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EARLY TO RISE MAKES A PLANT HEALTHY, WEALTHY, AND WISE

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Abstract. Seedling emergence time is a crucial event in the life cycle of a plant, determining its fitness via different components including survival, growth, and fecundity. Precocious emergents usually survive, grow, and/or reproduce earlier in the life cycle, but for perennials it is unknown whether these benefits are maintained throughout the life of the plant. Here, we examine for the first time whether fitness benefits due to the early emergence of perennial plants are perpetuated or vanish with time. For nine years, in a Mediterranean gorse community, we followed the fate of 2118 seedlings belonging to the four dominant woody species. We estimated phenotypic selection gradients on emergence time for three fitness components (survival, growth, and fecundity), under two experimentally simulated scenarios (fire and fire + erosion), at two different times in the life of the plant (3 and 9 years). Fire and erosion represent two potential selective forces constraining the temporal window of seedling emergence in Mediterranean habitats. All the species exhibited selection for early emergence, but through different fitness components. Directional selection favoring early emergence via survival in both fire scenarios was detected in the two Cistaceae species (*Helianthemum marifolium* and *Cistus albidus*), in which precocious emergents had higher fitness values late in the life cycle (9 years). In contrast, Fabaceae species (*Ononis fruticosa* and *Ulex parviflorus*) were not selected for early emergence via survival. Early emergents of all species in both fire scenarios had higher fitness values through growth early in the life cycle; these benefits decreased slightly with time but remained statistically significant, except in *H. marifolium*. Finally, late fecundity was enhanced by early emergence in both fire scenarios in *C. albidus* and *U. parviflorus* but not in *H. marifolium*. In conclusion, benefits acquired by emerging early are perpetuated for at least nine years.

Key words: Cistaceae; early emergence; Fabaceae; plant fitness; seedling emergence; seedling fecundity; seedling growth; time of emergence.

Introduction

The timing of seedling emergence is one of the key events in the life cycle of plants because it determines plant performance and success (Harper 1977, Weiner 1988). Time of emergence is influenced by a complex combination of different abiotic and biotic factors that determine the mode by which natural selection acts on emergence time (Venable 1984). A recent review has shown that emergence time influences plant fitness components such as survival, growth, and fecundity in different ways (Verdú and Traveset 2005). Such selection studies on individual components have been limited to fragmented portraits of lifetime selection that can be unrealistic if the positive effect of a single trait on a fitness component is altered by an opposite effect on another fitness component (see for example Alcántara and Rey 2003, Gómez 2004).

Moreover, the effects of emergence time on fitness components may change throughout the life of a plant. The early benefits associated with one trait may disappear later or even counteract other fitness components (Moles and Westoby 2004, Verdú and Traveset 2005). For example, early reproduction could reduce the availability of resources for growth and future reproduction (Stearns 1992).

In this context, long-term studies that consider the effects of emergence time both on early and late stages of the life cycle are needed to obtain realistic conclusions. Few studies have recorded fitness as an integration of effects during different phases of the life cycle, and most evidence comes from annual species. However, this knowledge cannot be extrapolated to perennials because the effects of emergence time on fitness components are remarkably different between the two growth forms. This knowledge gap is a consequence of the long time required to monitor fecundity in perennials, beyond the usual duration of published studies (median 7 months, range 2–36 months; data from Verdú and Traveset [2005]).

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The timing of seedling emergence is critical to plant performance in habitats subject to frequent disturbances (Quintana et al. 2004). In Mediterranean fire-structured shrublands, seedling emergence of many species is temporally constrained by the appearance of a disturbance such as fire. A temporal "window of opportunity" for seedling establishment is opened after fire because of the reduced competition for resources (Lavorel et al. 1994*a*, *b*, Buhk et al. 2007). Under these conditions, mechanisms that optimize seedling-emergence time after fire will be under strong selection (Meyer et al. 1997), and natural selection may favor early emergence that increases lifetime fitness (Daws et al. 2002, Verdú and Traveset 2005). On the other hand, early emergents may also have a higher risk of mortality due to seasonal hazards (e.g., Marks and Prince 1981, Jones and Sharitz 1989). In Mediterranean habitats, these seasonal hazards are unpredictable torrential rainfalls producing extreme erosive events, usually occurring after fire (De Luis et al. 2003). Extreme rainfall events producing high rates of water runoff and sediment transport reduce seedling survival by seedling uprooting or burial (De Luis et al. 2005*a*, *b*). If this happens, between-population differences in the occurrence of torrential rainfalls may provoke spatial variation in the selection pressures and ultimately different evolutionary trajectories to the optimal emergence time (Thompson 1994).

Here, we estimate the effects of emergence time on early (3 years) and late (9 years) fitness components in four dominant shrub species present on Mediterranean gorse shrublands after an experimental fire. We hypothesized that early emergence would have positive effects on plant fitness, as precocious seedlings become better competitors because they can access resources earlier. We also predicted that these positive effects will be maintained throughout the life cycle. Finally we explore if these early and late benefits are maintained in a different experimental scenario (fire + erosion) that potentially selects against early emergence.

