UNIVERSIDAD DE EXTREMADURA

CENTRO UNIVERSITARIO DE PLASENCIA

DEPARTAMENTO DE INGENIERÍA DEL MEDIO AGRONÓMICO Y FORESTAL

Limitaciones de la regeneración en poblaciones marginales de *Taxus baccata* y *Betula alba* en ambientes mediterráneos

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El doctorando	**El director**
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Plasencia, Octubre 2008

A mis padres

A Laura

A Marisol

"Hubo árboles antes que hubiera libros, y acaso cuando acaben los libros continúen los árboles. Y tal vez llegue la humanidad a un grado de cultura tal que no necesite ya de libros, pero siempre necesitará de árboles, y entonces abonará los árboles con libros"

Miguel de Unamuno

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Índice

Capítulo 1

Introducción y objetivos

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Las plantas en ambientes marginales

La distribución actual de las plantas responde a la interacción de factores de tipo climático, con precipitación y temperatura como principales parámetros responsables, además de los condicionantes derivados del tipo de sustrato (Woodward 1987). A estos factores abióticos debemos unir las interacciones que las especies vegetales establecen con los factores bióticos y que tienen relevancia en los patrones de distribución de las especies a diferentes escalas espaciales (Arroyo et al. 2004). Las especies pueden ocupar amplias áreas de territorio, de tal modo que la intensidad con la que se manifiestan los factores aludidos, tanto abióticos como bióticos, variará considerablemente dependiendo de la posición geográfica a lo largo del rango de distribución de las especies (Arroyo et al. 2004, Crawford 2008).

Las poblaciones marginales son aquellas que ocupan la periferia del areal de una especie (Crawford 2008). La marginalidad geográfica describe el efecto de unas condiciones ecológicas particulares sobre las poblaciones situadas en los bordes del área de distribución de una especie (Gaston 2003). Algunas características comunes a estas poblaciones son su reducido tamaño, el aislamiento y un elevado grado de estrés ambiental en su entorno, lo que las hace más vulnerables que las poblaciones centrales desde una perspectiva demográfica (Nantel & Gagnon 1999). Por tanto, podemos decir que en estas situaciones las especies ocupan hábitats marginales donde según diversos autores los factores abióticos presentan un papel más limitante que los factores bióticos (García & Zamora 2003, Forbis & Doak 2004). Sin embargo, no hay que olvidar que estas caraterísticas que las convierte en vulnerables también determinan estructuras genéticas peculiares, por lo que son consideradas como poblaciones reservorio de diversidad genética (Safriel et al. 1994, Hampe & Petit 2005).

Las especies de plantas relictas presentan en la actualidad una distribución claramente más restringida que en el pasado (Hampe 2004). En el caso de los relictos arbóreos su relictualidad está intimamente ligada con la marginalidad geográfica, que responde al efecto de los factores históricos y climáticos en la delimitación del área actual de distribución (Arroyo et al. 2004, Pulido et al. 2008, Rodríguez-Sánchez 2008). A las caracteristicas antes mencionadas para las poblaciones marginales debemos sumar que las especies relictas ocupan, en estos márgenes, los enclaves que reproducen en mayor o menor medida las condiciones ecológicas que les son más favorables. Estos lugares se denominan en sentido amplio refugios y, en general, se trata de enclaves riparios o de elevada humedad edáfica que suavizan los efectos del clima mediterráneo (Cox & Moore 1993, Thompson 2005).

Aunque se han realizado un buen número de estudios que comparan genéticamente poblaciones marginales y centrales (Eckert et al. 2008), son menos los que abordan aspectos demográficos (Hampe & Petit 2005). Por otra parte, las últimas revisiones que comparan la variabilidad genética entre poblaciones centrales y periféricas ponen de manifiesto las carencias en el conocimiento de los mecanismos demográficos responsables de la redución de la diversidad en poblaciones periféricas (Eckert et al. 2008).

Los árboles relictos boreales en las montañas mediterráneas: paleohistoria del tejo (*Taxus baccata*) y del abedul (*Betula alba*)

Se considera que el clima típico de la Cuenca Mediterránea aparece hace unos 3.2 millones de años (Suc 1984), mientras que la distribución de los bosques mediterráneos depende en gran medida de los cambios climáticos acaecidos durante el Cuaternario (Arroyo et al. 2004). Numerosas especies vegetales originadas en ambientes templados y boreales sufrieron desplazamientos hacia el sur en periodos glaciales del Cuaternario (Bennett et al. 1991, Tzedakis et al. 2002). Durante los periodos interglaciales, por el contrario, estas especies retrocedieron dejando en el sur poblaciones acantonadas en refugios climáticamente favorables. En el caso del tejo y el abedul, su distribución en la Región Mediterránea se ajusta al concepto de “planta rara”, pues presentan una distribución amplia, con poblaciones de tamaño reducido y acusada especificidad de hábitat (Rabinowitz et al. 1986). Este patrón de distribución es consecuencia del clima dominante hace varios millones de años.

En la península Ibérica se ha reseñado la aparición de polen de *Taxus*, en los bosques mixtos del género *Quercus*, desde los 6000 BP (antes del presente) hasta la actualidad (Peñalba 1994, Cortés et al. 2000). Esta presencia se hace más rara hacia el sur peninsular. El abedul aparece en los registros polínicos de manera muy importante a principios del Holoceno en las áreas del centro y sur (Janssen & Woldringh 1981). Tanto *T. baccata* como *B. alba* pueden considerarse relictos climáticos cuya distribución actual atiende a cambios históricos en el clima (Cox & Moore 1993) y cuyo factor limitante sería la temperatura y los efectos asociados a ésta (Arroyo et al. 2004).

Estas poblaciones relictas de especies leñosas en las sierras y montañas del ámbito mediterráneo son de enorme interés desde el punto de vista genético y biogeográfico. El aislamiento sufrido por estas especies podría explicar que la mayor parte de la variación genética se concentre en las áreas más meridionales (Hampe & Petit 2005). Esta diversidad se pone de manifiesto a escala regional, ya que estas poblaciones suelen ser genéticamente poco diversas a nivel intrapoblacional (Petit et al. 2003).

Debido a sus singulares patrones de distribución los táxones citados se incluyen en la mayoría de los catálogos regionales de especies amenazadas, lo que reconoce su importante valor biogeográfico en los ambientes mediterráneos (Devesa & Olivenza 2004). Esta consideración ha estimulado la dedicación de fondos públicos para el estudio de los procesos que limitan en la actualidad la regeneración natural de estas especies, ya que la calidad de la información disponible puede condicionar el éxito en la aplicación de medidas de conservación de las especies.

La regeneración natural de especies arbóreas relictas en ambientes de montaña mediterránea

Los ambientes de montaña mediterráneos constituyen un interesante campo de estudio para la ecología de la regeneración de especies arbóreas en el margen de su área de distribución. Así, en las últimas décadas se han llevado a cabo un buen número de estudios en la península Ibérica sobre la dinámica regenerativa de estas especies en áreas montañosas del centro y sur de la península (Arista 1994, Medán 1994, García et al. 1999, Camarero & Gutiérrez 1999, Castro et al. 1999, García et al. 2000a, García 2001, Hampe & Arroyo 2002, Mejías et al. 2002, Castro et al. 2004, Hampe 2005, Arrrieta & Suárez 2005, 2006, Pulido et al. 2008, Rodríguez-Sánchez & Arroyo 2008).

Entre los factores que limitan la regeneración podemos hablar de factores abióticos y factores bióticos. En el primer caso, las condiciones abióticas son especialmente duras en los ambientes mediterráneos durante el período de sequía estival. La marcada estacionalidad en las precipitaciones determinará los patrones de humedad del suelo a lo largo del año siendo este un condicionante para la distribución y abundancia de especies leñosas (Marañon et al. 2004). La escasez de agua durante el estío supone una importante pérdida de plántulas, que no sobreviven al primer verano, efecto este que incide negativamente en el reclutamiento de nuevos individuos para la población y que aparece bien documentado en diversas especies leñosas (Hampe & Arroyo 2002, Gulias et al. 2004, Arrieta & Suárez 2005, 2006). En relación a los factores bióticos, los individuos que forman parte de pequeñas poblaciones pueden presentar fenómenos de erosión genética y depresión endogámica, con la consiguiente reducción de la calidad y cantidad de semillas viables (Lawton 1993, García et al. 2000b, Vucetich & Waite 2003). Por otra parte las poblaciones de reducido tamaño presentan un mayor efecto de borde, lo que en ocasiones implica una mayor tasa de depredación de sus semillas (Santos & Tellería 1997). Así, la depredación posdispersa de semillas presenta valores muy elevados en numerosas especies leñosas presentes en ambientes mediterráneos y que mantienen poblaciones de reducido tamaño (Hulme 1997, Castro et al. 1999, Hampe & Arroyo 2002).

La regeneración natural del tejo y el abedul ha sido descrita con mayor o menor profusión en las áreas centrales de su área de distribución (véase Thomas & Polwart 2003 y Atkinson 1992 para revisiones de ambas especies) pero los estudios son mucho más escasos en áreas marginales, siendo incluso inexistentes en el caso del abedul.

Existen trabajos previos, principalmente en la Iberia húmeda, que abordan diferentes aspectos de la regeneración en las etapas posdispersivas en el caso del tejo (García et al. 2000, García & Obeso 2003, García & Obeso 2005, García et al. 2007) y son mucho más escasos en el abedul, para el que existen trabajos en la Iberia húmeda relacionados únicamente con la germinación, producción y emergencia de plántulas en bosques de clima atlántico (Reyes et al. 1997, Álvarez-Uría 2000, Laskurain et al. 2002, Herrera et al. 2002, Reyes & Casal 2003). No obstante, el efecto de condicionantes bióticos pre- y posdispersivos y su interacción con el efecto de un clima típico de montaña mediterráneo no ha sido estudiado hasta la fecha de forma integrada en el caso de ninguna de las dos especies.

Para terminar, cabe apuntar que estas especies que hoy en día son testigo de climas del pasado se enfrentan en las próximas décadas a un nuevo cambio global, conocido por todos como el cambio climático. No son pocos los trabajos que están abordando el problema del cambio climático usando como modelo de estudio estas especies de flora u otras de fauna que en no pocas ocasiones comparten una historia similar y que son un modelo de estudio apropiado para testar hipótesis sobre cómo afectará el futuro cambio en el clima a la distribución de los seres vivos (Thuiller 2005, Troung et al. 2007, Araújo & Luoto 2007). Recientemente se ha comprobado (Nogués et al. 2008) el efecto del futuro calentamiento global sobre las áreas de montaña mediterráneas. Las conclusiones son poco halagueñas puesto que predicen un marcado aumento en las temperaturas y una importante disminución en las precipitaciones, principalmente durante la primavera. Junto al efecto que el cambio en el clima pueda tener sobre la distribución futura de las especies tanto vegetales como animales conviene no olvidar los cambios en el manejo del campo que han acaecido en Europa en las últimas decadas (Bengssston 1993). En las áreas de montaña, el abandono de los usos tradicionales de ganadería extensiva y agricultura de subsistencia han generado un nuevo paisaje, definido por un aumento de las formaciones vegetales arbustivas y un escenario de recuperación del bosque autóctono en detrimento de las áreas abiertas de pastizales y matorrales de pequeño porte (Pulido et al 2007). Paralelamente, ha aumentado la incidencia de los grandes incendios forestales con el consiguiente riesgo de homogeneización del paisaje hacia la matorralización y un potencial peligro sobre los "refugios" donde habitan las especies amenazadas objeto del estudio.

Objetivos generales y estructura de la tesis

Aunque los trabajos comentados abordan el problema de la regeneración de estas especies desde múltiples perspectivas y son válidas para la comprensión de la dinámica de la regeneración en ambientes de clima templado, resultan difícilmente trasladables a los ambientes mediterráneos, en los que estas especies pueden sufrir diversos procesos de limitación demográfica sujetos a la existencia de factores abióticos o bióticos limitantes. Por ello los objetivos principales de la tesis son:

(1) Analizar la ecología de la regeneración del tejo y el abedul como representantes de una flora relicta boreal en ambientes mediterráneos.

(2) Evaluar el papel de los efectos abióticos y bióticos asociados a la condición marginal de las poblaciones de tejo y abedul.

(3) Comparar la respuesta a la marginalidad de dos especies relictas boreales que difieren en rasgos ecofisiológicos y reproductivos básicos.

(4) Generar información sobre las restricciones ambientales que afectan a especies arbóreas amenazadas por la condición marginal de sus poblaciones, de cara a su aplicación en proyectos de conservación en ambientes mediterráneos de montaña.

La presente Memoria consta esencialmente de cinco apartados (capítulos 2-6) que adoptan la estructura habitual de artículos científicos de ámbito internacional, por lo que aparecen redactados en inglés. Inevitablemente, ésto implica la reiteración de algunos de los contenidos a lo largo de algunos capítulos. Para facilitar la comprensión global del trabajo se ha incluido como capítulo 7 una Discusión general además de unas conclusiones que cierran la tesis. A continuación se describe brevemente el contenido de los capítulos 2 al 6 de la presente Memoria.

En el **Capítulo 2** se examina el efecto de una variable abiótica, en este caso la disponibilidad hídrica, y en qué medida la abundancia de ésta determina la regeneración natural de *T. baccata* a lo largo de su área europea de distribución, realizándose una aproximación desde diferentes escalas espaciales. Se analizó el efecto de la disponibilidad hídrica sobre la regeneración de la especie desde una escala local pasando por la regional hasta la continental. Para ello se utilizaron diferentes aproximaciones metodológicas que fueron desde la monitorización y seguimiento de la emergencia y supervivencia de las plántulas a la utilización de herramientas SIG para estudiar el efecto de las precipitaciones medias anules y estivales sobre el índice de regeneración en poblaciones europeas. En el **Capítulo 3** se profundiza en el estudio de diferentes etapas del ciclo de regeneración de *B. alba* con el fin de determinar cuales son los estadios críticos que limitan su regeneración natural en la región de estudio. Por otra parte, son escasos los trabajos que abordan el fenómeno de la polinización anemófila en una especie dioica, en este caso el tejo, distribuida en pequeñas poblaciones marginales y cual es el efecto de la distancia entre machos y hembras para el éxito reproductivo de cada árbol y por lo tanto el éxito evolutivo de esa población; este fue el objeto del **Capítulo 4**.

El **Capítulo 5** parte del hecho de que algunos trabajos han abordado cómo es la depredación posdispersiva en poblaciones marginales de estos árboles relíctos y en particular de *T. baccata* en poblaciones del margen sur (Hulme 1997) y últimamente comparando poblaciones del centro y sur (García-Castaño et al. 2006). Aún así, no carece de interés describir el proceso a lo largo de un período largo de tiempo en el que las semillas ocupan el suelo, así como relacionar el consumo de las semillas con la distancia a la planta madre además de estudiar si las tasas de depredación son mayores en poblaciones del margen con respecto a las centrales. Por último, el **Capítulo 6** se centró en el estudio del efecto del microhabitat (matorral *vs.* pastizal) sobre la supervivencia de las dos especies estudiadas *T. baccata* y *B. alba* en la periferia de su área de distribución, en ausencia de herbívoros, explorando su relación con parámetros abióticos como el ambiente lumínico y la humedad del suelo.

El tejo y el abedul en el el área de estudio

Las poblaciones de estudio se encuentran situadas en la periferia sur de sus respectivas áreas de distribución. En la región se extienden por zonas de media montaña de la cara sur del Sistema Central, al norte de la provincia de Cáceres dentro de la Comunidad Autónoma de Extremadura (Fig 1). Son áreas montañosas de accidentada topografía. En general, abundan los sustratos graníticos en las comarcas del este y centro-este y pizarrosos en la comarca de las Hurdes, al oeste del sistema montañoso. Las poblaciones se extienden entre los 900 y 1700 m.s.n.m, por lo que biogeográficamente ocupan el horizonte superior del piso mesomediterráneo y la totalidad del piso supramediterráneo (Rivas Martínez 1987). El clima, de tipo mediterráneo, se caracteriza por presentar inviernos relativamente lluviosos y fríos y veranos con altas temperaturas y escasas precipitaciones (Pulido et al. 2007). Las temperaturas medias anuales para las estaciones meteorológicas más cercanas a las poblaciones indican una temperatura media anual comprendida entre los 13.3 ° C en el área oeste (Cerezal, Las Hurdes), los 14.3 °C en el centro (Nogaledas y Papúos, Barrado) y los 16.8 ° C en el este (Regaderas, Madrigal de la Vera) y una precipitación media anual comprendida entre los 1321 mm del Cerezal al oeste y los 1053 mm de Madrigal de la Vera al este. Si bien hay que constatar que las estaciones meteorológicas se sitúan en altitudes muy inferiores a las ocupadas por las poblaciones de estudio, por lo que tomaremos estas cifras como orientativas. Las poblaciones se encuentran en asociación a cauces permanentes o estacionales; gargantas con exposición norte o noroeste en la mayoría de los casos. Cuando los cauces son permanentes, tejos y abedules suelen aparecer en el subvuelo de un bosque de galería dominado por alisos (*Alnus glutinosa*), pero en otras muchas situaciones, se encuentran asociados a cursos de agua estacionales entre brezales y escobonales típicos de zonas de media montaña. Los brezales están dominados por brezo rojo (*Erica australis*) y brezo blanco (*Erica arborea*) y en los escobonales se mezclan diferentes especies de escobas (*Genista florida*, *Genista cinerascens*) y piornos (*Cytisus oromediterraneus*). En la comarca de Las Hurdes (Cerezal) la presencia del tejo está asociada a una vegetación típica del piso mesomediterráneo con ombroclima húmedo. Se encuentra presente en formaciones maduras de madroñal (*Arbutus unedo*) con encinas (*Quercus ilex* subsp. *ballota*).

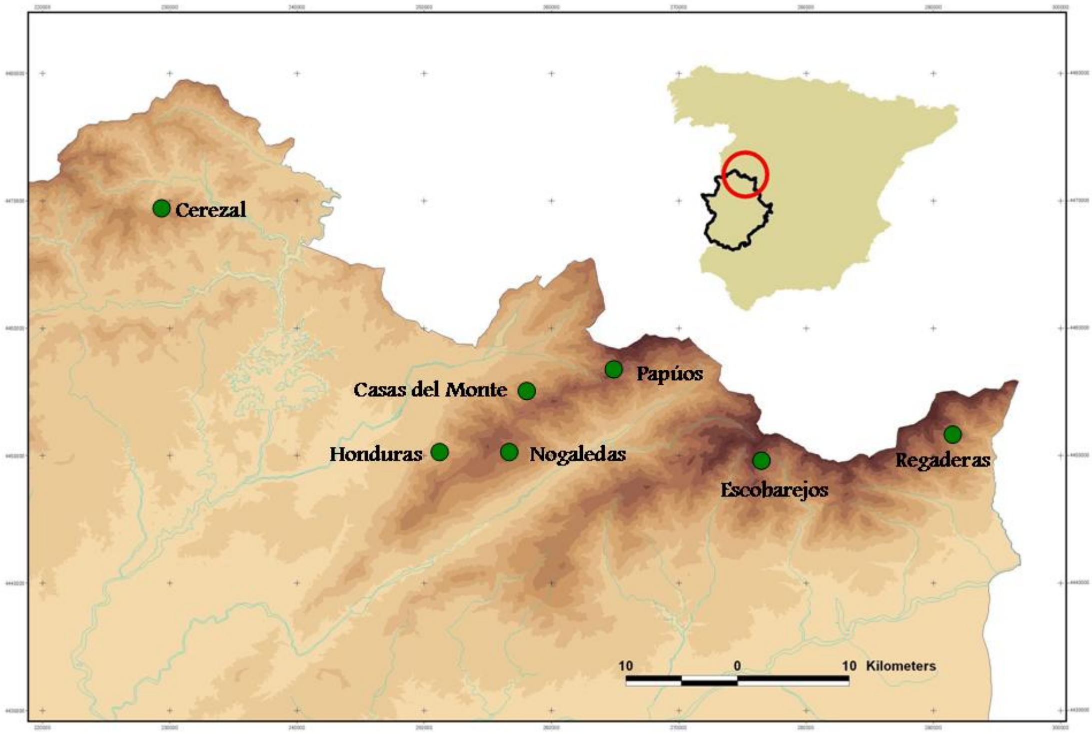

Figura 1. Poblaciones de estudio.

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Capítulo 2

Predicción de mecanismos a diferentes escalas espaciales: el efecto amplificado de las limitaciones abióticas sobre el reclutamiento del tejo (*Taxus baccata*)

Predicting mechanisms across scales: amplified effects of abiotic constraints on the recruitment of yew (*Taxus baccata*)

Predicting mechanisms across scales: amplified effects of abiotic constraints on the recruitment of yew (*Taxus baccata*)[1]

Abstract

Could we predict at large scale the main biological mechanisms that drive the local performance of species populations? Efforts to disentangle the mechanisms underlying large-scale spatial patterns must necessarily rely on multi-scale approaches from population level to the geographical range of species. We illustrate this key issue by analyzing the spatial consistence across scales of the effects of abiotic constraints on the regeneration success of the English yew (*Taxus baccata*) throughout its whole European range. We hypothesized that the recruitment rates in a given population would be strongly affected by water availability, which in turn should result in a predictable pattern of regeneration success at regional and continental scales. Therefore, we formulated the following predictions: (1) at the regional scale water availability should be higher in sites occupied by yew populations than in random locations; (2) at the regional scale regeneration success should decrease when water availability is lower; and (3) at the continental scale, regeneration success should also decrease where water availability is lower, resulting in a geographical trend of decreasing regeneration southwards. To test these predictions we first monitored seedling emergence and survival in two central Spanish populations during two years, and confirmed that yew recruitment is mainly limited by water availability at the local scale. Also, our analysis supported predictions 1 and 2: water availability strongly affected yew presence and regeneration success. At the continental scale (prediction 3), our results fulfilled the expectancy of lower regeneration in southern European populations as compared to central European ones. We propose that assessing the effect of climatic constraints across scales in key parameters for the persistence of populations is a crucial issue to improve large-scale assessments of impacts of climate change on biodiversity.

Introduction

Macroecology has been intensively describing large-scale biological patterns under the promise that they could be explained by a mechanistic evaluation of processes operating at different spatial scales (Brown 1999). However, one crucial

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[1] Sanz, R., Pulido, F. & Nogués-Bravo, D. Predicting mechanisms across scales: amplified effects of abiotic constraints on the recruitment of yew (*Taxus baccata*). En revisión en *Ecography*.

issue is still unresolved, that is, the evaluation of the effect of mechanisms in macroecological patterns across scales. Firstly, only few macroecological studies incorporate the mechanisms responsible for biotic diversity gradients in spatially explicit models (e.g., Rahbek 2007, Rangel 2007). Secondly, the progress in documenting mechanisms and testing their effects on emerging large-scale patterns across the whole hierarchy of scales has been only modest, most likely because of the difficulty to incorporate biotic variables at each relevant scale in a rigorous empirical evaluation framework. Advances in this topic is of most importance for the own development of Macroecology as mature discipline but also because understanding and predicting effects of global change on biodiversity require of integrative studies across scales (Kühn et al. 2008). Herein, we illustrate a potential way to progress in this issue.

