Topsoil properties and seedling recruitment in *Lavandula latifolia*: stage-dependence and spatial decoupling of influential parameters

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This paper investigates the influence of topsoil texture and chemistry on long-term patterns of seedling recruitment in *Lavandula latifolia* (Labiatae), an evergreen Mediterranean shrub. The questions addressed are: (1) Are spatial patterns of seedling emergence and survival probabilities related to spatial variation in soil properties? (2) Are the two components of recruitment similarly influenced by the same soil parameters or, alternatively, are they influenced in different ways and/or by different soil parameters? (3) If the latter applies, then do the sets of soil parameters influencing emergence and survival show congruent patterns of spatial variation? Seed progenies from fourteen maternal families were sown at ten widely spaced field sites (between-site distances in the scale of a few kilometers). Sites differed in average soil characteristics. There was also considerable variation in some soil parameters within sowing sites (distances between soil sampling points in the scale of meters). The seedling recruitment process was monitored for six years. Both the probability of one seed of *L. latifolia* giving rise to an emerged seedling, and the probability of an emerged seedling remaining alive six years past emergence and entering the juvenile age class, were significantly related to topsoil properties. Seedling emergence and survival tended to be influenced by largely non-overlapping sets of soil properties that were related, respectively, to texture- and fertility-related gradients. These two soil gradients tended to be uncorrelated at the scale of the study, and differed in the apportionment of variance among small (within sites) and large (between sites) spatial scales. While most variance in the emergence-influencing, texture-related gradient occurred at the between-site scale, a considerably greater fraction of variance in the survival-influencing, fertility-related gradient occurred at the within-site scale. It is suggested that, because of fine scale variability in soil fertility, local adaptations of *L. latifolia* to soil textural properties enhancing seedling emergence will be easier to evolve than adaptations to fertility-related features enhancing seedling survival.

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"Since soils too differ widely we must also speak of them, for these too come under the head of nature"

Theophrastus (372–288 B.C.)

The dynamics of natural plant populations depend critically on spatial and temporal patterns of recruitment (Harper 1977). These patterns, in turn, result from the combination of patterns of arrival and survival of seeds, seedling emergence, and seedling survival (Schupp et al. 1989, Eriksson and Ehrlén 1992, Houle 1992, 1998, Herrera et al. 1994, Schupp 1995). While patterns of arrival are determined basically by the mechanisms of seed dispersal, those related to subsequent stages depend on an intricate combination of biotic and abiotic factors operating at the seed landing site. The complexity and multifariousness of the interactions involved, and their important implications for the persistence of plant populations, justify the considerable effort devoted by plant ecologists to elucidating the ecological correlates and

population consequences of spatio-temporal patterns in postdispersal seed survival, seedling emergence, and seedling establishment. Among biotic factors, spatial variation in the incidence of seed predators (Díaz 1992, Molofsky and Fisher 1993, Hulme 1997, Hammond et al. 1999), pathogens (Augspurger 1984, De Nooij 1987, Packer and Clay 2000), herbivores (Núñez-Farfán and Dirzo 1988), overlying plant cover (Maguire and Forman 1983, Tremlett et al. 1984, Herrera et al. 1994), and intra and interspecific competition (Sacchi and Price 1992, Shabel and Peart 1994, McMurray et al. 1997, Gordon and Rice 2000), have been most frequently investigated as causal agents of spatial patterns of postdispersal seed survival and seedling recruitment. Studies considering the influence of abiotic factors, on the other hand, have most often focused on spatial variation in light regime (Burton and Mueller-Dombois 1984, Ustin et al. 1984, Sork 1987, MacDougall and Kellman 1992, Valverde and Silvertown 1995), soil moisture levels (Harrington 1991, Sacchi and Price 1992), amount of litter (Fowler 1988, Molofsky and Augspurger 1992, Eriksson 1995), and soil surface characteristics (Chambers et al. 1991). In view of the extensive attention received in the ecological literature by the array of factors that influence spatial patterns of seedling recruitment in wild plant populations, it is remarkable that the possible role of spatial variation in physical and chemical soil characteristics remains comparatively unexplored (but see, however, Horvitz and Schemske 1986, Chambers et al. 1991, Eriksson 1995, Walters and Reich 1997, Stratton and Bennington 1998). A number of field studies have focused on the effect of "soil" on seedling recruitment (Battaglia and Reid 1993, Schupp 1995, Godínez-Alvarez and Valiente-Banuet 1998), but these have most often classified soils into discrete qualitative categories, rather than actually measuring soil properties (e.g., chemistry, texture).