METHODS

Study site

The study was carried out in three 33 × 33 m plots in the Sierra de Onil (00°39′ E, 38°43′ N; 800 m above sea level), 40 km northwest of Alicante (Spain). Plots were located on slopes facing south, northeast, and north, with slope angles ranging between 21° and 27°. According to the nearest weather station (Bañeres, 7 km away), the climate is dry-Mediterranean (mean annual precipitation is 466 mm) and the mean monthly temperature is 13.8°C. Soils are loamy Typic Calcixeroll developed on Miocenic marls (De la Torre and Alías 1996) with a high carbonate content (pH = 7.7; García-Cano et al. 2000).

The three plots studied consist of a stage in the degradation of a former Aleppo pine (*Pinus halepensis*) forest burned in 1994, which afterward formed a Mediterranean gorse shrubland dominated by *Ulex parviflorus* (Fabaceae). The seeds of these species, as well as those of the rest of the subdominant shrubs such as *Cistus albidus* (Cistaceae) and *Rosmarinus officinalis* (Labiatae), are able to germinate after fire (i.e. seeder species; De Luis et al. 2004*a*).

Experimental design and seedling monitoring

In October 1996, after the first autumn rains and on windless days, we burned the three plots. Plots were previously delimited by a 5 m wide firebreak in which the vegetation was eliminated by mechanical brushing. The fires were ignited in the upper part of each plot with the fire fronts being made in a continuous line downhill.

Immediately after fire and for the next three years, seedling recruitment, survival, growth (height), and fecundity (number of flowers per plant) of all species presented in four 2×0.5 m^2 subplots established within each experimental plot were monitored (fire scenario). Germinating seedlings were tagged monthly at first, then once every two months and then each season. An additional sampling was made in autumn of 2005 (9 years after fire). Biomass estimation of each plant at each time was derived through specific allometric relationships between height and basal diameters from individuals harvested in an adjacent area (see De Luis et al. 2006).

Two months after fire, a rainfall simulation treatment was applied in two of the four 2×0.5 m^2 subplots (fire + erosion scenario) in each of the three plots. Rainfall intensity applied was 2.6 mm/min for 105 min and produced soil losses between 60 and 800 g/m^2, representing soil losses between 0.2 and 1 mm (De Luis et al. 2003). Erosion treatments had no effect on seedling emergence (De Luis et al. 2005*a*), but significantly affected seedling survival (De Luis et al. 2005*b*), seedling growth (De Luis et al. 2001), and also herbaceous recovery (De Luis et al. 2004*b*). Therefore fire and fire + erosion treatments represent different scenarios for vegetation recovery, where time of emergence may have different effects.

Study species

Over this time, 2477 seedling emergences were recorded belonging to 15 different species. The most abundant species were two Cistaceae (*Cistus albidus* with 931 individuals and *Helianthemum marifolium* with 578) and two Fabaceae species (*Ulex parviflorus* [327 individuals] and *Ononis fruticosa* [282 individuals]). Eleven other species were present, but not used in this study because of their low abundance.

The presence of a "hardseededness" with heat-stimulated germination is a characteristic of both Cistaceae as Fabaceae species (Thanos et al. 1992, Doussi and Thanos 1994, Arianoutsou and Thanos 1996). Also, the four focal species display short-range dispersal distance (Bastida and Talavera 2002, Baeza and Vallejo 2006), short life cycles (15–20 years; Lloret et al. 2003, Baeza and Vallejo 2006) with early first

TABLE 1. Number of seedlings per species emerging and surviving 3 and 9 years after the experimental fire in two experimentally simulated scenarios representing two potential selective forces constraining the temporal window of seedling emergence in Mediterranean habitats (fire and fire + erosion).

	Number of emerging seedlings		Plants alive at third year		Plants alive at ninth year	
Species	Fire	Fire + erosion	Fire	Fire + erosion	Fire	Fire + erosion
Helianthemum marifolium	281	297	86	82	37	26
Cistus albidus	405	526	133	108	95	72
Ulex parviflorus	148	179	36	26	21	17
Ononis fruticosa	169	113	52	6	3	0
Total	1003	1115	307	222	156	115
Grand total	2118		529		271	

reproduction events (1–3 years), and full reproductive capacity at ~5 years (Roy and Sonié 1992, Thanos et al. 1992, Ne'eman and Izhaki 1999, Ferrandis et al. 2001, Bastida and Talavera 2002). Seeds of these four species remain viable for at least 20 years. All these traits allow species to create persistent soil seed banks, which have been related to a high probability of persistence on frequently disturbed habitats (Pausas et al. 2004).

Across the four focal species there appears to be a trade-off between seed number and seed size. Fabaceae seed production is considerably lower in quantity, but seeds are substantially bigger than those of Cistaceae (Thanos et al. 1992, Hanley and Fenner 1998, Baeza and Vallejo 2006).

Fitness components and phenotypic selection

We estimated phenotypic selection on emergence time separately for the three different fitness components: survival, growth, and fecundity. These estimates were done under two scenarios (fire and fire + erosion) at two different times of the life of the plants (3 years and 9 years). In both scenarios, we grouped together data from all six 2×0.5 m^2 subplots with the same rainfall treatment.

