

## TEMPORAL AND SPATIAL DISPERSAL SYNDROMES

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### INTRODUCTION

The role of wildfires in the reproductive biology of mediterranean climate shrubs has dominated attention of ecologists for a long time. In California chaparral and other ecosystems species are conveniently designated as resprouters or seeders. Some taxa, referred to as "obligate resprouters" have long been noted to regenerate after wildfires strictly by resprouting and examples are present in all mediterranean communities (Keeley 1986). These species seldom if ever recruit seedlings after fire, in contrast to "facultative" or "obligate seeding" species. This feature of the postfire response has led to analysis of these life history differences in terms of various theories such as r- and K-selection. Very simply put, postfire seeders colonize postfire environments with masses of seedlings and thus are presumably r-selected whereas obligate resprouters are viewed as K-selected.

Based on arguments of Cody (1966), r-selected seeders should allocate a greater proportion of resources to seed reproduction than resprouters, however, this is not well supported. Based on a few studies and a great deal of casual observation, it appears as though there is little evidence that postfire obligate resprouters are allocating any less energy to reproduction than postfire seeders (Keeley and Keeley 1977, 1988, Mooney 1977, Zedler 1981). In other words obligate resprouting shrubs allocate a lot of energy to reproduction, yet they fail to establish seedlings after fire. This state of affairs has led Paul Zedler to ask, half-jokingly, "should these species consult a genetic counselor?" Indeed, it has been suggested that due to their conservative mode of postfire regeneration, these resprouters have not kept up with the pace of evolution seen in seeders (Wells 1969, Raven 1973). I suggest an alternative interpretation of these patterns, based on differences in dispersal strategy.

### DISPERSAL STRATEGIES IN CHAPARRAL

Chaparral shrubs can be conveniently divided into 1) temporal dispersers and 2) spatial dispersers.

#### Temporal Dispersers

Taxa such as Adenostoma, Arctostaphylos and Ceanothus produce refractory seeds that are stimulated to germinate by heat shock or charred wood generated by wildfires (Keeley 1991). Seedling recruitment by these species is restricted to the first growing season after fire, arising

from a persistent seed bank. These species might best be referred to as "fire recruiters" or "gap dependent" species. Dispersal is largely passive and the bulk of the seed pool is distributed near the parent (Keeley 1991). Safe sites for successful seedling recruitment are spatially abundant but temporally rare. Thus, these species are selected to develop a persistent seed bank that disperses the seeds in time rather than in space.

### Spatial Dispersers

Taxa such as *Quercus*, *Rhamnus* and *Prunus* are obligate resprouters after wildfires. Lack of postfire seedling recruitment arises from the fact that these species have a transient seed bank (Parker and Kelly 1989); their seeds are not refractory and germinate soon after dispersal (Keeley 1991). Seeds are bird dispersed and potentially are moved quite widely, at least relative to temporal dispersers (Fig. 1).

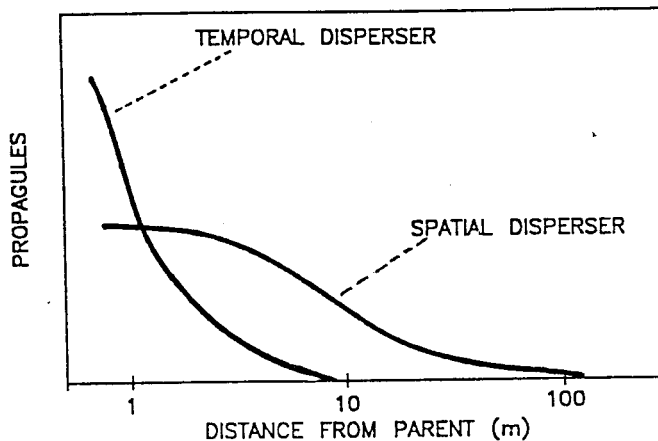


FIGURE 1. Dispersal curves for temporal and spatial dispersers.

I suggest that the differences observed in reproductive mode between temporal and spatial dispersers arises from differences in the distribution of safe sites for seedling recruitment.

### Safe Sites for Seedling Recruitment

As mentioned, safe sites for temporal dispersers occur only after fire. Safe sites, however, for spatial dispersers are present between fires, although the abundance may increase with time since fire (Fig. 2). Recent studies indicate that seedling recruitment by these spatial dispersing taxa is most frequent in older stands of chaparral (50 - 100 yrs without fire) (Lloret and Zedler 1991, Keeley still in review). On such sites seedlings are generally restricted to the deep litter layers beneath the shade of the shrub canopy; these species might be described

as "gap avoiding" species (Table 1).

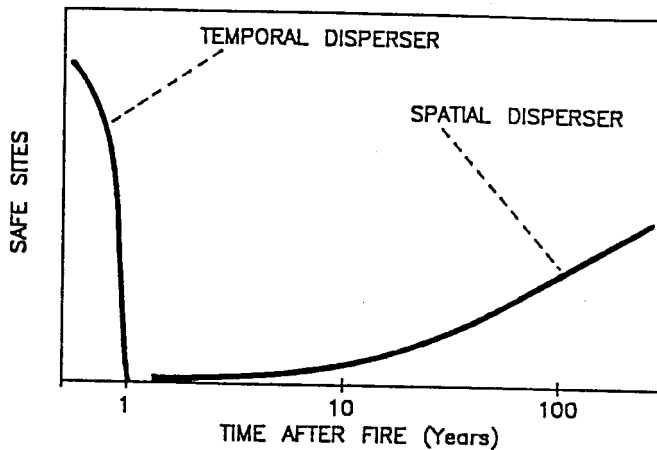


FIGURE 2. Distribution of safe sites after fire.

