

Seed Longevity of Non-Fire-Recruiting Chaparral Shrubs

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CALIFORNIA'S CHAPARRAL is a fire-prone plant community noted for its resilience under a condition of periodic disturbance, recovering by means of both vegetative resprouts and seedling recruitment. Those many shrubs, as well as annuals, that employ the latter means after a fire for completion of their life cycles are described as having "disturbance-dependent recruitment," this made possible by long-lived, deeply dormant seed banks.

It is of some interest that, on the contrary, significantly many members of the dominant woody flora—e.g., species of *Heteromeles*, *Prunus*, *Quercus*, *Rhamnus*, and *Umbellularia*—fail to recruit seedlings after fire and persist in such fire-prone environments because they are vigorous resprouters (Keeley 1992a). So puzzling is this anomaly that one prominent ecologist once remarked that perhaps this component of the vegetation was in serious need of genetic counseling (P. Zedler, personal communication circa 1985)—a rather casual reference to the idea that reproduction might perhaps be tied more to phylogenetic constraints than to adaptive evolution (e.g., Herrera 1992).

Much has been written on fire-stimulated germination of "disturbance-dependent" species, most of which have long-lived seeds that are induced to germinate by either heat shock or chemicals from smoke or charred wood (Keeley 1991, Keeley and Fotheringham 1997). Those species that fail to recruit after fire are known to have "non-refractory" seeds—i.e., those which germinate readily when fresh but may require cold stratification when older (Emery 1988, Young and Young 1992). It is unclear whether the naturally transient nature of such soil seed banks is due to absence of seed dor-

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mancy, resulting in germination of the entire seed bank each growing season, or to naturally short life of the seeds.

The purpose of this study was to investigate the longevity of seeds under different conditions of storage in the laboratory, and the effect of cold stratification and light on their germination.

SPECIES AND METHODS

Species selected for study included the chaparral shrubs *Heteromeles arbutifolia*, *Prunus ilicifolia*, *Quercus berberidifolia*, *Rhamnus californica*, and *R. crocea*, and the often-associated woodland element *Umbellularia californica* (nomenclature according to Hickman 1993). All of these produce fleshy animal-dispersed propagules that mature in fall and winter. After collection at altitudes between 500 and 1000 m in the San Gabriel Mountains, fruits were soaked in water for removal of the pericarp from all but the acorns. The initial germination test, designated as that performed at time 0 (fig. 1), was performed on seeds still moist from soaking. Subsequent germination tests, performed after 1, 6 and 12 months' storage, were of seeds that had been either allowed to dry at room conditions (relative humidity approximately 50%) or stored on trays covered by plastic (90% relative humidity). Testing was carried out by placing 20 seeds in a 10 cm polystyrene Petri dish (with filter paper) and initiating germination by adding 3 ml distilled water. Each treatment was done in triplicate. Treatments tested were: (1) incubation in light with 12-hour photoperiod @ 20°C, (2) incubation in dark @ 20°C, (3) one month's cold-moist stratification prior to incubation as in (1), and (4) two months' stratification prior to incubation as in (1). Mean germination for each treatment was compared statistically with analysis-of-variance test on arc-sine transformed data.

RESULTS AND DISCUSSION

Age Effects

Seeds were tested immediately after collection, and 1, 6, and 12 months later. In all species there was a highly significant effect of age (table 1). In general, peak germination occurred in seeds less than 1 month of age and dropped off rapidly with time (fig. 1). After 12 months' storage, all species exhibited highly significant drops in germination, and half the species—*Heteromeles arbutifolia*, *Quercus berberidifolia*, and *Rhamnus californica*—largely failed to germinate after a year of storage (fig. 1).