Relative fitness was estimated by dividing the absolute growth (or fecundity) of each individual by the population mean (Arnold and Wade 1984). For survival, the transformed logistic regression procedure of Janzen and Stern (1998) also provided selection coefficients on the relative fitness scale. Calculations of relative fitness were done separately for the different fire scenarios and years. The study trait (emergence time in days since the fire) was standardized to 0 ± 1 (mean ± SD) to facilitate comparisons of the strength of selection across different fire scenarios and years.

Linear selection gradients on the different fitness components were estimated by fitting generalized linear models (GLM). More specifically, standard least-squares regressions, following Lande and Arnold (1983) were used for the growth and fecundity fitness components whereas logistic regressions, following the transformation proposed by Janzen and Stern (1998), were used for survival. Statistical significance of the least-square regressions was obtained by estimating 95% confidence intervals with bootstrapping (1000 iterations).

We plotted the relative fitness function against the observed emergence time to detect local minima or maxima indicative of nonlinear (disruptive or stabilizing) selection (Brodie et al. 1995, Sandring et al. 2007). None of the plots showed a clear minimum or maximum, and therefore nonlinear selection gradients were not included in the GLM models.

RESULTS

Temporal distribution of seedling emergence

We tagged and followed for survival, growth, and flowering a total of 2118 seedlings belonging to the four dominant species. Three years after the fire treatments, 529 individuals were still alive, and this number decreased to 271 individuals nine years after the fires (Table 1).

There was rapid germination of the species in this community. During our experiment, most of the seedlings (mean 94%, range 87–98%; Fig. 1) emerged during the first year and no seedlings emerged after the second year after the fires.

Cistaceae species (*Helianthemum marifolium* and *Cistus albidus*) showed a rapid response to fire stimuli, with nearly 60% of total seedlings emerging in the first two months after fire. In contrast, maximum seedling emergence for the Fabaceae species (*Ononis fruticosa* and *Ulex parviflorus*) was observed during the autumn following fire (Fig. 1). In spite of these differences, in the first year after fire seedling emergence was manifested as a continuous process in all species involved.

Phenotypic selection

Survival.—After a fire, precocious emergents of the two Cistaceae species had a higher fitness via survival early in the life cycle (3 years), as the significant negative selection gradients indicate (−0.53 for *H. marifolium* and −0.40 for *C. albidus* [Table 2]). Interestingly, such benefits increased strongly with time, because selection gradient values increased twofold at 9 years (−1.14 for *H. marifolium* and −0.86 for *C. albidus*). As an example, we can estimate from these equations that emerging three weeks later decreases the probability of survival in

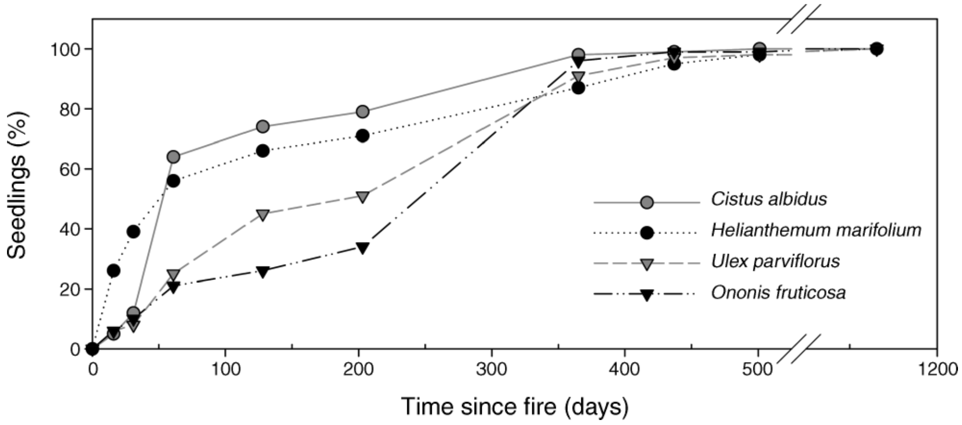

Fig. 1. Relative seedling emergence curves after fire of the four study species (*Cistus albidus*, *Helianthemum marifolium*, *Ulex parviflorus*, and *Ononis fruticosa*). Both scenarios (fire and fire + erosion) are pooled.

Helianthemum from 0.22 to 0.16, or to 0.09 if the delay is of two months.

When erosion acted after the fire, the same picture was observed for *C. albidus*, with survival benefits enhanced over time. However, survival benefits for early emergents of *H. marifolium* did not appear until some years later in the life cycle (Table 2, Fig. 2). In contrast, Fabaceae species (*O. fruticosa* and *U. parviflorus*) were not significantly selected for early emergence in terms of survival because none of the selection gradients were significantly negative. In contrast, some of these coefficients were positive, but these effects became nonsignificant later in the life cycle of the plants (Table 2, Fig. 2).

Growth.—Early emergents of all species had higher fitness values through growth early in the life cycle (Table 3, Fig. 3). The growth benefits slightly decreased with time, but remained significant, except in *H. marifolium*. The picture was similar in both postfire scenarios (Table 3, Fig. 3).