From the "microecological" side, integrative studies on plant population dynamics have shown that biotic and abiotic interactions may be partly responsible for plant distribution at a broader, landscape scale (Chown et al. 2004). Theoretically these bottom-up effects across scales could also take place from the regional to the continental scale (Anderson et al. 2002). In practice, however, bottom-up effects of biotic or abiotic interactions are most commonly tested in a limited spatial context, that is, at the level of landscapes or regions (Davis et al. 1998, Lipscomb & Nilsen 1999). Though top-down and bottom-up approaches have been used in the above empirical studies, their practitioners have usually emphasized one of the extremes, while little effort has been devoted to analyze the consistence of mechanisms across the whole continuum of scales, from population to the geographical range of species.

Problems involved in tracking the multi-scale effect of any given abiotic factor on ecological processes can be partly overcome in the case of certain organisms under particular conditions. This could be the case of widely distributed plants that are highly sensitive to abiotic stress (Rabinowitz et al. 1986). Climate-induced limitations might exert a strong influence on these plants at various scales, for example by locally influencing the chance of seedling recruitment or by determining the species' ability for successful regeneration in a given region (Pigott & Pigott 1993, Brèda et al. 2006). Hence, successful recruitment is a prerequisite for the maintenance of viable populations, which in the long term shape species' range boundaries (Gaston 2003, Pulido et al. 2008). Thus, one outstanding consequence of variation in recruitment success through a species' range is the centre-periphery gradient in population ability for persistence, which tends to be explained by range-wide variation in climatic stress (Brown et al. 1996, Vucetich & Waite 2003).

Here we examine the spatial consistence across scales of the effects of abiotic constraints on the process of plant recruitment. By using the English yew (*Taxus baccata*) as a model species, we scale-up the effect of water availability from the local to the regional to the continental scale. We hypothesized that the recruitment rates in a given population would be affected by water availability, which in turn should result in a predictable pattern of regeneration success at regional and continental scales. Therefore, we formulated the following predictions: (1) at the regional scale water availability should be higher in sites occupied by yew populations than in random locations non-occupied by yew; (2) at regional scale regeneration success should decrease when water availability is lower; and (3) at the continental scale, regeneration success should also decrease when water availability is lower, resulting in a geographical pattern with the southern European populations, growing in dryer zones, showing lower regeneration success. In addition, we evaluated whether the predicted continental trend could be extrapolated to the whole species' range by including populations at the northern edge.

Methods

Yew distribution

The English yew is a dioecious, long-lived tree species with a Eurasian distribution. Yew populations are present in Europe, East Asia and North Africa (Schutt 1995, Thomas & Polwart 2003; Figure 1). Most regions occupied by yew occur in Europe, where the species lives from 63° to 36° N latitude. Despite its broad distribution yew is considered in most regions as a threatened species (Thomas & Polwart 2003). The regeneration of yew is closely related to abiotic factors such as water and light availability (Svenning & Magard 1999, García et al. 2000a, Dovciak 2002, Iszkulo & Boratynski 2006). Previous studies have also shown that biotic interactions, such as the dispersal of seed by avian frugivores and browsing by ungulates can shape local demographic structure and landscape distribution patterns (García & Obeso 2003, García & Ortiz-Pulido 2004).

Local scale

The study at the local scale addressed the factors determining recruitment success of yew. Field work was conducted in the western Sistema Central mountain range (Cáceres province), a central Spanish region located in the southern edge of the species' range (Figure 1). The climate is continental Mediterranean with dry summers and cold winters. An intensive research was conducted in two populations, namely

Escobarejos and Cerezal, that were 62 kilometres apart. The Escobarejos population was located at 1350 m elevation and it comprised 34 adult trees associated to seasonal streams surrounded by shrublands dominated by *Erica australis* and *Cytisus oromediterraneus.* Fleshy-fruited tree species (*Sorbus aucuparia* and *Ilex aquifollium*) were also present in low numbers. The Cerezal population was located at 900 m elevation and it comprised 53 adult trees that grew close to streams in the understorey of a mixed montane forest with *Quercus ilex* and *Arbutus unedo* as dominant species.

On the basis of previous studies on Mediterranean woody plant recruitment rates (Jordano et al. 2004), on regeneration of fleshy-fruited gymnosperms in drought-prone environments (García et al. 1999, 2000b), and in our own information for yew (Sanz, *unpublished data*), we focussed our attention on the emergence and the fate of seedlings as the main determinants of population recruitment. The study was performed with seedling cohorts from two reproductive cycles (2004-2005 and 2005-2006; 2005 and 2006 hereafter). First, we established the study area of both populations as the minimum convex polygon defined by all the trees present. Within this area a complete survey of seedlings emerged each year was carried out monthly in late May, June, and July, when emergence was completed. Secondly, for each seedling found we noted the distance (m) to the nearest stream as a proxy variable for water availability, as well as the microhabitat in which it grew: under fleshy-fruited shrubs, under non fleshy-fruited shrubs, under the canopy of adult yew and open ground. Also we noted the microsite in which the seedling grew, as it could reflect the moisture environment experienced: bare ground, moss, and small patches of grass. Survival of seedlings was checked at 3-month intervals from May 2005 to November 2006. Finally, to evaluate the degree of microhabitat selectivity, we estimated the percentage cover of the different microhabitats and we compared it with the percentage of seedlings emerging in them. Cover of microhabitats was estimated by randomly selecting 200 points (5 m apart from each other) along parallel transects defined in each stand. On each point we placed a stick vertically and noted the type of microhabitat contacted.

We tested for the effect of environmental variables on seedling recruitment by means of Generalized Linear Models (GLZ) with cohort, population, microhabitat, and microsite as factors, and distance as a continuous predictor. We included only three factors at a time with microhabitat or microsite in the models to facilitate their interpretation, provided some levels of the "microsite" factor did not appear in some levels of the "microhabitat" factor. Survival was considered as a dichotomous response variable (0, 1) with a binomial distribution. We used the logit link function and the Wald statistic for significance testing. For evaluating whether the emergence of new seedlings was randomly distributed between the different microhabitats and between different distances to stream classes, the observed and expected frequencies were compared with Chi-square tests.

Regional scale

The study at the regional scale addressed the effect of water availability on the distribution and the regeneration success of yew populations. The region studied was approximately 300 km^2 in area. At this scale we made a complete survey to locate isolated yew trees and populations. On each site we counted the number of saplings and juveniles within a distance of 20 m at both sides of the spring where adults were found. In addition we recorded the coordinates, size (diameter at breast height at 1.3 m, DBH), and sex of adult trees. From this information we derived frequency

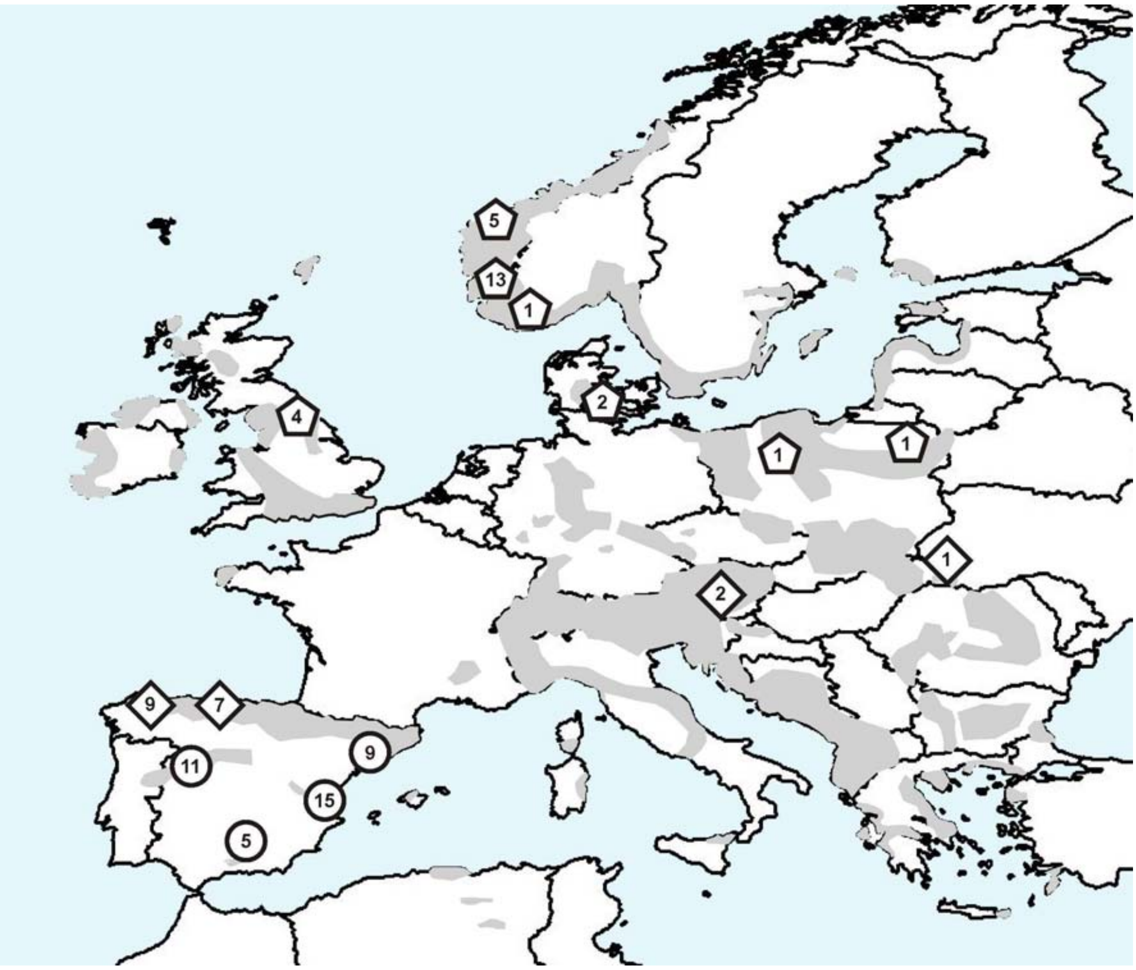

Figure 1. Distribution of yew (*Taxus baccata*) in Europe (shaded area) redrawn and modified from Schütt (1995) and Thomas & Polwart (2003). Also shown is the location of the sites for which indices of regeneration were available. Different polygons refer to different latitudinal zones, the figure inside de polygon indicating the number of sites sampled (see Appendix 1 for a complete list).

distributions of size classes and a regeneration index computed as the ratio of saplings plus juveniles to the total number of individuals including adults. This calculation rendered a standardized index ranging from 0 to 1 (recruits fraction, RF hereafter). Saplings were individuals above one year old and up to 50 cm, while juveniles were non-reproductive individuals above 50 cm. Trees were considered as "adults" if they bore reproductive structures. Estimates of size as a surrogate of age have been widely used in previous studies of yew (see e.g., Hulme 1996). On this basis we used size structures as descriptors of age structures of populations, whereas RF was used as a common estimate of the success of the regeneration process through all spatial scales.

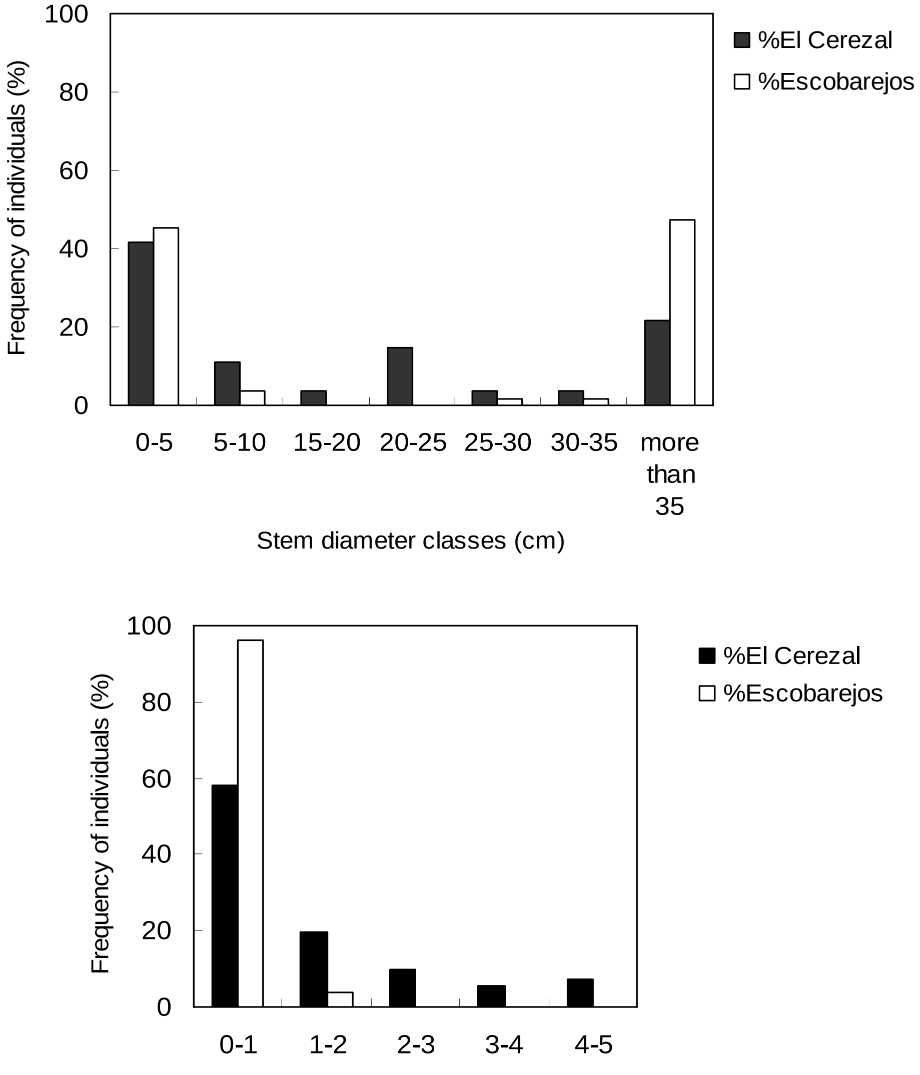

Figure 2. Size structure of the two populations used in the intensive demographic study as estimated by the stem diameter measured at 1.3 meters. The upper graph shows the frequency distribution for the whole range of size and the lower graph depicts the frequency of classes up to 5 cm in stem diameter (non adult individuals).

To evaluate the influence of water availability on yew presence we tested whether yew distribution departed significantly from random with respect to several proxy variables related to water availability. We first obtained the values of these variables for random and yew points by introducing their coordinates in a Digital Terrain Model with Sextante upon gvGIS 0.1 version (Olaya 2005). Then we recorded the values of elevation, slope, aspect, and distance to the nearest stream for 182 points with presence of yew trees and for 222 points selected at random within the altitudinal range of yew (903-1703 m) in the study region. Comparison of data for locations with yew populations and locations randomly selected non-occupied by yew populations allowed us to test prediction 1. We used parametric tests (Student t) when data of physiognomic variables had a normal distribution or when they could be normalized, and non-parametric tests (Mann-Whitney U) when data could not be normalized.

In addition, using data from 16 meteorological stations and a Digital Terrain Model we estimated the amount of annual and summer precipitation by spline interpolation. In addition irradiance, water flow accumulation and wetness index were estimated to account for topographical effects on water availability (Olaya 2005). By testing for the effects of these indices on RF by means of multiple regression analysis we evaluated prediction 2.

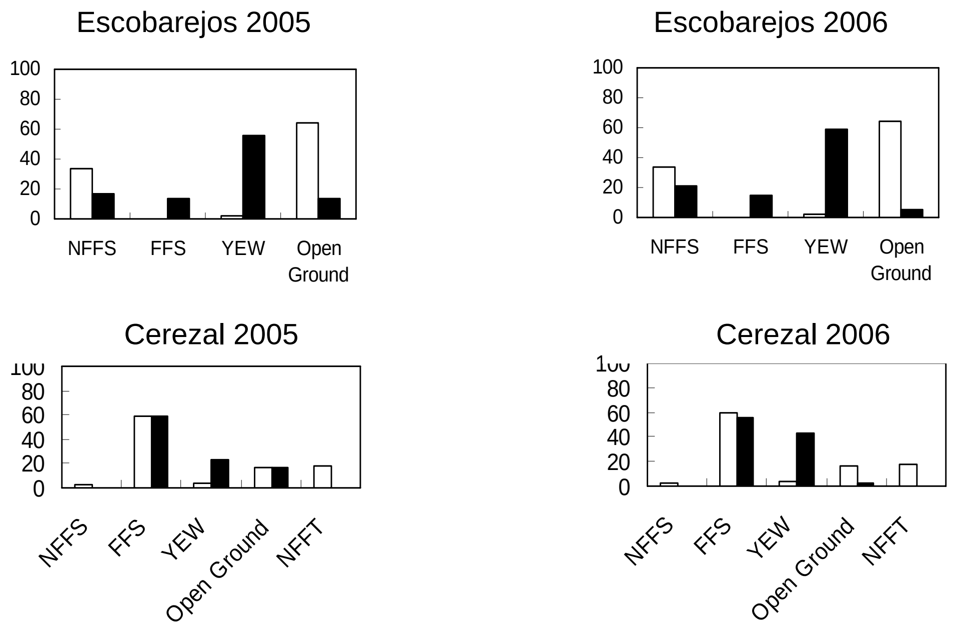

Figure 3. Comparison of availability (percentage cover) and use (percentage seedlings emerged) of microhabitats in two cohorts of each population used in the intensive demographic study.

Table 1. Results from Generalized Linear Models analysis testing for the effects of year, population, and microsite on seedlings establishment after the first summer.

Effect	Wald	df	p
Distance to stream	12.374	1	< 0.001
Year	0.200	1	0.654
Population	11.362	1	< 0.001
Microsite	5.650	1	0.017
Year × Population	11.484	1	< 0.001
Year × Microsite	1.283	1	0.257
Population × Microsite	0.501	1	0.479
Year×Population × Microsite	0.000	1	0.999

Continental scale

We conducted an analysis at a continental scale to test for the effect of water availability on regeneration success as estimated by RF. We took advantage of the large number of studies addressing stand structure in Europe covering the whole latitudinal range of the species (Figure 1). By checking published journal articles or unpublished reports we obtained the number of saplings, juveniles, and adults in each population, which was defined as a stand with five or more adult trees. In two regions in central and eastern Spain for which a very large number of nearby populations had been studied, we randomly selected 15 stands to increase the independence of the data. For the resulting 88 European sites (Appendix 1) we obtained figures of summer and total annual precipitation. We used data form the period 1961–1990 for calculations (New et al. 1999).

For testing our prediction 3 we used data only from central and southern yew populations (n = 61; see below). We excluded northernmost populations because we had no *a priori* reason to expect any given trend concerning the effect of water availability in the northern margin. Using population and climatic data for the remaining sites we evaluated the existence of a driving effect of water availability in the regeneration status of yew. We calculated the Pearson *r* correlation between RF and summer rainfall and annual rainfall for 19 central and 42 southern populations (n = 61). We accounted for the effect of the spatial auto-correlation on the degrees of freedom following Dutilleul (1993). We also used multiple regressions to control for the possible effect of population size on RF.

A supplementary analysis was conducted to test for the existence of a latitudinal trend in RF at the scale of the whole European range. The 50° N latitude was established as the border line separating central and northern populations, whereas the 43° N line was established as the border between central Temperate and southern Mediterranean zones (Figure 1). Firstly, we used linear and non-linear regression techniques with latitude (N degrees) as an independent variable and RF as response variable. Secondly, we used General Linear models for an ANOVA design to test for differences among latitudinal zones in RF while accounting for the effect of population size, which was treated as a covariate. Throughout the text means are shown ± 1 standard error (SE) unless otherwise stated. For data analysis we used the packages Statistica (release 6.0, StatSoft Inc. 2003), Idrisi Kilimanjaro (Clark Labs 2003) and SAM (Rangel et al. 2006).

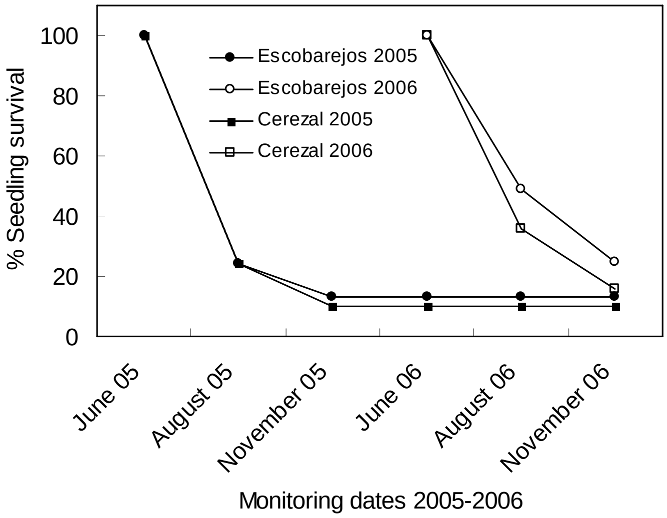

Figure 4. Curves depicting survival of seedlings from two cohorts of each of the two populations used in the intensive demographic study. For each population the 2005 cohort correspond to seedlings emerged in spring 2005 and the 2006 cohort corresponds to seedlings emerged in spring 2006.

Results

Local scale: size structure and recruitment

Data on adult tree size found at this scale showed that the Cerezal population had a inverse J-shaped size structure indicating continuous input of recruits, whereas the Escobarejos populations had an ageing structure due to the lack of established juveniles (Figure 2). A total of 490 newly emerged seedlings were monitored in the two study years. This figure included 307 in the 2005 cohort (122 in Escobarejos and 185 in Cerezal) and 183 in the 2006 cohort (80 in Escobarejos and 103 in Cerezal). Almost all seedlings emerged at very short distances from the closest stream (our proxy variable for water availability), that is, within the first distance class (0-10 m). This emergence pattern was consistent for all populations and years, as shown by strong deviation of the frequencies of emergence in four different distance classes from random expectations ($\chi^2 = 27.47$, df = 3, $p < 0.001$ in all possible combinations). In addition, emergence was significantly concentrated with respect to microhabitat, in such a way that, along stream banks, almost all seedlings were found beneath yew trees or under fleshy-fruited shrubs (Figure 3).

Seedling survival was extremely low in all populations and years. Only 15.9% of the seedlings monitored survived after the first summer when all the data were pooled (Figure 4). This figure contrasts with survival for the second summer, with all second-year seedlings surviving after such period (Figure 4). There were significant effects of distance to stream, population, and microsite on the probability of seedling

Table 2. Percentage seedling survival in different microhabitats in 2005 and 2006 in the populations of Escobarejos and Cerezal. Sample sizes are shown in parentheses.

