Postfire regeneration of resprouting mountain fynbos shrubs: differentiating obligate resprouters and facultative seeders

K. E. Marais · R. B. Pratt · S. M. Jacobs · A. L. Jacobsen · K. J. Esler

Abstract Plant species in Mediterranean-type climate regions have a diversity of traits that facilitate their persistence under a given fire regime. Obligate resprouters (OR) are dependent on resprouting to persist through a burn episode, as their seeds are killed by fire. Facultative seeders (FS) combine strategies by resprouting and recruiting new seedlings after fire. We hypothesised that these life history differences would lead to differential resprout success and we predicted that OR would be more successful than FS. We performed a 2-year study to assess resprout success of co-occurring Western Cape mountain fynbos FS and OR species, and to determine predictors of resprout success following a wildfire. All the FS species recruited seedlings postfire, whereas the OR did not. OR demonstrated near complete (99 %) survival after 2 years and all resprouted within 4 months postfire. In contrast, only 81 % of FS resprouted with only 65 % surviving 2 years postfire. Numerous factors were linked to resprout success: decreased lignotuber exposure and pre-fire vigour (number of pre-fire shoots) were significantly associated with postfire resprouting, while early resprouting (days to first resprout) and growth rate were significant predictors of post-resprout survival. The difference in resprout survival between the FS and OR may also be partially due to phylogenetic differences. These findings confirm the heterogeneity and complexity of postfire resprouting and support the distinction of OS and FS life history types.

Keywords Facultative seeders · Fire · Mediterranean-type ecosystems · Obligate resprouters · Postfire succession · Resprouting

Introduction

The five Mediterranean-type ecosystems of the world have been identified as biodiversity hotspots of global conservation concern (Cowling et al. 1996; Myers et al. 2000). Apart from Chile, the stability of these ecosystems is fire dependant (Keeley et al. 2012). Fire frequency has increased in many areas due to human activities and global climate change and this alteration in fire regime may have a destabilizing effect on these ecosystems (Syphard et al. 2006; van Wilgen et al. 2010). To predict how these systems respond to altered fire regimes, we need to understand how plants react to fire and what make them resilient to this disturbance.

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Like all Mediterranean-type ecosystems, South African fynbos vegetation is well adapted to intermittent crown fires, and plant species generally regenerate rapidly following fire. Plants use different mechanisms for postfire regeneration. Some species, termed obligate seeders (OS), are killed by fire as adults and persist by recruiting seedlings postfire from a fire-cued seed bank (Bond et al. 1984). Other species resprout after fire from lignotubers below-ground or above-ground organs (resprouters). Many studies have sought to compare resprouters and seeders (Bond and van Wilgen 1996; Bond and Midgley 2001, 2003; Vesk and Westoby 2004a; and Verdú et al. 2007). This binary system captures some important variations in plant traits (Vesk and Westoby 2004a), but fails to distinguish the relative importance of resprouting versus seedling recruitment as a postfire persistence strategy. One reason for this is that there are different types of resprouters. Some species are obligate resprouters (OR) after fire because their seeds are fire sensitive and thus they do not recruit seedlings after fire. Seedling recruitment for OR species occurs in fire-free intervals and is rare, meaning that individual fitness is dependent on resprout success and longevity to maximise seedling recruitment opportunities (Bond and Midgley 2001; Cowling et al. 1997). Other species, referred to as facultative seeders (FS), adopt a dual strategy that includes postfire resprouting and seedling recruitment from a fire-cued dormant seed bank (Keeley and Bond 1997; Keeley et al. 2006). It is convenient to refer to these different resprouting/ seeding types as categories, but it is more precise to describe resprouting and seeding as a continuum where OS and OR are extremes in postfire seeding and resprouting, respectively, and a given FS species falls somewhere in between the two.

Species with different resprouting and seedling recruitment strategies after fire diverge in a suite of life history traits and are commonly referred to as different life history types (Keeley et al. 2012). An important paradigm in comparing differences among life history types is the concept of tradeoffs (Bellingham and Sparrow 2000; Clarke et al. 2013; Keeley et al. 2012). For example, the loss of resprouting in many cases is a derived characteristic, and this loss should free up resources to support enhanced growth and reproduction (Midgley 1996; Schwilk and Ackerly 2005). In other cases, a loss in resprouting may be associated with increased stress tolerance (Pratt et al. 2012a).

Differences between the FS and OR resprouting types have not been widely studied, but some important differences between these two types have been identified (Crandall and Platt 2012). For example, woody OR and FS fynbos species differ in their resistance to drought (Pratt et al. 2012b). Moreover, woody chaparral seedlings differ in root allocation such that OR allocate more biomass to roots than FS, and they differ in a host of other functional traits, including shade tolerance (Pratt et al. 2012a). These functional differences are important because they are linked to differences in demography that define a particular life history type.

Resprouting is a complex process that involves at least three steps to achieve resprout success (Moreira et al. 2012; Malanson and Trabaud 1988; Le Maitre et al. 1992). First, plants need to survive the fire and initiate resprouting. Second, the resprouting needs to be vigorous to compete for above-ground space lost due to the fire, and to re-establish a canopy that can supply carbon to support the metabolic demands of the root system and continued vigorous resprouting. Third, survival after resprouting is necessary to complete re-establishment. Each of these factors has been shown to affect resprout success (Moreira et al. 2012).