The relative neglect in the ecological literature of topsoil properties as possible causal agents of spatial patterns of recruitment in natural plant populations is striking in the light of the following two considerations. First, the soil science and ecological literature are replete with documentation demonstrating that physical and chemical topsoil parameters are strongly patterned at spatial scales directly relevant to the recruitment process, ranging from the habitat level down to the microsite scale at distances of only a few meters or even centimeters (Beckett and Webster 1971, Blyth and MacLeod 1978, Nortcliff 1978, Arp and Krause 1984, Webster 1985, Robertson et al. 1988, Boerner and Koslowsky 1989, Bringmark 1989, Boettcher and Kalisz 1990, Grigal et al. 1991, Bell et al. 1993, Pelletier et al. 1999; among many others). Even in cultivated fields which are actively managed to reduce soil heterogeneity, up to half of the variance in soil parameters may already be present within any square meter of the field (Beckett and Webster 1971, Webster and Butler 1976). And second, the importance of topsoil properties for seedling emergence, establishment and growth, long known to farmers and stressed by Theophrastus more than two thousand years ago, is firmly established in both the agronomical and silvicultural literature (Cook et al. 1995, Cussans et al. 1996, Minotta and Pinzauti 1996, Misra and Gibbons 1996, Roldán et al. 1996, Townend et al. 1996, Jones and Rees 1997, Walters and Reich 1997, Pabin et al. 1998; among many others). The pervasiveness of spatial variability of physical and chemical soil parameters at a broad range of spatial scales, coupled with their influence on seedling emergence and survival, are expected to influence spatial patterns of seedling recruitment in natural plant populations in ways independent of the influence of those biotic and abiotic factors customarily considered in ecological studies. In a certain sense, therefore, soil-generated spatial patterns of recruitment may be seen as the initial templates over which other biotic and abiotic factors would subsequently act as modifiers.

In this paper, results of a long-term field experiment are used to evaluate the potential influence of topsoil texture and chemistry on patterns of seedling recruitment in *Lavandula latifolia* (Labiatae), a Mediterranean evergreen shrub. By concurrently measuring soil properties and seedling recruitment at two contrasting spatial scales, and decomposing the recruitment process into short-term seedling emergence and long-term seedling survival stages, the following questions will be addressed: (1) Are spatial patterns of seedling emergence and survival probabilities on a per seed basis influenced by spatial patterning of top soil properties? (2) Are the two components of recruitment similarly influenced by the same soil parameters or, alternatively, are they influenced in different ways and/or by different soil parameters? (3) If the latter applies, then do the sets of soil parameters influencing emergence and survival show congruent patterns of spatial variation? Most of the seedling recruitment data used in this paper were analyzed in detail by Herrera (2000) in an investigation that focused exclusively on aspects related to maternal differences in progeny viability and its components. The present paper addresses the soil correlates of spatial variation in recruitment, an aspect which was not considered in that earlier publication.

Methods

This study was conducted during 1992–1998 in the Sierra de Cazorla, an extensive mountain area in Jaén province, southeastern Spain. Mature seeds were collected in September–October 1992 from 14 *L. latifolia* shrubs at a population growing around the intersection of Arroyo Aguaderillos and the track joining Rob-

lehondo and Hoyos de Muñoz, in the Reserva de Navahondona-Guadahornillos. In January 1993, seeds were sown at ten broadly spaced localities in the same general area as the seed collecting site and differing in habitat type and elevation. The two most distant localities were 8.5 km apart, and the two closest ones only 150 m apart, and they were located in evergreen oak forest and scrubland, oak-pine mixed forest, and montane pine forest (see Herrera 2000: Table 1, for further details on localities). When selecting the experimental sites, I deliberately avoided those with established *L. latifolia* populations to minimize possible interferences from a pre-existing seed bank. Nevertheless, wild plants of *L. latifolia* did exist within 350 m or less of all experimental sites, thus corroborating the suitability of general environmental conditions for the persistence of this species.

