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Regeneration of Tree Species and Restoration Under Constrasted Mediterranean Habitats: Field and Glasshouse Experiments

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ABSTRACT

Understanding the processes of tree population recruitment and their limitations, is the scientific basis to assure the forest natural regeneration, and to improve techniques of restoration and afforestation. We present here preliminary results of a collaborative project (HETEROMED). The environmental heterogeneity of Mediterranean forests was related to natural patterns of seedling establishment. Factorial design experiments of seed addition were carried out and the resulting emergence and survival were related to the conditions of light and soil moisture. The fieldwork was carried out at two natural areas in South Spain: Sierra Nevada National Park (higher mountains on the Southeast) and Los Alcornocales Natural Park (lower mountains in Sierra del Aljibe range, on the southern tip of the Iberian Peninsula). The experiments were focussed in seven target species - *Quercus suber*, *Quercus canariensis*, *Quercus ilex*, *Quercus pyrenaica*, *Pinus sylvestris*, *Acer granatense* and *Sorbus aria*. In addition, a glasshouse factorial experiment investigated the differential response of the four *Quercus* species to the combined effects of shade and drought.

In both field sites (Sierra Nevada and Sierra del Aljibe) seedling emergence differed among species, but was not significantly affected by habitat (light availability). In Sierra Nevada, seedling survival after dry summer was statistically different between tree species, habitat type and irrigation treatment. Summer drought was the main cause of seedling mortality. Survival was higher in deep shade habitats than in open stands. Irrigation boosted survival in open areas (full light) and under shrublands (medium shade), but had scant effect inside woodland stands (deep shade). In Sierra del Aljibe, there were significant differences in seedling survival of *Quercus suber* between habitat types. Most surviving seedlings after the dry summer were in habitats with medium shade (under tree canopy), rather than in full light (open areas) or deep shade (closed forest) habitats. In the glasshouse study, the seedling mass (after six months of growth) was statistically different between species, and between light and water treatments. In the deep shade treatment seedling mass was not affected by stopping irrigation (simulating seasonal drought), unlike in the full light.

A comparison of field and glasshouse results is carried out. A conflict between components of regeneration (seedling emergence, survival, and growth) is demonstrated as common in Mediterranean forests. The implications for ecological restoration are discussed and future perspectives of HETEROMED project are advanced.

Key Words: Drought, Growth analysis, *Quercus*, Regeneration niche, Seedling emergence, Shade.

INTRODUCTION

Current forest policy in Europe has shifted the emphasis from multi objective to sustainable forestry (MCPFE 1998). Sustainability is a complex issue that requires simultaneous action at all levels of biological organization, from the genetic to the landscape. In order to accomplish these management goals it is urgent that we identify the main problems associated with the sustainability of Mediterranean forests before any action can be taken.

The Mediterranean Basin has been much deforested in historical times. The climatic change, agricultural clearance, exploitation for timber and fuel, wars and invasions, fire and overgrazing, have been cited as main agents of deforestation in the region (Thirgood 1981). In Spain, a country of about 505,000 km^2, at the western end of the Mediterranean Basin, the forested land occupies a 28% (MMA 2000), but only a 0.2% can be considered as natural or seminatural (Marchand 1990). Under this scenario, habitat restoration is perceived as one of the most effective approaches to reverse deforestation trends. In particular, restoration is needed in those areas where sustainability is a mandatory goal, as well in areas where agricultural practices are not profitable. Thus, potential targets for restoration include abandoned agricultural lands, burned vegetation, plantations of exotic species and seminatural forests in which traditional management has ceased. The ecological restoration in these areas should be based on the scientific knowledge of regeneration requirements of Mediterranean tree species (Jordano et al. 2001). For example, as opposed to the traditional reforestation techniques on shrub-cleared ground, the benefits of using shrubs as nurse plants for the reforestation of *Pinus sylvestris* has been demonstrated in S.E. Spain (Castro et al. 2004, Gómez et al. 2004).

The regeneration of existing tree populations in Mediterranean areas can be impeded by a lack of recruitment due to several causes, such as the scarce production and dispersion of seeds, and the high mortality of seedlings. The severity of summer drought, and the overgrazing by domestic and wild herbivores are main causes of this mortality (Herrera et al. 1994, Rey and Alcántara 2000, Jordano et al. 2001, Zamora et al. 2001, Gómez et al. 2003). The seedling stage is crucial in the dynamics of plant populations (Harper 1977). Environmental factors affecting the seedling features vary at small spatial scales, thus they act on a microsite-depending way altering the seedling survivorship probability (Castro et al. 2004a, Schupp 1995). The ecological restoration of degraded lands, as well as the assisted regeneration of key tree species in seminatural forests, will be benefited by a sound understanding of the relationship between environmental heterogeneity, regeneration success and the ecological factors governing these processes. This scientific knowledge will help to develop a new Mediterranean silvicultural science suited to current European and World strategies of sustainable forestry.

