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Original article

Effects of soil enrichment, watering and seedling age on establishment of Mediterranean woody species

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A B S T R A C T

Vegetation restoration in strongly degraded lands has inherent limitations. Among the most relevant limitations in Mediterranean Mountains are severe drought and stressful levels of irradiance during summer. Thus, it is common that seedlings planted in open ground incur high rates of early mortality. In the context of a project of restoration of a burned area in Southern Spain, we evaluate the efficiency of watering and enrichment with native soil, and the influence of seedling age on survival and growth of 9 late-successional tall shrubs and trees planted in open ground. We also explore how small-scale variation in environmental variables relates to establishment success. Our results show an overall positive effect of watering on the survival of planted seedlings, while the effects of enrichment with native soil and age of planted seedlings were species-specific. Seedling establishment varied markedly with the presence of ravines, which duplicated seedling survival. This suggests that ravines may be more easily restored, improving their role as corridors in landscape designs of restoration. Independently of the treatment applied, *Rosa* sp. and *Crataegus monogyna*, both fleshy-fruited species, had the highest rates of establishment. In conclusion, this study shows the viability of low aggressive restoration techniques to assist vegetation recovery in fire-degraded environments. Specifically, watering and planting in ravines should be considered where restoration practices are applied in areas lacking vegetation cover. Some species highly attractive for animal dispersers and of easy establishment (*Rosa* sp. and *Crataegus* sp.) could be used to enhance spontaneous regeneration within and beyond corridors through increasing seed attraction and dissemination.

1. Introduction

The prevailing paradigm in restoration ecology involves returning a degraded system to some desired state by reinitiating succession (Hobbs and Norton, 1996). This would allow recovering the diversity and, more importantly, the dynamics of the community. Thus, knowledge of successional dynamics and the processes driving them must be used to implement restoration techniques for degraded areas. Mediterranean-type vegetation is dominated by fire-tolerant species which are able to resprout or which show enhanced germination after fire (Pausas et al., 2004). These fire-tolerant plants are key in the development of successional processes since, through nurse effects (Maestre et al., 2003; Castro et al., 2004; Gómez-Aparicio et al., 2004), they catalyze the expansion of late-successional shrubs and trees which will eventually dominate the mature community (Siles et al., 2008). Accordingly, many studies propose the use the nurse plants in the restoration of Mediterranean vegetation (Gómez-Aparicio et al., 2004; Rey et al., 2009).

Unfortunately, a high recurrence of fire (or a long history of land degradation before fire) may overwhelm the capacity of fire-tolerant plants (Pausas, 2004), resulting in a rare spontaneous recovery of the vegetation. Under these circumstances, the availability of spontaneous nurse plants may be too scarce to be of any use for restoration. Restoration in such cases requires the establishment of nurse plants as a first step in restarting the successional dynamics. However, successful establishment of shrubs in the absence of nurse plants can be limited by the altered balance of nutrients in degraded soils (Gimeno-García et al., 2000) and the lowered capacity of soil water retention, and elimination or reduction of fungi and other components of the soil biota after fire (Allen, 1991; De Roman and De Miguel, 2002; Requena et al., 2001). Techniques for increasing the survival and growth of planted seedlings of these species are thus needed in degraded ecosystems.

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Mycorrhizas enhance nutrient availability for plants (Querejeta et al., 1998), improve soil structure (Barea and Olivares, 1998; Caravaca et al., 2002) and decrease water deficit (Augé, 2001). The importance of mycorrhiza for the establishment of forest plantations is widely recognized (Allen, 1991). Their function has been studied in relation to forest plant production (Torres and Honrubia, 1993, 1994) and growth of seedlings planted in the field (Maestre et al., 2002; Miller and Jastrow, 2000). Several studies have shown the utility of the mycorrhizal inoculation in restoration with shrub species in semiarid environments (Caravaca et al., 2002; Palenzuela et al., 2002; Requena et al., 2001), while other studies did not find any advantage in terms of seedling survival (Maestre et al., 2002). A critical aspect to optimize the use of mycorrhiza is the fungal choice for each soil–plant system. Some studies have shown that, compared to allochthonous mycorrhizal fungi, a mixture of native fungi has a higher efficiency for forest restoration, especially in the long term (Requena et al., 2001). This suggests that enriching degraded soils with soil obtained from undisturbed places surrounding the area to be restored, might increase the establishment success of the species planted.

