Journal of Ecology 2005
93, 1194–1202

Microhabitats shift rank in suitability for seedling establishment depending on habitat type and climate

LORENA GÓMEZ-APARICIO*, JOSE M. GÓMEZ and REGINO ZAMORA

Grupo de Ecología Terrestre, Departmento de Ecología, Facultad de Ciencias, Universidad de Granada, E-18071 Granada, Spain

Summary

1 Spatial patterns of seedling establishment have been shown to be largely affected by differences at the microhabitat scale. However, it is far from clear whether such differences are consistent both in space and time, and how they influence the spatial structure of plant populations.

2 We analyse the spatiotemporal variability in microhabitat quality for seedling emergence and survival of the Mediterranean tree *Acer opalus* ssp. *granatense*, examining seedling dynamics at the microhabitat scale in two maple populations intermingled in pine forests and two established on stony slopes during three consecutive years with different climatic conditions.

3 Seedling establishment varied markedly between microhabitats. In general, seedlings benefited from the presence of pre-established vegetation, with lower emergence and survival of maple seedlings in open interspaces than under adult maples, non-conspecific trees and shrubs.

4 However, the quality of most microhabitats depended on both habitat type and year. Emergence and survival under adult maples, heterospecific trees and in open interspaces was higher in forest than in stony-slope populations, and increased significantly with summer rainfall. Shrubs, on the contrary, showed relatively high values of seedling emergence and survival at all sites and in both dry and wet years. Consequently, the benefits of living under shrubs were comparatively greater at lower precipitation levels.

5 The different microhabitats found in heterogeneous landscapes such as Mediterranean forests vary, over relatively large spatiotemporal scales, in quality for seedling establishment. Shrubs showed the highest consistency in patterns of both seedling emergence and survival. This finding, together with the predominance of dry years in Mediterranean areas, may explain why *Acer opalus* ssp. *granatense* has a stable spatial distribution at a geographical scale with most saplings associated with shrubs. Spatiotemporal patterns of seedling dynamics at the microhabitat scale may cascade through later demographic stages, eventually impacting the spatial structure of plant populations.

Key-words: *Acer opalus* ssp. *granatense*, climate, facilitation, habitat types, hierarchical effects, Mediterranean mountain, microhabitat quality, seedling emergence and survival, spatiotemporal variability

Journal of Ecology (2005) **93**, 1194–1202
doi: 10.1111/j.1365-2745.2005.01047.x

Introduction

The period between seed germination and seedling establishment is considered one of the most vulnerable transitions in the life cycle of plants and, consequently, it has long been a focus of ecological research (Harper 1977; Kitajima & Fenner 2000). Many abiotic and biotic factors can affect seedling establishment, such as litter (Facelli & Pickett 1991; Molofsky & Augspurger 1992), light (Kobe *et al.* 1995; Nicotra *et al.* 1999), microtopography (Augspurger 1984; Huenneke & Sharitz 1986), soil physical and chemical characteristics (Herrera

---

*Present address and correspondence: Lorena Gómez Aparicio, Institute of Ecosystem Studies, 65 Sharon Turnpike, PO Box AB, Millbrook, NY, 12545–0129, USA (fax 845 677 5976; e-mail gomezl@ecostudies.org).

2002), seed arrival (Dalling *et al*. 2002; Russo & Augspurger 2004), herbivory (Ostfeld & Canham 1993; Gómez *et al*. 2003), pathogens (Augspurger 1983; Packer & Clay 2000) and competition with herbs (De Steven 1991).

All these factors are highly heterogeneous in space (Mack & Pyke 1983; Streng *et al*. 1989; Houle 1992), varying at different scales, such as among geographical areas (García *et al*. 1999; Castro *et al*. 2004), among habitats in a region (Herrera *et al*. 1994; Traveset *et al*. 2003), or among microhabitats within a habitat (Chambers 2001; Garrido 2003). In a recent review of the variation of demographic processes at different scales, Kollmann (2000) suggested that patterns of seedling establishment are affected mainly by differences between microhabitats. Therefore, an examination of which microhabitats, under which environmental conditions, constitute safe sites (*sensu* Harper *et al*. 1961) for seedling establishment is essential to understand the spatial structure and dynamics of plant populations. Nevertheless, as most studies analysing regeneration dynamics have been conducted in only one or two populations (Clark *et al*. 1999), it is far from clear whether differences between microhabitats are consistent in space or highly dependent on the study sites.

Even fewer studies extend the discussion of differences in microhabitat quality to temporal scales. Consequently, it is poorly understood whether levels of seedling establishment are strongly differentiated between microhabitats in some years, but not in others. Some studies point in that direction, showing the quality of microhabitats for recruitment to fluctuate interannually due to variation in climatic conditions (Greenlee & Callaway 1996; Tielbörger & Kadmon 2000; Ibañez & Schupp 2001). High temporal instability in the environmental mosaic faced by seedlings is important because it could translate into a population without a stable spatial distribution (Fowler 1988), whereas strong temporal consistency would result in spatial association with high-quality patches.

Our main goal is to analyse spatiotemporal variability in microhabitat quality for seedling emergence and survival of the Mediterranean tree *Acer opalus* ssp. *granatense* (Boiss.) Font Quer & Rothm (Aceraceae) by following seedling dynamics in four populations during three consecutive years with different climatic conditions. Across its range, this species occupies contrasting habitat types, such as forests and stony slopes, enabling the analysis of seedling dynamics under potentially different limitations for establishment. Maple populations occur as a mosaic of soil patches covered by different tree and shrub species, interspersed with bare ground. As wind-dispersed maple seeds reach all these microhabitats (Gómez-Aparicio 2004), seedling emergence and survival constitute a key filter of dispersal patterns, determining spatial population structure over the long-term. We address the following questions. (i) Do between-microhabitat differences in seedling emergence and survival depend on the study site? (ii) Is the suitability of a microhabitat for seedling establishment consistent over time? (iii) Do all microhabitats show the same spatiotemporal variation in quality?

