed that good germination and recruitment of two proteoid shrubs did occur after spring burns. Bradstock and Bedward (1992) suggest that variation in annual rainfall is more important than the season of burn in determining levels of post-fire recruitment in proteoid species in eastern Australia.

Second, the seasonality of fire regimes differs markedly between the eastern fynbos biome and those areas to the west. Using the United States Fire Danger Rating System's burning index, van Wilgen and Burgan (1984) showed that in the strongly winter-rainfall western biome, weather conducive to large fires was strongly seasonal. Days with extreme fire danger (defined as those days in which the top 5% of burning indices occur) were common in summer and did not occur in winter; the mean burning indices in summer were more than five times those in winter. In the east, the occurrence of conditions conducive to fires was not seasonal. Extreme fire danger days were as likely to occur in winter as they were in summer, and the mean burning indices in summer were equal to or at most double those in winter. These differences in fire climate, and their potential relevance to fire management, were recognized by van Wilgen (1984), who hypothesized that fire season would have less effect on post-fire recruitment patterns in the east than the west.

Third, there is a shift from winter/spring to summer/autumn flowering, both across and within lineages (Johnson 1993). Midgley and Vlok (1986) showed that among proteoid shrubs in *Leucadendron*, there was a trend for eastern species to flower later in the year (spring–summer) than western ones (winter–spring); accordingly, they recommended autumn fires in the east because this period coincides with maximum size of viable seed banks. Furthermore, Cowling (1987) noted a shift from winter to summer flowering of *Protea repens* in eastern fynbos, relative to western parts of the biome.

Fourth, large tracts of mid-slope and foothill landscape in the eastern fynbos biome lack an overstorey of proteoids; instead, these areas support grassy fynbos, a vegetation type dominated by sprouting shrubs

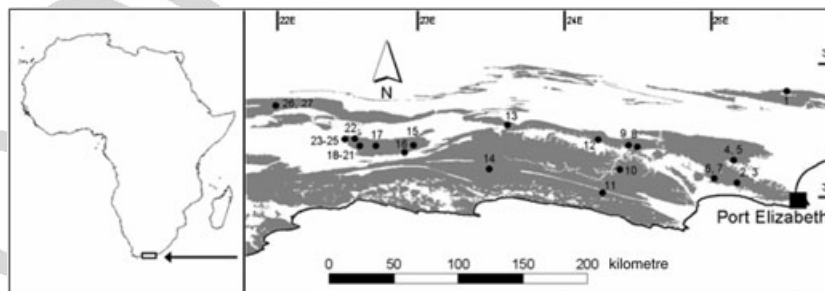


Fig. 1. Location of study sites in the eastern fynbos biome, South Africa. Inset shows the location of the region in Africa. Shading depicts the extent of fynbos vegetation in the region (Mucina *et al.* 2005).

(including a depauperate Proteaceae flora) and having a high cover of grasses, especially C4 species that are rare further west (Campbell 1985). In the central and western biome, non-sprouting, serotinous Proteaceae are a dominant feature in these landscapes, and the associated vegetation type is termed proteoid fynbos (Campbell 1985).

In this paper we assess fire season effects in the eastern fynbos biome on the recruitment of the proteoid shrubs growing in proteoid fynbos in our study domain (Cowling 1984; Campbell 1985): *Protea neriifolia* R. Br., *P. repens* (L.) L., *Protea lorifolia* (Salisb. ex Knight) Fourc. and *Leucadendron eucalyptifolium* H.Buek ex Meisn. The post-burn seed attrition hypothesis predicts that recruitment would be highest after warm-season burns, as is the case in the central and western fynbos biome (Bond *et al.* 1984; van Wilgen & Viviers 1985). Alternatively, as mentioned above, bimodal rainfall pattern would produce a bimodal recruitment pattern. This pattern would also be consistent with the post-burn seed attrition hypothesis, provided that seeds of eastern populations are able to germinate under a wider range of temperatures than western populations.

The pre-burn seed reserve hypothesis predicts that recruitment would be highest after fires that coincide with the peak in canopy-stored seed bank size (Jordaan 1949, 1965; Midgley & Vlok 1986). Consequently, we collated data on the flowering phenology of the study species across their distributions in the fynbos biome. All four of the species we encountered span the longitudinal range of the fynbos biome (Rebelo 2001). In the weakly serotinous *Protea* species (van Staden 1978; Bond 1985), seed bank size will peak about 6–9 months after flowering, when seeds have ripened (Jordaan 1982; Midgley & Vlok 1986; Mustart & Cowling 1992). The phenology data enabled us to test the pre-burn seed reserve hypothesis: a shift to summer flowering in the eastern fynbos biome would result in higher recruitment after cool- than warm-season fires.