Another factor frequently limiting seedling establishment under Mediterranean climate is the typical summer drought, particularly critical during the first year after planting. Summer water deficit is the main factor of stress and mortality for seedlings of Mediterranean shrubs and trees (Castro et al., 2006; García-Fayos and Verdú, 1998; Herrera et al., 1994; Rey and Alcántara, 2000; Traveset, 1993). Shading can reduce water stress and, consequently, established shrubs frequently facilitate seedling establishment of woody species in the region (García et al., 2000; García, 2001; Ramírez et al., 2006; Rey and Alcántara, 2000), thus exerting a nurse effect useful for restoration (Castro et al., 2004; Gómez-Aparicio et al., 2004; Padilla and Pugnaire, 2006). However, immediately after fire, shrub cover is normally insufficient for the widespread use of nurse plants. Several studies have shown that watering increases the establishment and growth of seedlings planted in open ground (Castro et al., 2005; Jiménez et al., 2004; Montesinos, 2007; Rey et al., 2004; Rey-Benayas, 1998), and that the advantage of shading for the seedlings is less manifest when watered (Montesinos, 2007; Padilla and Pugnaire, 2009; Rey-Benayas and Camacho-Cruz, 2004). Nevertheless, irrigation practices are seldom used in reforestation in southern Spain because it is considered expensive and it may prevent seedling acclimation to natural field conditions (but see Rey-Benayas and Camacho-Cruz, 2004). In any case, stress levels and establishment success in Mediterranean ecosystems depend on the particular rainfall conditions of the year of planting (Castro et al., 2004; Gómez-Aparicio et al., 2005a; Mendoza, 2008; Siles, 2008). Other environmental variables can vary at small scale, for example, topography and aspect. This variability may have important effects in seedling establishment and thus in restoration success. Nevertheless, the relationship between establishment success and environmental variables at small scales has been scarcely explored in studies for restoration of degraded areas (but see Gómez-Aparicio et al., 2005a, 2005b).

Seedling age can also influence survival of woody plants under Mediterranean summer stress. For naturally emerged seedlings, mortality decreases after the first summer (see for example, Rey and Alcántara, 2000; Traveset et al., 2003). However, seedlings used for restoration are usually one or two-years-old. To our knowledge, little attention has been paid to the influence of age of planted seedlings on their establishment and growth in reforestation.

The objective of this study was to evaluate the performance of different planting practices for the establishment of late-successional Mediterranean tall shrubs and trees, as important target species in restoration of fire-degraded areas in Mediterranean climate regions. More specifically, our aims were: (1) assess the effects of limited of small summer watering and enrichment with native soil on survival and growth of planted saplings of tall shrubs and tree species; (2) explore how small-scale variation in environmental variables relates to establishment success; and (3) evaluate the influence of the age of planted seedlings on establishment and growth.

2. Materials and methods

2.1. Study area

The study site is located in the Natural Park of "Sierras de Cazorla, Segura y Las Villas" (Jaén province, SE Spain), in an area of 850 ha burnt in August 2001. The climate is Mediterranean subhumid (Rivas, 2004), with hot and dry summers and rainfall distributed in spring and autumn. The potential native vegetation is a mixed forest of *Pinus nigra*, *Quercus ilex* subsp *ballota*, hereafter *Q. ilex*, and *Quercus faginea* (Valle, 2003). However, as a result of traditional management for forestry and cattle raising, the vegetation before fire is dominated by old afforestation stands and spontaneous colonization of *Pinus pinaster*, *P. nigra* and *Pinus halepensis*, with a sparse undergrowth of native shrub and tree species, and small patches of open native scrubland (Luque, 1995). At the beginning of our study, two years after fire, the vegetation present in the burned area formed a heterogeneous landscape with patches exhibiting different degrees of recovery, some still having mostly bare soil, others with dense resprouting and colonization by woody shrubs, and some scattered small patches of vegetation that had escaped the fire. The mean cover of pioneer shrub, tall shrub and tree species across the burned area was 19.2% (range 0–97%). The area is a limestone outcrop with interspersed patches of shallow soils. The topography is very steep, with altitude ranging from 760 to 1390 m. The average annual precipitation in the two closest weather stations is 770.7 and 1155.6 mm, with mean annual temperatures of 14.2 and 11.6 °C respectively. During the study years, rainfall in the burned area was very variable: 2003/2004 = 897 mm; 2004/2005 = 293 mm; 2005–2006 = 672 mm; 2006–2007 = 1000 mm (data from 12 pluviometers placed in our study zones, see below). Total cumulative rainfall during the four years of study varied between zones, ranging between 1856 and 2721 mm; cumulative precipitation in 4 summers ranged between zones from 98 to 163 mm ($N = 12$ zones).

2.2. Experimental trials

Experiments were carried out in 25 experimental plots distributed in 12 zones throughout the burned area (see Table 1). Plots (10 × 10 m) were fenced to prevent ungulate grazing. Each zone was characterized in terms of aspect, altitude, and the presence or absence of ravines (very small valleys, with non-permanent water course, formed by surface water erosion). A pluviometer was installed in each zone and the cumulative precipitation over the four years was used to characterize the variation in precipitation across plots. Planted seedlings of 8 species (see below) were produced at the forest nursery of Junta de Andalucía sited in Lugar Nuevo (Andujar), located 133 km from the study site, and were moved to a nursery sited in Escuela de Capacitación Forestal de Vadillo-Castril (Sierra de Cazorla) in spring of 2003 and 2004 for acclimation. Most plants were produced from seeds collected from Sierra de Cazorla. The seedlings were planted in manually drilled holes of 40 × 40 × 40 cm. We recorded survival and growth at the end of the summer (September–October) and at the end of the winter (April–May) during four and three years (experiment 1 and 2, respectively, see below).