TABLE 1. Seedling density, irradiance and litter depth in canopy gaps and beneath the shrub canopy of an 89 yr old stand of chaparral (N = 50 plots of 2m x 2m,  $\bar{X} \pm$  S.D., from Keeley still in review).

	Canopy Gaps	Beneath Canopy	P
Seedlings/plot	0.0 + 0.0	12.6 + 9.5	< 0.001
Irradiance (% of full sun)	95 + 7	22 + 11	< 0.001
Litter depth (mm)	1 + 5	69 + 32	< 0.001

#### Selection for Dispersal Strategies

In arid land systems drought plays a fundamental role in the evolution of shrub taxa. Some are conveniently described as drought toleraters and others as drought avoiders (Mooney and Miller 1985).

Drought toleraters are physiologically able to withstand extreme water stress. All temporal dispersers, *Adenostoma*, *Arctostaphylos* and *Ceanothus* are well described as drought toleraters as they are able to withstand extremely low xylem water potentials ( $\ll -7$  MPa) (Poole et al. 1981). This was likely selected because most or all of the population must develop its root system *de novo* after each fire. As a consequence they have rapid growth rates on open sites but are shade intolerant (Schlesinger et al. 1982).

Drought avoiders have very deep root systems and avoid low xylem water potentials by penetrating deep rock fractures that store water. Spatial dispersers are all deep rooted drought avoiders. Since these shrubs resprout after fire, well established individuals may have massive root

systems. Based on xylem characteristics these shrubs are described as having a high mesomorphy ratio (Carlquist and Hoekmann 1985), which likely contributes to their inability to withstand low water potentials; these shrubs will succumb at xylem water potentials markedly higher than is lethal for temporal dispersing species. One consequence of this strategy is that seedlings of these spatial dispersers are particularly vulnerable to soil drought and readily succumb on sites where seedlings of temporal disperser species thrive (Davis 1989). Thus, safe sites for spatial dispersers are microsites where water stress is minimized and the subsurface topography is sufficiently fractured to allow for deep penetration of roots.

#### Distribution of Safe Sites

Safe sites for temporal disperser species exist during a narrow window of time, but because fires are effective in clearing the landscape, safe sites occupy a large proportion of the landscape.

Safe sites for spatial disperser species are present during a much longer duration of time but the conditions necessary for successful seedling establishment are such that they represent a relatively small portion of most arid landscapes. In addition they are likely distributed in widely scattered sites.

There are theoretical reasons (Green 1983, Ellner and Shmida 1981) for suggesting that as the proportion of the landscape suitable for seedling establishment decreases, selection will favor adaptations that increase the breadth of the dispersal curve (Fig. 1). Therefore, the fleshy fruits of Rhamnus and Prunus or the meaty acorn of Quercus are readily understandable as adaptations for wide dispersal by birds.

Based on the observation that adult shrubs of Quercus and other spatial dispersers appear to be very long lived and relatively immune to mortality, I would guess that seedling recruitment into the adult population is a relatively infrequent event. If the probability of a propagule finding a safe site for establishment is extremely low, then there should be selection for increasing the opportunities; viz., searching each season rather than once per fire cycle as in temporal dispersers. Thus, having non-refractory seeds that germinate soon after dispersal, but fail to accumulate a persistent seed bank, would be favored in these spatial dispersers.

#### SUMMARY

A summary of characteristics associated with these two dispersal syndromes is given in Table 2.

Many of these characteristics may be interpreted as coevolved traits. For example, large seed size in spatial dispersers may reflect the low light conditions of safe sites. Late season fruit maturation may reflect selection for seed dispersal as close to winter germination period as

possible, in order to reduce predation and other losses (likely to be greater due to large size) and utilize dispersal services of migratory birds.

TABLE 2. Temporal vs Spatial Dispersers

TAXA	TEMPORAL DISPERSERS	SPATIAL DISPERSERS
	----- <u>Adenostoma</u> <u>Arctostaphylos</u> <u>Ceanothus</u>	----- <u>Quercus</u> <u>Rhamnus</u> <u>Prunus</u>
DISPERSAL MODE	PASSIVE	ANIMAL
BREADTH	NARROW	WIDE
SAFE SITES	POSTFIRE GAPS	MESIC, FRACTURED SUBSTRATES
SEED GERMINATION	FIRE DEPENDENT	SEASONAL
SEED BANK	PERSISTENT	TRANSIENT
ROOT/SHOOT	LOW	HIGH
MESOMORPHY INDEX	LOW	HIGH
DROUGHT TOLERANCE	HIGH	LOW
SHADE TOLERANCE	LOW	HIGH
SEED SIZE	SMALL	LARGE
FRUIT MATURATION	SPRING	SUMMER-FALL

Although space does not permit a detailed comparison here, there is abundant evidence in the literature that these two syndromes are present in other mediterranean ecosystems.

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