Journal of Vegetation Science 17: 729-738, 2006
© IAVS; Opulus Press Uppsala.

Regeneration of a marginal *Quercus suber* forest in the eastern Iberian Peninsula

Pausas, J.G.[1*]; Ribeiro, E.[1]; Dias, S.G.[1]; Pons, J.[1,2] & Beseler, C.[1,3]

[1]*CEAM Fundación Centro de Estudios Ambientales del Mediterráneo, C/ Charles R. Darwin 14, Parc Tecnológic,*
46980 Paterna, València, Spain; [2]*E-mail pep@ceam.es,* [3]*E-mail cbeseler@ceam.es*
[*]*Corresponding author; Fax +34 961318190; E-mail pausas@gmail.com, juli@ceam.es*

Abstract.
Question: Small and marginal forest populations are a focus of attention because of their high biodiversity value as well as the risk of population decline and loss. In this context, we ask to what extent a small, marginal *Quercus suber* (Cork oak) population located in the eastern Iberian Peninsula (Valencia, Spain) has the capacity for self-regeneration and what are the factors that determine its recruitment variability.
Location: *Quercus suber* forest in Pinet (Valencia, Spain).
Methods: We performed a spatially explicit sampling both of the recruitment and of the potential parameters that could account for the recruitment variability. Using regression techniques we model the recruitment occurrence and abundance, and then we test to what extent the model obtained is still constrained by the spatial dependence.
Results: *Quercus suber* recruitment density ranges from 0 to 18.66 individuals/25m^2 (mean = 1.46, SD = 2.8), with a very skewed distribution. Recruitment is similar under *Q. suber* forests and under *Pinus* forests, but it is almost absent under shrublands. Thus the parameters that explain most of the recruitment variability in local vegetation types are: the presence and cover of shrubs (negative relationship with recruitment), the basal area of *Q. suber* and *Pinus* and the amount of bare soil (all positively related to recruitment). These parameters are strongly related to the ecological processes driving recruitment (i.e. dispersal and predation) and they remove most of the spatial dependence of recruitment. Most recruiters, however, are small, forming a seedling bank rather than growing to successfully colonize new habitats.
Conclusion: The results suggest that although recruitment densities are not very high, they do not limit potential regeneration in the Pinet *Q. suber* forest. However, successful regeneration is not observed. If we aim to increase the Pinet *Q. suber* population size, land management measures need to provide appropriate conditions for both seedling establishment in shrublands (e.g. shrub clearing) and seedling growth in woodlands (e.g. *Pinus* logging).

Keywords: Autocorrelation; Mediterranean forest; Recruitment; Seedling; Spatial.

Abbreviations: AI = Aspect index; GLM = Generalized linear model; GPS = Global positioning system.

Introduction

Species distribution ranges are usually not continuous; they often show a core area and some marginal (geographically peripheral) populations. In the core area, populations strongly interact with each other through gene flow. However, peripheral populations undergo minimal interaction with conspecific populations. Available evidence suggests that peripheral populations are often genetically, morphologically and/or functionally divergent from central populations (Blows & Hoffmann 1993; Johansson 1994; Lönn & Prentice 2002), and often hold an important proportion of the species' genetic diversity (Petit et al. 2003; Hewitt 2004). Thus, they are potentially important sites for future speciation events. As such, conservation of marginal populations is important as a protection of the evolutionary processes likely to generate future diversity (Lesica & Allendorf 1995, Hampe & Petit 2005). However, the isolation and genetic erosion of small peripheral populations may also reduce their viability and fecundity, and drive the populations to extinction (Lawton 1993; Vucetich & Waite 2003). Furthermore, small marginal populations may be subject to higher predation rates (Tellería et al. 1991; Santos & Tellería 1994, 1997) and they may be highly sensitive to global changes in climate, disturbance regimes and pathogen agents (Thomas et al. 2004; Hampe & Petit 2005).

The importance of studying the regeneration of marginal populations is enhanced in the case of trees with socio-economic and cultural value. This applies to *Quercus suber* (Cork oak) populations in the eastern Iberian Peninsula. *Q. suber* forests are protected by the European Union (Habitat Directive 92/43EEC) and most *Q. suber* occur on acidic soils in the centre and western half of the Iberian Peninsula (the core area). However, in the east (Mediterranean coast), where calcareous soils are dominant, *Q. suber* also occurs in several peripheral populations, and they show genetic differences from the core populations (Jiménez et al. 1999). In the Valencia region (eastern Iberia), the main *Q. suber* forest patches range from ca. 8000 ha to ca. 80 ha (Pausas et al. 2004a, Pons & Pausas 2006) and are considered marginal, fragmented and with a questionable future (Díaz-Fernández et al. 1996, Jiménez et al. 1999, Anon. 2002-2005). There is also one, even smaller, population located further south in Carrascoy, Murcia (southeastern Iberian Peninsula), with very few individuals only (Díaz-Fernández et al. 1996). Part of the fragmentation may be due to the past elimination of oaks for terracing and cultivation, but indiscriminate and uncontrolled cork extraction (García-Fayos 1991) and increased fire frequency (Pausas 2004) may also have contributed to the reduction of *Q. suber* trees.

The southernmost *Q. suber* forest of the Valencia region is the Pinet forest, which is an isolated ca. 80 ha mixed forest patch of *Q. suber* and *Pinus pinaster*, 90 km south from the closest patch (Calderona, ca. 800 ha), and a substantial distance from the *Q. suber* core area. Furthermore, the Pinet patch is located in an area with environmental conditions that are considered to be near the limit of this species's environmental requirements (Blanco et al. 1997), in terms of low rainfall and non-acid soil derived from dolomites. Thus the Pinet *Q. suber* patch seems to be geographically, climatically and edaphically isolated. In such a situation we ask about the future of this small, marginal *Q. suber* patch: Can it regenerate by itself? Or alternatively, are land management measures required to conserve it?. What factors determine the appropriate habitat for its regeneration?

