Research

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Spatiotemporal patterns of seed dispersal in a wind-dispersed Mediterranean tree (*Acer opalus* subsp. *granatense*): implications for regeneration

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Seed dispersal can severely limit the quantity of plant recruits and their spatial distribution. However, our understanding of the role of dispersal in regeneration dynamics is limited by the lack of knowledge of seed deposition patterns in space and time. In this paper, we analyse the spatiotemporal variability of seed dispersal patterns in the Mediterranean maple, *Acer opalus* subsp. *granatense*, by monitoring seed rain along two years at a broad spatial scale (2 mountain ranges, 2 populations per range, 4 microhabitats per population). We quantified seed limitation and its components (source and dispersal limitation), and explored dispersal limitation in space by analysing dispersal distances, seed aggregation, and microhabitat seed distribution. *Acer opalus* subsp. *granatense* was strongly seed-limited throughout the gradients explored, being always dispersal limitation much higher than source limitation. The distribution of seeds with distance from adult individuals was leptokurtic and right-skewed in all populations, being both kurtosis and skewness higher the year of the highest seed production. Dispersal distances were shorter than expected by random in the four populations, which suggests distance-limited dispersal. Dispersal patterns were highly aggregated and showed a preferential direction around adults. At the microhabitat scale, most seeds accumulated under adult maples. However, there were no more seeds under trees and shrubs other than maple than in open interspaces, implying that established vegetation does not disrupt patterns of seed deposition by physically trapping seeds. When compared with patterns of seedling establishment, limited dispersal ability and inter-annual spatial concordance in seed rain patterns suggest that several potentially safe sites for recruitment have a very low probability of receiving seeds in most maple populations. These findings are especially relevant for rare species such as *Acer opalus* subsp. *granatense*, and illustrate how dispersal studies are not only crucial for our understanding of plant population dynamics but also to provide conservation directions.

Seed dispersal plays a key role in the organization and dynamics of plant communities (Harper 1977, Venable and Brown 1993, Chambers and Macmahon 1994, Schupp and Fuentes 1995). The spatial pattern of dispersal will not only determine the distribution of a species, but also the environmental variability encountered by its seedlings and saplings and thus, ultimately, the probability of incorporation of new adults into the population (Gómez et al. 2004). Despite their relevance, the patterns of seed deposition were for a long time scarcely included in dispersal studies under the general assumption that seed dispersal does not limit recruitment. However, in 1995, Schupp and Fuentes explicitly highlighted the relevance of the spatial relation of dispersed seeds both to seed sources and among patches in the landscape. Since then, dispersal patterns have been analysed in several demographic studies as crucial for understanding plant regeneration dynamics (Jordano and Herrera 1995, Rey and Alcántara 2000, Gómez 2003, Hampe 2004).

Seed dispersal can limit regeneration if seeds are dispersed only to a fraction of suitable sites for recruitment (Primack and Miao 1992, Hurtt and Pacala 1995, Tilman 1997, Zobel et al. 2000). This phenomenon, called seed limitation, can be due to a limited number of seeds available (source limitation) or to low dispersal capacity (dispersal limitation; Clark et al. 1998). In addition, dispersal limitation can be caused when most seeds are distributed at short distances from the parent tree (limitation in distance), and/or in a spatially aggregated manner (limitation in space; Jordano and Godoy 2002). Seed shadows of zoochorous species seem to be more aggregated than those of wind-dispersed species, mainly due to non-random movements of dispersers (Godoy 2002, Jordano and Schupp et al. 2002, Gómez 2003). However, anemochorous species can also show highly heterogeneous seed rain for reasons such as the aggregation of seed sources in space (Muller-Landau et al. 2002) or the occurrence of prevailing wind directions (Stewart et al. 1998, Bullock and Clarke 2000). Microhabitat patchiness can also play a major role in generating heterogeneous patterns of seed arrival, although it has frequently been ignored especially for wind-dispersed species. Given the capacity of the vegetation to act as barriers to primary dispersal (Nathan et al. 2002), more seeds should be expected to reach covered microhabitats than open spaces (Bullock and Moy 2004), which in turn could have relevant demographic effects (e.g. seed-seedling conflicts, Schupp 1995) if subsequent recruitment phases are also microhabitat-dependent (Nathan and Muller-Landau 2000).

