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# Ecological and evolutionary differences between Mediterranean seeders and resprouters

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**Abstract.** Differences in allocation patterns between seeders and resprouters in several Mediterranean plant communities (Australia, California and South Africa) have led to the prediction that seedlings of seeders grow faster than those of resprouters. In the Mediterranean Basin, it has also been hypothesized that regeneration strategy of plants after fire is associated with several other life history traits. This paper tests both hypotheses for the dominant plants in the Mediterranean Basin from literature data. Results show that seeders from the Mediterranean Basin grow significantly faster and allocate more biomass to leaf plus paracotyledons than resprouters. Seeders are mainly non-sclerophyllous, anemochorous, dry-fruited, small-seeded species that evolved in the Quaternary (post-Pliocene) and are associated with earlier successional stages. Resprouters are mainly sclerophyllous, vertebrate-dispersed, fleshy-fruited, large-seeded species that evolved in the Tertiary (pre-Pliocene) and are associated with late successional stages.

**Keywords:** Fire; Mediterranean shrubland; Seedling growth.

## Introduction

Resprouting and seeding are two regeneration strategies followed by plants after a disturbance, such as fire, in Mediterranean-type ecosystems (Keeley 1986, 1995; Whelan 1995; Bond & van Wilgen 1996). Resprouter taxa have buds in underground organs or in stems that allow them to resprout after fire (James 1984). Seeder taxa die after fire but their released seeds are able to germinate (Hanes 1971; Keeley 1987, 1991; Zedler 1995).

It has been observed that these regeneration strategies differ in resource allocation patterns (Pate et al. 1990; Hansen et al.1991; Bell et al. 1996). Resprouters allocate more of their resources to the underground organs where buds are formed. In contrast, seeders lack these organs and their investment is directed to aboveground growth (Kruger et al. 1997). Hansen et al. (1991) investigated for two congeneric understory shrub-legumes in Australian Mediterranean-type ecosystems and showed that the major investment in seeder species corresponded to shoots whereas that of the resprouter species was to roots. Concentrations of starch have been found to be considerably less in roots of seeder than in resprouter species of *Erica* from South Africa (Bell & Ojeda 1999). Pate et al. (1990) found, across a taxonomically diverse range of juvenile plants from Mediterranean Australia, that seeders generally had a threefold greater total plant dry weight and more than a fourfold greater shoot:root dry weight ratio than resprouters. Other authors have also documented resource allocation differences between seeder and resprouter taxa (Keeley & Keeley 1977; Zammit & Westoby 1987; Pate et al. 1991).

Bond & van Wilgen (1996) argue that these studies provide clear evidence for trade-offs between allocation to roots for future fire survival in resprouters and to shoots for immediate seedling growth in seeders. Because seeders allocate more resources to stems, it is expected that seeder seedlings grow faster than resprouter seedlings. Kruger et al. (1997) found that seeders in South Africa better colonized tall forests because their seedlings grew faster than those of resprouters, acquiring an advantage in this light limited habitat. Following the same arguments, Midgley (1996) found that seeders tended to be taller than congeneric resprouters.

In the Mediterranean Basin, higher seedling growth rates allow seeders to establish rapidly after fires (Lloret 1998), behaving as ‘disturbance-dependent recruiters’. Resprouters that recruit independently of fire behave as ‘disturbance-free recruiters’ (*sensu* Keeley 1998). It has been hypothesized that these two recruitment strategies have several morphological and physiological correlates (reproductive syndromes of Keeley 1998 and functional types of Pausas 1999). Among these correlates, characters such as life span, root systems, seed size, leaf consistency and seasonality, pollination and dispersal type and seedling establishment have also been associated with regeneration strategy after fire (Herrera 1987; Izhaki et al. 1992; Keeley 1995; Keeley 1998; Pausas 1999), although few quantitative analyses have tested this hypothesis (but see Herrera (1987) for a test about the relationship between fruit production and resprouting ability). Herrera (1984, 1992) quantitatively analysed character syndromes of woody plants from the Mediterranean Basin in a different context than fire ecology. With the aim of exploring the evolutionary processes explaining covariation of life-history traits in the flora of Southern Spain, he found that the age of lineage (pre- *vs.* post-Pliocene) significantly distinguished two character syndromes; group I: early colonizers (relative to successional stages), non-sclerophyllous, anemochorous, dry-fruited, small-seeded taxa; group II: late colonizers, sclerophyllous, vertebrate-dispersed, fleshy-fruited, large-seeded taxa. Many characters of Herrera's analysis correspond to the functional types hypothetically linked to Mediterranean seeders and resprouters, so it is possible to quantitatively test the association between these morphological and functional characters and the regeneration strategy after fire.