In this paper we report preliminary results from a collaborative project (HETEROMED), aimed to study the relationships between the environmental heterogeneity and the regeneration niches of keystone woody species in Mediterranean forests. The results will help to understand the possible factors limiting the natural regeneration, in a global change scenario, and to improve the techniques of afforestation and restoration. We have followed a new, multi-scale and multi-faceted evaluation of regeneration performance for representative tree species in relation to environmental heterogeneity. Variation in spatial scales ranged from regional to local. At regional level, two localities were selected in contrasted geographical areas, that is Sierra Nevada, a high mountain at the SE Iberian Peninsula, and Sierra del Aljibe, a low mountain range at the southern tip of the Iberian Peninsula. At local level, habitat heterogeneity within sampling plots was examined. The degree of experimental control ranged from semi-manipulative experiments on field conditions to detailed glasshouse experiments, in which the environmental factors (hypothesized to be relevant) were under precise control.

Physical factors considered as key regulators of regeneration success in Mediterranean habitats are soil moisture and light intensity (see Pigott and Pigott 1993, Sack and Grubb 2002, Sack et al. 2003, Castro et al. 2004a). Under field conditions, we investigated the effect of these two factors on seedling emergence and survival. The effect of soil moisture was tested by applying an irrigation treatment with water addition, and having a non-irrigated control. The effect of light was analysed using a gradient of habitats receiving different light intensity, from open areas (full light), to areas with intermediate vegetation cover (medium shade), and to areas with dense canopy cover (deep shade). Under glasshouse conditions, we investigated the seedling performance with a subset of tree species (*Quercus ilex*, *Quercus suber*, *Quercus pyrenaica* and *Quercus canariensis*), cultivated under contrasted levels of water and light availability. We hypothesise that seedling recruitment of these tree species will be limited by a conflict between survival (lower under dry, sunny habitats; higher in shaded, mesic habitats) and growth (higher in sunny habitats; lower in deep shade). We discuss the consequences of the analysed regeneration patterns for forest restoration.

MATERIAL AND METHODS

Field Experiments

The two field experiments followed a factorial design with three factors: (1) tree species; (2) type of habitat, selecting a range of light availability from habitats receiving full light to medium shade and deep shade; and (3) soil moisture, by irrigation of seedlings during summer as opposed to rainfed (control) treatment. Light conditions in the field sites were about 100% of full light in open microsites, 16-30% in semi shade under shrubs or isolated trees, and 3-5% inside dense forest with shrub understorey. Water addition simulated conditions of a year with a rainy summer, which represents a sporadic event in the Mediterranean area.

Seeds of the selected tree species were planted in each habitat type, following a factorial design. They were protected with a wire cage of 1.3 cm mesh size to exclude rodents. After sowing, sampling points were monitored periodically, noting emergence, survival, and cause of dead.

The two study localities have a Mediterranean type climate, with heaviest rainfall in autumn and spring, and warm dry summer. At Sierra Nevada site, the climate is more continental and typical of higher elevation mountains, with stronger summer drought and colder winter; snow is common persisting up to two months, and frost occurs from November to April. The average rainfall was 859 mm per year (within the period 1991-2001) and the mean temperature was 11.5°C. The mean of the minimum temperature in the coldest month (January) was -0.9°C and the mean of the maximum temperature in the hottest month (July) was 29°C. At Sierra del Aljibe, the climate is more oceanic and typical of lower elevation mountains, with weaker summer drought and milder winter. The average rainfall was 985 mm per year, and the mean temperature was 17°C; the mean of the minimum temperature in the coldest month was 3°C and the mean of the maximum temperature in the hottest month was 34°C (data from the *Pantano de los Hurones* meteorological station).

Sierra Nevada site

The first field experiment was carried out at *La Cortijuela* Botanical Garden, in the locality of Trevenque (37°05′ N, 3°28′ W), part of the Sierra Nevada range. The bed rock is mostly calcareous, with scattered patches of dolomitic rocks and occasional filites outcrops; predominant soils are regosols and cambisols, with slopes ranging between 5-15°. The landscape is a mosaic of mixed forests dominated by *Pinus sylvestris*, *Quercus ilex*, *Quercus pyrenaica*, *Acer granatense* and *Sorbus aria*, conifer plantations mostly of *Pinus sylvestris* and *Pinus nigra*, large gaps of successional shrublands, and intermigled areas of bare ground. Summer drought, and to a lesser extend ungulate herbivores, are the main factors constraining regeneration in these forests (Zamora et al. 2001, Castro et al. 2004). Historical management of forest resources included logging, shrub slashing for fuel and charcoal, and livestock raising; since 1999 this area has been protected in Sierra Nevada National Park.