Dispersal limitation can undergo substantial inter-annual variation (Houle 1998), mainly as a consequence of differences in seed production. It has been shown that in years of high production maximum dispersal distances increase due to a greater probability for at least one seed landing farther than usual (Dirzo and Domínguez 1986) or because of a trade-off between seed size and number, resulting in the production of lighter seeds with greater flying capacity (Clark et al. 1998). In addition, seed aggregation can also be influenced by annual reproduction patterns, spatial homogeneity increasing with the number of reproductive individuals (Houle 1998).

Overall, due to the strong spatiotemporal variability in seed dispersal patterns, to know the extent to which they can limit regeneration requires the analysis of dispersal processes in different locations and years. However, such analyses have rarely been made (Clark et al. 1999, Nathan and Muller-Landau 2000, Hampe 2004). The main goal of this study is to analyse the spatiotemporal variability of seed dispersal patterns in the Mediterranean wind-dispersed tree, *Acer opalus* subsp. *granatense*. We monitored abundance and spatial distribution of seeds over two years (2001 and 2002) and across a broad spatial scale (2 mountain ranges, 2 populations per range, 4 microhabitats per population). Specifically, our objectives were to: 1) quantify seed limitation and its components (source and dispersal limitation) 2) explore dispersal limitation with distance and in space, and 3) determine the spatiotemporal congruence of seed dispersal patterns and its implications for natural regeneration at the local scale. We consider that understanding the relative importance of source and dispersal limitations as well as the spatial patterns of seed dispersal relative to favourable microsites is essential to assess conservation status and planning restoration efforts for threatened or rare species such as *Acer opalus* subps. *granatense*.

Material and methods

Study species

Mediterranean maple *Acer opalus* subsp. *granatense* is an Iberian-Mauritanian endemic deciduous tree catalogued as Vulnerable by the IUCN (Anon. 2000) and included in the Red List of threatened vascular plants of Andalusia (Blanca et al. 2000). Maple has undergone reductions in number and size of populations in recent decades due to human disturbance (e.g. tree felling, deforestation, over-grazing; Blanca et al. 1998). Currently its distribution is composed of many small patches scattered throughout medium and high mountains (1100–2000 m a.s.l.) in the SE Iberian Peninsula, Balearic Islands and north Morocco (López-González 1994). Maple is a small tree, adults rarely surpassing 7–8 m in height. Individuals of this species are usually intermingled with Mediterranean evergreens such as *Pinus sylvestris*, *Pinus nigra*, or *Quercus ilex*. Populations are sexually polymorphic, composed of 50% of protogynous trees, the other 50% comprising males and protandrous (G. Gleiser pers. comm.). Since seed production in protandrous individuals is very low, ca 50% of the maple adults can be considered to contribute to the seed pool in each population (seeding adults, hereafter). The indehiscent fruits are composed of two samaras with convergent wings, each weighting ca 20–50 mg. Parthenocarpic development of fruits is rather common (de Jong 1976), especially in years of low seed production (Gómez-Aparicio unpubl.). Dispersal occurs between September and December.

Study areas

The study was conducted in two mountain ranges of SE Spain, Sierra Nevada (SN) and Sierra de Baza (SB), situated ca 80 km apart. The climate in the zone is continental Mediterranean, with cold winters and hot, dry summers. Rainfall averages 846.5 ± 55.7 mm yr^{-1} in SN and 527.4 ± 40.9 mm yr^{-1} in SB (mean 1991–2002), with most of the precipitation falling in autumn and spring. Two maple populations were chosen per mountain range, one intermingled within a *Pinus*

Table 1. Summary of the main characteristics of the four study populations of *Acer opalus* subsp. *granatense*. Adult density and height were sampled using 25 × 10 m transects (n = 10) haphazardly distributed in a representative area of each population 1-ha in size. Seed mass was calculated from seeds collected in traps during autumn 2002. Mean ± 1SE [minimum-maximum] are shown.

	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
Adult density (no. ha^{-1})	17.2 ± 6.5	80.2 ± 12.2	111.5 ± 18.8	61.1 ± 10.9
Adult height (m)	7.1 ± 0.3 [6.0–8.0]	4.5 ± 0.2 [2.5–6.0]	3.5 ± 0.2 [2.0–4.5]	5.5 ± 0.3 [3.0–8.0]
Seed mass (mg)	22.1 ± 0.4 [20.4–35.8]	20.2 ± 0.9 [19.1–44.8]	21.7 ± 1.1 [18.9–35.3]	26.9 ± 0.6 [23.9–39.6]