MATERIALS AND METHODS

Study sites

We identified 27 suitable sites in the eastern fynbos biome, in areas receiving an annual rainfall of between 500 and 800 mm (Schulze 1997), most of them located in protected areas (Fig. 1). All sites are underlain by Table Mountain Group sandstone, except for sites 6 and 7, which are located on Cretaceous sandstone, a rock type that yield soils chemically and physically similar to Table Mountain Group sandstone (Cowling 1984). Our westernmost sites (Groot

Swartberg and Kammanassie Mountains) overlapped the area sampled by Bond *et al.* (1984). Site location was constrained by the relatively low extent of proteoid fynbos that had been burnt in recent years. None of the sites had been subjected to grazing by domestic livestock or any other anthropogenic disturbance.

CapeNature, the conservation organization responsible for the management of provincial protected areas in the Western Cape Province, provided data – collected between 1983 and 1988 – for sites 17–19 and 22–25, all on the Kammanassie Mountains at the western margin of our study domain. Two of the authors (S.H. and Ş.P.) sampled the remaining sites between August and December 2003. Sites 2 and 3, and 4 and 5, comprised different areas of the same large fire that included different species. In the case of sites 6 and 7, we sampled two fires about 1 km distant that were initiated on separate days: we treated these sites as replicates. At sites 8, 19 and 23 two species co-occurred and were treated as replicates. Therefore, the total number of independent sites was 30.

Fires were classified seasonally as follows: cool season (winter and spring) June–November; warm season (summer and autumn) December–May. Protected area managers and landowners provided fire dates. Species occurrences were as follows: *P. neriifolia* (six cool-season fires; four warm-season fires), *P. repens* (four and eight, respectively), *P. lorifolia* (four and two, respectively), and *L. eucalyptifolium* (one and one, respectively). Although *L. eucalyptifolium* is moderately serotinous (i.e. viable seeds are retained in cones for up to 4 years), the three *Protea* spp. are weakly so (Bond 1985; Xxxxxx 0000, pers. obs.).

The age of parent plants at the time of each fire was determined by counting nodes on the stem of at least 30 individuals at each site (Bond *et al.* 1984). This was 8 years or greater at all sites (cool season: 10.7–3.0, warm season: 13.5–2.9), a period sufficient for at least 4 years of flowering and seed production before the fire. At all sites, the time since fire (hereafter TSF) was <5 years. Mean TSF (in months) for cool-season fires was 30.7 ± 17.7 , and for warm-season fires 22.9 ± 12.2 .

Post-fire recruitment data

At each site over 50 plots were sampled (minimum: 51, maximum: 315). The plots were 1 m × 1 m and located at 3- to 5-m intervals along transects (the interval depending on the size of the fire), according to the method used by Bond *et al.* (1984). In each plot the number of parent plants (as burnt skeletons) was counted, as well as the number of seedlings for each of the proteoid species present. For each site, we computed the number of seedling per parent for each species (Bond *et al.* 1984; van Wilgen & Viviers 1985).

The data provide an estimate of post-fire population growth for each species at each site.

Following Bond *et al.* (1984), we depicted the seedling per parent data on a log scale, but for two fire seasons only: cool-season and warm-season burns. Bond *et al.* (1984) depicted data separately for summer and autumn. However, we had insufficient replicates to do this. Bond's (1984) post-fire attrition hypothesis would nonetheless predict significant differences between warm- and cool-season burns, as defined above. We tested for differences in the numbers of seedlings per parent (log-transformed) between each season using a one-way ANOVA. Owing to the large variation in TSF, and the fact that seedling mortality is positively related to this variable (Midgley 1989; Lamont *et al.* 1991), we included TSF as a covariable in this analysis.

In order to depict recruitment data in relation to the bimodal march of precipitation in the study domain, we presented the data for each species at a monthly scale, and calculated the mean proportion of annual rainfall recorded in each month, using long-term (>37 years) rainfall data from 15 weather stations evenly distributed across the study domain. We subjectively categorized periods as favourable and unfavourable for recruitment, and tested for differences in the number of seedlings per parent between these periods using a one-way ANOVA with TSF as a covariable.

Phenology data

We used data collected by the Protea Atlas Project (Rebello 1991) to analyse patterns of flowering phenology for our study species throughout their range across the fynbos biome. Distributional data were collected between 1991 and 2001 at 500 m diameter localities, with coordinates accurate to within 100 m. Flowering data were collected for each species at each locality in the following classes: buds (mainly buds present), flowering (mainly flowerheads open, but buds and post-peak (finished) flowerheads also present), peak flowering (almost all flowerheads open), over (flowerheads present, but few buds and many flowerheads finished), cone (flowering finished and seeds not yet released), and none (no flowerheads or cones on plants).

