

Response of tree seedlings to the abiotic heterogeneity generated by nurse shrubs: an experimental approach at different scales

Lorena Gómez-Aparicio, Fernando Valladares, Regino Zamora and José L. Quero

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Spatial heterogeneity of abiotic factors influences patterns of seedling establishment at different scales. In stress-prone ecosystems such as Mediterranean ones, heterogeneity generated by shrubs has been shown to facilitate the establishment of tree species. However, how this facilitation is affected by spatial scale remains poorly understood. We have experimentally analysed the consequences of the abiotic heterogeneity generated by pioneer shrubs on survival, growth and physiology of seedlings of three important tree species from Mediterranean mountains (*Acer opalus* ssp. *granatense*, *Quercus pyrenaica* and *Quercus ilex*). Patterns of abiotic heterogeneity and seedling performance were studied at two scales differing in grain: 1) the microhabitat scale, by using open interspaces as controls of the effect of different shrub species, and 2) the microsite scale, analysing the effects of fine-grain heterogeneity (within-microhabitat heterogeneity). Results showed that, at the microhabitat scale, seedling establishment of the three tree species significantly benefited from the modification of the abiotic environment by nurse shrubs. However, we found shrub-seedling interactions to be species-specific, due to differential modification of both aboveground (light availability) and belowground (soil compaction, water content, and fertility) abiotic factors by nurse shrub species. Heterogeneity at the within-microhabitat scale was rather high, although it did not significantly affect seedling performance of any of the tree species. The study demonstrates that the effects of the abiotic heterogeneity generated by shrubs are not consistent across the range of spatial scales considered. The regeneration niche of tree species becomes very complex at fine spatial scales, and thereby estimators of abiotic heterogeneity are valuable descriptors of spatial patterns of seedling establishment only when microsite “noise” is averaged out at greater scales.

L. Gómez-Aparicio (gomezl@ecostudies.org), R. Zamora and J. L. Quero, Grupo de Ecología Terrestre, Dpto. Ecología, Fac. de Ciencias, Univ. de Granada, E-1807, Spain. – F. Valladares, Centro de Ciencias Medioambientales-CSIC, Serrano 115, Madrid, E-28006, Spain (present address of L. G.-A.: Inst. of Ecosystem Studies, 65 Sharon Turnpike, P.O. Box AB, Millbrook, NY, 12545-0129 USA).

Awareness of environmental heterogeneity appeared early in the history of ecology (McIntosh 1991). However, renewed interest in scales and patterns of heterogeneity has arisen in the recent decades, due to the shift from the simplifying assumptions of homogeneity of the 1960s to the incorporation of heterogeneity into ecological theory (Wiens 2000). Recent empirical studies have provided further support for the importance of including

environmental heterogeneity in the research of plant regeneration dynamics (Beckage and Clark 2003, Jurena and Archer 2003). Nevertheless, studies on spatial heterogeneity of abiotic factors and how it affects patterns of establishment remain scant.

Organisms are one of the most important sources of heterogeneity in ecosystems (Pickett et al. 2000). Consequently, they have been taken as the relevant scale for

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study in most works analysing causes and consequences of heterogeneity. The use of this approach has brought about concepts such as “keystone species” (Paine 1969, Bond 1994), “organism engineers” (Jones et al. 1994, Lawton and Jones 1995), or “foundation species” (Bruno et al. 2003), that explicitly recognize that specific kinds of organisms in a community can modulate the availability of resources and influence the function of the entire system. In this respect, studies analysing spatial patterns of woody plant establishment in Mediterranean ecosystems have found such patterns to be strongly affected by the habitat structure, with regeneration typically occurring under pre-established vegetation (Herrera et al. 1994, Rey and Alcántara 2000, García 2001, Valladares 2003, Gómez 2004, Castro et al. 2004a, Gómez-Aparicio et al. 2005a). Specifically, shrubs have been considered key organisms in Mediterranean forests and shrublands, since they promote succession by facilitation (*sensu* Connell and Slatyer 1977) by a nurse effect on seeds and seedlings of late-successional woody species (Maestre et al. 2003, Castro et al. 2004b, Gómez-Aparicio et al. 2004).

The habitat-modifying capacity of organisms in general, and nurse shrubs in particular, can vary highly among species because of differential morphology and size, as well as other specific traits (Callaway 1998). Consequently, shrub species can have distinctive nurse quality if they differentially modify key environmental variables influencing seedling establishment patterns (Gómez-Aparicio et al. 2004). Among abiotic characteristics, reduction of light availability has been emphasized as a main facilitation mechanism in Mediterranean-type ecosystems (Maestre et al. 2001, Gómez-Aparicio et al. 2005b). In addition, nurse plants can also affect below-ground variables in a positive way for understory seedlings. Soils under established vegetation have been shown to be richer in organic matter than bare areas (Moro et al. 1997), have a higher macroporosity (Joffre and Rambal 1988, 1993), and show less compaction (Verdú and García-Fayos 1996). These structural characteristics influence soil water storage capacity and seedling root penetration (Mósen and Dillenburg 2004), thereby exerting significant effects on seedling survival, growth and physiology (Bengough and Mullins 1990, Kozłowski 1999, 2002). Despite all these studies exploring the heterogeneity generated by organisms, most have focused on just one species. As a result, there is a lack of analyses at the community level exploring species differences in habitat modification and quantifying differential nurse effects of co-occurring species (Callaway et al. 2002, Pugnaire et al. 2004).

A direct consequence of considering the organism as the smallest scale of the study is the scarcity of information on how abiotic heterogeneity influences patterns of establishment at finer spatial scales. This lack is particularly notable in Mediterranean-type

ecosystems, despite the fact that some studies have shown abiotic conditions to vary significantly at the centimetre scale within the area influenced by a given shrub (Moro et al. 1997). Because heterogeneity exists beyond the organism, a “plant’s eye view” approach (Turkington and Harper 1979) focused on the habitat structure directly surrounding the seedlings would be the most accurate approach to understand how abiotic factors determine probabilities of plant establishment (Collins and Good 1987, Gibson and Good 1987, Collins 1990, McCarthy and Facelli 1990).

