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Does shelter enhance early seedling survival in dry environments? A test with eight Mediterranean species

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Abstract

Question: Do solid-walled polyethylene tubes and mesh fabric tubes improve the short-term survival of eight Mediterranean tree and shrub species often used in the restoration of arid environments?

Location: We conducted two experimental plantations in degraded field sites in the province of Almería (SE Spain), under arid Mediterranean conditions.

Methods: One-year-old seedlings of *Ceratonia siliqua*, *Juniperus phoenicea*, *Olea europaea*, *Pinus halepensis*, *Pinus pinaster*, *Quercus coccifera*, *Quercus ilex* and *Tetraclinis articulata* were planted either sheltered by one of the above shelter tubes, or by being left unsheltered. Survival was recorded the first growing season after planting, which was a very dry season.

Results: Overall, seedling survival ranged from as little as 0% to 24%, and tree shelters consistently enhanced survival in *Quercus* species only, ranging from 16% in walled shelters to 8% in mesh shelters. Shelters failed to boost survival in the six remaining species.

Conclusion: The results of this study suggest that both walled and mesh shelters were mostly ineffective at increasing seedling survival for the Mediterranean species used in this experiment; these species coincide with those used in restoration programs. The use of shelters in restoration programs conducted in arid environments should be reconsidered, while walled shelters might be advisable for Mediterranean *Quercus* species only. Further research is necessary to develop and assess improved types of shelters for arid environments.

Introduction

Seedling survival is critical in restoration programs conducted in dry Mediterranean environments, as seedlings are very sensitive to several hazards. These include extreme temperatures and irradiance, soil desiccation, strong winds, and herbivory (Moles & Westoby 2004; Padilla et al. 2009). Excessive light and extreme temperatures may damage seedlings, strong, desiccant winds may snap twigs and exacerbate water stress caused by low rainfall, and the seedling's green sprouts may be browsed by cattle and wild fauna (Bainbridge 1994). Seedlings are mostly unable to face these threats by themselves in disturbed environments and large casualties have been reported in projects carried out in arid and semi-arid Mediterranean environments (Alloza & Vallejo 1999; Maestre et al. 2002; Sánchez et al. 2004).

Restoration initiatives in arid environments are often at risk because of a low survival rate amongst transplants. Several procedures have been developed to provide seedlings with better protection in an effort to enhance survival rates (Ludwig & Tongway 1996; Rey-Benayas 1998; Padilla & Pugnaire 2006). The use of a wide array of tree shelter-types is by far the most common practice given its low cost, ease of use, and efficiency (Bainbridge 1994; Pemán & Navarro 1998; Ponder 2003), yet their effectiveness for non-traditional species in very dry environments has yet to be examined.

Tree shelters, usually made out of plastic or similar materials, and available in several designs, can protect plants against damage from domestic or wild fauna (Dubois et al. 2000; Sharrow 2001; Chaar et al. 2008) and wind (Bainbridge 1994), while at the same time may

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increase internal air humidity as a result of dew deposition and transpiration condensation inside their walls (del Campo et al. 2006). Furthermore, shelters may decrease excessive irradiance and buffer extreme temperatures (Bellot et al. 2002; Jiménez et al. 2005; del Campo et al. 2006) thereby reducing evapotranspiration (Bergez & Dupraz 1997). However, low levels of ventilation caused by some shelters may increase internal air temperature (Bergez & Dupraz 2009), which together with a decrease in photosynthetically active radiation reaching the leaves could constraint CO_2 fixation and plant growth (Dupraz & Bergez 1999). Moreover, in dark-colored tubes overheating is common if used in sunny and hot areas (Ward et al. 2000). Thus, the overall net balance between shelter benefits and costs determines their efficiency.

Forest restoration in Mediterranean ecosystems is particularly risky because of the low, unpredictable rainfall, long summer drought, high temperatures and irradiance, and frequent grazing (Pausas et al. 2004). Under these limiting conditions, shelters may provide suitable microsites. Mesh-walled and solid-walled shelters (both ventilated and unventilated) are commonly used in Mediterranean restoration programs (Bellot et al. 2002; Jiménez et al. 2005; Oliet et al. 2005; del Campo et al. 2006). However, most research with these shelters has been restricted to the most popular species (e.g. *Quercus ilex*), and their effectiveness in improving survival of other relatively slow-growing species characteristic of dry Mediterranean climates, remains to be examined (Oliet & Jacobs 2007). Therefore, research that tests the effects of tree shelters under very dry conditions is necessary to improve the success of restoration projects.