For our purposes flowering and peak flowering were summed as 'flowering' and other categories were ignored. Data were binned into longitudinal bands of one degree from 18°E to 26°E. Localities with less than five observations were not included in the analysis. Sample sizes for each month exceeded 250 for all species.

We used contour plots (StatSoft 2001) to depict phenological trends across the species' ranges, and smoothed the data using distance-weighted least

squares. We used a generalized linear model in R (R 2005) with a quasipoisson distribution and log-link function to explore the relationship for each species between proportion of plants in flower (response variable), and month and longitude as explanatory variables. Significant month-longitude interactions would indicate significant seasonal changes in flowering phenology across the biome.

RESULTS

Post-fire recruitment

Of the 30 sites sampled, 15 had been last burnt during the cool season and 15 in the warm season. Considering patterns for all four species, where each datum comprised the number of seedlings per parent of each species at each site (thus, $n = 15$ for both warm- and cool-season burns), the following patterns were evident (Table 1): overall, there was no significant difference in recruitment levels between seasons, and recruitment failure (fewer than 1 seedling per parent) was recorded at a similar frequency after both cool- (four sites) and warm- (three sites) season fires (Fig. 2). Data for *P. neriifolia* and *P. repens* showed a similar pattern, with recruitment failure occurring after both warm- and cool-season fires (Fig. 2). The month-scale analysis indicated two periods that could be regarded as favourable for recruitment: February–March, and August–October (Fig. 3). However, even in these periods, low levels of recruitment (numbers of seedling per parent fewer than 2) were observed. Variation in recruitment between these periods was significant. Both favourable periods coincided with the period immediately before, and inclusive of, the autumn and spring rainfall peaks characteristic of the eastern fynbos biome. In none of the cases was TSF a significant covariable (Table 1).

Phenology

The model revealed significant results (month-longitude interaction) only for *P. repens* and *P. neriifolia* (Table 2). For *P. repens*, flowering shifted from winter to summer along the west–east gradient; in the eastern fynbos biome (i.e. east of 22°E), flowering peaked from late autumn to mid-summer (Fig. 4). In *P. neriifolia*, flowering was concentrated in the winter months west of about 22°E (i.e. in the central and western fynbos biome); east of this longitude, there was a marked trend for flowering to shift to autumn, whereas the populations at the extreme east of its range show a marked summer peak. The other species showed no significant trends for phenology to shift across the biome:

Table 1. Results of one-way ANOVAs to assess the effects of fire season on post-fire recruitment (parent to seedling ratio: log-transformed) of proteoid shrubs in the eastern fynbos biome

| Source | Case/species | Sum of squares | D.f. | Mean square | F-ratio | P-value |
|--|----------------|----------------|------|-------------|---------|---------|
| Covariate: time since fire (TSF) | 1. All species | 0.081 | 1 | 0.081 | 0.04 | 0.835 |
| | 2. Pn and Pr | 0.062 | 1 | 0.062 | 0.03 | 0.866 |
| | 3. All species | 0.002 | 1 | 0.002 | 0.00 | 0.972 |
| Main effect: fire season | 1. All species | 0.842 | 1 | 0.842 | 0.46 | 0.503 |
| | 2. Pn and Pr | 2.472 | 1 | 2.472 | 1.17 | 0.292 |
| | 3. All species | 7.157 | 1 | 7.157 | 4.49 | 0.043 |
| Residual | 1. All species | 49.312 | 27 | 1.826 | | |
| | 2. Pn and Pr | 40.045 | 19 | 2.108 | | |
| | 3. All species | 42.997 | 27 | 1.592 | | |
| Total (corrected) | 1. All species | 50.444 | 29 | | | |
| | 2. Pn and Pr | 42.639 | 21 | | | |
| | 3. All species | 50.444 | 29 | | | |

Separate analyses are presented for cool- versus warm-season burns for data for all four species combined (Case 1), and for *Protea neriifolia* (Pn) and *Protea repens* (Pr) combined (Case 2), and for favourable versus unfavourable recruitment season burns for all species combined (Case 3). For each analysis, TSF was used as a covariable. All F-ratios are based on the residual mean square error and Type III Sums of Squares were used.

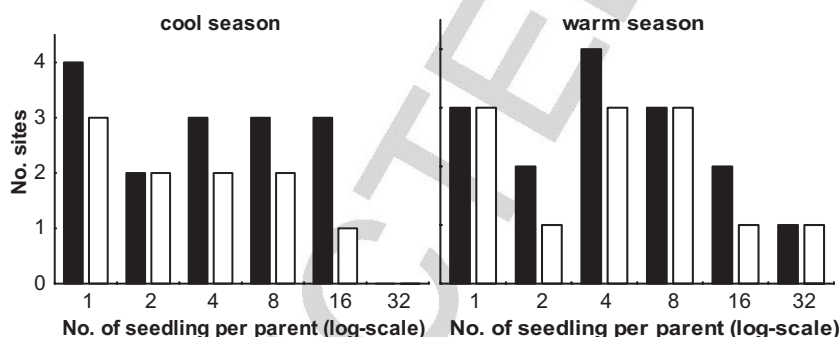


Fig. 2. Post-fire recruitment of all four study species (black bars) ($n = 15$ fires), and *Protea neriifolia* and *P. repens* (white bars; see Table 1) after cool- (June–November) ($n = 10$) and warm- (December–May) ($n = 12$) season fires in the eastern fynbos biome. Histogram bars represent the number of sites with the particular seedling to parent ratio. First category shows 0–1 seedlings per parent and so forth.