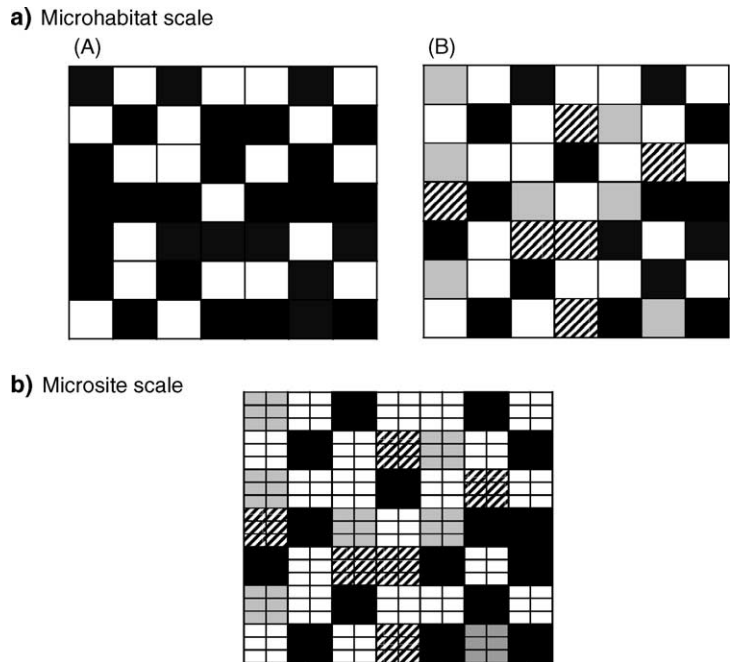
In this paper, we experimentally analyse the consequences for tree seedling performance of the abiotic heterogeneity (both above- and belowground) generated by pioneer shrubs in a Mediterranean mountain (SE Spain). The study was conducted at two spatial scales characterised by a same extent (the size of the study area being considered, *sensu* Turner et al. 2001) but different grain (the spatial resolution of the study, *sensu* Turner et al. 2001): the microhabitat and the microsite (Fig. 1). At the microhabitat scale (Fig. 1a), the consequences of the abiotic heterogeneity generated by shrubs was analysed with two levels of resolution: exploring the general effect of shrubs on seedling performance (Fig. 1aA), and distinguishing between shrub species in order to analyse the species-specificity of the nurse effect (Fig. 1aB). At the microsite scale (Fig. 1b), the effect of fine-grain heterogeneity (within-microhabitat heterogeneity) was analysed with a “plant’s eye view” approach. Specifically, we seek to determine: 1) the generality of the positive nurse effect of shrubs at the community level; 2) the species-specific nature of the interaction between shrubs and tree seedlings; 3) the relative impact of abiotic factors (light, soil compaction, moisture and fertility) on these interactions; and 4) the influence of the spatial scale on the effect of nurse shrubs on abiotic heterogeneity and tree seedling performance.

Methods

Study site

The study was conducted at the Sierra Nevada National Park (Granada, SE Spain), on the north-western slope of Loma de los Panaderos (Trevenque area, 37°5'N, 3°28'W, 1800–1850 m a.s.l.). The soil parent material is colluvium and residuum derived predominantly from limestone, with slopes ranging between 5 and 15 degrees. The climate is subhumid Mediterranean, with rainfall (846.5 ± 55.7 mm yearly average, mean \pm 1SE for 1991–2002) concentrated in autumn and spring, alternating with cold winters and hot, dry summers (47.3 ± 5.5 mm from June to August, mean \pm 1SE for 1991–2002). The study years (2001 and 2002) presented especially dry (10.0 mm) and wet (76.5 mm) summers, respectively. The mean minimum temperature in the coldest month

Fig. 1. Schematic illustration of the spatial scales at which the seedling response to abiotic heterogeneity generated by nurse shrubs was analysed. The extent remained constant throughout the study, but the grain changed from the microhabitat (a) to the microsite (b). At the microhabitat scale, seedling response was analysed with two levels of resolution: (A) comparing seedling performance in open interspaces (white squares) vs shrubs (black squares), and (B) distinguishing between shrub species (black, grey and cross-hatched squares) in order to analyse the species-specificity of the nurse effect.



(January) is -0.9°C , the mean maximum of the hottest month (July) is 29.0°C , and the mean annual temperature is 11.5°C . Frost occurs from November to April, and snow is common during winter, persisting up to 2 months. The study area was formerly a mixed forest of Scots pine *Pinus sylvestris* var. *nivadensis* and holm oak *Quercus ilex*, together with other tree species such as *Acer opalus* ssp. *granatense*, *Quercus pyrenaica* and *Sorbus aria*. In 1983, a fire in the study area burned ca 8 ha of the original pine forest. Today, the area has been recolonized by pioneer shrub species intermingled with interspaces of bare ground 1–3 m in diameter (see Castro et al. 2002 for a detailed description of the habitat structure).

Experimental design

In March 2001, one-year old seedlings of three tree species, *Acer opalus* ssp. *granatense*, *Quercus pyrenaica* and *Quercus ilex* were planted in four microhabitats: 1) under the canopy of *Salvia lavandulifolia* ssp. *vellerea*, 2) under the canopy of *Genista versicolor*, 3) under the canopy of *Prunus ramburii*, and 4) in open interspaces without vegetation. These nurse shrub species were chosen because of their abundance in the study area and their different morphological characteristics. *Salvia lavandulifolia* is a stunted evergreen shrub (<50 cm height and 2 m in diameter) with foliage almost to the ground. *Genista versicolor* is also an evergreen shrub with a canopy reaching the soil surface, but taller (>50 cm) than *Salvia* and additionally with N-fixing capacity.