Based on this theoretical scenario, this paper tests the following hypotheses: 1. Seeders from the Mediterranean Basin grow faster than resprouters. Because high growth rate of seeders must be a consequence of higher allocation to above-ground parts (Bond & van Wilgen 1996), I also tested whether leaf biomass allocation of seeders is higher than that of resprouters; 2. Seeders and resprouters from the Mediterranean Basin correspond to the functional types described by Herrera (1984, 1992).

## Methods

Data for this analysis were obtained from the literature. Innate mean relative growth rate *sensu stricto* (RGRss) and leaf + paracotyledon (green, leaf-like cotyledons) weight fraction (LPWF) data were obtained from Cornelissen et al. (1996). RGRss was the mean relative growth rate, excluding thick cotyledons from plant weight and LPWF was the ratio of total dry weight of leaves plus cotyledons to plant dry weight. Only evergreen shrubs or subshrubs present in shrublands from the Mediterranean Basin were included to avoid differences in growth rate associated with characters, other than regeneration strategies after fire – e.g. leaf habit (deciduous species grow faster than evergreen species) and life form (climbing plants grow faster because they do not need to invest in woody tissue for physical support). The selected taxa were classified as seeders or resprouters based on both literature (Naveh 1975; Allue Andrade 1983; Herrera 1987; Mesléard & Lepart 1991; Keeley 1995; Ojeda et al. 1996; González-Melero et al. 1997; Herranz et al. 1998; Pausas 1999) and personal observations. Taxa were classified according to the dominant strategy utilized. Although intermediate strategies between seeding and resprouting may occur (e.g. resprouting recruiters), there is insufficient information to consider this class. Thus, in this paper, I will only consider the seeder and resprouter strategies.

The final data base contains some of the most abundant species in the Mediterraean Basin communities. In the Mediterranean Basin, most seeders belong to a few families with many species (*Cistaceae*, *Labiatae*, *Leguminosae*) whereas resprouters belong to many families with few species (*Anacardiaceae*, *Rhamnaceae*, *Caprifoliaceae*, *Thymeleaceae*). This extreme taxonomic disparity between seeders and resprouters results in few taxa containing closely related species with different regeneration strategies. Phylogenetically independent contrasts cannot therefore be used to take into account in the common ancestry of taxa.

After checking for normality, RGRss and LPWF were compared between seeders and resprouters by one-tailed *t*-tests, using pooled variance estimations when variances were homogeneous and separate variance estimations when they were not.

To test if recruitment strategy after fire differs between the two character syndromes found by Herrera (1984, 1992), genera included in his analysis were classified as seeders (if seeds germinate after fire) or resprouters (if adults resprout profusely and their seeds usually die after fire). The same statistical test performed by Herrera (1992) – a General Linear Model fitted with Type III sum of squares – was run to compare the mean values of the scores of seeders and resprouters along the first dimension of the Nonmetric Multidimensional Analysis (DIM1 hereafter; see the appendix in Herrera 1992).

## Results and Discussion

The seeder species tested grow significantly faster ($t = 2.08$, d.f. = 5.83, $p = 0.04$, RGRss, Table 1) and allocate more biomass to leaf plus paracotyledons than resprouters ($t = 2.24$, d.f.=12, $p = 0.02$, LPWF, Table 1). These data were collected under controlled environmental conditions (Cornelissen et al. 1996) so it can be deduced that differences are innate. These results are consistent with the prediction that differences in allocation patterns between seeders and resprouters lead to faster seedling growth of seeders than resprouters (Midgley 1996; Kruger et al. 1997). Nevertheless, this interpretation must be taken with caution due to the low number of species tested.

In the Mediterranean Basin, seeders may immediately recruit after or between fires. Lloret (1998) showed that seedlings of seeders had higher growth rates and survival after a wildfire than before and that seedling growth was not correlated with vegetation cover in periods between fires. On the other hand, recruitment of resprouters only occurred during periods between fires, and was positively associated with the presence of vegeta-

**Table 1.** Mean relative growth rate s.s (RGRss) and leaf + paracotyledon weight fraction (LPWF) for seeder and resprouter taxa (data from Cornelissen et al. 1996). S = Seeder, R = Resprouter.

| Species | Strategy | RGRss | LPWF |
|---|---|---|---|
| *Calluna vulgaris* (*Ericaceae*) | S | 0.054 | 0.599 |
| *Cistus albidus* (*Cistaceae*) | S | 0.099 | 0.845 |
| *Cistus clusii* (*Cistaceae*) | S | 0.083 | 0.776 |
| *Cistus laurifolius* (*Cistaceae*) | S | 0.113 | 0.797 |
| *Helianthemum squamatum* (*Cistaceae*) | S | 0.046 | 0.690 |
| *Rosmarinus officinalis* (*Labiatae*) | S | 0.107 | 0.681 |
| Mean seeders | | 0.083 ± 0.011 | 0.731 ± 0.036 |
| *Arbutus unedo* (*Ericaceae*) | R | 0.076 | 0.702 |
| *Daphne gnidium* (*Thymeleaceae*) | R | 0.056 | 0.527 |
| *Pistacia lentiscus* (*Anacardiaceae*) | R | 0.067 | 0.737 |
| *Quercus coccifera* (*Fagaceae*) | R | 0.050 | 0.451 |
| *Quercus rotundifolia* (*Fagaceae*) | R | 0.049 | 0.427 |
| *Rhamnus alaternus* (*Rhamnaceae*) | R | 0.054 | 0.640 |
| *Rhamnus lycioides* (*Rhamnaceae*) | R | 0.064 | 0.601 |
| *Viburnum tinus* (*Caprifoliaceae*) | R | 0.055 | 0.713 |
| Mean resprouters | | 0.058±0.003 | 0.599±0.042 |

