14 Coupling Demography, Physiology and Evolution in Chaparral Shrubs

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14.1 Introduction

Historically, since fire is a recurrent catastrophic disturbance, mediterranean-climate shrubs have been classified by their mode of postfire regeneration, i.e., obligate seeders, facultative seeders or obligate resprouters. While these terms are useful, they are too restrictive in that they only refer to a species' response to fire and do not adequately describe modes of reproduction for all taxa.

Two modes of seedling recruitment in mediterranean climate regions are (1) *disturbance-dependent* species that restrict recruitment to postfire conditions (gap species) and (2) *disturbance-free* species that successfully recruit only in the long-term absence of fire (gap-avoiding species). The former exploit post-fire environments for population expansion and the latter require unusually long fire-free conditions for population expansion.

Here I will contrast these two recruitment modes, provide evidence that they are closely tied to physiological patterns of water use, and speculate on the evolutionary scenario around their development.

14.2 Disturbance-Dependent (Gap) Recruitment

Disturbance-dependent species establish seedlings in the first year after fire, and rarely do so in later years. Demographically, these species are characterized by dense cohorts of even-aged shrubs that thin dramatically with time after fire. Mature shrubs produce fruits that are not animal dispersed but tend to be deposited locally; being dormant the seeds disperse more in time than in space (Keeley 1992c). Seedlings arise after fire from a long-lived "permanent" soil seed bank and germination is cued either by intense heat or by chemical stimulus from smoke or charred wood (Keeley 1991). Such species have been referred to as "seeders." In chaparral many species of

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Arctostaphylos and *Ceanothus* lack the ability to regenerate vegetatively from lignotubers and are often referred to as "obligate seeders." Other species in these genera, and the widespread *Adenostoma fasciculatum*, are referred to as "facultative seeders" because they are capable of regenerating vegetatively, as well as reproducing by seed after fire.

14.3 Disturbance-Free (Gap-Avoiding) Recruitment

In chaparral, species of *Prunus*, *Quercus*, *Rhamnus*, and *Rhus* seldom establish seedlings after fire, however, they resprout vigorously and thus, with respect to fire, are termed "obligate-resprouters." Seedling recruitment occurs in older, more mesic stands and dense cohorts of seedlings are rare (Keeley 1992a,b). Successful reproduction is generally restricted to beneath the shrub canopy and is absent from gaps; recruitment is correlated with, and seemingly facilitated by, more mesic conditions of low light and high litter depth. Mature shrubs produce large fruit crops that are widely dispersed by animals (Keeley 1992c). Soil seed banks are transitory because seeds are short-lived (<1 year) and germinate readily with adequate moisture (Keeley 1991, 1997); a dormant seed bank does not accumulate, accounting for the lack of postfire seedling recruitment.

14.4 Morphological and Physiological Correlates

14.4.1 Root Systems

In general, species with disturbance-dependent recruitment are shallow rooted whereas species with disturbance-free recruitment have substantially deeper root systems (Hellmers et al. 1955; Kummerow et al. 1977). While some of this difference is accounted for by species-specific differences in root development, much of it is likely to be accounted for by vast differences in age of rootstocks. Species with disturbance-dependent recruitment have root masses initiated after the most recent fire, whereas disturbance-free recruiters resprout after fire from root masses that are of considerable age and depth. These latter species have roots that may penetrate bedrock to 9 m or more, or penetrate rock fractures. During summer this weathered rock mantle is capable of holding more water within a matric potential range accessible to shrubs than the overlying soils (Jones and Graham 1993).

14.4.2 Water Relations

Correlated with rooting habit are marked differences in exposure to, and tolerance of, water stress. During summer drought shallow-rooted shrubs are subjected to extremely negative soil water potentials; shallow rooted *Ceanothus* and *Arctostaphylos* commonly have predawn stem xylem water potentials of −6.5 to −8 MPa (Parsons et al. 1981; Poole et at. 1981; Davis and Mooney 1986). These species are capable of tolerating even more extreme water stress, e.g., Schlesinger et al. (1982) reported pre-dawn water potential of −12 MPa for *Ceanothus*. *Ceanothus* and others capable of sustaining extreme soil water potentials have seasonal and diurnal osmotic adjustments (Bowman and Roberts 1985) and Davis (1989, Chapter 17; this volume) anatomical characteristics, which reduce embolism at high tensions, are an important factor in tolerance of high water stress.