L. eucalyptifolium flowered in spring, irrespective of longitude, whereas *P. lorifolia* flowered in winter. Consequently, we did not visually depict data for these two species.

DISCUSSION

Overall, we found no differences between cool- and warm-season burns in recruitment success for our proteoid species, as predicted by van Wilgen (1984) based on the fact that fires are likely at anytime of the year in the eastern fynbos biome. Thus, our results are not consistent with those of Bond *et al.* (1984) and van Wilgen and Viviers (1985) for the central and western fynbos biome, respectively, nor with those from Mediterranean-climate scrub-heath in Australia (Cowling & Lamont 1987); they are, however, broadly consistent with patterns for two strongly serotinous

proteoids – *Petrophile sessilis* and *Hakea sericea* – from south-eastern Australia, an area lacking pronounced rainfall seasonality (Whelan & York 1998).

The most favourable recruitment periods for our proteoid species were late summer to autumn (February–March) and late winter to early summer (August–October), both of which coincided with the bimodal rainfall peaks recorded for the eastern fynbos biome. Therefore, fires that immediately precede, or coincide with these peak rainfall months produce the highest, albeit variable, recruitment. Fires that coincide with the dry winter and summer months produce significantly lower recruitment. Our results suggest that highest recruitment is linked to periods of high soil moisture, which would favour germination. Higher temperatures in autumn than spring (Deacon *et al.* 1992), which could result in lower rainfall effectiveness and lower soil moisture in autumn, do not appear to influence recruitment.

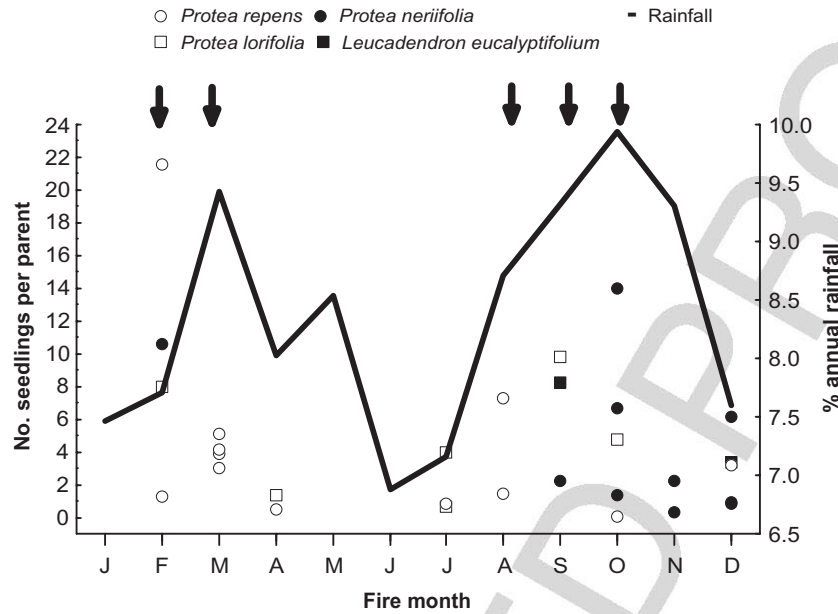


Fig. 3. Post-fire recruitment (numbers of seedlings per parent) of four proteoid species in the eastern fynbos biome in relation to month of burn and rainfall seasonality. Arrows indicate periods subjectively categorized as favourable for recruitment. Solid line shows the long-term rainfall average.