We assessed the contribution of two shelter types, mesh-walled and solid-walled, to enhance early seedling survival of a wide range of tree and shrub species commonly used in restoration programs carried out in arid mountains of SE Spain. Recurrent restoration failure has been reported in these sites. Here, given the harsh environmental conditions, we expected shelters to enhance seedling survival.

Methods

Experimental sites

This study was conducted at two deforested sites approximately 52 km apart in the province of Almería (SE Spain), the Santillana and Cortijo La Sierra sites. The expansion of dry-farming, grazing and logging until the beginning of the 20th century eroded almost completely natural vegetation in these areas (Latorre et al. 2001). Natural recovery of these arid landscapes is rather slow (Pugnaire et al. 2006) and restoration efforts have tried to speed up succession (Bonet 2004). However, recurrent restoration failure has been reported in these sites.

The climate in both sites is Mediterranean, with a dry season from Jun to Sep, and irregular precipitation throughout the rest of the year. Temperatures are moderately low in winter and high in summer. The two sites differed in rainfall and potential vegetation, so tree shelters were tested on different species to account for such a contrast. The Santillana site (37°6′ N, 2°45′ W) was placed facing north in the Sierra Nevada range at 1300 m elevation on a 20% slope. Annual precipitation averages 393 mm, and the mean annual temperature is around 13°C (Red de Información Ambiental de Andalucía, 1961–1990). Soils are loamy-sandy, eutric regosols developed over a shallow mica-schist bedrock. The stand community was a shrubland dominated by the large shrubs *Retama sphaerocarpa* and *Genista cinerea* with scattered juveniles of *Q. ilex*. The Cortijo La Sierra site (37°1′ N, 2°10′ W) was located on a 35% south-facing slope in the Sierra Alhamilla range, at 700 m elevation. The mean annual temperature is 17.3°C and annual precipitation is 309 mm. Soils are loamy-sandy, calcic regosols developed over a mica-schist bedrock (Lucdeme 1989). The plant community was a scrubland dominated by the small shrubs *Anthyllis cytisoides* and *Artemisia barrelieri*, with scattered juveniles of *Olea europaea* var. *sylvestris*.

At each experimental site we selected an area of nearly 4 ha. In each area, sites were chosen on opposite slopes with similar plant communities and soils, and differed only in aspect. In Santillana, slopes faced north-east and south-east, while in Cortijo La Sierra slopes faced north and south.

Species and tree shelters

We used the Phoenician juniper (*Juniperus phoenicea* L.), Kermes and Holm oaks (*Quercus coccifera* L. and *Q. ilex* L., respectively), and the maritime pine (*Pinus pinaster* Aiton) on a relatively wet site (Santillana), and the Carob tree (*Ceratonia siliqua* L.), Phoenician juniper, wild olive (*Olea europaea* L. var. *sylvestris* Brot.), Aleppo pine (*Pinus halepensis* Mill.) and the Araar (*Tetraclinis articulata* (Vahl) Mast) on the drier site (Cortijo La Sierra). All these species are native to Mediterranean woodlands and correspond with the potential vegetation in each site (Valle et al. 2003). The use of such species has been subsidized for the restoration of old fields by the regional government (Decree 127/1998, Junta de Andalucía).

One of the tree shelters tested consisted of a cylindrical, green, polyethylene tube, 8 mm mesh size (Redplanton, Projar SA, Valencia, Spain; hereafter 'mesh shelter'); the other shelter was made of 0.5 mm-thick beige polyethylene (Plastimer SA, Almería, Spain) with 48 lateral 20 mm