A key hypothesis addressed in this study is that OR and FS species will differ in their resprout success. Moreover, it was a goal of this study to evaluate what step or steps in the resprouting process may limit resprout success and if this varies between these two life history types. To our knowledge, such a comparison of FS to that of OR has not been done. We examined numerous traits that could affect resprout success including fire severity (Moreno and Oechel 1993), how exposed to fire lignotubers were (Drewa et al. 2002), and plant size (Le Maitre et al. 1992; Stohlgren et al. 1984). For resprout vigour, we examined growth rate, number of shoots before fire and the ability to resprout early (Le Maitre et al. 1992; Malanson and Trabaud 1988). Finally, we monitored resprout survival for 2 years after fire as the final step determining resprout success. We also monitored postfire seedling recruitment of OS and FS species in the form of seedling to parent ratios. This is an important context for interpreting resprout success among FS species because resprouting failure may be offset by seedling recruitment and this provides important information about where species fall along

the seeding–resprouting continuum of life history types. Because a main goal of this study was to identify determinants of resprout success that required time-consuming measurements, we chose to intensively study a single field site where FS and OR species were co-occurring, following a wildfire.

Materials and methods

Study site and species

We conducted a 2-year repeated observation study, documenting postfire regeneration in mountain fynbos following a wildfire that occurred from 3 to 7 March 2009 in the Paarl Mountain Nature Reserve (33°44′S, 18°55′E) close to Cape Town, South Africa. The fire was typical for mountain fynbos: moderately hot and patchy, with some areas burning hotter than others (Fig. 1). Massive intrusive granite boulders characterise the reserve. The vegetation is classified as Boland Granite Fynbos at higher altitudes and Swartland Granite Renosterveld on the lower slopes (Mucina and Rutherford 2006). The mean annual rainfall on the mountain plateau is estimated to be 960 mm (van Wilgen 1974; Zucchini 1992; Milton 2003), with most of the rainfall occurring during the winter months, from May to September. The summer months are generally hot and dry, typical of a Mediterranean-type climate. The study site was situated on a northeast facing aspect at an elevation of 600 m, with fine textured soils derived from granite. The site last burned 18–20 years before the studied fire (L. de Roubaix, Paarl Mountain Nature Reserve manager, personal communication). Pre-fire, the site was dominated by ericoid and proteoid shrubs (Milton 2003).

This was a natural experiment and we did not survey our study area before the fire. Burnt bark traits as well as scorched leaves and fruit on or around burnt plants were used to identify species. To further aid, identification of burned species and their life history types, we selected an adjacent, topographically similar site directly across the road and within 20 m of our burned site, which had burnt 2 years previously. From the list of possible species, we selected those that could be classified as either OR or FS (Table 1) according the to previously documented life history descriptions of the species and our own field observations. A seedling survey including the most abundant obligate seeder species (OS) on the site was done to confirm our species assignment to life history types as well as to compare seedling to adult ratios between the FS and OS species. Nomenclature follows Goldblatt and Manning (2000), except for the *Searsia* spp., which follow Yi et al. (2004).

Data collection

Fieldwork started 19 days postfire, on 23 March 2009. A rain gauge was set up to monitor rain and a data logger to monitor temperature (HOBO pendant data logger, Onset Computer Corporation, MA, USA) at the study site. Individual burnt stumps were visually assessed and selected by walking transects across the study site. We tagged 349 plants, aiming for 40 individuals per species. Some species were, however, less abundant and the target could not be reached. Burnt stumps were marked with numbered fireproof tags. For the dioecious species, *Leucadendron salignum,* we tagged a minimum of 40 male and 40 female plants. Tagged plant identification, based originally on bark characteristics of burnt stumps were verified following resprouting and were generally accurate (of the hundreds of tagged and resprouted plants, only six plants were found to have been originally misidentified). Moreover, individuals of a particular species were sampled regardless of their size, i.e. they were randomly sampled. We did find and sample some very small individuals, which was possible because, in general, the fire was not so severe as to completely remove all standing biomass. Nevertheless, it is possible that some small plants were totally destroyed by the fire and did not resprout, leading to a bias in our data. Because the complete destruction of small plants was very rare for this fire, any size bias in our data will likely be of small effect.

