

Resilience of mediterranean shrub communities to fires

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Abstract

All mediterranean shrub communities are resilient to wildfires at a frequency range of every 20–50 years. These communities, however, are not unique in this respect. Many non-mediterranean shrub communities are dominated by species capable of resprouting and thus are resilient to occasional wildfires. Certain mediterranean shrub communities are unique in that they are dominated by species which have specialized their reproductive cycle to fires. These species recruit seedlings only in the first postfire year and since the burned shrubs are incapable of vegetative regeneration, they are referred to as obligate seeding shrubs. Such species require fires for rejuvenation and population expansion. Communities dominated by obligate seeding species are not resilient to wide deviations from this modal fire frequency. Fires at shorter intervals readily eliminate species with this life history mode. Likewise, extremely long intervals between fires could eliminate such species, though the upper limit of tolerance is unknown. California chaparral obligate seeding shrubs are largely resilient to fire-free intervals of 100 years or more but this may not be universally true for obligate seeding shrubs in other regions. Mediterranean-climate shrub communities dominated by resprouting shrubs are resilient to a much shorter fire recurrence interval. Certain of these species however fail to establish seedlings after fire and it appears that these obligate resprouters require extended fire-free periods for seedling establishment. Many of these resprouting species are capable of continually rejuvenating their canopy by sprouting from the base and there is reason to believe that communities dominated by such species would be resilient to very long fire recurrence intervals. The abundance of species with different life history modes varies between the different mediterranean-climate regions as well as along geographical gradients within regions. Thus, resilience of these communities is spatially variable.

Introduction

By most definitions mediterranean-climate shrub communities would be considered resilient to fires. Following such a perturbation, community structure is altered only briefly and, under most burning regimes, the species composition at a given time after fire does not change appreciably from one fire cycle to the next.

Consider for example the response of California chaparral to wildfires which typically kill all aboveground biomass (Fig. 1). The evergreen sclerophyllous shrub component re-establishes itself rapidly after fire by resprouting from belowground vegetative parts and/or by recruitment of seedlings from soil-stored seed. Also in the first spring there is a flush of deciduous suffrutescent and herbaceous plants which arises from soil-stored seed, or

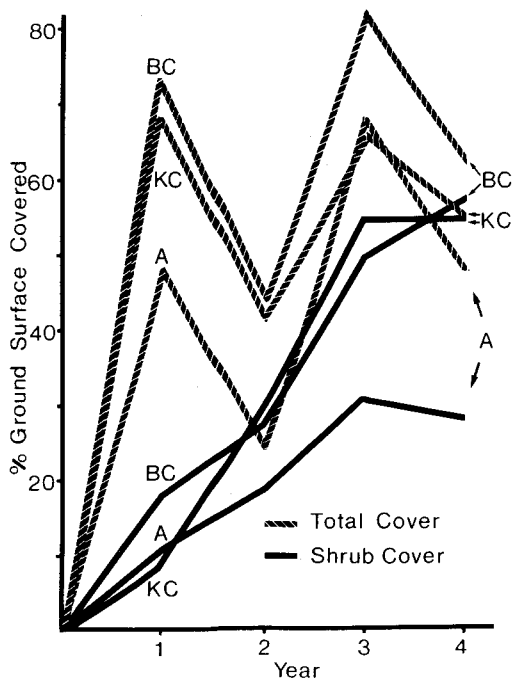


Fig. 1. Postfire changes over four years in total cover (temporary herbaceous and suffrutescent species plus shrubs) and shrub cover alone in California chaparral: A = a low elevation site, BC = a mid-elevation site and KC = a high elevation site (from Keeley & Keeley 1981).

dormant bulbs or other underground parts. As the shrub cover closes in, this temporary component returns to its prefire dormant state. Concomitantly, the relative abundances of shrub species return to prefire levels as the species which recruited large numbers of seedlings are thinned out. If we define resilience in terms of rapid return to the pre-perturbation (equilibrium) state, then both the 'successional' and 'climax' components of the chaparral are highly resilient to fire. This paper will explore the factors responsible for this resilience.

Community resilience

Attempts to understand community resilience simply in terms of changes in species diversity following perturbation are unlikely to tell us much about the mechanisms responsible for community resilience. The resilience of plant communities to perturbations is a function of the composite re-

siliences of the assemblage of different species populations in the community. Different life histories will carry with them different resiliences to perturbation.

In Californian chaparral there is a diversity of life history types which respond quite differently to fire (Table 1). Some species of dominant evergreen shrubs establish very few seedlings but these shrubs are vigorous resprouters. At the other extreme are obligate seeding shrubs which establish many seedlings but are incapable of resprouting. These modes of reestablishment produce very different demographic patterns after fire (Fig. 2). Obligate seeders survive fire only as a dormant seed pool in the soil. Recruitment is restricted to the first year after fire, producing a large even-aged cohort, which suffers extreme mortality (and intense selection?) after every fire. Obligate resprouters in contrast show little demographic change after fire and they regain their original cover more rapidly than obligate seeders. Other shrub species have a mixed mode of recovery involving both seedlings and resprouts (Table 1).

Chaparral has a wide array of non-evergreen subordinate species which are abundant in the first few years after fire and gradually decrease in importance (Fig. 1). Their response to fire shows as great a range as with the dominant evergreen shrubs (Table 1). Just contrasting the different perennial components of this 'successional' flora we see that subshrubs and suffrutescents establish largely from seed whereas herbaceous perennials establish from vegetative sprouts. As the dominant shrub canopy closes, all of these species become a minor part of the flora, but each exploits a different form of refuge until the next fire. Subshrubs and suffrutescents largely survive as dormant seeds in the soil, although they may remain within gaps in the canopy. Herbaceous perennials often lie dormant as tubers or bulbs in the soil until the next fire, although in favorable years they may initiate leaves under the canopy. Vines (both herbaceous and woody) respond to fire in the same manner as herbaceous perennials, although they are able to grow into the canopy and thus are active, both vegetatively and florally, each year.

Even in annuals, which by definition must all

Table 1. Postfire reproductive and regenerative characteristics of the various plant life history types in Californian chaparral.