Materials and methods

STUDY SPECIES

Acer opalus ssp. *granatense* is an endemic Iberian-Mauritanian deciduous tree. It has a fragmented distribution composed of small patches scattered throughout the mountains of the south-eastern Iberian Peninsula, Balearic Islands and northern Morocco (López-González 1994). It has been catalogued as vulnerable by the IUCN (2000) and included in the recent Red List of Threatened Vascular Plants of Andalusia (Blanca *et al*. 2000). Populations appear at 1100–2000 m a.s.l. on north-facing slopes, in shady ravines or near riverbanks, i.e. where Mediterranean summer drought is partially mitigated by special topographic or soil conditions. Seeds disperse from September to December and seedlings emerge the following spring (April–June), although some seeds may require two periods of low temperatures to break dormancy and germinate.

STUDY DESIGN

Two study sites were located in the Sierra Nevada National Park and two in the Sierra de Baza Natural Park, the two mountain ranges approximately 80 km apart in southern Spain. The climate is Mediterranean, with precipitation concentrated in late autumn and winter (often as snow) and hot, dry summers. Sierra Nevada receives higher annual precipitation than Sierra de Baza (846.5 ± 55.7 mm vs. 527.4 ± 40.9 mm; 1991–2002), although both have similarly low summer rainfall (June–August, 47.3 ± 5.5 mm and 46.1 ± 4.3 mm, 1991–2002). Winters are cold and snow is common, persisting up to 2 months, and frost occurs from November to April. The bedrock is calcareous. In each mountain range, one site consisted of maple intermingled with *Pinus sylvestris* forest (forest populations, hereafter) and the other a maple population situated 2–4 km away on a stony slope (stony-slope populations). Site types differed mainly in soil substrate and canopy cover, with stony-slope populations on a substrate largely composed of bare soil with loose stones, compared with forest populations, which have stable substrate and higher tree cover (Table 1). We identified four microhabitat types (i.e. distinct homogeneous patches of habitat ranging from < 1 m to several metres in diameter; García 2001): Maple, under the canopy of adult maples; Canopy, under the canopy of non-conspecific adult trees together with shrubs > 1.5 m in height (one to two species per site, Table 1); Shrub, under the canopy of shrubs < 1.5 m in height (one to three species per site, Table 1); and Open, open interspaces among woody vegetation.

Table 1 Main characteristics of the four study sites. The cover of the different microhabitats was determined by means of 25 × 2 m transects ($n = 10$ per site), visually estimating cover percentages at each 1 × 2 m square

	Site			
	Sierra Nevada		Sierra de Baza	
	Forest	Stony-slope	Forest	Stony-slope
Location (UTM)	30SVG5905	30SVG5904	30SWG1438	30SWG1433
Altitude (m a.s.l.)	1850	1920	1850	2000
Orientation	NW	NW	NW	NE
Slope (°)	40	40	30	35
Microhabitat cover (%)				
Maple	15.0	21.9	25.8	13.0
Canopy*	17.1	2.5	20.1	13.5
Shrub†	29.9	11.3	9.7	15.1
Open	27.9	55.5	38.6	43.1

*Canopy includes *Pinus sylvestris* and *Taxus baccata* in the forest population of Sierra Nevada, *Amelanchier ovalis* in the stony-slope population of Sierra Nevada, and *Pinus sylvestris* in the two sites of Sierra de Baza.

†Shrub includes *Ononis aragonensis*, *Juniperus communis* and *Berberis hispanica* in the forest population of Sierra Nevada, *Ononis aragonensis* in the stony-slope population of Sierra Nevada, *Prunus ramburii* and *Crataegus monogyna* in the forest population of Sierra de Baza, and *Juniperus communis* and *Berberis hispanica* in the stony-slope population of Sierra de Baza.

SEEDLING EMERGENCE

Emergence was experimentally studied by sowing seeds in the field. Seeds were collected in November 2001 from five to six parent maples per mountain range, and kept at constant temperature (3–5 °C) at La Cortijuela Botanical Garden (1640 m a.s.l., Sierra Nevada National Park) until sowing. Seeds from different trees were mixed to provide two seed pools, one for Sierra Nevada and another for Sierra de Baza, and used for sowing at the two sites within the corresponding mountain range. In the laboratory, a fraction of each pool ($n = 100$) was weighed and examined (by removing the pericarp) to estimate viability. Previous experience has shown that embryos estimated visually as viable have proven viable after a tetrazolium test in more than 90% of cases (author's unpublished data). Seed weight and viability rates were similar in both pools (37.3 ± 1.2 mg and 12% viability in Sierra Nevada, 35.5 ± 1.1 mg and 10% viability in Sierra de Baza). In December 2001, groups of five seeds were sown in 30 haphazardly assigned points per microhabitat ($n = 3150$ seeds). Within each group, seeds were sown 2 cm apart and at 2 cm depth. In the Canopy and Shrub microhabitats, sowing points were replicated for each of the canopy and shrub species present at that particular site. The number of seeds per point was chosen as a compromise to maximize the probabilities of having at least one emergence per point (due to low seed viability) while avoiding density-dependent effects. Each sampling station was protected by a wire cage to prevent seed predation and additional seed rain and all naturally occurring seeds were removed before sowing. Emergence was monitored fortnightly from 1 April to the end of June, when no additional emergence was registered. Survival of emerged seedlings was reviewed at the end of the summer (mid September). Throughout the paper, emergence is corrected for viability rates, i.e. percentage emergence is divided by 0.12 and 0.10 in Sierra Nevada and Sierra de Baza populations, respectively.