Finally, *P. ramburii* is a deciduous spiny shrub usually taller than 50 cm and with a shape that leaves open the surface beneath. We planted 60 seedlings per species and microhabitat, representing 720 experimental seedlings in total. Planting sites were randomly chosen, being always >1 m apart from each other. When planted under shrubs, seedlings were totally covered by the nurse canopy. Seedlings used in the experiment were grown in the Cortijuela Botanical Garden (Sierra Nevada National Park, 1685 m a.s.l.) from seeds collected from local populations. Seeds were sown in 0.3-liter pots ($58 \times 58 \times 180$ mm) filled with native mineral soil, organic matter and vermiculite in 2-1-1 proportions. Pots were placed in full light and irrigated twice weekly. At the time of planting, seedlings were transplanted to 40-cm-deep holes made with an automatic auger 12 cm in diameter.

Analysis of the abiotic heterogeneity generated by shrubs

To analyse the effect of the presence of shrubs on abiotic conditions, we characterized the aboveground (light availability) and belowground (soil compaction, textural and chemical characteristics, and soil water content) environment in each of the four microhabitats where the seedlings were planted. Light availability was quantified by hemispherical photography. Photographs were taken at ground level using a horizontally-levelled digital camera (CoolPix 995 digital camera, Nikon, Tokyo,

Japan) and aimed at the zenith, using a fish-eye lens of 180° field of view (FCE8, Nikon). The images were analysed using Hemiview canopy analysis software ver. 2.1 (1999, delta-T Devices, Cambridge, UK). The software estimates direct and indirect site factors (DSF and ISF), which are defined as the proportion of direct and diffuse radiation for clear sky conditions at our study site, respectively (Rich 1990). Site factors range from 1 (open sky) to 0 (complete obstruction). Indirect light was estimated under standard overcast conditions. Direct and indirect site factors were combined into a global site factor (GSF) using weights that represent the proportion of diffuse vs direct light at our study site (10% ISF vs 90% DSF). DSF and GSF were calculated for clear days.

Soil compaction was measured using a penetrometer (Penetrologger, Eijkelkamp Agrisearch Equipment, Giesbeek, The Netherlands). As opposed to common penetrometers, this model does not provide just the average compaction of the perforated soil, but a value of resistance to penetration at every cm in depth. The result for each point sampled is a profile describing the variation of soil compaction with depth. From these profiles, we derived two variables that can affect rooting penetration and consequently seedling performance: the maximum compaction in the profile (MPa), and the depth at which this maximum value was encountered (cm).

Light availability and soil compaction were measured after the first winter review (see Analysis of seedling performance) in the same sample points, which were located immediately adjacent to a fraction of seedlings alive at that time (after the first year in the field) and to a proportional number of seedlings that died during the same period ($n = 125$, 10–12 seedlings per species and microhabitat combination). We employed this approach in order to use GSF and soil compaction values in two ways. For comparisons at the microhabitat scale, average values were calculated for each of the four microhabitats considered. For exploring the relationship at the micro-site scale among the three abiotic variables and seedling performance, we related seedling survival, growth, and fluorescence to the values of light availability, maximum compaction, and depth of maximum soil compaction measured next to it.

To analyse the textural and chemical soil characteristics, we sampled the upper 15 cm of the soil. Ten soil samples were collected from each treatment, placed in plastic bags and transported to the laboratory, where they were mixed daily and allowed to air-dry with the sides of the bags rolled down. Air-dry soils were sieved and the <2-mm fraction was analysed for routine chemical and physical properties (Anon. 1994) at the Food and Agriculture Laboratory of Granada (Santa Fe). Soil water content was measured in 10 sampling stations per microhabitat during spring and summer of 2001 (April–September, measurements made in the third

week of each month) using ThetaProbe sensors (Delta-T Devices, Cambridge, UK). Measures were taken once a month at the same sample points at 20 cm deep, carefully filling up each hole after the measurement. Measures in August were not taken.

Analysis of seedling performance

We used seedling survival, growth, and photochemical efficiency (estimated by chlorophyll fluorescence) as response variables to evaluate seedling performance. Survival was sampled three times: 1) after the first summer, once the autumn rains arrived (October 2001); 2) after the first winter, before the beginning of the summer drought (April 2002); and 3) once the second summer had ended (October 2002). In each survey, we also recorded the most likely cause of mortality (distinguishing between summer drought, winter frost and damage by herbivores) and seedling height. We calculated the accumulated Relative Height Growth (RHG) over the entire study period as $RHG = (\ln H_2 - \ln H_1) / (t_2 - t_1)$, where H_2 and H_1 represent the final and initial height, and $t_2 - t_1$ the time elapsed between measurements. Chlorophyll fluorescence was measured with a portable pulse-modulated fluorometer (model FMS2, Hansatech Instruments, Kings Lynn, UK) in June and July 2002 (at the beginning and in the middle of the summer, respectively). The maximum efficiency of the photosynthetic energy conversion of photosystem II (F_v/F_m) was measured at midday (14–16 h solar time) in a fraction of the surviving seedlings for which light availability and soil compaction were quantified ($n = 3–5$ microhabitat and species). F_v/F_m was measured after 30-min of dark adaptation using the standard leaf clips supplied by the manufacturer.

Data analysis

We examined the differences in light availability, soil compaction, and soil textural and chemical properties between microhabitats by one-way ANOVAs (Proc GLM, Anon. 2002). Microhabitat was introduced as fixed factor. Differences between levels of significant factors were determined by post hoc Bonferroni tests. Throughout the paper, we applied the fixed Bonferroni correction at $\alpha < 0.05$ to reduce type-I error when multiple comparisons were made (Cabin and Mitchell 2000). Soil water content was analysed using a repeated-measures ANOVA (Proc GLM) where microhabitat was introduced as between-subject factor and month as within-subject factor. Additionally, we examined the concordance in the variation of light and soil compaction within microhabitat by using Pearson product-moment correlations.