	Seed germination		Resprouting potential	Lignotuber
	After fire	In fire-free interval		
Dominant evergreen shrubs:				
Obligate resprouters (OR)	nil	low	v. high	induced
Facultative resprouters (FR)	high	0	moderate	ontogenetic
Obligate seeders (OS)	v. high	0	0	-
Subshrubs/suffrutescents	high	low	nil - low	none
Herbaceous perennials/vines	nil	low	high	ontogenetic (fleshy tubers)
Annuals:				
Opportunistic-annuals	high	low-moderate	0	-
Fire-annuals	v. high	0	0	-

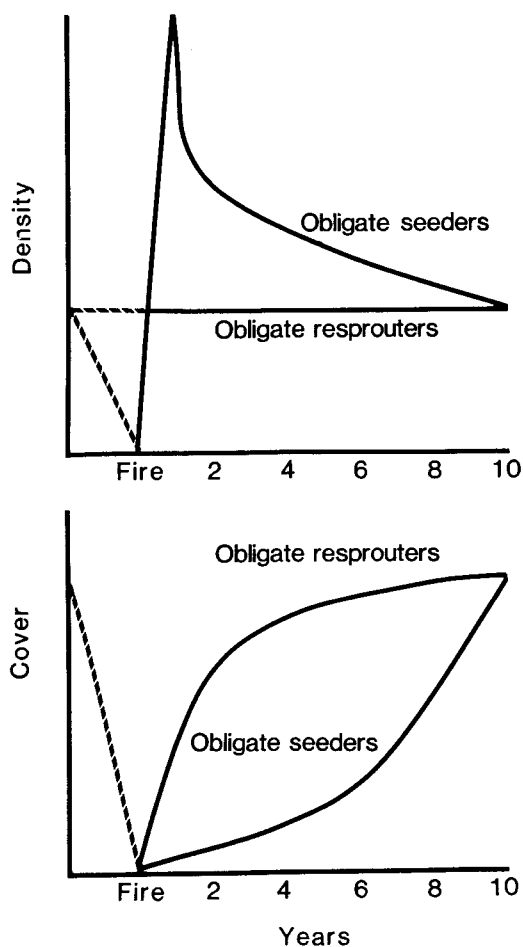


Fig. 2. Schematic description of demographic changes in obligate resprouters and obligate seeders in the immediate postfire environment.

establish from seed, we see a range of demographic patterns. Some species are present in gaps in mature chaparral and are seldom prominent after fire. Others readily colonize and establish in gaps but are most prominent after fires. Still others specialize on the postfire environment and are otherwise quite rare. It is clear from the different seed germination characteristics observed for annuals (Table 2) that there has been selection for different germination physiologies in these different modes. At one extreme are annuals which germinate readily, and at the other extreme are species with refractory seeds that show a very marked dependence upon some cue, in this case charred wood, to indicate a postfire environment. Between these extremes are a great many annuals that have a mixed strategy in which a quarter to a third of the seeds germinate readily and another portion of the seed pool requires a fire related cue such as heat pulse or charred wood.

In summary, resilience of the chaparral community to fires is a function of species specific mechanisms.

Resilience to fires: costs

It is clear from theoretical as well as field work done since MacArthur and Wilson (1967) introduced the concepts of r- and K-selection, that resilience to perturbation often selects for species

Table 2. Germination of chaparral annuals in response to heat shock and charred wood (J. & S. Keeley unpublished data). Treatments with the same superscript are not significantly different at $P < 0.05$ with one-way ANOVA and Fishers Least Significant Difference test.

Species	Percentage germination		
	Control	120° C (5 min)	Charred wood
<i>Antirrhinum nuttallianum</i>	69 ^a	56 ^a	58 ^a
<i>Cordylanthus filifolius</i>	57 ^a	27	62 ^a
<i>Camissonia hirtella</i>	30 ^a	66	26 ^a
<i>Lotus salsuginosus</i>	24 ^a	40	20 ^a
<i>Gilia capitata</i> (burn)*	20 ^a	25 ^a	69
<i>Gilia capitata</i> (mature)	15 ^a	27 ^a	67
<i>Silene multinervia</i>	36 ^a	43 ^a	83
<i>Antirrhinum coulterianum</i>	2 ^a	3 ^a	42
<i>Emmenanthe penduliflora</i>	0 ^a	0 ^a	75

* Seed collected from a burned site and an adjacent mature chaparral stand.

which specialize and even become dependent on disturbances. Examples from chaparral are the 'fire-annuals' such as *Emmenanthe penduliflora*. This species' life cycle is restricted to the first postfire year after which it largely 'disappears' until the next fire. The degree of specialization to this environment is illustrated by the fact that its seeds germinate only in the presence of charred wood (Table 2). Often such specialization carries with it a cost in terms of resilience to lack of perturbation. Thus, a question related to my overall focus is, how resilient are mediterranean shrub communities to fire-free intervals? This is relevant because wild-fires are likely to have played a stochastic role in the evolution of chaparral and other mediterranean-climate taxa.

'Temporary' vegetation

In the case of many annuals, polymorphic seed germination behavior (Table 2) may account for the persistence of certain species in an environment in which fires are an unpredictable component. A portion of the seed pool of a single species lies dormant until fire and another portion responds to conditions within gaps in the mature chaparral canopy. If the fire-free intervals were long enough we might expect selection for an increasingly larger portion of the seeds to be non-fire dependent, assuming of course that the polymorphism is genetic. However, such lability could be non-adaptive in

that as the fire-free interval increases, the probability of fire increases. The marked similarity in germination between *Gilia capitata* seeds collected from plants on a first year burn and from plants in an adjacent mature chaparral stand, indicates that plants in canopy gaps have not 'tracked' the environment in this manner (Table 2).

There are however other, 'safer', ways of tracking the environment. *Salvia mellifera* is a semi-deciduous subshrub often found in gaps within the chaparral canopy as well as after fire. Its germination behavior shows that seeds in the dark largely require the cue of charred wood for germination (Table 3). However, that same portion of seeds germinate readily when exposed to the light and this response is greatly enhanced when seeds are exposed to alternating diurnal temperatures such as would occur near the soil surface of a gap in the mature canopy.

Therefore, for short-lived species, there may be various mechanisms for ensuring their presence under extended fire-free conditions.

Obligate resprouters vs obligate seeders: role of fire frequency

Reproductive characteristics of obligate resprouting species and obligate seeding species likewise suggest differences in resilience to fire recurrence intervals of various lengths (Table 4). Obligate seeding shrubs, specifically species of *Ceanothus*

Table 3. Seed germination of the semi-deciduous chaparral subshrub *Salvia mellifera* after heat treatment or with charred wood (n = 3 dishes of 50 seeds each) (J. Keeley unpublished data). Treatments were compared with one-way ANOVA.

Incubation	Percentage germination					
	Control	70° C (1 hr)	70° C (5 hr)	120° C (5 min)	Charred wood	P
Constant 23 °C						
Dark	1	2	5	0	24	<0.01
Light	23	24	17	25	25	>0.05
23 °C day/13 °C night						
Dark	4	5	9	3	37	<0.01
Light	50	54	55	50	55	>0.05

and *Arctostaphylos*, require 5–25 years for seed crops sufficient to replenish the seed pool in the soil. Fires at more frequent intervals may eliminate these species from chaparral (Arnold *et al.* 1951, Zedler *et al.* 1983). These shrubs produce substantial seed crops annually or biennially. In general, obligate seeding shrub species do not have well developed dispersal properties and their long-lived seeds require a germination cue from fire such as heat or charred wood as observed for the fire-annuals.