SURVIVAL OF NATURAL SEEDLINGS

For three years (2000, 2001 and 2002), 100–200 newly emerged seedlings (depending on the natural availability) were marked individually per microhabitat ($n = 7200$ seedlings). In Canopy and Shrub microhabitats, 100–200 seedlings were marked under each species present. In the stony-slope population of Sierra de Baza, seedlings were marked only in 2001 and 2002. Seedlings were censused twice a year after summer (September) and after winter (April). The most likely cause of any death was recorded, distinguishing between drought (seedlings brown and shrivelled), frost (seedlings uprooted due to frost heave), herbivory (seedlings with the epicotyl consumed), physical damage (due to trampling, substrate movements or fallen branches) and light limitation (seedlings with extremely thin and almost transparent green leaves). Seedlings that were not relocated were excluded from the analyses.

DATA ANALYSES

Seedling emergence and survival were analysed using Generalized Logit Models (Proc CATMOD, SAS Institute 2002). For emergence, the presence/absence of emerged seedlings per sowing point was introduced as dependent variable (the number of seedlings per point was not used because it was zero in 81.3% of the cases). We fitted the dependent variable to a binomial function, with mountain range, site (nested in mountain range) and microhabitat as main factors. The same model was used for the analyses of survival after the first summer of seedlings that had emerged in the experimental sowings, but with seedling state (alive vs. dead) as the binomial dependent variable. For the survival of naturally established seedlings, mountain range, site (nested in mountain range), microhabitat and year were introduced as main factors and survival after the first summer (for cohorts 2001 and 2002) as binomial dependent variable. Data for the 2000 cohort were not included in the analysis due to the lack of data for one site. When a factor was significant, differences among levels were explored using paired χ^2 tests. To control for experiment-wise type I error produced by multiple comparisons, we adjusted the probabilities of error to $\alpha = 0.05$, using the sequential Bonferroni technique (Rice 1989). Non-significant interactions among sources of variation were pooled with the error term to improve the test (Zar 1996).

We used regressions to explore the relationship between summer rainfall (cumulative rainfall in June, July and August) and seedling survival after the first summer. Climatic data were obtained from the nearest meteorological station to the study sites (La Cortijuela Botanical Garden for both Sierra Nevada sites and Narvaez Meteorological Station for Sierra de Baza sites) and regressions were performed on mean survival of the two populations in a mountain range (except for Sierra de Baza in 2000) and study year ($n = 6$), in order to avoid pseudoreplication. Means are shown ± 1 SE.

Results

SEEDLING EMERGENCE

Experimental emergence was no higher than 7% in any site, but correction for the low viability rates increased mean total emergence to 36.6%. Emergence varied between sites and microhabitats (Table 2). It was higher in the two forest populations (48.3% in Sierra Nevada and 54.8% in Sierra de Baza, corrected values) than in the two stony-slope populations (21.6% and 21.5%). Emergence was highest under heterospecific canopies and lowest in open interspaces (Fig. 1), although differences between microhabitats depended on study site (significant Site [Mountain range]–Microhabitat interaction term, Table 2). Thus, increased emergence under conspecific and heterospecific canopies was observed only in forest populations (Fig. 1). Emergence under shrubs did not, however, vary between study sites, being consistently higher than in open areas.

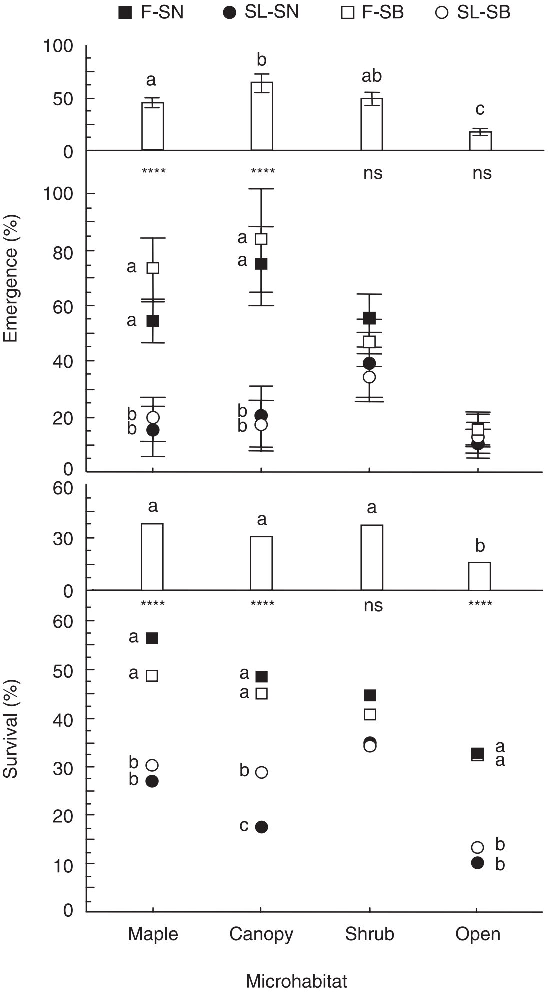

Fig. 1 Emergence (corrected for seed viability) and survival of experimental seedlings in 2002. In the upper plot for each cohort, bars represent the average per microhabitat (all the sites pooled). In the lower plot, symbols represent the mean per site and microhabitat combination. Values for emergence are mean ± SE (percentage of seed emergence per sowing point). Different letters show significant differences between sites within microhabitat at $\alpha < 0.05$ after Bonferroni correction. Asterisks denote the significance of the between-site differences in microhabitat quality. ****$P < 0.0001$, ***$P < 0.001$, **$P < 0.01$, *$P < 0.05$. F = forest population; SL = stony-slope population; SN = Sierra Nevada; SB = Sierra de Baza.

