Species identity and water availability determine establishment success under the canopy of *Retama sphaerocarpa* shrubs in a dry environment

Francisco M. Padilla* and Francisco I. Pugnaire

Estación Experimental de Zonas Áridas, Consejo Superior de Investigaciones Científicas, C/ General Segura 1, ES-04001 Almería, Spain. Phone +34 950281045, Fax +34 950277100

Running title: *Retama* shrubs and restoration

*fpadilla@eeza.csic.es

Summary

Seedling establishment in harsh environments is often enhanced by the proximity of adult shrubs. This information has been used in restoration work by placing seedlings of species being restored under the canopy of some shrubs. However, monitoring this process is often restricted to a single species, and comparisons with practices that protect planted seedlings against harsh conditions are scant. Similarly, few studies have supplied seedlings with water in the summer to observe the effects of water availability on the interaction. We compared sapling survival of three woody species (*Olea europaea*, *Pistacia lentiscus* and *Ziziphus lotus*) under the leguminous shrub *Retama sphaerocarpa* and in gaps covered with piled branches that mimicked a shrub canopy. After three years, survival of saplings planted under *Retama* differed depending on species identity and water supply. Survival of *Olea* saplings placed under *Retama* shrubs was twice that under piled branches if not watered (35±8 *vs.* 17±2 %, respectively) whereas survival of saplings under *Retama*, if watered, was less (48±11 *vs.* 68±8%, respectively). *Retama* shrubs had a negative effect on *Ziziphus*; most saplings died under its canopy, while survival in piled branches ranged 10-54%. *Pistacia* was neither facilitated nor outcompeted by *Retama*. Facilitation of *Olea* by *Retama* shrubs was more apparent under dry conditions where watering increased competition and decreased facilitation. Overall, we conclude that *Retama* shrubs can help dry land restoration to a greater extent than artificial shade for *Olea* when not watered. The critical role played by water supply in determining nursing success rates warrants further study.

Keywords: artificial shade, degraded environments, Mediterranean ecosystems, reforestation, ecological restoration, facilitation, nurse plants, plant interactions, sapling survival, watering.

Introduction

Seedlings are very susceptible to hazards like extreme temperatures and radiation, soil desiccation and herbivory (Franco & Nobel 1989). High mortality rates are often associated with the seedling stage. One of the ultimate determinants of recruitment success is the microsite where plants grow (Schupp 1995). Competition with existing vegetation has been pointed out as a factor involved in recruitment failure (Tyler & D'Antonio 1995; Ladd & Facelli 2005). However, seedling establishment in harsh environments is often enhanced, or facilitated, in the vicinity of adults of some species that act as nurses (the "nurse effect") (Niering et al. 1963). Research over the last few decades showed complex and likely synergistic mechanisms underlying the nurse effect, coarsely related to climatic amelioration (Franco & Nobel 1989; Valiente-Banuet & Ezcurra 1991), soil fertility (García-Moya & McKell 1970; Gutiérrez et al. 1993; Pugnaire et al. 2004) and protection against herbivory (Rousset & Lepart 2000; Callaway et al. 2005; Smit et al. 2008).

Establishment of seedlings under the canopy of some species does not preclude negative effects of nurses. While providing shelter, nurses can interfere both directly and indirectly with understory seedling success rates (Brooker et al. 2008), and survival may increase or decrease depending on whether positive effects balance negative ones (Callaway & Walker 1997; Holmgren et al. 1997; Pugnaire & Luque 2001). The importance of such effects changes through time and space (Holzapfel & Mahall 1999; Tielbörger & Kadmon 2000; Armas & Pugnaire 2005), as does the net balance in response to conditions like seedling stress tolerance and competitive ability (Bertness & Hacker 1994; Liancourt et al. 2005) and abiotic harshness (Pugnaire & Luque 2001; Callaway et al. 2002; Sthultz et al. 2007).

Applying facilitation to ecosystem restoration has received increased attention in recent years (see review in Padilla & Pugnaire 2006). The area under the canopy of certain species that act as nurses has been shown to be an appropriate site to place seedlings of perennial species being restored in a wide range of environments. However, most research on the use of nurse plants in restoration was conducted by comparing seedling performance under nurse plants and in control gaps, which differs greatly from common restoration practices that provide seedlings artificial protection from tube shelters (Pemán & Navarro 1998). Other protective procedures have been suggested as a way to foster natural recolonization (Ludwig & Tongway 1996), including artificial shade (Rey-Benayas et al. 2005) and piled shrub branches. The latter method is of great interest since it can mimic a nurse plant canopy while reducing the visual impact of tube shelters.

Comparing seedling success rates under nurse plants and artificial shade treatments is essential to understanding the potential of facilitation in restoration practice. This is of particular importance if nurse plants were found to provide seedlings with a better habitat resulting in higher survival rates than artificial shading. In addition, research on the use of nurse plants in restoration has suffered from a very short-term monitoring (but see Castro et al. 2004). Research conducted with more long-term monitoring and under varying sets of ecological conditions is still necessary (Brooker et al. 2008).

In dry Mediterranean ecosystems, the leguminous shrub *Retama sphaerocarpa* is well known for its facilitative effects. The *Retama* canopy buffers extreme temperatures and radiation reaching the soil surface, while its open structure allows adequate amount of light to pass through. Moreover, soils under *Retama* have higher organic matter and microbial activity, nitrogen, water content, and improved clay fraction and texture compared to between-shrub spaces (Pugnaire et al. 1996; Moro et al. 1997a,b; Pugnaire et al. 2004; López-Pintor et al. 2006).