	Escobarejos		Cerezal	
	2005	2006	2005	2006
Fleshy-fruited shrubs	23.5 (17)	75 (12)	26.4 (110)	22.8 (57)
Non fleshy-fruited shrubs	42.8 (21)	88.2 (17)	0 (1)	-
Yew	0 (68)	17 (47)	11.9 (42)	2.3 (44)
Open	12.5 (16)	25 (4)	28.1 (32)	50 (2)

establishment after the first summer, as shown by GLZ modelling (Table 1). When microhabitat was included in the model its effect was not significant, though both shrub categories pooled clearly enhanced survival as compared to yew and open microhabitats (Table 2). The most important factor causing seedling death in all populations and years was water availability in summer, which accounted for 52 and 67% mortality in 2005 and 2006, respectively. Second in importance were trampling by large herbivores in Escobarejos (between 29% - 40%) and accidental burial in Cerezal (between 15%-21%).

Regional scale: distribution and regeneration status

Distance to the nearest stream was by far the most significant variable explaining yew presence (mean value for random points was 151.4 ± 135.0 m as compared to 4.5 ± 2.1 for yew points). Statistical comparisons of mean values for yew points and random points indicated very significant selectivity for streams (U = 15.94, $p < 0.001$), whereas no selection was evident for altitude ($t = 0.31$, $p = 0.760$). Also the species was more likely to occur in northeast orientations (U = 6.04, $p < 0.001$) and steeper slopes ($t = 5.82$, $p < 0.001$) than available. Overall, these results support our prediction 1.

Figure 5. Frequency distribution of the index of regeneration (RF all), computed as the ratio of saplings plus juveniles to the total number of individuals including adults in a given population (n = 43 sites). Also shown are a RF estimated for saplings (recent regeneration) and a RF estimated for juveniles (older regeneration).

Yew stands in the study region were typically small in size. Out of 43 stands found only six had 10 or more adults (mean 5.58, median 2). The size structure of populations showed a general regeneration failure as indicated by the low frequency of non-adult age classes, which were present in only 16.3% of the stands. Frequency distribution of RF was extremely right-skewed even when the index was decomposed by separately using saplings (recent regeneration) and juveniles (past regeneration; Figure 5). A multiple regression analysis including all physiognomic and climatic variables and population size as predictors showed significant effects of summer precipitation ($p = 0.040$) and population size ($p = 0.00008$; Table 3). When we considered only 11 populations with five or more adults, the multiple model was not significant (results not shown), but summer precipitation successfully predicted RF in a simple linear regression ($t = 2.398$, $df = 9$, $p = 0.039$).

Table 3. Results from multiple regression analysis at a regional scale (n = 43 yew sites) using physiognomic and climatic variables, and population size as predictors of the regeneration success (recruits fraction, RF). Results for the whole model are: $R^2 = 45.54\%$, F = 4.868, df = 8,29, p = 0.0007).

	B	SE β	B	SE B	t	p
Elevation	0.362	0.169	0.000	0.000	2.145	0.040
Irradiance	-0.343	0.137	-0.003	0.001	-2.297	0.018
Flow accumulation	0.118	0.195	0.000	0.000	0.607	0.548
Wetness index	-0.020	0.192	-0.003	0.024	-0.109	0.913
Summer rainfall	0.432	0.201	0.015	0.007	2.147	0.040
Annual rainfall	-0.211	0.199	-0.001	0.001	-1.056	0.299
Distance to stream	0.027	0.131	0.000	0.001	0.207	0.836
Population size	0.594	0.129	0.011	0.002	4.589	8×10^{-5}

Table 4. Results from multiple regression analyses at a continental scale with summer and annual rainfall and population size (number of adult trees) as predictors, and the index of regeneration (recruits fraction, RF) as dependent variable.

	β	SE β	B	SE B	t	p
Intercept			0.121	0.163	0.741	0.462
Population size	0.119	0.138	0.000	0.000	0.895	0.394
Annual rainfall	0.037	0.188	0.000	0.000	0.200	0.841
Summer rainfall	0.637	0.203	0.002	0.001	3.123	0.003

Continental scale: regeneration status

Fifty-one (60%) out of 88 populations had values of RF below 0.5 and virtually no regeneration (RF < 0.1) was found in 27 (32%) populations (Appendix 1). For testing prediction 3 we computed the Pearson r correlation between RF and water availability using the values from central and southern populations. RF was significantly affected by water availability when considering either summer precipitation (n = 61, r = 0.532, p = 0.019) or annual precipitation (n = 61, r = 0.567, p = 0.032). The values of RF increased linearly with water availability (Figure 6), supporting our prediction 3. This was confirmed when, besides precipitation, population size was included as a predictor of RF in a multiple regression analysis, which showed also a significant effect of summer precipitation and a non-significant effect of population size (Table 4).

To evaluate the strength of whole-range trends in RF we performed the above analyses including also data for 27 populations in the North zone (n = 88; Appendix 1). There were significant differences in RF between latitudinal zones after removing the influence of population size in an ANCOVA (F = 10.213, df = 2,83, p = 0.0001). On average central European populations showed significantly higher RF values than populations located at the northern (p = 0.00002) and southern extremes (p = 0.0001; Fisher LSD post hoc tests). Therefore, the relationship between RF and latitude was much better described by quadratic rather than lineal models (R^2 = 14.62%, p = 0.0002 in a linear model and R^2 = 32.49%, p = 0.0000001 in a quadratic model; Figure 7).

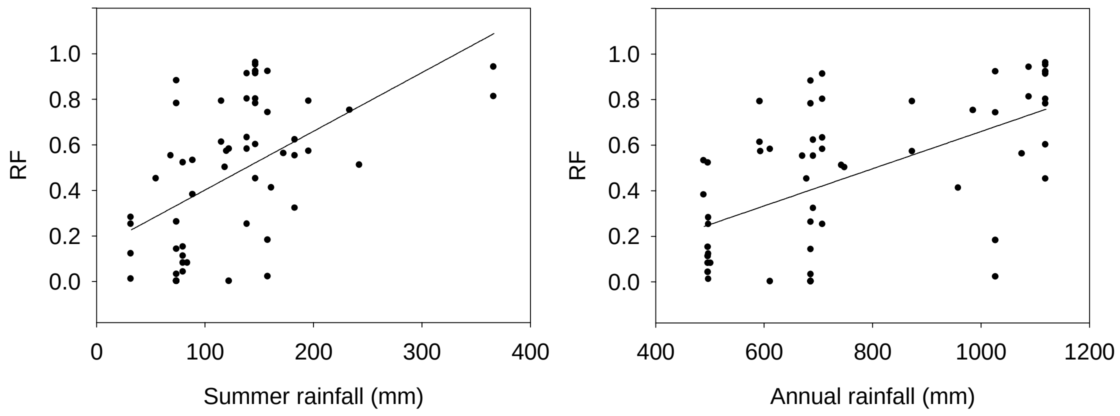

Figure 6. Relationships between the amount of summer and annual of rainfall and the regeneration success of yew (as estimated by the recruits fraction, RF), for 61 central and southern European populations of yew. Partial correlations between RF and rainfall, after accounting for population size, are $r = 0.408$, $p = 0.004$ for annual rainfall, and $r = 0.560$, $p < 0.001$ for summer rainfall.

Discussion

Water-driven recruitment limitation: direct and indirect effects at local scale

Our results were conclusive as regard to the strong dependence on soil water availability for recruitment of yew at a local scale. Seedling emergence and survival were consistently enhanced in moister places in both study populations and years. Thus, both demographic processes were controlled by a simple abiotic effect, as they depended just on a close spatial association with water sources, as commonly found with other relict tree species in the Mediterranean (Pigott & Pigott 1993, Brèda et al. 2006, Pulido et al. 2008). However, in the case of yew, meeting water requirements of seeds and seedlings also depended on biotic interactions influencing the likelihood of a given propagule reaching well-watered places. Thus, within riparian vegetation, seedling emergence was significantly concentrated under the canopy of fleshy-fruit producing trees (including yew). This spatial pattern of emergence cannot be explained just by shared microhabitat requirements of seedlings and adult trees, but also by directional dispersal by frugivorous birds using fleshy-fruited trees as perches while foraging (for similar results on yew see García et al. 2000a, García & Obeso 2003, Sanz, *unpublished data*).

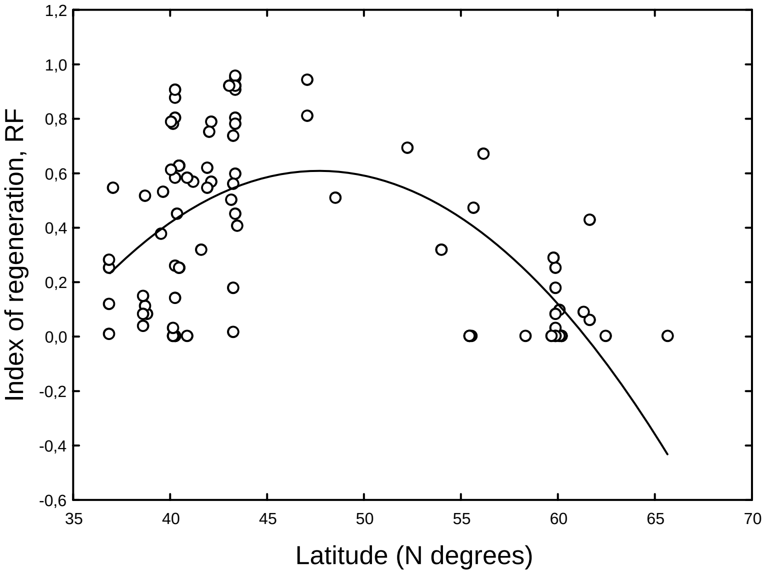

Figure 7. Relationship between latitude (N degrees) and the index of regeneration (RF) for 88 European populations of yew. The best fit was that of a quadratic model: $RF = -10.55 + 0.48 * L - 0.01 * L^2$ ($R^2 = 35.30\%$).

Apart from the above animal-mediated effect, two additional plant-mediated effects could help to explain the spatial arrangement of yew recruits. First, we found clear differences between microhabitats in seedling survival, in such a way that transition from seedling to sapling was more likely to occur under shrubs. This survival pattern could be the result of nurse effect involving microclimate amelioration, a mechanism that has been previously documented in Mediterranean populations of several gymnosperms (García et al. 2000a, Castro et al. 2004). Second, a highly significant positive effect of mosses on seedling survival was also found. Presence of mosses has been previously reported as a good predictor of survival in marginal populations of *Rhododendron ponticum* in southern Spain (Mejías et al. 2002). The high water retention capacity of mosses could explain their facilitative role in seedling emergence and establishment (Dovciak et al. 2008). Summarizing, seedling establishment strongly depended on the water availability, and the need for reaching moist microsites could be met just by passive means, by interacting with avian dispersal agents or with nurse plants.

Abiotic constraints acting at a regional scale

At a regional scale adult yew trees grew in close spatial association with streams, where they experienced lower water demands, thus supporting prediction 1. This clear cut pattern of distribution could be also influenced by anthropogenic disturbances, such as burning and grazing, whose impact could be lower in the less accessible mountain streams where yew stands are usually found. Nevertheless, several pieces of evidence point to abiotic stress as the main factor shaping yew regional distribution. First, drought stress was by far the most important cause of seedling death in all years and populations in our intensive study. Second, yew stands concentrated not only in the close vicinity of streams, but also in north-facing slopes, where summer drought could be alleviated due to reduced incidence of solar irradiance. Hence, as compared to anthropogenic disturbances, the distribution of water sources seemed to exert an overwhelming influence on the presence of yew.

Besides yew distribution, the regeneration success at a regional scale was significantly affected by, among other variables, summer precipitation, thus supporting prediction 2. We can thus conclude that the main abiotic constraint acting at the population level also shaped the spatial structure and regeneration success of yew at a regional level.

Scaling up the continental scale

A trend towards decreased regeneration in the southern edge has been correctly predicted, since the prevailing climate in the southern edge is characterized by a pronounced summer drought which is critical for tree recruitment, in agreement with results obtained at the local and regional levels. In addition, the recent and predicted trend towards decreased precipitation in the Mediterranean (IPCC 2001) can be hypothesized to affect range dynamics by (1) lowering population viability in the southern belt (the rear edge) and (2) by increasing it in the leading edge (*sensu* Hampe & Petit 2005). Our results show that the former process is in fact taking place and it may well increase the risk of extinction of the southern populations in the coming decades.

The trend towards water-driven increased regeneration northwards did not hold when including populations at the highest latitudes (beyond 50° N). In fact, regeneration values in this zone were significantly lower than those recorded for central and southern populations. These results illustrate the existence of a centre-periphery trend towards decreased population viability in both northern and southern marginal areas of the range (Lawton 1993, Brown et al. 1996, Vucetich and Waite 2003). In the case of yew, factors other than water supply limit regeneration in the current northern edge. These factors include light availability (Iszkulo & Boratynski 2006) and frost and/or herbivore damage (Dovciak 2002, Mysterud & Ostbye 2004, Iszkulo & Boratynski 2005). Therefore, our results suggest a disparity in the factors regulating yew persistence across its range (Stewart Jr. & Nilsen 1995, Santamaría et al. 2003), a finding that deserves further investigation to fully understand range dynamics (Gaston 2003).

Concluding remarks

We have shown in this study that water availability controls one of the direct mechanisms, recruitment, which enables yew populations to persist at local and regional scales. This in turn allowed us to predict the pattern of regeneration success at a continental scale and to gain insight into the ability of populations to face climate change. A plethora of recent studies using climatic envelope models (CEMs; Pearson & Dawson 2003), have assessed the risk of extinctions of thousand of species during the 21st century due to climate change (Thuiller et al. 2005). However, it is increasingly recognized that climate alone cannot adequately predict species distributional responses (Araújo & Luoto 2007, Svenning & Skov 2007). Thus, we propose that our future challenges should be: (1) to incorporate historical and biotic drivers into models predicting distribution shifts (Diniz-Filho & Bini 2008), and (2) to clarify how environmental factors control processes involved in species persistence through multiple scales (Whittaker et al. 2001). The approach developed in this paper shed light on one of the potential ways to achieve this second goal.

Acknowledgements

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Appendix 1. Location and values of the ratio of recruits (saplings plus juveniles) to the sum of individuals from all age classes including adults (RF) for 85 populations of yew (*Taxus baccata*) in Europe.

Country	Lat º N	Zone	Site	Adults	RF	Source
Norway	62.50	North	Klyvelia	81	0.00	1
Norway	61.67	North	Barlindflaten	67	0.06	1
Norway	61.67	North	Berge	23	0.43	1
Norway	61.56	North	Sandviksbotn	33	0.00	1
Norway	61.38	North	Kåda	10	0.09	1
Norway	60.23	North	Yddal	9	0.00	1
Norway	60.22	North	Flotaneset	23	0.00	1
Norway	60.22	North	Hestabotn	36	0.00	1
Norway	60.05	North	Børevika	21	0.00	1
Norway	60.05	North	Ånuglo	85	0.10	1
Norway	59.85	North	Eidesvatnet	18	0.18	1
Norway	59.85	North	Gjuvslandlia	40	0.25	1
Norway	59.85	North	Sæbøskårane	59	0.03	1
Norway	59.85	North	Tveitabotn	34	0.00	1
Norway	59.85	North	Tveitane	23	0.08	1
Norway	59.85	North	Ølveshovda	33	0.00	1
Norway	59.80	North	Brandviknes	112	0.29	1
Norway	59.67	North	Langebudalen	20	0.00	1
Norway	58.35	North	Lindborgvatnet	18	0.00	1
Denmark	56.13	North	Marselisborg		0.67	2
Denmark	55.68	North	Munkebjerg		0.47	2
England	55.58	North	Greta Gorge		0.00	3
England	55.48	North	Castle Eden Dene		0.00	3
England	55.48	North	Hawthron Dene		0.00	3
England	55.48	North	Horselyhope Ravine		0.00	3
Poland	54.03	North	Cisowy Jar		0.32	4

Country	Lat º N	Zone	Site	Adults	RF	Source
Poland	52.25	North	Kornik Arboretum		0.69	5
Ukraine	48.50	Central	Knyazhdvir	8600	0.51	6
Austria	47.05	Central	Leininger Riese	828	0.94	7
Austria	47.11	Central	Stiwollgraben	2236	0.81	8
Spain	43.37	Central	1		0.95	9
Spain	43.37	Central	2		0.80	9
Spain	43.37	Central	3		0.92	9
Spain	43.37	Central	4		0.60	9
Spain	43.37	Central	5		0.45	9
Spain	43.37	Central	6		0.96	9
Spain	43.37	Central	7		0.78	9
Spain	43.37	Central	8		0.91	9
Spain	43.37	Central	9		0.92	9
Spain	43.43	Central	Sueve	42	0.41	10
Spain	43.29	Central	Peña Mayor	42	0.02	10
Spain	43.28	Central	Teixeu	38	0.18	10
Spain	43.27	Central	Río Color	30	0.56	10
Spain	43.23	Central	Aramo	41	0.74	10
Spain	43.13	Central	Sierra Sobia	49	0.50	10
Spain	43.05	Central	Agüeria	44	0.92	10
Spain	42.15	South	Alta Garrotxa	57	0.79	11
Spain	42.11	South	Collsacabra	18	0.57	11
Spain	42.05	South	Montsec	2	0.75	11
Spain	41.92	South	Centelles	42	0.62	11
Spain	41.92	South	Montseny	17	0.55	11
Spain	41.61	South	Montserrat	73	0.32	11
Spain	41.20	South	Prades	30	0.57	11
Spain	40.93	South	Cardó-Tivissa	33	0.58	11

Country	Lat º N	Zone	Site	Adults	RF	Source
Spain	40.90	South	Ports de beseit	34	0.00	11
Spain	40.44	South	Mas de les Covetes	6	0.25	11
Spain	40.43	South	Barranc de L'Horta	91	0.63	11
Spain	40.38	South	Escobarejos	30	0.45	12
Spain	40.27	South	Majacerezo	6	0.14	12
Spain	40.27	South	Papúos	10	0.88	12
Spain	40.22	South	Hornito	5	0.00	12
Spain	40.22	South	Asperones	5	0.00	12
Spain	40.22	South	Piornalego	14	0.26	12
Spain	40.22	South	Nogaledas	6	0.00	12
Spain	40.18	South	La Hoz	7	0.00	12
Spain	40.18	South	Las Meñas	19	0.00	12
Spain	40.18	South	El Cerezal	53	0.78	12
Spain	40.17	South	Las Yeguas	34	0.03	12
Spain	40.44	South	Mas de les Covetes	6	0.25	13
Spain	40.43	South	Barranc de L'Horta	91	0.63	13
Spain	40.26	South	Barranc Mas Roig	382	0.91	13
Spain	40.25	South	Mas de Vela	31	0.80	13
Spain	40.24	South	Barranc la Pegunta	326	0.58	13
Spain	40.06	South	Barranco Saladillo	46	0.61	13
Spain	40.04	South	Barranco de Jorge	36	0.79	13
Spain	39.62	South	Pico Ropé	9	0.53	13
Spain	39.57	South	Fuente de la Puerca	8	0.38	13
Spain	38.86	South	Circ de la Safor	12	0.08	13
Spain	38.70	South	Serra Xortà	16	0.11	13
Spain	38.67	South	Morró de la Moleta	62	0.52	13
Spain	38.66	South	Font Roja	115	0.08	13
Spain	38.66	South	Serra de Bèrnia	11	0.15	13

Country	Lat º N	Zone	Site	Adults	RF	Source
Spain	38.65	South	Serra d'Aitana	46	0.04	13
Spain	37.10	South	Trevenque		0.55	14
Spain	36.90	South	Salto del caballo	85	0.12	15
Spain	36.90	South	Tacita de Plata	18	0.25	15
Spain	36.90	South	Mal Infierno	13	0.28	15
Spain	36.90	South	Barranco del Sol	73	0.01	15

1. Mklestad 2005; 2. Svenning & Magard 1999; 3. Hulme 1996; 4. Iszkulo 2001; 5. Iszkulo & Boratynski 2005; 6. Iszkulo et al. 2005; 7. Dhar et al. 2007; 8. Dhar et al. 2006; 9. Villarino & Trevín 2003; 10. García & Obeso 2003; 11. Caritat & Bas 2007 ; 12. Authors' unpublished data ; 13. Andrés et al. 2005 ; 14. García et al. 2000; 15. Navarro & Pulido 2003.

Capítulo 3

Procesos demográficos determinantes del área de distribución: el caso del abedul (*Betula alba*) en el límite sur de su distribución

Demographic processes explaining range dynamics: the case of downy birch (*Betula alba*) at its southern distribution limit

Demographic processes explaining range dynamics: the case of downy birch (*Betula alba*) at its southern distribution limit[2]

Abstract

The mechanisms determining the persistence of plant populations in the edges of species' range are poorly known, a fact that hampers prediction of future ranges. Here we asked which are the critical demographic processes determining recruitment in marginal populations of downy birch (*Betula alba*) at the southern limit of the species' range.

We studied four remnants populations (11-27 individuals) located in central Spain under dry Mediterranean climate and growing as part of riparian mountain vegetation.

In 2005 and 2006 seed production and the wind-generated spatial pattern of seed rain were evaluated by means of seed traps, whereas emergence and survival was monitored for a sample of 604 tagged seedlings.

The number of seeds produced (6287-30655 seeds/m^2 in two years) was not indicative of source limitation of recruitment. Seed dispersal by wind was primarily a within-stand phenomenon in all populations, since 86.7% of the seeds were trapped under mother trees and only 0.29% were dispersed more than 100 m. This restricted dispersal enhanced the likelihood of reaching safe (moist) microsites but severely reduced the chances for colonization of empty suitable habitat patches. Germination success was only 3.6-19.8%. Ninety-two percent of seedlings emerged at a distance less than 5 m from the stream, while but 93.1% died because of desiccation during the first summer drought.

Microsite limitation and low seed viability can be considered as the main bottlenecks for within-stand replacement. Restricted dispersal and strong dependence on wet microsites makes extremely unlikely the colonization of suitable habitat patches. Riparian habitats could act as local topographic refuges buffering distribution shifts.

Introduction

A central tenet in macroecology states that a species' performance decreases from the centre to the periphery of the range, with marginal populations being characterized by a smaller size, higher isolation, and lower ability to face

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[2] Sanz, R., Pulido, F. & Camarero, J. J. Demographic processes explaining range dynamics: the case of downy birch (*Betula alba*) at its southern distribution limit. Enviado a *Plant Ecology*.

environmental changes (Brown et al. 1996, Gaston 2003). Tests of geographic variation in fitness-related traits have measured variation in morphology (Kollmann & Bañuelos 2004), ecophysiology (Santamaría et al. 2003), fecundity (García et al. 2000, Rasmussen & Kollmann 2004), demography (Sanz et al. in prep.), or genetic make-up (Eckert et al. 2008). However, in most cases the mechanisms underlying geographical patterns remain unclear, which is especially true of the distributional limits of species (Sagarin & Gaines 2002, Hampe & Petit 2005, Geber 2008). Since the shape and extension of species' ranges are largely determined by processes affecting peripheral populations (Brown et al. 1996, Lennon et al. 1997), our knowledge of ecological processes operating at the range boundaries must be improved to fully understand range structure and dynamics (Gaston 2003).