The three most common types of habitat found in these mountain forests were chosen: (1) "Full light", areas of bare ground or with scant vegetation; (2) "Medium shade", sites under the canopy of shrubs; and (3) "Deep shade", sites under the canopy of woodland stands. At each habitat, we randomly assigned 20 sampling stations, in which we sowed seeds of the five most common woody species in these forests - *Quercus ilex*, *Quercus pyrenaica*, *Acer granatense*, *Sorbus aria*, and *Pinus sylvestris* -, each in a frame of 20×30 cm. For *Quercus ilex* and *Quercus pyrenaica* we sowed five acorns per sampling station, whereas for the rest of species we used 15 seeds per sampling station (9,900 seeds in total).

Half of the sampling stations were used as a control (non-watered), and the other half for a watering treatment. This experimental protocol was replicated three times per habitat. Plots assigned to irrigation were sprinkler-irrigated at seven-day intervals from 09 June to 30 September 2003 (when the first major rainfall was recorded). Irrigation consisted of adding ca. three litres of water at each application time, which in total made about 342 litres (3 litres × 114 days).

Sierra del Aljibe site

The second field study was carried out at Panera (36°31′ N, 5°34′ W), about 450 m altitude, in the Sierra del Aljibe (S. Spain). The main geologic substrate is sandstone, originating acidic and sandy soils. Cork oak (*Quercus suber*) and the deciduous oak *Quercus canariensis* (in wetter and richer soils) are dominant trees. Forest management includes periodic shrub clearing to facilitate cork harvest (every nine years). Game ungulates (red and roe deer) and free-range livestock (cows, goats and pigs) feed on oak seeds and browse the saplings (see ecological description of the area in Ojeda et al. 2000).

The three habitat types chosen in this forest were: (1) "Full light", sites in open areas of bare ground or grassland; (2) "Medium shade", sites under isolated trees without shrubs underneath; and (3) "Deep shade", sites inside dense forest patches with shrub understorey. At each habitat, we randomly assigned 20 sampling stations, in which we sowed seeds of the two most common tree species - *Quercus suber* and *Quercus canariensis* -, each in a frame of 20×30 cm. Five acorns were sown (on December 2002) per sampling station, making a total of 1,200 seeds.

During the summer months, half of the sampling points (randomly chosen) were watered by adding one litre (per experimental unit of 600 cm^2) at 21 days intervals; while the other half was left unwatered as control.

Glasshouse Experiment

Four target species were selected for the growth analysis experiment under controlled conditions (in a glasshouse), corresponding to the two field sites studied. Two oak species (*Quercus ilex* and *Quercus pyrenaica*) were abundant in Sierra Nevada, and other two species (*Quercus suber* and *Quercus canariensis*) were co-dominant in Sierra del Aljibe. The experiment was carried out in a glasshouse of the University of Córdoba (Spain), with automatic irrigation system and regulation of air temperature. Single acorns were individually weighed, and then sown (on December 2002) in pots of five litres and 50 cm height (to avoid as much as possible the interference during root growth). Replicates were randomly mixed within each experimental unit.

Oak seedlings were subjected to three light levels: (1) "Full-light" treatment, receiving the 100% of the available radiation inside the glasshouse, and equivalent to open field conditions; (2) "Medium shade" treatment, covered by a green screen, and receiving about 25% of full-light radiation; and (3) "Deep shade" treatment, covered by a green cloth, and receiving only about 3% of full-light radiation. The mean ± s.d. of photosynthetic active radiation measured (with EMS7, canopy transmission metre, PP-system, UK) on 28 May 2003, in each light treatment were 760±424 (in Full light), 187±76 (in Medium shade) and 23±5 (in Deep shade) μmoles m^{-2} s^{-1}, respectively.

At the beginning of the growth experiment, pots were watered weekly. Once emerged the seedlings and after four months of growth, a drip-irrigation system was inserted in half of the pots (W treatment), while the other half did not receive any water until the end of the experiment (NW treatment). These treatments simulated therefore a typical Mediterranean situation of summer drought (NW treatment) versus a summer with reduced or no drought (W treatment), and their results will be comparable with those of the field experiments. The mean ± s.d. values of soil moisture (in volumetric water content), measured at 20 cm depth (with a TDR mod 100, Spectrum Technologies, Inc.) on March 2003, were 14±2% (for W treatment) and 6±1% (for NW).

Seedlings were harvested on March (initial harvest), May (second harvest) and July (third harvest, i.e. six months after sowing). Sixteen replicates per species and treatment were analysed, making a total of 192 seedlings in the first and second harvests, and 384 seedlings in the third harvest (when the water treatment was added). In this paper we are presenting preliminary results based on plant fresh weight (FW) of the third harvest.

Data Analysis

Treatment effects were analysed with factorial ANOVAs in all the experiments, considering species, habitat (light intensity in the case of glasshouse experiment), and soil moisture (irrigation) as main factors. Multiple comparison of means was analysed by post-hoc Tukey test. The programs STATISTICA v 6.0 and JMP v 5.0 were used for statistical analyses. Data were arcsine or log-transformed to satisfy the homocedasticity assumption.