For three years we monitored sapling survival of three shrub species transplanted under *Retama* shrubs and in gaps covered with piled branches. We supplied water in summer to see how water availability during drought affected the interaction between nurse plants and saplings. Although tube shelters are the most common protectors used in restoration practices in the Mediterranean, we used piled branches because of the similarity to a nurse canopy. We expected higher survival rates of saplings under *Retama* shrubs than under piled branches because of the reported effects of *Retama* on soil resources, given that both piled branches and *Retama* shrubs would considerably lower temperature and radiation in the understory.

Materials and Methods

Experimental site

We selected two 1-ha plots on opposite, moderate slopes in the foothills of the Sierra Alhamilla range (Almería, Spain, 37º99'N, 02º99'W, *ca.* 650 m elevation). Plant communities, soils, and slopes were very similar in both plots, differing only in aspect. One plot was on a relatively more humid, east-facing slope, the other on a relatively drier, west-facing slope (Figure 1). The climate is Mediterranean semi-arid with a mean annual temperature of 17.3 ºC and 282 mm of annual precipitation, with a marked drought period from June to September. Temperatures are mild in winter and high in late spring and summer. Soils are loamy-sandy, calcic regosols developed over a mica-schist bedrock.

The plant community consists of a degraded shrubland dominated by the drought-deciduous shrub *Anthyllis cytisoides* L. and scrub such as *Artemisia barrelieri*

Bess. and *Thymus hyemalis* Lange, interspersed with the large shrub *Retama sphaerocarpa* (L.) Boiss and annual grasses and herbs. Late-successional shrubs belonging to this community but almost absent are *Olea europaea* L. var. *sylvestris* Brot. (Oleaceae), *Pistacia lentiscus* L. (Anacardiaceae) and the thorny *Ziziphus lotus* (L.) Lam. (Rhamnaceae; Mota et al. 1997). Hereafter we refer to this species by their generic name only.

Species and experimental design

Retama, a large leguminous shrub, spreads throughout the western Mediterranean Basin. The shrub has an open canopy that dampens temperatures and radiation reaching the soil, and a dual root system with dense layer of fine roots, mainly in the top 20 cm of the soil, and several deeply penetrating tap roots (Haase et al. 1996). This dual system is believed to maximize water uptake from deep sources during the seasonal drought, and from the upper soil horizons when water is available following rainfall or watering (Schwinning et al. 2002).

We tested the effect of *Retama* shrubs on *Olea*, *Pistacia*, and *Ziziphus* seedlings. All three species share reproductive traits such as fleshy fruits and large seeds, and functional traits such as sclerophylly, deep roots, and low drought tolerance revealed by little negative pre-dawn xylem water potentials, pointing to a Tertiary origin (Herrera 1992).

In January 2004, between 20 and 30 one-year-old saplings of these three species, provided by local nurseries and grown under identical conditions, were transplanted on both slopes either under the *Retama* canopy (*Retama* shrubs hereafter) or randomly in gaps covered with piled branches of the shrub *Anthyllis* (piled branches, Figure 2), planting one sapling per shrub and gap. By using piled branches we did not aim to mimic *Retama*'s canopy, but rather to compare sapling survival under *Retama* against survival under artificial shade. We selected *Anthyllis* branches for several reasons: the shrub was very common shrub in the study area; they provide general similarities with nurse plant's canopies; and we believe more natural, less impacting artificial shade materials should be used in restoration practices.

Selected *Retama* shrubs were similar in age and height (*ca.* 2 m), and lacked perennial species in their understories to avoid competition. Seedlings were planted as close to the trunk of *Retama* as possible since amelioration of climatic extremes and improved availability of resources decrease from the canopy center outwards (Moro et al. 1997a), and on the upslope side of the shrub to take advantage of the small soil mounds formed by sediment accretion. At transplant, we dug a 0.5-m-deep hole using an auger (BT 120 C, Stihl AG & Co. KG, Waiblingen, Germany). Since summer drought is the major constraint on seedling survival and competition for water is often more important than competition for light or nutrients in dry habitats (Casper & Jackson 1997), in the summer of 2004 and 2005 half the seedlings were watered six times every three weeks on average between June and September. Around 2.5 L of water were supplied at the root level of each sapling through a fine pipe buried 20 cm in the soil close to the sapling roots. This amount had proven sufficient to keep seedlings alive in an earlier experiment (Sánchez et al. 2004). No additional water was supplied at transplant.

Temperature and radiation

We used sensors to record soil temperature (Campbell Scientific Ltd, Leicestershire, UK) and photosynthetically active radiation (PAR quantum sensor SKP 215, Skye Instruments Ltd, Powys, UK) at ground level under three randomly selected

Retama shrubs, in three gaps covered with piled branches, and in two gaps, in a flat area located in the east-facing plot. Although our experimental design did not include a control treatment in gaps, we decided to monitor abiotic conditions in this environment to quantify how *Retama* shrubs and piled branches reduced radiation and temperature compared to gaps. Data collected for six days in March 2006 during a sunny spell were recorded every minute and averaged every ten minutes in a CR10X data logger (Campbell Scientific Ltd, Leicestershire, UK). Rainfall was collected with a pluviometer (Davis Instruments Corp, Hayward, CA, USA) and recorded daily (Hobo, Onset Computers, Pocasset, MA, USA) during the three years of experimentation.