Differences in cumulative seedling survival were analysed with Generalized Logit Models (Proc CATMOD, Anon. 2002), using the maximum likelihood as estimation method (Stokes et al. 1995). Microhabitat and tree species were included as independent variables. Differences between levels of significant factors were determined by partial χ^2 tests. Between-microhabitat differences in seedling RHG were analysed for each tree species using one-way ANOVAs (Proc GLM), considering only those microhabitats with more than one surviving seedling at the end of the experiment. RHG data were previously log-transformed to improve homoscedasticity (Zar 1996). Chlorophyll fluorescence (F_v/F_m) was analysed using a repeated-measures ANOVA (Proc GLM), where microhabitat and species were introduced as between-subject factors and time as within-subject factor.

To synthesise the differences among performance estimators, nurses and tree species in the strength and sign of the shrub-tree seedling interactions, we used the Relative Neighbour Effect (RNE, sensu Markham and Chanway 1996). This index ranges from -1 to 1 , with negative values indicating facilitation between neighbours, and positive values indicating competition. However, to facilitate the interpretation of the results, we multiplied RNE values by -1 , positive values thereby showing facilitation (Callaway et al. 2002). RNE was calculated for each performance estimator as the difference in seedling performance (accumulated survival, RHG and fluorescence in the middle of the summer) with and without nurses (averaged for the three shrub species) relative to the case with the greatest performance in the pair. RNE was calculated for each nurse and tree species in a similar way using survival values.

The relationships at the microsite scale between seedling performance (survival, RHG and fluorescence) and the abiotic variables (GSF, maximum soil compaction (MPa), and depth of maximum soil compaction (cm)) were analysed using multiple logistic regressions (Proc LOGISTIC, Anon. 2002) in the case of survival, and multiple linear regressions (Proc REG, Anon. 2002) in the case of RHG and fluorescence. For each performance estimator, we conducted one analysis per microhabitat and species combination, introducing the three abiotic factors as independent variables. Throughout this paper, means are shown ± 1 SE.

Results

Abiotic heterogeneity generated by shrubs

The four microhabitats differed in GSF values ($F_{3,121} = 56.17$, $p < 0.0001$). A gradient was found from the open microhabitat showing the highest values (0.81 ± 0.03), through *S. lavandulifolia* and *P. ramburii* presenting similar intermediate values (0.54 ± 0.02 and 0.51 ± 0.02 ,

respectively), to *G. versicolor* showing the lowest values (0.27 ± 0.02) (Fig. 2a). Microhabitats did not show significant differences in maximum soil compaction (MC) ($F_{3,121} = 2.28$, $p = 0.082$), which ranged between 4.40 ± 0.28 MPa under *P. ramburii* and 5.36 ± 0.18 MPa under *G. versicolor*, with *S. lavandulifolia* and open showing intermediate values (4.97 ± 0.24 MPa and 4.84 ± 0.32 MPa, respectively). However, depths at which these maximum values were registered (DMC) differed significantly among microhabitats ($F_{3,121} = 5.58$, $p = 0.001$) (Fig. 2a), being shallower in open (15.58 ± 2.40 cm) than in *S. lavandulifolia* (25.65 ± 1.40 cm), *P. ramburii* (24.44 ± 1.41 cm) and *G. versicolor* (28.60 ± 1.84 cm). At the microsite scale, light availability varied independently of soil compaction in all microhabitats ($p > 0.05$ for all GSF-MC and GSF-DMC Pearson product-moment correlations), giving rise to a wide array of combinations of light availability and soil compaction within each microhabitat (Fig. 2b).

Microhabitats differed significantly only in 3 of the 9 textural and chemical soil properties considered (Table 1). pH was higher in *S. lavandulifolia* than in any other microhabitat, although in all cases values were rather similar (around 7 or very slightly alkaline). Available P and K were lower in open than in the three other microhabitats. For both nutrients, the three shrub species showed no significant differences, although the highest P content was found under *G. versicolor* and the highest K content in soils under *S. lavandulifolia*.

Soil water content significantly differed between microhabitats ($F_{3,35} = 3.43$, $p = 0.027$) and especially between months ($F_{4,140} = 640.22$, $p < 0.0001$). Soil water content underwent the sharpest decrease from May to June, reaching minimum values in July. However, its variation in time differed among microhabitats ($F_{12,140} = 3.76$, $p < 0.0001$, interaction Month \times Microhabitat). In April and May soil water content differed only between open and *G. versicolor*, these differences disappearing in June (Fig. 3). However, significant differences appeared again in July, when *P. ramburii* showed the lowest value and *S. lavandulifolia* the highest.

Seedling performance

Only 29.7% of the seedlings initially planted survived until the end of the experiment, the highest mortality occurring during the first summer (96.5% of the accumulated mortality at the end of the experiment). Summer drought was the main cause of mortality (94%), winter frosts and damage by herbivores causing just 2.3 and 3.7% of the total mortality, respectively. Cumulative seedling survival significantly varied between microhabitats (L-R $\chi^2 = 18.25$, DF = 3, $p = 0.0004$) and species (L-R $\chi^2 = 40.62$, DF = 2, $p < 0.0001$). The highest survi-