Initial measurements included: (1) lignotuber circumference, as a measure for stored reserves, available bud bank and/or an estimate of plant age (Moreno and Oechel 1991; le Maitre et al. 1992; Bell and Ojeda 1999; Paula and Ojeda 2006); (2) number of pre-fire shoots, as a measure of pre-fire vigour (le Maitre et al. 1992); (3) burnt branch diameter of terminal branches, as an index of fire severity (greater diameter of burnt branches corresponds to a more severe fire (Moreno and Oechel 1993; Pérez and Moreno 1998; Euston-Brown et al. 2004; Keeley 2009); and (4) lignotuber height above soil (lignotuber exposure) as well as slope, as a measure of erosion potential. After the
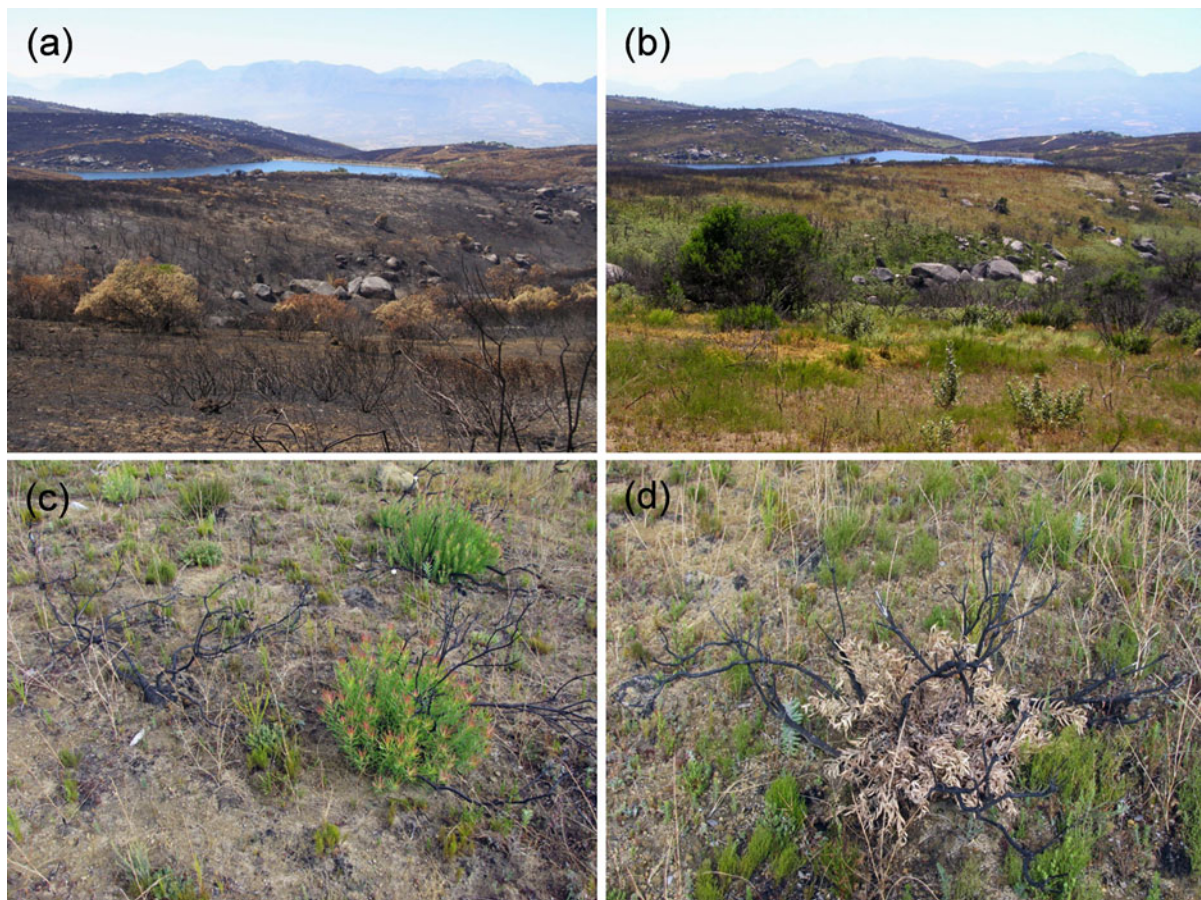
Fig. 1 Photographs showing the field site about 7 days following the fire at Paarl Mountain, South Africa (**a**) and the same view of the site about 1 year after the fire (**b**). Some shrubs failed to resprout after the fire (**c**; individual of *Leucadendron salignum* that failed to resprout is visible on the *left side of panel*), although many individuals successfully resprouted (**c**; two individuals of *L. salignum* on the *right side of the panel*). Most shrubs that exhibited mortality at the site were able to resprout, but then subsequently died (**d**; a dead *L. salignum* is visible in the *centre of the panel*). The shrubs in *panels* **c** and **d** are about 0.5 m tall

initial survey, field surveys were conducted every other week for the first 2 months, then monthly for the rest of the first year postfire and then seasonally (winter, spring, summer and autumn) for the second year. Measurements taken at each site visit included: (1) if plants had resprouted (yes/no), (2) number of resprouted shoots, (3) elongation of longest shoot (in cm) and (4) evidence of herbivory (yes/no). When counting the resprouts, we limited the count to resprouts not more than 0.05 m away from the lignotuber. This was done to focus on a single main ramet, because without extensive excavation or genetic fingerprinting it was not feasible to study whole genets for root suckering species.

Two seedling counts were conducted in April after the first autumn rains, 1 and 2 years after the fire. Twelve 100 m^2 plots (10 m × 10 m) were randomly located across the study site. Pre-fire adult populations in each of the twelve plots were determined by counting the skeletal remain as well as resprouted individuals during the first survey 1 year after the fire. All seedlings (dead and alive recorded separately) for each species were recorded in a total of 48 1 m × 1 m subplots, with four subplots located within each of the twelve 10 m × 10 m plots. Seedling mortality was assessed at 1 and 2 years postfire. All species included in the seedling surveys are included in Table 1.

Table 1 Target species and families, including their life history type (LHT; *OR* obligate resprouter, *OS* obligate seeder; *FS* facultative seeder), sample size (*n*), growth form, seed storage and dispersal vectors, mean lignotuber circumference (MLC) with standard error (SE) in brackets as well as percentage survival at 2 years postfire