Fecundity.—The effects of emergence time on early fecundity could only be tested in *C. albidus*, which flowered at 3 years. Precocious emergents of such species had greater fecundity than later ones (Table 3, Fig. 4). Six years later, the benefits of early emergence were still very strong and significant although varied with the postfire scenario: compared with year 3, fecundity benefits halved in the fire scenario but doubled in the fire + erosion scenario (Table 4). The other two species for which we obtained data show different trends, with late fecundity enhanced by early emergence in *U. parviflorus* but not in *H. marifolium* (Table 4, Fig. 4).

Correlations between fitness components.—Aerial plant growth during first development stages (3 years) was low in all species studied, perhaps because resources were allocated more for root development. However, growth in this early phase is of critical importance in subsequent plant development. Late survival (3–9 years) was significantly higher in plants that were larger in year 3. This is especially true for the two Cistaceae species. In the case of Fabaceae, statistical significance is only observed for *Ononis fruticosa* (Fig. 5). Fecundity results also mirror growth results. Larger plants are able to

Table 2. Directional selection acting on seedling emergence time via survival fitness component in two different scenarios and two different ages in the life cycle of the plant species.

	Fire				Fire + erosion			
Survival and species	α	SE	*P*	βavggrd	α	SE	*P*	βavggrd
Early survival (3 years)								
H. marifolium	−0.83	0.19	0.000	−0.53	0.07	0.13	0.602	0.05
C. albidus	−0.63	0.13	0.000	−0.40	−0.34	0.14	0.015	−0.27
U. parviflorus	0.11	0.19	0.542	0.09	0.47	0.19	0.014	0.39
O. fruticosa	0.36	0.19	0.055	0.24	1.23	0.69	0.076	1.11
Late survival (9 years)								
H. marifolium	−1.41	0.44	0.001	−1.14	−1.38	0.50	0.006	−1.21
C. albidus	−1.26	0.22	0.000	−0.86	−0.87	0.27	0.001	−0.73
U. parviflorus	−0.25	0.26	0.348	−0.21	−0.12	0.27	0.660	−0.11
O. fruticosa	−0.79	0.51	0.122	−0.76				

Notes: The selection gradient (βavggrd) was calculated following the transformed logistic regression procedure of Janzen and Stern (1998). The parameter of the logistic regression model (α), its standard error (SE), and statistical significance (*P*) are also shown. A negative selection gradient means that early emergents survive more often than later ones. Empty cells indicate that no data are available.

Table 3. Directional selection acting on seedling emergence time via growth fitness component in two different scenarios and two different ages in the life cycle of the plant species.

Growth and species	Fire			Fire + erosion		
	β	SE	95% boot CI†	β	SE	95% boot CI†
Early growth (3 years)						
H. marifolium	−0.25*	0.07	(−0.33, −0.17)	−0.44*	0.09	(−0.58, −0.34)
C. albidus	−0.37*	0.07	(−0.64, −0.23)	−0.24*	0.09	(−0.88, −0.14)
U. parviflorus	−0.74*	0.25	(−1.83, −0.28)	−0.57*	0.35	(−1.74, −0.17)
O. fruticosa	−0.57*	0.12	(−1.44, −0.12)			
Late growth (9 years)						
H. marifolium	−0.05	0.09	(−0.38, 0.24)	0.11	0.08	(−0.81, 0.24)
C. albidus	−0.22*	0.06	(−0.41, −0.13)	−0.21*	0.07	(−0.41, −0.13)
U. parviflorus	−0.72*	0.15	(−1.24, −0.29)	−0.47*	0.23	(−0.91, −0.02)
O. fruticosa						

Notes: The selection gradient (β) was calculated following the standard least-squares regressions procedure of Lande and Arnold (1983). A negative selection gradient means that early emergents grow more than later ones. Empty cells indicate that no data are available.

* Significant selection gradients at $\alpha = 0.05$.

† Confidence intervals (95%) obtained with bootstrapping (1000 iterations).

produce flowers while those not reaching a minimum size had not still flowered 9 years after fire (Fig. 6).

Discussion

Although the fitness components we measured are differentially affected by emergence time in the different study species, all four of the focal species were ultimately subjected to selection for early emergence (Table 5). None of the studies previously describing the benefits of early emergence had considered the long-term effects of emergence time in perennial plants and consequently nothing was known about how fecundity—one of the most relevant fitness components—is affected by emergence time or how later events may compensate the benefits of the early emergents (Verdú and Traveset 2005). Here, we provide, for the first time, empirical evidence on the fecundity benefits associated with early emergence and the perpetuation of all measured fitness benefits of early emergence throughout the life of the perennial plants.

Environmentally induced covariance between early emergence and fitness has been described as an important constraint in isolating effects of early emergence on different components of plant fitness (Rausher 1992, Stinchcombe et al. 2002). It might be expected that seeds located in better microsites germinate earlier and at the same time, and that these microsites may allow seedlings to grow and reproduce more. However, we found no differences in the microsite characteristics we measured (prefire vegetation cover, slope incline, ash and litter content on soil) among cohorts of the same species (De Luis et al., *in press*), although a possibility exists that "safe sites" for germination occur on a smaller scale (centimeters to meters) than we measured in the local environment (Harper 1977). We clearly need a better understanding of the environmental sources of the variation in seedling

Table 4. Directional selection acting on seedling emergence time via fecundity fitness component in two different scenarios and two different ages in the life cycle of the plant species.