Table 2 Summary of models analysing differences between microhabitats, and their interaction with the site, in emergence and survival of experimental seedlings in 2002

Variable	Factors	d.f.	L-R χ^2	*P*
Emergence	Mountain range	1	1.51	0.2228
	Site [mountain range]	3	9.78	0.0205
	Microhabitat	3	15.74	0.0013
	Site [mountain range] × microhabitat	9	19.71	0.0198
	Model	16	40.28	0.0007
Survival	Mountain range	1	2.09	0.1579
	Site [mountain range]	3	10.82	0.0127
	Microhabitat	3	15.91	0.0012
	Site [mountain range] × microhabitat	9	21.45	0.0108
	Model	16	44.09	0.0002

SEEDLING SURVIVAL

The survival of experimental seedlings varied between sites and microhabitats (Table 2). It was higher in the two forest populations (46.1% in Sierra Nevada and 41.2% in Sierra de Baza) than in the two stony-slope populations (21.3% and 29.4%). Survival in open areas

Table 3 Summary of models analysing the differences between sites, microhabitats and years in survival after the first summer of natural seedlings in 2001 and 2002

Factors	d.f.	L-R χ^2	*P*
Mountain range	1	0.49	0.4798
Site [mountain range]	3	33.45	< 0.0001
Microhabitat	3	115.24	< 0.0001
Year	1	231.79	< 0.0001
Site [mountain range] × microhabitat	9	120.05	< 0.0001
Microhabitat × year	3	86.21	< 0.0001
Model	20	1171.82	< 0.0001

was significantly lower than in the other three microhabitats (Fig. 1). Survival in all microhabitats except under shrubs was significantly higher in the two forest than in the two stony-slope populations (Fig. 1, significant Site [Mountain range]–Microhabitat interaction term in Table 2), indicating that the quality of a microhabitat for survival of experimental seedlings varied with site. Spatial patterns of survival of naturally established seedlings were similar to those found for experimental seedlings, varying among sites and microhabitats (Table 3). Average survival was around 30%, with 84.9% of the observed mortality due to summer drought (5.3% frost, 2.5% herbivory, 2.2% physical damage and 5.1% light limitation). Survival was lower in the two forest populations than in the two stony-slope populations, and in open areas than in any other microhabitat. However, differences between microhabitats varied depending on the site considered (significant Site [Mountain range]–Microhabitat interaction, Table 3). Thus, between-site differences in survival were consistently less significant under shrubs than in any other microhabitat in the three study years (Fig. 2).

Survival varied significantly among years (Table 3), being more than twofold higher in 2002 (53.2%) than in 2001 (22.3%). Although not included in the model, survival in 2000 showed a similar magnitude (23.9%) and between-microhabitat distribution as in 2001 (Fig. 2). Between-microhabitat differences in survival were not consistent across years, as shown by the significant Microhabitat–Year interaction term (Table 3). Thus, although overall survival was higher in 2002 than in 2001, survival under shrubs was the least affected at all sites, so that this microhabitat had the highest survival in 2001 but was among the lowest in 2002 (Fig. 2). Regressions of rainfall and first summer survival showed that survival increased significantly with rainfall in all microhabitats except under shrubs (Fig. 3).

Discussion

SPATIAL PATTERNS OF SEEDLING EMERGENCE AND SURVIVAL

Our results show that both emergence and survival of maple seedlings at all four sites is highly microhabitat-dependent, being much lower in open interspaces than under pre-established vegetation, either trees or shrubs. This result agrees with other studies conducted in Mediterranean systems, where pre-existing vegetation facilitates emergence and survival of woody seedlings (Herrera *et al.* 1994; García 2001; Garrido 2003; Gómez *et al.* 2003; Castro *et al.* 2004). We found that even adult maples benefited seedlings, despite the negative interactions between seedlings and conspecific adults that