Species	Family	LHT	n	Growth form	Seed storage and dispersal	MLC (cm)	% survival
Diospyros glabra (L.) De Winter	Ebenaceae	OR[a,b]	45	Dioecious shrub/small tree	Vertebrate dispersed	219.5 (13.3)	100
Searsia rosmarinifolia (Vahl) F.A. Barkley	Anacardiaceae	OR[b]	13	Dioecious scrambling shrub	Vertebrate dispersed	36.5 (5.2)	100
Searsia tomentosa (L.) F.A. Barkley	Anacardiaceae	OR[b,c]	29	Dioecious large shrub	Vertebrate dispersed	79.3 (16.2)	97
Diosma hirsuta L.	Rutaceae	FS[b]	37	Ericoid shrublet	Soil stored, myrmecochory	27.0 (1.6)	89
Cliffortia juniperina L.f.	Rosaceae	FS[d]	34	Ericoid shrublet	Soil stored	60.2 (4.2)	59
Cliffortia ruscifolia L.	Rosaceae	FS[b,c]	21	Small leaved, spiny shrub	Soil stored, myrmecochory	25.1 (4.3)	29
Aspalathus bracteata Thunb.	Fabaceae	FS[e]	51	Scrambling shrublet	Soil stored, myrmecochory	29.8 (2.1)	82
Leucadendron salignum P.J. Bergius	Proteaceae	FS[b]		Small proteoid shrub	Serotinous, winged, myrmecochory		
Male			44			58.3 (4.1)	61
Female			43			53.3 (3.3)	56
Gender unknown			7			39.4 (6.1)	0
Searsia angustifolia (L.) F.A. Barkley	Anacardiaceae	OR[f]	N/A	Dioecious scrambling shrub	Vertebrate dispersed		
Searsia lucida (L.) F.A. Barkley	Anacardiaceae	OR[f]	N/A	Dioecious shrub/small tree	Vertebrate dispersed		
Leucadendron rubrum Burm.f.	Proteaceae	OS[g]	N/A	Large, erect proteoid shrub	Serotinous, wind dispersed		
Leucospermum grandiflorum (Salisb.) R.Br.	Proteaceae	OS[g]	N/A	Large, erect proteoid shrub	Soil stored, myrmecochory		
Cliffortia erectisepala Weim.	Rosaceae	OS[d]	N/A	Erect shrub	Soil stored, myrmecochory		
Total			325				

Species in bold text were target species in both the resprout and seedling study, whereas other species were included only in the seedling study

[a] Cowling et al. (1997)

[b] van Wilgen and Forsyth (1992)

[c] Keeley and Bond (1997)

[d] Whitehouse (2002)

[e] Stirton, personal communication

[f] Personal field observations

[g] Rebelo (1995)

Statistical analyses

Sample sizes were not uniform and species could only be confirmed after resprouting. Species with sample sizes of less than ten were excluded from the species-specific analyses. To analyse mortality data, a general linear mixed model was used with a binary response variable (Bates et al. 2013). Life history type was included as fixed effect, and species were random effects nested within life history type. Other covariates included basal circumference, branch diameter, number of pre-fire shoots, slope, lignotuber height above the soil, lignotuber exposure above ground per unit basal area, and days to first resprout for those individuals that resprouted. In analysing models, non-significant variables were removed to identify the best model, which were determined as the one with the lowest AIC value. Three models were run, analysing mortality at different stages after the fire. The first model analysed all mortality due to fire (i.e. plants that did not resprout after the fire); the second model analysed mortality after resprouting (i.e. plants that resprouted and subsequently died); and the third model analysed the overall mortality after 2 years, regardless of when the mortality occurred. In some cases, separate models were also run for mortality of FS to exclude possible confounding effects by the OR. Furthermore, a binary logistic regression for mortality of FS species that suffered mortality due to fire was run, with branch diameter as the predictor.

Comparison of relative growth between species was done using a four-parameter logistic equation (also called the sigmoid dose–response curve) which was chosen because this model fit best when used across the different species to compare growth over time. The following equation was used:

$$Y = Bottom + (Top - Bottom)/(1 + 10^{((EC50-X)*HillSlope)}),$$

where the parameters have the following meaning: bottom represents lower level where growth starts, top represents upper level indicating maximum growth, EC50 represents time taken to reach half the growth between bottom and top and hill slope represents measure of steepness of the growth.

However, because growth starts at zero, the bottom parameter was set to zero and not estimated. Thus, it

was a three parameter equation that was fitted to the data.

STATISTICA was used for all analyses (STATISTICA v. 10, StatSoft, Inc., Tulsa, OK, USA), except the general linear mixed models that used the R package lme4 (Bates et al. 2013), and logistic regression was done using Minitab (v. 16.1, State College, PA, USA).

Results

Postfire survival

One hundred percent of the OR resprouted after the fire compared to 81 % of the FS. After 2 years, the survival rate was 99 % for the OR compared to that of 65 % for the FS ($P < 0.001$). Among the FS species that resprouted, post-resprouting mortality was generally greatest during the summer dry seasons (Fig. 2). Some *L. salignum* plants resprouted well in the summer and others not until the second year after the fire (Fig. 2).

Factors influencing postfire survival

A number of factors predicted survival (i.e. plants that resprouted after the fire). Pre-fire vigour was an important predictor of survival, where more pre-fire shoots were associated with lower mortality (Table 2). This factor was significant even when analysed within the FS life history type to avoid confounding by the OR life history type ($Z = 3.017$, $P = 0.002$). Lignotuber exposure was significantly higher for plants that did not survive fire (Table 2). Fire severity, estimated as the smallest terminal branch diameter, was not a significant predictor of survival ($Z = -0.454$, $P = 0.649$), even when each of the FS were analysed separately to account for species–specific effects ($P > 0.05$ for all species). Plant size, estimated by lignotuber circumference, was not significantly associated with survival ($Z = -0.915$, $P = 0.359$). Plants were not widely divergent in size, even between the two life history types, except one outlier species (*Diospyros glabra*) that was larger than all the rest (Fig. 3).