Table 2. Results of a generalized linear model to assess the effect of longitude and month on the proportion of flowering individuals of proteoids in different months and sites across the longitudinal extent of the fynbos biome

| Species | Coefficients | Estimates | Std. Error | <i>t</i> -value | <i>P</i> -value | Rd (D.f.) |
|---------|-------------------|-----------|------------|-----------------|-----------------|-------------|
| Le | Intercept | -5.629 | 6.702 | -0.840 | 0.404 | |
| | Month | 0.842 | 0.752 | 1.119 | 0.267 | |
| | Longitude | 0.306 | 0.297 | 1.029 | 0.307 | |
| | Month × longitude | -0.031 | 0.033 | -0.924 | 0.359 | 1489.4 (69) |
| Pl | Intercept | -5.361 | 3.989 | -1.344 | 0.183 | |
| | Month | 0.695 | 0.578 | 1.204 | 0.233 | |
| | Longitude | 0.407 | 0.180 | 2.264 | 0.027 | |
| Pn | Month × longitude | -0.035 | 0.026 | -1.348 | 0.182 | 2302.4 (70) |
| | Intercept | -1.596 | 1.754 | -0.910 | 0.365 | |
| | Month | 0.483 | 0.252 | 1.920 | 0.058 | |
| Pr | Longitude | 0.250 | 0.079 | 3.164 | 0.002 | |
| | Month × longitude | -0.026 | 0.011 | -2.220 | 0.029 | 2255.3 (90) |
| | Intercept | -1.758 | 2.063 | -0.852 | 0.397 | |
| | Month | 0.564 | 0.316 | 1.785 | 0.078 | |
| | Longitude | 0.266 | 0.096 | 2.776 | 0.007 | |
| | Month × longitude | -0.033 | 0.015 | -2.236 | 0.028 | 1659.9 (84) |

D.f., degrees of freedom; Le, *Leucadendron eucalyptifolium*; Pl, *Protea lorifolia*; Pn, *P. neriifolia*; Pr, *P. repens*; Rd, residual deviance.

Our data are not consistent with the predictions of the post-fire attrition hypothesis as articulated by Bond and van Wilgen (1996). This hypothesis argues that recruitment levels are a consequence of the time period for which seeds are exposed to post-dispersal attrition: longest after winter burns – because seeds germinate only at the start of the following cool season – and shortest after autumn burns, when highest recruitment levels are observed (Bond 1984; Cowling & Lamont 1987). However, it might be true that popu-

lations of eastern proteoids, unlike their central and western counterparts, which require cool temperatures for germination (Midgley 1989; Mustart & Cowling 1991), have seeds capable of germinating over a wide range of temperatures. If this were the case, then seed attrition may well control recruitment: germination would be least delayed after fires that coincide with the wet, warm autumn and wet, cool spring periods. Testing this would require data on the variation in temperatures optimal for germination along the

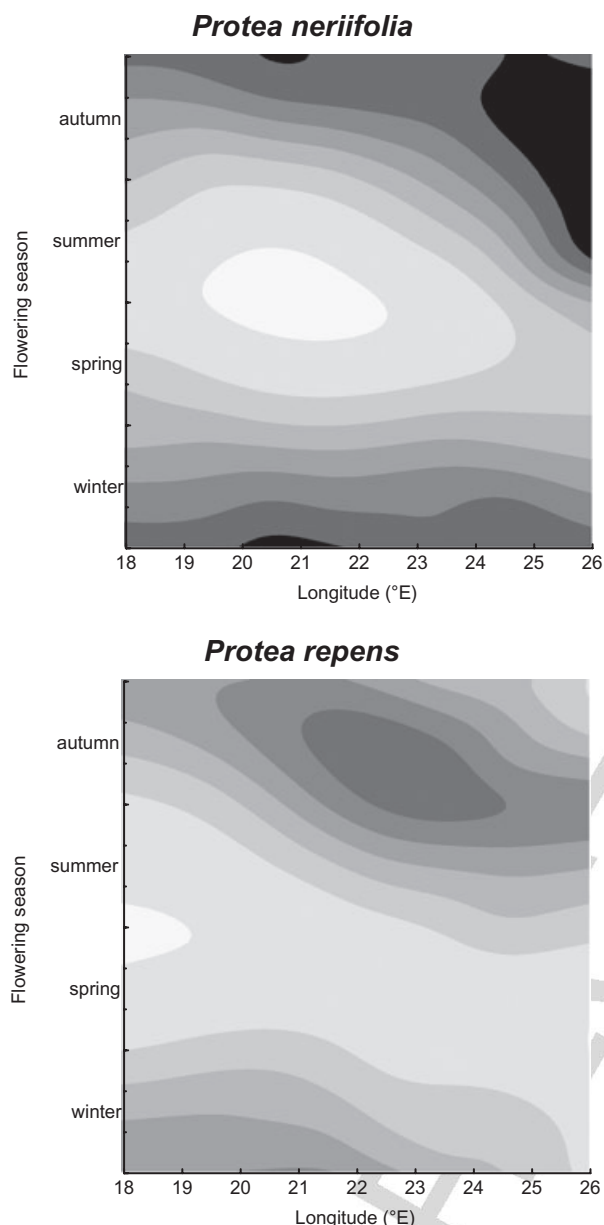


Fig. 4. Phenology of two proteoid species in the fynbos biome. Level of flowering is binned into eight shades, ranging from white (0%) to the black (70%) black. Although the analysis is per month, the following austral seasons were used to depict flowering patterns: winter (June–August), spring (September–November), summer (December–February), autumn (March–May).

east–west gradient of rainfall seasonality in the fynbos biome.