sylvestris forest (forest population [F], hereafter) and another on a stony slope (stony-slope population [SL], hereafter). Density of adult maples in these populations ranged between 17 and 111 individuals m^{-2}, mean adult height varied between 3.5 and 7.1 m, and mean seed mass varied between 20 and 27 mg (Table 1). We defined four microhabitats per population: 1) "Maple", under the canopy of adult maples; 2) "Canopy", under the canopy of heterospecific adult trees and shrubs > 1.5 m in height (1–2 species per population); 3) "Shrub", under the canopy of shrubs < 1.5 m in height (1–3 species per population); and 4) "Open", in open interspaces between woody vegetation. Tree and shrub species were chosen according to their availability. The Canopy microhabitat included *Pinus sylvestris* and *Taxus baccata* in F-SN, *Amelanchier ovalis* in SL-SN, and *P. sylvestris* in F-SB and SL-SB. The Shrub microhabitat included *Ononis aragonensis, Juniperus communis* and *Berberis hispanica* in F-SN, *O. aragonensis* in SL-SN, *Prunus ramburii* and *Crataegus monogyna* in F-SB, and *J. communis* and *B. hispanica* in SL-SB.

Seed rain sampling

Seed rain of *A. opalus* subsp. *granatense* was quantified during two consecutive years (2001 and 2002) by placing seed traps (0.045 m^2 aluminium trays) in a 1-ha study area per population. Traps were located randomly (and consequently without any reference adult), implying that sampling effort was not equitably distributed among distance ranges but, as strongly recommended by Willson (1993), proportional to their abundance in each population (median distance to the nearest seeding adult [Q25%–Q75%]: 8.5 m [4.8–12.7] in F-SN; 6.7 m [4.1–10.6] in SL-SN; 6.0 m [3.9–10.3] in F-SB; and 8.0 m [5.1–11.9] in SL-SB). Traps were placed at 30 points per microhabitat and population, each point containing 2 adjacent traps. In Canopy and Shrub microhabitats, sampling points were replicated for each species. The total number of traps was 420 in F-SN, 240 in SL-SN, 300 in F-SB and 300 in SL-SB (n = 1260 traps). The distance distribution of traps did not differ between the Canopy, Shrub and Open microhabitats ($p > 0.05$ in all cases, Kolmogorov-Smirnoff tests), implying that the different microhabitats were similarly distributed in relation to adult maples. Traps were covered with 1.3-cm diameter mesh in order to avoid post-dispersal predation. This mesh size has been shown to effectively restrict predators in seed predation experiments conducted in the four study sites (Gómez-Aparicio 2004). Traps were sampled fortnightly during the dispersal period (September–December), and their content transported to the laboratory, where seeds were individually weighed.

Since the number of seeds found in a trap depends both on its position in relation to the sources and on the amount of seed production, we calculated a seed availability index (SAI) for each trap (see Russell and Schupp 1998 for a similar approach). By using this index as a covariate, we can discern the role of the microhabitat in determining spatial patterns of dispersal regardless of its location. Thus, for each trap, we recorded the distance and orientation to the five nearest maples. Seed production for each adult was quantified in a semi-quantitative scale from 0 (no production) to 5 (very high production). SAI was calculated for each trap as:

$$\mathrm{SAI} = \sum_{i=1}^{5} \frac{p_i}{d_i}$$

where p is the seed production for each of the 5 nearest adult maples, and d its distance to the trap. This index is considered to represent the true relevance of being near maples, since factor 1 (distance to the nearest adult) explained 70% of the variability in the index, factor 2, 3, 4 and 5 explaining 19, 7, 3, and 1%, respectively (averages for the four populations).

Data analysis

Analysis of seed limitation and its components: source limitation and dispersal limitation

For each population, we quantified seed limitation and its components (source limitation and dispersal limitation) at the 0.09 m^2 spatial scale (pair of seed traps per sampling point). Seed limitation is defined as the proportion of empty traps over the time period: source limitation as the expected proportion of empty traps if seeds were uniformly distributed across space (uniform distribution defined stochastically as a random distribution); and dispersal limitation as the proportion of sampling points that received seeds in relation to sampling points that would receive them if seeds were randomly distributed (Clark et al. 1998, Nathan and Muller-Landau 2000). By using this approach, we assessed seed limitation in maple populations by describing spatial variation in natural seed rain patterns, an alternative to experimental manipulations. Therefore, seed limitation calculated in this way refers to "fundamental" and not "realized" seed limitation, assuming optimal conditions for seedling emergence. However, this method provides accurate information concerning the role of dispersal patterns in regeneration (Dalling et al. 2002, Muller-Landau et al. 2002), and enables the monitoring of a wider area, which is especially useful for studies covering several populations, as in the present study. Limitation measurements were calculated for every year (2001 and 2002), at the 1-yr scale (average of both years) and at the 2-yr scale (considering the total fallen seeds in both years). Limitation values range from 0 (no limitation) to 1 (maximum limitation).