Fecundity and species	Fire			Fire + erosion		
	β	SE	95% boot CI†	β	SE	95% boot CI†
Early fecundity (3 years)						
H. marifolium						
C. albidus	−0.70*	0.58	(−2.28, −0.08)	−0.27*	0.28	(−1.22, −0.09)
U. parviflorus						
O. fruticosa						
Late fecundity (9 years)						
H. marifolium	−0.04	0.24	(−0.77, 0.73)	−0.10	0.42	(−2.54, 0.52)
C. albidus	−0.34*	0.16	(−0.87, −0.10)	−0.49*	0.17	(−1.07, −0.10)
U. parviflorus	−1.06*	0.46	(−1.99, −0.33)	−0.74*	0.38	(−1.49, −0.01)
O. fruticosa						

Notes: The selection gradient (β) was calculated following the standard least-squares regressions procedure of Lande and Arnold (1983). A negative selection gradient means that early emergents reproduce more than later ones. Empty cells indicate that no data are available.

* Significant selection gradients at $\alpha = 0.05$.

† Confidence intervals (95%) obtained with bootstrapping (1000 iterations).

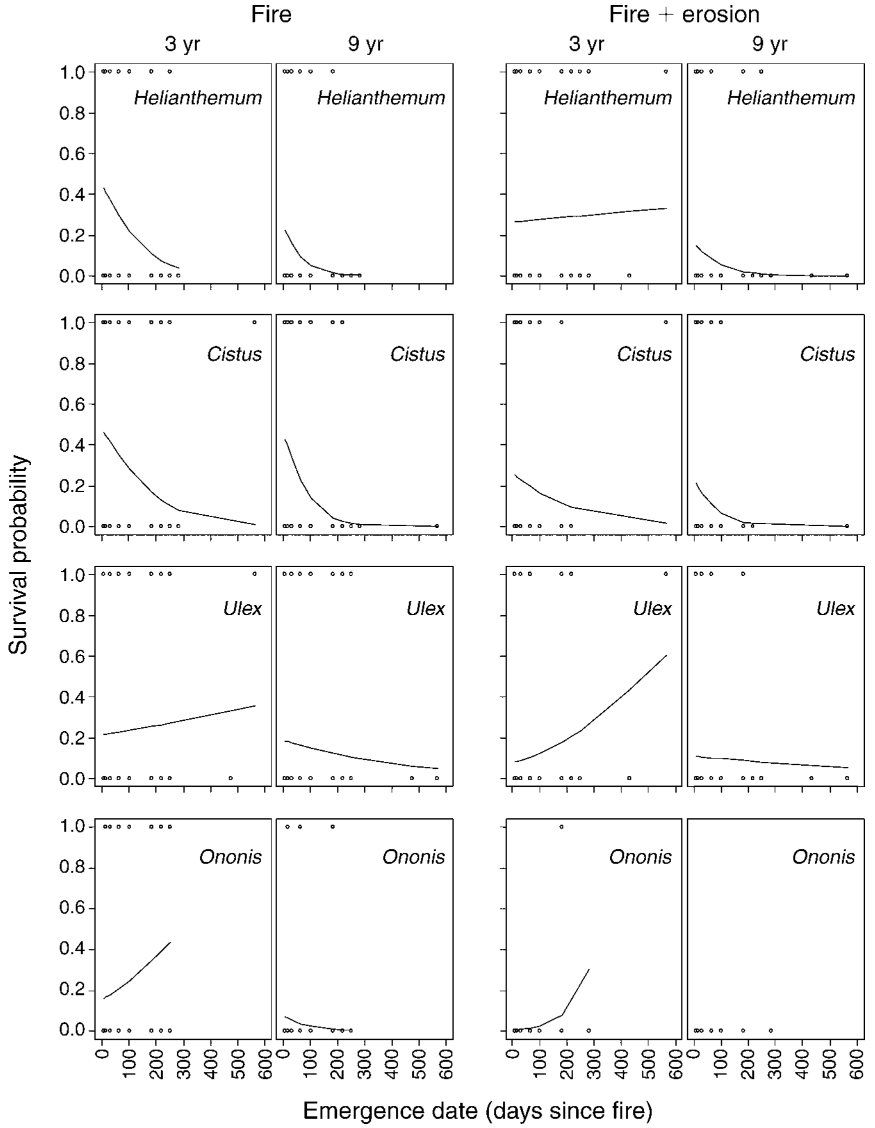

FIG. 2. Plant survival probability as a function of the emergence time 3 and 9 years after the experimental fire in both scenarios (fire and fire + erosion). The observed values (circles) are shown together with the fitted logistic regression line following the procedure of Janzen and Stern (1998) to estimate selection coefficients on the relative fitness scale.

TABLE 5. Summary of the results showing whether directional selection is acting toward early (E) or late (L) emergence time on different fitness components under two different scenarios at two different ages in the life cycle of the plant species.