Survival analyses

Since summer drought is the main threat to seedlings in the Mediterranean, and we focused on survival at the end of this period rather than on the temporal pattern of sapling casualties, survival was recorded before and after the summer of 2004, 2005 and 2006, recounting dead saplings on each date and checking for resprouts. Survival rate after one, two and three years in the field was calculated as a percentage of plants alive in spring 2004, excluding seedling deaths caused by transplant. Sapling survival after one, two and three years in the field was performed by simple binary logistic regression where survival data was the dependent variable, and aspect (east or west), watering (irrigated or control), and canopy (*Retama* shrubs or. piled branches) were the predictor factors. We ran independent logistic regressions for each species. This is an appropriate method for analyzing categorical variables where one of them is clearly the response variable (Agresti 2002). For *Olea* and *Ziziphus*, the statistical design consisted of a three-factor factorial (Aspect x Watering x Canopy). For *Pistacia*, however, the design comprised two factors (Watering x Canopy) because replication in the east plot was very small. Logistic regression started from the saturated model, and significance of interactions and main factors were determined through backwards elimination, first of higher-order interaction terms 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). Sample size of each treatment ranged from 15 to 28 plants because of differing dieback caused by transplant. Analyses were conducted with the SPSS v14.0 statistical package (SPSS Inc., Chicago, IL, USA) with significant differences set at P< 0.05. Data are presented as means ± 1 standard error.

Results

Sapling survival

After three growing seasons, survival of *Ziziphus* saplings planted under *Retama* shrubs was significantly lower than in piled branches (0-3 *vs.* 10-53%, respectively, P<0.001, Figure 3). Conversely, *Retama* shrubs significantly enhanced *Olea* survival when compared to piled branches, but this effect depended on water supply, as reflected by the significant Watering x Canopy interaction (P<0.01, Table 1), with survival being 48-56% higher for non-irrigated saplings planted under *Retama* shrubs than for those in piled branches (35±8 *vs.* 17±2 %, respectively). In contrast, more watered saplings survived under piled branches (48±11 *vs.* 68±8%, respectively, Figure 3), with most of the mortality occurring in the dry summer of 2005 (Table 2). We detected no significant effect of canopy on survival rates of *Pistacia*.

Watering did enhance survival rate in all three species (P<0.01, Table 1), with irrigated saplings of *Olea* and *Pistacia* showing survival rates close to 100% in autumn of 2004, and above 50% in *Ziziphus* under piled branches. Watering during the second summer reduced mortality in both this year and the following one, and watered saplings showed higher survival than non-irrigated saplings at the end of the experiment (Figure 3).

Abiotic environment

Both *Retama* canopies and artificial shade buffered air temperature and radiation reaching the soil surface. Daily mean temperature in both treatments was reduced by 3ºC compared to open areas (Table 3). Both canopies also ameliorated extreme temperatures, although the buffering was greater under artificial shade (up to 17 ºC lower than in gaps) than under *Retama* canopy (9 ºC). Radiation levels under treatments at noon were similar at around 500 µmol m^{-2} s^{-1}, which contrasts with radiation >1200 µmol m^{-2} s^{-1} in gaps. Daily mean PAR under artificial protection and *Retama* microsites was reduced by 70% and 56 % respectively compared to gaps; maximum PAR was reduced by 40% in both treatments.

Discussion

Our hypothesis that survival of saplings planted under the canopy of the leguminous shrub *Retama sphaerocarpa* would be higher than under piled branches was only partially substantiated. Seedling placement under *Retama* shrubs was beneficial for *Olea europaea* var. *sylvestris*, whereas it was apparently neutral for *Pistacia lentiscus* and detrimental for *Ziziphus lotus*. These differences in nursing success indicate that the interaction of these species with *Retama* shrubs is species-specific (*sensu* Callaway 1998), in consistency with other reports (Gómez-Aparicio et al. 2004; Liancourt et al. 2005).

We found that survival of non-watered *Olea* saplings planted under *Retama* shrubs was double that under piled branches after three growing seasons. Since we did not test seedling performance in gaps, the absolute effect of *Retama* canopies could not be assessed. However, this result is important considering that both piled branches and *Retama* shrubs ameliorated radiation and temperature in the understory. This indicates that shrubs can provide better habitat for *Olea* than artificial shade, which concurs with reports showing enhanced survival of the con-specific *Olea europaea* var. *cuspidate* under the canopy of the nurse *Euclea racemosa* when compared to open gaps in very dry Afromontane savanna woodland (Aerts et al. 2007).

Our experimental design does not allow us to distinguish between soil *versus* canopy effects underlying facilitation by *Retama*, but it is likely that *Olea* saplings benefited from both effects rather than from protection against radiation and temperature alone, as suggested by the lower survival under piled branches. Canopy protection has often been pointed out as the primary mechanism involved in the nurse effect (Valiente-Banuet & Ezcurra 1991; Maestre et al. 2003), but the soil environment is also very important (García-Moya & McKell 1970; Gutiérrez et al. 1993; Pugnaire et al. 2004). Gómez-Aparicio et al. (2005) found that seedlings of tree species in a Mediterranean mountain survived better under nurse plants than under artificial shade, and similar findings were reported by Smit et al. (2008) in Mediterranean open woodlands. The facilitative mechanisms of *Retama* over woody and herbaceous species naturally occurring in the understory have been extensively addressed in the literature, and include shade provided by the canopy and improvements in the neighboring soil environment (Pugnaire et al. 1996; Moro et al. 1997b; Rodríguez-Echeverría & Pérez-Fernández 2003; Pugnaire et al. 2004; López-Pintor et al. 2006). Since facilitation was reported in absence of water (both after the summer drought and in non-watered plants), soil moisture and hydraulic lift by *Retama* roots (I. Prieto & Z. Kikvidze, unpublished) could be a key process responsible for survival in this microsite, although further research is needed to determine the real contribution of this process. It should be noted that shade could be negative if radiation is limiting (Rey-Benayas et al. 2005). However, this is unlikely in our study because mid-day radiation levels under the sparse canopy of *Retama* and piled branches was >500 μmol m^{-2} s^{-1}, usually a non-limiting level for Mediterranean species (Valladares et al. 2005).