Although some information is available on the regeneration of *Q. ilex* (Retana et al. 1999; Lookingbill & Zavala 2000; Plieninger et al. 2004), very little is known about the recruitment and regeneration of *Q. suber*. Very few studies have been published for *Q. suber*, and most of these were carried out within the core area a long time ago (reviewed by Montero et al. 1994). As with most oaks, *Q. suber* regeneration is accomplished through acorns. If there is sufficient acorn production, the regeneration may depend on acorn dispersal by vertebrates (mainly the European jay *Garrulus glandarius*), acorn and seedling predation (mainly by mouse and wild boar) and seedling establishment and growth. All these processes vary spatially, depending on habitat characteristics such as forest structure and site conditions (Grime & Hillier 2000; Gómez 2003, 2004a). Thus, in the present work we evaluate the potential regeneration of Pinet *Q. suber* by quantifying the observed recruitment and their height and development stages; we assume that this may provide a first indication of the future of the studied population. Thus, we hypothesise that *Q. suber* recruitment should be highly variable in space, with a patchy pattern, and that parameters related to micro-environmental characteristics and community structure should account for most of the *Q. suber* recruitment variability. Recruitment is defined as the establishment of new individuals; to what extent this recruitment implies a clear regeneration will depend on the opportunities for growth.

Sampling the recruitment of a small population patch may violate the assumption of independence, and be subject to pseudoreplication and spatial autocorrelation problems (Legendre & Legendre 1998). This is because the mean distance between two points in a small population is shorter than the spatial area of influence of the underlying ecological phenomenon, e.g. acorn dispersal. In such systems, spatial structure may be very relevant for ecosystem functioning. Thus, to account for the spatial structure (i.e. autocorrelated data), we perform a spatially explicit sampling that both includes ca. 50% of the Pinet forest patch and that accounts for most of the topographic, geologic and vegetation structural variability in the area. This sampling allows us to validate the effect of spatial autocorrelation on recruitment and to test to what extent independent variables may account for the spatial effect (Legendre & Legendre 1998).

Methods

The species

Quercus suber is an evergreen Mediterranean tree rarely reaching 20 m height, with sclerophyllous leaves and a thick, rugged, corky bark. It is relatively abundant in the western parts of both Morocco and the Iberian Peninsula, as well as in western Italy, the large islands between Italy and Spain and in North Africa (Morocco, Algeria and Tunisia) (Tutin 1964; Anon. 2000-2005; Fig. 1). In the Iberian Peninsula, most *Q. suber* occur on acidic soils in the centre and western half of the Peninsula (the core area).

Q. suber grows in non-carbonated soils such as acidic soils on granite, schist or sandy substrate and occasionally on neutral soils over dolomitic bedrocks. It occurs in regions with an annual precipitation normally above 600 mm and a mean temperature around 15 ºC (Blanco et al. 1997). It can form relatively dense, monospecific forests or it can participate in mixed forest communities, open woodlands or, usually together with *Q. ilex,* in the anthropogenic savanna-like agrosystems known as *dehesas*, *montados* or *pascolos arbolatos*.

As is the case for all oaks*, Q. suber* produces male and female (unisexual) flowers in different inflorescences on the same individual. Pollination is by wind (anemophily) and flowers mature into a dry fruit with one seed, the acorn. *Q. suber* produce both annual and biennial acorns (Díaz-Fernandez et al. 2004); annual acorns mature in the same year as the flowering, while biennial acorns mature in the autumn of the following year. Acorn dispersal is assured primarily by the European jay (*Garrulus glandarius*), as in most European oaks (Bossema 1979); mice are the main acorn predators but they may also contribute to short-distance dispersal (Gómez 2004b).

Study area

The Pinet forest patch is located in the south of the Valencia Province, eastern Spain (Iberian Peninsula, Fig. 1), 12 km from the Mediterranean coast (38°59' N, 0º18' W) and 600 m a.s.l. It is considered one of the smallest peripheral Iberian populations. Mean annual rainfall is ca. 700 mm, with strong interannual variability. The lithology of the area is a complex system of hard limestones with dolomites producing soils with a pH range of 5.6 to 8.4. The vegetation of the area is dominated by shrublands generated from multiple fires in the area (Pausas 2004) including *Quercus coccifera*, *Ulex parviflorus*, *Cistus* species, *Q. ilex* shrubs, *Rosmarinus officinalis, Thymus* species and *Brachypodium retusum* (as a dominant herbaceous species). However, the strong post-fire regeneration capacity of *Q. suber* (Pausas 1997) has enabled the small Pinet forest to persist within a large matrix of shrublands. The vegetation of the area is not the typical oak agrosystem of western Iberia (*dehesa*), but rather a mosaic of *Q. suber* forest, pine forests (*Pinus pinaster*) and shrublands. Cork was probably extracted some time ago in Pinet, but this use has been abandoned.

Sampling

We selected an area of ca. 47 ha that crossed the whole Pinet forest patch; we assume that the selected area accounts for most of the variability in the area. The area is complex, especially in terms of topography (aspect, slope) and vegetation structure (woodland, shrubland), which makes a stratified sampling design difficult. Furthermore, the size of the study area is too small for designing a sampling of independent plots as *Quercus* dispersal distances may be more than 500 m (Gómez 2003; Pons & Pausas unpubl.). We thus decided to perform a spatially explicit sampling on homogeneous units in relation to topography and vegetation structure. Using a GPS (Global positioning system), we delimited all necessary polygons within the sampling area that were visually homogeneous in their topographic and vegetation features. In this way, we obtained 140 polygons that varied in size (mean = 3383 m^2, median = 2274, SD = 4040) and shape. In each polygon we recorded both the DBH for all tree species (only for the trees with DBH > 4 cm) and the topographic characteristics (slope, aspect). Three soil samples from the top 10 cm of the soil were collected in each polygon, and the pH was analysed in the lab.

In each polygon we set three, four or five 5 m × 5 m plots, depending on polygon size (< 4000, 4000-6000, > 6000 m^2, respectively), for a total of 473 plots. On each plot we visually estimated the cover in each stratum (herbaceous, shrubs, trees), the proportion of bare soil and the stone and outcrop cover. Then, on each plot, we counted and measured the height of all individuals of all *Quercus* tree species that were less than < 3 m in height and classified them as: acorn seedling (with acorn attached), seedlings and resprout (with several stems and evidence of top-killing and resprouting). The oak species occurring were the evergreen *Q. suber*, *Q. ilex* and *Q. coccifera*, and the semi-deciduous *Q. faginea* (with marcescent leaves). *Q. coccifera* is a rhizomatous shrub that constitutes a dominant species in the Mediterranean garrigue shrublands, but its shoots from rhizomes are difficult to distinguish from seedlings, and thus the recruitment of this shrub oak was not quantified. From now on, when we use the term *Quercus* we refer to the three tree oaks only.