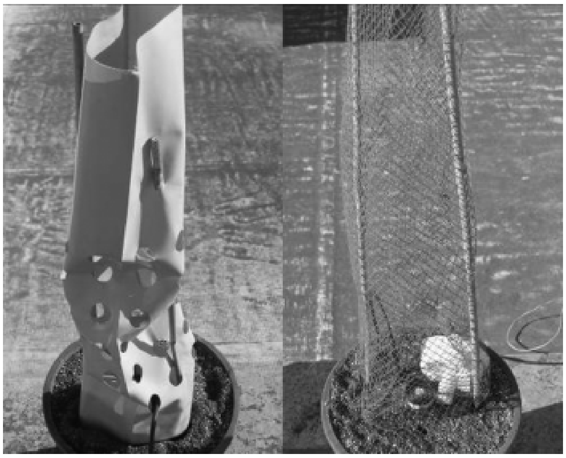

Fig. 1. Partial view of the solid-walled (left) and mesh-walled (right) shelters used in this study.

diameter holes on the lower half of the shelter (hereafter 'solid shelter'). Both mesh and solid shelters were anchored by two sticks, were 60 cm in high and 15 cm diameter, and open at the top (Fig. 1). Seedling survival in shelters was compared to survival of seedlings in controls.

Experimental design

In January 2003, 1-yr-old seedlings of standard size grown under identical conditions in a nearby forestry nursery (Padules, Spain; 36°59′ N, 2°46′ W, 740 m elevation), were transplanted to the field. Seeds were of local provenance. At the time of transplant, species were distributed on each aspect at random in gaps at a distance of at least 1 m from any perennial species, and were assigned to one of the following treatments: (a) mesh-walled shelter, (b) solid-walled shelter or (c) no shelter (control). Only one seedling was planted in each tube. In all cases, we dug a small micro-catchment (1 m^2) using a hoe to increase water collection following traditional techniques. In Sep 2002, subsoiling with one ripper to a depth of 0.5 m was carried out twice at each site. As summer drought is one of the major constraints on survival, half of the planted seedlings received two irrigation pulses in May and Jul, with around 1.5-3 l of water supplied at root level through a fine pipe buried 20 cm into the soil close to the roots (Sánchez et al. 2004); the other half remained unwatered throughout. Watered seedlings were chosen at random.

The experimental design was factorial with two fully-crossed factors: watering (irrigated versus control) and shelter type (mesh versus solid versus control). Aspect was not taken into account as we lacked plot replication; data from north and south aspects were therefore pooled for each site. Survival was recorded in Oct 2003, after the first autumn rains. Survival was determined by the presence of living sprouts. The sample size per treatment combination (species × watering × shelter) ranged from 60 to 100 seedlings in Santillana and from 60 to 80 seedlings in Cortijo La Sierra.

Rainfall in each experimental site was collected with a pluviometer (Davis Instruments Corp, Hayward, CA, USA) and recorded daily (Hobo, Onset Computers, Pocasset, MA, USA) from Apr to Oct. Rainfall from preceding months was taken from the nearest meteorological station. Overall rainfall during the course of the experiment was 28% and 36% below the latest historical records in Santillana and Cortijo La Sierra, respectively. Despite this lower rainfall, it is worth noting that climate change scenarios for our region predict a 30% reduction in precipitation (IPCC 2007). Hence, our findings could provide insights into future restoration trends.

Micro-environmental conditions in tree shelters

At the end of the experiment we recorded photosynthetically active radiation (PAR, quantum sensor SKP 215; Skye Instruments Ltd, Powys, UK), relative air humidity and temperature (Hobo Pro; Onset Computers, Pocasset, MA, USA) at ground level in shelters placed in pots at the Experimental Station of Arid Zones (CSIC, Almería; 36°50′ N, 2°27′ W, 30 m elevation). These measurements aimed to shed light on the mechanisms underlying differing survival between tree shelters, and not to characterize growing conditions inside. Data, collected over a 5-d period in Sep 2003 during a sunny spell, allowed for a relative comparison on microclimatic amelioration between tree shelters and controls.

Micro-environmental data were recorded every minute and averaged every 10 min in a CR10X data logger (Campbell Scientific Ltd, Shepshed, UK). We used three replicates for each shelter type and two for controls. Vapor pressure deficit (*VPD*, kPa) was calculated from air temperature (*T*, °C) and relative air humidity (*RH*, %) following Rosenberg et al. (1983):

$$VPD = \left(1 - \frac{RH}{100}\right) \times 0.61078 \times e^{\left(\frac{17.269 \times T}{T + 237.3}\right)} \quad (1)$$

Statistics

Differences in seedling survival between shelters and control were tested by using simple binary logistic regression where survival was the dependent variable, and watering and shelter-type were the predictor factors. In each site, we ran independent logistic regressions for each species. Logistic regression started from the saturated model (watering × shelter), and significance of the interaction and main factors were determined through backwards elimination, first of interaction, and then of main factors, and by comparing the goodness-of-fit (G^2) between the model with an eliminated term and the preceding model, using the χ^2 distribution as a significance contrast (Tabachnick & Fidel 2001).