Table 1
Characteristic of experimental plots: zone (distribution of experimental plots throughout the burned area), experiment (1: assay of the effects of watering and enrichment with native soil on establishment; 2: seedling age effect on survival of tall shrubs), Ravine (0: absence; 1: presence); Aspect (N/S/E/W) and altitude (m.).

Plot	Zone	Experiment	Ravine	Aspect	Altitude
1	1	1	0	W	1218
2	2	1	0	W	1020
3	3	1	0	E	1170
4	4	1	0	E	1238
5	5	1	0	E	1282
6	6	1	0	W	1188
7	7	1	0	W	1188
8	8	1	0	E	1265
9	9	1	0	E	1265
10	10	1	0	E	810
11	11	1	0	E	860
12	12	1	0	E	950
13	10	1	1	E	800
14	11	1	1	E	860
15	12	1	1	E	950
16	4	1	1	E	1210
17	1	2	0	SW	1220
18	2	2	0	W	1010
19	3	2	0	E	1180
20	4	2	0	SE	1210
21	7	2	0	W	1188
22	8	2	0	E	1275
23	10	2	0	E	805
24	11	2	0	E	855
25	12	2	0	SE	930

2.2.1. Enrichment with native soil

The native soil used with each plant species was a sample of rhizosphere soil taken under conspecific individuals naturally growing in unburned vegetation surrounding the study site. To propagate the native soil biota, we cultivated barley on commercial peat mixed with the native soil samples. After several months, barley was removed and the substratum was used to pot the seedlings of the inoculation treatment. A parallel assay under common garden conditions (at the Experimental Garden of the University of Jaén) verified that this procedure was efficient. As an example of microorganism colonization, we compared the presence of ecto- and arbuscular-mycorrhizas in seedlings under enriched and non-enriched soil treatments, After seven months of transplanting to inoculated soil, the percentage of root colonization by arbuscular mycorrhiza (the most frequent micorrhizal association in Mediterranean plants; Barea et al., 1999a, 1999b) was double in enriched than in control plants ($F_{1,96} = 23.39$, $p < 0.0001$), but it was also to some extent plant species-specific (interaction effect of treatment by plant species becoming marginally significant: $F_{11,96} = 1.81$, $p = 0.06$).

2.2.2. Watering

This treatment consisted in adding 0.5 l of water per seedling every fortnight, from 15 June to 15 September, during the first two years after planting. This dose was spread in a radius of 25 cm around each seedling to make it equivalent to 8 mm/m^2 (totalling 56 mm/m^2 in the whole summer, approximately the average summer rainfall in the study area). This treatment increased water availability 3.11 times over the natural summer rainfall in 2004 (18 mm/m^2), and 0.67 times in 2005 (82.5 mm/m^2).

Experiment 1. Assay of the effects of watering and enrichment with native soil on establishment.

The planted species were *Buxus sempervirens*, *Crataegus monogyna*, *Pistacia lentiscus*, *Pistacia terebinthus*, *Prunus spinosa*, *Quercus coccifera*, *Q. ilex* and *Rosa* sp. These species are characteristic of dry-subhumid Mediterranean scrublands, and most of them could be used as nurse plants for forest species in restoration plans (Siles et al., in press). The experiment was conducted in 16 experimental plots and started in autumn 2003. The experiment followed a randomized-block design with two fully-crossed factors (enrichment with native soil: inoculated vs. not inoculated; and watering: watered and not watered). All combinations of these treatments were replicated 4 times for each species planted within each plot. Three or four species were used per plot, and thus each plot had 48 or 64 planted seedlings. In total, 8 target species and 943 one year-old seedlings were planted.

Seedling survival was analyzed using a binomial error distribution and logit link-function. The treatments (watering and enrichment with native soil) and their interaction were considered fixed factors. Block (each study zone), species (nested within zone), and the interaction effect of species with each experimental treatment were considered random factors. Data was analyzed with the procedure GLIMMIX of SAS/STAT (SAS Institute Inc. 2003). If the interaction between species and treatments was found significant, we analyzed separately for each species the effect of treatment. Seedling growth, as increase in height of the survived seedlings, was also analyzed by generalized linear model with GLZ module of STATISTICA (Statsoft Inc, 1998). We used normal distribution and identity link-function, and the factors in this analysis were enrichment with native soil and watering, and their interaction.

The relationship between survival at the end of the experiment and the environmental variables (aspect, altitude, cumulative rainfall over the 4 study years, and presence of ravines) was modelled by a binomial regression (GLZ module of STATISTICA), with average survival at each plot as dependent variable and each environmental feature as independent variable.

Experiment 2. Seedling age effect on survival of tall shrubs.