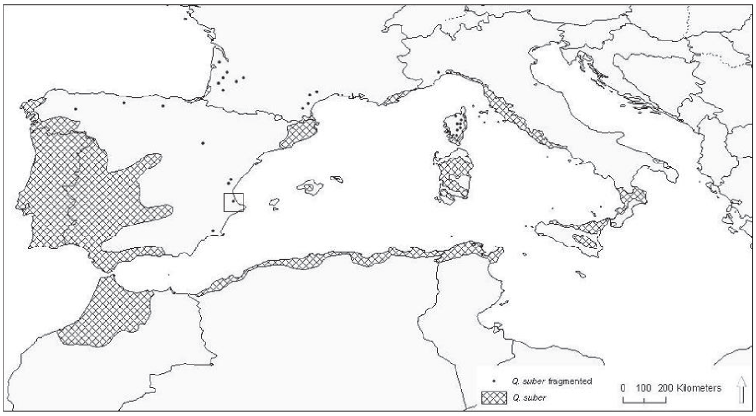


Fig. 1. Distribution of *Quercus suber* (modified from Anon. 2000-2005) and location of the Pinet forest (square).

Data analysis

We first computed the area of each polygon using the Splancs software (Rowlingson & Diggle 1993). Then, for each polygon, we computed the tree density and basal area of all the tree species present which included *Quercus* (*Q. suber*, *Q. ilex*, *Q. faginea*) and *Pinus* (*P. pinaster, P. halepensis*). However, by far the most prevalent tree species found were *Q. suber* and *P. pinaster*. Two qualitative variables related to the community type observed in the polygon were generated: Type 2 (with two categories: Wooded polygon or shrubland) and Type 3 (with three categories: polygon dominated by *Pinus*, by *Quercus* or by shrubland). Aspect was transformed to a quantitative moisture index (Aspect Index, *AI*) following: $AI = \cos(\alpha - 22.5)$, where a is the facing angle (in radians); AI ranges between 1 (northeast facing slopes) and –1 (southwest facing slopes) (Pausas et al. 2004b). The means of three soil pH measures of each polygon were calculated.

Recruitment density was computed as the mean of the number of individuals with height < 3 m in the different 5 m × 5 m plots. Unless otherwise stated, recruitment density is expressed as the number of individuals per 25 m^2. Similarly, mean plot-level cover values (vegetation, bare soil, outcrops and stoniness) were calculated for each polygon.

The statistical modelling of *Quercus* recruitment was performed only for *Q. suber*, it being the most abundant *Quercus* tree species on the study site. To find the parameters that determine the *Q. suber* recruitment density, we use a regression model approach, with recruitment density (individuals/25 m^2) as dependent variable and site and forest structural parameters as independent variables. Specifically, the variables used were (units or classes in brackets): *Q. suber* basal area (m^2/ha), *P. panaster* basal area (m^2/ha), total polygon basal area (m^2/ha), *Q. suber* tree density (individuals/ha), *P. pinaster* tree density (individuals/ha), total polygon tree density (individuals/ha), shrub cover (%), herbaceous cover (%), Type 2 (Wooded vs Shrubland), Type 3 (*Quercus*, *Pinus* or Shrubland), aspect index (AI, from –1 to 1), slope (%), bare soil (%), stoniness (%), outcrops (%) and soil pH.

However, recruitment density did not follow a normal distribution, and no transformation was found to normalise it. Thus, we decided to split the model and use a two-step regression approach. We separately modelled (a) the recruitment occurrence and (b) the amount (density) of recruitment. Splitting the model also provides additional biological information on the difference between occurrence and abundance. Recruitment occurrence was modelled as the presence/absence of recruitment in relation to independent variables using a Generalized linear model (GLM) with Binomial error distribution and logit link function. For polygons where recruitment occurred, the recruitment density was normalised by a log-transformation and regressed with the independent variables assuming a normal error distribution. For both models, the selection of the variables that explain most variability was assessed by a forward stepwise procedure. Only linear terms were included as there was no evidence of complex responses. The χ^2 (for the occurrence model) and the *F* (for the density model) criteria were used to add/remove variables in the model.

Spatial autocorrelation of all variables studied was quantified using Moran's *I* statistic for quantitative variables and the joint-count statistic for qualitative variables (Cliff & Ord 1981). Neighbour polygons are considered to be those with contiguous boundaries that share more than one point. To evaluate the adequacy of the environmental regression models, we generated spatial correlograms of the raw recruitment data and the residual of the models obtained. Any spatial pattern remaining in the residual would indicate that a spatially patterned variable not included in the analysis is probably contributing to the recruitment variability (Diniz-Filho et al. 2003). Autocorrelation and correlograms were computed using the spdep software (Bivand 2005). We used the version of the two spatial analysis programs (Splancs and spdep) as implemented in the R language (Bivand & Gebhardt 2000; Anon. 2005).

Table 1. Mean (SD) and maximum regeneration density (individual/ 25 m^2) of the different *Quercus* species, for all polygons (overall), for the polygons where they appear, for the polygons where *Quercus suber* is dominant (86 polygons; QS) and for the polygons where *Pinus pinaster* is dominant (28 polygons; PP). Dominance is assumed here as having the largest basal area. Differences between means in QS and PP are not significant for any species.

	Overall		Polygons with occurrence		QS	PP
	Mean (SD)	Max.	Polygons (%)	Mean (SD)	Mean (SD)	Mean (SD)
Q. suber	1.46 (2.82)	18.66	50.0	2.92 (3.41)	1.54 (2.84)	2.56 (3.48)
Q. ilex	0.17 (0.48)	3.00	25.0	0.71 (0.73)	0.21 (0.55)	0.26 (0.44)
Q. faginea	0.30 (1.04)	7.33	21.4	1.38 (1.92)	0.41 (1.2)	0.21 (0.94)
Total	1.93 (3.18)	20.67	61.7	3.19 (3.57)	2.15 (3.27)	3.03 (3.69)