RESULTS

Field Experiments: Seedling Emergence

Seedling emergence at Sierra Nevada differed among species (P<0.0001), but was not significantly affected by habitat (light availability; Table 1). *Pinus sylvestris* and *Quercus ilex* showed the highest emergence rates while *Acer granatense* did the lowest (Figure 1). At Sierra del Aljibe, seedling emergence also differed significantly between species (P<0.001, Table 1), being *Quercus suber*

Table 1. Summary of the ANOVA results for seedling emergence and survival, at the field study sites of *Sierra Nevada* (SN) and *Sierra del Aljibe* (SA). Factors are Species (five in SN and two in SA), Light (a gradient of three habitat types with different light availability), and Water (irrigation treatments of emerged seedlings).

	Sierra Nevada			Sierra del Aljibe		
	df	F	P	df	F	P
Seedling Emergence						
Species	4	140.24	<0.0001	1	34.52	<0.0001
Light	2	1.47	0.232	2	0.95	0.389
Species * Light	8	10.58	<0.0001	2	4.32	0.015
Residual	885			114		
Seedling Survival						
Species	4	78.73	<0.0001	1	1.63	0.209
Light	2	34.21	<0.0001	2	1.70	0.194
Water	1	302.77	<0.0001	1	3.42	0.071
Species * Light	8	5.70	<0.0001	2	0.02	0.982
Species * Water	4	2.84	0.023	1	2.79	0.102
Light * Water	2	19.29	<0.0001	2	1.16	0.324
Species * Light * Water	8	1.56	0.134	2	0.26	0.770
Residual	698			46		

emergence higher than that of *Quercus canariensis* (Figure 1). On the other hand, there was no significant overall effect of habitat on seedling emergence, but a significant interaction species x habitat (Table 1). That is, *Quercus suber* seedlings emerged significantly better (Tukey test) in the deep shade than in full light conditions, while emergence in the medium shade was intermediate. For *Quercus canariensis* there was no significant effect of habitat on seedling emergence (Figure 1).

Field Experiments: Seedling Survival

At Sierra Nevada field site, survival after summer drought depended significantly on all the factors considered (Table 1). Watering treatment was the factor with highest effect, increasing survival from 35.8±2.2% to 76.7±1.7% (all species pooled). Species identity had also a strong effect on survival, ranging from roughly 70% for *Quercus* species to 24% for *Pinus sylvestris* (Figure 2). The habitat type also affected seedling survival, beeing higher in "Deep shade" (woodland) stands than in "Full light" (open) stands (Figure 2). The highly significant light × water interaction in the ANOVA (Table 1) indicated that the magnitude of the effect of irrigation depended on the habitat; thus seedling survival increased in watered open and shrubby microsites but watering had scant effect inside woodland stands (Figure 2).

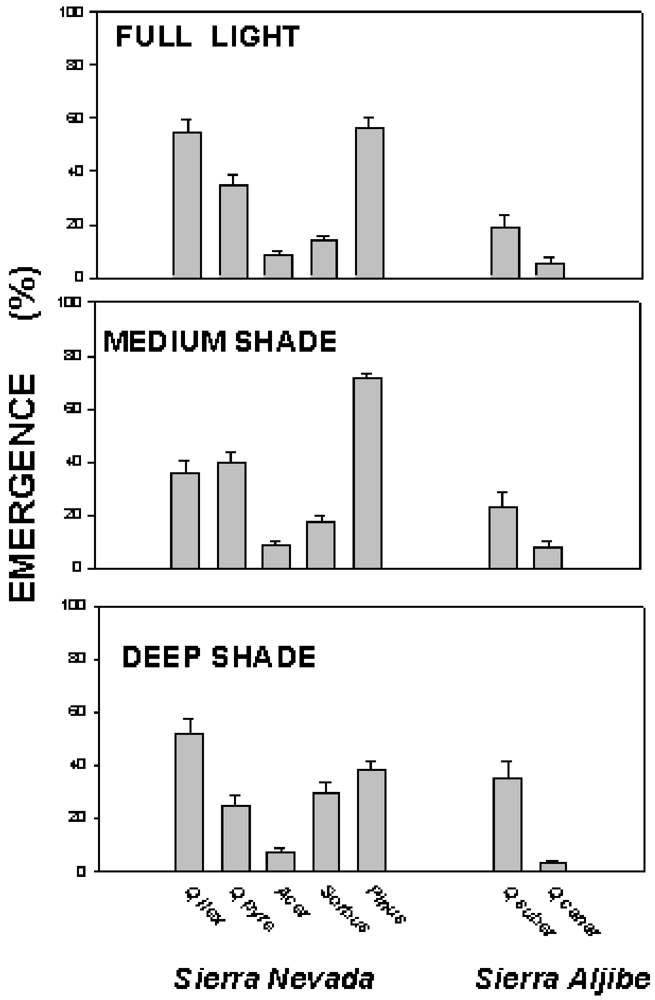

Figure 1. Seedling emergence (mean and s.e.) in the field sites of *Sierra Nevada* (five species) and *Sierra del Aljibe* (two species). Three habitat types: Full light (open microsites), Medium shade (under shrubs or isolated trees) and Deep shade (inside the forest) were distinguished.