Contrary to our expectations, survival of *Ziziphus* saplings planted under *Retama* shrubs was much lower than in gaps covered with piled branches. This fact would partly rule out shade as the main cause of death in *Retama* microsites. Competitive ability may account for differences in nursing success. Facilitation by nurse plants is expected in species that tolerate the negative effects of neighbors (i.e., have strong competitive ability), minimizing such costs of spatial proximity as sharing soil resources, and maximizing benefits like climatic amelioration and improved soil resources (Liancourt et al. 2005). Given that both canopy treatments ameliorated microclimate, higher survival in piled branches would suggest that *Ziziphus* did not tolerate competition from the shallow roots of *Retama* and from understory herbs. Reports have shown that the herbaceous community under *Retama* has negative effects on seedling establishment (Espigares et al. 2004), and although mortality in *Ziziphus* occurred mostly in summer when annual species are senesced, it is possible that herbs strongly competed with *Ziziphus* early in the growing season and depleted its reserves by the onset of drought.

As for *Pistacia*, we found that survival did not differ significantly between microsites. However, it is worth noting that *Pistacia* was not negatively affected when living close to *Retama* shrubs. There are reports of positive effects of the nurses *Stipa tenacissima* and *Pinus halepensis* on *Pistacia* saplings in semiarid ecosystems (Maestre et al. 2003; 2004). It should be noted that in these cases the control treatment consisted of a plantation with uncovered gaps greatly exposed to extreme temperature and radiation, which would bring about more stressful microsites than our piled branches. Given the lack of replication in our east-facing plot, we are unable to state whether the nonsignificant results obtained with this species reflect a neutral balance between facilitation and competition or are simply due to low statistical power underlying the low sample size for this species.

All species benefited from watering, but we found that watered saplings of *Olea* survived better under piled branches than under *Retama* shrubs, indicating that higher water availability during summer reduced facilitation by *Retama* and led to competitive interactions. Facilitation decreased and competition increased as water stress was alleviated by watering. Because of the dual root system of *Retama*, watered saplings under nurses may have been subjected to competition from *Retama*'s shallow roots, whereas saplings placed in gaps were not. We would have expected a stronger effect of *Retama* canopy over survival in the drier, more stressful west-facing plot than in the more humid eastern plot. However, we found that aspect had no significant effect on survival, probably because the east and west aspect of our plots exhibit less contrasting gradients than north and south aspects.

Overall, *Retama* shrubs can help dry land restoration to a greater extent than artificial shade for *Olea* if not watered. *Retama's* role in dry land restoration for other species should be carefully scrutinized. Water supply plays a critical role in determining nursing success since irrigation in gaps is not affected by sharing with the nurse roots, and should be considered and evaluated.

Implications for practice

- Survival of the shrub *Olea europaea* var. *sylvestris* saplings placed under *Retama sphaerocarpa* shrubs was higher than under piled branches that created artificial shade, so using *Retama* shrubs should be considered over artificial shade for this species in dry Mediterranean environments.
- Our results provide more evidence of the importance of the identity, and likely competitive ability, of the target species for the nursing success. However, in most cases it is impossible to infer the expected outcome without testing.
- Irrigation when planting close to nurse shrubs might not be recommended since nurse plants and target saplings would compete for the water provided, whereas saplings placed away from nurses would not.
- Long-term monitoring of this technique is still needed, as along with experiments under varying sets of abiotic conditions and with different competitive abilities to discover the actual potential for practitioners.

Acknowledgements

We are very grateful to Serfosur SL for technical assistance in this project, and especially to Rafael Ortega for suggestions on the experiment. We also thank Alejandro Moreno for field help, and Cristina Armas, Fernando T. Maestre and anonymous reviewers for comments on an earlier draft of this manuscript. Appreciation is also extended to Joan Deely for assistance with language editing. This project was funded by the Spanish Ministry of Education and Science (grants AGL2000-0159-P4-02 and CGL2004-00090/CLI) and FMP was supported by an I3P fellowship (CSIC-European Social Fund).

References

Aerts, R., A. Negussie, W. Maes, E. November, M. Hermy, and B. Muys. 2007. Restoration of dry Afromontane forest using pioneer shrubs as nurse-plants for *Olea europaea* ssp. *cuspidata*. Restoration Ecology **15:**129-138.

Agresti, A. 2002. Categorical Data Analysis, 2nd ed. Wiley-Interscience, New Jersey, USA.

Armas, C., and F. I. Pugnaire. 2005. Plant interactions govern population dynamics in a semi-arid plant community. Journal of Ecology **93:**978-989.

Bertness, M. D., and S. D. Hacker. 1994. Physical stress and positive associations among marsh plants. The American Naturalist **144:**363-372.

Brooker, R. W., F. T. Maestre, R. M. Callaway, C. L. Lortie, L. A. Cavieres, G. Kunstler, P. Liancourt, K. Tielbörger, J. M. J. Travis, F. Anthelme, C. Armas, L. Coll, E. Corcket, S. Delzon, E. Forey, Z. Kikvidze, J. Olofsson, F. I. Pugnaire, C. L. Quiroz, P. Saccone, K. Schiffers, M. Seifan, B. Touzard, and R. Michalet. 2008. Facilitation in plant communities: the past, the present, and the future. Journal of Ecology **96:** 18-34.