Differences in daily mean, maximum and minimum temperatures, VPD, and PAR between shelter types were tested through one-way ANOVA, followed by Tukey tests. For these tests, we randomly selected 1 day from our 5-day dataset, since measurements were taken on a relatively uniform, sunny spell. For PAR analysis we considered only the daylight time period, between 8:00 and 17:30 solar time.

Analyses were conducted with the SPSS v15.0 statistical package (SPSS Inc., Chicago, IL, USA), and significant differences were set at $P < 0.05$.

Results

Seedling survival

Santillana site

There were no significant differences in seedling survival among shelter treatments in *J. phoenicea* ($P > 0.3$, Table 1, Fig. 2A). Summer irrigation enhanced survival from 12% to 24% (control versus watered seedlings, respectively; $P < 0.001$). Among *P. pinaster* seedlings, survival was very low, with figures ranging from 0% to 7%. Survival of watered seedlings was close to 4% in all treatments, but non-irrigated seedlings only survived in mesh-walled shelters (watering × shelter, $P < 0.02$). Overall, survival of *Q. coccifera* seedlings was significantly higher in shelters ($P < 0.001$), particularly in solid-walled shelters (17%) followed by mesh-walled shelters (11%), while only 3% of the control seedlings survived. Watering increased survival almost four times across treatments (4% versus 15 %; $P < 0.001$). *Quercus ilex* also survived better in both types of shelters than in control ($P < 0.003$) with higher survival in watered treatments ($P < 0.001$). The highest survival rate was found in solid-walled shelters (15%) followed by mesh-walled shelters (7%) with only 4% in control seedlings. Survival of watered seedlings was four-fold that of unirrigated ones.

Cortijo La Sierra site

Most of the seedlings planted at this site died in summer, with survival ranging from 0% to 6% (Fig. 2B). There was a weak effect of tree shelters on survival of *C. siliqua* ($P < 0.05$) and *T. articulata* ($P < 0.04$; Table 1), with seedlings in solid-walled shelters surviving slightly better (4%) than those protected with mesh-walled shelters or living in control (< 1%). Tree shelters had no effect at all on survival of *J. phoenicea*, *O. europaea* and *P. halepensis*. Similarly, irrigation did not enhance survival in any species other than *T. articulata* ($P < 0.03$).

Micro-environmental conditions in tree shelters

The PAR was significantly lower in solid-walled than in mesh-walled shelters and controls; daily mean and max PAR recorded in solid-walled shelters was 75% below that recorded in control and near 30% in mesh-walled shelters (Table 2). Thus, solid-walled shelters diminished PAR reaching the soil surface to a greater extent than mesh shelters. The VPD tended to be lower in tree shelters than in control, as shelters retained air moisture. Not only were there differences among shelters in mean VPD, but also in min. and max. values (Table 2). By contrast, mean, max. and min. air temperature inside tree shelters and in control did not differ. Overall, the lowest PAR and VPD levels were found in solid shelters, while the highest were recorded in the control; mesh shelters were in between the two.

Table 1. Results of logistic regression performed with seedling survival as the response variable and watering supply (watered and non-watered) and tree shelters (soil, mesh and control) as predictor variables for each species. No data are available for *J. phoenicea* at Cortijo La Sierra site because all seedlings died. Bold letters indicate significant differences at $P < 0.05$.