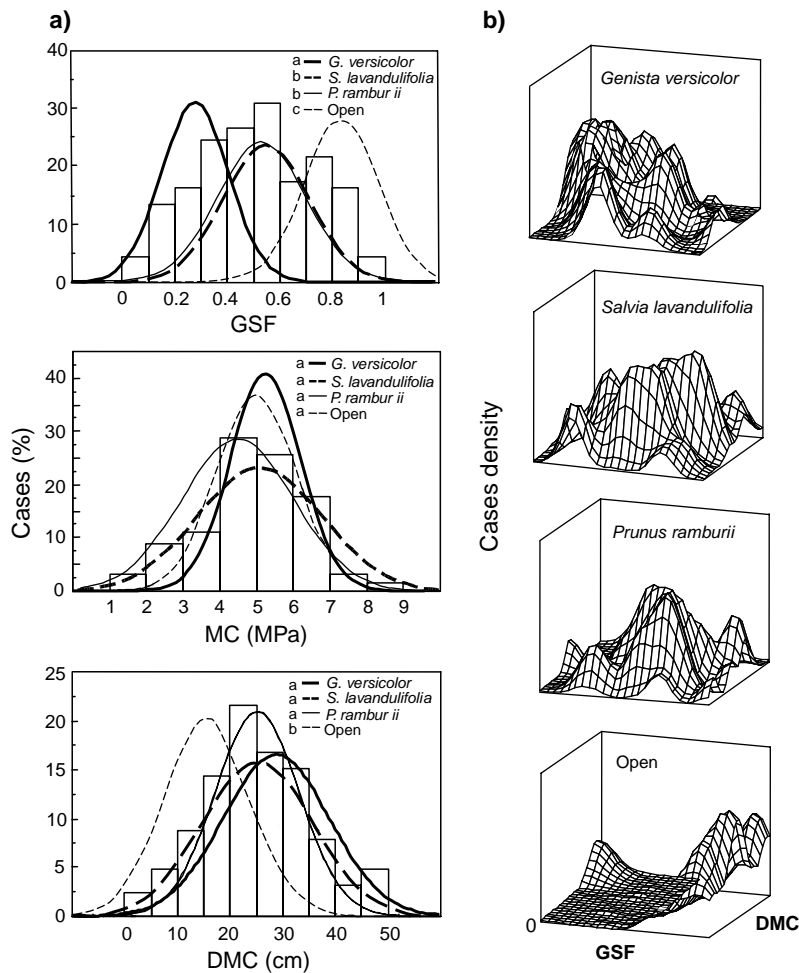


Fig. 2. a) Distribution of Global Site Factor (GSF), maximum compaction (MC) and depth of maximum compaction (DMC) values measured next to seedlings in the four microhabitats of study ($n=10-12$ seedlings per species and microhabitat combination). Different letters show significant differences at $\alpha < 0.05$ after Bonferroni correction. b) Abiotic heterogeneity within microhabitat estimated over a grid of GSF (X-axis) and DMC (Z-axis). Y-axis represents the density of microsites with each combination of GSF and DMC. The smooth surface was modelled using nonparametric density estimation.

val was registered under *S. lavandulifolia* (46.0%), followed by *G. versicolor* (31.6%), *P. ramburii* (20.7%) and open (20.67%, Fig. 4a). Between species, survival of

A. opalus ssp. *granatense* (10.34%) was significantly lower than survival of *Q. pyrenaica* (35.67%) and *Q. ilex* (39.78%). The three species showed the same pattern of

Table 1. Summary of the textural and chemical soil characteristics measured in the four microhabitats studied ($n=10$ sampling stations per microhabitat). Variables for which significant differences between microhabitats were found are in bold. Different letters indicate significant differences for each soil variable according to one-way ANOVAs (after Bonferroni correction at $\alpha < 0.05$).

Variable*	<i>Salvia lavandulifolia</i>	<i>Genista versicolor</i>	<i>Prunus ramburii</i>	Open
Clay (%)	31.10±0.81	28.59±1.06	26.74±1.07	30.58±1.04
Sand (%)	19.71±0.57	24.74±1.65	22.68±2.93	23.39±2.76
pH	7.58±0.08^a	7.13±0.12^b	7.04±0.12^b	7.19±0.04^b
CEC (cmol _c kg ⁻¹)	17.49±0.67	20.19±1.27	20.28±1.86	19.12±1.38
Ca (cmol _c kg ⁻¹)	13.54±0.59	13.88±0.94	13.83±0.91	15.39±0.93
OM (%)	5.46±0.33	5.37±0.40	6.59±0.73	5.05±0.48
N (%)	0.31±0.02	0.33±0.02	0.40±0.04	0.29±0.02
P (mg kg ⁻¹)	6.10±0.78^{ab}	8.56±0.53	8.30±1.37^b	4.10±0.41^b
K (mg kg ⁻¹)	204.50±15.36^a	166.67±9.65^b	171.50±13.52^b	138.00±10.52^b

*Soil variables were determined as followed: clay and sand by the Bouyoucos hydrometer method; available water capacity (AWC) as the difference in the amount of soil water between field capacity (pf 1/3) and permanent wilting point (pf 15) in a pressure chamber; pH with a pH meter in a 1:2.5 mass:volume soil and water suspension; cation exchange capacity (CEC) and exchangeable Ca by removal of soluble fraction, extraction with ammonium acetate and concentrations measures using atomic emission spectroscopy; organic matter (OM) by lost of mass by combustion at 430°C; total N by Kjeldahl method; available P by colorimetry with bicarbonate of soda; and available K (soluble plus exchangeable) by extraction with ammonium acetate and atomic emission spectroscopy.

Fig. 3. Monthly evolution of volumetric soil water content during the spring and summer 2001 in the four microhabitats under study (mean \pm 1 SE, $n=10$ sampling stations per microhabitat). Due to technical problems, measures in August were not conducted. Different letters show significant differences between microhabitats for the same month at $\alpha < 0.05$ after Bonferroni correction.