Resprouter life history type, days to first resprout, number of pre-fire shoots and growth rates were significant predictors of survival post-resprouting.
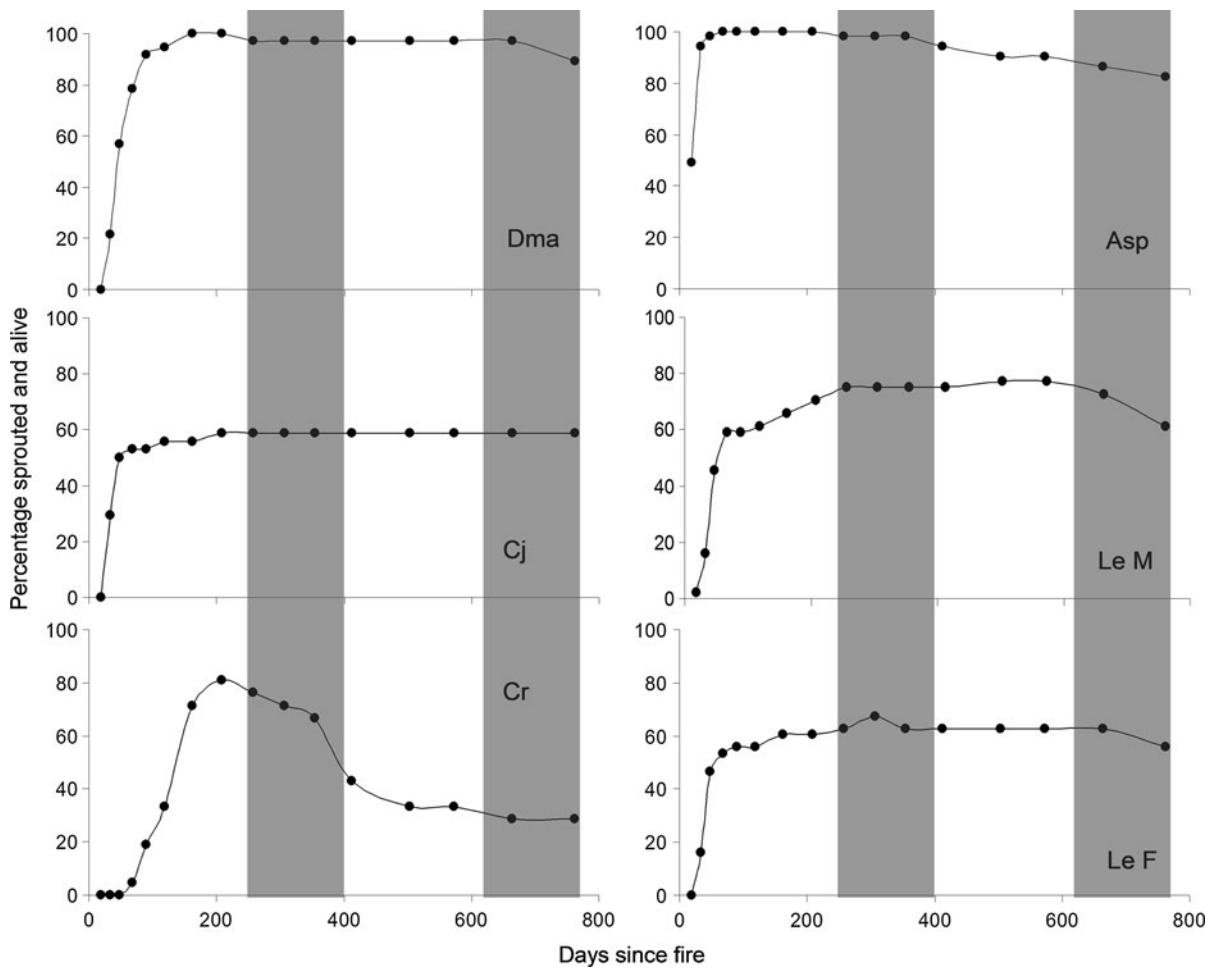
Fig. 2 A time series plot of the percentage tagged facultative seeder species that resprouted after the fire as well as the mortality that occurred during the 2-year sampling period. The *shaded area* depicts the dry summer months. *Diosma hirsuta* (Dma), *Aspalathus bracteata* (Asp), *Cliffortia juniperina* (Cj), *C. ruscifolia* (Cr) and *L. salignum* male and female (Le M & F). OR were omitted from figure because they had about 100 % survival

Table 2 Mean and SE of significant covariates (denoted by P values) from a general linear mixed model analysing survival of fire as a dependent variable

	Survived	Number of pre-fire shoots	Lignotuber height above soil
Mean ± SE	Yes	15.31 ± 0.93	3.53 ± 0.24
	No	9.35 ± 0.69	6.76 ± 0.63
P value		<0.001	0.034

Among the OR life history type, 99 % that resprouted survived until the final survey, whereas only 80 % of the resprouted FS survived ($Z = 2.548$; $P = 0.010$). The plants that resprouted earlier had a better chance of survival (Table 3). This result was significant even when analysing the FS species separately to exclude potential confounding by OR species ($Z = -2.762$; $P = 0.005$). Although the OR took on average 45 days to resprout postfire compared to that of 65 days for the FS, this difference was not significant ($P = 0.71$). Having more pre-fire shoots were significantly associated with survival (Table 3); however, this result was not significant when analysed for FS separately ($Z = 1.678$; $P = 0.093$) indicating that the OR have a confounding effect on this conclusion and that it is not supported. Plant size, fire severity, slope and lignotuber exposure were not significantly associated with mortality that occurred after resprouting.
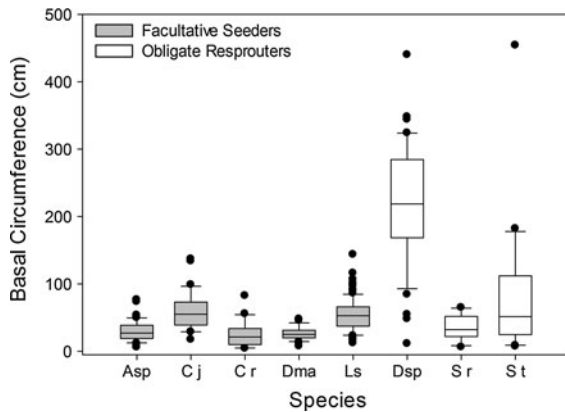
Fig. 3 Box and whisker plot showing median basal circumference, as well as the 10th, 25th, 75th, and 90th percentiles including outliers (circles). Aspalathus bracteata (Asp), Cliffortia juniperina (Cj), Cliffortia ruscifolia (Cr), Diosma hirsuta (Dma), Leucadendron salignum (Ls), Diospyros glabra (Dsp), Searsia rosmarinifolia (Sr) and Searsia tomentosa (St)