	Fire						Fire + erosion					
	Survival		Growth		Fecundity		Survival		Growth		Fecundity	
Species	3 yr	9 yr	3 yr	9 yr	3 yr	9 yr	3 yr	9 yr	3 yr	9 yr	3 yr	9 yr
H. marifolium	E	E	E	ns		ns	ns	E	E	ns		ns
C. albidus	E	E	E	E	E	E	E	E	E	E	E	E
U. parviflorus	ns	ns	E	E		E	L	ns	E	E		E
O. fruticosa	ns	ns	E				ns	ns				

Notes: A cell containing "ns" (nonsignificant) means that there is no evidence that natural selection is acting through such fitness components. Empty cells indicate that no data are available.

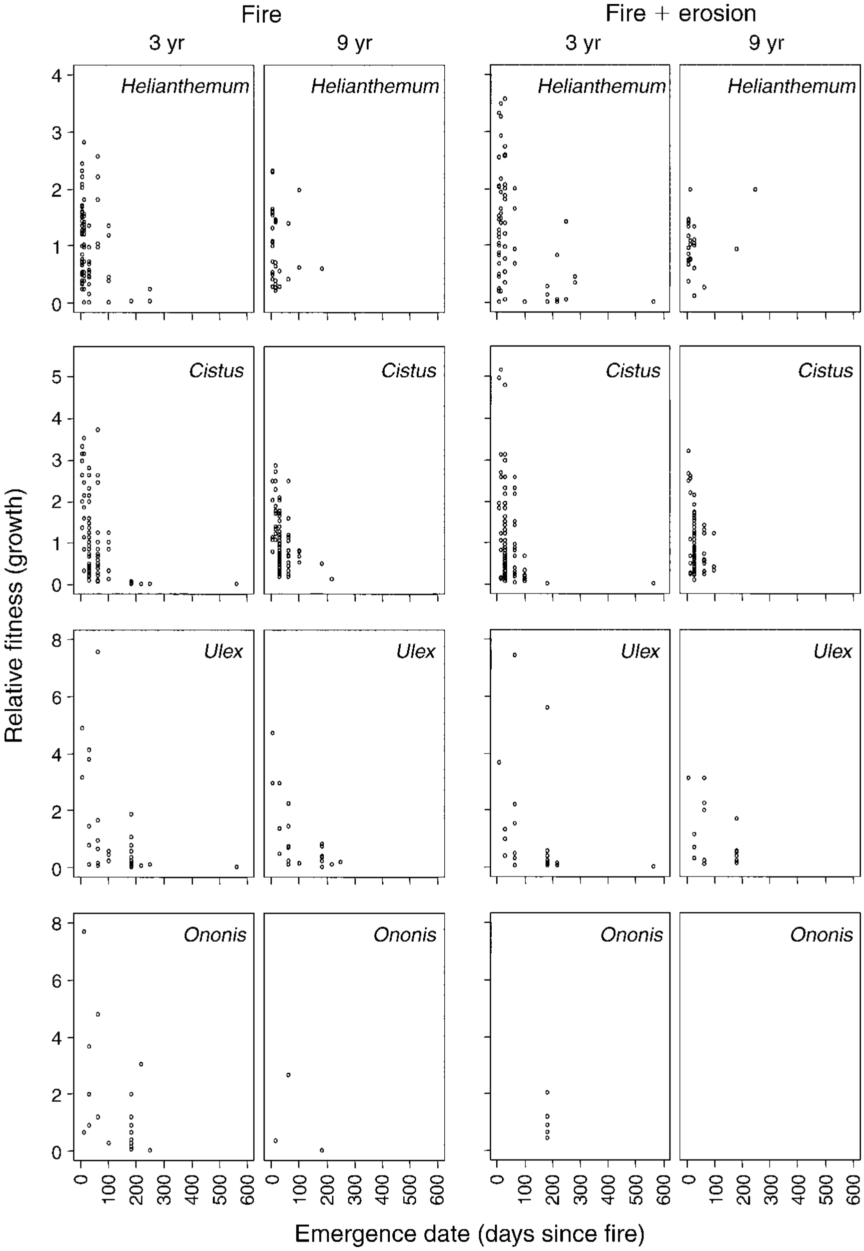

FIG. 3. Relative fitness via plant growth as a function of the emergence time 3 and 9 years after the experimental fire in both scenarios. Circles represent the relative fitness of each individual estimated as the ratio between its absolute growth and the population mean.

germination times, as there is evidence that different sets of genes contribute to variation in germination behavior in different seasonal conditions and geographic locations (Donohue et al. 2005). Ultimately, the complexity of the genetic mechanisms of fitness traits interacting with environmental factors could maintain genetic variation in traits under strong directional selection (Merilä and Sheldon 1999). For this reason, the strong directional selection toward early emergence detected here does not deplete genetic variability of fitness-related traits, and late emergents may exist in our populations. The existence of such variation is relevant to coping with rare, catastrophic events in which early emergence may be lethal (i.e., severe winter frosts).