Analysis of dispersal limitation in distance and space

The distribution of seed density with distance to the nearest seeding maple was described by 6 parameters: kurtosis, skewness, mean, median, mode and maximum. For each study year, differences among populations in the 6 parameters were analysed using Welch t-tests (Zar 1996). To explore any effect of distance on dispersal limitation, the density of seeds collected in the different distance classes during the 2 yr of the study was compared to the density expected in each class if seeds were dispersed at random, the latter being approximated as the density of seed traps per distance interval. Since the nearest reproductive individual was assumed as the seed source, dispersal distances reported in this study are not "real" but "conservative" distances of dispersal, a proportion of the seeds probably coming from a more distant adult.

Aggregation of seeds in space was analysed using Morisita's index of dispersion (Morisita 1959), calculated for each population at the sampling point (i.e. pair of traps) level. Deviations from random distributions were analysed by χ^2 tests with q-1 degrees of freedom (Greig-Smith 1983). We also determined the directionality of seeds around adult maples by using circular statistics (Oriana 2.0, Kovach Computing Services). Since the angular distribution of seeds depends partially on the position of traps, we first explored whether trap location follows a regular distribution in the circular space (or von Mises distribution) by using Rayleigh tests (Batschelet 1981). Values were not significant for any population ($p > 0.05$ in the four cases), showing that traps were uniformly distributed around maple adults and that therefore sampling effort was not biased towards any specific direction around adults. Consequently, we also applied Rayleigh tests to analyse whether seeds were distributed uniformly around maple adults. Finally, Watson's F tests (Batschelet 1981) were used to compare the distribution of the seeds around maple adults in the two years of the study.

The role of the microhabitat in determining spatial patterns of dispersal was analysed by using Generalized lineal mixed models (Proc MIXED, Anon. 2002), using the maximum likelihood as estimation method (Stokes et al. 1995). For each population, total seed number recorded per sampling point was adjusted to a Poisson distribution, using Log as link function. Microhabitat was introduced as a fixed factor and year as a random. The seed availability index (SAI) was introduced as a continuous predictor. Differences among microhabitats were explored with post-hoc Bonferroni tests. To control for the experiment wise type I error produced by multiple comparisons, we adjusted the probabilities of error to $\alpha = 0.05$ by using the sequential Bonferroni technique (Rice 1989).

Results

Analysis of seed limitation and its components: source limitation and dispersal limitation

The four populations registered high values of seed limitation (0.63–1) in the two years of study (Table 2). Seed limitation decreased from 2001 to 2002 in all populations, matching an increase in seed density. However, this inter-annual difference affected mostly the shorter distance classes, as seed limitation in all cases was $\geq$ 0.90 at 6–8 m from the nearest seeding maple (Fig. 1). Seed limitation was lower when calculated at the 2-yr scale (0.60–0.80) than at the 1-yr scale (0.74–0.90). The magnitude of source limitation in all populations was much lower than the magnitude of dispersal limitation, especially at the 2-yr scale, when seed limitation was due almost entirely to dispersal limitation (Table 2).

Table 2. Seed density (seeds m^{-2}; mean ± 1SE) and limitation measurements at the sampling point spatial scale (0.09 m^2) for the four study populations of *Acer opalus* subsp. *granatense*. Values were calculated for each year independently, as well as at the 1-yr (mean ± 1SE of the 2 yr) and 2-yr (sum of the 2 yr) scale. Limitation values were between 0 (no limitation) and 1 (maximum limitation).