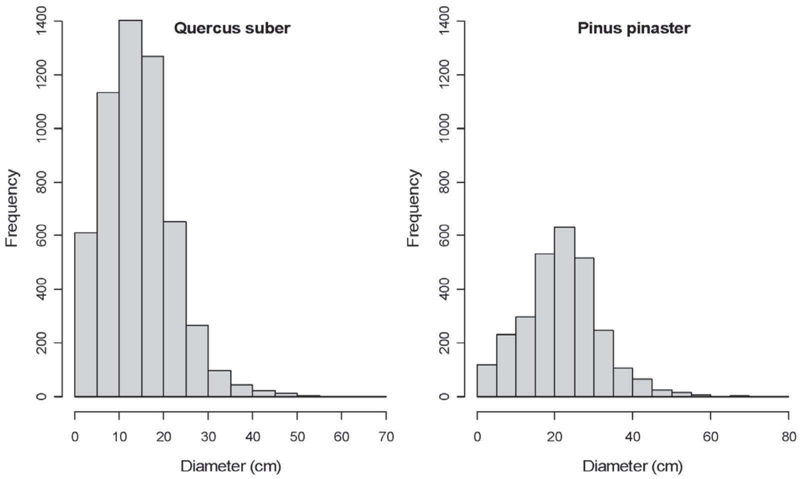


Fig. 2. Diameter class frequency distribution of the two most abundant tree species in the Pinet forest, *Quercus suber* and *Pinus pinaster*, for trees with DBH > 4 cm.

Results

Pinet forest structure

8777 trees were measured in the 140 polygons, 63% of them were *Q. suber*, 32% *P. pinaster* and the remainder were *Q. faginea*, *Q. ilex* and *P. halepensis* (3.6, 1.0, 0.7 %, respectively). The Pinet forest is a mosaic of shrublands (16.4% of the polygons have no trees) and woodlands of *Q. suber* and *P. pinaster* with a variety of densities. In the wooded polygons, total tree densities range from 1.22 to 898 trees/ha (mean = 242.7, SD = 204.8). *Q. suber* trees appear in 78% of the polygons and *P. pinaster* in 61%; in the polygons where they appear, *Q. suber* densities range from 1.18 to 867 trees/ha (mean = 178, SD = 185) and *P. pinaster* densities from 3.22 to 784 trees/ha (mean = 85.4, SD = 143.7). Both tree species appear together in 57% of the polygons. *P. halepensis, Q. ilex* and *Q. faginea* trees appear in 7, 8 and 27% of the polygons, and always with low densities (26, 39 and 27 trees/ha, respectively).

Diameter class distribution of the two main trees shows a dominance of thin classes for *Q. suber* (median = 14.3 cm) and a more balanced size class distribution for *P. pinaster* (median = 21.9 cm) (Fig. 2). Shrub and herb layers are found in all polygons, ranging from 17 to 93% shrub cover (mean = 57, SD = 16), and from 5 to 82% herb cover (mean = 40, SD = 19). Shrub cover, herb cover and basal area values are all uncorrelated with each other ($|r| < 0.17$, $p > 0.05$).

Quercus recruitment variability

A total of 908 oak individuals < 3 m in height were found on the 473 plots in the study area; 77% were *Q. suber,* 14% *Q. faginea* and 9.5% *Quercus ilex* (Fig. 3). For all tree species we found some individuals in all three categories: seedlings, seedlings with attached acorns and resprouts; seedlings, however, were dominant in all species (64%; Fig. 3).

Q. suber recruitment density ranges from 0 to 18.66 individuals/ 25 m^2 (mean = 1.46, SD = 2.8, Table 1), with a very skewed distribution (Fig. 4a). Half of the polygons (50%) presented some recruitment of this species; for these polygons, the mean density was 2.92 individuals/25 m^2 (Table 1). The log transformation of the recruitment densities in the polygons with recruitment shows a distribution that does not differ from a normal distribution (Shapiro test, $W = 0.972$, $p = 0.117$) (Fig. 4b). Mean recruitment density tends to be higher under *P. pinaster* than under *Q. suber*, but the variability is very high making the differences non-significant (Table 2). *Q. suber* did not recruit in polygons with pure shrubland (Table 1); in such situations, the only *Quercus* seedlings found were from the shrub *Q. coccifera*, but they were not quantified. *Q. ilex* and *Q. faginea* recruitment appears in 25% and 21% of the polygons, with lower densities than *Q. suber* (Table 1).

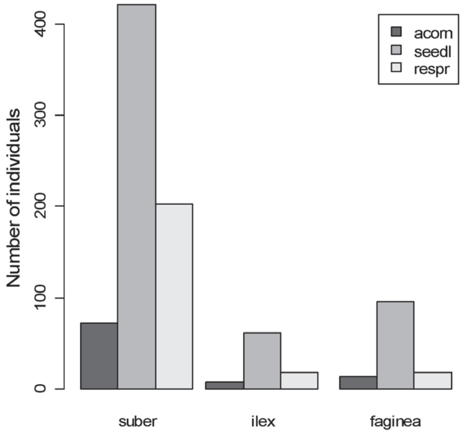


Fig. 3. Number of recruiting individuals found in the 140 polygons by *Quercus* species and type (acorn seedlings, seedlings and resprouts).

Table 2. Mean and SD values of the independent variables for the study area (140 polygons) and sign and significance (*p*-values) of the model for regeneration occurrence and for regeneration density. ns: $p > 0.05$. The sign of the relationship is indicated for the significant variables only.

			Occurrence		Density	
Variable	Mean	SD	sign	*p*	sign	*p*
Plant community structure						
Quercus suber basal area	3.35	4.02	+	< 0.0001		ns
Pinus pinaster basal area	2.40	5.99	+	< 0.0001	+	0.0017
Total polygon basal area	6.04	7.27	+	< 0.0001	+	0.0001
Quercus suber tree density	138.62	179.46	+	< 0.0001		ns
Pinus pinaster tree density	51.89	119.30	+	< 0.0001	+	0.0019
Total polygon tree density	202.79	202.73	+	< 0.0001		ns
Shrub cover	56.92	16.20		ns	-	< 0.0001
Herbaceous cover	40.08	18.94	+	0.0001		ns
Type 2	.	.		< 0.0001		N/A
Type 3	.	.		< 0.0001		0.033
Site conditions						
Aspect index (AI)	0.21	0.79	+	0.026		ns
Slope	28.51	14.52		ns	-	0.0013
Bare soil	2.43	4.70	+	0.0001	+	0.042
Stoniness	18.70	18.04	-	< 0.0001		ns
Outcrops	4.79	10.83	-	0.035		ns
Soil pH	6.73	0.54	-	< 0.0001		ns