The planted species were *Berberis hispanica*, *C. monogyna*, *P. lentiscus*, *P. terebinthus*, *Q. coccifera* and *Rosa* sp. All plants were enriched with native soil and watered during the summer. The experiment was conducted in nine plots and started in autumn 2004. Thirty two seedlings of four target species were planted per plot (four replicates of each treatment per plot for each species) with half of the seedlings of 1-year-old and the other half 2-years-old. In total, we planted 288 seedlings following a randomized-block experimental design with only one treatment factor (seedling age).

We compared the establishment success (i.e. survival probability) for seedlings of different age using generalized linear mixed models (GLIMMIX procedure of SAS/STAT; SAS Institute Inc., 2003) and considering binomial error and logit link-function. Seedling age was considered a fixed effect, while species and its interaction with seedling were random factors. Seedling growth was analyzed as in Experiment 1.

3. Results

3.1. Effects of watering and enrichment with native soil on shrub establishment

Seedling survival after four years of study averaged 0.36 ± 0.02 (mean ± standard error). Survivorship stabilized in September 2005 in each treatment, that is, after two years since planting (Fig. 1). *Rosa* sp. and *C. monogyna* showed the highest survival probability over the four study years (0.71 ± 0.03 and 0.44 ± 0.03, respectively), while *B. sempervirens* and *P. lentiscus* had the lowest survival (0.11 ± 0.04 and 0.15 ± 0.06, respectively). The effects of inoculation and watering on survival were fairly consistent through time. After each summer a positive effect of watering was apparent (Table 2), which was still significant at the end of the study (Fig. 2,

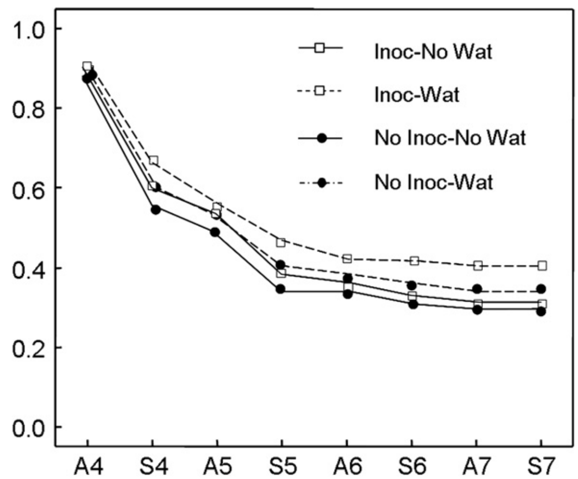

Fig. 1. Curves of mean cumulative survival probability (across species) by treatment. Error bars have been omitted for clarity. Tests of the treatment effects are shown in Table 2. Treatments are indicated as Inoc (native soil enrichment) and Wat (watering every 15 days during the first two summers after plantation). The *x*-axis indicates the month (A: April; S: September) and year (4–7: 2004–2007) of monitoring.

0.37 ± 0.07 for watered seedlings compared to non-watered ones, 0.24 ± 0.05). This positive effect was independent of the species (species times irrigation interaction, $p > 0.05$). In contrast, after the first summer, not all species had the same response to enrichment with native soil (inoculation times species interaction, $p < 0.01$). *C. monogyna* and *P. lentiscus* showed a positive effect of native soil enrichment on survival ($p < 0.05$, for both species at each date), and this effect remained at the end of the study (Table 3). In particular, this effect was very strong in *P. lentiscus*, with average survival of enriched seedlings of 0.33 ± 0.11, while it was 0.03 ± 0.03 for non-inoculated ones (Fig. 3). Yet, *P. terebinthus* and *P. spinosa* responded negatively to enrichment with native soil, and this was evident after the second summer since planting (see Table 3, $p < 0.05$). We did not find any significant effect of enrichment with native soil on survival for the remaining species. In contrast to survival, we found no significant effect of watering and enrichment on growth of survived seedlings at the end of the experiment ($p > 0.05$). The only significant effect on growth was the variation among species (species nested in zone: $F_{35,288} = 9.49$; $p < 0.001$). The species with highest growth were *Rosa* sp. (41 ± 2.63 cm), *C. monogyna* (13.06 ± 1.75 cm) and *P. terebinthus* (12.78 ± 1.80 cm). Only *Rosa* plants flowered through the course of the experiment, with some individuals reaching reproductive maturity after two years since planting. Four years after planting, 30% of *Rosa* plants had flowered.

Table 2
Results of Generalized Linear Models testing effects of enrichment with native soil (Inoc), watering (Wat), species nested within zone (Sp (zone)) and their interactions (Inoc × Wat; Inoc × Sp(zone); Wat × Sp(zone)) on seedling survival in open ground. Enrichment with native soil, watering and their interactions are fixed effects, and the rest are random effects. F statistics are used for fixed effects, and *Z* statistics for random effects. Significance of effects is indicated as **p* < 0.05; ***p* < 0.01; ****p* < 0.001.