Unlike the winter-rainfall part of the fynbos biome (Cowling *et al.* 2005), rainfall seasonality is highly unpredictable in the eastern fynbos biome: although long-term rainfall data do indicate clear spring and autumn peaks, good rains might occur at any time of the year, as can dry periods (Procheş *et al.* 2005). As

pointed out above, this unpredictability might contribute to the high variation in recruitment success, even within the so-called favourable periods (Bradstock & Bedward 1992; Whelan & York 1998).

The shift to summer flowering of *P. repens* and *P. neriifolia* in the eastern fynbos biome suggests that the pre-burn seed reserve hypothesis might also contribute to explaining post-fire recruitment patterns of these two proteoids in the eastern reaches of the fynbos biome: spring fires would coincide with highest seed reserves in weakly serotinous proteoids such as these two species (Jordaan 1949; Jordaan 1965, 1982; Midgley & Vlok 1986). However, fire in autumn – a period favourable for recruitment – coincides with the lowest seed reserves, thereby refuting the pre-burn seed reserve hypothesis. Relatively high recruitment after spring burns was also recorded for the spring-flowering *L. eucalyptifolium* and winter-flowering *P. lorifolia*: a pattern inconsistent with the pre-fire seed reserve hypothesis. However, the low number of sites (*L. eucalyptifolium*) and poor representation of warm-season fires (*P. lorifolia*) constrain generalizations regarding fire season effects for these species.

More research will be required on fire season effects on seed bank sizes, germination, pre- and post-dispersal seed mortality, and patterns of seedling mortality of proteoids in order to conclusively assess the relative importance of the various hypotheses, in explaining fire seasonal effects on recruitment of proteoids in the eastern fynbos biome. There are other possible explanations for the observed patterns, invoking both seed availability and seedling mortality. Many of our populations were less than 15 years old at the time of burn, this age being regarded as optimal for recruitment for proteoids, and hence for assessing patterns (Bond *et al.* 1984; van Wilgen *et al.* 1992). However, mean stand age of proteoids at the time of burn in sites associated with favourable recruitment periods was not significantly different from sites burnt in other months (Student *t*-test; $t = 1.481$, $P = 0.150$).

Fire intensity, through its effects on seed mortality and retention in serotinous cones, may also influence post-fire recruitment (Lamont *et al.* 1991). However, as judged by the diameter of the finest branches remaining on the parent plants (Xxxxxx 0000, unpubl. obs.), fires were of similar intensity, irrespective of their time of year. Conditions suitable for intense fires occur frequently throughout the year in the eastern fynbos biome (van Wilgen & Burgan 1984).

Although very high pre-fire density of proteoids (*c.* 8 individuals m^{-2}) may depress recruitment (Bond *et al.* 1984; Bond *et al.* 1995), at none of our sites did density exceed 2.35 individuals m^{-2} . Consequently, density is unlikely to be a factor in poor recruitment of our study species. Another hypothesis argues that sprouting graminoids, in particular fast-growing C4 grasses (Pierce & Cowling 1984) that are common in

1 many eastern fynbos communities (Cowling 1984;
2 Campbell 1985), may outcompete slower-growing
3 proteoid seedlings, thereby reducing post-fire popula-
4 tion sizes (Vlok & Yeaton 2000). However, Heelemann
5 (2005) was unable to demonstrate negative interac-
6 tions between sprouting graminoids (grasses, sedges
7 and restios) and proteoid seedlings across a wide range
8 of sites in the eastern fynbos biome, except for a single
9 case: *Ehrharta ramosa* (a C3 grass) and *Protea lorifolia*,
10 and this at one site only. Finally, in the eastern fynbos
11 biome, where prolonged dry and hot spells might
12 occur at any time of the year – including the peak
13 rainfall periods in autumn and spring – recruitment
14 success might be a consequence of abiotic factors,
15 namely weather conditions conducive to high seedling
16 mortality. The frequency of these conditions is likely to
17 have a high stochastic component and their impacts
18 may confound factors that influence recruitment in a
19 more deterministic manner. In eastern Australia,
20 where rainfall patterns are non-seasonal, the lack of
21 fire season effects on the recruitment of proteoids has
22 been attributed to unpredictable variation in post-fire
23 conditions owing to stochastic rainfall patterns
24 (Bradstock & Bedward 1992; Whelan & York 1998).
25 Generally, fire season effects on proteoid recruitment
26 appear to be most pronounced in regions with strongly
27 seasonal rainfall (Knox & Clarke 2006).