On the other hand, obligate resprouting species, e.g., *Heteromeles arbutifolia*, *Quercus dumosa*, *Prunus ilicifolia*, *Rhamnus* spp. and *Cercocarpus betuloides* are quite resilient to frequent burning. These species also have a marked competitive advantage over obligate seeders during the first decade after fire. Resprouters recover rapidly and even begin producing seed crops at an early (resprout) age. Fruit crops are often substantial and in some, *H. arbutifolia* for example, fruit production is usually annual. These species are quite unlike obligate seeding species in that their seeds are adapted for long-distance dispersal via birds (fleshy berries and acorns, Bullock 1978, Hom 1984) or

wind (plumose achenes). Uniformly, these seeds are short-lived (J. Keeley unpublished data) and thus a seed pool does not accumulate in the soil. This, coupled with the observation that these seeds are generally quite sensitive to high temperatures, explains why seedling recruitment does not occur after fires. The lack of postfire seedling recruitment, particularly in light of the large energetic investment in seed production, suggests that these species are poorly adapted to the fire-prone chaparral environment, or as Paul Zedler suggests, ‘these species failed to consult their genetic counselor’.

In the absence of fires these obligate resprouting species often gain dominance over obligate seeding species. An example of this is seen in a very old stand of scrub oak chaparral in southern California. *Quercus dumosa* is the clear dominant at this site which has remained unburned for >100 years (Table 5). Such stands are often described in the literature as ‘decadent’, ‘senile’ or ‘senescent’, terms which I prefer to avoid. These terms are based largely on the observation that certain species, often obligate seeders, are dying out, as is the case with *Ceanothus crassifolius* in this stand. How-

Table 4. Reproductive characteristics of obligate resprouting and obligate seeding shrubs in California chaparral.

	Time after fire to substantial fruiting	Fruit crops	Dispersability	Seed longevity	Unusual germination requirements
Obligate resprouters (OR)	2 yrs	Mod-High	High	1–2 yrs	None
Obligate seeders (OS)	5–25 yrs	Mod-High	Low	>100 yrs (?)	Heat Charred wood

ever, several of the sprouting species in the stand are not dying out and in fact appear to represent a relatively stable community. There are several reasons for this. These obligate resprouter species:

- (1) are quite long-lived,
- (2) they continually rejuvenate their canopy by initiating new sprouts from their bases in the absence of fire,
- (3) they apparently require fire-free intervals of 100 years or more for recruitment of new individuals.

These patterns are illustrated for *Q. dumosa* where the age distribution of stems on established shrubs (Fig. 3A) indicates continual recruitment of

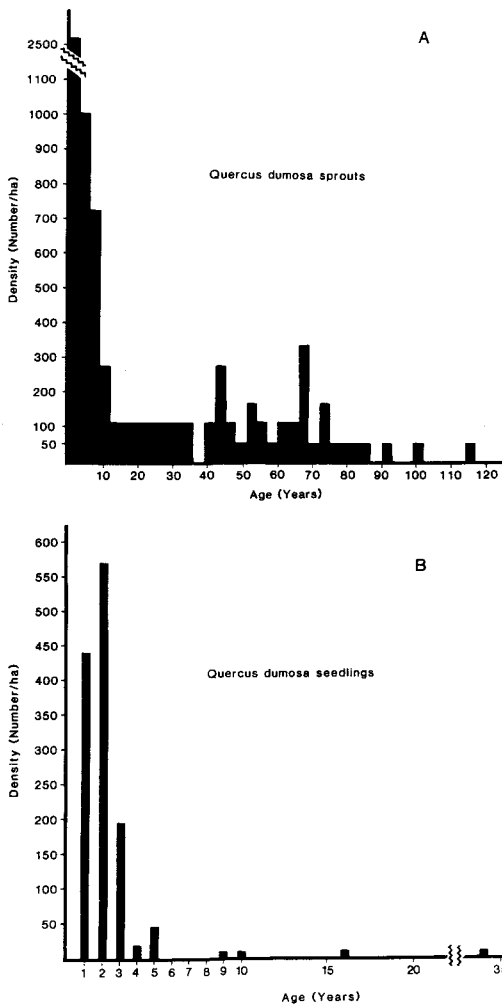


Fig. 3. Age distribution of *Quercus dumosa* (A) stems arising from established rootcrowns and (B) seedlings, in the same stand shown in Table 5.

shoots into the canopy. Active seedling recruitment by this species is also occurring in the stand (Fig. 3B). Although it is not apparent from these figures, there is a gap (of >60 yrs) between the oldest 'seedling' (defined as an individual not arising from a well-established rootcrown present since the previous fire >100 years ago) and the shrub population. The largest seedling, at 34 years, was <1 m tall which is far below the upper canopy height of 3 m. It appears that population expansion requires long fire-free periods but even then the rate of successful seedling recruitment into the population is low.

These conclusions are true for all of the obligate resprouting species mentioned above, with the caveat that seedling recruitment is never very abundant. In addition to a long fire-free period, seedling establishment requires a mesic site with a well developed litter layer and possibly a temporal pattern of high precipitation, which produces a substantial seed crop, followed by above average precipitation for successful seedling establishment (Zedler 1981, 1984).

I suggest that obligate resprouting and obligate seeding shrubs differ in their resilience to high and low fire recurrence intervals in a pattern like that shown in Fig. 4. All species are resilient to a burning regime with a recurrence interval between 10 to 100 years.

Obligate resprouters are tolerant of large deviations from this regime and require extended fire-free periods for seedling establishment and *population expansion*. Thus, in chaparral, the species

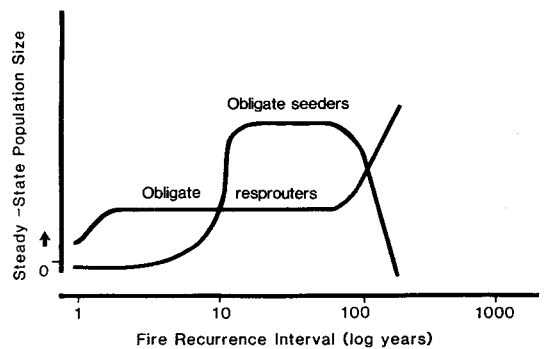


Fig. 4. Hypothetical resilience of obligate resprouters and obligate seeders across a range of fire recurrence intervals in Californian chaparral.

which are the least specialized to fire, are the species most resilient to the greatest range of fire frequencies.