Callaway, R. M. 1998. Are positive interactions species-specific? Oikos **82:**202-207.

Callaway, R. M., and Walker, L. R. 1997. Competition and facilitation: a synthetic approach to interactions in plant communities. Ecology **78:**1958-1965.

Callaway, R. M., R. W. Brooker, P. Choler, Z. Kikvidze, C. J. Lortie, R. Michalet, L. Paolini, F. I. Pugnaire, B. Newingham, E. T. Aschehoug, C. Armas, D. Kikodze, and B. J. Cook. 2002. Positive interactions among alpine plants increase with stress. Nature **417:**844-848.

Callaway, R. M., Kikodze, D., Chiboshvili, M. and Khetsuriani, L. 2005. Unpalatable plants protect neighbors from grazing and increase plant community diversity. Ecology **86:**1856-1862.

Casper, B. B., and R. B. Jackson. 1997. Plant competition underground. Annual Review of Ecology and Systematic **28:**545-570.

Castro, J., R. Zamora, J. A. Hódar, J. M. Gómez, and L. Gómez-Aparicio. 2004. Benefits of using shrubs as nurse plants for reforestation in Mediterranean mountains: a 4-year study. Restoration Ecology **12:**352-358.

Espigares, T., A. López-Pintor, and J. M. Rey-Benayas. 2004. Is the interaction between *Retama sphaerocarpa* and its understorey herbaceous vegetation always reciprocally positive? Competition-facilitation shift during *Retama* establishment. Acta Oecologica **26:**121-128.

Franco, A. C., and P. S. Nobel. 1989. Effect of nurse plants on the microhabitat and growth of cacti. Journal of Ecology **77:**870-886.

García-Moya, E., and C. M. McKell. 1970. Contribution of shrubs to the nitrogen economy of a desert-wash plant community. Ecology **51:**81-88.

Gómez-Aparicio, L., R. Zamora, J. M. Gómez, J. A. Hódar, J. Castro, and E. Baraza. 2004. Applying plant facilitation to forest restoration: a meta-analysis of the use of shrubs as nurse plants. Ecological Applications **14:**1128-1138.

Gómez-Aparicio, L., J. M. Gómez, R. Zamora, and J. L. Boettinger. 2005. Canopy *vs.* soil effects of shrubs facilitating tree seedlings in Mediterranean montane ecosystems. Journal of Vegetation Science **16:**191-198.

Gutiérrez, J. R., P. L. Meserve, L. C. Contreras, H. Vásquez, and F. Jaksic. 1993. Spatial distribution of soil nutrients and ephemeral plants underneath and outside the canopy of *Porlieria chilensis* shrubs (Zygophyllaceae) in arid coastal Chile. Oecologia **95:**347-352.

Haase, P., F. I. Pugnaire, E. M. Fernández, J. Puigdefábregas, S. C. Clark, and L. D. Incoll. 1996. An investigation of rooting depth of the semiarid shrub *Retama sphaerocarpa* (L.) Boiss. by labelling of ground water with a chemical tracer. Journal of Hydrology **177:**23-31.

Halpern, B. S., B. R. Silliman, J. D. Olden, J. P. Bruno, and M. D. Bertness. 2007. Incorporating positive interactions in aquatic restoration and conservation. Frontiers in Ecology and the Environment **5:**153-160.

Herrera, C. M. 1992. Historical effects and sorting processes as explanations of contemporary ecological patterns: character syndromes in Mediterranean woody plants. The American Naturalist **140:** 421-446.

Holmgren, M., M. Scheffer, and M. A. Huston. 1997. The interplay of facilitation and competition in plant comunities. Ecology **78:**1966-1975.

Holzapfel, C., and B. E. Mahall. 1999. Bidirectional facilitation and interference between shrubs and annuals in the Mojave Desert. Ecology **80:**1747-1761.

Ladd, B. M., and J. M. Facelli. 2005. Effects of competition, resource availability and invertebrates on tree seedling establishment. Journal of Ecology **93:**968-977.

Liancourt, P., R. M. Callaway, and R. Michalet. 2005. Stress tolerance and competitive-response ability determine the outcome of biotic interactions. Ecology **86:**1611-1618.

López-Pintor, A., A. Gómez Sal, and J. M. Rey Benayas. 2006. Shrubs as a source of spatial heterogeneity –the case of *Retama sphaerocarpa* in Mediterranean pastures of central Spain. Acta Oecologica **29:**247-255.

Ludwig, J. A., and D. J. Tongway. 1996. Rehabilitation of semiarid landscpaes in Australia II. Restoring vegetation patches. Restoration Ecology **4:**398-406.

Maestre, F. T., S. Bautista, and J. Cortina. 2003. Positive, negative and net effects in grass-shrub interactions in Mediterranean semiarid grasslands. Ecology **84:**3186-3197.

Maestre, F. T., J. Cortina, and S. Bautista. 2004. Mechanisms underlying the interaction between *Pinus halepensis* and the native late-successional shrub *Pistacia lentiscus* in a semiarid plantacion. Ecography **27:** 776-786.

Moro, M. J., F. I. Pugnaire, P. Haase, and J. Puigdefábregas. 1997a. Effect of the canopy of *Retama sphaerocarpa* on its understorey in a semiarid environment. Functional Ecology **11:**425-431.