Table 3 Mean and SE for significant covariates (denoted by P values) from a general linear mixed model with post-resprout survival as a dependent variable

	Survived	Number of pre-fire shoots	Days to first resprout
Mean ± SE	Yes	16.48 ± 1.05	51.10 ± 3.11
	No	8.35 ± 1.14	100.7 ± 13.8
P value		0.043	0.004

Higher rates of growth were significantly associated with greater resprout survival; however, this conclusion was affected by an outlier. One FS species, A. bracteata, had a different growth form than the other shrub species; it was a scrambling shrublet that produced ground spreading shoots that were not mechanically self-supporting resulting in it being an outlier within shoot elongation measures (Fig. 4a). When analysed with this species removed, growth rate was a highly significant predictor of resprout survival ($Z = 4.056$; $P < 0.001$). This result was significant even when analysing the FS species separately from the OR species ($Z = 3.383$; $P < 0.001$). The mean growth rate ±1 SE of the FS survivors was 2.54 ± 0.08 and those resprouts that died had growth rates of 1.72 ± 0.20 mm/day.

Comparing growth rates of life history types, obligate resprouter species had greater shoot

elongation than the FS species. We compared these data with the outlier A. bracteata removed. This resulted in an increased difference between OR and FS species (Fig. 4b). The OR species also reached the halfway mark of their total shoot elongation over 2 years in a much shorter time (184 ± 28 days) than the FS species (277 ± 39 days).

Evaluating overall survival, thus not separating when mortality took place, the resprouter life history type, the number of pre-fire shoots, as well as the lignotuber exposure above ground were significantly associated (Table 4). The OR had 99 % survival compared to 65 % for the FS ($Z = 3.191$; $P = 0.001$). Individuals having more pre-fire shoots and having a less exposed lignotuber had greater levels of survival (Table 4). Lignotuber size was not a significant predictor ($Z = -1.358$; $P = 0.174$), and nor was the fire severity ($Z = 0.916$; $P = 0.359$) or slope ($Z = -0.722$; $P = 0.471$).

Seedling survey

None of the OR species recruited seedlings during the study period, except Searsia tomentosa. The obligate seeder (OS) species recruited far more seedlings per adult than the FS. Both the OS and FS life history types recruited enough seedlings to offset their adult mortality (Table 5).

Discussion

Overall, there was a difference in survival among the two resprouter life history types. More than a quarter of FS individuals died, including plants that never resprouted after the fire and resprouts that died within the first 2 years postfire. In contrast, mortality among OR species was limited to one small S. tomentosa plant that appeared to be a juvenile (small diameter, single stem) (Manders and Richardson 1992; Manders et al. 1992). The near total survival of OR individuals supports the hypothesis that the OR life history type is associated with greater resprout success than those of FS species. However, FS species recruited abundant seedlings after fire and 2 years postfire, there were more seedlings than those of pre-fire adults (Le Maitre et al. 1992). As expected, OR recruited no seedlings after fire. Obligate seeders (OS) recruited the most seedlings and no adult plants survived the fire. The differences in
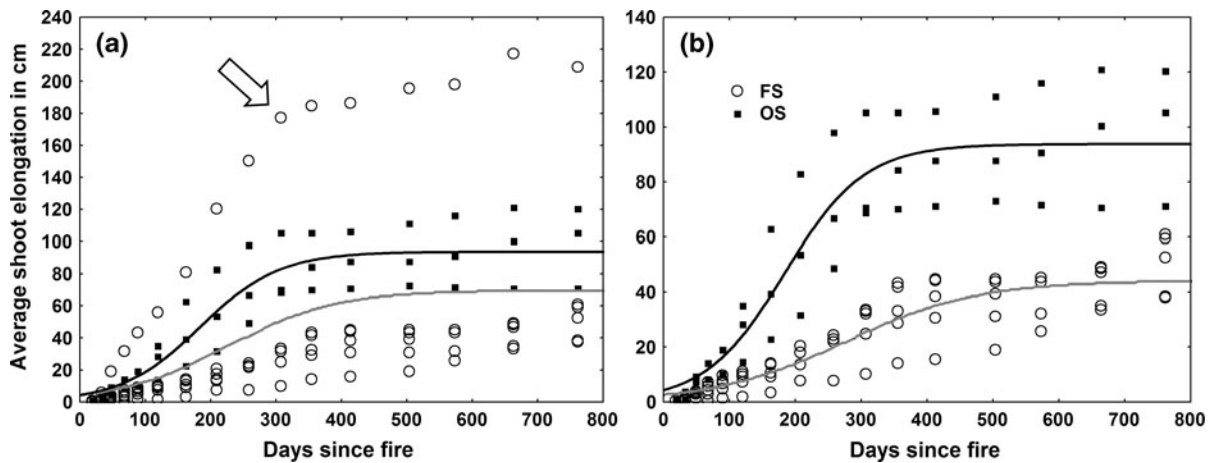
Fig. 4 Growth curves (shoot elongation) of pooled OR species and FS species over the 2 year study period. The *arrow* in graph **a** identifies the ground-spreading *A. bracteata*, which was an outlier within the FS group. In graph, **b** *A. bracteata* has been excluded