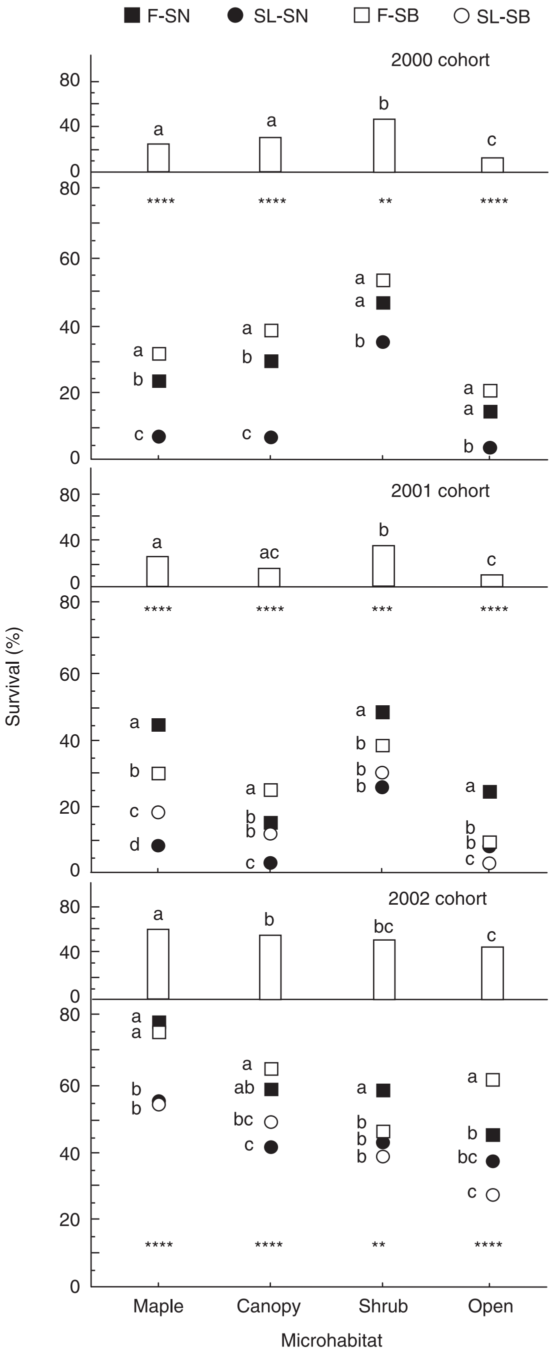

Fig. 2 Survival of natural seedlings after the first summer during the three years of study. In the upper parts, bars represent the average per microhabitat (all the sites pooled). In the lower parts of the boxes, symbols represent the mean per site and microhabitat combination. Statistical conventions as in Fig. 1.

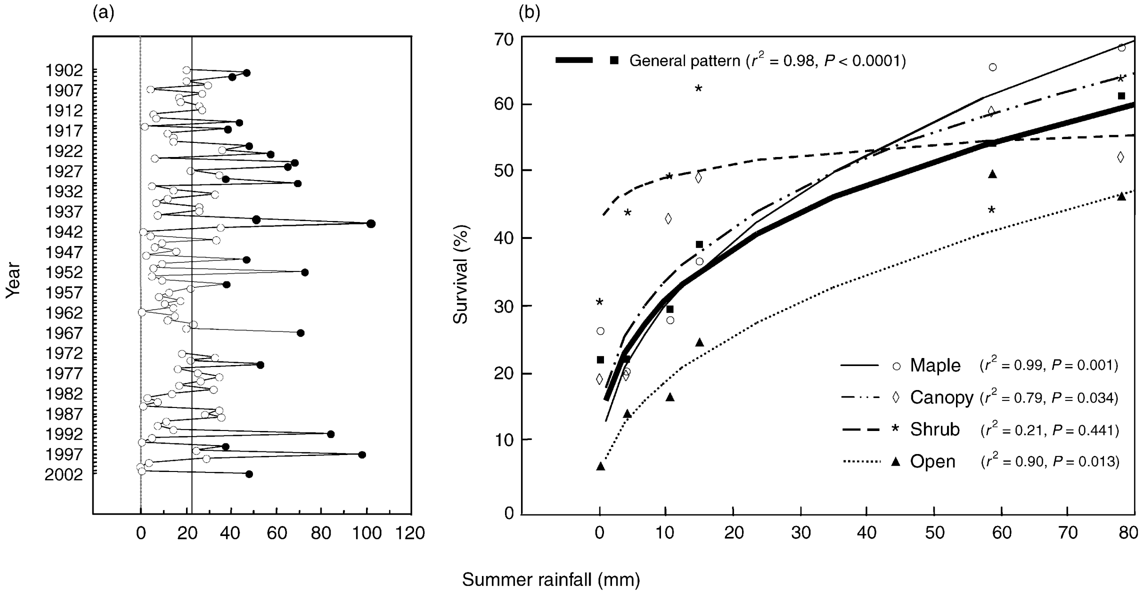

Fig. 3 (a) Summer rainfall over the last century (1902–2002). Data come from the Observatory of Cartuja (750 m a.s.l., Granada) and show a highly significant correlation with data available in the nearest meteorological stations to the study sites, both in Sierra Nevada (La Cortijuela Botanical Garden, 1650 m a.s.l.; $r^2 = 0.73$, $n = 12$, $P = 0.0002$) and Sierra de Baza (Narvaez Meteorological Station, 1390 m a.s.l.; $r^2 = 0.69$, $n = 12$, $P = 0.004$). The black line indicates the mean for the sere (24.01 ± 2.22 mm), and black points represent years with summer rainfall deviating above the mean by > 25%. (b) Regressions between summer rainfall (cumulative rainfall in June, July and August) and seedling survival after the first summer, with and without distinguishing among microhabitats; $n = 6$ in all cases, with one data point per mountain range (mean of the two populations, except for Sierra de Baza in 2000) and study year.

have been commonly reported in other Mediterranean (Herrera *et al.* 1994; Nathan *et al.* 2000; Rey & Alcántara 2000) and non-Mediterranean systems (Augspurger 1984; Streng *et al.* 1989; Kollmann & Grubb 1999). Emergence and survival could have been facilitated by several mechanisms, such as the reduction of radiation and soil desiccation (Kitzberger *et al.* 2000; Schenk & Mahall 2002), production of litter that diminishes water evaporation losses (Evans & Young 1970; Fowler 1988), reduction of soil compaction (Verdú & García-Fayos 1996) or increase of soil macroporosity and water storage (Callaway *et al.* 1991; Joffre & Rambal 1993). Among all of these factors, our previous experimental work suggests that the 'canopy effect', that is, the modification of the above-ground microclimate by established vegetation, constitutes a major facilitation mechanism of seedling establishment in Mediterranean systems that can be even more relevant than the modification of soil properties (Gómez-Aparicio *et al.* 2005b).