In contrast, deep-rooted species of *Quercus*, *Prunus*, *Rhus*, and *Rhamnus* are generally subjected to substantially higher summer water potentials in the range of −3 MPa (Poole and Miller 1981; Oechel 1988; Davis 1989). When exposed to extremely low water potentials, usually only experienced at the seedling stage, they suffer high mortality. Oechel (1988) reported a minimum non-lethal water potential for *Quercus* seedlings of −7.5 MPa, far greater than that observed for a shallow-rooted obligate-seeding *Ceanothus*. Even at more moderate water stress, deep rooted species (e.g., *Rhus*) exhibit stomatal closure at far lower water stress than shallow-rooted species (e.g., *Ceanothus*) (Miller 1981).

The critical role rooting depth plays in tolerance of water stress is illustrated in a study by Thomas and Davis (1989). During the summer drought, deep-rooted *Rhus* (*Malosma*) *laurina* shrubs were exposed to very little water stress whereas shallow-rooted *Ceanothus megacarpus* were exposed to substantially higher water stress. On the other hand, seedlings of both species, having roughly similar root mass development, were exposed to remarkably similar summer water stress. However, the *Rhus* seedlings failed to survive, due to much greater susceptibility to water-stress-induced embolism. *Rhus* exhibits a 50% loss in hydraulic conductivity when branches reach a xylem pressure potential of only −1.6 MPa, whereas the obligate-seeding *Ceanothus* does not exhibit 50% embolism until −11 MPa (Kolb and Davis 1994; Jarbeau et al. 1995; Davis, Chapter 17, this Vol.). These patterns may be tied to differences in the size of pores in xylem pit membranes. In *Rhus*, larger vessels and wider pores contribute to greater xylem efficiency when adults have access to water that is available via deep roots, but contributes to greater vulnerability to embolism when water is limited by lack of sufficient root development, as is the case with seedlings (Jarbeau et al. 1995). Based on anatomical surveys (Carlquist and

Hoekmann 1985), this hypothesis predicts that deep-rooted species of *Quercus*, *Prunus*, *Rhamnus*, *Rhus* and others, produce seedlings that are more vulnerable to drought than shallow-rooted species such as *Ceanothus*.

14.5 Coupling Demography, Physiology and Evolution

Adenostoma, *Arctostaphylos*, and *Ceanothus* have adapted their reproductive biology to exploit wildfires for seedling recruitment and population expansion (disturbance-dependent recruitment). In contrast, *Quercus*, *Rhamnus*, *Prunus*, and *Rhus* have not, and these taxa require long fire-free intervals for seedling recruitment (disturbance-free recruitment). These demographic modes are characterized by character syndromes that reflect physiological and morphological divergence (Table 14.1).

Disturbance-dependent recruitment derives from the ready availability of resources in postfire environments, which have placed high selective value on delaying germination to postfire conditions. Summer droughts in these hot, high light environments, however, have imposed strong selection for physiological tolerance of water stress. As a consequence, these disturbance-dependent species have evolved vascular cells more resistant to embolism and greater osmotic tolerance to extremely low water potentials. Recruitment in postfire gaps has selected for rapid growth rates and may have selected against developmental patterns that generate adventitious buds and lignotubers, leading to the obligate-seeding mode. In turn, this obligate-seeding mode, with the increased frequency of sexual reproduction, may have allowed for a greater physiological and anatomical fine-tuning of adaptation to drought. Additionally, with enhanced drought tolerance, there is less selective value to resprouting, an adaptation which can be interpreted as a means of maintaining an established root system with access to year-round moisture. Safe sites for recruitment are rare in time but when they occur are spatially extensive, putting little premium on mechanisms that enhance spatial dispersal but a high premium on maintenance of deep dormancy, with germination cued to fire.

Disturbance-free recruitment restricts seedling establishment to cooler, low light, moister conditions under the shrub canopy. These species are highly susceptible to drought-induced embolism and thus avoid summer drought by maintaining year-round access to water with deep massive root systems. This drought avoidance strategy works well for adults but makes seedling recruitment in a drought-prone environment precarious, thus, there has been no effective selection for delaying seed germination to postfire conditions, and seeds are neither dormant nor long-lived (Keeley 1997). Additionally, safe sites for seedling recruitment are rare and thus these taxa all have highly attractive animal-dispersed propagules.