Site	Species	Watering		Shelter		Watering × Shelter	
		χ^2	P	χ^2	P	χ^2	P
Santillana	*Juniperus phoenicea*	13.465	< **0.001**	2.307	0.316	2.234	0.327
	Pinus pinaster	1.505	0.220	2.959	0.228	9.226	**0.010**
	Quercus coccifera	12.855	< **0.001**	19.852	< **0.001**	4.788	0.091
	Quercus ilex	17.430	< **0.001**	12.222	**0.002**	4.008	0.135
Cortijo La Sierra	*Ceratonia siliqua*	0.306	0.580	6.215	**0.045**	1.249	0.536
	Juniperus phoenicea	–	–	–	–	–	–
	Olea europaea	2.452	0.117	5.721	0.057	3.409	0.182
	Pinus halepensis	0.721	0.396	1.021	0.600	4.957	0.084
	Tetraclinis articulata	5.063	**0.024**	6.866	**0.032**	1.560	0.458

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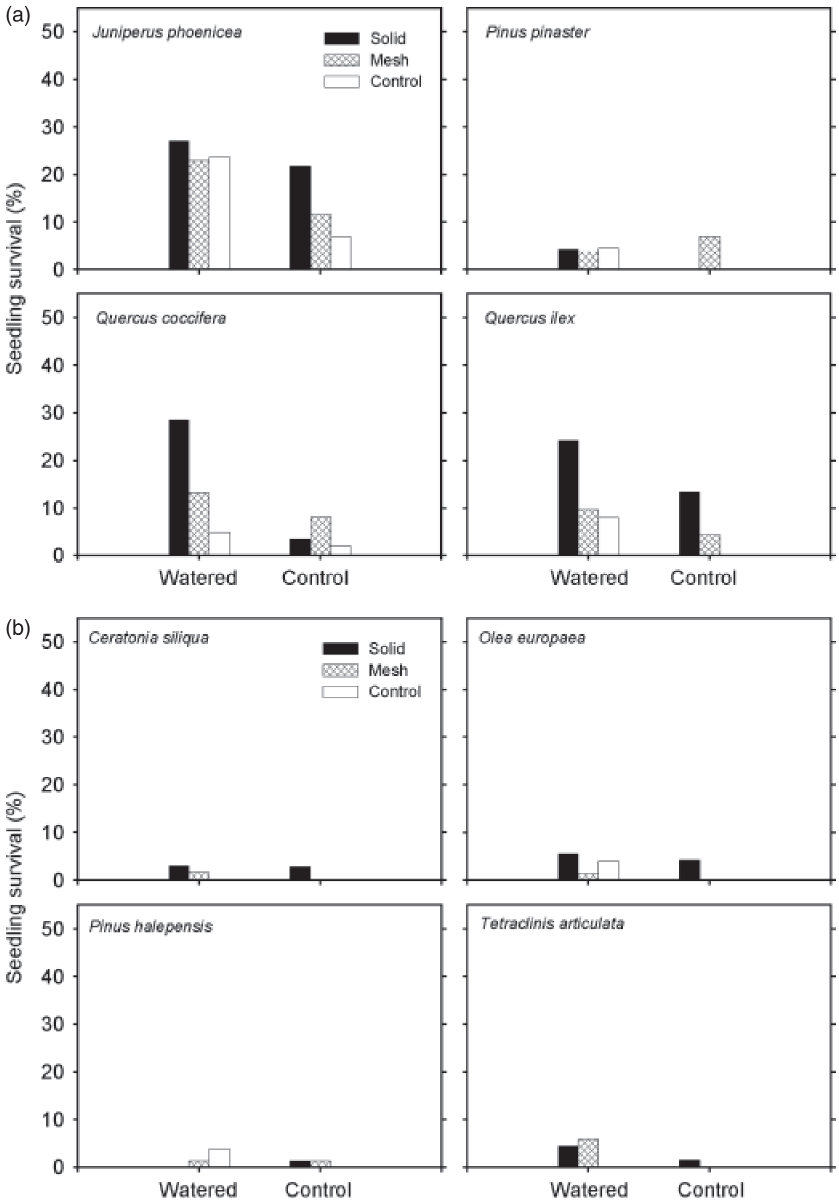

Fig. 2. Survival rate in autumn (after 9 months), of eight Mediterranean species grown in two different types of shelters (mesh-walled and solid-walled) and unsheltered (control) in Santillana (a) and Cortijo La Sierra (b) experimental sites. Note that *Juniperus phoenicea* does not appear in the Cortijo La Sierra site because all seedlings died.