	Sep-04	Apr-05	Sep-05	Apr-06	Sep-06	Ab-07	Sep-07
zone	0.81	0.09	0.32	0.48	0.47	0.23	0.2466
Sp(zone)	**3.08****	**3.48*****	**3.35*****	**3.43*****	**3.45*****	**3.42*****	**3.41*****
Inoc × Sp(zone)	1.65	1.61	**2.52***	**2.35***	**2.23***	**2.18***	**2.1971***
Wat × Sp(zone)	0.3	–	1.19	1.37	1.25	1.65	1.7107
Inoc	**5.34***	1.49	2.3	1.31	1.81	1.64	1.79
Wat	**6.62***	1.68	**8.54****	**5.78***	**7.76****	**9.88****	**10.18****
Inoc × Wat	0.01	1.01	0.03	0.21	0.56	1.42	1.22

The bold values showed the effect with $p < 0.05$.

3.2. Relationship of seedling survival to environmental variables

Seedling survival in ravines was significantly higher than far from ravines ($F_{1,14} = 11.41$, $p < 0.01$; average probability of survival in ravines = 0.59; 95% confidence interval: 0.43–0.73; average survival in non-ravines = 0.31, 95% confidence interval: 0.24–0.39). In contrast, there was no effect of aspect ($F_{1,14} = 0.04$, $p = 0.85$). Rainfall variation across the burned area did not relate to survival ($F_{1,11} = 0.24$, for cumulative rainfall over 4 years; $F_{1,11} = 0.01$, for cumulative rainfall over four summer periods; $p > 0.5$, in both cases), However, we did find some marginal trend toward a decreasing survival with the increase in altitude (binomial regression, $b = -0.0019 \pm 0.0009$, $p = 0.06$, g.l. = 1,14).

3.3. Effect of seedling age on survival and growth

Seedling survival after three years in this experiment was 0.21 ± 0.02, and stabilized in September 2005, that is, one year after planting. As with Experiment 1, *Rosa* sp. and *C. monogyna* had the highest survival over the course of the experiment (0.59 ± 0.06 and 0.21 ± 0.06, respectively in September 2007), while all specimens of *B. hispanica* and *P. lentiscus* were dead at the end of the experiment. Results of this assay showed a consistent effect over time of planting zone (block) and age of the seedling, though the latter was species-specific as shown by the significant interaction between species and seedling age ($p < 0.05$ since the first summer, see Table 4). Because of no survival for some species, the slices (or partition) of the interaction effect could not be conducted, but examination of Fig. 4 clearly shows the higher establishment success of the two year-old specimens for all species with some survival excepting *P. terebinthus*.

Regarding seedling growth, we found an effect of both zone of planting and age of seedling, though the latter was species-specific (interaction effect, $p < 0.01$). Growth of 2-year-old seedlings of *P. terebinthus* and *C. monogyna* (12.67 ± 5.69 cm and 9.66 ± 3.63, respectively) was higher than growth of 1-year-old ones (7.00 ± 2.31 and 4.75 ± 4.75 cm). In contrast, growth of *Rosa* sp. specimens was higher for 1-year-old than for 2-years-old seedlings (21.87 ± 3.19 and 12.06 ± 2.79 cm, respectively).

4. Discussion

Our results show an overall positive effect of watering on the survival of planted seedlings, which was fairly consistent across species, while the effects of enrichment with native soil and age of planted seedlings were species-specific. We discuss each of these effects in turn.

4.1. Effect of native soil addition

Many studies in the Mediterranean region have shown a reduction in soil microorganisms after fire. In particular, mycorrhizal communities have been shown to become poorer for several years after fire compared to nearby non-burned areas (Allen, 1991; De Roman and De Miguel, 2002), what may constitute a limitation for plant establishment (Allen, 1991). In our study, we did not find a consistent effect of enrichment with native soil across species. While the effect on survival was positive in some species, it was negative in others. The balance of the interaction of the plant and microorganisms seems to change along with plant ontogeny. It turned from an overall positive effect of enrichment with native soil on seedling establishment, in the beginning of the experiment, to a gradual loss of efficiency for the plant, becoming even negative for *P. terebinthus* and *P. spinosa*, after four years. This change can be produced by the natural recovery and colonization of the soil by