Convergent and parallel evolution is evident in the very similar pattern of disturbance-dependent and disturbance-free recruitment in the Mediterranean macchi or garrigue of Europe. Here, *Cistus*, *Cytisus*, and others

Table 14.1. Reproductive syndromes correlated with tolerator and avoider strategies of water stress

Examples:	*Ceanothus* *Arctostaphylos* *Adenostoma*	*Quercus* *Prunus* *Rhamnus*
Water stress mode:	Tolerators	Avoiders
Mechanism:	Physiological Anatomical	Morphological (deep roots)
Potential drought-induced mortality:		
-Adults:	Moderate	Very low
-Seedlings:	Moderate	Very high
Recruitment mode:	Disturbance-dependent	Disturbance-free
Gaps:	Gap species	Gap-avoider
Safe sites:	Burned sites	Under canopy
Availability		
-In time:	10–100 year	1 year
-In space:	Extensive	Limited
Seed dormancy:	Deep	Weak
Seed bank:	Persistent (10–100 year)	Transient (<1 year)
Germination cues:	Heat Smoke, char	(Cold)
Dispersal strategy:	Temporal	Spatial
-Mode:	Passive	Animal
-Shadow:	Narrow	Widespread
-Season:	Spring-summer	Fall-winter
Seed size:	Small	Large
Ecological pattern:		
-Niche width:	Narrow	Wide
Evolutionary pattern:		
-Speciation in chaparral:	Low – very high	Low – moderate
Biogeography Pattern:		
-Chaparral endemics:	>75%	<3%
-Outside North America:	<1%	>75%

are disturbance-dependent whereas many taxa such as *Quercus, Prunus, Rhamnus,* and others require fire-free conditions for recruitment. Particularly remarkable is the marked degree of similarity between California and Europe in the character syndromes tied to these demographic modes (Keeley 1994). The former species have passively dispersed seeds that accumulate in soil seed banks and are fire stimulated, whereas the latter taxa have animal dispersed fruits and transitory seed banks. As in chaparral, disturbance-dependent recruiters such as *Cistus* are physiologically more tolerant of drought stress than disturbance-free recruiters such as *Quercus* (Rundel 1995).

Herrera (1992), however, offers an alternative explanation for such character syndromes. Invoking historical effects, he argues that the regeneration mode in gap-avoiding species is ill-adapted to the mediterranean climate and represents evolutionary inertia. I agree with Herrera on the importance of phylogeny; indeed, it is clearly reflected in that many of the same genera are gap-avoiders in both California and the Mediterranean Basin. The fact that post-fire gap species are much more distantly related between these two regions suggests this is a more recent evolutionary step.

It is noteworthy that the character syndrome expressed by gap-avoiding species in both California and the Mediterranean Basin is widely shared outside of these regions and likely quite ancient. Kollmann (1995) describes the regeneration niche for "fleshy-fruited" shrubs in northern Europe as one in which seedling establishment is greatest under the canopy of mature scrub, largely because this vegetation is the focal point of dispersal. Successful recruitment of saplings, however, is hindered by low light (Kollman and Reiner 1996) and thus successful recruitment is more likely on intermediate "successional" sites that provide better light environments and are somewhat attractive to dispersers. As a consequence of these environmental constraints, Kollman (1995) suggests that there is a relatively narrow window of time during which successful recruitment may occur. If mediterranean climate gap-avoiders share such an evolutionary pathway, an alternative to the view that this syndrome is ill-adapted to the contemporary setting is that the window of opportunity for successful dispersal, seedling establishment, and sapling recruitment has narrowed.

In other words, in the current environment, disturbance-dependent gap species are adapted to recruitment in a postfire environment that is temporary but widespread. The mediterranean climate summer drought has dramatically increased the predictability of such safe-sites for recruitment. Thus, taxa in both California and the Mediterranean Basin, adapted to such conditions, are relatively recently evolved. In contrast, disturbance-free gap-avoiding species are adapted to recruiting in a "niche" that in this contemporary setting is less abundant and spatially disjunct. Prior to the onset of the mediterranean climate, this regeneration niche may have been more widespread and the same may have been true of these species. Today the window has simply narrowed, but it is still there.

14.6 Conclusions

Competition for limiting resources such as water, light and nutrients, selects for different adaptive options. In mediterranean-climate ecosystems some shrub species physiologically *tolerate* extreme summer drought whereas others *avoid* drought by maintenance of deep roots. Seedling access to resources differs from access by adults and thus mode of handling drought stress may greatly affect mode of regeneration (Table 14.1). *Drought tolerators* are capable of establishing on severe sites and thus capitalizing on the predictable availability of high light and nutrients after fire. Many of these species restrict seedling establishment to the immediate postfire environment and thus have disturbance-dependent recruitment. *Drought avoiders* depend upon deep root systems to avoid lethal drought stress, but this strategy is unavailable to their seedlings. Instead, successful reproduction must avoid burned sites and thus these species have disturbance-free recruitment that is generally restricted to more mesic sites under the shrub canopy.

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