Obligate seeding species are clearly specialized to fire-prone environments and *population expansion* is dependent upon fires. However, this is specialization with a vengeance in that fires at too frequent intervals produce localized extinction. Very long fire-free periods may likewise be intolerable, although the upper limit to combined plant and seed longevity may exceed 200 years. Clearly the species most highly specialized to the chaparral fire cycle are also the least resilient to the full range of possible fire frequencies.

California chaparral is an assemblage of shrubs with different resiliences. Why haven't these species converged in their life history responses to fire? One hypothesis is that their coexistence is dependent upon a fire regime of variable recurrence intervals. These community patterns may have been favored in the past by a stochastic pattern of natural (lightning) fires. While some view fire frequency as a deterministic process (a predictive event closely tied to fuel load), in pre-human times ignition sources were not ubiquitous in time and space (Keeley 1977b, 1982).

Obligate resprouters vs obligate seeders: role of habitat selection

Another factor which could explain the wide range

of fire responses is the observation that obligate resprouting and obligate seeding species are not distributed randomly across the landscape. In fact obligate resprouting species are commonly replaced by obligate seeding species on more xeric or nutrient deficient sites. In general, the latter species are most successful on equator-facing slopes, on ridge tops and on the desert slopes of most ranges (Fig. 5).

Table 6 gives an example of the overall success of one obligate seeding species on mesic vs xeric slopes. On the drier slope, plants are significantly larger, suffer less mortality and produce many more seeds than on the mesic slope.

On xeric sites the patterns observed as chaparral ages may be quite unlike those observed for the pole-facing stand dominated by the obligate resprouter *Quercus dumosa* (Table 5). Table 7 describes a very old chaparral stand on a site noticeably more xeric than the *Q. dumosa* site. Dominating this drier slope is the obligate seeding *Arctostaphylos glauca*. In this stand, unburned for 88 years, there were no seedlings of any species. The apparent vigor of the shrubs suggests that this site could remain free from fire for a much longer period without significant changes in community composition.

There are morphological and physiological differences which, within limits, we can ascribe to obligate resprouters and obligate seeders (Miller 1981) and which may explain some of the spatial

Table 5. Pole-facing slope of southern California chaparral unburned for >100 years (J. Keeley unpublished data).

		Density (individuals/ha)	Basal coverage (m ² basal area/ha)
<i>Quercus dumosa</i> (OR)*	Alive	3400	31.1
	Dead	700	1.5
	Seedlings	1300	<.1
Other			
	Obligate resprouters (4 spp)		
	Alive	2100	5.0
	Dead	200	0.8
	Seedlings	1000	<.1
Facultative resprouters (2 spp)	Alive	2200	4.4
	Dead	400	2.5
Obligate seeder (1 spp)	Alive	600	5.7
	Dead	1100	4.8

* OR = obligate resprouter.

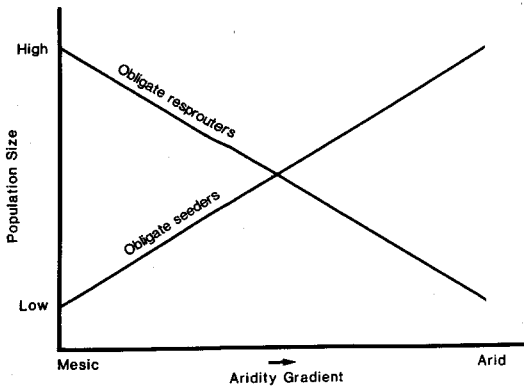


Fig. 5. Apparent 'success' of obligate resprouters and obligate seeders in relation to aridity of the site.

variation in distribution of these types (Table 8). Obligate resprouters have very extensive root systems which, in most years, can tap deep underground soil moisture reserves throughout the summer drought (Fig. 6). To some extent these shrubs are drought avoiders and are seldom exposed to the same degree of water stress as the shallow-rooted obligate seeders. These sprouters however have poorer stomatal control and carbon uptake is stopped at much lower water stress than is the case with the more drought tolerant obligate seeders. Under adequate soil moisture conditions, obligate seeders often have much higher stomatal conductances and higher growth rates. These species also have highly specialized leaf structures such as the deeply sunken stomatal crypts of *Ceanothus* (section *Cerastes*) or the near vertical amphistomatous isofacial leaves of many *Arctostaphylos* species. Although the physiological mechanism is unclear, it is obvious from field observations that obligate seed-

ers are readily shaded out by other shrubs whereas obligate resprouters are markedly shade tolerant.

In summary, obligate resprouters and obligate seeders are syndromes which reflect selection for a suite of characters (Table 9). Safe sites for obligate resprouters are deep soils or fissures in the substrate with underground water available during the summer drought (at least in most years). Such sites are distributed in patches across the landscape. To find such sites these species were selected for high dispersability and immediate establishment. Once a favorable microsite is found it is held for a long time through continued replacement of the canopy (e.g., Fig. 3A) and repeated resprouting after fires. Obligate seeders have less critical demands in terms of soil depth. These species readily establish on most substrates. They have rapid growth rates and high drought tolerances, factors which may be physiologically linked to low shade tolerance. They readily establish after fire and are maintained in gaps between sprouters. Thus as the frequency of safe sites for sprouters goes down the abundance of safe sites for seeders goes up (Fig. 5). Once established, new sites are available only after disturbance, typically fire. Seed longevity is great and since fires will come to them, dispersability is low.

Thus, while different life history types have different resiliences to fire, different environments favor different life history types. Therefore it is to be expected that community resilience will vary across the distributional range of environments for that community type. Coexistence of obligate seeders and obligate resprouters may be enhanced by spatial heterogeneity of suitable habitats as well as temporal heterogeneity due to fire frequency.

Table 6. Pole- vs equator-facing slope comparison of the obligate seeder *Ceanothus crassifolius* in southern California (n = 30). Shrubs were 24 years old at the end of the study (J. & S. Keeley unpublished data). Slope faces were compared with a two-tailed t-test.

	Pole-facing	Equator-facing	P
Total plant cover (% ground surface)	>100%	<80%	-
<i>C. crassifolius</i>			
Height (m)	2.6	2.6	ns
Areal coverage (m ² /individual)	2.6	5.6	<0.01
Mortality over 6 years (%/year)	2.9	0	<0.01
Fruit production over 6 years (fruits/m ² areal coverage)	254	481	<0.01

Table 7. Equator-facing slope of southern California chaparral unburned for 88 years (J. Keeley unpublished data).