Moro, M. J., F. I. Pugnaire, P. Haase, and J. Puigdefábregas. 1997b. Mechanisms of interactions between a leguminous shrub and its understorey in a semi-arid environment. Ecography **20:**175-184.

Mota, J. F., J. Cabello, M. Cueto, F. Gómez, E. Giménez, and J. Peñas. 1997. Datos sobre la vegetación del Sureste de Almería. Universidad de Almería, Almería, Spain.

Niering, W. A., R. H. Whittaker, and C. H. Lowe. 1963. The Saguaro: A population in relation to environment. Science **142:**15-23.

Padilla, F. M., and F. I. Pugnaire. 2006. The role of nurse plants in the restoration of degraded environments. Frontiers in Ecology and the Environment **4:**196-202.

Pemán, J., and R. Navarro. 1998. Repoblaciones forestales. Universitat de Lleida, Lleida, Spain.

Pugnaire, F. I., P. Haase, and J. Puigdefábregas. 1996. Facilitation between higher plant species in a semiarid environment. Ecology **77:**1420-1426.

Pugnaire, F. I., and M. T. Luque. 2001. Changes in plant interactions along a gradient of environmental stress. Oikos **93:**42-49.

Pugnaire, F. I., C. Armas, and F. Valladares. 2004. Soil as a mediator in plant-plant interactions in a semi-arid community. Journal of Vegetation Science **15:**85-92.

Rey-Benayas, J. M., J. Navarro, T. Espigares, J. M. Nicolau, M. A. Zavala. 2005. Effects of artificial shading and weed mowing in reforestation of Mediterranean abandoned cropland with contrasting *Quercus* species. Forest Ecology and Management **212**: 302-314.

Rodríguez-Echeverría, S., and M. A. Pérez-Fernández. 2003. Soil fertility and herb facilitation mediated by *Retama sphaerocarpa*. Journal of Vegetation Science **14:**807-814.

Rousset, O., and J. Lepart. 2000. Positive and negative interactions at different life stages of a colonizing species (*Quercus humilis*). Journal of Ecology **88:**401-412.

Sánchez, J., R. Ortega, M. Hervás, F. M. Padilla, and F. I. Pugnaire. 2004. El microrriego, una técnica de restauración de la cubierta vegetal para ambientes semiáridos. Cuadernos de la SECF **17:**109-112.

Schupp, E. W. 1995. Seed seedling conflicts, habitat choice, and patterns of plant recruitment. American Journal of Botany **82:**399-409.

Schwinning, S., K. Davis, L. Richardson, and J. R. Ehleringer. 2002. Deuterium enriched irrigation indicates different forms of rain use in shrub/grass species of the Colorado Plateau. Oecologia **130:**345-355.

Smit, C., J. Den Ouden, and M. Díaz. 2008. Facilitation of *Quercus ilex* recruitment by shrubs in Mediterranean open woodlands. Journal of Vegetation Science **19:** 193-200.

Sthultz, C. M., C. A. Gehring, and T. G. Whitham. 2007. Shifts from competition to facilitation between a foundation tree and a pioneer shrub across spatial and temporal scales in a semiarid woodland. New Phytologist **173:**135-145.

Tabachnick, B G., and L. S. Fidel. 2001. Using multivariate statistics, 4th ed. Allyn & Bacon, Massachusetts, USA.

Tielbörger, K., and R. Kadmon. 2000. Temporal environmental variation tips the balance between facilitation and interference in desert plants. Ecology **81:**1544-1553.

Tyler, C. M., and C. M. D'Antonio. 1995. The effects of neighbors on the growth and survival of shrub seedlings following fire. Oecologia **102:**255-264.

Valiente-Banuet, A., and E. Ezcurra. 1991. Shade as a cause of the association between the cactus *Neobuxbaumia tetezo* and the nurse plant *Mimosa luisana* in the Tehuacan Valley, Mexico. Journal of Ecology **79:**961-971.

Valladares, F., I. Dobarro, D. Sánchez-Gómez, and R. W. Pearcy. 2005. Photoinhibition and drought in Mediterranean woody saplings: scaling effects and interactions in sun and shade phenotypes. Journal of Experimental Botany **56:**483-494.

TABLES

Table 1. Results of logistic regression performed with sapling survival in autumn after one (2004), two (2005) and three (2006) years in the field with the response variable, and aspect (A), watering supply (W), and canopy treatment (C) as predictor variables for each species (*Olea europaea* var. *sylvestris*, *Pistacia lentiscus* and *Ziziphus lotus*). Bold letters show significant differences at P<0.05. Analyses could not be performed for *Pistacia* because of the low replication in the east aspect.

		Aspect (A)		Watering (W)		Canopy (C)		A x W		A x C		W x C		A x W x C	
Year	*Species*	χ^2	*P*	χ^2	*P*	χ^2	*P*	χ^2	*P*	χ^2	*P*	χ^2	*P*	χ^2	*P*
2004	*Olea*	0.114	0.736	49.434	**<0.001**	0.048	0.827	2.654	0.103	0.319	0.572	0.001	0.975	0.000	1.000
	Pistacia	-	-	20.995	**<0.001**	2.653	0.103	-	-	-	-	0.759	0.384	-	-
	Ziziphus	0.005	0.944	31.773	**<0.001**	8.718	**0.003**	0.709	0.340	1.299	0.254	0.003	0.956	3.588	0.058
2005	*Olea*	0.015	0.903	17.555	**<0.001**	0.983	0.321	0.241	0.623	0.251	0.616	5.281	**0.022**	0.552	0.458
	Pistacia	-	-	16.123	**<0.001**	0.633	0.426	-	-	-	-	1.239	0.266	-	-
	Ziziphus	0.064	0.800	28.441	**<0.001**	16.541	**<0.001**	1.521	0.217	1.492	0.222	0.191	0.662	0.000	1.000
2006	*Olea*	0.100	0.752	15.691	**<0.001**	0.052	0.820	3.808	0.051	0.014	0.906	6.879	**0.009**	0.195	0.659
	Pistacia	-	-	8.463	**0.004**	0.109	0.741	-	-	-	-	0.607	0.436	-	-
	Ziziphus	0.060	0.806	15.958	**<0.001**	28.972	**<0.001**	1.521	0.217	1.425	0.233	0.180	0.671	0.000	1.000