Population	Measure	Time scale			
		2001	2002	1-yr	2-yr
Sierra Nevada					
Forest	Seed density	0	34.18±10.95	17.1±5.51	34.07±10.92
	Seed limitation	1	0.80	0.90±0.10	0.80
	Source limitation	1	0.04	0.52±0.48	0.04
	Dispersal limitation	‡	0.80	‡	0.80
Stony-slope	Seed density	8.11±4.42	22.42±6.81	15.2±4.12	30.46±9.23
	Seed limitation	0.91	0.69	0.80±0.11	0.67
	Source limitation	0.48	0.13	0.30±0.17	0.06
	Dispersal limitation	0.82	0.64	0.73±0.09	0.65
Sierra de Baza					
Forest	Seed density	11.32±4.21	15.57±3.82	13.4±2.85	28.59±7.99
	Seed limitation	0.79	0.71	0.75±0.04	0.64
	Source limitation	0.33	0.27	0.30±0.03	0.01
	Dispersal limitation	0.68	0.63	0.65±0.02	0.63
Stony-slope	Seed density	10.35±4.93	33.36±8.33	21.8±4.94	43.63±11.45
	Seed limitation	0.85	0.63	0.74±0.11	0.60
	Source limitation	0.39	0.05	0.22±0.17	0.02
	Dispersal limitation	0.74	0.60	0.67±0.07	0.59

‡Note: since no seeds were produced in the forest population of Sierra Nevada in 2001, seed and source limitation were given the maximum value (1), and thereby dispersal limitation could not be calculated.

Analysis of dispersal limitation in distance and space

The distribution of seeds with distance to the nearest seeding tree was leptokurtic and right-skewed in all populations, both leptokurtosis and skewness increasing in the second year of study (Fig. 2). Although there were differences among populations and years, in all cases the mean ranged between 2 and 4 m, the median was <4 m, the mode was ca 2 m, and the maximum observed distances ranged 7–12.5 m. The observed distribution of seeds per distance class significantly differed from the distribution expected if seeds were dispersed at random ($p < 0.05$ in the four populations, Kolmogorov-Smirnoff tests), the observed median distances being in all cases much shorter than expected (3.5 vs 8.5 m in F-SN; 2.1 vs 6.7 m in SL-SN; 2.5 vs 6.0 m in F-SB; and 3.2 vs 8.0 m in SL-SB). Seed mass was not related to dispersal distance in any population ($p > 0.05$ in all cases, Spearman rank correlations).

Seeds showed a significant spatial aggregation in all populations and years (Table 3), which was generally higher in 2001. The density of seeds around adult maple trees differed significantly from uniformity in 6 of the 7 combinations of population and year explored ($p < 0.05$, Rayleigh tests; Table 3). There was no inter-annual difference in seed distribution around parent maples in any of the populations ($p > 0.05$, Watson tests).

Microhabitat identity did significantly affect seed density in all populations, even after introducing the seed availability index (SAI) as a continuous predictor (Table 4). In all populations and years, seed deposition was much higher under Maple than in any other microhabitat (67% of the seeds trapped). Shrub and Open showed similar values in all cases, whereas Canopy presented the lowest seed density (Fig. 3). The inter-annual variation in seed density was not the same for all microhabitats, as indicated by significant microhabitat × year interactions in the four populations (Table 4). Thus, although seed density was higher in 2002 than in 2001 in all microhabitats, the increase was comparatively higher under Maple and generally lower under Canopy.

Discussion

Seed limitation, source limitation and dispersal limitation

Acer opalus subsp. *granatense* was strongly seed-limited throughout the spatiotemporal gradient explored. Seed limitation at the 1-yr scale ranged 0.74–0.90 in all populations, despite their differences in two key characteristics influencing the values of the index, adult height (which indirectly influences seed production) and abundance (Muller-Landau et al. 2002). When compared with other populations throughout