		Density (individuals/ha)	Basal coverage (m ² basal area/ha)
<i>Arctostaphylos glauca</i> (OS)*	Alive	2000	41.8
	Dead	1700	8.1
<i>Ceanothus crassifolius</i> (OS)	Alive	1400	17.3
	Dead	2800	16.6
<i>Adenostoma fasciculatum</i> (FR)	Alive	5200	21.9
	Dead	4900	9.7
<i>Quercus dumosa</i> (OR)	Alive	200	2.3
	Dead	30	<.1

* OS = obligate seeder, FR = facultative resprouter, OR = obligate resprouter.

Table 8. Morphological and physiological comparison of obligate resprouters and obligate seeders in Californian chaparral (from Miller 1981).

	Rooting depth (m)	Minimum xylem water potential (MPa)	Xylem water potential@ stomatal closure (MPa)	Maximum stomatal conductance (cm s ⁻¹)	Tolerance	
					drought	shade
Sprouters	>>1	-4	-2 to -4	2 to 4	Low	High
Seeders	<1	<-6	-6 to -8	3 to 5	High	Low

Table 9. Obligate resprouter and obligate seeder syndromes of the dominant evergreen shrubs in Californian chaparral.

	Sprouters	Seeders
Development:		
Safe sites	Deep soil, fissures	Gaps between sprouters
Drought tolerance	Low	High
Growth rates	Low-moderate	High
Shade tolerance	High	Low
Longevity		
Shrub	V. great (continuous replacement of canopy with sprouts)	Moderate
Seeds	Nil	V. Great
Demography:		
Distribution of safe sites	Patches	Widespread after fires
Dispersal	High potential	Low potential
Recruit seedlings	Under canopy	Fire created gaps
Population expansion	In absence of fire	After fire
Tolerance		
High fire frequency	Very tolerant	Intolerant
V. low fire frequency	Very tolerant	Weak tolerance

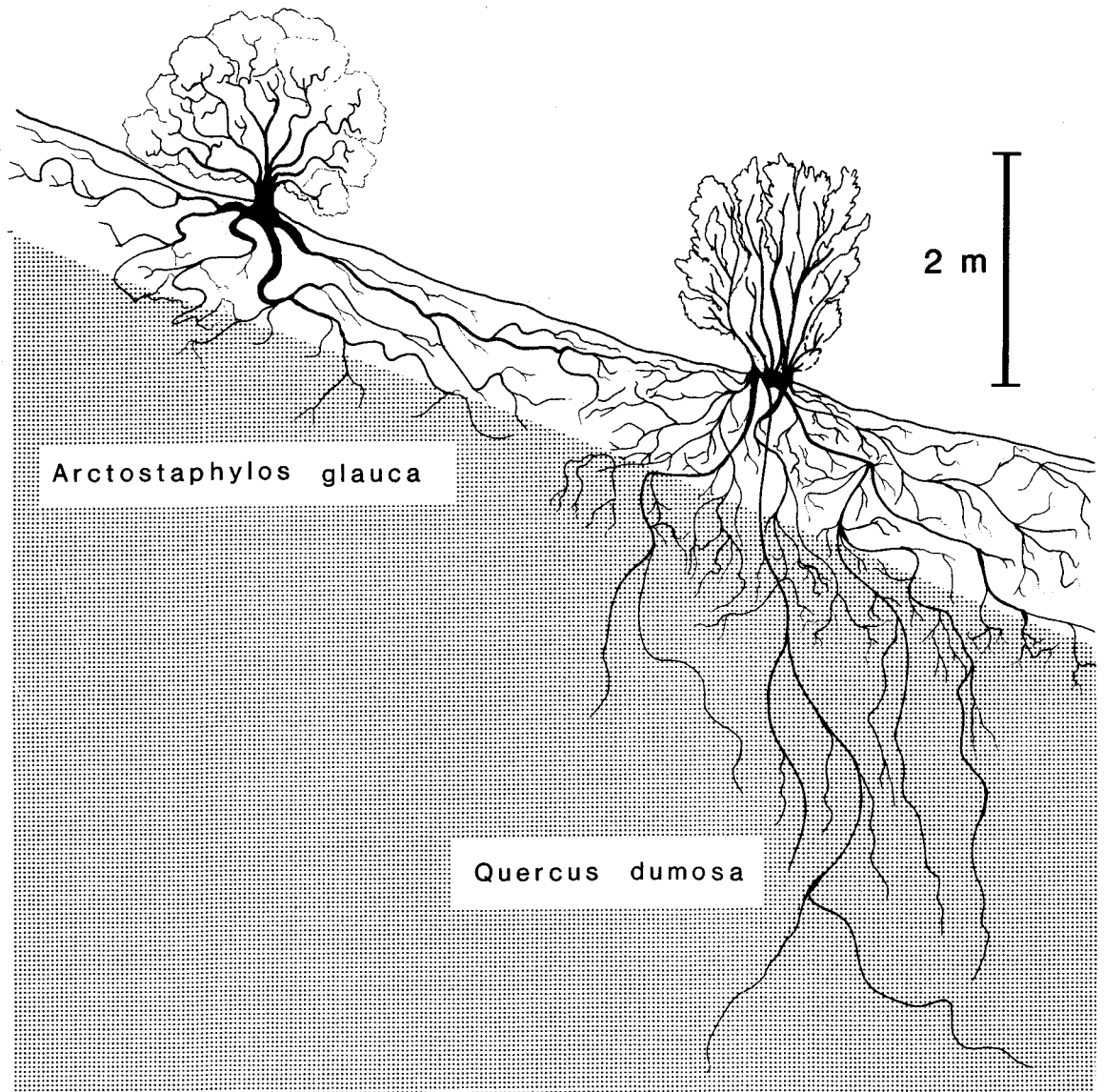


Fig. 6. Root distribution of an obligate seeder *Arctostaphylos glauca* and an obligate resprouter *Quercus dumosa* (redrawn from Hellmers *et al.* 1955, by T. Montygierd-Loyba).

Facultative resprouters

Intermediate to these extremes are species which combine the characteristics of obligate resprouters and obligate seeders. By sprouting, these shrubs are clearly more resilient to frequent fires than obligate seeders and they are potentially more resilient to long fire-free periods because of their ability to replace their canopy with new basal

sprouts in the absence of fire in the same manner as observed for *Quercus dumosa* (Fig. 3A). Unlike obligate resprouters, these facultative resprouters do not recruit new individuals into the community in the absence of fire and thus they are dependent upon fires for population expansion. *Adenostoma fasciculatum* is one of the most important of these species and is dominant on relatively xeric sites. In some respects this species is a 'switch-hitter', i.e.,

behaving as a seeder on some sites and a sprouter on other sites (Keeley 1977b). Also, in terms of rooting depth and physiology, *Adenostoma* exhibits remarkable flexibility (Miller 1981). *Arctostaphylos* and *Ceanothus* are two other genera with facultative resprouting species. In general, these species occur in more mesic microsites than congeneric obligate seeding species (Keeley 1977b, Musick 1972, Ball *et al.* 1983).