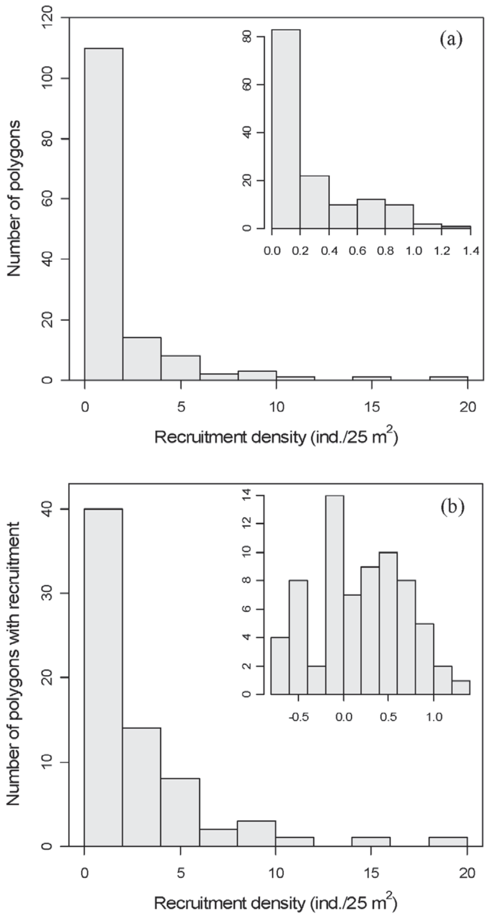


Fig. 4. Frequency distribution of (**a**) regeneration density (individuals / 25 m^2) in all polygons and (**b**) in the polygons with regeneration density greater than 0. Inset figures are the frequency distribution of the data after log-transformation.

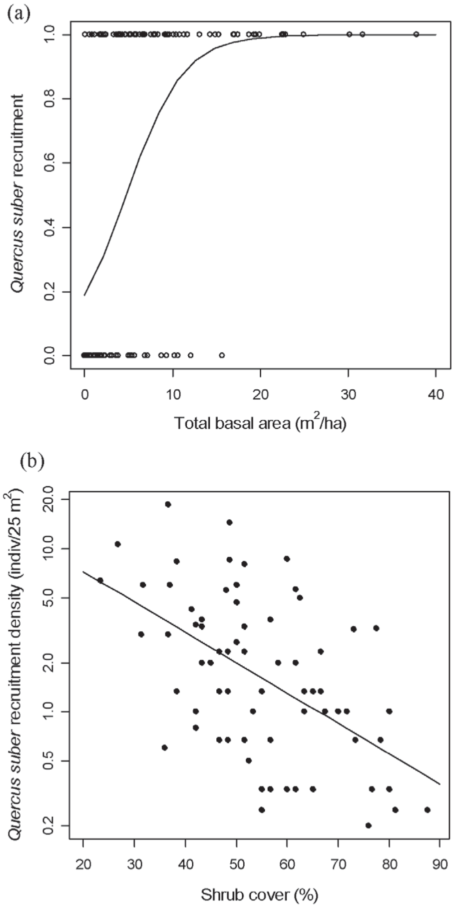


Fig. 5 a. Occurrence of *Quercus suber* regeneration as a function of total polygon basal area (m^2/ha); **b.** Amount of *Quercus suber* regeneration (individuals per 25 m^2, log scale) in the polygons where regeneration occurs, as a function of shrub cover (%). Lines are significant fits with $p < 0.00001$ (Table 1).

Table 3. Summary of the stepwise selection model for the occurrence of *Quercus suber* regeneration. All quantitative parameters show a positive relation; Type2 was positive for Wooded polygons and negative for Shrubland. Explained deviance = 43.5%.

	Residual *df*	Residual deviance	AIC	*df*	Deviance	*p*
Null	139	194.08	196.1			
+ Type2	138	157.65	161.6	1	36.44	< 0.0001
+ *P. pinaster* density	137	136.93	142.9	1	20.72	< 0.0001
+ *Q. suber* basal area	136	121.02	129.0	1	15.91	0.0001
+ bare soil	135	114.82	124.8	1	6.19	0.013
+ herb cover	134	109.69	121.7	1	5.13	0.023

The mean height of all *Quercus* recruiting individuals was 20.21 cm (SD = 16.5), with significantly ($p < 0.001$) lower height for *Q. suber* (19.4 cm) than for *Q. faginea* (21.3 cm) and *Q. ilex* (25.5 cm). Only ca. 2.8% of the individuals were taller than 50 cm, and 90% of the individuals were shorter than 32 cm.

Quercus suber recruitment

Recruitment occurrence was significantly related to most of the variables tested except shrub cover and slope (Table 2). Recruitment was positively related to forest structural parameters (tree basal area and tree density of both *Quercus* and *Pinus*), to the cover of herbaceous plants and to the proportion of bare soil (Table 2, Fig. 5a). Recruitment was negatively related to stoniness, soil pH and the proportion of outcrops in the polygon.

The most parsimonious model obtained to explain the occurrence of *Q. suber* recruitment includes five parameters and explains 43.5% of the deviance (Table 4). Recruitment is observed mainly in wooded polygons and is almost absent in shrublands; variables Type 2 and Type 3 explain similar variability suggesting that the tree species present in the polygon (*Quercus* or *Pinus*) are much less relevant than the wooded vs shrubland factor. Once the Type 2 parameter is in the model, the variables that explain most variability were *P. pinaster* density, *Q. suber* basal area, amount of bare soil and herb cover. All these parameters show a positive relationship with recruitment occurrence. Thus, most recruitment occurs in forests with *P. pinaster* and *Q. suber*, with high herb cover but with some bare patches on the forest floor.

Some recruitment was observed in 70 of the polygons. The most important variable explaining recruitment density in these polygons was shrub cover, which shows a negative relationship (Table 2, Fig. 5b). Total and *P. pinaster* basal area and *P. pinaster* density show a positive relationship. Slope and the proportion of bare soil also show a significant relationship (negative and positive, respectively).

In these polygons, 41% of the variability in the amount of recruitment (density) is explained by three parameters (Table 4): shrub cover, pine density and the amount of bare soil, with a negative relationship for the former and a positive for the others.