28 Irrespective of the underlying mechanisms, the post-
29 fire recruitment of proteoids in the eastern fynbos
30 biome shows a weak, bimodal seasonal signal:
31 although recruitment does show autumn and spring
32 peaks, low levels might occur at any time of the year.
33 Indeed, along with quick rotation burns (Cowling
34 1984), stochastic recruitment failure may explain the
35 low extent of proteoid fynbos in the east, relative to the
36 central and western parts of the biome. Our results
37 suggest that generalizations regarding fire manage-
38 ment for the maintenance of diversity derived from
39 data in the central and western fynbos biome do not
40 necessarily hold for the east.

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REFERENCES

- Bond W. J. (1984) Fire survival of Cape Proteaceae – influence
of fire season and seed predators. *Vegetatio* **56**, 65–74.
- Bond W. J. (1985) Canopy-stored seed reserves (serotiny) in
Cape Proteaceae. *S. Afr. J. Bot.* **51**, 181–6.
- Bond W. J. & van Wilgen B. W. (1996) *Fire and Plants*. Chapman
& Hall, London.
- Bond W. J., Vlok J. H. J. & Viviers M. (1984) Variation in
seedling recruitment of Cape Proteaceae after fire. *J. Ecol.*
72, 209–21.
- Bond W. J., Maze K. E. & Desmet P. G. (1995) Fire life history
and the seeds of chaos. *Ecoscience* **3**, 252–60.
- Bradstock R. A. & Bedward M. (1992) Simulation of the effect
of season of fire on post-fire seedling emergence of two
Banksia species based on long-term rainfall records. *Aust. J.*
Bot. **40**, 75–88.
- Bradstock R. A. & O'Connell M. A. (1988) Demography of
woody plants in relation to fire: *Banksia ericifolia* L.f. &
Petrophile pulchella (Schrad.) R. Br. *Aust. J. Ecol.* **13**, 505–
18.
- Campbell B. M. (1985) A classification of the mountain vegeta-
tion of the fynbos biome. *Mem. Bot. Surv. S. Afr.* Botanical
Research Institute, Department of Agriculture and Water
Supply, S.A. **50**, 1–121.
- Cowling R. M. (1984) A syntaxonomic and synecological study
in the Humansdorp region of the Fynbos Biome. *Bothalia*
15, 175–227.
- Cowling R. M. (1987) Fire and its role in coexistence and spe-
ciation in Gondwanan shrublands. *S. Afr. J. Sci.* **83**, 106–12.
- Cowling R. M. & Lamont B. B. (1987) Post-fire recruitment of
four co-occurring *Banksia* species. *J. Appl. Ecol.* **24**, 645–58.
- Cowling R. M., Lamont B. B. & Pierce S. M. (1987) Seed bank
dynamics of four co-occurring *Banksia* species. *J. Ecol.* **75**,
289–302.
- Cowling R. M., Ojeda F., Lamont B. B., Rundel P. W. &
Lechmere-Oertel R. (2005) Rainfall reliability, a neglected
factor in explaining convergence and divergence of plant
traits in fire-prone Mediterranean-climate ecosystems.
Global Ecol. Biogeogr. **14**, 509–19.
- Deacon H. J., Jury M. R. & Ellis F. (1992) Selective regime and
time. In: *The Ecology of Fynbos. Nutrients, Fire and Diversity*
(ed. R. M. Cowling) pp. 6–22. Oxford University Press,
Cape Town.
- Heelemann S. (2005) *Post-fire seedling recruitment of non-sprouting
serotinous Proteaceae in fynbos vegetation: a study of the eastern
Cape Floristic Region (South Africa)* (Unpublished Diploma
Thesis). University of Rostock, Rostock.
- Johnson S. D. (1993) Climatic and phylogenetic determinants of
flowering seasonality in the Cape flora. *J. Ecol.* **81**, 567–72.
- Jordaan P. G. (1949) Aantekeninge oor die voortplanting en
brand periodes van *Protea mellifera* Thunb. *J. S. Afr. Bot.*
15, 121–5.
- Jordaan P. G. (1965) Die invloed van n winterbrand op die
voortplanting van vier soorte van die Proteaceae. *Tydskrif
Vir Natuurbeewaaring* **5**, 27–31.
- Jordaan P. G. (1982) The influence of a fire in April on the
reproduction of three species of the Proteaceae. *J. S. Afr.
Bot.* **48**, 1–4.
- Knox K. J. E. & Clarke P. J. (2006) Fire season and intensity
effect shrub recruitment in temperate sclerophyllos
woodlands. *Oecologia* **149**, 430–739.
- Lamont B. B., Le Maitre D. C., Cowling R. M. & Enright N. J.
(1991) Canopy seed storage in woody plants. *Bot. Rev.* **57**,
277–317.