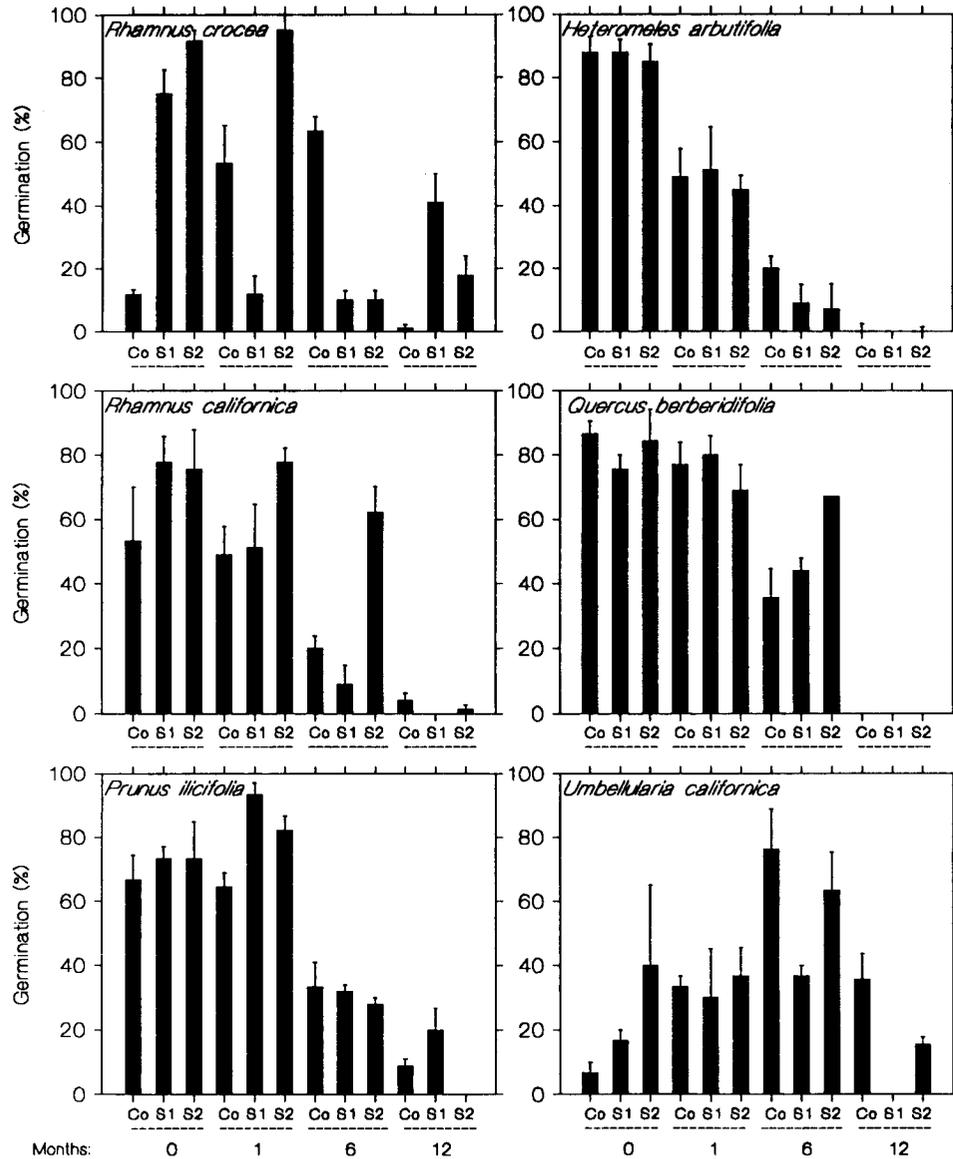


Figure 1. Germination of fresh seeds or seeds aged 1, 6, or 12 months under control conditions (Co), or after cold stratification for 1 month (S1) or 2 months (S2).

Of course, storage conditions may greatly affect seed longevity (Emery 1988, Young and Young 1992). It is recognized that in the cold or under vacuum, seeds can be kept alive for longer periods. Results presented here, however, fairly approximate the longevity of seeds under field conditions.

Other Effects

Storage conditions had a highly significant effect on subsequent germination for all species (table 1), but the response to conditions varied. *Quercus berberidifolia* was highly sensitive to drying, all seeds stored dry for 1 month or more failing to germinate (data not shown). But seeds of *Umbellularia californica* stored best under dry conditions, seeds of all ages stored under humid conditions having significantly less germination (data not shown). All other species also germinated best under dry storage.

Cold stratification had no significant effect except on *Rhamnus californica* (table 1), which germinated best after two months of it. For the other species, cold stratification failed to improve germination, no matter what the seeds' ages. This finding is at odds with the generalization about these species in the literature: that although fresh seed germinates without treatment, "stored seed" often requires cold stratification.