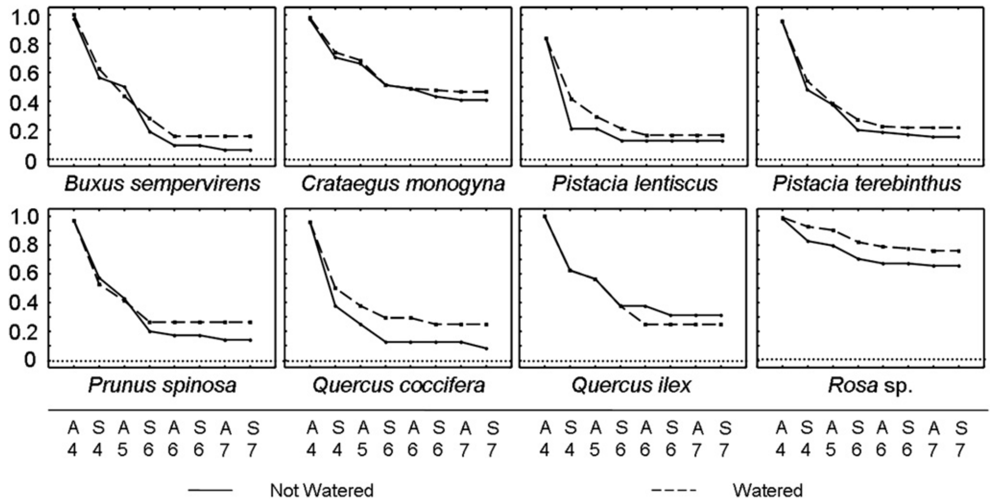

Fig. 2. Curves of cumulative survival probabilities for each species in the watering treatments. Tests of the treatment effects are shown in Table 2. The *x*-axis indicates the month and year of survey (A: April; S: September).

native microorganisms thorough time. In other studies, similar results were found with mycorrhizal inoculation. Some authors had suggested that the relative loss of efficiency of inoculation with mycorrhiza in degraded zones through time might reflect the natural colonization of soil by mycorrhizal fungi (Diaz and Honrubia, 1995; Maestre et al., 2002; Requena et al., 1996), which might be more beneficial than nursery inoculation. In the particular case of *Quercus* species, *Q. ilex* and *Q. coccifera*, the lack of benefit of enrichment with native soil is congruent with the results of Maestre et al. (2002) with *Q. coccifera*. It is worth noting that the two species with highest survival and growth (*Rosa* sp. and *C. monogyna*) were favoured by enrichment with native soil (though in the former the effect was not significant). In contrast, species with very low overall levels of survival were negatively affected by enrichment (*P. spinosa*, *P. terebinthus* and *Q. ilex*). This suggests the possibility that under pronounced water stress, the association with some soil microorganisms, for example mycorrhizal fungi, turns to a negative balance for the less stress-tolerant species.

4.2. Effect of irrigation

The positive effect of watering confirms the findings of numerous studies and prove that it helps to overcome the high water stress that juveniles suffer during the Mediterranean summer drought (Castro et al., 2005; Mendoza, 2008; Montesinos, 2007; Rey and Alcántara, 2000; Rey-Benayas and Camacho-Cruz, 2004; Rey-Benayas, 1998). Watering is a common practice in restorations of semiarid zones of Magreb (Gupta, 1991; Raggabi, 1996). In Spain, watering was historically a cultural practice in reforestations under conditions of strong water limitation (called reforestation with baby's bottle, cited in Serrada et al., 2005). Moreover, recent studies have shown an increase in the survival and growth of watered seedling during the first summer after planting (Jiménez et al., 2004; Navarro and Martínez, 1996; Rey-Benayas, 1998; Sánchez et al., 2004). Paradoxically, seedling irrigation is nowadays frequently advised against in reforestation, and not used, under the idea that, besides increasing the economic cost, the watered plant increases its water demand, becoming less tolerant to drought. (but see Rey-Benayas and Camacho-Cruz, 2004 for a positive effect of watering during the first three years after plantation in *Q. ilex*). Our results refute this view, since 7 out of 8 species significantly increased their survival by watering. *Q. ilex* was the single species where the effect of watering was not positive (see Fig. 2), turning negative (but not statistically significant) after the severe drought of the second year of the experiment. In contrast to our data, Rey-Benayas and Camacho-Cruz (2004) found a positive effect of irrigation on survival and growth of this species under higher precipitation conditions (400–500 mm). It is possible that this species, one of the most used in current reforestations in Spain, does increase its water demand after watering in years of high water stress, becoming less tolerant to drought.

Table 3
Effect of enrichment with native soil on seedling survival. Significance of effects is indicated as (*) $p < 0.1$ (marginally significant); $^{*}p < 0.05$; $^{**}p < 0.01$; $^{***}p < 0.001$.

Species	Sep-04	Apr-05	Sep-05	Apr-06	Sep-06	Ab-07	Sep-07
Buxus sempervirens	3.63(*)	0.79	1.97	2.19	2.19	1.2	1.2
Crataegus monogyna	**9.74****	**9.79****	**16.06*****	**10.77****	**11.36*****	**11.7*****	**11.7*****
Pistacia lentiscus	**6.92***	**5.07***	**6.42***	**5.34***	**5.34***	**5.34***	**5.34***
Prunus spinosa	0.15	1.1	3.84(*)	3.33(*)	3.33(*)	**4.21***	**4.21***
Pistacia terebinthus	0.07	0.42	3.02(*)	**4.49***	3.27(*)	3.65(*)	3.65(*)
Quercus coccifera	**4.85***	1.03	0.03	0.03	0.22	0.22	0.6
Quercus ilex	0.13	0.03	1.17	0.32	1.12	1.12	1.12
Rosa sp.	0.01	0.18	0.28	0.26	0.38	1.08	1.08

The bold values showed the effect with $p < 0.05$.