Recent simulations on the ability of temperate tree species to respond to climate change predict that species with large range sizes will lose climatically suitable area, and that the suitable climate space will shift polewards (Ohlemüller et al. 2006). These predictions, derived from Bioclimate Envelope Models, rely on the assumption that factors other than climate are not influential at the relevant scale (Hampe 2004a). However, predictions concerning range boundaries could be flawed if species are able to find local refuges buffering latitudinal shifts at the eroding edge (Camarero et al. 2005, Troung et al. 2007, Pulido et al. 2008), or if they are not able to disperse to predicted climatically suitable areas at the leading edge (Svenning & Skov 2007). In the case of eroding edges, where populations are expected to be in decline, knowledge of the factors limiting tree recruitment at a local to regional scale and of the ability to track environmental change through dispersal is essential for understanding the persistence of populations (Hampe & Petit 2005). More specifically, both the role of abiotic and biotic factors, as well as their interactions, need to be addressed to determine future responses.

Here we examine factors affecting population dynamics in the southernmost populations of the downy birch (*Betula alba*), a dominant tree species in temperate forests of Europe whose abundance decreases southwards (Tutin et al. 1993), and that is currently experiencing an upward shift in the northern edge of the range (Troung et al. 2007). Mediterranean stands of the species are generally considered as relict and endangered due to the small population size, restriction to particularly benign environments surrounded by inhospitable landscapes, and a number of anthropogenic hazards (Devesa & Olivenza 2004). Though central and northern European populations have been intensively studied (Kinnaird 1974, Miles & Kinnaird 1979, Kullman 1986, Skoglund & Verwijst 1989, Holm 1994, Laskurain et al. 2002, 2003, Reyes & Casal 2003), their southern counterparts have not been addressed despite their potential for genetic differentiation and extinction risk (Devesa & Olivenza 2004).

The purpose of this study was to integrate the analysis of the different phases of the reproductive cycle of downy birch to detect the main bottlenecks hampering tree recruitment in marginal populations. We hypothesized that the declining status of this species could be explained by a sequence of bottlenecks related to the marginal location of the studied Mediterranean populations. Specifically we predicted that (1) seed production and/or viability should decrease due to abiotic stress affecting tree vigour; (2) seed dispersal should be unlikely to result in the foundation of new populations due to the scarcity of suitable habitat patches; and (3) seedling recruitment should be strongly constrained by water availability as usually found in Mediterranean habitats. By means of this approach we seek to elucidate the factors determining population viability in southern peripheral populations increasingly exposed to climate change (IPCC 2007).

Methods

Study species

Downy birch occurs in Europe and in Central and North Asia (Atkinson 1992). Birches grow in few remnant populations in the Sistema Central mountain range of the central Iberian Peninsula, where this species reaches its southern range limit (Castroviejo et al. 1990). Downy birch is a monoecious tree, with male and female flowers occurring in separated inflorescences or catkins. The species is wind pollinated and mostly self-incompatible (Pelham et al. 1984, Atkinson 1992). The nutlets developed in the female catkins are winged and they are dispersed by the wind. From August to November birch trees produce large amounts of seeds that are dispersed either individually or as part of complete catkins fallen to the ground (Atkinson 1992, Reyes et al. 1997).

Study populations

Birch populations studied here were located in the centre of the Sistema Central mountain range, in the North of Cáceres province, W Spain (40° 15’ N, 5° 45’ W; Figure 1). The climate is of a mountain Mediterranean type with cold winters and hot and dry summers, with mean annual precipitation of 1100 mm. Scattered individuals or small groups (less than 50 trees) of this species occur at 950-1750 m

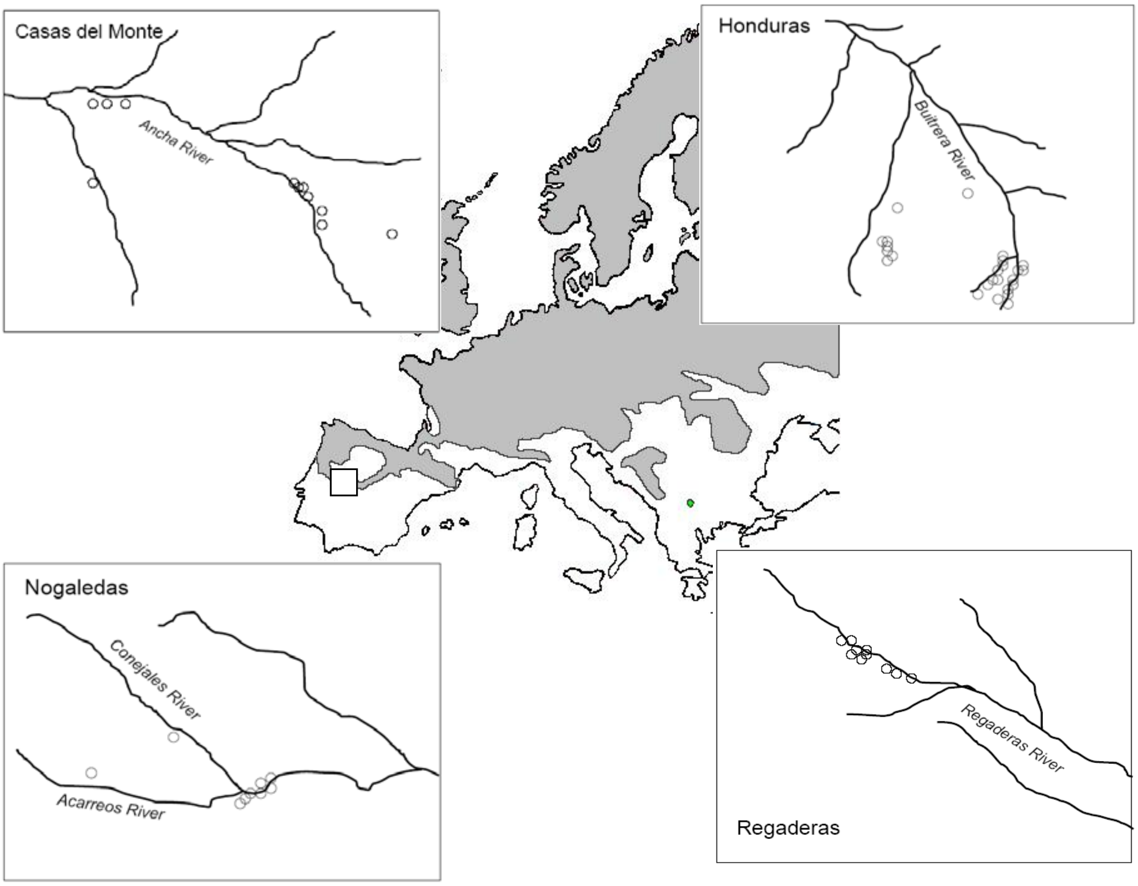

Figure 1. Maps showing the distribution of downy birch (grey area; based on Atkinson 1992, and Svenning & Skov 2007) and the study area (empty square), as well as the spatial arrangement of birch trees within experimental populations (approximate scale 1: 100.000).

above sea level. The dominant vegetation around birch stands is composed by heathers (*Erica arborea* and *E. australis*) and brooms (*Genista florida* and *Cytisus oromediterraneus*). In all cases, birch trees grow on north-facing slopes along mountain streams, that is, the species behaves as riparian (Figure 1).

This study was conducted in four populations, with a maximum distance of 42 km between them. From west to east the studied sites were: Honduras, Casas del Monte, Nogaledas, and Regaderas (Figure 1). We choose these populations from a complete set of 51 stands within the study region on the basis of a minimum number of individuals (> 10 adult trees). The total area of each population was determined by using the minimum convex polygon defined by all the trees present in the stand. To describe the size structure of all populations we defined the following classes: saplings (individuals more than one year old and up to 50 cm in height), juveniles (non-reproductive trees more than 50 cm tall), and adults (trees bearing reproductive structures).

Seed production

Tree fecundity and the degree of source limitation were analyzed in three of the four populations. Between 24 and 37 circular seed traps (plastic glasses 12 cm in diameter, 14 cm in depth, and 0.011 m^2 in area) were placed under the fruiting trees in each population in July 2005. Traps were in operation from this date to the end of 2006. Traps were placed on the ground underneath the tree canopies. Since a pilot study showed no seed predation by ants or birds in the traps, we did not cover them with mesh. This procedure allowed seeds to freely fall into traps, that would otherwise have been covered with litter fallen on the mesh. The content of traps was collected at biweekly sampling periods from mid-July to mid-December. In the laboratory the dry content of the trap was weighted and then a 1 g sample (> 10% of the total mass) was extracted to count all the seeds present. The number of seeds fallen in the trap was computed by multiplying the number of seeds in the sample by the total weight of the material collected. When the number of seeds in the trap was low we counted all of them.

Seed dispersal

The strength of dispersal limitation of recruitment was assessed by quantifying seed rain during two consecutive years (2005 and 2006). We used the same type of seed traps described above. Following Saura-Mas & Lloret (2005) traps were placed along four lines with north (from 316° to 45°), east (from 46° to 135°), south (from 136° to 225°) and west (from 226 to 315°) orientations. Each line consisted of 12 groups of five traps located at 10, 20, 30, 40, 50, 60, 70, 80, 90, 100, 110, and 120 m from the centre of the stand. We collected the whole content of traps two times during the dispersal period between late-summer and late-autumn. The number of seeds fallen in the traps was estimated as described above.

Seed germination

Seed viability was tested in a glasshouse experiment during the first study year (2005). We collected 20 mature catkins from five mother trees in each population at the time of dehiscence (mid-October). One-hundred seeds from each tree were sown in 40 × 25 cm plastic trays filled with a 3:1 peat-sand mixture. Trays were always well-watered (three applications per week) in order to mimic conditions in natural riparian habitats. Seedling emergence was monitored monthly during one year from the date of sowing.

Seedling emergence and survival

We conducted a complete survey of recently emerged seedlings in the four populations in 2005 and 2006. The area surveyed was established by using the minimum convex polygon as described above. To detect seedlings emerged outside existing stands, we also searched in a total of 16 transects (20 × 5 m), evenly distributed in the left and right margins and in the upstream and downstream. Seedling emergence was monitored three times during June and July, and survival of seedlings was checked in November in the two study years. The distance of each seedling to the nearest stream was measured. We also noted the microsite (bare ground, moss and pasture) and microhabitat (beneath birch, alder, fleshy-fruited shrubs and non-fleshy fruited shrubs and open ground) in which seedlings were found.

Data analysis

To test for population and year effects on seed production we used General Linear Models (GLM) with factorial ANOVA design. The heterogeneity between populations in germination rates was evaluated by means of GLM with one-way ANOVA design. Pairwise differences between populations or years were tested with post-hoc Fisher LSD tests. To test for the effects of population, year and microhabitat on the density of seeds dispersed up to 120 m from the centre of the stands we used GLM with factorial ANOVA design. Generalized Linear Models (GLZ) were used to test for the effects of cohort, population, microhabitat, and microsite on seedling survival, with distance to the nearest stream as a continuous predictor. Survival was considered as a dichotomous variable with a binomial distribution. We used the logit link function to account for the relationships between dependent and independent variables. The likelihood ratio (LR) was used to evaluate the significance of effects in the model. We used the Statistica package (version 6.0, StatSoft Inc. 2003) for all the preceding analyses.

A detailed analysis of the spatial patterns of seed dispersal was conducted by fitting density-distance curves to negative exponential functions for all the orientations, populations, and years. We used Moran's I correlograms to evaluate the spatial pattern in the (log-transformed) seed density data of all years, populations and orientations (Houle 1998, Fortin & Dale 2005). Under the null hypothesis of no spatial autocorrelation, I takes an expected value close to zero, with positive (usually from 0 to +1) and negative (usually from 0 to -1) values indicating positive and negative spatial autocorrelation, respectively. We calculated I for ten equal-distance classes of 10 m and each *I* value was tested for significance. The correlogram was regarded as globally significant if at least one value of *I* was significant ($p < 0.05$) at the Bonferroni-corrected $p' = p / k = 0.005$, where *k* is the number of distance classes considered. The distance at which the value of spatial autocorrelation reaches the expected value of no autocorrelation is regarded as the "spatial range" of the studied pattern (Fortin & Dale 2005). All spatial analyses were performed with SAM v. 2.0 (Rangel et al. 2006).

Results

Demographic structure

The four study populations were very small in size, with the number of adult individuals ranging from 11 in Nogaledas to 27 in Honduras (mean population size 17.25 ± 7.41). These values are higher than the mean (8.25 ± 8.77) population size in the study region. In general, populations showed an ageing size structure as indicated by their low percentage of saplings or juveniles (recruits). The proportion of recruits was 0.0% in Regaderas, 32.5% in Honduras, 26.6% in Nogaledas, and 45.4% in Casas del Monte (Figure 2). Non-adult individuals were mostly juveniles in Nogaledas and Honduras, while saplings was the only size class occurring in Casas del Monte.

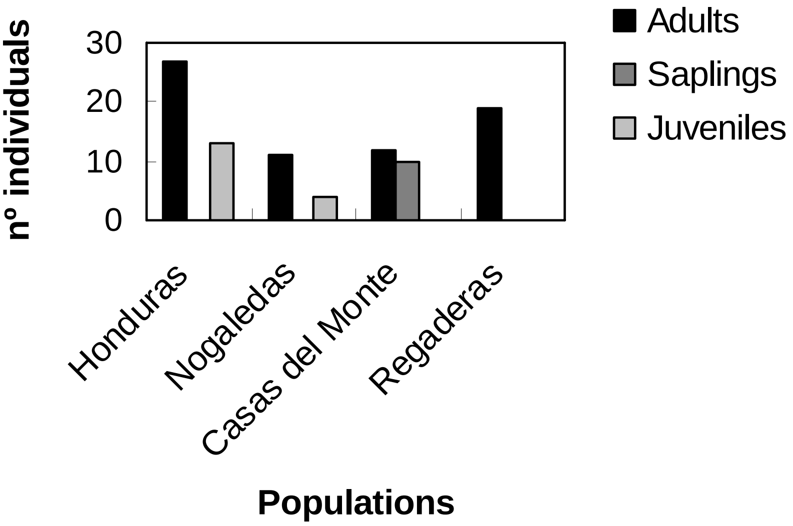

Figure 2. Demographic structure in the four populations studied.

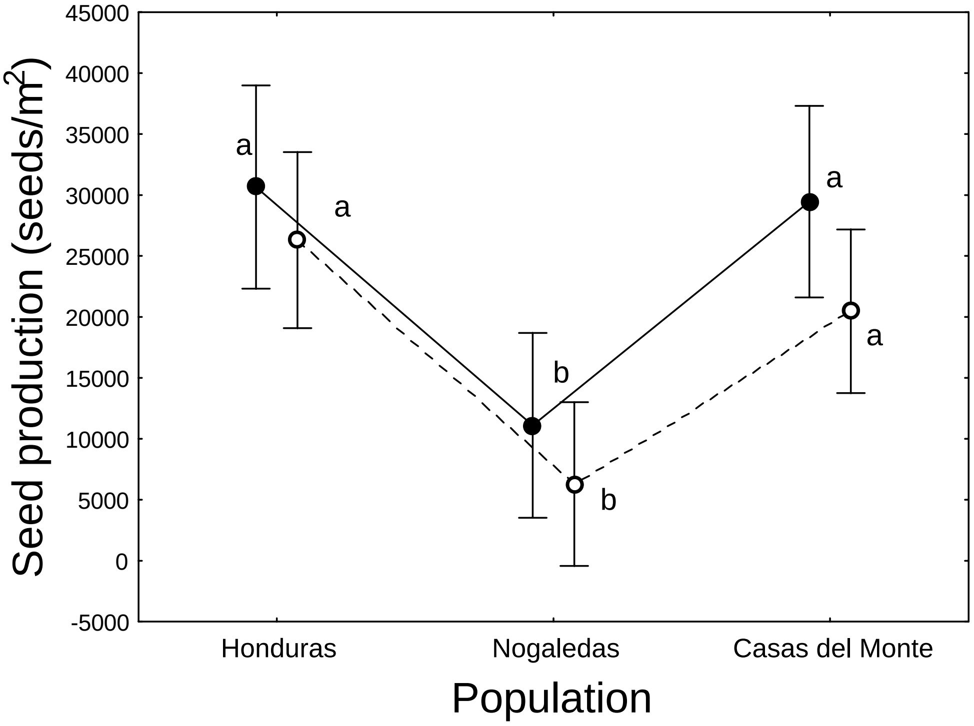

Figure 3. Seed production in three marginal populations of downy birch in central Spain. Filled circles correspond to 2005 and empty circles correspond to 2006 data. Different letters indicate significant ($p < 0.05$) differences between sites.

Seed production

The three populations studied showed considerable differences in tree fecundity as estimated by seed density beneath birch trees. Seed production varied between a maximum of 30655 ± 4223 seeds/m^2 in Honduras in 2005 and a minimum of 6287 ± 3401 seeds/m^2 in Nogaledas in 2006 (Figure 3). A highly significant effect of population on seed production was noted, while the effect of year was marginally significant due to a decrease in fecundity in 2006 in all populations (Table 1). Seed production was higher in Honduras and Casas del Monte, with Nogaledas showing much lower values. This pattern was consistent among years (Table 1).

Seed dispersal

In contrast to the analysis of seed production, this section deals with the whole seed shadow, extending from 0 to 120 m from the centre of a given stand. Maximum seed densities were observed at the smallest distance from the stand (Table 2). The seed-dispersal curves were leptokurtic in the four orientations and both years, and they were successfully fitted to negative exponential functions (Table 2; Figure 4). The parameter describing the exponential decay (*b*) was significantly greater in the year 2006 (0.27 ± 0.02) than in 2005 (0.18 ± 0.02) (ANOVA, F = 9.13, p = 0.007). The correlograms of seed density corresponded to spatial gradients confirming the sharp decrease in seed density at greater distances from the stands (Figure 5).

The "spatial range" of the seed-density patterns in the year 2005 was ca. 45 m in most populations and orientations. Note that 90-95% of all the dispersed seeds per populations were detected from 0 up to 50 m apart from the studied stand, and this distance corresponds to the levelling of the seed-density values when expressed in a logarithmic scale (Figure 4 and Figure 5). In the year 2006, the spatial correlograms corresponded again to gradients and they indicated a smaller "spatial range" of seed dispersal (ca. 35 m), especially in Nogaledas and Casas del Monte, which agrees with the exponential functions described above.

Concerning long-distance dispersal events, on average only 0.29% of the seeds trapped were dispersed beyond 100 m (0.45% in Honduras, 0.07% in Nogaledas and 0.22% in Casas del Monte). These proportions give a general picture of whether dispersed seeds could reach suitable habitats (springs) close to existing birch stands. The mean distance from each stand to the five nearest streams were 95.3 ± 18.4 m in Honduras, 203.75 ± 97.5 m in Casas del Monte, and 153.1 ± 72.9 m in Nogaledas. Thus, it seems that the capacity of wind transport for ensuring dispersal to neighbour streams was low and it varied between populations.

Table 1. Results from General Lineal Models (ANOVA design) testing for the effects of population and year on seed production within birch stands.

Effect	df	F	p
Population	2. 180	16.099	0.000
Year	1. 180	3.885	0.050
Population*Year	2. 180	0.233	0.792

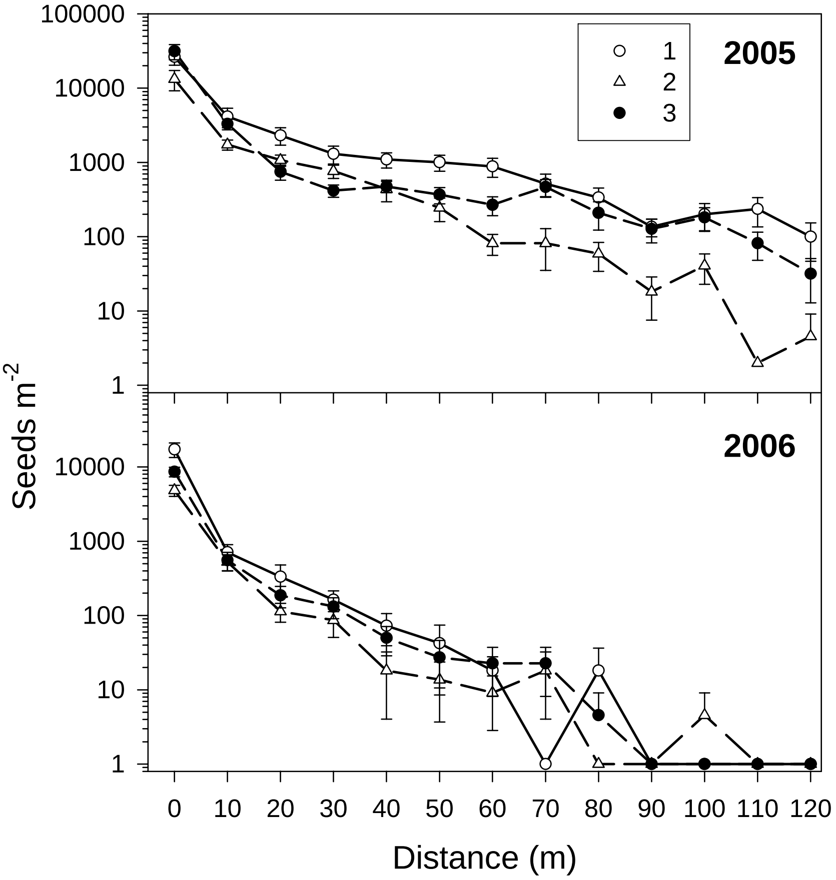

Figure 4. Variation of seed density with distance in 2005 in Honduras (1, circles), Nogaledas (2, triangles), and Casas del Monte (3, filled circles) sites. Values of seed density at each distance were computed as the mean number of seeds fallen in five traps. Note the logarithmic scale on the vertical axis.

The short-distance dispersal pattern also had consequences for the distribution of seeds delivered to different microhabitats. Thus, 86.7% of the seeds were trapped under birch trees, with few seeds reaching other microhabitats (8.5% of seeds were trapped in open ground and 4.7% in shrubs). A three-way ANOVA with seed density as a dependent variable showed a highly significant effect of year, population and microhabitat (including birch; Table 3). In addition, all the interactions involving the "microhabitat" factor were significant, indicating a strong spatiotemporal inconsistency in the pattern of seed rain among microhabitats.