At each locality, twenty-eight (14 maternal parents × 2 replicates) 30 × 30 cm plots ("quadrats" hereafter) were set over a surface of roughly 50 m², and randomly assigned to maternal parents. Contiguous quadrats were 15–30 cm away, and the most distant quadrats in a site were 4–7 m apart. Each quadrat received 100 seeds from a single maternal parent, which were distributed as homogeneously as possible over the soil surface. Prior to sowing, litter and coarse woody debris were removed by hand from all the quadrats to eliminate the possible influence of variation among localities and quadrats in litter depth. To initially hold seeds in place and protect them from seed predators, each quadrat was covered with a piece of dense fiberglass net which was tightly affixed to the ground with nails. Nets were removed three months later, when seedlings started to emerge. None of the nets showed any sign of damage by rodents at the time of removal. This fact, and the observation that granivorous ants were not active at any site in the period from sowing to the end of seedling emergence, made me confident that there were no pre-germination seed losses to seed predators. The number of seeds from some maternal parents was insufficient to fulfill the design, and one or the two replicates for these individuals were missing from some of the sites. Furthermore, seedling emergence was negligible at one of the sites (site AT, Herrera 2000: Table 1), where < 4% of sown seeds emerged (in contrast to 12–54% at other localities) and the few resulting seedlings died during the first summer after emergence. Seedling data from this site have been excluded from all the analyses of seedling emergence and survival, which were eventually based on data from 9 localities (elevation range 1030–1645 m), 229 quadrats, and 22800 seeds sown. Data from two quadrats that were heavily disturbed by wildboars in the course of the study were excluded from the survival analyses.

Experimental sites were visited every ten days during February–July 1993, and quadrats examined for newly-emerged seedlings. On each occasion, new seedlings emerged since the last visit were marked on one of the cotyledons with a small dot of fast-drying black ink, thus allowing for a precise determination of the cumulative number of seedlings emerged per quadrat during the whole germination season (late April–early June in 1993). A few seedlings emerged in the experimental quadrats in 1994, but their importance was negligible and this study will consider only the data for the 1993 seedling cohort. After the 1993 seedling emergence period finished, experimental sites were monitored every three months until June 1994, and at progressively longer intervals until the completion of the study in late December 1998. In each inspection, the number of surviving seedling was recorded for each quadrat. By the end of the study, 6th-year survivors had already become well-established juveniles. Mortality became negligible at seedling ages > 3 yr, hence these 6-yr old survivors can properly be considered as actual recruits to the population, some of which would have reproduced for the first time only 2–3 yr after the completion of the study (Herrera 2000).

Five soil samples (top 15–20 cm soil, after excluding surface litter and coarse debris) were collected at each

Table 1. Summary statistics for the combined set of $N = 50$ soil samples considered in this study (10 sowing sites × 5 soil samples per site).

Soil parameter	Range	Median	Coefficient of variation (%)	Fraction of variance (% of total)		Difference among sites	
				Among sites	Within sites	$F_{9,40}$	P-value
Texture:							
Sand (%)	7.3–72.3	28.9	47.1	90.4	9.6	48.05	<0.0001
Clay (%)	5.5–62.6	40.1	40.7	91.9	8.1	57.88	<0.0001
Silt (%)	19.0–48.3	29.8	22.9	73.1	26.9	14.59	<0.0001
Chemistry:							
pH	7.0–8.1	7.7	5.1	88.6	11.4	39.69	<0.0001
Organic matter (%)	2.3–9.6	5.1	31.3	56.6	43.4	7.51	<0.0001
N (%)	0.08–0.40	0.23	33.5	66.8	33.2	11.04	<0.0001
P (μg/g)	0.3–8.5	2.0	80.8	67.5	32.5	11.37	<0.0001
K (mg/g)	0.05–0.52	0.28	42.9	90.4	9.6	48.07	<0.0001

of the ten planting sites in February 1997. Although some soil parameters may vary seasonally and annually (e.g., Ehrenfeld et al. 1997, and references therein), accounting for this possibility would have required repeated collection of soil samples from the relatively small area of planting sites over the 6-yr duration of this study, a sampling scheme that would have compromised the normal development of seedlings. In absence of data on possible seasonal and annual variation in soil parameters, it seems reasonable to assume that the magnitude of such variation would be comparatively minor in relation to the broad levels of variation found between sampling points and planting sites. Soil sampling points were always located in the open space between two neighboring quadrats, and their location was chosen to maximize the total number of planting quadrats in the site that fell within 50 cm of some sampling point. Nearest sampling points at each site were 1.25–1.75 m apart. In each site, the location of soil sampling points was recorded on maps where the location of planting quadrats had been also represented. Using this information, the seedling emergence and survival data from each planting quadrat were then associated with the soil variables from the nearest sampling point for the purposes of statistical analyses (see further details in next section). Texture (percent sand, silt and clay content) and chemical (pH, organic matter, total nitrogen, and available potassium and phosphorus) characteristics were determined on soil samples using standard soil analytical procedures. Particle-size distribution (<2 mm) was determined by the hydrometer method (Gee and Bauder 1986). Chemical properties were determined using procedures in Page et al. (1982): pH in water extract, organic matter by the Walkley-Black method, total nitrogen by the Kjeldahl method, available phosphorus by the Olsen method, and available potassium by amonium acetate extraction.