Emerging early in the season allows seedlings to be the first to capture the resources and therefore to grow faster to cope with competition in better condition (Arendt 1997). This selective scenario might be particularly important for plant species whose persistence in fire-prone habitats depends on postfire seed germination, as is the case for all our species under study. Such "seeder" species are selected for fast growth rates and high

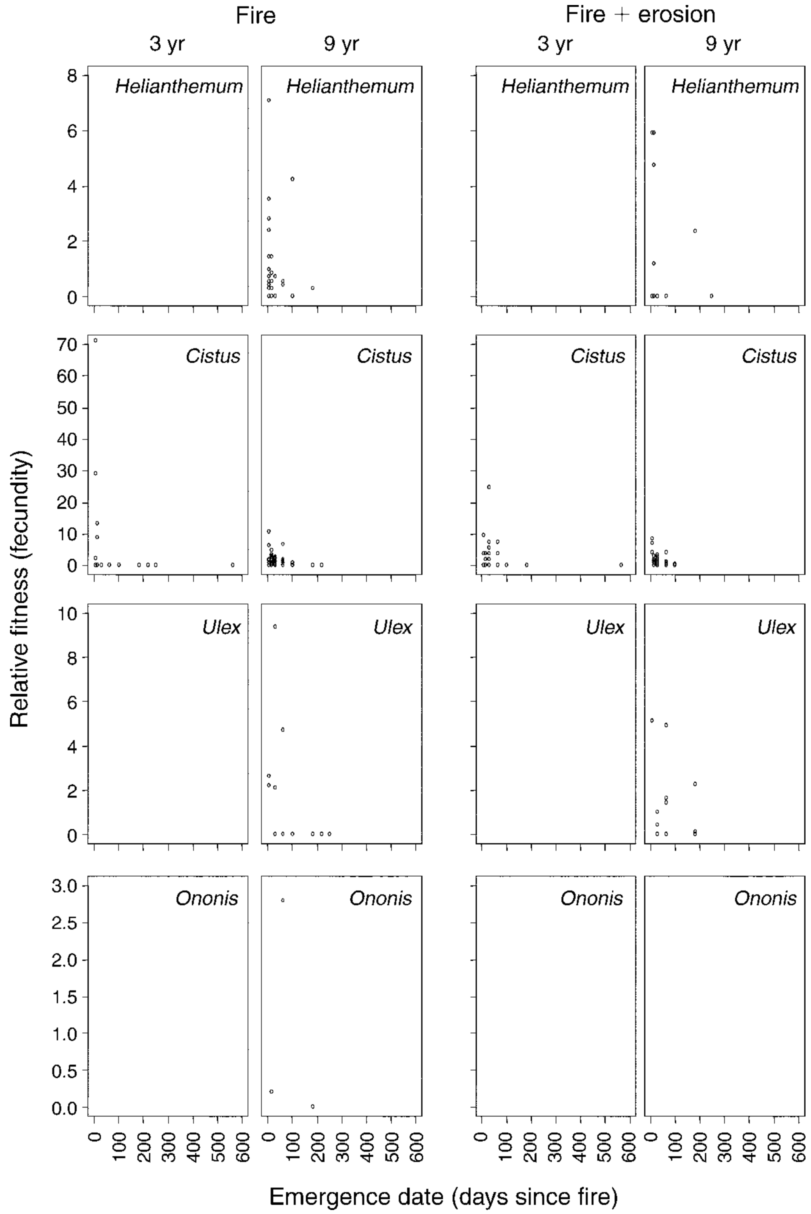

FIG. 4. Relative fitness via plant fecundity as a function of the emergence time 3 and 9 years after the experimental fire in both scenarios. Circles represent the relative fitness of each individual estimated as the ratio between its absolute fecundity (number of flowers) and the population mean.

fecundities because they need to minimize the immaturity risk, or in other words, to grow and reproduce before fire kills them (Keeley and Fotheringham 2000, Verdú 2000, 2002, Pausas and Verdú 2005, Verdú et al. 2007).

Our results show that faster growth rates and high fecundity are intercorrelated traits that are acquired by emerging early in the season. Consequently, natural selection under fire scenarios was favoring early emergents because of their higher growth and fecundity rates.

Alternatively, environmental uncertainty may select for strategies consisting of spreading the mortality risk by continuous emergence instead of concentrating emergence early in the season (Mathias and Kisdi 2001). We have shown that emerging early is a favored strategy even under an uncertain scenario such as that imposed by strong erosion produced after torrential rainfalls. This may be explained because of the omnipresence of a strong critical period, summer drought, for seedling establishment in a Mediterranean climate (De Luis et al. 2005*b*). Seedlings emerging later may avoid the risk of dying from being buried or unearthed by sediments produced by rainfalls (De Luis et al. 2005*b*), but they might be too small to cope with