In view of the ability of these facultative resprouters to couple both resprouting and seeding in their mode of postfire recovery, the advantages to obligate seeders become blurred. Clearly it would seem that a species which could both resprout and recruit seedlings after fire might have an advantage over species limited to just seedling recruitment. Why haven't chaparral communities converged to assemblages of facultative resprouters with the elimination of obligate seeders?

One advantage to obligate seeding could be related to the fact that facultative resprouting species produce a lignotuber at the seedling stage and continuing throughout their lifespan. Such a structure undoubtedly carries with it an energetic and nutrient cost. Allocation arguments suggest that there may be trade-offs between the advantages of lignotuber formation and additional seed production to be gained by eliminating the basal burl (Keeley and Keeley 1977).

Under what conditions would this be favored? In some respects we could think of closely-related obligate seeders and facultative resprouters representing contrasts similar to annuals vs perennials or semelparity vs iteroparity with years or lifespans, respectively, being replaced by fire cycles. Based on arguments proposed by Charnov and Schaffer (1973), an obligate seeder would have to increase its offspring production each generation by a factor which is a function of seedling survival until fire and probability of sprouting shrubs surviving fire.

I have attempted to evaluate these trade-offs in an iterative computer model of competition between facultative resprouters and obligate seeders. In this iterative model equal numbers of sprouter seeders and obligate seeders are positioned along a one dimensional axis with the same canopy width but a maximum of 50% overlap. In this model each

shrub disperses propagules. Fires result in the killing of all obligate seeder shrubs and a portion of the sprouters. For simplicity all seeds are allowed to germinate and any within proximity of a resprout (half the radius of the mature canopy) do not survive. It is assumed that seeds of sprouters and seeders are equal in survival and thus thinning is imposed randomly by type with the stipulation that the mature plant canopies do not overlap by more than 50%. This model is then iterated through a series of fire cycles but under different conditions of sprouter mortality and proportion of seed production by sprouters vs obligate seeders.

Fig. 7A shows the behavior of these populations over a period of many fire cycles under conditions of 20% sprouter mortality each fire cycle, but with equal seedling establishment after fire. Not surprisingly after 20 generations the obligate seeder goes extinct. Other simulations show that depending upon the level of sprouter mortality and the differential in seedling establishment between seeders and sprouters, one can get different outcomes (i.e., obligate seeders 'winning' as in Fig. 7B or coexistence as in Fig. 7C). Numerous simulations of this model allow a comparison of how postfire mortality interacts with the proportion of sprouter-seeder seed production (Fig. 8). From this model we see that as the postfire mortality of sprouters increases, the seed production differential necessary for obligate seeders to 'win' decreases. This in itself is not surprising, but it does provide predictions which could be empirically tested.

The very limited field data available do support these conclusions in a qualitative way. For example, sprouting *Ceanothus* generally have similar seed production and seedling establishment levels as do obligate seeding species of *Ceanothus* and the sprouters in this genus also typically suffer very high mortality. *Arctostaphylos* sprouting species on the other hand suffer low mortality and the differential in seedling establishment between these species and congeneric obligate seeders is high (e.g., Keeley 1977a, Keeley and Zedler 1978). However, what remains unknown is the mechanism responsible for these differences. In one study the obligate seeding *A. glauca* produced 6 times

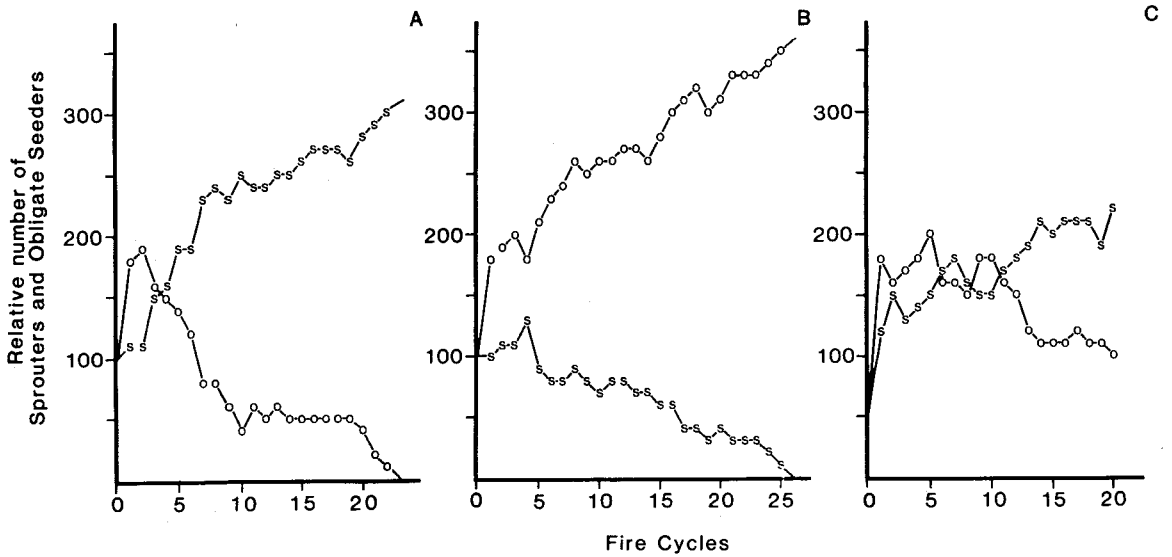
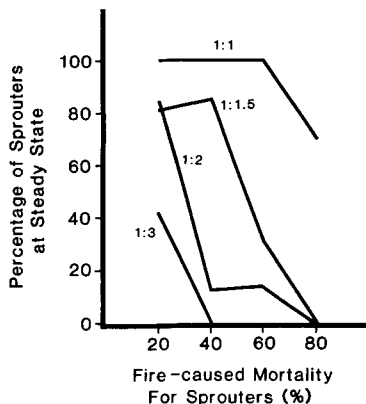


Fig. 7. Outcome of facultative resprouter (s) vs obligate seeder (o) competition model. Simulations are with: (A) equal seed production for both types and 20% fire-caused mortality of the sprouter; (B) three times greater seed production for the obligate seeder and 20% fire-caused mortality of the sprouter (but doubled to 40% every fifth fire cycle); (C) two times greater seed production for the obligate seeder and 20% (but 40% every fifth fire cycle) fire-caused mortality of the sprouter – the general pattern observed here remained unchanged for >100 fire cycles.

more seedlings after fire than the equally abundant sprouting *A. glandulosa* (Keeley 1977a). However, over 10 years of fruit production data indicate that the sprouting species actually produces greater numbers of fruits (J. and S. Keeley, unpublished data). The fruits of the obligate seeding species are much larger though, and over this 10 year period that species allocated approximately 6 fold greater

biomass to reproduction than the sprouting species.