Statistical analyses

The effects of soil texture and chemical variables on the probability of one seed yielding an emerged seedling (= "seedling emergence probability" hereafter, measured as seedlings emerged/seeds sown), and the probability of one emerged seedling eventually yielding an established, 6th-year juvenile (= "seedling survival probability" hereafter, measured as surviving juveniles/ seedlings emerged), were assessed by fitting generalized linear models to the data using SAS procedure GENMOD (SAS Institute 1996a). Individual quadrats were used as experimental units, and the soil descriptor parameters for the nearest soil sampling point were incorporated to the models as independent variables. Estimates of seedling emergence probability and

seedling survival probability for each quadrat were modeled using logits and the binomial probability distribution. The overdispersion scale parameter, used to adjust likelihood ratio statistics, was estimated by the square root of the deviance of the model divided by its degrees of freedom (SAS Institute 1996a). Differences among planting sites in elevation were likely to have some influence on seedling emergence and survivorship through their influence on, for example, temperature and patterns of rainfall. To account for this possibility, site elevation was also included in the models as a covariate. Furthermore, mother plants differed significantly in seedling emergence and survival probabilities (Herrera 2000), hence emergence and survival data from quadrats with seeds from the same mother were expected to be correlated. To adequately account for this effect and statistically remove the "nuisance effect" of differences among mother plants, models were fitted using the Generalized Estimating Equations (GEE) method, with mother plant treated as the SUBJECT effect and an unstructured covariance structure (Stokes et al. 1995, SAS Institute 1996b).

Analyzing the effect of soil properties on seedling survival by focusing only on the binary information of whether an emerged seedling was alive or not by the end of the study may result in reduced statistical power, as this analysis is insensitive to possible effects on the timing of seedling death and thus the shape of survivorship curves. For this reason, the effect of soil descriptors on seedling survivorship was also tested by fitting a Cox proportional hazards regression model (Allison 1995) to seedling survivorship data consisting of information on time durations from emergence to death (noncensored observations) or to the end of the study (censored observations). Site elevation was also included as a covariate in this analysis. To account for the effect of differences among mother plants in seedling survivorship (Herrera 2000), mother plant was added to the model as a random, or "frailty" effect. Computations were carried out using survival analysis functions in S-Plus 2000 (Mathsoft 1999).

Sets of soil variables are often closely correlated (Webster and Butler 1976, Arp 1984, Arp and Krause 1984), and this multicollinearity may affect the reliability of significance tests for individual effects in linear models and regressions. For this reason, scores of soil samples on rotated principal components, rather than the values of the eight original soil variables, were used as soil descriptors in linear models and Cox regression. The principal components analysis was carried out on the correlation matrix using SAS procedure FACTOR. The three components with associated eigenvalues >1 were retained.

The number of soil sampling points per site was smaller than the number of planting quadrats, thus the set of soil descriptor variables for any given sampling point was associated in the analyses with more than one

seed planting quadrat. As the distance between individual quadrats and its nearest soil sampling point was roughly the same for all quadrats and sites, this procedure did not pose any particular statistical problem except for reducing the "signal-to-noise" ratio and thus the probability of detecting small-scale trends, which would fall on the conservative side. However, to test for any possible effect on the results of slight variations in the distances between planting quadrats and their associated soil sampling points, I performed two additional variants of the analyses described above. In one of them, quadrats with centers located at > 0.5 m of its nearest soil sampling point (29.3% of quadrats) were excluded. In the other, all quadrats were included but data were weighed in the analyses inversely to the distance from the quadrat's center to the nearest soil sampling point. In the two instances, results were essentially identical to those obtained using all quadrats and no data weighing scheme, thus these latter results will be the only ones reported below.