Discussion

We tested whether solid-walled and mesh-walled shelters, both commonly used in arid restoration programs of SE Spain, enhanced survival of Mediterranean woody species. Overall, survival was significantly higher in solid-walled shelters than in mesh-walled shelters, or in controls in four out of the eight species tested. However, this effect was almost negligible in two of these species, as survival was so low ($< 3\%$) in shelters that the effect is irrelevant in management terms. This leads us to conclude that under very dry conditions such as those at our field sites, shelter alone does not ensure establishment, as found elsewhere when using the shelter provided by piled shrub branches in a nearby area (Padilla & Pugnaire 2009).

Solid-walled shelters reduced the amount of radiation reaching the soil surface to a greater extent than did mesh-walled shelters, whereas both shelter types resulted in higher air moisture than in control. Although we did not record levels of herbivory explicitly, we did observe some browsed shoots, particularly in control seedlings,

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Table 2. Photosynthetically active radiation (PAR), vapor pressure deficit (VPD) and air temperature in mesh- and solid-walled shelters, and in controls, measured at soil level in experimental pots in Sep 2003 at the end of the experiment. *F* and *P* are values of one-way ANOVA. Significant differences among shelter treatments are indicated at $P < 0.05$ by bold type, differing lower-case letters after Tukey test. Values are means ± 1 SE.

	Mesh	Solid	Control	ANOVA	
				$F_{2,4}$	P
PAR (μmol m^{-2} s^{-1})					
Mean	**580 ± 15^a**	**113 ± 10^b**	**823 ± 9^c**	1419.69	< 0.001
Max	**1264 ± 40^a**	**200 ± 17^b**	**1750 ± 13^c**	1523.60	< 0.001
Min	**114 ± 5^a**	**21 ± 1^b**	**111 ± 3^a**	474.11	< 0.001
Air temperature (°C)					
Mean	24.74 ± 0.07^a	25.24 ± 0.02^a	25.09 ± 0.05^a	0.80	0.498
Max	33.44 ± 0.26^a	34.10 ± 0.67^a	35.29 ± 0.52^a	0.78	0.508
Min	21.34 ± 0.10^a	21.65 ± 0.13^a	21.11 ± 0.09^a	0.81	0.497
Air humidity (%)					
Mean	**76.1 ± 2.4^{ab}**	**86.3 ± 7.3^b**	**52.7 ± 0.0^a**	**9.61**	**0.019**
Max	**96.3 ± 1.1^a**	**99.9 ± 0.7^a**	**90.1 ± 0.0^b**	**26.97**	**0.002**
Min	37.4 ± 4.8^a	58.9 ± 21.1^a	19.5 ± 0.0^a	1.71	0.272
VPD (kPa)					
Mean	**0.89 ± 0.09^a**	**0.86 ± 0.02^a**	**1.82 ± 0.02^b**	34.86	0.003
Max	**3.18 ± 0.24^a**	**3.33 ± 0.22^a**	**5.76 ± 0.20^b**	24.71	0.006
Min	**0.10 ± 0.03^a**	**0.02 ± 0.02^a**	**0.25 ± 0.00^b**	17.82	0.010

while shelters prevented rabbits and mice from browsing on the protected seedlings. *Quercus coccifera* and *Q. ilex* had beneficial protection from browsers and intense summer radiation in solid-walled shelters when compared with mesh-walled shelters and controls. These findings are in agreement with reports that highlight the preference of these species to dark-colored, solid-walled shelters in the Mediterranean. Bellot et al. (2002) found that brown plastic protectors were most beneficial for Kermes oak, probably owing to radiation interception to optimum levels for the species. Rey-Benayas (1998) reported greater survival under artificial shade than in controls, and Oliet & Jacobs (2007) recommended shelter tubes for planting Holm oaks in Mediterranean areas. Furthermore, the regeneration niche of these *Quercus* species is linked to the shaded understorey (Broncano et al. 1998; Puerta-Piñero et al. 2007; Smit et al. 2008), thus higher levels of shelter, such as those provided by our solid-walled shelters, are appropriate over mesh-walled shelters or unsheltered planting for these *Quercus* species, as these shelters intercept radiation and protect against herbivory.