TABLE I
SUMMARY OF ANALYSIS OF VARIANCE IN GERMINATION
IN RESPONSE TO CONDITIONS
(P < 0.01 = highly significant effect; N.S. = not statistically significant)

Species	Age	Storage Conditions	Cold Stratification	Light
<i>Heteromeles arbutifolia</i>	P < 0.01	P < 0.01	N.S.	N.S.
<i>Prunus ilicifolia</i>	P < 0.01	P < 0.01	N.S.	N.S.
<i>Quercus berberidifolia</i>	P < 0.01	P < 0.01	N.S.	N.S.
<i>Rhamnus californica</i>	P < 0.01	P < 0.01	P < 0.01	N.S.
<i>Rhamnus crocea</i>	P < 0.01	P < 0.01	N.S.	P < 0.01
<i>Umbellularia californica</i>	P < 0.01	P < 0.01	N.S.	P < 0.01

Tests for dark inhibition, done only on fresh seeds, indicated that most species were light-neutral (table 1). Only *Rhamnus crocea* and *Umbellularia californica* exhibited slightly significant increases in germination in the dark.

Because of the unusual fruit structure of *Rhamnus crocea*, germination was conducted on two sets of seeds. This species produces a fleshy capsule, as do some Old World species of *Rhamnus* (Izhaki and Safriel 1990). Seeds of these species are not released until the pericarp is removed and the endocarpal capsule dries to a tension sufficient to cause spontaneous opening. After pericarp removal, one set of seeds, still enclosed in their moist capsules, was tested. Without drying, these capsules never opened, and consequently, none of the seeds germinated. All results presented for this species (fig. 1, table 1) were for another set of seeds: seeds that had been ejected from the capsule.

CONCLUSIONS

Many chaparral shrubs restrict seed germination and seedling recruitment to the immediate post-fire environment; they are best described as "disturbance-dependent recruiters." Other shrubs, however, persist in this fire-prone ecosystem strictly by resprouting. They are often termed "obligate resprouters"—a term that describes their regenerative response to fire but says nothing about their mode of reproduction. These latter species, the focus of the present study, restrict seedling recruitment to mature vegetation, often to that in long-unburned stands. They are best described as "disturbance-free recruiters" (Keeley 1992a). Seeds of such species, lacking innate dormancy, will germinate readily after removal of the potentially inhibiting pericarp. If their seeds fail to germinate within the first growing season, it is unlikely that they will survive the summer drought and, hence, that they will ever contribute to recruitment (fig. 1). This accounts for the lack of post-fire seedling establishment in these species.

Failure of these latter species to exploit post-fire conditions for seedling recruitment perhaps can be explained by phylogenetic constraints (e.g., Herrera 1992). As their global distribution implies, genera such as *Quercus*, *Prunus*, and *Rhamnus* are old. Quite possibly their reproductive strategy evolved in a different climate, perhaps one where fire was of minor significance. Their vigorous resprouting ability (a likely pre-adaptation to fire) has prevented their being extirpated from modern fire-prone sites, but phylogenetic constraints may be holding these species back from evolving the ability to exploit the post-fire environment for seedling recruitment.

An alternative may be that there is strong stabilizing selection to maintain the present pattern of disturbance-free recruitment. In California's summer-drought climate it is to be expected that in order to reduce interspecific competition, communities should comprise species with different water-use strategies. Species recruiting after fire—e.g., *Ceanothus*, *Arctostaphylos*, *Adenostoma*—are far more "drought-tolerant" than species recruiting in the absence of fire—e.g., *Heteromeles*, *Quercus*, *Prunus*, *Rhamnus*—and this is tied to physiological and anatomical differences (Keeley 1997). The latter taxa avoid drought stress largely because they maintain extensive root systems capable of tapping water stored in deep soil and rock layers. Although such a "drought-avoiding" strategy is highly effective for adult shrubs, this option is unavailable to seedlings, which cannot begin growth with well-developed root systems. It is likely, therefore, that post-fire sites will be avoided for recruitment, seedlings standing the greatest chance of surviving summer drought beneath the canopy of mature vegetation. Establishment under such conditions has not selected for seed dormancy or seed longevity.

Correlated with the differences in patterns of seedling recruitment are differences in seed dispersal. Species recruiting after fire arise from dormant seed banks that have been dispersed in time. Fires create extensive spatial gaps for recruitment, and in consequence little is to be gained from widespread spatial dispersal of the fruits of such species. But species that recruit in the absence of fire require special microsites: those that are perhaps more mesic or more conducive to rapid establishment of a deep root system. In the case of these shrubs, it follows, there has been selection for fruits that are attractive to animals and hence dispersed throughout the chaparral. It is no coincidence, then, that disturbance-free recruitment is typically associated with fleshy-fruited animal-dispersed shrubs.

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