Results

Spatial variation in topsoil properties

With the single exception of pH, which remained within relatively narrow limits, all the soil parameters considered exhibited considerable variability when all the soil samples were considered together (Table 1). Variability occurred at both the within and among locality spatial scales. Localities differed significantly in mean soil parameters, both for each parameter considered individually (univariate analyses; Table 1) and when all parameters were treated simultaneously in a multivariate analysis of variance ($F_{72,208} = 10.7$, $P < 0.0001$). The broad ranges of locality means for sand (10.5–62.1%), clay (8.4–61.2%) and silt (22.4–44.8%) percent content illustrate the textural variability represented in the sample of sites, which included clay, clay loam, silty clay, sandy loam, and loam soils. Broad ranges also occurred in the locality means for organic matter (2.9–6.7%), total nitrogen (0.11–0.31%), available phosphorus (0.96–6.56 μg/g) and available potassium (0.07–0.49 mg/g). No obvious relationship could be detected across localities between elevation and mean soil characteristics. None of the correlations between the former variable and the eight soil parameters considered was statistically significant (range of P-values = 0.15–0.93).

In addition to the broad-scale, statistically significant differences among localities in mean soil properties, some soil parameters also exhibited important variation at the within-locality, small-scale level. This applies particularly to organic matter, N and P, for which the within-locality component accounted for as much as 30–40% of total variance (Table 1; variance partitioning performed using SAS procedure VARCOMP). This means that about one third of the total regional variance in these soil parameters was represented at the very local scale of the few meters separating the five points sampled in each locality. The situation differs for other soil parameters, like sand, clay and K content. In these cases, the small-scale, within-locality level accounted for only a small fraction (8–9%) of total variance, and variability mainly occurred at the between-site scale.

Principal components analysis of the correlation matrix of soil parameters (across the $N = 50$ sampling points, all localities combined) revealed the existence of three major independent gradients of variation in soil properties (Table 2). The first gradient (PC1) may be interpreted as predominantly reflecting a soil texture gradient running from high sand content on the negative extreme to high clay content on the positive extreme. The close positive correlation between K and PC1 (Table 2) is also to be linked to textural variation, as available K in these soils is mainly derived from the decomposition of clay minerals. For this reason, I will hereafter consider PC1 as a prevailingly textural gradient. The second gradient (PC2) clearly corresponds to a fertility gradient, mainly reflecting the coordinated variation of organic matter, phosphorus, nitrogen and pH. The positive and negative extremes of the gradient would correspond, respectively, to the most fertile and infertile soils. These first two components account altogether for 68% of total between-sample variance. The third gradient (PC3) accounts for only an additional 16% of variance, and reflects variation in silt content, thus another texture-related gradient. The three axes resulting from the principal components analysis have a clear biological meaning and summarize satisfactorily the variation of the eight soil parameters considered. There are thus both biological and statistical justifica-

Table 2. Principal components analysis of soil texture and chemical composition parameters, conducted on the correlation matrix of soil parameters from all experimental planting sites combined ($N = 50$ soil samples). Main entries are the correlations of original variables with rotated principal components. Significant values are shown in bold type ($P < 0.05$, Bonferroni-corrected to account for multiplicity of simultaneous tests).

Soil parameter	Correlation with principal component (PC)		
	PC1	PC2	PC3
Potassium	**0.917**	−0.143	−0.228
Clay	**0.909**	−0.297	−0.248
Sand	**−0.918**	0.283	−0.203
Organic matter	−0.111	**0.837**	0.056
pH	−0.181	**0.839**	0.096
Phosphorus	−0.278	**0.749**	−0.355
Nitrogen	−0.336	**0.756**	0.274
Silt	−0.153	0.081	**0.956**
Proportion of variance (%)	34.60	34.14	16.01

tion to use scores of individual samples on these three axes as simplified, non-correlated descriptors of soil characteristics in the rest of statistical analyses.

Seedling emergence and survival

A total of 7507 seedlings emerged from the 22 800 seeds sown, and there was at least one emerged seedling in 96.1 % of the $N = 229$ quadrats (the 9 localities combined). Mean (± 1 SD) seedling emergence probability per quadrat was 0.330 ± 0.205 emerged seedlings/seed (Range $= 0$–0.76). Variation among quadrats in seedling emergence probability was satisfactorily explained by variation in PC1–PC3 scores, elevation, and maternal family, as revealed by the close fit of the data to the linear model (scaled deviance $= 1.074$, df $= 226$, $P > 0.99$). After statistically accounting for site elevation and maternal differences in progeny recruitment prospects, the probability of a seed producing an emerged seedling depended significantly on PC1 (directly) and PC3 (inversely) scores, the two soil gradients related to textural properties, but not on PC2 scores, the gradient related to soil fertility (Table 3). Seedling emergence probability declined with increasing clay content, and increased with increasing sand and/or silt content. Site elevation had a significant negative incidence on seedling emergence probability.