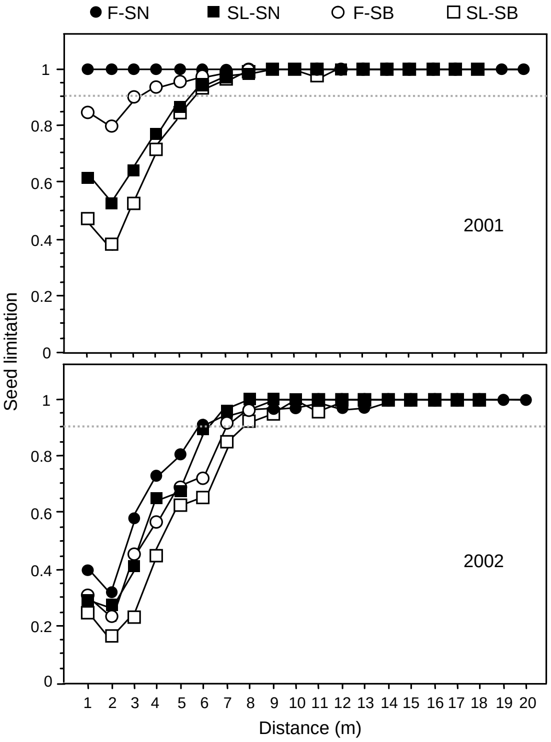

Fig. 1. Variation in seed limitation with distance (in m) to the canopy edge of the nearest seeding maple for each population and year of study. Seed limitation is calculated as the proportion of sampling points not receiving seeds in the time period. Sampling points were classified in 18 distance classes (20 for the forest population in Sierra Nevada) of 1 m. The grey line indicates the position of the value 0.9 of seed limitation. F, forest population; SL, stony-slope population; SN, Sierra Nevada; SB, Sierra de Baza.

the range of the species in the Iberian Peninsula, our four populations covered the whole range of possibilities for both adult size and density (Gómez-Aparicio 2004). Therefore, seed limitation at the 1-yr scale could be considered as a general pattern in maple populations across broad spatial scales. In addition, we did not detect any strong reduction in seed limitation calculated at the 2-yr scale. Thus, although our temporal scale was not long enough to rule out possible limitation changes over the long term (Muller-Landau et al. 2002), our results suggest that maple populations in Mediterranean mountains undergo high seed limitation at least over the short term, as reported for other tree species in tropical (Harms et al. 2000, Muller-Landau et al. 2002) and temperate forests (Clark et al. 1998).

The relative contribution of the two components of seed limitation (source and dispersal limitation, sensu Clark et al. 1998) showed a high spatiotemporal congruence, with source limitation being consistently much lower than dispersal limitation. Source limitation decreased in 2002 due to a higher seed production. Consequently, when calculated at the 2-yr scale, seed limitation was almost entirely due to dispersal limitation, as in other *Acer* species (Clark et al. 1998).

Dispersal limitation in distance and space

Dispersal distances were shorter than expected according to a random distribution in the four populations, which suggests the existence of limitation in distance even at high densities of conspecific trees (>100 individuals ha^{-1}). In fact, 50% of the seeds dispersed were located <4 m from the nearest seeding tree, and no seeds were found beyond 13 m. Moreover, maximum dispersal distances did not differ in our two years, despite the variation in seed production and the fact that an increase in seed number is an important parameter for enlarging seed shadows (Dirzo and Domínguez 1986, Tanaka et al. 1998). Two main factors that generally affect dispersal in anemochorous species could constrain the dispersal distance of the species, source height and seed mass (Augspurger and Franson 1987, Thiede and Augspurger 1996, Nathan et al. 2001). The small size of maple trees restricts the horizontal reach of seeds (Cousens and Rawlinson 2001, Nathan et al. 2002). In fact, differences of adult height in our populations likely influenced dispersal distances, since the two populations with the tallest maples (forest population in Sierra Nevada and stony-slope population in Sierra de Baza) presented maximum dispersal distances as much as 5 m longer (i.e. 30–40% of the overall dispersal distance) than the two populations including shorter adults. On the other hand, the mass of maple seeds ranged between 20 and 40 mg, being much heavier than seeds of most co-occurring wind-dispersed trees such as *Pinus nigra* or *Pinus sylvestris* (e.g. 5–12 mg for *P. sylvestris* in Castro 1999). Moreover, the range of mass variation of maple seeds did not appear to be big enough to influence dispersal distances, since lighter seeds did not travel farther (Augspurger and Franson 1987).

Morisita indices showed aggregated dispersal patterns in all four maple populations. This high heterogeneity in seed shadow may be a consequence of a large fraction of seeds falling near parent trees (Venable and Brown 1993), but also implies that those that travelled farther were deposited in clumps. The formation of such clumps could be influenced by directional dispersal related to local wind regimes, because most seed concentrated in specific orientations in relation to adults. Moreover, >50% of the traps that received seeds in 2001 also did it in 2002, suggesting a high degree of inter-annual concordance in seed rain patterns