Table 2. Seasonal and annual rainfall (in mm) in the years 2004, 2005, and 2006, and average of the 1950-2000 period in the experimental site.

Year	Season				Annual
	Winter	Spring	Summer	Autumn	
2004	90	205	2	18	315
2005	73	35	6	30	145
2006	113	90	26	52	281
Average	91	82	16	92	281

Table 3. Air temperature and photosynthetically active radiation (PAR) in the daylight time period, between 7:00-17:30 solar time when PAR > 100 µmol m^{-2} s^{-1}, in spring 2006 under *Retama* shrubs, in piled branches, and in gaps. Daily temperature and PAR values are means (± 1 SE) of six days with three replicates for *Retama* islands and artificial protection, and two replicates for gaps.

		In gaps	Piled branches	*Retama* shrubs
Temperature (ºC)	Mean	16.1±0.6	13.1±0.2	13.3±0.3
	Max	40.9±1.0	23.8±0.5	31.8±0.8
	Min	2.1±0.4	5.3±0.2	3.1±0.3
PAR (µmol m^{-2} s^{-1})	Mean	902±23	275±21	397±14
	Max	1554±18	901±91	954±32
	Min	124±6	44±2	66±2

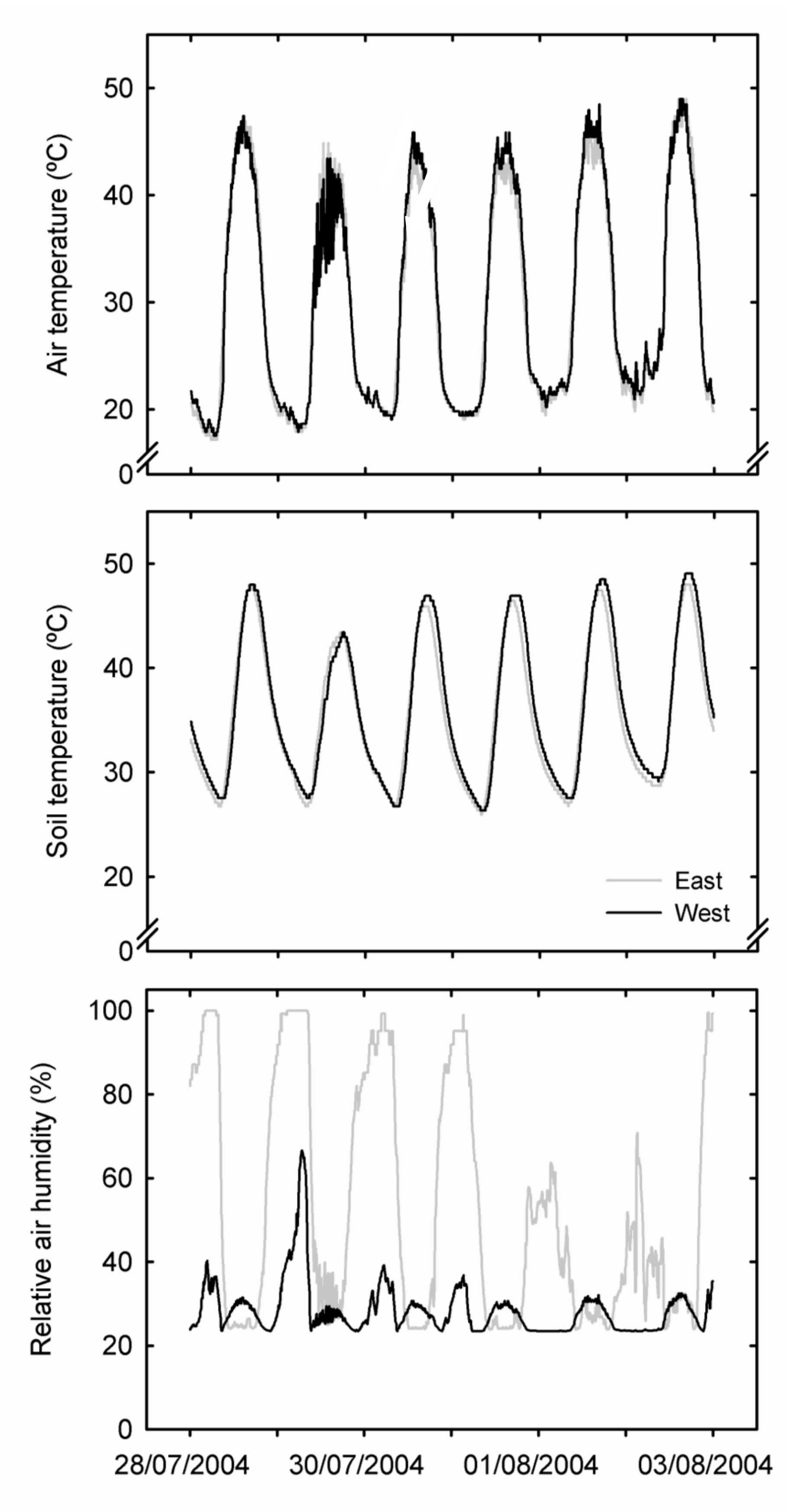
FIGURE LEGENDS

Figure 1. Air temperature (above), soil temperature (middle) and relative air humidity (below) in east (pale grey) and west-facing slopes (dark grey) in the experimental site over a six-day period in summer 2004. Soil temperature was measured at 5 cm depth (Hobo, Onset Computers, Pocasset, MA, USA) and relative air humidity and temperature at 20 cm height (Hobo Pro).