Only 410 seedlings remained alive six years past emergence, or a 0.055 overall survival probability. There was at least one surviving seedling in 32.8 % of quadrats, but the mean number of surviving seedlings per quadrat was very low (Mean $\pm$ SD $= 1.79 \pm 4.08$ seedlings/quadrat). Variation among quadrats in seedling survival was satisfactorily accounted for by variation in PC1–PC3 scores, elevation, and maternal family, as shown by the close fit of the data to the linear model (scaled deviance $= 0.655$, df $= 222$, $P > 0.99$). Among emerged seedlings, the probability of remaining alive by the end of the sixth year depended significantly and directly on the fertility-related PC2 scores, but was not significantly related to variation in the texture-related PC1 and PC3 scores (Table 3). Once

emerged, therefore, the chances of a seedling remaining alive for the next six years increased with increasing pH, organic matter, phosphorus, and nitrogen content. There was also a significant negative effect of site elevation on long-term seedling survival prospects.

Fitting a Cox proportional hazards regression model to the seedling survivorship data over the 6-yr study period yielded quite similar results to the preceding analysis based exclusively on the simple binary information of whether a seedling was alive or not by the end of the study (Table 4). The effect of PC1 on seedling survival remained nonsignificant, while the effects of PC2 and elevation remained both highly significant and their significance levels were considerably enhanced. The Cox regression analysis revealed also a significant effect of PC3 on seedling survival which had remained undetected in the preceding analysis. Relative risk values ($=$ exp [regression coefficients]) associated with both PC2 and PC3 denote a negative impact of these two variables on seedling death risk, i.e., increases in both variables were associated with a reduction in the risk of seedling death. The impact on seedling survivorship was strongest for PC2, as each one-unit increase in this variable leads to an estimated decline of 12% in the risk of seedling death, in comparison to only a 7% risk reduction per one-unit increase in PC3.

Discussion

Soil parameters and seedling recruitment

All soils in the Sierra de Cazorla study region originate from some variant of calcite or dolomite limestone bedrock, yet the broad range of physiographic and environmental conditions occurring in the area have contributed to their differentiation over relatively small distances, as stressed by González Parra et al. (1984, 1985a, b) and confirmed by this study. Variation of textural and chemical topsoil properties takes place at scales ranging from a few meters to several kilometers, and this study has shown that such variation is statistically related to variation in potential recruitment of *L.*

Table 3. Statistical significance of effects of principal components describing textural (PC1 and PC3) and chemical (PC2) soil properties (Table 2) and site elevation on seedling emergence and seedling survival rates, tested by fitting generalized linear models to quadrat-level seedling emergence and survival data (see Methods: Statistical analyses for further details).

Independent variables	Dependent variable					
	Seedling emergence			Seedling survival		
	Parameter estimate	χ^2	P	Parameter estimate	χ^2	P
PC1	**−0.225**	10.70	**0.001**	0.235	2.51	0.11
PC2	−0.059	1.40	0.24	**0.380**	6.32	**0.012**
PC3	**0.148**	6.91	**0.009**	0.164	0.63	0.43
Elevation	**−0.002**	12.83	**0.0003**	**−0.005**	8.87	**0.003**

Table 4. Results of fittting a Cox proportional hazards regression model to the quadrat-level seedling survivorship data for the six-year study period. The effect of differences among mother plants in seedling survivorship was statistically accounted for by including mother plant as a random ("frailty") effect in the model.

Independent variable	Coefficient	Relative risk	χ^2	P
PC1	−0.0173	0.983	1.9	0.17
PC2	−0.1145	0.892	60.7	≪0.0001
PC3	−0.0726	0.930	16.2	<0.001
Elevation	0.0018	1.002	336.2	≪0.0001

latifolia populations on a per seed basis. Both the probability of one seed of *L. latifolia* giving rise to an emerged seedling, and the probability of an emerged seedling remaining alive six years after emergence, are significantly related to topsoil properties. There are no reasons to suspect that these results are due to anything other than the actual influence of topsoil characteristics on these two sequential recruitment stages. First, the effects of locality elevation and maternal parent were statistically accounted for in all the models fitted, hence the possibility that observed results are a spurious consequence of the slight imbalance of the experimental design with regard to maternal provenance of seeds, or of some correlation between elevation and soil characteristics, can be safely ruled out. And second, it is quite unlikely that results reflect a spatial association between soil characteristics and some influential biotic factor like, e.g., seed predation or seedling herbivory. Seeds remained protected from seed predators from sowing to germination, and signs of invertebrate herbivory or pathogen damage on newly emerged seedlings were extraordinarily infrequent.