Table 4 Mean and SE of significant covariates (denoted by *P* values) from a general linear mixed model with overall survival as the dependent variable

	Survived	Number of pre-fire shoots	Lignotuber height/basal area
Mean ± SE	Yes	16.48 ± 1.05	0.026 ± 0.005
	No	8.88 ± 0.64	0.071 ± 0.014
P value		0.002	0.003

Output is for all plants alive versus all plants dead 2 years postfire, not taking into account when the mortality occurred

resprouting and seedling recruitment may be due to life history type differences or phylogenetic effects (see end of "Discussion" section).

Differential ability to survive the fire was related to several factors, with the ability to resprout early appearing particularly important. Early resprouting was a significant factor when analysed for FS only, thus this conclusion is not solely affected by differences between the two life history types. Early resprouting likely confers a competitive advantage and may also be important for carbon balance. When a resprout is top killed, the root system and adventitious buds remain alive and require the energy from stored carbohydrates. These carbohydrates initially come from stores in the lignotuber and roots, but these stores are finite and new shoots must be quickly deployed to acquire carbon via photosynthesis. Species that initiated resprouting earlier spent a shorter duration with no capacity for carbon gain. Early resprouting is also

likely a competitive advantage for two reasons. First, early resprouters that reclaim above-ground space lost during the fire would outcompete others nearby that resprouted later for both light and space. Second, after fire, there is a flush of nutrients (Christensen and Muller 1975) in the ash of the burned organic material that early resprouters may be better able to acquire and translocate to their new shoots. This may be especially important in the nutrient poor soils of the South African Cape region.

Pre-fire plant vigour appeared an important driver of postfire resprouting, which is consistent with numerous other studies (Malanson and Trabaud 1988; Le Maitre et al. 1992; Vesk et al. 2004). Greater numbers of shoots pre-fire could indicate a greater bud bank (Malanson and Trabaud 1988) or a greater pre-fire canopy and carbohydrate stores (Drewa et al. 2002). It is possible that there is a link between pre-fire vigour and early resprouting. Another key component is vigour during the resprouting stage (Moreira et al. 2012; Le Maitre et al. 1992; Malanson and Trabaud 1988), the advantages of which are the same as already discussed for early resprouting. The OR resprouts and the surviving FS resprouts grew faster than FS species that did not survive and this may have been important in re-establishing a balanced root to shoot ratio after the fire and in competing for resources, including water. The results of these analyses generally held when analysed for the FS only indicating that they were not solely driven by differences between the two life history types.

Table 5 Attributes and demography of 13 species monitored for 2 years after a late summer season fire

Species	Life history	Pre-fire density (mean ± SE) individual/1 m²	Postfire density (mean ± SE) alive individual/1 m² after 2 years	Initial seedling/ parent ratio	Seedling/ parent ratio after 2 years	Pre- and postfire plot presence	Seedling survival 2 years postfire (%)	Resprout survival 2 years post fire (%) (sample size in brackets)	Proportion live seedlings from live population 2 years post fire
Diospyros glabra	OR	0.007 ± 0.004	0.007 ± 0.004	0	0	9/9	–	100 (8)	0
Searsia angustifolia	OR	0.004 ± 0.002	0.004 ± 0.002	0	0	4/4	–	100 (5)	0
S. lucida	OR	0.003 ± 0.001	0.003 ± 0.001	0	0	9/9	–	100 (4)	0
S. rosmarinifolia	OR	0.029 ± 0.006	0.029 ± 0.006	0	0	4/4	–	100 (35)	0
S. tomentosa	OR	0.023 ± 0.006	0.106 ± 0.056	14.8	3.7	4/4	25	100 (27)	0.78
Diosma hirsuta	FS	0.180 ± 0.090	0.703 ± 0.376	4.2	3.0	10/10	72	90 (216)	0.77
Aspalathus bracteata	FS	0.058 ± 0.021	0.742 ± 0.233	22.5	11.8	8/11	52	93 (70)	0.92
Cliffortia juniperina	FS	0.016 ± 0.007	0.114 ± 0.060	31.6	6.6	4/5	21	63 (19)	0.91
C. ruscifolia	FS	0.018 ± 0.010	0.060 ± 0.032	5.7	2.3	4/4	40	100 (22)	0.62
Leucadendron salignum	FS	0.077 ± 0.019	0.161 ± 0.066	1.9	1.4	9/10	71	74 (92)	0.65
L. rubrum	OS	0.010 ± 0.005	0.813 ± 0.433	252.1	81.3	4/10	32	–	1
Leucospermum grandiflorum	OS	0.003 ± 0.002	0.083 ± 0.083	166.7	33.3	2/1	20	–	1
C. erectisepala	OS	0.017 ± 0.006	3.438 ± 0.664	446.3	206.3	7/12	46	–	1

OR obligate resprouter, FS facultative seeder, OS obligate seeder

Plant size has been found to be an important determinant of resprout success. Paula and Ojeda (2006, 2009) found that plants with larger lignotubers had higher mortality rates after disturbance and this was assumed to be related to age, i.e. older plants with bigger lignotubers have been exposed to more disturbed events that may have depleted their bud banks (Drewa et al. 2002). In contrast, other studies have found that plants with smaller lignotubers had higher postfire mortality (Stohlgren et al. 1984; Moreno and Oechel 1991). In our study, the largest individuals were among the OR, but there was considerable overlap in size among life history types. Across different life histories and also within the FS, there was no clear difference in mortality related to lignotuber size.