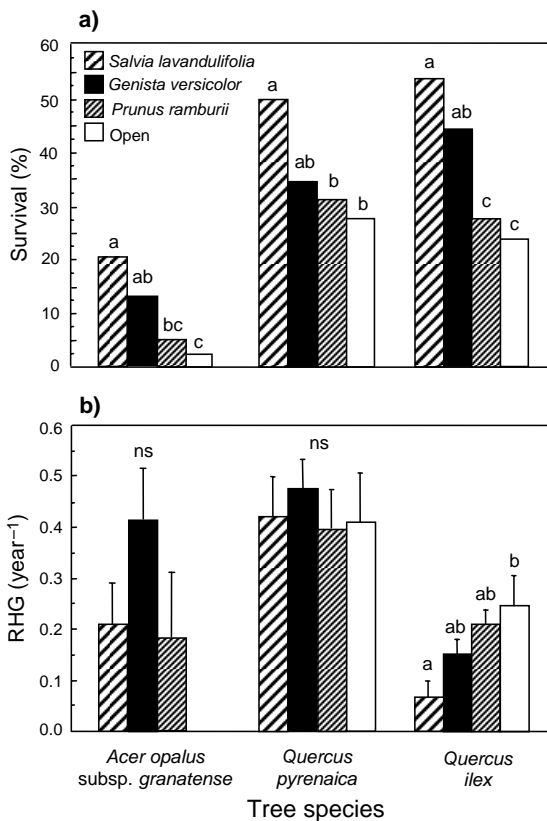
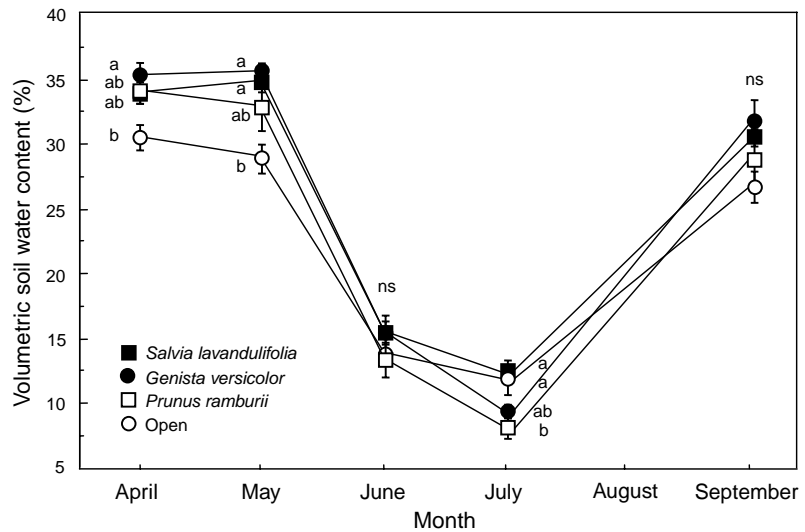


Fig. 4. a) Accumulated survival and b) Relative Height Growth (RHG) of 1-yr-old seedlings planted in the four experimental microhabitats (mean \pm 1 SE). Different letters show significant differences between microhabitats for the same species at $\alpha < 0.05$ after Bonferroni correction. The RHG of *Acer opalus* ssp. *granatense* was calculated only for the three microhabitats where more than one seedling survived until the end of the experiment.

survival among microhabitats (absence of Microhabitat \times Species interaction).

RHG varied significantly between microhabitats for *Q. ilex* ($F_{3,44} = 3.45$, $p = 0.024$), but not for *A. opalus* ssp. *granatense* ($F_{2,9} = 2.39$, $p = 0.142$) or *Q. pyrenaica* ($F_{3,12} = 0.46$, $p = 0.715$). *Quercus ilex* seedlings had the highest RHG in open (Fig. 4b), although it only differed significantly from RHG values of seedlings in *S. lavandulifolia*, where the lowest growth occurred.

Chlorophyll fluorescence differed significantly between microhabitats ($F_{3,35} = 3.39$, $p = 0.028$), but not between species ($F_{2,35} = 2.41$, $p = 0.105$). Seedlings under the three shrub species had similar values of F_v/F_m in June, and higher than seedlings in open (Fig. 5). However, F_v/F_m suffered a significant change with time ($F_{1,35} = 8.75$, $p = 0.005$), decreasing from June to

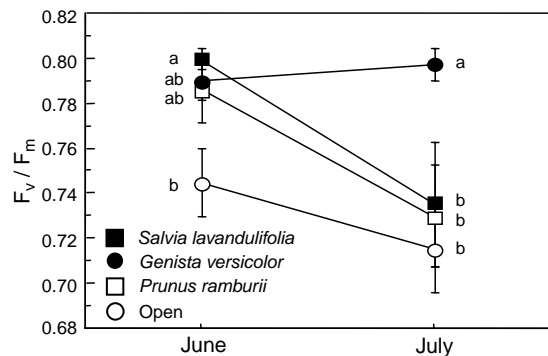


Fig. 5. Midday measurements of the maximum photochemical efficiency of photosystem II (F_v/F_m) for seedlings in the four microhabitats studied. Measures were made at the beginning (14–15 June) and in the middle (27–28 July) of the summer of 2002 (means \pm 1 SE, $n=3-5$ per microhabitat and species combination) after 30-min of dark adaptation. Different letters show significant differences between microhabitats for the same month at $\alpha < 0.05$ after Bonferroni correction.

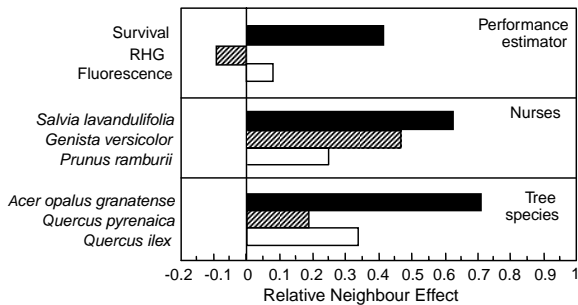


Fig. 6. Summary of the differences between performance estimators, nurses and tree species in the sign and strength of the shrub-tree seedling interactions by using the Relative Neighbour Effect (RNE). Positive and negative values of the RNE indicate facilitation and competition, respectively. RNE for each performance estimator was calculated as the difference in seedling performance with and without shrubs (averaged for the three shrub species) relative to the case with the greatest performance in the pair. The RNE was calculated for each tree and nurse species in a similar way using survival values.