Under natural field conditions, the emergence of *L. latifolia* seedlings was related to soil texture (negatively to clay content, positively to sand content), while their long-term survival was related to soil fertility (positively to organic matter, nitrogen, and phosphorus). Although results of this kind are infrequent in the ecological literature for wild plants under natural field conditions (see also Eriksson 1995, Walters and Reich 1997, Stratton and Bennington 1998), these findings are not unexpected on biological grounds. Investigations on cultivated plants have often shown that a high clay content increases mechanical impedance of soils to root penetration and reduces seedling emergence in some species (Cook et al. 1995, Misra and Gibbons 1996, Townend et al. 1996, Pabin et al. 1998). For several species of small-seeded weeds, Vleeshouwers (1997) documented the adverse effect of high soil penetration resistance on seedling emergence and growth. *Lavandula latifolia* seeds are small (mean seed mass = 1.3 mg), thus early radicle growth and hypocotyl elongation are expected to be quite sensitive to variations in mechanical impedance and thus be seriously hampered by very clay-rich soils, which may

account for the inverse relationship between seedling emergence probability and PC1. This interpretation is supported by the frequent observation during this study of newly-emerged, withering *L. latifolia* seedlings with coiled radicles following failure to get into very clay-rich soils.

Field and glasshouse studies on cultivated and wild plants have consistently documented a positive effect of soil fertility, particularly nitrogen and phosphorus content, on seedling growth rates (McColl 1970, Wang et al. 1994, Minotta and Pinzauti 1996, Roldán et al. 1996, Walters and Reich 1997, Duarte et al. 1998). Growth rate enhancement is also most likely the proximate mechanism accounting for the positive effect of soil fertility (PC2) on long-term survival of *L. latifolia* seedlings found here. Mortality of *L. latifolia* seedlings mostly takes place during the first summer after emergence, as a consequence of the severe summer drought characteristic of Mediterranean habitats (Lloret et al. 1999, Herrera 2000). First-summer survival is markedly size-dependent, with larger seedlings surviving better than smaller ones (C. M. Herrera, personal observation). By enhancing early seedling growth, therefore, increased soil fertility may allow a greater size to be reached by summer, which will in turn result in decreased susceptibility to water stress and enhanced long-term survival. The inverse relationship between elevation and seedling survival may likewise be explained by the size-dependence of first-summer survival. There was a distinct elevational trend in timing of seedling emergence, which tended to occur later as elevation increased, and by early summer seedlings were smaller on average at higher localities and thus more prone to death from desiccation. None of the 869 seedlings that emerged at the two highest localities (1640 and 1645 m elevation) survived past the first summer.

Stage-dependence and spatial decoupling

Emergence and survival of *L. latifolia* seedlings tended to be mainly related, respectively, to texture (PC1, PC3) and fertility (PC2) gradients. Since principal components are, by definition, uncorrelated to each other, the probabilities of a seed producing a seedling

(affected by PC1 and PC3) and of a seedling surviving until the established stage (affected by PC2) are also expected to be uncorrelated. This is strongly supported by the near-zero correlation coefficient between seedling emergence and seedling survival probabilities across quadrats, partialled on site elevation ($r_{.elevation} = 0.077$, $N = 227$, $P = 0.25$). This means that if a spot on the forest floor has the soil textural properties that favor the emergence of *L. latifolia* seedlings, this says next to nothing on whether it possesses or not the fertility features that would enhance the early growth and subsequent survival of these seedlings. Spatial decoupling of this kind, ultimately generated by the independent variation of the two sets of soil properties that influence the two recruitment stages, may help to explain the instances of spatial discordance between recruitment stages often reported in the literature. For example, several investigations have reported situations where seed rain and seedling abundance of individual species are spatially decoupled, and this has been interpreted as reflecting secondary dispersal of seeds or the action of pathogens and seed predators (Houle 1992, 1998, Herrera et al. 1994). Without negating the potential importance of these factors, results of this investigation suggest that patchiness in soil properties affecting seedling emergence and survival should also be taken into consideration to explain spatial discordances between seed and seedling abundance.