Plants with more exposed lignotubers were less likely to resprout after the fire, which may be related to heat-induced damage to the exposed lignotuber (Drewa et al. 2002). We do not know why some lignotubers were more exposed than others. Our slope measurements were not related to lignotuber exposure and there were no obvious species differences. Also, we did not observe animal activities that could explain the movement of soil that could expose lignotubers.

Fire severity was not linked to mortality per se. This conclusion is based on measuring minimum branch diameters to estimate fire severity. Because we used different species, this may have introduced errors that confounded our analyses. To address this, the association between branch diameter and mortality was analysed separately for each FS species that suffered mortality due to fire. We found no significant correlation between fire severity and branch diameter suggesting that fire severity was not a significant factor affecting mortality (Drewa et al. 2002). We do not think this result is due to any unusual aspect of the fire site we studied. Our site contained areas that had a broad range of fire severities with most of the site experiencing moderate fire as evidenced by the amount of standing biomass and ash left behind (Fig. 1). The fire was also typical of the fynbos fire regime in timing (about 20 years after the last fire and during the hot and dry rainless season).

The final step in re-establishing after fire is surviving after resprouting. Within 2 years, after the fire, many of the FS species exhibited resprout mortality. Virtually all of the resprout mortality occurred during the summer dry season, suggesting that the hot and dry summer months may have played a role in mortality among some FS species (Pratt et al. 2014). Pratt et al. (2012a) found that OR species were more vulnerable to water-stress-induced cavitation than FS species, suggesting that OR species would be more vulnerable to drought. However, OR species did not succumb during the summer months indicating that they avoided water stress. Early and rapid growth may have allowed the OR to support their extensive existing root systems, and to avoid significant root dieback due to carbon limitations. This may have allowed them to maintain ample access to soil moisture during the summer, and thus avoid water stress. Moreover, the stem xylem of OR is more efficient (greater xylem specific hydraulic conductivity), which would allows OR stems and leaves to maintain less negative water potentials for a given transpiration rate assuming an equal leaf area supplied by the stem xylem for both life history types (Pratt et al. 2012a). By contrast, the FS may be more shallowly rooted or have less carbohydrate stores that led to mortality of roots due to carbohydrate starvation. Shallower roots for the FS could have led them to experience greater water stress (West et al. 2012), and may have superseded their increased resistance to water stress leading to mortality. More work is needed to test the role of root mortality and pruning on the survival of resprouts.

Resprout success is hypothesised to be determined by three factors: fire survival; resprouting vigour; and post-resprouting survival (Le Maitre et al. 1992; Malanson and Trabaud 1988; Moreira et al. 2012). This hypothesis is significant in that it recognises resprouting as a complex process that may be limited at different stages. The observation that some species die after resprouting suggests that in some cases mortality is ultimately controlled by factors other than fire (Le Maitre et al. 1992). This hypothesis also emphasises the importance of plant traits as a determinant of resprout success. Some traits recognised as being important in the resprout process are carbohydrate storage and adventitious bud traits (Clarke et al. 2013; Jones and Laude 1960; Vesk and Westoby 2004b). However, there are many other traits, particularly related to carbon balance, that are likely under strong selection in resprouters (Moreira et al. 2012). The present study lends support to the hypothesis of resprouting as a multi-stage process and that certain plant traits are linked to resprout success. We find all three of the above-mentioned factors are important in limiting FS species from resprouting and

surviving, when compared to the highly successful co-occurring OR species.

The role of phylogeny is an important factor that needs to be considered in resprouts success. This was a natural experiment comparing co-occurring species with different life history types, thus we had little ability to control for phylogenetic effects with our taxon sampling. FS and OR are generally distant relatives, thus contrasting closely related taxa, as had been frequently done to study OS and FS types (Schwilk and Ackerly 2005), is not a generally viable approach (however see Crandall and Platt 2012). There are other approaches to controlling the role of phylogeny in comparative studies (Bond and Midgley 2003; Harvey and Pagel 1991), and additional studies using these methods will be valuable. However, phylogeny may not be a chief factor explaining resprout success if there are traits that are strongly associated with resprout success (Clarke et al. 2013). This is because these traits are likely to be under strong selection that takes place after every fire. We found that variables that were significant predictors of resprout success were generally significant when analysed in models that excluded the OR species. This indicates that our conclusions about the importance of these variables are robust and independent of the phylogenetic differences between OR and FS taxa. Consistent with this, resprout success and predictors of resprout success were found to vary intraspecifically, i.e. in a phylogenetic independent fashion (Moreira et al. 2012).

The goal of this study was to compare resprouts success between FS and OR life history types and determine factors that contributed to this success. Because of the intensive nature of the sampling to address these goals we were limited to one field site, which limits the scope of the present study.

Conclusion

Our findings confirm that resprouting is influenced by multiple factors and that resprouters are heterogenous, which supports the distinction of OR and FS life history types. This is consistent with the hypothesised trade-off between persistence and longevity on the one hand, as exemplified by the OR, and recruitment of seedlings and shorter life span on the other hand, exemplified by the obligate seeders, with the facultative seeder life history type falling in between these two extremes.

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