The quality of a microhabitat for seedling establishment was highly dependent on the habitat type. Thus, whereas open areas and shrubs always presented, respectively, low and high quality for emergence, the quality of conspecific and heterospecific canopies varied significantly between forest and stony-slope populations (Fig. 1). These two microhabitats showed the highest emergence percentages in forest populations, but when located in stony-slope populations, emergence diminished threefold to values comparable with those registered for open areas. Similarly, the greatest intersite variation in microhabitat quality for seedling survival occurred under tree cover (both conspecific and heterospecific) and in open areas, whereas emergence under shrubs was similarly high in forest and stony-slope populations (Figs 1 and 2). This shift was presumably mediated by differences in a local-scale factor: substrate in forest populations is composed largely of stable mineral soil, whereas in stony-slope populations the well-developed soil is concentrated under shrubs and the ground in the remaining microhabitats is covered by loose stones. Such substrate negatively affects seedling emergence due to a low root-soil contact (Chambers 1995; Vilá & Lloret 2000), and its mobility implies an additional risk for seedling survival. In fact, although summer drought was the main cause of mortality, many dried seedlings in stony-slope populations were also uprooted or covered by stones, implying that damage from mobile stones could have led to death by desiccation. Therefore, local characteristics (substrate type) dilute differences among microhabitats (specifically between open areas, conspecific canopies and heterospecific canopies) in quality for seedling establishment, showing the hierarchical control that larger spatial scales can exert on the expression of differences at smaller scales (Kotliar & Wiens 1990; Turner *et al.* 2001).

INTERACTION BETWEEN THE TEMPORAL AND THE SPATIAL SCALE OF SEEDLING ESTABLISHMENT

Seedling survival varied greatly interannually (see also De Jong & Klinkhamer 1988; Traveset *et al.* 2003), from around 20% in dry years (2000 and 2001) to > 50% in the wet year (2002). Summer 2002 was one of 21 years in the last century where rainfall was > 25% above the mean, whereas 2000 and 2001 represent two of the driest years since 1902 (Fig. 3a). The positive effect of rainfall allowed a high percentage of seedlings in 2002 to survive their critical first summer.

Our results also show that interannual climatic variation can alter not only the magnitude of seedling survival, but also its spatial distribution between microhabitats. Whereas in dry years survival was highest under shrubs, shrub understories turned out to be one of the least suitable microhabitats for survival in 2002, with percentages even lower than open interspaces. When survival after the first summer was related to summer rainfall for each microhabitat considered, shrubs proved to be the best microhabitat for seedling survival at low precipitation levels (Fig. 3b), perhaps because shrubs not only reduce radiation by percentages similar to those of trees, but also present thicker litter layers and lower soil compaction than any other microhabitat (author's unpublished data). These abiotic modifications should improve seedling water status by reducing evapotranspiration losses and by allowing roots to explore a larger soil profile, thereby increasing the seedling's probability of withstanding summer drought.

However, as rainfall increased, survival under conspecific and heterospecific canopies, as well as in open areas, rose by a logarithmic function, whereas under shrubs it remained constant at around 50%. Shrubs were the only microhabitat where summer rainfall and survival did not significantly correlate so that in the mid-range of the gradient explored, survival under shrubs was equivalent to survival under tree canopy, both conspecific and heterospecific. As precipitation increased still further, shrubs became even lower quality microhabitat than tree species (maple and canopy, Fig. 3b), probably due to a higher overlap in resource use among seedlings and shrubs than among seedlings and trees. These findings show that the quality of a microhabitat for recruitment is highly dependent on climatic variables. Consequently, the landscape can change from being, at low precipitation levels, a low-quality matrix for recruitment with high-quality patches (shrubs), to become, at high precipitation levels, a high-quality matrix where only open interspaces constitute patches of comparatively lower quality.

CONSISTENCY OF MICROHABITAT QUALITY THROUGH SPACE AND TIME

The great variability reported here limits the categorization of a specific microhabitat as a safe site for recruitment, at least in environments, such as Mediterranean forests, characterized by high spatiotemporal heterogeneity. The same microhabitat differed in suitability depending on the habitat type (forests vs. stony-slopes), due to a hierarchy of abiotic factors influencing recruitment (soil substrate over canopy effects). Such hierarchies have rarely been documented in the literature, but are crucial to understand which factors limit the regeneration of a species on broad spatial scales. The connection of large spatial scales with relatively large temporal scales enabled us to show that, even within the same population, microhabitat quality can vary substantially with climatic conditions and therefore with the level of abiotic stress in the system. Moreover, the spatiotemporal variability in quality appears not to affect all the microhabitats evenly. The shrub microhabitat showed spatial and temporal consistency, and had a significant advantage over the remaining microhabitats in dry years. The general positive effect of shrubs on seedling establishment, together with the fact that dry summers are the rule in the Mediterranean, could explain why populations of *Acer opalus* ssp. *granatense* have a stable spatial distribution at a geographical scale, with most saplings found under shrubs throughout its range in the Iberian Peninsula (Gómez-Aparicio *et al.* 2005a). Spatiotemporal patterns of seedling emergence and survival at the microhabitat scale may be strong enough to cascade through later demographic stages, eventually impacting the spatial structure of plant populations.