This investigation has also suggested that major soil gradients influencing *L. latifolia* recruitment differ in the structure of their spatial variance. While the variance of textural soil variables contributing to PC1 and PC3 is mainly accounted for by differences between localities, the fertility-related variables contributing to PC2 have a considerable small-scale variance component at the within-locality level. Since PC1 and PC3 mainly affect to the success of seeds while PC2 affects to the success of seedlings, such differential apportionment of spatial variance implies that the relevant scales of spatial heterogeneity are different for seeds and seedlings. From the perspective of *L. latifolia* seed progenies, therefore, the forest floor would be "perceived" as made up of larger homogeneous patches, while seedling progenies will "perceive" it as much more fine-grained. This suggests the possibility that seeds and seedlings of *L. latifolia* may have contrasting opportunities for local adaptation. Under conditions of consistent selective pressures and restricted gene flow relative to the spatial scale of relevant environmental parameters, spatial heterogeneity may lead to local adaptation and spatial genetic structuring in plant populations (Schemske 1984, Stratton 1995, Stratton and Bennington 1998, and references therein). Gene flow in *L. latifolia* is rather restricted via both pollen and seeds (Herrera 1987). Seeds lack special mechanisms for dispersal and are

primarily dispersed within 1 m of the mother plant. This means that the seed progenies of individual plants will be spread over soils patches that, with regard to the textural properties which influence seedling emergence, are both relatively homogeneous and predictably similar to that of either of their parents. The resulting seedling progenies, however, will be distributed over an area where the relevant variables influencing their long-term survival vary at a much more restricted scale, and only a relatively small fraction of them will occupy microsites similar to those faced by their parents when they were at the seedling stage. Under these conditions, it may therefore be predicted that morphological and/or physiological adaptations to the textural properties of local soil that would enhance seedling emergence will be easier to evolve than local adaptations to soil fertility features that would enhance seedling survival. Further studies will be needed to examine these and other possible adaptive consequences of stage-dependence and spatial decoupling of influential soil parameters on the recruitment of *L. latifolia*.

Concluding remarks

Few previous investigations seem to have simultaneously documented stage dependence *and* independent variation of the soil parameters related, respectively, to seedling emergence and seedling survival. Schupp (1995) reviewed studies where the relative survival values of microsites for seeds and seedlings had been simultaneously determined, but in the investigations considered microsites were defined in function of biotic factors (e.g., cover, disturbance, habitat type) or, in a few instances, qualitative soil-type categories. There are reasons, however, to expect that soil-caused decoupling of microsite quality for seeds and seedlings is more frequent than hitherto acknowledged. As noted in the Introduction (see references there), patchiness in soil parameters seems to be the rule in nature, and it can arise from many sources and occur at many different scales. In forests, stemflow close to the base of the trunk of trees, and the mosaics associated with litter fall, decomposition and nutrient uptake rates under different species of trees or shrubs, seem to play the predominant role (Zinke 1962, Gersper and Holowaychuk 1971, Crozier and Boerner 1984, Boerner and Koslowsky 1989, Boettcher and Kalisz 1990, Kleb and Wilson 1997). In addition to spatial heterogeneity in soil properties, different soil parameters tend to exhibit spatially uncorrelated patterns of variation over small and medium-sized scales (Blyth and Macleod 1978, Nortcliff 1978, Arp and Krause 1984, Webster 1985, Robertson et al. 1988, Grigal et al. 1991, Lechowicz and Bell 1991). Uncorrelated patterns of spatial varia-

tion of different soil parameters are revealed, for example, by contrasting profiles of accumulating variance with increasing spatial scale (Nortcliff 1978, Webster and Butler 1976, Webster 1985) or, as found here and in other studies, by differential patterns of variance apportionment among various nested spatial scales (Beckett and Webster 1971). Furthermore, the soil science and ecological literature provide indications that, as found here, patchiness of fertility-related variables generally tends to occur at much smaller spatial scales than texture-related ones (Nortcliff 1978, Boettcher and Kalisz 1990, Goovaerts and Chiang 1993, Jackson and Caldwell 1993, Gross et al. 1995). Given the apparent generality of the phenomena that contribute to the patterns revealed by this study on *L. latifolia*, it seems safe to predict that similar results will most likely be obtained for other species.

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