July in all microhabitats but under *G. versicolor*, where values remained near the optimum 0.8 (Demmig-Adams and Björkman 1987).

The Relative Neighbour Effect (RNE) varied widely between performance estimators, nurses and tree species (Fig. 6). Shrubs had a highly positive effect on seedling survival (RNE = 0.41) and slightly positive in photochemical efficiency (RNE = 0.07), but rather negatively affected growth (RNE = -0.09). Among nurses, RNE values varied from 0.62 for *S. lavandulifolia* to 0.25 for *P. ramburii*, *G. versicolor* showing an intermediate value (RNE = 0.46). Finally, among tree species the positive effect of shrubs was much higher for *A. opalus* ssp. *granatense* (RNE = 0.70) than for *Q. ilex* (RNE = 0.34) and especially than for *Q. pyrenaica* (RNE = 0.19).

At the microsite scale, neither GSF, maximum soil compaction (MC) nor depth of maximum compaction (DMC) significantly influenced seedling survival, growth or fluorescence for any species and microhabitat combination ($p > 0.05$ for all factors and interactions in the 36 models, data not shown). This lack of significance persisted even when grouping all the species by microhabitat in order to improve the power of the tests ($p > 0.05$ in the 12 models, data not shown).

Discussion

Facilitation at the microhabitat scale: the influence of performance estimators and species interacting

Our results show that tree seedling establishment is highly dependent on the microhabitat, with shrubs having an overall positive effect on seedling performance. However, the strength and even the sign of the interaction varied depending on the estimator of performance considered and the interacting species. The high-

est positive effect of shrubs was on seedling survival (RNE = 0.41, Fig. 6), survival percentage under shrub canopies (34.8%) being two-fold that of bare soil (17.3%). Maximum photochemical efficiency of photosystem II (F_v/F_m) also improved in the middle of the summer under the canopy of shrubs (RNE = 0.07), due to a reduction in the diurnal photoinhibition typically caused by high light intensities (Cornic 1994, Alves et al. 2002). Although the improvement was minor, and, in July, only seedlings in the shadiest microsite (*G. versicolor*) maintained efficiency values near the optimum 0.8 (Demmig-Adams and Björkman 1987), seedlings in the open, as early as June, showed lower F_v/F_m values than in any other microhabitat. This finding suggests that the stress period for seedlings in the open was longer than for seedlings under shrubs. Finally, the Relative Height Growth (RHG) showed minor and negative responses to the presence of shrubs, being slightly lower under nurses than in open spaces (RNE = -0.09). However, in all cases growth rates were considerably low. Thus, seedlings planted under shrubs exhibited higher survival and better physiological performance, although with a cost in terms of height growth (for similar contrasting results among performance estimators see Callaway et al. 1996 and Maestre et al. 2001). However, taking into account that mortality of seedlings during summer is a main factor limiting regeneration of many Mediterranean woody species (Herrera et al. 1994, Rey and Alcántara 2000, Gómez et al. 2001, Traveset et al. 2003), the benefits of enhanced survival can be considered to more than compensate for a minor reduction in height growth, the net effect of shrubs on the performance of tree seedlings being thus highly positive.

The three nurse species had a positive effect on seedling performance, showing facilitation to be common at the community level. However, the strength of the facilitative effect was highly variable (Fig. 6, see Callaway and D'Antonio 1991 for a similar result). Seedling survival under *P. ramburii* was similar to survival in the open, whereas it increased twofold under *G. versicolor* and almost three-fold under *S. lavandulifolia*. Thus, shrub-tree seedling interaction proved species-specific, the benefactor species not being interchangeable (Callaway 1998). A similar pattern was found for the beneficiary species, a result that agrees with previous studies showing that even species of the same family can be differentially facilitated due to subtle differences in physiological and morphological characteristics (see Callaway et al. 1996 and references therein). Thus, although the three tree species were affected by the microhabitat, *A. opalus* ssp. *granatense* benefited from the presence of shrubs much more than did the two *Quercus* species (Fig. 6). In fact, seedlings of *A. opalus* ssp. *granatense* are reportedly extremely sensitive to high radiation levels, suffering significantly higher mortality

and photoinhibition when growing in full sunlight than seedlings of *Q. ilex* and *Q. pyrenaica* (Gómez-Aparicio 2004). These findings suggest that, among late-successional trees, stress-sensitive species such as *A. opalus* ssp. *granatense* depend longer on facilitative interactions for establishment than do more stress-tolerant species such as *Q. ilex* and *Q. pyrenaica*. Additionally, the three species responded similarly to the nurse identity, the worst (*P. ramburii*) and the best nurse (*S. lavandulifolia*) being the same for every seedling species. Therefore, the facilitation of the tree seedlings studied did not differ in quality (identity of the best nurse shrub), but in quantity (strength of the interaction).

The overall strong facilitative effects that shrubs had on seedling survival, together with the differences in the strength of the interaction found between nurse and seedling species, and the fact that the three beneficiary species studied preferred the same nurse, suggest that certain pioneer shrub species can be considered “foundation species” (Bruno et al. 2003) – i.e. species that shape successional communities under stressful Mediterranean conditions by creating appropriate habitats for the establishment of late-successional tree species (see also Gómez-Aparicio et al. 2004).