tion cover (i.e. *Arbutus unedo, Pistacia lentiscus, Daphne gnidium*; Mesléard & Lepart 1991; Verdú & García-Fayos 1996, 1998; García-Fayos & Verdú 1998). In this ecological scenario, where wildfires release resources for establishment, seeders may benefit from high seedling growth rates while adult resprouters are resprouting.

Recruitment strategy after fire differs significantly between the character syndromes found by Herrera (1984, 1992) ($F = 32.8$; d.f.=1,58; $p < 0.001$; see App. 1 for taxa included in the analysis). The fitted model, accounting for 35% of the observed (intergeneric) variance of DIM1, indicates that resprouter genera tend to score significantly lower on DIM1 than seeder genera. A very good discrimination on DIM1 is made by the recruitment strategy after fire as 95% of seeders scored values of DIM1 > 0.65 and 97.5% of resprouters scored values of DIM1 < 0.65. The only exceptions were the seeder *Pinus* scoring like a resprouter (DIM1 = –1.24) and the resprouter *Erica* scoring like a seeder (DIM1 = 0.91). Therefore, seeders are mainly non-sclerophyllous, anemochorous, dry-fruited, small-seeded species associated with early colonization whereas resprouters are mainly sclerophyllous, vertebrate-dispersed, fleshy-fruited, large-seeded species associated with late successional stages. These features are consistent with the theoretical models of Keeley (1998) and Pausas (1999).

Herrera (1992) also explained the difference between taxa of different successional stages by the age of the lineage, accounting for 27.5% of the observed variance of DIM1. At least for the Mediterranean Basin, the age of lineage is associated with regeneration strategy after fire: seeders correspond to taxa evolved in the Quaternary (post-Pliocene) and resprouters with taxa evolved in the Tertiary (pre-Pliocene). For example, Quaternary genera such as *Cistus, Helianthemum, Tuberaria, Rosmarinus, Thymus, Lavandula, Phlomis, Lotus, Argyrolobium, Anthyllis*, and *Coronilla* behave as seeders (Troumbis & Trabaud 1987; Parker & Kelly 1989; Arianoutsou & Thanos 1994; Keeley 1995) whereas Tertiary genera such as *Pistacia, Daphne, Quercus, Rhamnus, Smilax* and *Phyllirea* behave as resprouters (Herrera 1987). From an evolutionary point of view, the differences between seeders and resprouters reported in this paper may be due to phylogenetic inertia (*sensu* Harvey & Pagel 1991; e. g. seeders grow faster because they share a common ancestor with fast growth) or to stabilizing selection within each group (*sensu* Westoby et al. 1995; i.e. seeders grow faster because they share the same selection pressures). The study of growth rate, allocation patterns and ecological correlates of the few closely related species with different strategies known in the Mediterranean Basin (e.g. *Genista triacanthos* vs. *G. tridens*, Ojeda et al. 1996; *Ulex parviflorus* vs. *U. europaeus*, Mansanet 1985; Puentes et al. 1985) would help in understanding the ecological and evolutionary response of plants to fire.

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**App. 1.** Classification of the genera listed in the analysis of Herrera (1992) regarding the reproductive strategy after fire. Mean values and S.E. of Herrera's DIM1 for seeders and resprouters are also shown.

**Seeders** (DIM1= 0.78 ± 0.11): *Calicotome, Calluna, Cistus, Colutea, Coronilla, Cytisus, Dorycnium, Fumana, Genista, Halimium, Helianthemum, Lavandula, Phlomis, Pinus, Rosmarinus, Satureja, Stauracanthus, Teucrium, Thymus, Ulex.*

**Resprouters** (DIM1= – 0.39 ± 0.13) *Amelanchier, Arbutus, Asparagus, Berberis, Celtis, Ceratonia, Chamaerops, Clematis, Coriaria, Crataegus, Daphne, Erica, Ephedra, Hedera, Ilex, Jasminum, Juniperus, Laurus, Lonicera, Myrtus, Nerium, Olea, Osyris, Phyllirea, Pistacia, Prunus, Quercus, Retama, Rhamnus, Rhus, Rosa, Rubia, Rubus, Ruscus, Smilax, Sorbus, Thymelea, Ulmus, Viburnum, Vitis.*