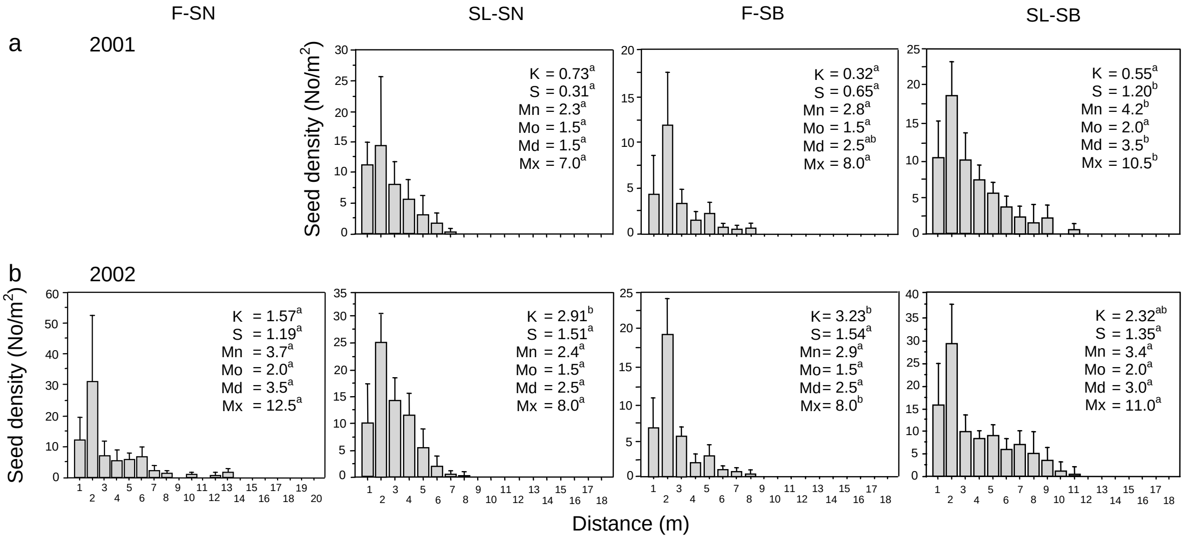

Fig. 2. Average seed density (mean ± 1SE) as a function of distance (in m) from the canopy edge of the nearest seeding adult in (a) 2001 and (b) 2002. For each population and year, characteristics of the shape and central tendencies of the dispersal distributions are given (K, kurtosis; S, skewness; Mn, mean; Mo, mode, Md, median, Mx, maxima). Different letters show statistical differences among populations (within the same year) after Welch t-tests. No seeds were produced in the forest population of Sierra Nevada in 2001. Letter codes same as Fig. 1.

($p < 0.05$ in the four populations, Kendall correlations), a result that in turn has being rarely reported for wind-dispersed species (Houle 1998, Nathan et al. 2000, Jones et al. 2005).

Seed deposition patterns were significantly affected by microhabitat. However, this influence was restricted basically to Maple, which consistently showed much higher seed density than any other microhabitat. Contrary to our expectations of higher seed arrival to covered microhabitats (Canopy and Shrubs) than to the Open microhabitat, the magnitude of seed dispersal did not differ among the three microhabitats. These findings agree with those reported by Russell and Schupp (1998) for *Cercocarpus ledifolius,* and Castro et al. (1999) for *Pinus sylvestris*, but differ with several reports that reached the opposite conclusion (Fuentes et al. 1984, McEvoy and Cox 1987, Thiede and Augspurger 1996, Bullock and Moy 2004). Therefore, seed trapping seems to be highly dependent on the species and system considered.

Table 3. Description of seed aggregation patterns in the two study years. Values of the Morisita's index of dispersion significantly higher than 0 indicate aggregated patterns, whereas values non-significantly different from 0 indicate a regular distribution. Mean angle (in degrees) represents the prevailing dispersal direction around adult maples. Concentration represents the deviation of the seed distribution around adult maples from a uniform distribution in the circular space (or von Mises distribution), and was evaluated with Rayleigh tests.

Year	Population	Morisita index	Angular distribution	
			Mean angle (±1SE)	Concentration
2001	Sierra Nevada			
	Stony-slope	35.51****	216.25±4.28	5.12****
	Sierra de Baza			
	Forest	18.10****	359.92±10.01	1.05****
	Stony-slope	34.73****	274.82±20.38	1.02*
2002	Sierra Nevada			
	Forest	22.17****	327.13±3.90	1.58****
	Stony-slope	11.69****	223.39±20.95	0.59*
	Sierra de Baza			
	Forest	10.74****	54.56±18.12	0.51**
	Stony-slope	9.99****	226.91±80.18	0.08

**** $p < 0.0001$, *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$.

Table 4. Summary of the Generalized lineal mixed model analysing differences among microhabitats in the four populations and during the two years of study. SAI (seed availability index) was introduced as a continuous predictor.