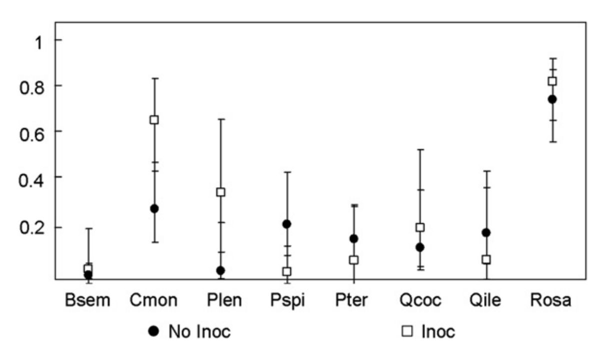

Fig. 3. Decomposition among species of the effect of soil enrichment on survival probability at the end of the experiment (September 2007). Symbols are least-square means and 95% confidence intervals. Tests of the treatment effects are shown in Table 3. Species are indicated as: Bsem (*Buxus sempervirens*), Cmon (*Crataegus monogyna*), Plen (*Pistacia lentiscus*), Pter (*Pistacia terebinthus*), Qcoc (*Quercus coccifera*), Qile (*Quercus ilex*) and Rosa (*Rosa* sp.).

Table 4
Results of the analyses testing the effect of seedling age at plantation (Age), fixed effect, and species (Sp) and zone (Zone) as random effects, on seedling survival and growth in open ground. Species effect was nested within zone since different species were used in each case. The interaction effect was considered random. F statistics are used for fixed effects, and *Z* statistics for random effects. Significance of effects is indicated as (*) $p < 0.1$ (marginally significant); *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$.

Effects	Survival						Growth
	Apr-05	Sep-05	Apr-06	Sep-06	Apr-07	Sep-07	03–07
Age	**7.78****	1.63	0.87	1.37	0.65	0.81	**8.15***
Zone	−1.07	−1.07	−0.72	−1.32	−0.92	−0.7	−1.91(*)
Sp (Zone)	**2.36***	**2.56***	**2.43***	**2.51***	**2.36***	**2.2***	1.56
Age × sp (Zone)	1.64	1.83(*)	**2.19***	1.92(*)	**2.31***	**2.47***	**−2.77****

The bold values showed the effect with $p < 0.05$.

In any case, on average, watering increased the probability of seedling survival and this difference arose mainly during the year of more severe drought (the hydrological year 2004/2005). Several additional particularities of our study reinforce our conclusion in favour of the use of watering: first, the positive effect emerged even after minimal watering (equivalent to summer storms); second, watering effect was invariant across zones of the burned area; and third, the benefit of watering was not only in the short term (in the first years after planting) but also after four years. Therefore, our results firmly advise the use of supplementary summer watering. To improve the establishment of tall shrubs in fire-degraded zones with Mediterranean dry-subhumid climate, watering should be considered where restoration practices based on seedling planting in open ground are to be implemented. With some exception, our results further contradict the supposition of increased future mortality risk by increased water demand. Moreover, reduction of summer rainfall and a prolonged drought period is a predicted scenario of Climate Change in the south of the Mediterranean region, which might make watering still more necessary in the future.

Recent techniques of forest restoration in the Mediterranean region advocate the use of established pioneer shrubs as microhabitats (nurses) for tall shrubs and tree seedling plantation (see Gómez-Aparicio et al., 2004; Siles et al., in press), under the main idea that shading by established shrubs reduces water and irradiance stresses, and protect the seedlings against ungulate grazing. Experimental results of nurse-based restoration in the same burned area (Siles et al., unpublished) have rendered a benefit of 2–9-fold increase in probability of seedling survival (depending on the annual rainfall) compared to planting in open ground without watering. Such advantage is clearly shortened if watering is used. In fact, in years with typical rainfall for the region (800–1100 mm) nurse-based planting has an overall success of around 70% of survival after the first year, which is comparable with the seedling survival after a year of watered plants in open ground (around 60%). This clearly means that part of the benefits of the use of nurse plants, in terms of juvenile establishment, might be compensated by watering. Some other studies have found that benefits of nurse plants or the artificial shading for seedling recruitment disappear with irrigation (Montesinos, 2007; Padilla and Pugnaire, 2009, respectively).