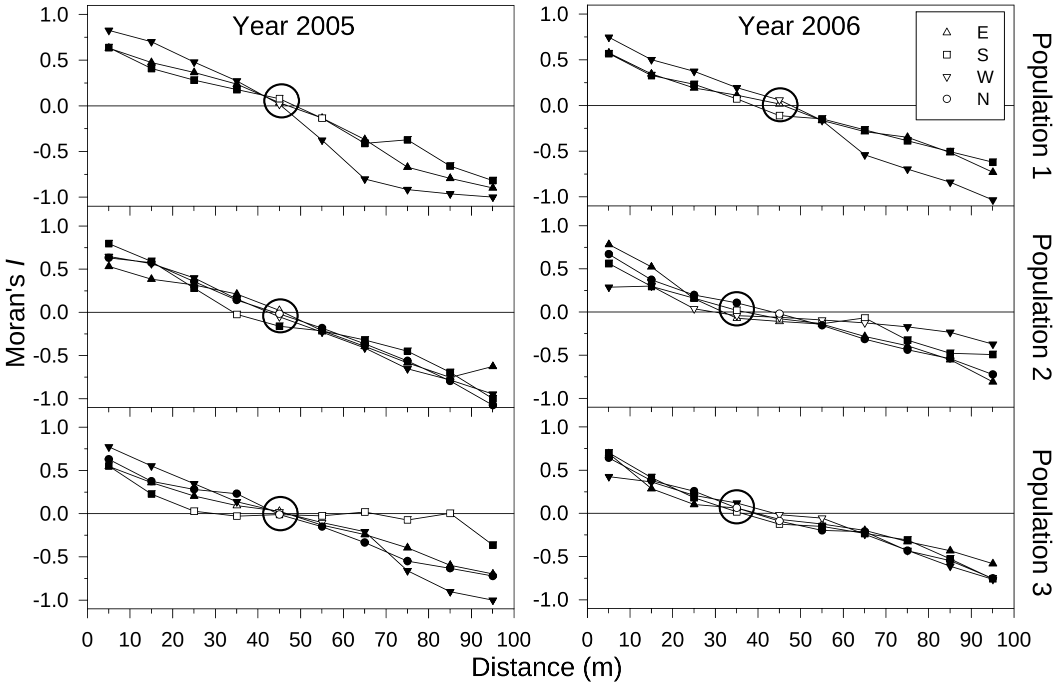

Figure 5. Moran's *I* spatial correlograms of seed density for all populations and orientations (different symbols) considering the two study years (2005, 2006). All correlograms were globally significant ($p < 0.05$). Solid symbols indicate significant coefficient values at $p = 0.05$. The circles indicate the "spatial range" of the seed-density patterns, i.e. where the *I* values cross the axis of $I = 0$. Population codes are as follows: 1: Honduras, 2: Nogaledas; 3: Casas del Monte.

Seed germination

Germination rates found in the 2005 experiment were generally low in all populations. Mean values found were 3.6% in Nogaledas, 4.6% in Casas del Monte, 17.8% in Regaderas, and 19.8% in Honduras (*n* = 5 trees in each population). A one-way ANOVA showed a highly significant difference between populations (F = 6.491, df = 3.16, p = 0.004), which could be attributed to differences in the pairs Nogaledas-Casas del Monte and Regaderas-Honduras (Figure 6).

Seedling emergence and survival

Seedling emergence started in mid-June and was completed by mid-July in both study years. There was great variation among years in the number of seedlings emerged, to the extent that we found 173 seedlings in 2005 and 431 in 2006 (all four populations pooled). As expected from adult and seed distributions, seedling emergence peaked in the vicinity of streams, with 92.4% of seedlings emerging closer than 5 meters from the riverbed. Most seedlings emerged (48.9%) were found under adult birches, whereas the proportion found in other microhabitats was generally low

Table 2. Descriptive statistics of seed density and exponential negative curve fits ($y = a \times e^{(-bx)}$) of distance-seed density relationships for the different populations and years. All fits were highly significant ($p < 0.001$).

Population	Year	Mean seed density (seed/m^2)	a	b	SE	R
Honduras	2005	3471 ± 796	26345.51	0.17	811.55	0.994
Nogaledas	2005	1369 ± 374	13231.16	0.19	362.07	0.995
Casas del Monte	2005	2926 ± 750	31367.35	0.22	308.61	0.999
Honduras	2006	1689 ± 510	17229.72	0.32	107.01	0.999
Nogaledas	2006	434 ± 102	4844.55	0.22	30.57	0.999
Casas del Monte	2006	740 ± 171	8612.90	0.27	62.74	0.999

(13.3% in alder, 6.1% in fleshy-fruited shrubs, 21.8% in non-fleshy fruited shrubs and 9.9% in open ground).

Survival rates were very low in all populations and in the two years. After the first summer, the percentage survival for all populations ranged from 0 to 1.5% in 2005 and from 3.9 to 5.5% in 2006. Overall, only 6.9% of seedlings found in all populations and years were alive after the first summer (n = 604 seedlings; Figure 7). In almost all cases (93.1%) seedling mortality occurred during the drought period with no signs of biotic damage. GLZ modelling showed highly significant effects of distance to stream and microsite on seedling survival (Table 4). Thus, seedling survival primarily depended on distance to water sources, with no seedlings surviving more than 3 meters apart. Within this distance interval, survival was significantly enhanced in the absence of grass competition, either on bare ground or in association with mosses. Mosses provide the best site for seedling survival: 6.5% of seedlings which emerged on moss survived, as compared to 1.1% of seedlings emerging on bare ground.

Table 3. Results from General Linear Models (ANOVA design) testing for the effect of population, year and microhabitat on the density of seeds dispersed up to 120 m from the centre of the stands.

Effect	df	F	p
Population	2.1340	14.445	0.000
Year	1.1340	41.976	0.000
Microhabitat	4.1340	227.539	0.000
Population * Year	2.1340	3.065	0.047
Population * Microhabitat	8.1340	16.654	0.000
Year * Microhabitat	4.1340	37.036	0.000
Population * Year * Microhabitat	8.1340	4.926	0.000

Discussion

Demographic structure: regeneration decreases near the border

Range-wide differences in population attributes are a common assumption of most approaches to plant biogeography. As stated by the centre-periphery hypothesis, marginal populations located at the species' boundaries should exhibit lower viability due to small population size and increased fragmentation (Brown et al. 1996). In the case of birches, available information on stand dynamics suggests the existence of geographical trends supporting the centre-periphery hypothesis. Thus, marginal populations of downy birch tend to be small in size (Kinnaird 1974, and this study), whereas central populations are larger (McVean & Ratcliffe 1962, Kinnaird 1968, Atkinson 1992). Concerning regeneration failure, as indicated by a low frequency of young age classes, it has been reported in some parts of the northern edge of the range such as Scotland (Atkinson 1992), Finland (Sarvas 1948), and Sweden (Skoglund & Verwijst 1989). Lack of regeneration has been explained by low shade tolerance of seedlings under the canopy of birch woods, by the impact of grazing, or by the existence of root competition (Atkinson 1992). On the opposite geographical extreme, southern relict populations studied in the Iberian Peninsula are also in decline due to regeneration failure. In this case, anthropogenic disturbance and drought seem to be the main explanations for the lack of juveniles in *Betula*, as in others relict riparian

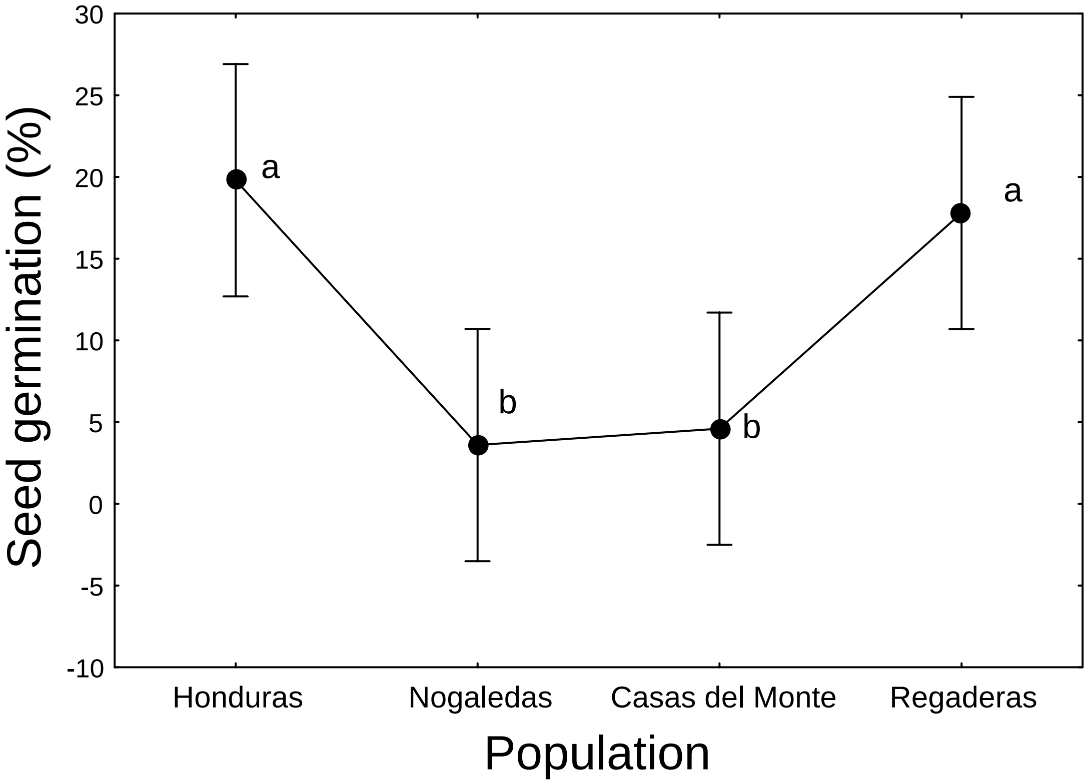

Figure 6. Mean values of seed germination rates in four populations of downy birch in a greenhouse experiment carried out in 2005. Different letters indicate significant ($p < 0.05$) diferentes between sites.

species (Peinado & Moreno 1989, Hampe & Arroyo 2002, Mejías et al. 2002, Pulido et al. 2008).

Seed production

Geographical variation in seed production of trees has been reported at continental scales, with the lowest values occurring in peripheral populations (for example García et al. 2000). In our case, seed production showed significant differences between populations and, to a lesser extent, between years. The same was true of populations of *Betula alleghaniensis* (Houle 1999) or *Betula pendula* (Holm 1994, Reyes & Casal 2000). The values of tree fecundity found in our populations were in the upper part of the range found in several birch species. Thus, Sarvas (1948) reported a maximum crop of 2300 filled seeds/m^2 in *B. pendula* in Finland. Seed crops between 3800 and 43000 seeds/m^2 were recorded in Scotland (Miles & Kinnaird 1979), whereas the range in northwestern Spain was 28659 - 62739 seeds/m^2 (Reyes & Casal 2003). Overall, we found no evidence of decreased fecundity in our marginal conditions, and it seems very unlikely that regeneration was hampered by source limitation (*sensu* Clark et al. 1999).

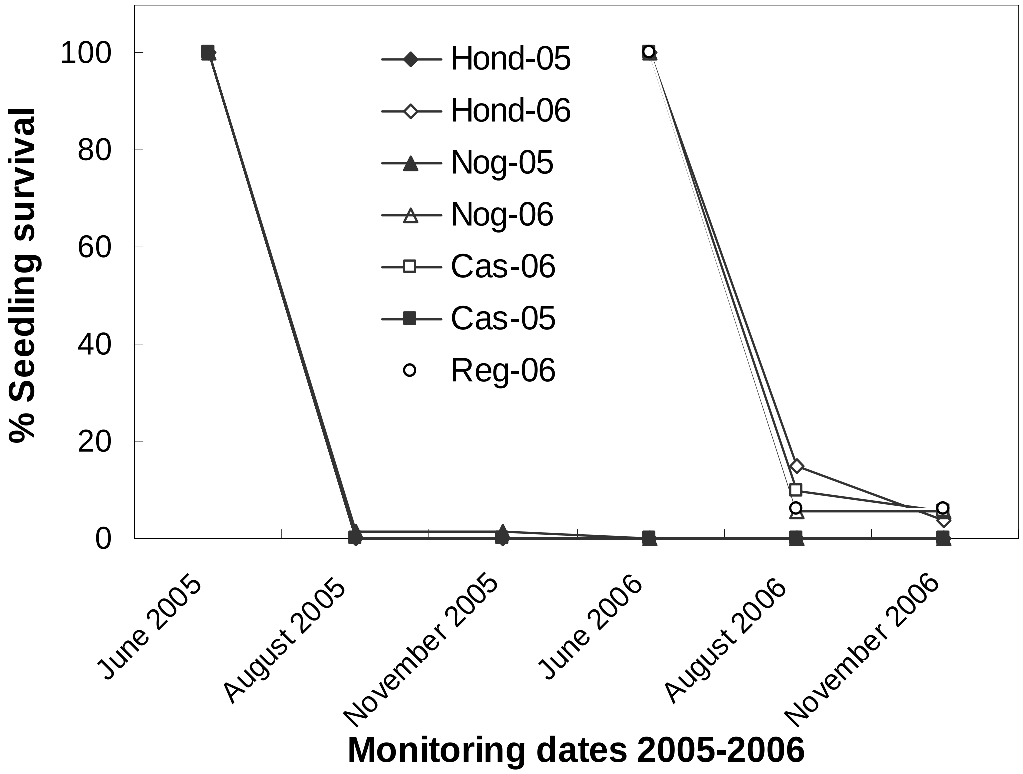

Figure 7. Cumulative proportion of seedlings surviving in the four study sites during 2005 and 2006. The 2005 cohort was monitored from June 2005 to November 2006, while the 2006 cohort was monitored from June 2006 to November 2006. Populations codes: Hond: Honduras, Nog: Nogaledas, Cas: Casas del Monte, Reg: Regaderas.

Seed dispersal: the unlikely colonization of empty habitat patches

We found that the magnitude and spatial pattern (distance and microhabitat distribution) of the seed rain were different between populations and years (see Houle 1998 for a similar result). In addition, secondary seed dispersal through snow (Matlack 1989, Greene & Johnson 1997), water flow (Hampe 2004b) and nutlet attachment to the body of large mammals (Moissie et al. 2005) could also have taken place, though these processes could not greatly modify the primary pattern of seed rain generated by gravity (within catkins) or by wind (single seeds). Most seeds (86.7%) did not leave the area of the birch stands. As opposed to predictions from classical hypotheses implying greater risk under mother trees (Janzen 1970), seed deposition under mother birch trees growing in riparian sites would in most cases ensure that water supply was sufficient for germination and establishment (see *Seedling emergence and survival* below).

Table 4. GLZ models testing for the effects of distance to stream, microsite, microhabitat, cohort and population on seedling survival.

Effect	df	χ^2	p
Distance to stream	1	24.902	< 0.001
Microsite	2	15.447	< 0.001
Microhabitat	4	3.390	0.495
Cohort	1	5.249	0.022
Population	3	3.100	0.376
Cohort * Population	0	1.387	0.300
Cohort * Microsite	3	1.935	0.586
Cohort* Microhabitat	2	2.881	0.237
Population * Microsite	4	6.766	0.148
Population * Microhabitat	2	8.611	0.135
Cohort * Population* Microsite	1	0.000	0.999
Cohort * Population * Microhabitat	1	0.000	1.000
Cohort * Population * Microhabitat * Microsite	1	0.000	1.000

In a regional context the most relevant question related with dispersal is whether seed transport can lead to colonization of suitable empty sites. Our results were in agreement with previous studies in that almost all seeds were deposited within a radius of 40-50 m of source trees (Sarvas 1948). Furthermore, in our case only 6.9% of the dispersal events occurred beyond 10 m from existing stands. Whether seed export can lead to establishment of recruits depends on the probability of reaching suitable microsites in nearby streams, which must generally occur through long-distance (> 100 m) dispersal.

Downy birch nutlets have been reported to disperse more than 400 m from the mother tree (Smith 1900) or even more than 1000 m (Van der Pijl 1982). Maximum dispersal distances for other birch species are 475 m in *B. papyrifera* (Greene & Johnson 1996), 80 m in *Betula lenta* (Matlack 1992), and 300 m in *Betula pubescens* ssp. *tortuosa* (Molau & Larsson 2000). Records of seeds dispersed more than 100 m are very scarce (5% in *Betula uber* according to Ford et al. 1983, and 0.29% in our study). On the basis of the amount of seeds dispersed far and the mean distance from stands to nearby streams, we concluded that seed arrival to suitable patches away from those already occupied could be possible (though very unlikely) in Honduras, but it would be virtually zero in the remaining populations. In addition, it must be taken into account that seeds must fall within a narrow belt of moist soil close to streams, which greatly reduces the probability of seeds landing in suitable microsites. Hence, the ability to colonize potentially suitable streams is strongly constrained by the low number of seeds reaching them and by the spatial arrangement of streams within catchments.

Seed germination

Germination success in our marginal populations was very low, indeed markedly lower than those reported for the central populations from which information is available (Reyes & Casal 2003 in Spain, Holm 1994 in Sweden, and Sarvas 1948 in Finland). Only Miles & Kinnaird (1979) recorded comparable values (15%) for Scotland, though our mean values were even lower (11.4%). As also noted by Reyes & Casal (2003), seed viability might be related to population structure (via its effects on pollen flow or genetic make-up), as it was lowest in the smallest population (Nogaledas) and highest in the largest one (Honduras).

The limiting role played by germination in population recruitment has been discussed by Kullman (1986), who suggested that seed germination was not an important bottleneck in the life-cycle of mountain birch (*Betula pubescens* subsp. *tortuosa*) because a large seed production could lead to the establishment of a dense seedling bank even with low germination success. This reasoning is valid for populations where there is no microsite limitation and viable seeds cannot saturate available safe sites for seedlings (Clark et al. 1999). In our case, close dependence on watered microsites could make low germination an important bottleneck in the regeneration process.

Seedling emergence and survival: a case for strong abiotic constraints

Seedling emergence concentrated in the vicinity of streams, with 92.4% of seedlings emerging within five meters of the riverbed, as expected from the spatial pattern of seed rain. Besides greater seed deposition, there could be a positive effect of moisture on emergence close to the stream. This could be explained by enhanced conditions in small, watered sand banks or by the role of mosses as germination seedbed. The facilitative role of mosses for seed germination has been reported in previous studies with *B. alba* and *B. pendula* (Kinnaird 1974), among other species. We suggest that, as compared with sand banks, cushions of mosses may buffer moisture fluctuations and provide attachment for dispersed seedlings.

We found extremely low values of seedling survival after the first summer. This was a common characteristic of our four populations and also of all previous studies on birches across Europe (Kinnaird 1974, Miles & Kinnaird 1979, Kullman 1986, Skoglund & Verwijst 1989, Laskurain et al. 2003). These studies also found frost-damage during the first winter to be the second cause of seedling mortality. Thus, available information demonstrates that early survival of seedlings is almost exclusively limited by abiotic factors. This also applies to our marginal populations, where soil moisture during the first summer is critical for survival (Sanz & Pulido, *submitted manuscript*). In a later stage of the life cycle, conversion of seedlings to woody saplings or juveniles most likely depends on protection from herbivore damage, as exemplified by the nurse effects of heaths found by Kinnaird (1974). In close agreement, saplings and juveniles in our populations were always found within dense heath patches (Sanz, *unpublished data*).

Synthesis: conservation prospects in a changing climate

Three main findings can be outlined from this study. First, the number of seeds produced is not suggestive of source limitation in marginal populations, thus contradicting prediction 1. Second, rare long-distance dispersal events to suitable empty habitats, combined with poor germination, might prevent the foundation of new birch populations, in agreement with prediction 2. Third, seed dispersal was primarily a within-stand phenomenon, and this short-distance dispersal enhances the likelihood of reaching safe (moist) microsites for seedling emergence and survival, as expected from prediction 3. The fact that the main results concerning the different steps of the regeneration process applied to all populations studied suggests that they might be representative for southern marginal populations of birch.

Abiotic constraints influencing seedling survival have been shown to be the main driving force of recruitment in relict populations of several species under Mediterranean climate (Mejías et al. 2002 for *Rhododendron ponticum*, Hampe & Arroyo 2002 for *Frangula alnus*, Pulido et al. 2008 for *Prunus lusitanica*). More generally, strong sensitivity of demographic processes to water stress has been stressed for many tree species growing under Mediterranean climate (Pigott & Pigott 1993, Brèda et al. 2006). In the case of southern peripheral populations of downy birch, strong microsite limitation of recruitment makes this species a strictly riparian one. Thus, mid-elevation streams can be considered as local refuges buffering distribution shifts such as those found in the northern edge of the species' range (Troung et al. 2007). The suitability of these habitats as local refuges can be predicted to decrease with increased climate warming and subsequent changes in the water regime (Ohlemüller et al. 2006). In this future scenario, colonization of suitable habitats through long-distance dispersal seems unlikely in view of the contrasting distributions of seed rain and mountain springs acting as suitable habitats for seedling establishment.

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Capítulo 4

El éxito en la polinización de un árbol dioico y anemófilo (*Taxus baccata*) en poblaciones marginales: variación individual en la limitación polínica y efecto de la distancia entre sexos

Pollination success of an anemophilous, dioecious tree (*Taxus baccata*) in marginal populations: individual variation in pollen limitation and effect of intermate distance

Pollination success of an anemophilous, dioecious tree (*Taxus baccata*) in marginal populations: individual variation in pollen limitation and effect of intermate distance[3]

Abstract

Pollen limitation is a likely factor constraining reproductive success of plants at their distributional limits. Here we examine the influence of the amount of pollen received and the spatial arrangement of male and female yew trees (*Taxus baccata*) on the success of fertilization and mature fruit production. Special emphasis was placed on the analysis of individual variation in reproductive performance and its temporal consistency. Spatiotemporal variation in fruit production was assessed in two populations during 2005 and 2006, whereas a pollen-addition experiment was performed in one of these populations (Escobarejos). Both populations were located in central Spain, close to the southern edge of the species' range. We hypothesized that marginality should have detrimental effects for yew reproduction, which should result from the effects of environmental and demographic stochasticity associated to marginality.

We found significant between-population and between-year variability in fruit production. The success of fertilization and fruiting in the experimental population were pollen-limited, and their significant individual variation was consistent from one year to the next. Female trees aborted ca. 70% of the fruit set in both years, and they did it independently of pollen supplementation and a higher flower load in treated branches. Thus, sink strength of branches was proportional to their load of developing fruits. Fruit set in control branches was significantly influenced by the females' neighbourhood, with fecundity decreasing exponentially with distance to the nearest male and mean distance to all males in both study years. Marginality seems to impose a high spatiotemporal variability in yew fecundity. Large and temporally consistent individual variation in fecundity related to the spatial arrangement of mates result in an uneven contribution of genotypes to the population seed pool, an indication of demographic stochasticity.

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[3] Sanz, R. & Pulido, F. Pollination success of an anemophilous, dioecious tree (*Taxus baccata*) in marginal populations: individual variation in pollen limitation and effect of intermate distance. Enviado a *International Journal of Plant Sciences*.