Spatial analysis

All the studied variables showed a strong spatial component. All independent variables showed a strongly significant autocorrelation index (Moran's I ranging from 0.25 to 0.48, p-values < 0.0001, except for bare soil for which $I = 0.12, p = 0.019$). Dependent variables (recruitment occurrence and density) are also spatially autocorrelated ($I > 0.30$, $p < 0.0001$). Both the occurrence and the density models greatly reduced the spatial effect, and the residuals show a low and marginally significant autocorrelation value ($I = 0.0099, p = 0.039$) for the occurrence model or a non-significant value ($I = –0.01$, $p = 0.482$), for the density model. Correlograms suggest that recruitment occurrence shows autocorrelation at longer distances (larger patches) than recruitment density (Fig. 6) and that the autocorrelation is strongly reduced at different spatial scales, specially at the first lag (Fig. 6). Thus, the predictor variables in the respective multiple regressions successfully account for most of the spatial autocorrelation.

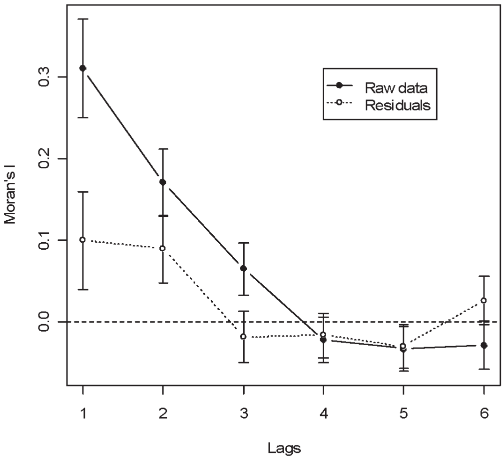
Table 4. Summary of the stepwise selection model for *Quercus suber* regeneration density. Shrub cover negative, *Pinus* density and bare soil positive. Explained variance = 41.3.

	Residual *df*	RSS	*df*	Sum of squares	*F*	*p*
Null	69	88.53				
+ shrub cover	68	62.99	1	25.541	32.43	<0.0001
+ *P. pinaster* density	67	55.18	1	7.806	9.91	0.0025
+ bare soil	66	51.99	1	3.196	4.06	0.048

Discussion

Overall, *Q. suber* in the Pinet forest patch recruits successfully, and at similar rates to those observed in other *Quercus* patches in the eastern Iberian Peninsula (Pons & Pausas 2006). Recruitment densities (Table 1) are in general at the low end of the recruitment range of the data compiled by Montero et al. (1994) for different Iberian sites over several years (850 to 22000 individual/ha in unmanaged sites, with mean = 7100, SD = 3900 individual/ha). In fact, our maximum values are close to their mean values. Our recruitment densities are also lower than the values reported for other evergreen Mediterranean *Quercus* forests such as *Q. ilex* forests (Retana et al. 1999; Lookingbill & Zavala 2000), but they are much higher than for *Q. ilex* dehesas (Plieninger et al. 2004).

(a) Occurrence



(b) Density

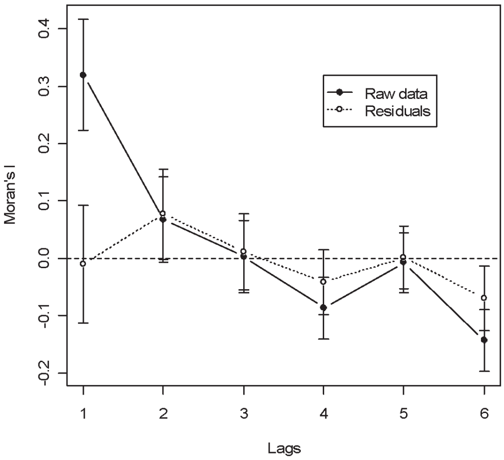


Fig. 6. Correlograms showing the reduction in the autocorrelation (measured as Moran's *I* index) from the raw data (solid line) to the residuals (dotted line) for (**a**) the model for *Quercus suber* regeneration occurrence and (**b**) regeneration abundance.

Nevertheless, *Q. suber* recruitment does not occur in shrublands, even if they are close to *Q. suber*, and it only occurs in wooded polygons, in both *Quercus* and *Pinus* forest. There are no oldfields in the Pinet area where *Q. suber* recruitment and growth would be expected, as has been observed in other eastern Iberian *Q. suber* woodlands (Pons & Pausas 2006). Recruitment densities are similar under both *Q. suber* and *Pinus* (Table 1), suggesting that the population has the capacity to colonize new forest environments (i.e. pine dominated polygons), but not shrublands. In fact, the next parameters entering into the model were *Pinus* density and *Q. suber* basal area, both showing a positive trend. Thus, *Pinus* forests are appropriate habitats for *Q. suber* recruitment. The movement of acorns from *Quercus* to *Pinus* forests has been described for other *Quercus* species and has been attributed to the European jay (Gómez 2003), which also occurs in the study area (Pons & Pausas 2004). The significance of *Q. suber* basal area may be related to the increasing acorn input. Two additional variables account for significant recruitment variability: the proportion of the floor covered by herbs and the proportion of bare soil. Both showed a positive relationship with recruitment occurrence, but because the amount of bare soil ranges only from 0 to 20%, they are not correlated with each other ($r = -0.042$, $p = 0.62$). Thus, it seems that recruitment is favoured in forests with grassy understorey and some open microsites. This may be due to the reduced competition in such systems or to the European jay's preference for this kind of floor when hiding acorns (Bossema 1979).

Once we know the conditions in which recruitment can occur, we ask under what conditions recruitment density is highest. The results suggest that the main parameter conditioning recruitment density is shrub cover, to the extent that the higher the shrub cover, the lower the recruitment density (Fig. 5b). *Pinus* density and the amount of bare soil also explain a significant part of the variability in recruitment density, in a way similar to the recruitment occurrence model. The absence of recruitment in shrublands and the decreasing pattern of recruitment density with increasing shrub cover may be due to an active avoidance of closed shrublands by jays (Bossema 1979; Kollmann 1995; Frost & Rydin 2000), to higher predator (mouse) densities in shrublands compared to forests (Torre & Díaz 2004) or to germination failure and competitive exclusion (Gómez et al. 2004); we cannot discriminate among these alternative causes. Lower mouse densities in forests have been attributed to the higher mouse predation risk in these environments (Kollmann & Schill 1996).