There are other considerations. As Wells (1969) pointed out, the obligate seeding mode results in a greater number of sexual generations and the potential for a greater fine-tuning of adaptation. This may have allowed for the evolution of specialized xerophytic adaptations. An additional advantage to obligate seeders may be in accelerated seedling growth rates due to the abandonment of the lignotuber and the laying down of adventitious buds. Both of these factors – closer evolutionary tracking of the environment and faster seedling growth rates – may have been far more important in the evolution of obligate seeders than any energetic or nutrient advantage accrued by not producing a lignotuber.



Comparison with other mediterranean shrub communities

Postfire regeneration characteristics for all five mediterranean-climate shrub communities are compared in Table 10. It is clear that there are

Fig. 8. Summary of the influence of seed production differential (between sprouters and seeders) and sprouter mortality, on the steady state proportion of sprouters (numbers on the curves give the proportion of sprouters:seeders propagule production).

Table 10. Comparison of postfire regeneration characteristics for the five mediterranean shrublands (+++ = very abundant, ++ = abundant, + = present, 0 = absent).

Fire response	California	Mediterranean	Chile	South Africa	Australia
Evergreen sclerophyllous shrubs:					
Obligate seeders					
(Seed storage in soil):	+++	(0)	0	+	+
(Seed storage on plant):	(+)	0	0	+++	+++
Facultative resprouters:	+++	++	+	++	++
Obligate resprouters:	++	+++	+++	++	++
Non-evergreen subshrubs & suffrutescents:					
Seeding	+++	+	+	+	+++
Sprouting	+	+	+	++	++
Herbaceous perennials:					
Seeding	0	0	0	0	0
Sprouting	+	++	++	+++	++
Annuals					
Opportunistic annuals:	++	+	+	+	+
Fire annuals:	+++	0	0	(0)	(0)

marked regional differences in life history attributes. This suggests that the communities may differ in their resilience to fire.

Obligate seeding shrubs

The Mediterranean maquis or garrigue and the Chilean matorral are distinctly unlike chaparral in the lack of the obligate seeding mode in the dominant evergreen shrub vegetation (Naveh 1974, Mooney 1977). In the case of Chile, evidence discussed by Mooney (1977) indicates that natural fires may have been an uncommon part of the evolutionary landscape. Considering their obvious specialization to fire, this may be sufficient explanation for the lack of obligate seeders in that region.

The Mediterranean represents a potentially different situation since natural lightning fires were apparently part of the evolutionary past (Le Houerou 1974). Naveh (1984) claims anthropogenic factors have played a major role in shaping vegetation structure in this region and it is distinctly possible that fire frequencies have increased markedly over the past 10,000 years (Naveh 1975). As a matter of conjecture it is possible that obligate seeders have been eliminated under such a regime (e.g., Fig. 4). It is clear from experimental work in

the garrigue of southern France (Trabaud and Lepart 1981) that this sclerophyllous shrubland is much more resilient to frequent fires than the California chaparral. However, other factors cannot be excluded. For example the bulk of the Mediterranean maquis and garrigue vegetation is at much higher latitudes than the Californian chaparral; thus climate can not be ruled out as playing a role in the balance of different life history types in this region.

Sclerophyllous shrublands in Australia and South Africa have a number of obligate seeding species (Kruger 1979, Gill and Groves 1981). As noted earlier for chaparral, there is evidence from the Australian heath that obligate seeding species increase in abundance with increasing aridity and decreasing foliage cover (Specht 1981).

In the Australian heath important obligate seeding species occur in the genera *Banksia*, *Hakea* (Proteaceae) and *Casuarina* (Casuarineaceae). In South African fynbos obligate seeding shrubs occur in the genera *Leucadendron*, *Protea* (Proteaceae) and *Erica* (Ericaceae). As is the case with *Arctostaphylos* and *Ceanothus* in Californian chaparral, these genera are relatively large and also have a number of lignotuberous resprouting species. The conclusions drawn from Californian chaparral on the resilience of obligate seeding shrubs largely

hold for fynbos and Australian heath. Fires at recurrence intervals less than 10 years can produce localized extinction (Gill and Groves 1981, Russell and Parsons 1978, Bond 1984, McMahon 1984b). Kruger and Bigalke (1984) proposed a model for resilience of fynbos obligate seeders vs resprouters (Fig. 9) with marked similarities to the model proposed earlier for chaparral (Fig. 4). Obligate seeders in both regions show reduced resilience to fires when the frequency deviates from some modal level. Kruger and Bigalke however consider resprouters at a disadvantage under a fire frequency of 20–30 years, something not observed in chaparral.

The obligate seeding shrub flora in South African fynbos and Australian heath differs from Californian chaparral in the abundance of species which store seeds on the plant rather than in the soil. In many species seeds are retained within woody fruiting structures and are released after being heated by fire. This trait is widespread in the Proteaceae, Myrtaceae and Casuarinaceae, but it is not restricted to obligate seeding species (Beadle 1940, Gardner 1957, Specht *et al.* 1958, Kruger 1979). As a result of this storage characteristic, the seeds of these species seldom possess a dependence on any fire related cue such as heat shock or charred wood and they germinate readily upon dispersal (Kruger 1979, Bond 1984, Zammit 1984). This is in marked contrast with chaparral shrub seeds which are stored in the soil and require a cue of heat or charred wood for germination. The southern hemisphere obligate seeders thus allocate a much greater amount of energy and nutrients to seed *protection*, but ultimately produce orders of magnitude fewer seeds than chaparral obligate seeders (c.f., Keeley 1977a, Cowling and Lamont 1984).

It is unclear what evolutionary forces have selected for seed storage on the plant as opposed to in the soil. Possibilities include:

1) Different phylogenetic lines may have been predisposed to one mode over another; e.g. hard seededness is more widespread in the Ericaceae and Rhamnaceae than the Proteaceae, Myrtaceae and Casuarinaceae. It may have been developmentally simpler for these southern hemisphere plant

families to adapt their reproductive cycle to a fire prone environment by modifying the timing of seed release rather than of seed dormancy. Such an argument may also apply to the few coniferous tree species associated with chaparral which possess serotinous cones.

2) There may be greater seed predation pressure in the southern hemisphere plant communities which could select for greater protection of seeds (Breytenbach 1984, O'Dowd and Gill 1984). My experience has been that although seed harvesting ants are common in disturbed areas they are uncommon under mature chaparral (see also Hunt 1977).