Introduction

A central tenet of biogeographical theory states that species' performance should decrease from the centre to the periphery of their range, with marginal populations being characterized by a smaller size and higher isolation between individuals (Brown 1984, Caughley et al. 1988, Brown et al. 1996, Crawford 2008). Knowledge of the mechanisms underlying the persistence of marginal populations is essential because range extension and shape are largely determined by processes affecting peripheral population and metapopulations (Brown et al. 1996, Lennon et al. 1997), and because such populations often harbor unique genotypes (Hampe & Petit 2005). In the particular case of sessile organisms such as plants, populations at the species' range boundaries usually experience high levels of stochasticity with respect to key environmental traits (Sagarin & Gaines 2002, Yakimowski & Eckert 2007, Crawford 2008). Furthermore, reduction of population size as a result of fragmentation in marginal habitats may result in decreased reproductive performance due to mate isolation (Allee effect; Knight 2003) and increased demographic stochasticity, with individual genotypes contributing unequally to population recruitment (Wagenius et al. 2007).

Individual variation in reproductive success is the basis for the changing genetic make-up of populations, which in turns constitute the template on which natural selection acts (de Jong & Klinkhamer 2005). Individual differences in the reproductive output of plants may to a great extent be related to the ability to achieve fertilization through the capture of pollen from compatible mates (Dudash 1993, Knight et al. 2005). The extent to which individual differences in pollination success result in significant changes in genotypic frequencies within populations depends on the temporal consistency of such differences (see e. g., Herrera 2004). By contrast, temporal inconsistency may result from individual differences being controlled by the temporal variability in local environmental conditions, including microclimate, effectiveness of pollen vectors, as well as their interaction, though these aspect has been largely ignored to date (Knight et al. 2005).

Apart from the above factors, the opportunity for selection to act upon pollination-related traits depends on whether or not individual differences in fertilization rates are maintained at later stages of the reproductive cycle (Ward & Johnson 2005, Hetland & Totland 2007). In the case of marginal populations, which are usually exposed to extreme climatic events such as frost or drought, the effect of abiotic factors may cancel out previous differences in the reproductive output (Rasmussen & Kollmann 2004, Hampe 2005). Thus, increased fruit set through

efficient pollination does not necessarily leads to increased fruit production, as the later depend on the plant's ability to fill growing fruits acting as sinks for assimilates (Stephenson 1981, Charlesworth 1989, Holland et al. 2004).

Sensitivity to environmental stochasticity in marginal populations should also vary according to species' mating systems (de Jong & Klinkhamer 2005, Wagenius et al. 2007). Thus, dioecious plants are generally more prone to pollen limitation of fruit set, since female individuals depend on pollen transfer from nearby male individuals (Charlesworth 1993). Since population decline affects sex ratios and inter-mate distances, reproductive success should strongly depend on the spatial arrangement of individuals, though this influence has rarely been analysed in marginal populations (Yakimowski & Eckert 2007).

In this paper we evaluate the contribution of pollen availability and intermate distance as determinants of individual differences in the reproductive output of a dioecious, anemophilous tree: the English yew (*Taxus baccata*). The study was conducted in a marginal region close to the southern distributional limit of yew, where populations are small and intermate distances are presumably large (Pulido et al. 2007). In addition, the dry Mediterranean climate of the area, that is known to influence population structure and recruitment of yew, is a likely factor affecting tree fecundity through its effect on fruit abortion due to water shortage (Sanz et al. unpublished data). Under the general hypothesis that marginality should have detrimental effects for yew reproduction, we asked four main questions: (1) Is the marginal population studied limited by pollen availability? (2) Do individual female trees show temporally consistent differences in their response to increased pollen load? (3) Do higher fertilization rates lead to higher mature fruit production under drought conditions in the fruiting period? (4) Do inter-mate distances contribute to explain individual differences in fecundity in our fragmented population?

Methods

Study species

Yew is an evergreen, wind-pollinated, and dioecious gymnosperm tree with a scattered distribution in Europe (Thomas & Polwart 2003). Reproductive organs are located in leaf axils near the end of the previous summer growth. Male parts consist of small cones, made up of 6-14 stalked peltate microsporophylls each with 4-9 pollen sacs. These strobili form clusters of up to 20-30 near branch ends. Female structures are 1.5-2.0 mm long, and they are located solitary or in pairs in leaf axils on the underside of shoots. They consist of several imbricate scales, with the uppermost one being fertile and bearing a single ovule (Thomas & Polwart 2003). In our study area, pollen is shed in male trees from late February to early April, whereas female flowers produce a single pollination drop during March and April (Sanz, personal observation). This ovular secretion provides a germination medium for pollen, but it might also play a role in reducing pollen pollution by foreign species (Gelbart & von Aderkas 2002). After fertilization a false fruit or pseudocarp develops, the seed being surrounded by a red, fleshy aril that attract avian and mammal dispersal agents. Throughout the text, the term “fruit” will be used as it is a common practice with yew species (Thomas & Polwart 2003).

Study sites

The study was conducted within a *ca.* 300 km^2 mountain area of the province of Cáceres (central Spain) where 11 yew populations (including five or more adults) are present. We selected two of these populations, namely Escobarejos (close to Losar de la Vera, 40° 12’ N, 5° 60’ W) and Cerezal (close to Nuñomoral, 40° 42’ N, 6° 23’ W). The Escobarejos site is located between 1300 and 1400 m a.s.l. in the upper limit of a semideciduous oak forest (*Quercus pyrenaica*). Here 22 adult trees (6 males and 16 females; proportion of males was 0.28) grow along three adjacent seasonal streams in a north-facing slope (Figure 1). Vegetation is dominated by tall and medium-sized shrubs, mainly *Erica australis*, *E. arborea*, and *Cytisus oromediterraneus*. The Cerezal site is located between 900 and 1000 m a.s.l. Here 53 yew trees grow along two seasonal streams within a forest dominated by *Arbutus unedo* and *Quercus ilex*. The sex of the trees could be determined for 29 individuals (15 males and 14 females; proportion of males was 0.51).

Experimental design and procedures

The production of fully developed, mature fruits was studied in 8 female trees in Cerezal and 16 female trees in Escobarejos during 2005 and 2006. Fruit counts were made in 8 marked branches per tree in Cerezal and in 4 marked branches in Escobarejos. Counts were performed in mid-August, just before the period of fruit removal by bird and mammal frugivores. As fruits were placed along easily measurable shoots, we estimated fruit production per unit branch length to obtain a fecundity estimate that was independent of branch size. This estimate was computed as the number of mature fruits present in the first one meter of branch, defined by the summed length of the corresponding shoots.

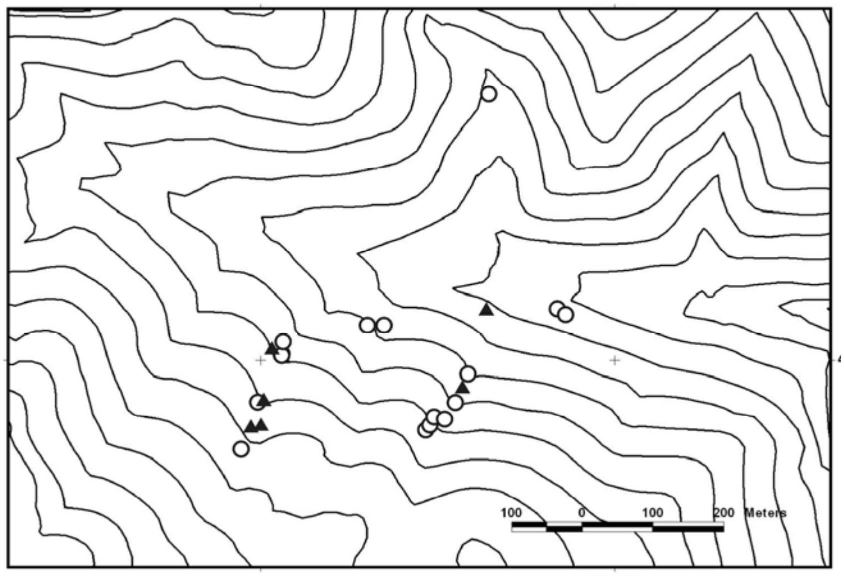


Figure 1. Map showing the location of all trees within the Escobarejos population. Circles indicate 16 female trees, and triangles correspond to 6 male trees.

To test for pollen limitation we conducted a pollen addition experiment in Escobarejos, the largest population, in 2005 and 2006. In this population, the sex-ratio (2.66) was female-biased (16 females: 6 males; Figure 1). This local proportion was clearly greater than the mean calculated for 11 populations in the study region (0.89), but it allowed us to work with the highest number of experimental female trees. Thus, we used 16 female trees as target plants and 6 male trees as pollen donors. In early February each year, we marked 8 branches per female trees. Four branches were left as controls (natural pollination) and four branches were treated by adding pollen. Each branch was defined as the cluster of adjacent modules bearing at least 50 female flowers. The mean value of initial flowers per branch in 2005 was 58.6 ± 0.9 for control branches and 58.4 ± 1.2 for treated branches. In 2006 the mean values were 54.2 ± 1.1 for control and 56.3 ± 1.3 for manipulated branches. Values for treated and control flowers were statistically indistinguishable in both years ($F_{1,126} = 0.010$, $p = 0.919$ and $F_{1,126} = 2.994$, $p = 0.861$ for 2005 and 2006, respectively). Hence, percentage fertilization and fruiting were estimated on the basis of the same sample sizes for control and treated branches.

From late February to mid March we collected pollen from available male trees by shaking small branches in the interior of a recipient. Pollen was transported to the lab and preserved at 4° C until hand pollination (Siregar & Sweet 2000). Artificial pollination started when a given tree had at least 30% of receptive (drop bearing) female flowers. To hand-pollinate female flowers we applied pollen with a fine paintbrush. This procedure was repeated three times during March and April (22, 31

March and 12 April in 2005, 14 and 28 March and 9 April in 2006) to ensure that all females received extra pollen at least once during its flowering period. During hand pollination, control branches were wrapped with a plastic bag to avoid deposition of manipulated pollen. Both treated and control branches were open to subsequent natural pollination after being hand pollinated. As a result of branch growth from one year to the next, and also due to branch damage in some cases, marked branches could not be the same in both years.

In June 2005 and 2006 we counted the number of developing and non-developing ovules in the treated and control branches to estimate fertilization success as the percentage of female flowers that were fertilized. Developing ovules were distinguished from non-developing ones by colour and size: the former were enlarged and white and the latter were brown and small (Sanz, *personal observation*, Allison 1990b). In mid-August each year we counted the number of mature fruits per branch to estimate fruiting success (percentage of female flowers that produced mature fruits) and the incidence of abortion (percentage of fertilized flowers that did not developed into mature fruits).

Data analysis

We used General Linear Models on a nested ANOVA design to test for the effects of year, population and female tree (nested within population) on fruit production. To test for the effect of year, treatment (hand pollination *vs.* control), and female tree on fecundity we used General Linear Models (GLM) with a fully factorial ANOVA design. We used fertilization success, fruiting success, and abortion rates as response variables. Finally, to test for the effect of female neighbourhood on fertilization we obtained data of distance from each female to the nearest male and mean distance from females to all males in the population by means of a Geographic Information System. The relationship between fertilization success and both distances were fitted to a negative exponential equation ($y = a * e^{-bx}$). Trough the text means are reported ± 1 standard error (SE). All statistical analyses were performed with the software Statistica 6.0 (StatSoft, Inc., Tulsa, USA 2003).

Results

Variability in fruit production

The production of mature fruits was similar in Cerezal and Escobarejos in 2005, but it was lower in Escobarejos in 2006 due to extensive fertilization failure. For the Escobarejos site, abortion rates were very high in 2005 and 2006 (Table 1).

Table 1. Mean (± SE) of the number of mature fruits produced (fruits per 1 m branch length) in the two years and populations studied. The percentage fertilization success (% Fruit set) and the percentage of aborted fruits (% Abortion) in control branches for the population where we estimated flower production (Escobarejos) is also shown.

Population	Year	% Fruit set	% Abortion	No. Mature fruits
Cerezal	2005	-	-	4.4 ± 0.6
Cerezal	2006	-	-	4.3 ± 0.6
Escobarejos	2005	18.6 ± 25.8	72.3 ± 4.9	4.1 ± 0.6
Escobarejos	2006	4.2 ± 8.3	73.8 ± 6.4	1.4 ± 0.5

We found significant effects of tree, population and year on mature fruit production (Table 2). In addition, inter-annual trend was different in both populations, as revealed by the significance of the interaction term (Table 2). Among-tree differences in fruit production were extremely high in both populations. For Cerezal a 12.7-fold difference among extreme values was noted in 2005 and a 28-fold difference in 2006. Corresponding figures for Escobarejos were 32.8-fold in 2005 and 17.4-fold in 2006.

Pollen limitation of fertilization and fruiting at the population level

Fertilization success and fruiting success were significantly lower in control branches as compared to treated ones (Figure 2). First, pollen addition had a highly significant effect on fertilization success (24.2 to 39.9 in 2005, and 8.2 to 24.0 in 2006), and this effect was consistent for both study years as revealed by the non-significance of the interaction term in Table 3. Pollen supplementation also increased significantly the fruiting success in treated branches (6.6 to 11.9 in 2005, and 3.1 to 8.1 in 2006; Figure 2). Again, the effect of treatment was consistent for both years (interaction terms in Table 3). In accordance with these results, percentage abortion was not affected by treatment ($F_{1,146} = 0.154$, $p = 0.694$) nor year ($F_{1,146} = 0.296$, $p = 0.587$). Percentage aborted fruits were very high in all cases: 72.3% (control) *vs.* 73.5% (treatment) in 2005, and 73.8% (control) *vs.* 69.9% (treatment) in 2006. The lack of difference in abortion rates indicated that, though treated branches had a higher load of fertilized flowers, the probability of transition from fertilized flower to mature fruit was not influenced by the treatment.

Table 2. Results from GLM (nested ANOVA design) used to test for the effects of year, population, and tree (nested within population) on the number of mature fruits per branch.

Effect	df	F	p
Tree (Population)	22	4.790	0.000
Population	1	5.738	0.017
Year	1	6.231	0.013
Population × Year	1	5.903	0.016

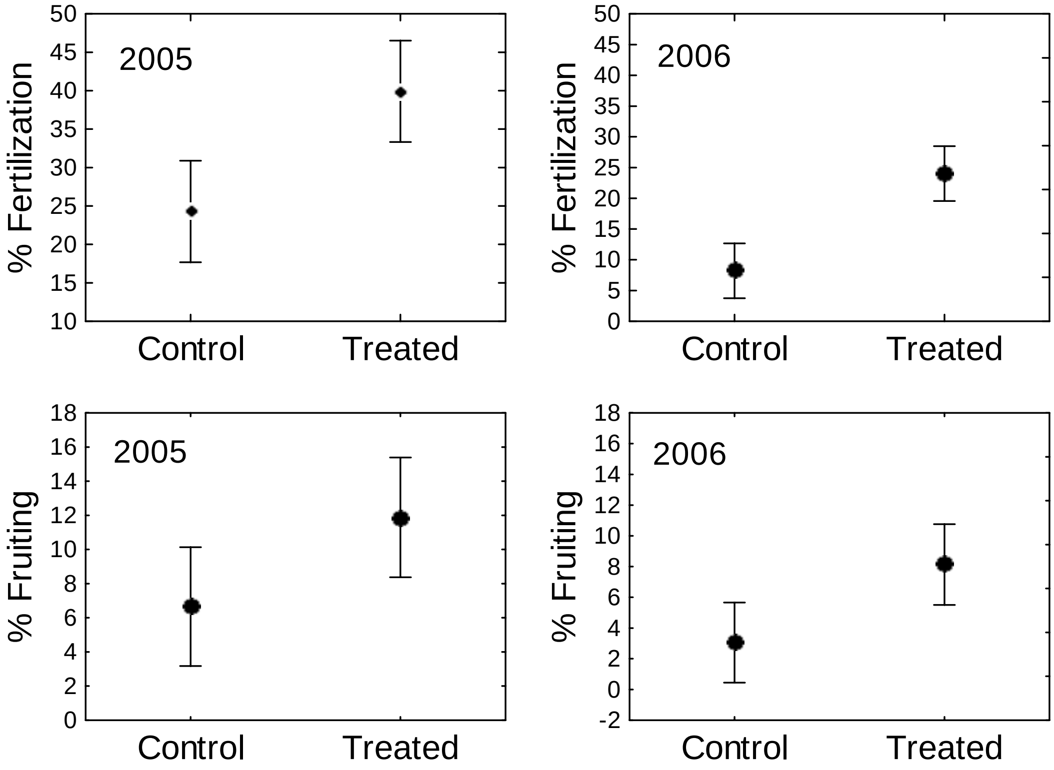


Figure 2. Fertilization success (proportion of females flowers that were fertilized) and fruiting success (proportion of female flowers that developed to mature fruit) in control and treated trees in 2005 and 2006. Values are means of four control and four treated branches for each of the 16 female trees present in the Escobarejos population. Note that, for a given process, the same scale is used for the vertical axis in both years.

Table 3. Results from GLM (fully factorial ANOVA design) testing for the effects of tree, year, and treatment (control *vs*. hand-pollination) on percentage fertilization success (flower to fruit set) and percentage fruiting success (flower to mature fruit).

Effect	Fertilization success			Fruiting success		
	df	F	p	df	F	p
Tree	15	22.635	0.000	1	26.567	0.000
Year	1	85.075	0.000	1	13.811	0.000
Treatment	1	82.340	0.000	15	23.008	0.000
Tree × Year	15	6.886	0.000	15	2.496	0.002
Tree × Treatment	15	2.273	0.003	15	1.889	0.027
Year × Treatment	1	0.003	1.000	1	0.020	0.887
Tree × Year × Treatment	15	0.772	0.700	14	0.887	0.574

Individual variation in reproductive performance and pollen limitation

Fruit production varied greatly also within populations (Table 2). More importantly, the percentage success of fertilization and fruiting varied significantly between female trees in the Escobarejos site (Table 3). Though there was a significant tree × year interaction for both variables (Table 3), the ranking of individuals from 2005 to 2006 was marginally consistent in the case of fertilization ($r = 0.475$, $p = 0.063$) and highly consistent for fruiting ($r = 0.744$, $p = 0.001$; Pearson's correlation coefficients for 16 female trees). Overall, these results show that certain individuals consistently contributed more to the seed pool of the population in the two years study period.

Individual variation in the degree of pollen limitation, estimated as the absolute increment in the success of fertilization or fruiting caused by pollen addition, is shown in Figure 3. The response of individuals in terms of increase in fertilization was highly variable but consistent between years ($r = 0.509$, $p = 0.044$ for the relationship between increments in 2005 and 2006). The values of individual increment (treatment minus control) were independent of the values of control branches in the case of fertilization ($r = -0.178$, $p = 0.507$ in 2005 and $r = -0.129$, $p = 0.633$ in

2006). Results were different for fruiting, in such a way that increments were not consistent between years (r = 0.420, p = 0.105). Also the increments in treated branches were marginally correlated with control values (r = 0.446, p = 0.083) in 2005 and significantly correlated (r = 0.576, p = 0.020) in 2006.

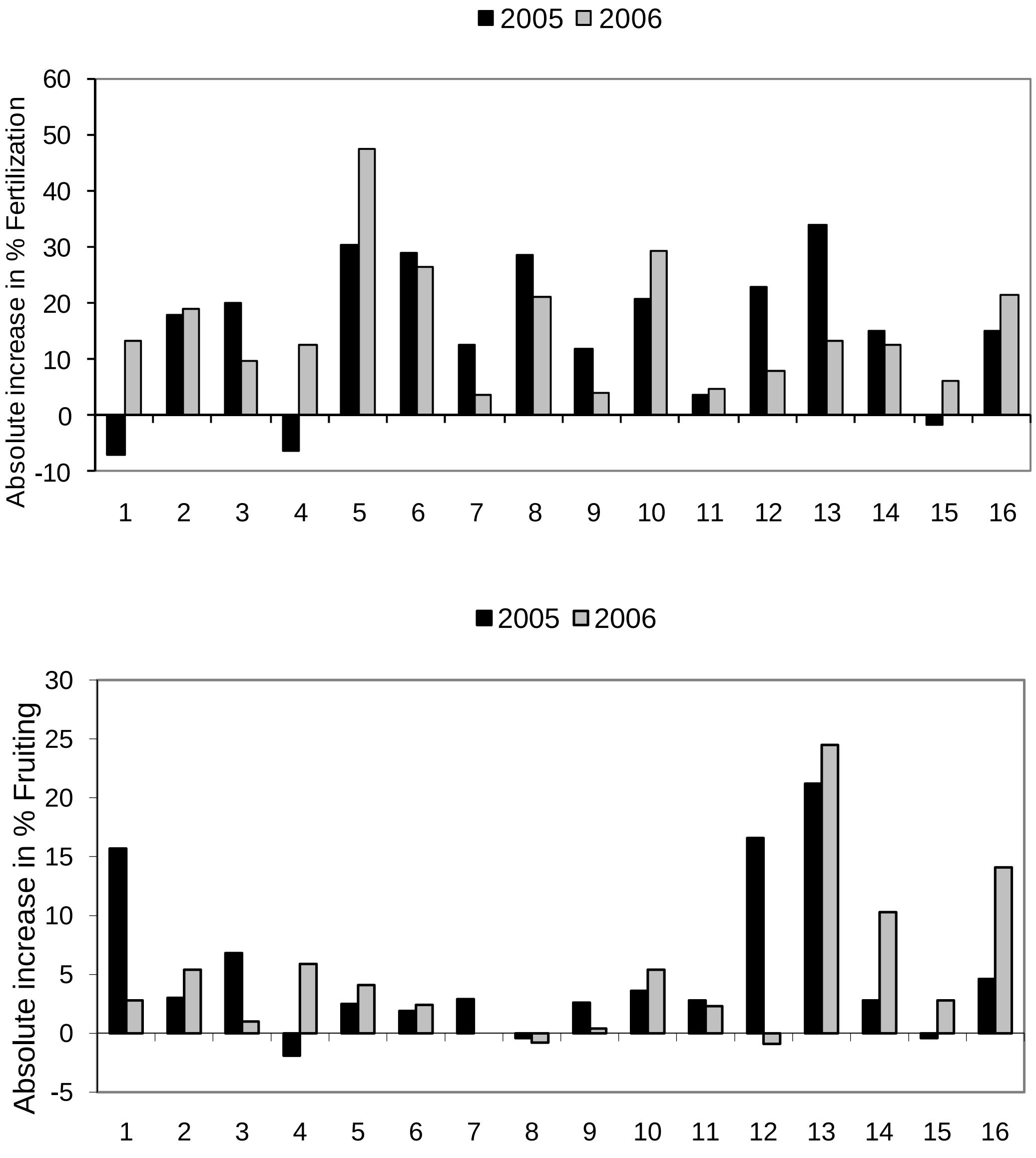
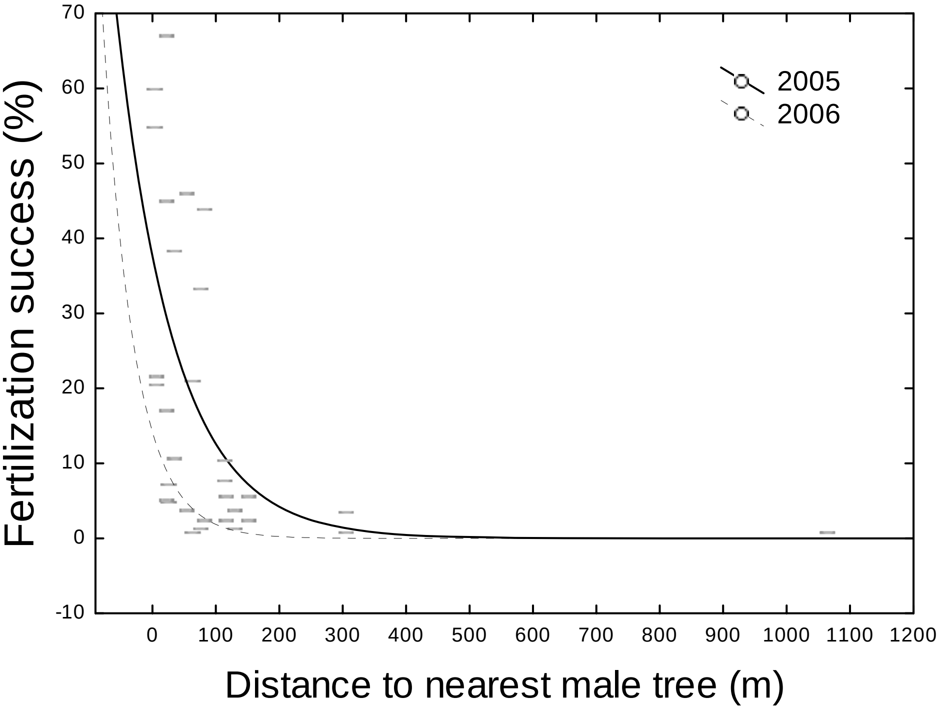


Figure 3. Individual variation in the response of female yew trees to pollen addition in 2005 and 2006. Data for the absolute increment in fertilization success (upper graph) and fruiting success (lower graph) are shown for each of the 16 females in the Escobarejos population.