Acknowledgements

We thank the Consejería de Medio Ambiente, Junta de Andalucía, for permitting our fieldwork in the Sierra Nevada National Park and Sierra de Baza Natural Park. We are especially grateful to Sergio de Haro, Elena Baraza and Jose Antonio Hódar for their help in the field. Peter Klinkhamer and two anonymous reviewers provided helpful comments on earlier versions of the manuscript. David Nesbitt improved the English version. This study was supported by a PFPU-MECD grant to L.G.A., the Andalusian government grant (PAI) rnm-220, and projects REN2001-4552-E and HETEROMED REN2002-04041-CO2-01/GLO from the Spanish Ministry of Science and Technology (MCYT).

References

Augspurger, C. (1983) Seed dispersal of the tropical tree, *Platypodium elegans*, and the escape of its seedlings from fungal pathogens. *Journal of Ecology*, **71**, 759–771.

Augspurger, C. (1984) Seedling survival of tropical tree species: interactions of dispersal distance, light-gaps, and pathogens. *Ecology*, **65**, 705–1712.

Blanca, G., Cabezudo, B., Hernández-Bermejo, J.E., Herrera, C.M., Muñoz, J. & Valdés, B. (2000) *Libro Rojo de Flora Amenazada de Andalucía*. Consejería de Medio Ambiente, Junta de Andalucía, Sevilla, Spain.

Callaway, R.M., Nadkarni, N.M. & Mahall, B.E. (1991) Facilitation and interference of *Quercus douglasii* on understorey productivity in central California. *Ecology*, **72**, 1484–1499.

Castro, J., Zamora, R., Hódar, J.A. & Gómez, J.M. (2004) Seedling establishment of a boreal tree species (*Pinus sylvestris*) at its southernmost distribution limit: consequences of being in a marginal Mediterranean area. *Journal of Ecology*, **92**, 266–277.

Chambers, J.C. (1995) Relationships between seed fates and seedling establishment in an alpine ecosystem. *Ecology*, **76**, 2124–2133.

Chambers, J.C. (2001) *Pinus monophylla* establishment in an expanding *Pinus-Juniperus* woodland: environmental conditions, facilitation and interacting factors. *Journal of Vegetation Science*, **12**, 27–40.

Clark, J.S., Beckage, B., Camill, P., Cleveland, B., HilleRisLambers, J., Lichter, J. *et al.* (1999) Interpreting recruitment limitation in forests. *American Journal of Botany*, **86**, 1–16.

Dalling, J.W., Muller-Landau, H.C., Wright, S.J. & Hubbell, S.P. (2002) Role of dispersal in the recruitment limitation of neotropical pioneer species. *Journal of Ecology*, **90**, 714–727.

De Jong, T.J. & Klinkhamer, P.G.L. (1988) Population ecology of the biennials *Cirsium vulgare* and *Cynoglossum officinale* in a coastal sand-dune area. *Journal of Ecology*, **76**, 366–382.

De Steven, D. (1991) Experiments on mechanisms of tree establishment in old-field succession: seedling survival and growth. *Ecology*, **72**, 1076–1088.

Evans, R.A. & Young, J.A. (1970) Plant litter and establishment of alien annual weed species in rangeland communities. *Weed Science*, **18**, 697–703.

Facelli, J.M. & Pickett, S.T.A. (1991) Plant litter: its dynamics and effects on plant community structure. *Botanical Review*, **57**, 1–25.

Fowler, N.L. (1988) What is a safe site? Neighbour, litter, germination date, and patch effects. *Ecology*, **69**, 947–961.

García, D. (2001) Effects of seed dispersal on *Juniperus communis* recruitment on a Mediterranean mountain. *Journal of Vegetation Science*, **12**, 839–848.

García, D., Zamora, R., Hódar, J.A. & Gómez, J.M. (1999) Age structure of *Juniperus communis* L. in the Iberian peninsula: conservation of remnant populations in Mediterranean mountains. *Biological Conservation*, **87**, 215–220.

Garrido, J.M. (2003) *Semillas y plántulas de* Helleborus foetidus *L. (Ranunculaceae): variación geográfica, ecológica y evolución*. PhD thesis. University of Jaén, Jaén, Spain.

Gómez, J.M., García, D. & Zamora, R. (2003) Impact of vertebrate acorn- and seedling-predators on a Mediterranean *Quercus pyrenaica* forest. *Forest Ecology and Management*, **180**, 125–134.

Gómez-Aparicio, L. (2004) *Papel de la heterogeneidad en la regeneración del* Acer opalus *subsp.* granatense *en la montaña mediterránea: implicaciones para la conservación y restauración de sus poblaciones*. PhD thesis. University of Granada, Granada, Spain.

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

Gómez-Aparicio, L., Zamora, R. & Gómez, J.M. (2005a) Regeneration status of the endangered *Acer opalus* subsp. *granatense* throughout its geographical distribution in the Iberian peninsula. *Biological Conservation*, **121**, 195–206.

Greenlee, J. & Callaway, R.M. (1996) Effects of abiotic stress on the relative importance of interference and facilitation in montane bunchgrass communities in western Montana. *American Naturalist*, **148**, 386–396.

Harper, J.L. (1977) *Population Biology of Plants*. Academic Press, London.

Harper, J.L., Clatworthy, J.N., McNaughton, I.H. & Sagar, G.R. (1961) The evolution of closely related species leaving in the same area. *Evolution*, **15**, 209–227.

Herrera, C.M. (2002) Topsoil properties and seedling recruitment: stage-dependence and spatial decoupling of influential parameters. *Oikos*, **97**, 260–270.