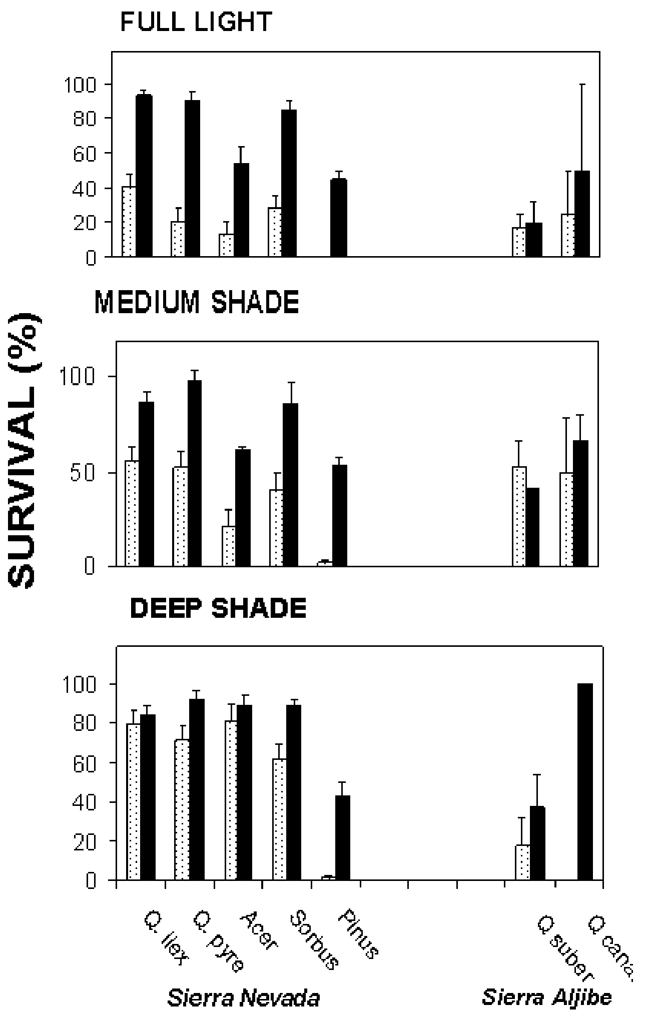

Figure 2. Percent survival (mean and s.e.) of seedlings after the summer drought, at the two field sites of *Sierra Nevada* and *Sierra del Aljibe*. Three habitat types are as shown in Figure 1. Irrigated seedlings are indicated with black bars, and non-irrigated with gray bars.

In the Sierra del Aljibe field experiment, there was a 20% of overall seedlings surviving at the end of the summer (September 2003), and apparently there were no differences between species and habitat (Table 1). However, data were unbalanced because the very low emergence of *Quercus canariensis*; and in a separate analysis of *Quercus suber* survival, habitat was found as a significant factor (ANOVA values of F=5.55, and P=0.006). Seedlings of cork oak had a higher survival rate (43%) in the semi shade (under isolated trees) microsites, than in open sites (15%) or inside closed forest (14%). The effect of water irrigation was not significant either on seedling survival, in this study site (Table 1). Compared to the Sierra Nevada study shown above, in this experiment the irrigation treatment was too weak (one litre per 600 cm^2 at 21 days intervals) to have a significant effect on the plant water balance and to increase seedling survival.

Glasshouse Experiment: Seedling Growth

The ANOVA results for the combined effects of light and water on seedling mass of four *Quercus* species are shown in Table 2. There was a significant difference between species, and a significant effect of both light and water treatments on seedling mass. The rank of seedling mass (fresh weight after six months growth on irrigation and full-light conditions) was: *Quercus pyrenaica* (mean ± s.d. = 32±7 g), *Quercus suber* (28±6 g), *Quercus ilex* (20±8 g) and *Quercus canariensis* (9±4 g). A similar pattern in the species ranking of seedling mass was found for the other water and light treatments. The constancy in the species ranking of seedling weight parallelled to their differences in acorn (seed) mass, following a similar rank: *Quercus pyrenaica* . *Quercus suber* > *Quercus ilex* > *Quercus canariensis*. Moreover, acorn mass and seedling mass were positively correlated (all species and treatments combined, r = 0.31, P<0.001).