3) Different fire regimes may have selected for these different modes of seed storage. Soil-stored seeds of chaparral obligate seeders are quite long-lived and can outlive the parent plant by a considerable period of time. In fynbos and heath, seeds stored on the plant are released and germinate with the death of the parent plant, regardless of fire (Gill 1976). Since successful seedling establishment usually (Hazard and Parsons 1977, Bradstock and Myerscough 1981), but not always (Hnatiuk and Hopkins 1980), requires fire, southern hemisphere obligate seeding shrubs may be even less resilient to long fire-free periods than chaparral obligate seeders. There is some evidence that this may be true. Bond (1980) showed that seedling densities in fynbos were much less after fire in 40–45 year old stands of Proteaceae than after fire in 20 year old stands. Kruger and Bigalke (1984) contend that obligate seeders in fynbos will decline steadily in importance as the average fire recurrence interval exceeds 30 years (Fig. 9). This is in marked contrast to obligate seeders in chaparral which will readily re-establish with fire recurrence intervals exceeding 100 years (Keeley and Zedler 1978, Keeley unpublished data).

Resprouters

Shrubs capable of sprouting from basal or underground vegetative parts are major constituents of all five Mediterranean shrub vegetations. Sprouting species which also produce lignotubers as a normal developmental stage are common in Cal-

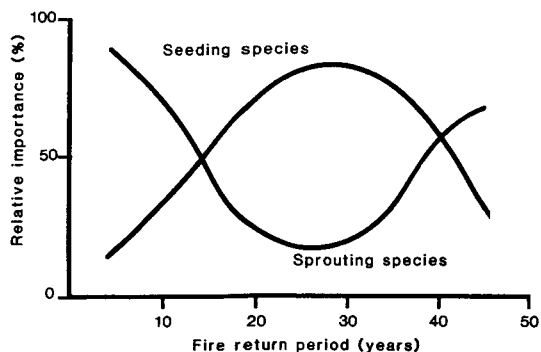


Fig. 9. Resilience of obligate seeding and resprouting fynbos species relative to average fire frequency (redrawn from Kruger & Bigalke 1984).

ifornian chaparral, South African fynbos and Australian heath and mallee, but apparently absent from the Mediterranean Region. The fact that shrubs from *most* non-mediterranean-climate regions lack this trait, despite, in some cases being exposed to frequent fires, argues strongly for its presence being a function of climate as well as fire (Gill 1975, Keeley 1981).

There is some evidence that sprouting species in other mediterranean systems share with chaparral shrubs the characteristic of continual sprouting throughout their lifespan, and thus rejuvenating their canopy in the absence of fire (Cochrane 1963, Holland 1969). This characteristic, coupled with the ability to resprout after fire, suggests that sprouting shrubs in all mediterranean regions would be resilient to both very short as well as very long fire recurrence intervals.

The postfire recruitment of seedlings by resprouting shrub species in other mediterranean regions shows the same range of responses as seen in Californian chaparral, i.e., obligate resprouters and facultative resprouters.

Obligate resprouters

All five mediterranean-climate sclerophyllous shrublands have dominant species which owe their presence after fire solely to resprouting. Such species dominate the Mediterranean Region scrub, e.g. *Quercus coccinea*, *Pistacia lentiscus* and *Rhamnus* spp. and the Chilean scrub, e.g. *Lithraea caustica*, *Schinus latifolius* and *Quillaja saponaria*. De-

spite poor seedling recruitment after fire these species are capable of substantial fruit production. As is the case with obligate resprouters in chaparral, most of those species listed above produce propagules suggestive of long distance dispersal. There are no data on when or how frequently these species recruit new individuals into their populations.

Facultative resprouters

Shrub species capable of resprouting and establishing seedlings after fire are important components of Californian chaparral, South African fynbos and Australian heath. This type of shrub is less common in the other regions although examples exist, e.g., *Arbutus unedo* in the Mediterranean (Naveh 1975) and *Trevoa trinervis* in Chile (Keeley and Johnson 1977).

Non-evergreen subshrubs, suffrutescents and herbs

In the Mediterranean there are a number of non-evergreen subshrubs similar to Californian species such as *Salvia mellifera*. These, e.g., *Cistus* and *Cytisus* species, are most important on xeric and nutrient poor sites and are often successional after fire in sclerophyllous shrublands. Many, if not all of these species are capable of resprouting; however, like *S. mellifera*, they are sensitive to fire intensity and under most burning regimes are functionally obligate seeders. They establish on burned sites from soil-stored seed which is dormant until stimulated to germinate by fire (Juhren 1966, Papanastasis and Romanas 1977). The rapid growth rate and early flowering of these species makes them resilient to relatively frequent fires. Their dormant seed pool and ability to survive in refuges of extremely xeric or nutrient deficient sites makes them resilient to very long fire-free periods.

The suffrutescent growth form (including both chamaephytes and hemicryptophytes) is important in fynbos and heath, represented for example by many taxa in the family Restionaceae. Seedling establishment is rare in these species but all are vigorous resprouters after fire (Kruger 1979, Specht 1981, van Wilgen and Kruger 1981). These plants often play a successional role and may be

replaced 15–20 years after fire (Kruger 1983). They are however capable of vegetative spread, and in open stands, there is evidence that they can remain important regardless of fire (McMahon 1984a). Nutrient poor soils and frequent fires in these regions keep the vegetation more open than is typical of chaparral, and these factors promote the persistence of this element (Low 1984).

All five mediterranean systems have a flora of herbaceous perennials, especially geophytes. In all regions their presence in the postfire environment is the result of sprouting from bulbs or corms. There is no evidence that any of these species have seeds which are stored in the soil and cue germination to the immediate postfire environment. However, all such species flower prolifically in the first year after fire, and some species have been noted to only flower after fire (Levyns 1966, Martin 1966). These species are resilient to relatively frequent fires. In the absence of fire they are capable of extended dormancy and there is no evidence that they die out (Taylor 1978).

Annuals

Californian chaparral is unique amongst the mediterranean systems in its abundant and diverse annual flora with life histories closely linked to fire. The lack of such a flora in Chile (Keeley and Johnson 1977) may be tied to the apparent lack of fire in that environment. In the Mediterranean there are annuals present in burned sites, though most of these species are not restricted to burns and they readily colonize other disturbances (Naveh 1974). The long history of anthropogenic factors in that region may have played a role in selecting for 'generalist-type' colonizing species. In South Africa and Australia annuals do not comprise a major part of the temporary postfire flora (Adamson 1935, Martin 1966, Gill and Groves 1981). Possibly the extreme nutrient deficiency of soils in these two regions makes the annual life history a non-viable option.

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