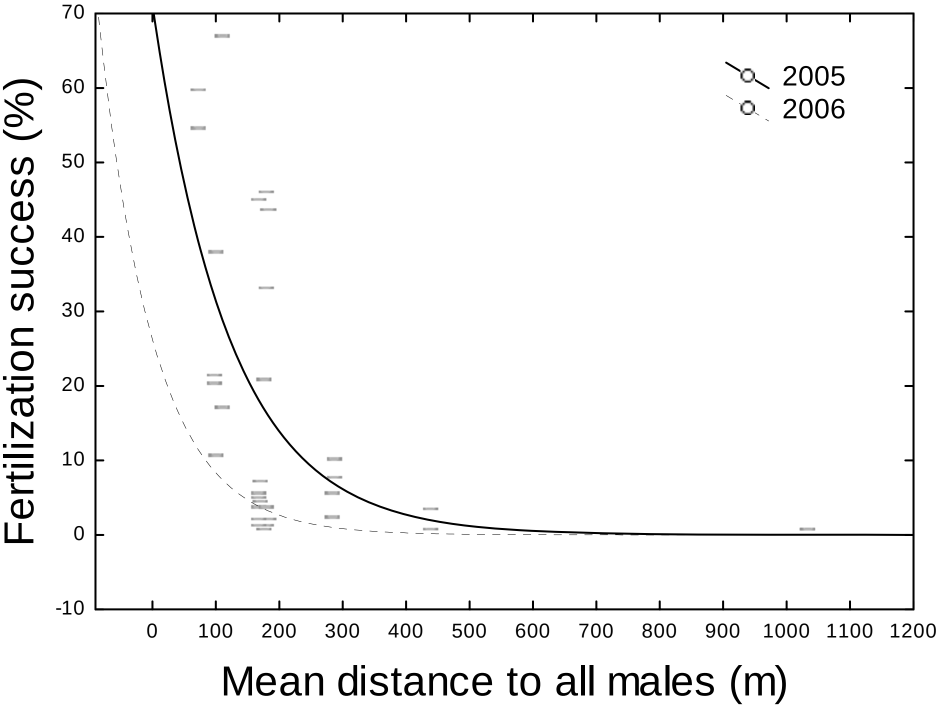


Figure 4. Relationships between percentage fertilization success and distance to the nearest male (upper graph) or mean distance to all males (lower graph). Each point corresponds to one female tree. For each predictor variable, data are shown for both study years. The equations for the models with higher fit were as follow: $y = 37.61 \times e^{-0.01x}$ in 2005 and near male distances, $y = 71.12 \times e^{-0.08x}$ in 2005 and mean distance to all males in population $y = 14.16 \times e^{-0.02x}$ in 2006 and near male distances, $y = 13.16 \times e^{-0.02x}$ in 2006 and mean distance to all males in population.

Effect of female neighbourhood on fertilization

The average value of female distance to the nearest male was 79.0 m, while the mean distance to all males in the population was 183.8 m (Figure 1 and Figure 4). Fertilization success of female trees (control branches) decreased significantly with distance to the nearest male tree ($R^2 = 64.6\%$, $p < 0.001$ in 2005 and $R^2 = 86.0\%$, $p < 0.001$ in 2006). Similar results were obtained when considering as predictor the mean distance to all male trees ($R^2 = 61\%$, $p < 0.001$ in 2005 and $R^2 = 97.1\%$, $p < 0.001$ in 2006). In all cases the best fit of data points followed a negative exponential function (Figure 4). Fertilization success dropped to extremely low values beyond 80 m to the nearest male and beyond 180 m mean distance to all males (Figure 4).

Discussion

Fecundity and pollen limitation at the population level

Our results showed significant between-population and between-year variation in fruit production. Furthermore, supra-annual changes in fruit production were site-dependent, as this variable remained constantly low in Cerezal and sharply decreased in Escobarejos. In the latter population, local climate conditions during flowering may be invoked as primary factors responsible for the extensive fertilization failure in 2006. First, previous studies have shown that only under conditions of high humidity can pollination drops be produced in female flowers of *Taxus* (Ziegler 1959). Low receptivity of female flowers due to air dryness could be an important limitation of fertilization, since both study years had lower-than-average values of winter precipitation, while in the following year (2007) fruit set increased in association with higher-than-average precipitation (Sanz*, unpublished data*). On the other hand, as shown by Melzack & Watts (1982), severe frost in early spring may cause tissue damage in male flowers, a widespread phenomenon observed in most trees in 2006.

Pollen addition in the Escobarejos population confirmed that natural fertilization levels were far from the maximum achievable, as fertilization increased significantly in treated branches in both years (65% and 193% increase in 2005 and 2006). Increased fruit set after pollen addition has been previously found in dioecious and monoecious species of *Taxus* (Allison 1990a, Di Fazio 1998), which suggests that fertilization success is generally low in this genus. This also seems to be the rule for most anemophilous trees in isolation or in small stands (Holm 1994, Knapp 2001).

Individual variation in reproductive performance: magnitude and temporal consistency

Within both study populations, individuals showed a huge variation in fruit production, and the amplitude of this variation was subjected to changes between populations and between years. Thus, the within-population range of fruit production increased from 2005 to 2006 in Cerezal, while it decreased in Escobarejos because of a much lower fruit production in the second year. The wide range of individual variation in reproductive performance, together with its strong spatiotemporal changes, are in line with what could be expected in populations subjected to high environmental stochasticity (Sagarin & Gaines 2002, Yakimowski & Eckert 2007, Crawford 2008).

All else being equal, strong within-population variability in reproductive performance is likely to result in uneven contribution of each individual to population recruitment, that is, few genotypes might be controlling the genetic make-up of the whole population (Jordano et al. 2007). In fact, we also found that the within-population ranking of fruiting success was highly consistent from one year to the next. Continued contribution to the population seed pool by the same female trees provides the basis for the action of selective pressures favouring such individual genotypes (Herrera 2004).

Studies on pollen limitation of reproduction have usually emphasized differences in the average values of control and treated individuals or modules, while little effort has been devoted to differences in individual responsiveness to pollen addition (Knight et al. 2005, but see Holm 1994). If we assume that reiterated hand-pollination was successful in saturating female flowers with pollen at the time of ovular receptivity, individual variation in responsiveness must be attributed to differences in events occurring after pollen arrival. Since pollen quality was expected to be similar as a result of mixing from different donors, the most likely explanation is the existence of genotypic differences in the suitability of the environment provided by female reproductive tissues for pollen tube growth (Rodríguez-Riaño & Dafni 2007).

Deferred consequences of pollen supplementation for fruiting success

Figures for percentage of aborted fruits were almost identical in all treatments and years, with three quarters of the initiated fruits being aborted prior to maturation. This high percentage of fruit loss during development has been also found in studies with tree species under Mediterranean climate, where water shortage during fruiting usually takes place (Jordano et al. 2004). Abortion of different *Taxus* species were a much less important cause of fruit loss for yew in studies conducted in temperate latitudes (Willson et al. 1996, Thomas & Polwart 2003).

Control and treated branches aborted a strikingly similar proportion of fruits in both years, despite hand-pollinated branches bearing a significantly higher load of fertilized flowers and thus potential number of carbohydrate sinks during fruit development (Lee 1988, Anderson & Owens 2001). The fact that increased load of initiated fruits in hand-pollinated branches did not result in higher abortion rates indicates that developing fruits experienced similar competition for assimilates in both treatments. In other words, the sink strength of branches was proportional to their load of developing fruits. Thus, we suggest that high abortion rates could be a necessary mean to allow trees to achieve a proportional allocation of resources to modules with different fruit loads (Lee 1988, de Jong & Klinkhamer 2005).

Effect of inter-mate distances

The sex ratio and the spatial arrangement of male and female trees are critical features of populations of dioecious species (Whitehead 1983), and it is generally accepted that the sex ratio becomes male-biased in low quality habitats (Freeman et al. 1976, Dawson & Bliss 1989). In fact, the mean sex ratio of 17 marginal yew populations in central Spain is slightly male-biased (0.89 ± 0.14; Sanz et al. unpublished manuscript). However, our experimental study was conducted in a female-biased population (sex ratio 2.66), which could be one of the major causes of low average pollination success.

Besides its biased sex ratio, our population was highly fragmented and hence distances between potential mates were generally large. Distances between males and females have been shown to affect pollination success in wind-pollinated species differing in size and mating strategy (Allison 1990a, Knapp 2001, Sork et al. 2002, Wilcock & Neiland 2002, Steven & Waller 2007). We confirmed the effect of distance between males and females on fertilization rates in both study years, even though fertilization rates were very low in most females in 2006. Furthermore, our results consistently showed a negative exponential decrease of fertilization with increasing distance, in such a way that success was very high at short distances and it sharply dropped to extremely low values. Interestingly, the distances corresponding to complete fertilization failure, either for the nearest male or for the mean of all males, were more than double in 2005 than in 2006 as a result of the sharp decrease in overall fertilization success in the latter year (Table 1, Figure 4).

Female isolation with respect to source males can be invoked as the main factor explaining low natural fertilization rates in our study. Other possible causes for fertilization failure could be related to factors acting after pollen arrival to female flowers, such as low ovular receptivity, low germination of pollen grains or low compatibility between pollen and ovules (Wilcock & Neiland 2002). However, the combined influence of these factors relative to that of female isolation is clearly low, as hand-pollination resulted in a dramatic increase in fertilization.

Implications of geographical marginality

Our results in two marginal populations showed significant spatiotemporal variation in fruit production. This contrast with previous results conducted in temperate forests experiencing conditions typical of the centre of the species' range (Thomas & Polwart 2003, Valdés 2006, García et al. 2007). In addition, the important role played by extreme climatic events (spring air dryness or late frost) would be in agreement with expectations for populations located in the species' distribution limit (Rasmussen & Kollmann 2004, Hampe 2005). Among these critical abiotic constraints, the effect of drought on fruit development could be considered as a further fecundity limitation of populations located in the southern rear edge of the species' range (García et al. 2000). Similar results were found in marginal populations of *Prunus mahaleb* (Pflugshaupt et al. 2002), *Sorbus torminalis* (Rasmussen & Kollmann 2004), and *Frangula alnus* (Hampe 2005). Finally, and besides abiotic drivers that impose a strong environmental stochasticity, the female-biassed sex-ratio and the large intermate distances can be viewed as two components of demographic stocochasticity inherent to peripheral populations.

Acknowledgements

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Capítulo 5

Depredación posdispersiva de semillas en un árbol relicto: ¿se incrementa el consumo por roedores en el borde del área de distribución del tejo (*Taxus baccata*)?

The post-dispersal seed fate of a relict tree: does predation by rodents increase in the range limit of yew (*Taxus baccata*)?

The post-dispersal seed fate of a relict tree: does predation by rodents increase in the range limit of yew (*Taxus baccata*)?

Abstract

Post-dispersal seed predation is a crucial phenomenon in the recruitment process of tree species, and its incidence could be decisive in marginal populations of threatened relict species, such as yew (*Taxus baccata*) growing in Mediterranean mountains of central Spain. Here we examine the spatial and temporal patterns of yew seed consumption by rodents and explore the potential consequences of living in the periphery of the species' range. We predicted that (1) the rates of seed predation should be higher than in central populations as a result of habitat fragmentation; (2) seed consumption should exhibit fine-grained spatial variation due to microhabitat specificity and distance to source trees; and (3) predation rates should be lower far from existing yew stands, as rodents are expected to forage on different food sources. We evaluated the effect of population, microhabitat, and distance to the nearest seed producing tree on percentage of seeds eaten in three marginal populations during 2005 and 2006. To evaluate whether seed predation could prevent the foundation of new yew patches, we estimated the loss of seeds that were experimentally dispersed far from existing stands in 2006.

Predation rates were extremely high to the extent that rodent almost completely depleted the experimental seeds before germination in all yew populations and years. We also found site-specific differences that paralleled supra-annual variation in seed crops. Our expectation of higher predation rates with increasing vegetation cover was fully confirmed, and it was consistent for all years and populations. This microhabitat effect outweighed the effect of distance to the nearest seed-producing tree. In 2006 overall predation rates were 23% lower in the absence of yew trees as compared with yew stands. We suggest that the mechanisms explaining seed depletion in marginal populations were primarily linked to the direct or indirect effects of habitat fragmentation. Finally, it is concluded that rodents selectively consumed the most valuable seeds in terms of their recruitment prospects, a fact that may be alleviated when seeds arrive to empty patches of suitable habitat.

Introduction

Post-dispersal seed predation is known to limit recruitment in plant populations, since it set the amount of potentially emerging seedlings (Janzen 1971, Crawley 2000). In the case of trees, that usually produce large seeds, rodent predators have been shown to be major agents determining seedling distribution and even regeneration of dominant species (see Hulme 2000, Hulme & Benkmann 2002 for reviews). Most studies have shown that predation rates are microhabitat-specific due to the effect of vegetation cover on the behaviour of rodents. This implies that the frequency of seed dispersal to different microhabitats strongly influences the fate of seeds (Calviño-Cancela 2007). In other cases, seed predation rates may be independent of microhabitat, mostly because consumers unselectively deplete a very high proportion of seeds, hence preventing recruitment at all (Verdú & García-Fayos 1996, Castro et al. 1999, Plucinski & Hunter 2001). Seed predation also exhibits considerable temporal variation within and between years (Kollmann et al. 1998, Plucinski & Hunter 2001, Feer & Forget 2002), to the extent that losses of seeds can be concentrated in the few days or weeks after exposure (Whelan et al. 1991, Schreiner et al. 2000).

While many studies have addressed the spatiotemporal variation in removal of seeds at a local level, the question whether predation by functionally similar rodent species follow a certain geographical trend has been scarcely explored (García-Castaño et al. 2006). Specifically, as predicted by common biogeographical hypothesis (Brown 1984, Caughley et al. 1988), seed survival is expected to be different in the centre with respect to the periphery of the plant species' range (García et al. 2000a). Thus, the fact that marginal plant populations tend to be more fragmented and to face greater environmental stress is well established (Crawford 2008). However, though it could be expected that this declining status may negatively affect tree fecundity and seed availability for animal consumers, it is hard to predict the impact of these animals on plant populations, as the geographical variation of predator and plant abundance may be decoupled (Garrido et al. 2002). For example, rodent predation has been shown to increase with the degree of habitat fragmentation (Santos & Tellería 1994, 1997), but whether this applies to fragmented marginal populations depends, among other factors, on predator population density at the plant's distribution margin.

Studies of plant-animal interactions in peripheral plant populations are scarce, and few studies have been conducted on seed predation by rodents (Hulme 1997, Castro et al. 1999, Hampe & Arroyo 2002, García-Castaño et al. 2006). In this paper we address this issue in marginal populations of yew (*Taxus baccata*) located in the southern range limit of the species (Thomas & Polwart 2003). The main objectives of the study were to quantify the magnitude and spatiotemporal variability of rodent predation on yew seeds, and to evaluate its potential impact on regeneration of marginal populations. The impact of this biotic interaction could add to that exerted by abiotic conditions (Sanz et al., Sanz & Pulido, unpublished manuscripts), thus severely reducing regeneration prospects. Thus we expected that: (1) the rates of seed predation should be high as a result of low tree fecundity and high habitat fragmentation; (2) seed consumption should show fine-grained spatial variation due to the combined effect of microhabitat and distance to seed producing trees; and (3) predation rates should be lower far from existing yew stands, as rodents are expected to forage on different food sources.

Methods

Study species

The English yew is a dioecious, long-lived tree species with a Eurasian distribution. Yew populations are presented in Europe, East Asia and North Africa. Most regions occupied by yew occur in Europe, where the species lives in mountain areas from 63° to 36° N latitude approximately. Yew is absent only at very high elevations or under the influence of very cold continental climate (Paule 1993). Despite its broad distribution yew is considered in most regions as a threatened species (Thomas & Polwart 2003). This declining status has been proposed for most peripheral populations, both at the northern and the southern edges (Svenning & Magard 1999, García et al. 2000b, Sanz et al. unpublished manuscript). The most commonly reported post-dispersal seed predator throughout Europe is the wood mouse (*Apodemus sylvaticus*). This species consumes a large amount of pulp-free seeds from fallen fruits or from animal regurgitates (Thomas & Polwart 2003, Hulme 1996, Hulme 1997, García et al. 2005, García-Castaño et al. 2006). Yew seeds are dark brown, spherical or slightly ellipsoidal. The range values of average fresh mass of this lipid-rich seeds is 43-77 mg (Thomas & Polwart 2003).

Study sites

The study was performed in the western Sistema Central mountain range (Cáceres province), a central Spanish region located in the southern edge of the species' range. The climate is continental Mediterranean with dry summers and cold winters. Research was conducted in the populations of Escobarejos, Cerezal, and Papúos, which are separated by a maximum of 62 kilometres. The Escobarejos population was located at 1350 m elevation and it comprised 34 adult trees associated to seasonal streams surrounded by shrublands dominated by *Erica australis* and *Cytisus oromediterraneus.* Fleshy-fruited tree species (*Sorbus aucuparia* and *Ilex aquifollium*) were also present in low numbers. The Papúos population was located at 1500 m elevation and it comprised 10 adult trees (3 females and 7 males) associated to seasonal streams surrounded by shrublands dominated by *Erica australis* and *Cytisus oromediterraneus.* Fleshy-fruited tree species (*Sorbus aucuparia* and *Ilex aquifollium*) were also present in low numbers. The Cerezal population was located at 900 m elevation and it comprised 53 adult trees, of which 29 could be sexed (15 males and 14 females). Yew trees were growing close to streams in the understorey of a mixed montane forest with *Quercus ilex* susbsp. *ballota* and *Arbutus unedo* as dominant species. All three populations have a long history of livestock grazing and associated burning for improving browse, but these practices are maintained only partially in Escobarejos and Papúos.

Experimental procedures

The experiments were carried out from September to March in two consecutive years (2005 and 2006). The experimental seeds used to analyze predation in a given population were of local origin. Seed removal was studied in the field using feeding stations consisting of plastic dishes (8 cm in diameter and 2.5 cm in deep) placed in three different microhabitats: under female yew, shrubs or in open areas (bare soil and/or herbs). Feeding stations had small holes in the bottom of the dish for water drainage and they were covered lightly by organic soil and litter in order to mimic natural conditions and to avoid the loss of seeds due to wind or rain. We placed 8-10 dishes per microhabitat with 30 seeds on each dish. All seeds had a barely visible green mark for distinguishing from other seeds out of the experiment. The number of predated seeds was noted in late October (early predation) and in late March (cumulative predation). We considered that a seed had been predated when there were easily identifiable teeth marks on the outer surface. We counted predated seed in the dishes and within a radius of 50 centimetres around the dish. No invertebrate activity was observed at dishes (Sanz, *personal observation*) and following other authors we considered removal of seeds by rodents as equivalent to predation (Hulme 1997, Hulme & Borelli 1999, García et al. 2005).

To test prediction 3, implying lower seed predation outside existing yew stands, we performed an experiment in a site were no yew tree was present but that could be considered as a potential yew site on the basis of local physiognomy. The site was a small valley including a seasonal stream surrounded by shrublands. In this experiment we analyzed the effect of the distance to the stream (0-1 *vs.* 1-3 metres) and the stream section (upper and bottom parts of the valley). Both factors could be expected to affect yew regeneration, as seedlings emerged from surviving seeds strongly depend on soil water supply (Sanz et al. unpublished manuscript). In each section we placed eight dishes with 10 seeds on each. In each section four dishes were close and four dishes were away from the spring. Apart from estimating the magnitude of predation when yew trees were absent, we tested whether both experimental factors affected the foraging patterns and the impacts of seed predators.

Data analysis

Data were analyzed with General Linear Models on an ANCOVA type design. Early and cumulative percentage seed predation were used as dependent variables, whereas microhabitat, population and year were included as categorical predictors. Distance to the closest female yew was used as covariate to remove its likely influence on the main effects. Differences between levels of significant predictors were tested with Tukey HSD tests. The effect of distance on cumulative predation rates were further explored by regressing both variables for each site per year combination. For studying seed removal in the absence of yew we used General Linear Models on a factorial ANOVA type design. Again cumulative predation was used as the dependent variable and distance to stream and section of the stream as categorical predictors. Prior to the above analyses the dependent variable was normalized by means of angular transformation. All statistical analyses were performed with the software Statistica 6.0 (StatSoft, Inc., Tulsa, USA).

Table 1. Results from General Linear Models on ANCOVA type design used to test the effect of microhabitat, population, and year on percentage cumulative predation at the end of the experimental period (March).