Herrera, C.M., Jordano, P., López-Soria, L. & Amat, J.A. (1994) Recruitment of a mast-fruiting, bird-dispersed tree: bridging frugivore activity and seedling establishment. *Ecological Monographs*, **64**, 315–344.

Houle, G. (1992) Spatial relationship between seed and seedling abundance and mortality in a deciduous forest of north-eastern North America. *Journal of Ecology*, **80**, 99–108.

Huenneke, L.F. & Sharitz, R.R. (1986) Microsite abundance and distribution of woody seedlings in a South Carolina cypress-tupelo swamp. *American Midland Naturalist*, **115**, 328–335.

Ibañez, I. & Schupp, E.W. (2001) Positive and negative interactions between environmental conditions affecting *Cercocarpus ledifolius* seedling survival. *Oecologia*, **129**, 543–550.

IUCN (2000) *IUCN Red List Categories*. IUCN, Gland.

Joffre, R. & Rambal, S. (1993) How tree cover influences the water balance of Mediterranean rangelands. *Ecology*, **74**, 570–882.

Kitajima, K. & Fenner, M. (2000) Ecology of seedling regeneration. *Seeds: the Ecology of Regeneration in Plant Communities*, 2nd edn (ed. M. Fenner), pp. 331–359. CAB International, Wallingford.

Kitzberger, T., Steinaker, D.F. & Veblen, T.T. (2000) Effects of climatic variability on facilitation of tree establishment in northern Patagonia. *Ecology*, **81**, 1914–1924.

Kobe, R.K., Pacala, S.W., Silander, J.A. & Canham, C.D. (1995) Juvenile tree survivorship as a component of shade tolerance. *Ecological Applications*, **5**, 517–532.

Kollmann, J. (2000) Dispersal of fleshy-fruited species: a matter of spatial scale? *Perspectives in Plant Ecology, Evolution and Systematics*, **3**, 29–51.

Kollmann, J. & Grubb, P.J. (1999) Recruitment of fleshy-fruited species under different shrub species: control by under-canopy environment. *Ecological Research*, **14**, 9–21.

Kotliar, N.B. & Wiens, J. (1990) Multiple scales of patchiness and patch structure: a hierarchical framework for the study of heterogeneity. *Oikos*, **59**, 253–260.

López-Gónzalez, G. (1994) *La Guía de Incafo de los Árboles y Arbustos de la Península Ibérica*. Editorial Incafo, Madrid, Spain.

Mack, R.N. & Pyke, D.A. (1983) The demography of *Bromus tectorum*: variation in time and space. *Journal of Ecology*, **71**, 69–93.

Molofsky, J. & Augspurger, C.K. (1992) The effect of leaf litter on early seedling establishment in a tropical forest. *Ecology*, **73**, 68–77.

Nathan, R., Safriel, U.N., Noy-Meir, I. & Schiller, G. (2000) Spatiotemporal variation in seed dispersal and recruitment near and far from *Pinus halepensis* trees. *Ecology*, **81**, 2156–2169.

Nicotra, A.B., Chazdon, R.L. & Iriate, S.V.B. (1999) Spatial heterogeneity of light and woody seedling regeneration in tropical wet forests. *Ecology*, **80**, 1908–1926.

Ostfeld, R.S. & Canham, C.D. (1993) Effects of meadow vole population density on tree seedling survival in old fields. *Ecology*, **74**, 1792–1801.

Packer, A. & Clay, K. (2000) Soil pathogens and spatial patterns of seedling mortality in a temperate tree. *Nature*, **404**, 278–281.

Rey, P.J. & Alcántara, J.M. (2000) Recruitment dynamics of a fleshy-fruited plant (*Olea europaea*): connecting patterns of seed dispersal to seedling establishment. *Journal of Ecology*, **88**, 622–633.

Rice, W.R. (1989) Analyzing tables of statistical tests. *Evolution*, **43**, 223–225.

Russo, S.E. & Augspurger, C.K. (2004) Aggregated seed dispersal by spider monkeys limits recruitment to clumped patterns in *Virola calophylla*. *Ecology Letters*, **7**, 1058–1067.

SAS Institute (2002) *SAS/STAT User's Guide*, Version 8.2. SAS Institute, Cary, North Carolina.

Schenk, H.J. & Mahall, B.E. (2002) Positive and negative plant interactions contribute to north–south–patterned association between two desert shrub species. *Oecologia*, **132**, 402–410.

Streng, D.R., Glitzenstein, J.S. & Harcombe, P.H. (1989) Woody seedling dynamics of an East Texas floodplain forest. *Ecological Monographs*, **59**, 177–204.

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

Traveset, A., Gulias, J., Riera, N. & Mus, M. (2003) Transition probabilities from pollinator to establishment in a rare deciduous shrub species (*Rhamnus ludovici-salvatoris*) in two habitats. *Journal of Ecology*, **91**, 427–437.

Turner, M.G., Gardner, R.H. & O'Neill, R.V. (2001) *Landscape Ecology in Theory and Practice*. Springer-Verlag, New York.

Verdú, M. & García-Fayos, P. (1996) Nucleation processes in a Mediterranean bird-dispersed plant. *Functional Ecology*, **10**, 275–280.

Vilá, M. & Lloret, F. (2000) Seed dynamics of the mast seeding tussock grass *Ampelodesmos mauritanica* in Mediterranean shrublands. *Journal of Ecology*, **88**, 479–491.

Zar, J.H. (1996) *Biostatistical Analysis*, 3rd edn. Prentice Hall, Englewood Cliffs, New Jersey.

Received 15 March 2005
revision accepted 18 May 2005
Handling Editor: Peter Klinkhamer