Population	Factor	DF	L-R χ^2	p
Sierra Nevada				
Forest	Microhabitat	3	21.38	<0.0001
	Year	1	96.25	<0.0001
	Microhabitat × year	3	20.09	0.0002
	SAI	1	1177.64	<0.0001
Stony-slope	Microhabitat	3	23.98	<0.0001
	Year	1	6.34	0.012
	Microhabitat × year	3	8.74	0.033
	SAI	1	325.53	<0.0001
Sierra de Baza				
Forest	Microhabitat	3	11.45	0.009
	Year	1	0.99	0.326
	Microhabitat × year	3	9.56	0.023
	SAI	1	314.26	<0.0001
Stony-slope	Microhabitat	3	17.47	0.0005
	Year	1	19.99	<0.0001
	Microhabitat × year	3	37.98	<0.0001
	SAI	1	556.20	<0.0001

Implications for regeneration

A direct consequence of limited dispersal ability of maple seeds is that they are unable to explore larger fractions of the landscape. Dispersal kernels were leptokurtic and right-skewed, especially in the year of highest seed production, seed limitation being above 0.9 just at around 7 m from the nearest seeding adult maple in all populations and years. Maple early recruitment has been reported to be highly dependent on the microhabitat, seedling and sapling survival being much higher under pre-established woody vegetation than in open interspaces (Gómez-Aparicio et al. 2005). Thus, the fact that the 50% of the seed traps randomly located under trees and shrubs were beyond 7 m from any adult maple implies that several suitable microhabitats for regeneration have low probabilities of receiving seeds. Furthermore, this pattern seems to be temporally stable, since the 2002 increase in seed availability decreased seed limitation but only at short distances (<6–8 m). This finding suggests that, in the long term, seed limitation could be expected to reach a minimum once seeds have saturated the space near maples whereas many safe sites remain empty because they are too far away (Schupp et al. 2002).

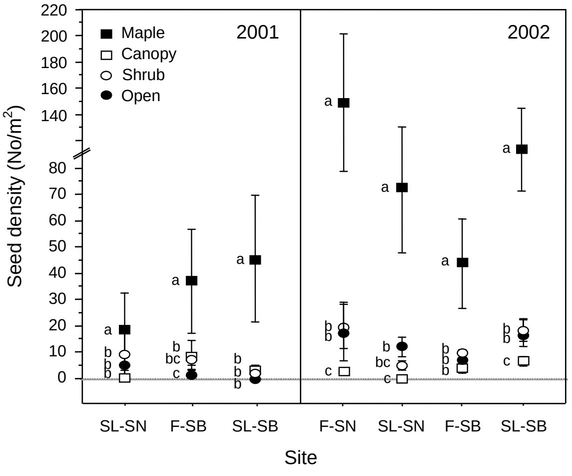

Fig. 3. Differences between microhabitats in seed density (mean ± 1SE) in the two years of study. Different letters show significant differences among microhabitats within populations at $\alpha < 0.05$ (after Bonferroni correction). Letter codes same as Fig. 1. No seeds were produced in the forest population of Sierra Nevada in 2001.

The fact that seed deposition was highly aggregated and spatially concordant over the years implies that even near maples seeds will land in the same microsites every year, reducing the number of sites colonized. Secondary seed dispersal could attenuate this aggregation by redistributing seeds, but it does not appear to substantially alter primary dispersal patterns, since emerging seedlings are highly aggregated around adults (Gómez-Aparicio 2004). Aggregated patterns of seed deposition could cascade through later demographic stages giving rise to intra-specific competition (Levin et al. 1984, Augspurger and Kitajima 1992, Hurtt and Pacala 1995), not only between individuals of the same cohort, but also of different cohorts.

The results presented here show that the variation in maple seed deposition patterns did not preclude seed and dispersal limitation throughout the spatiotemporal scope of the study. This is especially relevant for rare species such as *Acer opalus* subsp. *granatense*, since seed limitation slows down rates of abundance change

(Muller-Landau et al. 2002), presumably hampering the recovery of its past distribution. In these scenarios, protection of remaining reproductive individuals and the introduction of propagules in distant, high-quality, unoccupied microhabitats could counterbalance the negative consequences of restricted dispersal patterns for maple regeneration. This way, seed dispersal analyses become not only crucial for understanding plant population dynamics, but also for the conservation and restoration of natural populations of species that suffer from seed limitation (Eriksson and Ehrlen 1992, Primack and Miao 1992, Bullock et al. 2002, Turnbull et al. 2000, Makana and Thomas 2004).

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