This limited recruitment in shrublands may limit the expansion of *Q. suber* in the Pinet area because the mixed *Quercus-Pinus* forest of Pinet is within a large matrix of shrublands. Furthermore, most *Q. suber* recruiting individuals were small (mean height = 19.4 cm; 90% quantile = 28.6 cm), suggesting that they were not in the process of regeneration, but forming a seedling bank (Kohyama 1983; Antos et al. 2005). Thus, if expansion of this small patch is desired, land management techniques, such as shrub clearing and *Pinus* logging, would probably help to open the regeneration window (Kollmann 1995). That is, to create appropriate conditions for both the recruitment in shrublands and the growth and successful completion of the regeneration cycle in woodlands. Further analysis of seedling growth would help to unambiguously determine the dynamics of the regeneration process.

The split regeneration model explains ca. 44% of the variability in recruitment occurrence, and where recruitment actually occurs, it explains ca. 41% of the variability in recruitment density. As expected, at the scale studied, recruitment is spatially autocorrelated. This may be due to the different spatial organisation of vegetation and topography and to the spatial patterns of associated recruitment processes such as dispersal and predation. However, by modelling recruitment with spatially structured independent variables, we have removed most of the spatial effect on recruitment occurrence and density, which suggests that the model can be used as a predictive tool.

Further analysis will be needed to elucidate to what extent the small *Q. suber* Pinet population shows a reduced reproduction rate in comparison with to other *Q. suber* populations as a result of genetic erosion, overpredation, lack of dispersers or establishment problems. Nevertheless, our analysis allows us to conclude that this population has the potential capacity to regenerate itself. Parameters related to community structure (forest and understorey structure) are highly important for the recruitment of *Q. suber*, and these may be due to the habitat preferences of the dispersal and predation agents (Torre & Díaz 2004; Pons & Pausas 2004) as well as to the micro-environmental conditions appropriate for germination and establishment (Espelta et al. 1995; Gómez 2004a). In any case, we need to open the regeneration window if we aim to increase the *Q. suber* population size.

Acknowledgements. This work has been financed by the EU project CREOAK (QLRT-2001-01594) and the Spanish project VARQUS (CGL2004-04325/BOS). S. Dias and E. Ribeiro have benefited from an EU Leonardo da Vinci fellowship. We thank R. Bivand for comments and help on the spdep software and P. Garcia-Fayos for comments on the text. CEAM is funded by the *Generalitat Valenciana* and *Bancaixa*.

References

Anon. 2000-2005. *The European Forest Genetic Resources Programme (EUFORGEN)*. IPGRI (International Plant Genetic Resources Institute). URL: http://www.ipgri.cgiar.org/networks/euforgen/Euf_Distribution_Maps.asp [accessed date: 03.07.2004]

Anon. 2005. *R: A language and environment for statistical computing*. R Development Core Team, R Foundation for Statistical Computing, Vienna, AT.

Antos, J.A., Guest, H.J. & Parish, R. 2005. The tree seedling bank in an ancient montane forest: stress tolerators in a productive habitat. *J. Ecol*. 93: 536-543.

Bivand, R. 2005. *The spdep package. ver 0.3-12*. – On line documentation. URL: http://cran.r-project.org/doc/packages/spdep.pdf

Bivand, R. & Gebhardt, A. 2000. Implementing functions for spatial statistical analysis using the R language. *J. Geogr. Syst*. 2: 307-317.

Blanco, E., González, M.A.C., Tenorio, M.C., Bombín, R.E., Antón, M.G., Fuster, M.G., Manzaneque, A.G., Manzaneque, F.G., Saiz, J.C.M., Juaristi, C.M., Pajares, P.R. & Ollero, H.S. 1997. *Los bosques ibéricos. Una interpretación geobotánica*. Planeta, Barcelona, ES.

Blows, M.W. & Hoffmann, A.A. 1993. The genetics of central and marginal populations of *Drosophila serrata*. I. Genetic variation for stress resistance and species borders. *Evolution* 47: 1255-1270.

Bossema, I. 1979. Jays and oaks: an eco-ethological study of a symbiosis. *Behaviour* 70: 1-117.

Cliff, A.D. & Ord, J.K. 1981. *Spatial processes: Models and applications*. Pion, London, UK.

Díaz-Fernández, P.M., Gallardo M.I. & Gil, L.A. 1996. Alcornocales marginales en España. Estado actual y perspectivas de conservación de sus recursos genéticos. *Ecología* 10: 21-47.

Díaz-Fernández, P.M., Climent, J. & Gil, L. 2004. Biennial acorn maturation and its relationship with flowering phenology in Iberian populations of *Quercus suber*. *Trees Struct. Funct*. 18: 615-621.

Diniz-Filho, J.A.F., Bini, L.M. & Hawkins, B.A. 2003. Spatial autocorrelation and red herrings in geographical ecology. *Global Ecol. Biogeogr*. 12: 53-64.

Espelta, J.M., Riba, M. & Retana, J. 1995. Pattern of seedling recruitment in West-Mediterranean *Quercus ilex* forests influenced by canopy development. *J. Veg. Sci*. 6: 465-472.

Frost, I. & Rydin, H. 2000. Spatial pattern and size distribution of the animal-dispersed tree *Quercus robur* in two spruce-dominated forests. *Ecoscience* 7: 38-44.

García-Fayos, P. 1991. La vegetacion silicicola de la Sierra Calderona (Comunidad Valenciana). *Lazaroa* 12: 317-332.

Gómez, J.M. 2003. Spatial patterns in long-distance dispersal of *Quercus ilex* acorns by jays in a heterogeneous landscape. *Ecography* 26: 573-584.

Gómez, J.M. 2004a. Importance of microhabitat and acorn burial on *Quercus ilex* early recruitment: non-additive effects on multiple demographic processes. *Plant Ecol*. 172: 287-297.

Gómez, J.M. 2004b. Bigger is not always better: conflicting selective pressures on seed size in *Quercus ilex*. *Evolution* 58: 71-80.

Gómez, J.M., Valladares, F. & Puerta-Piñero, C. 2004. Differences between structural and functional environmental heterogeneity caused by seed dispersal. *Funct. Ecol.* 18: 787-792.

Grime, J.P. & Hillier, S.H. 2000. The contribution of seedling regeneration to the structure and dynamics of plant communities, ecosystems and larger units of the landscape. In: Fenner, M. (ed.) *The ecology of regeneration in plant communities*, pp. 361-374. CAB International, Wallingford, UK.

Hampe, A. & Petit, R.J. 2005. Conserving biodiversity under climate change: the rear edge matters. *Ecol. Lett.* 8: 461-467.