Overall, the light factor had a maximum effect on seedling mass (maximum F value in ANOVA; see Table 2). On average, seedlings receiving full light had more than three times higher mass than those under shade conditions (Figure 3). Interestingly, there was a differential response between *Quercus* species to the light treatments (significant species× light interaction; Table

Table 2. Summary of the three-way ANOVA for the effects of species, and the treatments of light and water, on seedling (fresh) mass after six months cultivation in a glasshouse.

	df	F	P
Species	3	134.38	<0.0001
Light	2	258.24	<0.0001
Water	1	71.07	<0.0001
Species * Light	6	2.45	0.025
Species * Water	3	2.51	0.060
Light * Water	2	4.39	0.014
Species * Light * Water	6	2.50	0.023
Residual	212		

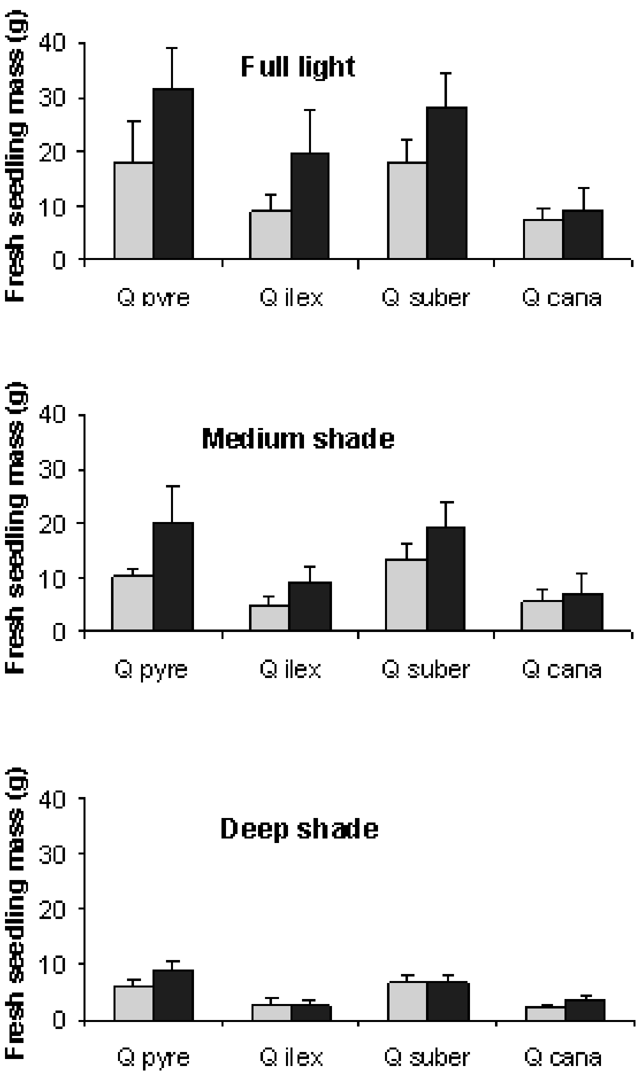

Figure 3. Mean seedling mass for the four *Quercus* species grown for six months in a glasshouse, under three levels of light: Full-light (100%), Medium shade (75%) and Deep shade (3%). Two irrigation treatments are indicated: (1) Continuous water supply by drip irrigation (black bars) and stopped irrigation after four months (grey bars).

2). Although all species responded negatively to deep shade (having lower mass than in full light), the two species *Quercus suber* and *Quercus canariensis* did not show significant mass reduction in medium shade treatment, compared to full light (Figure 3).

The water factor also had significant effect on seedling mass (Table 2). Seedlings suffering the seasonal shortage of water (not being irrigated after four months) had significantly lower mass than those receiving continuous drip irrigation (Figure 3).

Interestingly, there was a significant interaction between light and water treatments (Table 2). In deep shade conditions, seedling mass did not differ between the two watering treatments (post-hoc Tukey test was not significant, P=0.96; see Figure 3). There were also significant interactions between the seedling species and the treatments of light and water (Table 2, Figure 3), which means that the species varies in their responses according to the light and water treatments.

DISCUSSION

Environmental Heterogeneity and Tree Population Recruitment

Spatial heterogeneity of forest conditions affects the growth and survival of tree seedlings. The differential response between tree species, at the seedling stage, to the spatial and temporal heterogeneity (that is their differences in regeneration niches), may promote their coexistence and maintain forest biodiversity (Grubb 1977, Pacala and Tilman 1994). In addition, stochastic processes, combined to species niche overlap, may also contribute to forest species coexistence (Beckage and Clark 2003).

Environmental conditions optimal for one aspect of regeneration can be sub-optimal for others, originating demographic conflicts (Schupp 1995, Battaglia et al. 2000). In the Sierra del Aljibe site, there were contrasted responses between the emergence and establishment stages for *Quercus suber*. In the gradient of vegetation cover, the higher emergence of seedlings were inside closed forest (deep shade). On the contrary, survival rate was higher at intermediate stages. In Sierra Nevada, the deleterious effect of drought (experimentally demonstrated there), might create conflicts between seedling survival and growth, as shady habitats appropriate for survival might be unsuitable sites for seedling growth, due to the too low radiation levels there.