4.3. Effect of seedling age

Our results corroborate that the first year after planting is the most critical for seedling establishment (García-Salmeron, 1995; Mendoza, 2008; Rey et al., 2004; Rey-Benayas, 1998), and that the age of the planted seedlings may be important for many species to overcome this critical stage. It is, overall, advisable to use 2-year-old rather than 1-year-old seedlings. This is congruent with the frequent finding of increased survival after the first year for naturally emerged seedlings of woody and perennial herb species of the Mediterranean forest and scrublands (Garrido et al., 2007; Rey and Alcántara, 2000; Traveset et al., 2003, among many others). Nonetheless, the rainfall regime in subsequent years may still be important in the stabilization of survival curves, as shown by the high mortality for most species during the second year (of extremely severe drought) after planting in Experiment 1. This remarks the existence of a relationship between seedling mortality and the inter-annual variation in rainfall.

4.4. Spatial heterogeneity and the effect of ravines

Spatial heterogeneity in the environment normally influences establishment of naturally emerged seedlings in many species (e.g., Gómez-Aparicio et al., 2005a, 2005b; Rey and Alcántara, 2000), and it is expected to also affect establishment of planted seedlings (e.g., Rey et al., 2004). However, the high variation in rainfall among zones of the burned area was not related to variation in seedling

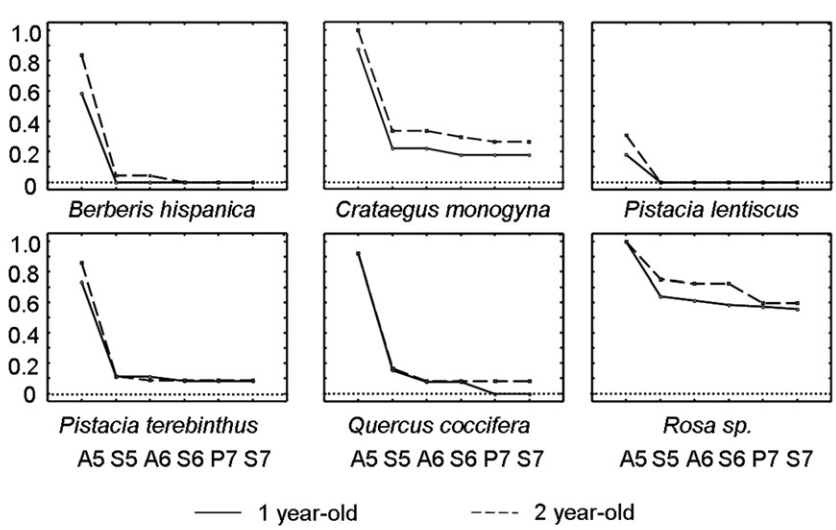

Fig. 4. Curves of cumulative observed survival probabilities for seedlings planted at different ages. Tests of the treatment effects are shown in Table 4. The *x*-axis indicates the month (A: April; S: September) and year (5–7: 2005–2007) of monitoring.

establishment. It is possible that most of such variation occurred during the moist periods of the year, when precipitation had less impact on seedling establishment, while spatial heterogeneity in rainfall was much smaller during summer (around 15 mm per year; 65 mm in four years), and probably insufficient to mark differences in establishment.

Of major importance for seedling establishment seems to be the spatial heterogeneity in edaphic humidity due to the occurrence of ravines. Seedlings duplicated their survival when planted in ravines compared to those planted far from ravines. Ravines may be thus an important element in restoration in Mediterranean mountains, especially for managing restoration from a landscape perspective. They can be used to obtain belts of tall scrublands rich in fleshy-fruited species (*Rosa*, *Crataegus*, *Berberis*, etc.), which would attract birds and carnivorous mammals (common seed disperser of these species), allowing further shrub colonization through seed dispersal into and outside ravines. Under this view, ravines would act as micro-ecological corridors by offering proper environment for animal seed dispersers.

5. Concluding remarks

A final important finding is that some thorny tall shrubs, like *Rosa* and *C. monogyna*, showed disproportionate survival and growth even without watering. These are fleshy-fruited species highly attractive to frugivorous birds and carnivorous mammals (see for example Herrera, 1989, 1995). These species (in particular, *Rosa*) reach reproductive maturity quickly and could rapidly increase the local woody cover. We propose them as keystone species for restoration of Mediterranean mountains: (i) besides being easily established in ravines, they can be easily established in other places; (ii) they can attract vertebrate seed dispersers and nucleate the arrival of other fleshy-fruited tall shrubs and trees (Herrera, 1984; Verdú and García-Fayos, 1996); and iii) these species are abundant in many native plant communities of the Mediterranean mountains.

In conclusion, the experiments conducted in this study to plant late-successional shrubs have shown the viability of the use of low aggressive restoration techniques to revegetate fire-degraded environments. Watering seems to be the most recommendable treatment. In most cases, supplementary watering during summer and/or particularly dry years will suffice, being unnecessary in subsequent years (Fig. 1). Its implementation within the frame of a landscape design of restoration is promising. This landscape design should take advantage of the particular suitability of ravines to seedling establishment and to be used as corridors for seed disperser animals. Some species highly attractive for seed dispersers and of particularly easy establishment (like *Rosa* sp. and *C. monogyna*) could become fundamental to extend the spontaneous regeneration into and beyond corridors by favouring seed dispersal.

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