- 1 Le Maitre D. C. (1990) The influence of seed ageing on the
2 plant on seed germination in *Protea neriifolia* (Proteaceae).
3 *S. Afr. J. Bot.* **56**, 49–53.
- 4 Le Maitre D. C. (1992) The relative advantages of seeding and
5 sprouting in fire-prone environments: a comparison of life
6 histories of *Protea neriifolia* and *Protea nitida*. In: *Fire in South*
7 *African Mountain Fynbos: Ecosystem, Community and Species*
8 *Response at Swartboskloof* (eds B. W. van Wilgen, D. M.
9 Richardson, F. J. Kruger & H. J. van Hendsbergen)
10 pp. 123–44. Springer-Verlag, Berlin.
- 11 Midgley J. J. (1989) Season of burn of serotinous fynbos Protea-
12 ceae: a critical review and further data. *S. Afr. J. Bot.* **55**,
13 165–70.
- 14 Midgley J. J. & Vlok J. H. J. (1986) Flowering patterns in Cape
15 Proteaceae. *Acta Horticult.* **185**, 273–6.
- 16 Mucina L., Rutherford M. C. & Powrie L. W. (2005) *Vegetation*
17 *Map of South Africa, Lesotho and Swaziland*. SANBI,
18 Pretoria.
- 19 Mustart P. J. & Cowling R. M. (1991) Seed germination of four
20 serotinous Agulhas Plain Proteaceae. *S. Afr. J. Bot.* **57**, 310–
21 13.
- 22 Mustart P. J. & Cowling R. M. (1992) Impact of flower and cone
23 harvesting on seed banks and seed set of serotinous Agulhas
24 Proteaceae. *S. Afr. J. Bot.* **58**, 337–42.
- 25 Mustart P. J., Cowling R. M. & Wright M. G. (1995) Clustering
26 of fertile seeds in infructescences of serotinous *Protea*
27 species: an anti-predation mechanism? *Afr. J. Ecol.* **33**,
28 224–9.
- 29 Parker V. T. & Kelly V. R. (1989) Seed banks in California
30 chaparral and other Mediterranean climate shrublands. In:
31 *Ecology of Soil Seed Banks* (eds M. A. Leck, V. T. Parker &
32 R. L. Simpson) pp. 231–56. Academic Press, San Diego.
- 33 Pierce S. M. & Cowling R. M. (1984) Phenology of fynbos,
34 renosterveld and subtropical thicket in the south eastern
35 Cape. *S. Afr. J. Bot.* **3**, 1–16.
- 36 Procheş & Scedil,., Cowling R. M. & du PreeZ. D. R. (2005)
37 Patterns of geophyte diversity and storage organ size in the
winter-rainfall region of southern Africa. *Divers. Distrib.* **11**,
101–9.
- R (2005) *R: A Language and Environment for Statistical*
Computing. R Foundation for Statistical Computing,
Vienna. [Cited xx xxxx xxxx.] Available from URL: [http://](http://www.R-project.org) 4
www.R-project.org
- Rebello A. G. (1991) *Protea Atlas Manual*. Protea Atlas Project,
Kirstenbosch.
- Rebello A. G. (2001) *A Field Guide to the Proteas of Southern*
Africa. Fernwood Press, Vlaeberg, Cape Town.
- Schulze R. E. (1997) Climate. In: *Vegetation of Southern Africa*
(eds R. M. Cowling, D. M. Richardson & S. M. Pierce)
pp. 21–42. Cambridge University Press, Cambridge.
- van Staden J. (1978) Seed viability in *Protea neriifolia*. I. The
effects of time of harvesting on seed viability. *Agroplantae*
10, 65–7.
- van Wilgen B. W. (1984) Fire climates in the southern and
western Cape Province and their potential use in fire control
and management. *S. Afr. J. Sci.* **80**, 358–62.
- van Wilgen B. W. & Burgan R. E. (1984) Adaptation of the
United States Fire Danger rating System to fynbos
conditions. Part II. Historic fire danger in the fynbos biome.
S. Afr. For. J. **129**, 66–78.
- van Wilgen B. W. & Viviers M. (1985) The effect of season of fire
on serotinous Proteaceae in the western Cape and the impli-
cations for fynbos management. *S. Afr. For. J.* **133**, 49–53.
- van Wilgen B. W., Bond W. J. & Richardson D. M. (1992)
Ecosystem management. In: *The Ecology of Fynbos: Nutrients,*
Fire and Diversity (ed. R. M. Cowling) pp. 345–73. Oxford
University Press, Cape Town.
- Vlok J. H. J. & Yeaton R. I. (2000) Competitive interactions
between overstorey proteas and sprouting understorey
species in South African mountain fynbos. *Divers. Distrib.* **6**,
273–81.
- Whelan R. J. & York J. (1998) Post-fire germination of *Hakea*
sericea and *Petrophile sessilis* after spring burning. *Aust. J. Bot.*
46, 367–76.

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