Under Mediterranean-type climate, summer drought tends to be the main factor causing seedling mortality. In fact, in the Sierra Nevada study it caused roughly 75% of seedling deaths. The different responses of the Sierra Nevada forest species upon summer drought, also suggests that species composition of Mediterranean forests, in general, might change under a scenario of global warming, favouring those species more tolerant to drought. Furthermore, given the predicted increase in both dryness and variability of rainfall regime (IPCC 2001, Rodó and Comín 2001), the already rare wet-summer events that barely allows recruitment will be even more sporadic, reducing even more the ability of these forests to regenerate naturally.

Comparison between Seedling Survival and Growth

Conflicts between components of regeneration can occur when a particular microsite is not favourable for early seedling survival, but once established there they grow faster. On the contrary, in certain microsites seedlings have more chances to survive but they can find growth restrictions by light limitation (as shown in the Sierra Nevada study).

The growth analysis of several tree species under controlled conditions (glasshouse experiment) showed a variety of responses between species, and also between light and water treatments. There was a clear, general trend of faster growth with increasing light, as expected because a higher radiation will induce a higher photosynthesis rate and carbohydrate synthesis (Lambers et al. 1998). From an ecological point of view, it was more interesting to demonstrate the differential responses between species to light, which may reflect different sensitivity to resource availability. Some species will be able to capitalize on opportunities in high-resource (full light) environments, while other species are relatively insensitive and will perform consistently across the resource (light) gradient (Kolb et al. 1990, Beckage and Clark 2003).

Drought was a limiting factor causing seedling mortality in field conditions. In glasshouse conditions, water treatment also had a major effect on seedling mass. The seasonal shortage of water (in pots not irrigated after four months) induced a significantly lower growth of seedlings of all the species. This mass reduction can be explained by the stress-induced closure of stomata and hence a decrease in CO_2 assimilation (Joffre et al. 2000). However, this pattern was not general, because seedlings in deep shade conditions did not show a mass reduction when irrigation was stopped. Most probably, in shaded pots the evapotranspiration was lower and hence soil water decreased more slowly, thus minimising the negative effect of stopping drip irrigation on seedling growth.

The combination of light and water effects on plant growth (as shown by the light and water interactions in the glasshouse experiment) is a complex ecophysiological phenomenon with profound ecological consequences (for example, see Kolb et al. 1990, Baruch et al. 2000, Sack and Grubb 2002, Sack et al. 2003). Moreover, the independence of the seedling responses to the light and water conditions would allow a wider array of regeneration niches and the coexistence of trees and shrubs in the forest (Sack and Grubb 2002).

In a comparative analysis of field and glasshouse results, we plotted the mean survival rate for two species "*Quercus ilex* and *Quercus pyrenaica*" in the three light conditions studied in Sierra Nevada, against the seedling mass of the same species in the three light levels provided in the glasshouse (Figure 4). The analysis was carried out separately for irrigated (both in field and glasshouse), and for non-irrigated conditions. In natural conditions, seedling survival was higher inside the forest (deep shade) and lower in the open (full light). Under equivalent glasshouse conditions, seedling growth was lower in deep shade and higher in full light. When the seasonal drought was eliminated by supplemental drip irrigation, seedling survival was similarly high in every microhabitat, but seedling growth stayed lower in shaded conditions, by shortage of light resources. Therefore, in Mediterranean forests, shaded microsites are favourable for seedling survival but they grow very slowly there, by light limitation. In forests of North America, a trade-off for tree species having a low survival in resource-poor environments, and able to grow faster in resource-rich environments, has been reported (Pacala et al. 1994, Kobe et al. 1995, Beckage and Clark 2003).

Restoration Ecology of Mediterranean Forests

Understanding the heterogeneity of the forest environment and the regeneration requirements of the tree species will help to design adequate practices for the ecological restoration of Mediterranean forests. The combination of summer drought and light intensity creates a gradient from open microhabitats, with high radiation and low soil moisture, to the forest floor, with deep shade and higher soil moisture; in this complex gradient the requirements for seedling survival and growth are uncoupled.

On one hand, recruitment under tree canopies is hampered because of deficient radiation levels. On the other hand, drought stress is usually the highest in areas of bare soil; only during an eventual wet summer seedlings will establish there. As a result, seedling establishment is mostly constrained to areas underneath the canopy of shrubs, as they provide intermediate values of radiation and moisture that allow survival, without hampering performance (Gómez et al. 2001, Castro et al. 2002b). Therefore, restoration strategies concerning either seeding or planting of seedlings, should consider shrubby species as regeneration niches to ensure establishment success in Mediterranean environments (see Jordano et al. 2001, Castro et al. 2004b, Gómez et al. 2004).