Hewitt, G.M. 2004. Genetic consequences of climatic changes in the Quaternary. *Phil. Trans. R. Soc. Lond.* B 359: 183-195.

Jiménez, P., Agundez, D., Alia, R. & Gil, L. 1999. Genetic variation in central and marginal populations of *Quercus suber* L. *Silvae Gen.* 48: 278-284.

Johansson, M.E. 1994. Life history differences between central and marginal populations of the clonal aquatic plant *Ranunculus lingua*: A reciprocal transplant experiment. *Oikos* 70: 65-72.

Kohyama, T. 1983. Seedling stages of two subalpine *Abies* species in distinction from sapling stage: a matter-economic analysis. *Bot. Mag.* 96: 49-65.

Kollmann, J. 1995. Regeneration window for fleshy-fruited plants during scrub development on abandoned grasslands. *Ecosience* 2: 213-222.

Kollmann, J. & Schill, H.P. 1996. Spatial patterns of dispersal, seed predation and germination during colonization of abandoned grassland by *Quercus petraea* and *Corylus avellana*. *Vegetatio* 125: 193-205.

Lawton, J.H. 1993. Range, population abundance and conservation. *Trends Ecol. Evol.* 8: 409-413.

Legendre, L. & Legendre, P. 1998. *Numerical ecology*. 2nd. English ed. Elsevier Science, Amsterdam, NL.

Lesica, P. & Allendorf, F.W. 1995. When peripheral populations are valuable for conservation. *Conserv. Biol.* 9: 753-760.

Lönn, M. & Prentice, H.C. 2002. Gene diversity and demographic turnover in central and peripheral populations of the perennial herb *Gypsophila fastigiata*. *Oikos* 99: 489.

Lookingbill, T.R. & Zavala, M.A. 2000. Spatial pattern of *Quercus ilex* and *Quercus pubescens* recruitment in *Pinus halepensis* dominated woodlands. *J. Veg. Sci.* 11: 607-612.

Montero, G., Torres, E., Cañellas, I. 1994. Regeneración de alcornocales. Síntesis biblográfica. *Ecología* 8: 271-283.

Pausas, J.G. 1997. Resprouting of *Quercus suber* in NE Spain after fire. *J. Veg. Sci.* 8: 703-706.

Pausas, J.G. 2004. Changes in fire and climate in the eastern Iberian Peninsula (Mediterranean basin). *Clim. Change* 63: 337-350.

Pausas, J.G., Pons, J. & Vallejo, R. 2004a. Cork Oak Restoration: developing techniques to enhance establishment of a threatened ecosystem (Spain). *Ecol. Rest.* 22: 289-290.

Pausas, J.G., Ribeiro, E. & Vallejo, R. 2004b. Post-fire regeneration variability of *Pinus halepensis* in the eastern Iberian Peninsula. *For. Ecol. Manage.* 203: 251-259.

Petit, R.J., Aguinagalde, I., de Beaulieu, J.L., Bittkau, C., Brewer, S., Cheddadi, R., Ennos, R., Fineschi, S., Grivet, D., Lascoux, M., Mohanty, A., Müller-Starck, G., Demesure-Musch, B., Palmé, A., Martín, J.P., Rendell, S. & Vendramin, G.G. 2003. Glacial refugia: hotspots but not melting pots of genetic diversity. *Science* 300: 1563-1565.

Plieninger, T., Pulido, F.J. & Schaich, H. 2004. Effects of land-use and landscape structure on holm oak recruitment and regeneration at farm level in *Quercus ilex* L. dehesas. *J. Arid Environ.* 57: 345-364.

Pons, J. & Pausas, J.G. 2004. Jay habitat selection in cork-oak landscapes of Eastern Iberian Peninsula. In: Brotons, L., Martin, J.L. & Prodon, R. (eds.*) A landscape perspective on Mediterranean vertebrate ecology*. Montpellier, France 25-26th, March. Book of abstracts. Centre d'Ecologie Fonctionelle et Evolutive-CNRS, Montpellier, FR.

Pons, J. & Pausas, J.G. 2006. Oak regeneration in heterogeneous landscapes: the case of fragmented *Quercus suber* forests in the eastern Iberian Peninsula. *For. Ecol. Manage.* 231: 196-204.

Retana, J., Espelta, J.M., Gracia, M. & Riba, M. 1999. Seedling recruitment. In: Rodà, F., Retana, J., Gracia, C.A. & Bellot, J. (eds.) *Ecology of Mediterranean Evergreen Oak Forests*, pp. 89-104. Springer, Berlin, DE.

Rowlingson, B. & Diggle, P. 1993. Splancs: spatial point pattern analysis code in S-Plus. *Comp. Geosci.* 19: 627-655.

Santos, T. & Tellería, J.L. 1994. Influence of forest fragmentation on seed consumption and dispersal of Spanish juniper *Juniperus thurifera*. *Biol. Conserv.* 70: 129-134.

Santos, T. & Tellería, J.L. 1997. Vertebrate predation on Holm Oak, *Quercus ilex*, acorns in a fragmented habitat: effects on seedling recruitment. *For. Ecol. Manage.* 98: 181-187.

Tellería, J.L., Santos, T. & Alcántara, M. 1991. Abundance and food-searching intensity of wood mice (*Apodemus sylvaticus*) in fragmented forests. *J. Mammal.* 72: 183-187.

Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C., Erasmus, B.F.N., Ferreira de Siqueira, M., Grainger, A., Hannah, L., Hughes, L., Huntley, B., van Jaarsveld, A.S., Midgley, G.F., Miles, L., Ortega-Huerta, M.A., Peterson, A.T., Phillips, O.L. & Williams, S.E. 2004. Extinction risk from climate change. *Nature* 472: 145-148.

Torre, I. & Díaz, M. 2004. Small mammal abundance in Mediterranean post-fire habitats: a role for predators? *Acta Oecol.* 25: 137-142.

Tutin, T.G. (ed.) 1964. *Flora Europaea*. Vol. 1. Cambridge University Press, Cambridge, UK.

Vucetich, J.A. & Waite, T.A. 2003. Spatial patterns of demography and genetic processes across the species' range: null hypotheses for landscape conservation genetics. *Conserv. Gen.* 4: 639-645.

Received 7 February 2006;
Accepted 2 June 2006;
Co-ordinating Editor: M.P. Austin.