What makes a nurse? Analysis of the habitat-modifying capacity of the shrub species

The three nurse species significantly modified the abiotic environment of their understory, although with species-specific differences. Light availability and presumably its correlates air temperature and evapotranspiration were lower under nurse shrubs than in open interspaces, modification that has been often used to explain the generally better performance of seedlings situated under a canopy than in the open (Valiente-Banuet and Ezcurra 1991, Callaway 1992, Vetaas 1992, Suzán et al. 1996, Gómez-Aparicio et al. 2004). However, differences among nurse species in canopy architecture and size differentially influenced light availability in the understory. *Genista versicolor* generated the shadiest environment, reducing incident light by almost 70%, whereas *S. lavandulifolia* and *P. ramburii* diminished radiation by only 40%. The fact that light availability under *S. lavandulifolia* and *P. ramburii* was the same but seedling survival below the canopies of these species significantly differed (two times higher in *S. lavandulifolia*), indicates that light was a relevant factor involved in the positive effect of shrubs, but not sufficient to explain differences among nurse species.

The influence of shrubs on belowground abiotic factors ranged from negligible to significant. Shrub species did not differentially influence the maximum soil compaction, which was rather high under all shrubs (>4.5 MPa; Bengough and Mullins 1990, Materechera

et al. 1991, Passioura 2002). However, when compared to the open microhabitat, the three shrub species significantly increased by >10 cm the depth at which maximum soil compaction was reached. This modification could be highly relevant for plant establishment, since less compaction allows seedlings to root easily and explore a wider soil profile (Yates et al. 2000, Kozłowski 2002), with a consequently increased capacity to absorb the scarce water available in Mediterranean ecosystems during summer. In fact, in the hottest month of the year (July) soil water content was very low, being ca 10% in the four microhabitats, which coincides with the estimated wilting point for loam soils such as those of the study site (Lambers et al. 1998). However, soil water content in July was higher under *S. lavandulifolia* (12.3%) than in any other microhabitat (8.1% under *P. ramburii*, 9.3% under *G. versicolor*, 11.7% in open). The particularly high positive effect that *S. lavandulifolia* had on seedling survival seems to be due at least in part to the combination of great depth of maximum soil compaction and soil water content above the wilting point.

Modification of soil texture and nutrients by nurse shrubs was minor, especially when compared to other systems such as arid and semiarid savannas, where they generate the so-called “islands of fertility” (Soriano and Sala 1986, Pugnaire et al. 1996a, b, Aguiar and Sala 1999). In fact, only available P under *G. versicolor* and available K under *S. lavandulifolia* were significantly higher than the respective values in open microhabitats. Potassium has been reported to increase plant resistance to drought, mainly due to osmotic adjustments and a reduction in transpiration rates, which in turns results in higher water-use efficiency (Christersson 1976, Bradbury and Malcom 1977, van den Driessche 1991). Consequently, high available K under *S. lavandulifolia* could also contribute to its high quality as nurse (see also Gómez-Aparicio et al. 2005b). Considering the whole array of abiotic modifications generated by shrub species, we suggest that when answering the question of what makes a shrub a good nurse, there is no single factor, but rather a complex suite of species-specific habitat modifications related to light availability, soil water content, soil compaction, and available nutrients (primarily K in our case).

Heterogeneity and facilitation at the microsite scale

Our results reveal high within-microhabitat abiotic heterogeneity. In fact, the total local variance in maximum soil compaction (1.5–8.5 MPa) and depth of maximum soil compaction (4–48 cm) was represented at each of the three shrub species (Fig. 2a). Within-microhabitat variability for light was rather lower, at least for some microhabitats (*G. versicolor* and open),

which showed just a fraction of the total light values in the study area (Fig. 2a). This high fine-grain heterogeneity, together with the fact that light availability and soil compaction varied independently in the four microhabitats, gave rise to a wide array of environmental combinations (see also Carlton and Bazzaz 1998) and consequently of microsite qualities for recruitment within each microhabitat (Fig. 2b). However, seedling performance was not significantly affected either by light availability, maximum soil compaction or depth of maximum soil compaction for any of the tree species. The high heterogeneity characterizing the environment at the scale of individual seedlings presumably led to the fate of the seedlings being affected by uncontrolled environmental variability, including factors not evident at higher spatial scales, such as the microtopography (Huenneke and Sharitz 1986, Cornett et al. 1997). Moreover, genetic differences between seedlings and small-scale stochastic events may also have contributed to override the effect of the abiotic variables explored in within-microhabitat patterns of survival (Hartgerik and Bazzaz 1984, Gibson and Good 1987). In fact, stochastic factors and their relative importance vs deterministic factors in the recruitment process have been proposed as a justification to why some authors have found regeneration niches (*sensu* Grubb 1977) in plant communities, while others have not (see Kubota and Hara 1996 and references therein).

Concluding remarks

Our results have shown that facilitation is a common interaction at the community level in our study site, the modification of the abiotic environment by shrubs benefiting seedling establishment of the three species studied during secondary succession in Mediterranean mountains. However, when analysing the same abiotic factors (light and soil compaction) at different scales, we found that their descriptive capacity of the seedling regeneration niche was restricted to the coarser scale of study (shrubs vs open comparison). In fact, open interspaces showed higher irradiance and lower depth of maximum soil compaction than any other shrub species studied, highlighting the general positive effect of shrubs on seedling performance (mainly survival) found in this study. However, when distinguishing among shrub species, light availability and soil compaction only partially explained the patterns of seedling survival. Other abiotic variables such as soil water content and nutrients were needed to understand why *S. lavandulifolia* had the highest positive effect on seedling performance. Finally, at the microsite scale, neither light nor soil compaction satisfactorily predicted seedling fate, which was presumably influenced by a broad variety of deterministic and stochastic factors acting at this small

spatial scale. The effects of the abiotic heterogeneity generated by nurse shrubs on seedling establishment were thereby dependent on the scale of study, the regeneration niche of tree species becoming more complex at finer scales. Consequently, a given set of estimators of abiotic heterogeneity (e.g. light availability and soil compaction) significantly accounted for the spatial patterns of seedling establishment only when microsite “noise” was averaged out at greater scales.

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