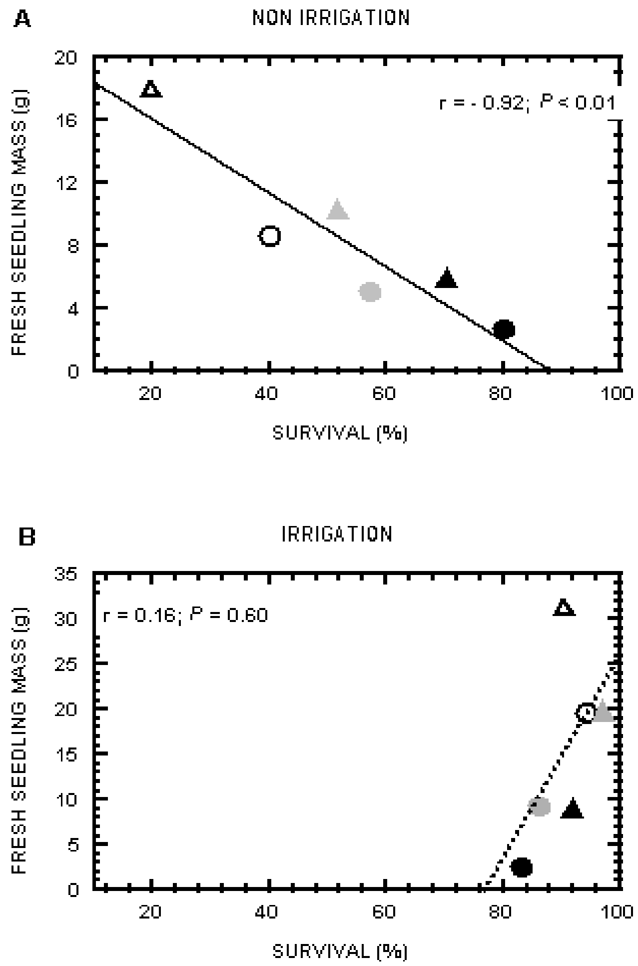

Figure 4. Comparative analysis of the seedling survival at field conditions in *Sierra Nevada* site and the seedling (fresh) mass at glasshouse conditions. Two species: *Quercus ilex* (circles) and *Quercus pyrenaica* (triangles), and three light conditions: Full light (white), Medium shade (grey) and Deep shade (black) are indicated. Regression analyses were carried out separately for the two irrigation treatments.

Future Perspectives

The HETEROMED project aims to increase our understanding of the regeneration processes of key Mediterranean tree species, so biologically-based diagnosis models can be developed. Regeneration success and stand dynamics in forest ecosystems are strongly linked to seedling and juvenile performance (Pigott and Pigott 1993). Thus, identifying critical factors influencing these stages is critical for developing sound forestry practices. Our main project goals are twofold. Firstly, we aim to improve reforestation practices, currently underway in Mediterranean forests, by incorporating biological knowledge; and doing so reforestation cost and seedling mortality will be minimized. By using reforestation methods "close to nature" (for example, use of shrubs as nurse plants) we can both decrease operation cost and minimize the risk of plant failure. We can also choose among several alternatives, such as selecting suitable microsites to maximize probability of seedling survival for each species, or deciding whether to seed or to transplant in each environment. All this acquired knowledge will be summarized in correlational probabilistic models that link seedling probability of mortality to microsite heterogeneity. Maximum likelihood estimators of seedling probability of mortality, as a function of limiting factors, will allow us to generate risk maps on a given terrain, so regeneration success can be optimised.

Our second and more ambitious goal is concerned with calibrating models of stand dynamics, so evaluation of successional trajectories of restored communities can be evaluated (Bradshaw 1995). Mediterranean forests exhibit multiple stable states induced by changes in soil water balance. Changes in ecological interactions during the recruitment process (for example, from facilitation to competition) has been shown to shift the system from one stable state to another (Zavala 1999). Thus, understanding regeneration success of different species in each habitat type is critical for developing a mechanistic understanding of forest succession in these ecosystems. The development of models of stand dynamics, calibrated with experimental data on species individual performance, will provide insight on the mechanisms controlling community structure and dynamics, and also allow to formulate a new, scientifically based, silviculture for Mediterranean forests. Based on previous maximum likelihood estimators of seedling performance, we will calibrate individual based models that predict stand composition in terms of species individual responses to resource limitation and ecological interactions among individuals (Shugart 1984, Pacala et al. 1996). The development of a new, mechanistic process-based forest simulator - well integrated to data - that captures the assembly mecha-nisms of these communities, will be a valuable diagnosis tool to guide local and regional decisions regarding the use of forest resources in this region, and in general in Mediterranean-type ecosystems.

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