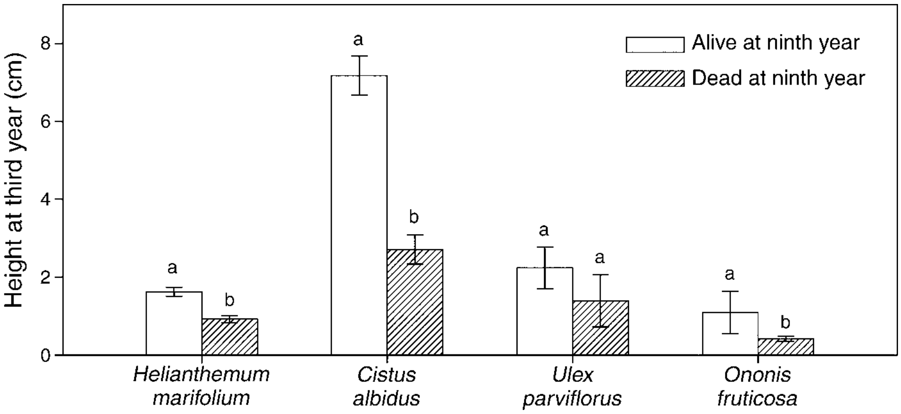

FIG. 5. Plants that survived from year 3 to year 9 were significantly taller in year 3 than plants that did not survive. Within a species, different letters above the bars indicate significant differences in height at $\alpha = 0.05$ (one-way ANOVA). Error bars indicate ±SD. Within a species, different letters above the bars indicate significant differences in height at $\alpha = 0.05$ (one-way ANOVA). All *Ononis fruticosa* plants flowered, and therefore the statistical test was not performed.

the summer drought. Empirical evidence of this process exists for *Pinus sylvestris* populations living in a Mediterranean climate, where the relative importance of drought as a mortality factor increased for late-emerged seedlings (Castro 2006). In this context, early emergence may represent a suitable evolutionary adaptation imposed by the summer period that allows seedlings to have more time for root system development, making them less sensitive to water stress (Moreno and Oechel 1992).

Despite the pervasive influence of early emergence on plant fitness, it is clear that not all species behave similarly (Quintana et al. 2004). Verdú and Traveset (2005) detected a phylogenetic signal in the effect of emergence time on seedling growth, meaning that closely related species behave more similarly than distant ones. Likewise, it was detected that seedling emergence behavior was more similar between species of the same family. Cistaceae species (*Helianthemum marifolium* and *Cistus albidus*) showed a rapid response to fire stimuli, since nearly 60% of total seedlings emerged in first two months after fire. In contrast, maximum seedling emergence for Fabaceae species (*Ononis fruticosa* and *Ulex parviflorus*) was observed during the autumn following fire. This phylogenetic pattern suggests that different traits related to postfire germination have been inherited by common ancestry (or favored by a common ecology) in the species of each family (Verdú and Pausas 2007). Tiny seeds of Cistaceae with germination induced by fire have been described as being unable to emerge from depths of more than 2–3 cm (Odion and Davis 2000), and therefore their germination is directly linked to the intensity of fire. In contrast, in Fabaceae seeds, the emergence process is not only linked to fire heating, since seeds are substantially bigger (Thanos et al. 1992, Hanley and Fenner 1998, Baeza and Vallejo 2006) and therefore capable of emerging from much deeper in the soil (Ne'eman et at. 1992, 1993, Westoby et al. 1992, Baeza et al. 2002). Such different germination behavior is translated into interspecific differences in the spatial

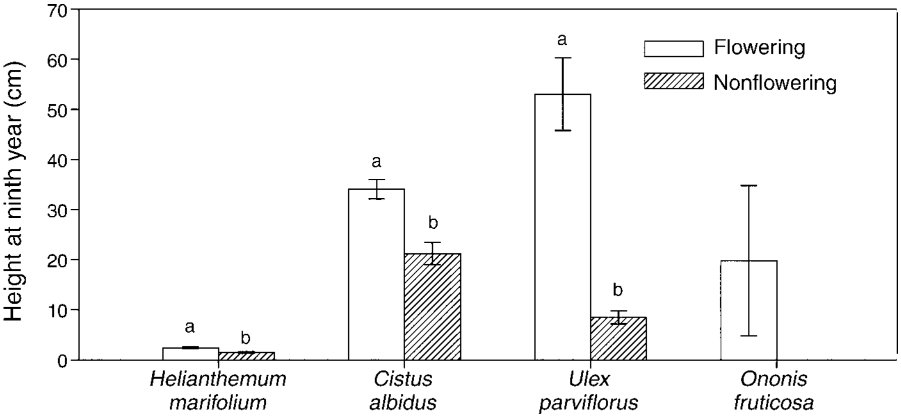

FIG. 6. Plants flowering at nine years were significantly taller than non-flowering plants. Different letters within a species indicate significant differences in height at $\alpha = 0.05$ (one-way ANOVA). Error bars indicate ±SD. All *Ononis fruticosa* plants flowered, and therefore the statistical test was not performed.

and temporal emergence patterns that ultimately allow the coexistence of species in these communities (De Luis et al., *unpublished data*).

The salient picture of our work is that early emergents are larger and reproduce more throughout the whole life cycle, supporting the idea that rapid growth evolves when a minimum size needs to be reached quickly, such as for sexual maturation (Arendt 1997). Given the profound demographic and evolutionary consequences of precocious sexual maturation (Verdú 2002), strong directional selection toward early emergence is largely expected. Furthermore, we show that this strategy has no delayed costs (sensu Yearsley et al. 2004), as trade-offs do not severely affect life-history episodes nor fitness components.

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