Shelters were also effective for *Ceratonia* and *Tetraclinis* in statistical terms. The fact that seedlings of *Ceratonia* performed similarly in mesh-walled shelters and in controls suggests that shade provided by soil-walled shelters, rather than browsing protection, mediated the shelter effect. *Ceratonia* is generally intolerant of deep shade, and establishes itself in well-lit gaps in open woodlands in Spain (Sack et al. 2003). However, this does not preclude that in our very dry site, saplings could profit from some shade; evidence reveals that in xeric and open habitats this species tends to occur in late-successional stages characterized by lower irradiance (Herrera 1984; Valle et al. 2003). Similarly, tree shelters had significant effects on *Tetraclinis articulata* and seedlings likely benefited from protection against herbivory rather than from irradiance, because performance in shade-providing, solid-walled tubes equaled survival in mesh-walled tubes. Shade does not seem to be a critical factor for the regeneration of this species, which mostly occurs in very harsh environments of northern Africa on a wide range of substrates. Rather, high grazing pressure limits the natural regeneration of the species (Abbas et al. 2006).

Neither solid-walled nor mesh-walled shelters consistently affected survival of the remaining species, *J. phoenicea* and *P. pinaster* in Santillana, and *O. europaea* and *P. halepensis* in Cortijo La Sierra. Despite the fact that differences were not significant, seedlings of *P. pinaster* tended to perform better in mesh tubes than in solid-walled tubes, most likely because the mesh protected buds against rodents and rabbits, while at the same time allowing light to pass through. This pattern is consistent with the behavior of such a helophytic species (Calvo et al. 2008). Some seedlings of *O. europaea* remained alive in solid-walled shelters, whereas in controls or in mesh tubes, survival tended to be lower (but not significantly). These findings would concur with previous work reporting that some sort of shelter could increase seedling recruitment of this species (Rey & Alcántara 2000). Survival of *P. halepensis* saplings was one of the lowest in

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the whole experiment regardless of shelter type, which is likely to be caused by the water stress in Cortijo La Sierra site being too intense even for this helophytic pine.

Research has shown that irrigation in spring and summer may provide seedlings with enough moisture to face summer drought (Rey-Benayas 1998; Bainbridge 2002; Sánchez et al. 2004; Banerjee et al. 2006; Alrababah et al. 2008), yet the amount of water supplied is critical (Allen 1995). The two pulses of water we supplied (in May and Jul) enhanced survival slightly at the more humid Santillana site, but did not increase survival at the drier Cortijo La Sierra site. Therefore, more frequent or intense watering schemes seem to be necessary in these extremely dry sites, in order to boost early seedling survival.

Overall, our findings suggest that neither of the shelter types assessed enhance seedling survival rates consistently for most of the species planted at these dry sites. We therefore suggest that the use of such shelters be reconsidered for environments similar to ours, as they are not worth the labor or costs at these sites. The shelter types tested here may have further drawbacks because they have a great visual impact, they remain in the field long term, and removals are typically expensive. These reasons, together with their low efficiency, make it necessary to develop new designs and to improve materials for shelters in arid environments. An alternative to tree shelters can be provided by using pre-existing vegetation or piled branches as nurse plants for seedlings of the shrub and tree species being restored (Ludwig & Tongway 1996; Padilla & Pugnaire 2006). Fertile and more moist soils may occur underneath living nurse plants, unlike tree shelters or piled branches, so the conjunction of sheltering and fertile, wetter soils in the understorey of nurse plants may result in enhanced seedling survival when compared with only sheltered seedlings (Gómez-Aparicio et al. 2005; Padilla & Pugnaire 2009; I. Prieto et al. unpubl. data). However, research comparing the effectiveness of nurse plants versus tree shelters or piled branches remains poorly understood, but is needed for more appropriate restoration procedures.

In conclusion, solid-walled shelters were most effective at enhancing seedling survival for *Q. coccifera* and *Q. ilex* in our very dry environments; however, the tree shelters tested were largely ineffective for the other six Mediterranean species. Despite these species being well-adapted to Mediterranean droughts, under the severe conditions of our Mediterranean summer, only in the drought-tolerant *Quercus* species were tree shelters beneficial both in statistical and management terms. Thus, the use of these tree shelter-types in arid environments should be reconsidered, especially under global change scenarios imposing drier conditions, as they have proven to contribute little to the enhancement of seedling survival, but often account for a significant proportion of the restoration budget. The real determining aspect of these sites is water, so further research is still necessary to validate mechanisms, either through artificial shelters, natural shelters or nurse plants, that alleviate water stress among seedlings in arid environments.

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