Figure 2. Plantation of a sapling under the canopy of the leguminous shrub *Retama sphaerocarpa* (above) and in a gap covered with piled branches of the shrub *Anthyllis cytisoides* (below) in a degraded environment in the Sierra Alhamilla range (Almería, SE Spain). White arrows point to introduced saplings.

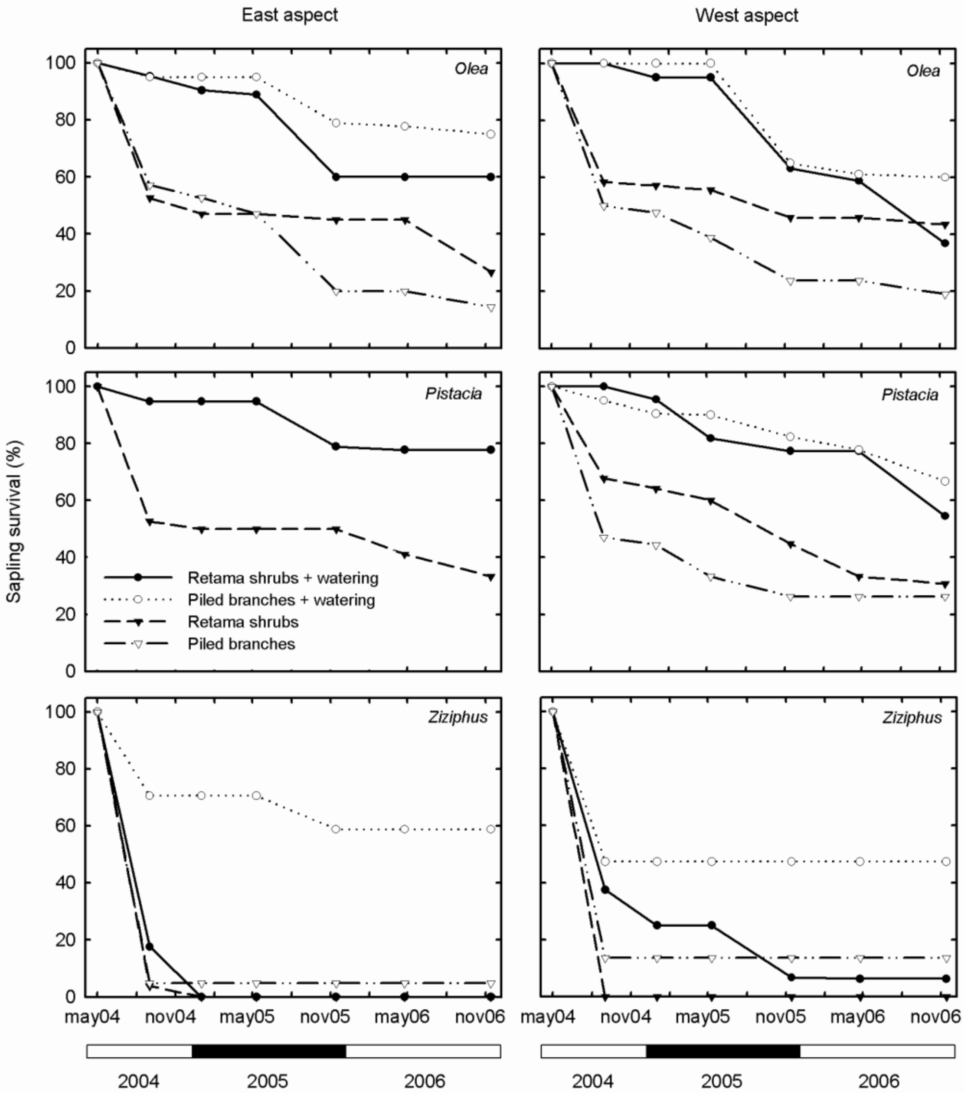
Figure 3. Sapling survival of *Olea europaea* var. *sylvestris*, *Pistacia lentiscus* and *Ziziphus lotus* in east and west-facing slopes, in *Retama sphaerocarpa* islands and under artificial canopies, and with summer irrigation and control (n = 15-28). Data for *Pistacia* in the east aspect are not available because of low replication.

Figure 1


Air temperature (ºC)
50
40
30
20
0
Soil temperature (ºC)
50
40
30
20
0
East
West
Relative air humidity (%)
100
80
60
40
20
0
28/07/2004
30/07/2004
01/08/2004
03/08/2004

Fegure 2

Figure 3



East aspect
West aspect
Olea
Pistacia
Ziziphus
Sapling survival (%)
Retama shrubs + watering
Piled branches + watering
Retama shrubs
Piled branches
may04
nov04
may05
nov05
may06
nov06
2004
2005
2006