Effect	df	F	p
Distance	1	0.005	0.943
Microhabitat	2	4.320	0.015
Population	2	1.344	0.264
Year	1	21.170	0.000
Microhabitat * Population	4	2.302	0.062
Microhabitat * Year	2	0.787	0.457
Population * Year	2	9.056	0.000
Microhabitat * Population *Year	4	1.808	0.131

Results

Variation in predation rates

We found very high rates of seed predation in the two study years, both for early and for cumulative consumption. For early predation (September-November) we found a significant effects of year (F = 20.321, df = 1, $p < 0.001$), that showed different trends for each population (F = 18.676, df = 2, $p < 0.001$; GLM on three-way ANCOVA design). This interaction was due to the Cerezal population showing greater predation in 2005, while the opposite was found in Escobarejos and Papúos (Figure 1). Predation rates also varied between microhabitats (F = 4.269, df = 2, p =

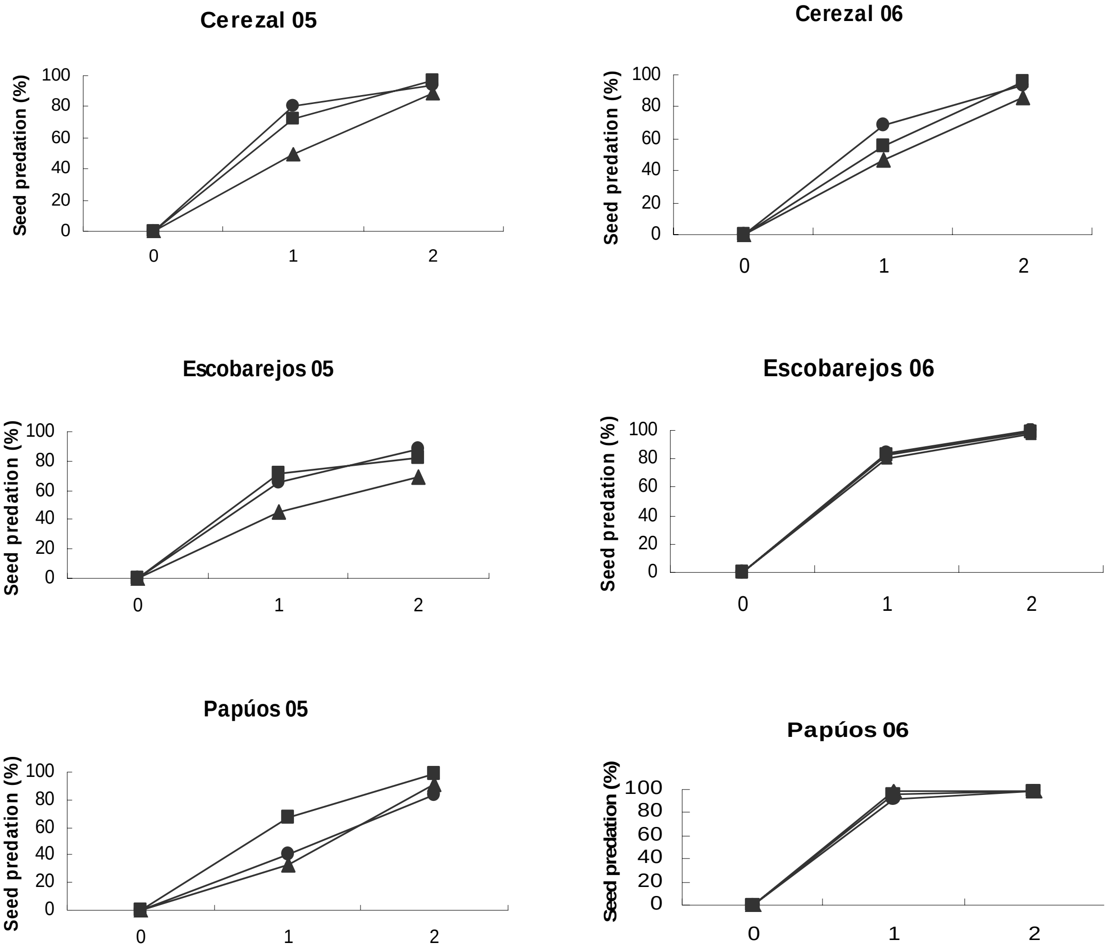

Figure 1. Temporal changes in mean values of cumulative percentage of seed removal in three populations and two years (2005 and 2006). Within each graph symbols represent different microhabitats (circles: yew microhabitat; triangles: open areas; squares: shrubs microhabitat). Figures in the horizontal axis refer to the sampling date (0: onset of the experiment in September; 1: early predation from September to November; 2: cumulative predation from September to March).

0.016). Averaged across populations, predation was especially intense under yew trees (61.6% ± 5.4 in 2005 and 81.6% ± 5.6 in 2006) and shrubs (70.0% ± 5.7 in 2005 and 79.6% ± 5.7 in 2006). The corresponding values were significantly lower in open areas especially in 2005 (42.0% ± 5.4 in 2005 and 77.6% ± 5.8 in 2006).

Cumulative predations rates (September-March) were 87.9% ± 2.9 in 2005 and 96.5% ± 1.4 in 2006 (figures averaged for all populations). The difference between years was significant (Table 1), and it depended also on population because predation increased from 2005 to 2006 in Escobarejos and Papúos, while it decreased in Cerezal (Table 1). The cumulative rate showed a significant microhabitat effect (Table 1), with predation being more intense under yew trees (87.4% ± 2.6 in 2005 and 97.8% ± 2.6 in 2006) and shrubs (90.6% ± 2.7 in 2005 and 98.0% ± 2.6 in 2006). However, predation in open areas was also very high at the end of the experimental period (80.6% ± 2.8 in 2005 and 94.5% ± 2.6 in 2006).

Effect of distance to female yew trees

The model including the effects of year, population, and microhabitat showed no effect of distance from the feeding station to the nearest female yew tree (Table 1). When distance was used as predictor of the cumulative predation rate in regression analyses, we found no significant effect in all population per year combination (Table 2). Only in the case of Escobarejos in 2007 did the relationship approached statistical significance (p = 0.077).

Seed predation in the absence of yew trees

Cumulative seed predation in 2006 was also high in the site were no yews were present (75% when all treatments were pooled), but it was lower than in the yew stands.

Table 2. Summary of the simple linear regression analyses predicting cumulative predation rates as a function of distance from the feeding stations to the nearest female tree in the three study populations and in two years.

		2005			2006	
	R^2	F	p	R^2	F	p
Cerezal	0.000	0.003	0.958	0.067	1.502	0.233
Escobarejos	0.107	3.356	0.077	0.074	1.926	0.178
Papúos	0.171	4.757	0.263	0.017	0.434	0.516

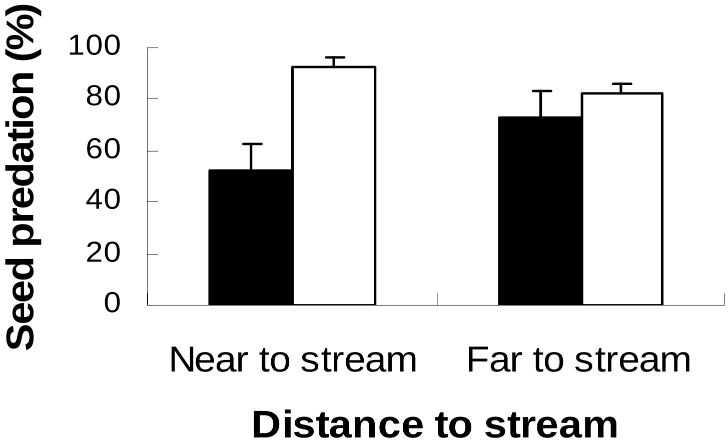

Figure 2. Mean (+ SE) values of seed predation rate as a function of distance to the stream and section of the stream in a site were yew is absent. Black columns: high section of the stream; white columns: low section of the stream.

Predation rates were significantly affected by the stream section but not by distance to the stream (Table 3). The cumulative values were 62.5% ± 7.5 in the upper valley and 87.5 ± 7.5 downstream. With respect to distance, predation was 77.5% ± 7.0 at the greater distance and 72.5% ± 10.3 in the stations adjacent to the stream (Figure 2).

Table 3. Results of factorial GLM analysis on an factorial ANOVA type design testing for the effects of stream section and distance to stream on cumulative seed losses in the absence of yew trees. See Figure 2 for the levels of the factors.

Effect	df	F	p
Section	1	5.660	0.035
Distance	1	0.226	0.643
Section * Distance	1	2.038	0.179

Discussion

Does seed predation increase at the range limit?

Predation rates reported in this study were extremely high within all yew stands considered, to the extent that rodent almost completely depleted the experimental seeds before germination. This result is comparable to those found in studies of seed predation with other tree species in southern marginal locations (Hulme 1997, Castro et al. 1999, Hampe & Arroyo 2002). Comparable studies carried out near the centre of the range (Central Europe) have predictably found lower predation rates in yew (Hulme 1996 -ca. 70%), Hulme & Borelli 1999 (38-60%), García et al. 2005 (ca. 70%)) and other forest species (García-Castaño et al. 2006). Therefore, postdispersal seed losses can be invoked as a potentially important driver of recruitment in peripheral populations, though this effect could be due to different ecological mechanisms acting at the species' margin. First, fragmentation of marginal populations can increase predation rates through an influx of generalist seed predators from the habitat surrounding isolates (Hulme 1997, Santos & Tellería 1997, Curran & Webb 2000). Second, low population numbers and isolation between individual trees can make them more vulnerable to seed predators because the location of seeds is more predictable (Hulme & Benkmann 2002). Third, as found in a previous study (Sanz & Pulido, *unpublished manuscript*), low density of individuals implies a decrease in the absolute number of seeds produced per unit area, which, all else being equal, may cause an increase in the impact of rodents. Fourth, high rates of predation could also be related to the low availability of alternative food sources in the study period. Thus, marginal populations in Mediterranean mountains tend to occur in disturbed habitats dominated by early successional shrublands where large-seeded species are very scarce, as it is the case of our study sites. Finally, among the large-seeded species present in this region (*T. baccata*, *Sorbus aucuparia*, and *Ilex aquifolium*) yew have been shown to be the most rewarding one for rodents (García et al. 2005, García et al. 2007). Overall, we suggest that mechanisms explaining seed depletion in marginal populations are primarily linked to the direct or indirect effects of habitat fragmentation (Santos & Tellería 1994, 1997, García & Chakoff 2007).

Spatial patterns of seed predation

At the population level, predation rates were generally very high, but we found site-specific differences that seem to be related to annual variation in seed crops (Sanz & Pulido, unpublished manuscript). Thus, one of the sites (Cerezal) showed similar crops in both study years, whereas one of the other two sites (Escobarejos) showed a decrease from 2005 to 2006. The impact of seed predators paralleled inter-annual changes in seed production, suggesting that predator satiation and crop depletion occurred in good and bad years, respectively (Kelly & Sork 2002).

At a within-population scale, rodent seed predation has been shown to be microhabitat-specific in most studies, a result that tends to be explained by risk-sensitive foraging (Fedriani & Manzaneda 2005, Calviño-Cancela 2007). In addition, predation rates are expected to decrease with increasing distance from the seed-producing trees, as seeds are progressively scarcer and their location is less predictable (Janzen 1971). Due to the likely effects of microhabitat and distance, we expected a fine-grained spatial variation in predation rates, a fact that was only partially supported by our data.

With respect to microhabitat specificity, our expectation of higher predation rates with increasing vegetation cover was fully confirmed. Furthermore, the between-microhabitat patterns were consistent for all years and populations. Thus, predators changed the spatial distribution of the seed rain especially intense under yew trees and shrubs (García et al. 2007). Concerning distance to the nearest yew tree, we did not find an effect on seed removal, and results suggest that the effect of microhabitat outweighed that of distance. The lack of effect of distance to the nearest seed source in other studies has been explained by considering the spatial distribution of seed-producing trees, in such a way that predictions from the classical Janzen-Connell's model are expected to hold for regularly distributed adult populations (Hyatt et al. 2003). When conspecific adults show a random or clumped distribution, as it is the case of our forest fragments, patterns of seed survival may depart from Janzen-Conell's expectations. In addition, existing data indicates that foraging by vertebrate granivores frequently deviates from this model, while less mobile invertebrate predators usually match it (Hammond & Brown 1998).

Seed predation and the potential for colonizing new sites

In the absence of yew trees rodents were expected to forage on different food sources, which, all else being equal, could reduce predation rates on yew seeds. Though no statistical comparison could be carried out, we found that in 2006 overall predation rates averaged 97% in yew stands and 75% in the absence of yews, which means 23% reduction in predator's incidence. Cumulative predation rates in 2006 were 63% and 86% in the two sites (upper and lower sections) were no yew were present, while the corresponding figures were 92%, 98%, and 99% in the three yew populations. Thus, it could be suggested that seed arrival to empty patches of suitable habitat would increase the probability of seed survival and recruitment. As the probability of seedling recruitment is extremely low in existing yew stands (Sanz et al. unpublished manuscript), the higher suitability of empty patches regarding seed survival could be the basis for the foundation of new populations of this threatened species.

Conclusion: implications for yew regeneration

The consequences of seed predation by rodents for the recruitment and persistence of marginal populations of yew depend on the amount of seeds surviving in suitable microsites for germination and establishment. We have shown elsewhere that the likelihood of seedling establishment boots in shaded and moist microsites and these conditions usually occurs under shrubs or trees growing close to streams (Sanz et al. unpublished manuscript). We have found in this study that predation is significantly more intense under yew and shrubs patches, and that the risk of seed consumption is lower in open areas. Therefore, predation by rodents was concentrated in potentially safe sites for seedlings (see also Hulme 1996, García et al. 2000). By contrast, predation of seed in open areas is demographically inconsequential, since few seeds are dispersed to this microhabitats and the survival probability provided germination occur is close to zero. It can thus be concluded that rodents selectively consumed the most valuable seeds in terms of their recruitment prospects, thus posing an important threat for yew persistence in marginal populations.

Acknowledgements

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Capítulo 6

¿Está atenuado el efecto de las plantas nodriza en los hábitat refugio de especies forestales? Una evaluación con dos especies de diferente tolerancia a la sombra

Are nurse-plant effects attenuated in refuge habitats of boreal relict species? A test with two species of contrasting shade tolerances

Are nurse-plant effects attenuated in refuge habitats of boreal relict species? A test with two species of contrasting shade tolerances

Abstract

Facilitation by nurse plants is a critical process in early regeneration of tree seedlings in stressing environments. However, little is known about its role in facilitating seedling survival in marginal populations growing in climatic refuges, where species may experience different resource levels. The aim of this study was to evaluate the relationships between shrubs and seedlings of two contrasting tree species, English Yew (*Taxus baccata*) and downy birch (*Betula alba*), growing in marginal populations where they behave as riparian, hence water stress could be buffered. We planted one-year seedlings of both species beneath shrubs and beneath open grassland in two herbivore exclosures. Seedling survival was monitored over two years. Soil moisture and irradiance were measured for each seedling at mid-summer to test for their influence on survival. Soil moisture and irradiance were significantly higher in open grassland of both study plots. Seedling survival was significantly affected by soil moisture in both populations and years, while no effect of shrubs was noticed for either seedling species. Results remained unchanged after the second summer in both species. It can be concluded that, in riparian refuge habitats, the relationships between seedlings and their otherwise nurse shrubs, may shift from facilitation to neutrality.

Introduction

The outcome of plant-plant interactions have been proposed to vary according to the level of environmental stress experienced by the participant species (Lortie & Callaway 2006, Brooker et al. 2008). Positive effects (facilitation) are well documented and they are hypothesized to occur under higher levels of abiotic stress (Bertness & Callaway 1994, Callaway et al. 2002, Brooker et al. 2008). Facilitation of tree seedlings by shrubs species acting as nurses in the face of abiotic stress have been repeatedly found in Mediterranean mountains, where alleviation of summer drought seems to be the main advantage of seedling association with nurse shrubs (Gómez-Aparicio et al. 2004, Castro et al. 2005, Gómez-Aparicio et al. 2008). In contrast, protection against biotic stress caused by herbivore damage seems to be of lower relative importance when compared with that of microenvironmental effects (Gómez-Aparicio et al. 2008). This view of shrubs-seedling interactions have been criticized on the basis of recent meta-analyses showing that the net result of the interaction depends on the response variable used as a proxy of fitness and on the resource axis considered to define the stress gradient (Maestre et al. 2005, 2006). For example, the relative importance of abiotic and biotic stress may change for different life stages within a species (García & Obeso 2003) or for different target species (Bertness & Callaway 1994, Holmgren et al. 1997, Brooker et al. 2008).

Studies on plant performance at their distributional limits have focussed on the direct effect of changing abiotic conditions on the target species (Brown et al. 1996, Gaston et al. 2003, Santamaría et al. 2003). However, changes in abiotic conditions may also have indirect effects through the modification of the strength of biotic interactions at the edge of species' distribution, a fact that has been largely ignored to date.

As the distance from the centre of the distribution increases, environmental conditions progressively depart from those found in central populations. Consequently, marginal populations will tend to concentrate in refuge habitats under benign conditions surrounded by inhospitable environments (Hampe & Petit 2005). For example, in dry Mediterranean environments many populations of tree relict species of subtropical or boreal origin exhibit habitat shift toward riparian environments, where the effect of summer drought can be buffered while the effect of excess light may be more pronounced (Hampe & Petit 2005, Pulido et al. 2008, Sanz et al. *submitted manuscript*). The effect of multiple forms of stress, acting in the same or in opposite directions, could lead to varying direct effects on plant performance (Pulido et al. 2008). In addition, under these changed abiotic conditions the performance of the target species may be altered due to the indirect effects on its biotic interactions. Here we illustrate this question by evaluating the effect of shrubs on the survival of tree seedlings in populations located in the southern distributional limit, where the abiotic environment presumably departs from that of central populations (Sagarin & Gaines 2002). Tree seedlings belonged to two species of boreal origin, yew (*Taxus baccata*) and downy birch (*Betula alba*), that occupy benign mountain riparian habitats in Mediterranean mountains (García et al. 2000, Sanz et al. *submitted manuscript*). In previous studies we found that seedling establishment of both species in marginal populations is controlled by soil moisture, but species-specific responses to the presence of shrubs are expected on the basis of their contrasting shade tolerances. Thus, all else being equal, yew seedlings are tolerant to deep shade and thus they are expected to benefit from the shade provided by shrubs (Hättenschwiler 2001, Izkulo & Boratynski 2006), whereas birch seedlings are shade intolerant and they are expected to be more successful in open areas (Miles & Young 1980, Atkinson 1992).

We experimentally evaluated how seedlings of both species responded to changed moisture and light conditions resulting from the presence of shrubs. Specifically we asked: (1) to what extent is seedling survival controlled by water availability in refuge riparian habitats?; (2) is seedling survival facilitated under shrubs when water supply is less limiting?; and (3) is the effect of shrubs different for *T. baccata* and *B. alba* as a result of their contrasting shade tolerances?.

Methods

Study species

The English yew is a dioecious, long-lived tree species with a Eurasian distribution. Yew populations are present in Europe, East Asia and North Africa (Thomas & Polwart 2003). Most regions occupied by yew occur in Europe, where the species lives from 63° to 36° N latitude approximately. Despite its broad distribution yew is considered in most regions as a threatened species (Thomas & Polwart 2003). The regeneration of yew is closely related to abiotic factors such as irradiance availability (Svenning & Magard 1999, Dovciak 2002, Iszkulo & Boratynski 2006), water availability, and frost damage (Sanz et al. *unpublished manuscript*, Iszkulo & Boratynski 2005). Downy birch is a monoecious tree with male and female flowers occurring in separated inflorescences or catkins. The species is wind pollinated and mostly self-incompatible (Pelham et al. 1984, Atkinson 1992). Downy birch occurs in Europe and in Central and North Asia (Atkinson 1992). At its southern distribution limit downy birch lives in few remnant populations in the Sistema Central mountain range of central Iberian Peninsula (Castroviejo et al. 1990). Within this region downy birch is distributed from Serra da Estrela in Portugal to Sierra de Ayllón in Spain as its eastern limit (Castroviejo et al. 1990). Regeneration patterns have been studied in Temperate and Boreal areas, where downy birch behaves as a pioneer species in forest clearings (Sarvas 1948, Miles & Kinnaird 1979a, 1979b, Miles & Young 1980, Holm 1994).

Study sites

The experiment was conducted in two fences sites located in the centre of the Sistema Central mountain range, in the North of Cáceres province. The “Nogaledas” site (40° 11´ N, 5° 51´ W) was located at 1200 m asl, while the “Regaderas” site (40° 13´, 5° 25´ W) was located at 1700 m asl. In both sites the climate is of a mountain

Mediterranean type with cold winters and hot summers. Mean annual temperature averages is 14.9° C and mean annual precipitation is 1100 mm. The dominant vegetation in both sites is composed by heathers (*Erica arborea* and *E. australis*) and brooms (*Genista florida*) mixed with riparian forest of alder (*Alnus glutinosa*) and herbaceous plants (*Festuca elegans* and *Pteridium aquilinum*) in grassland microhabitat.

Experimental design

We planted one-year old seedlings of *Betula alba* and *Taxus baccata* in a 200 m^2 exclosure on each site. Exclosures were established in autumn 2005 with 2-m high fences. Two cohorts of healthy seedlings grown in the glasshouse of the University of Extremadura were planted in March 2006 and March 2007. Within each exclosure we planted seedlings in two microhabitats: beneath shrubs (heathers) and in the open grassland (ferns and grasses). In each exclosure four experimental blocks of each microhabitat were established. In each block we planted 10 seedlings of each species. Minimum distance between seedlings was 10 cm. Seedlings were allowed to establish from March to June, when we confirmed that all seedlings were alive after transplantation.

Soil moisture and light measurements

Soil moisture in each experimental treatment (shrub and open grassland) was characterized by measuring volumetric soil water content. Measurements were taken for each seedling on 14-15 July 2006 and 19-20 July 2007 with a Thetaprobe Sensor (Delta-T Devices, UK), which recorded values in the uppermost 10 cm soil layer. Post-summer seedling survival of the 2006 cohort was checked in October 2006 and October 2007, while seedlings planted in 2006 were checked in October 2007.

A year-round integrated measurement of irradiance was obtained by taking hemispherical photographs over each seedling with a fish-eye camera during 2006. Images were treated with GlA: “Gap Light Analyzer” (GLA 2.0: Frazer & Caham 1999). The Direct Site Factor (DSF) was used as a dimensionless measure of light supply.

Data analysis

Our experiment involved a very large design with five categorical predictors (species, year, population, treatment –shrub present or absent-, and block) and a covariate (soil moisture). In addition, for the first year in which irradiance as also measured, the design included two covariates. To make this design simpler, we conducted separate analyses for each species. In addition, as our aim was to specifically testing for some of the above effects on seedling survival, we first conducted a main effect ANCOVA to test for the effects of block in an analysis including the remaining categorical predictors and moisture and irradiance as covariates. Since the effect of block was not significant we also conducted a factorial ANCOVA to check the influence of interactions on the significance of the main effects. We used the Statistica package (version 6.0, StatSoft Inc. 2003) for all the preceding analyses. Data used in the ANOVAs were tested for normality and homocedasticity and transformed when necessary.

Results

Abiotic characteristics of microhabitats

There was a statistically significant difference in moisture among microhabitat treatments (F = 11.858, df = 1.520, $p < 0.001$) and years (F = 13.991, df = 1.520, $p < 0.001$) at both study sites (F = 72.056, df = 1.520, $p < 0.001$). Mean soil moisture was in all cases higher in the open treatment than beneath shrubs, except in Nogaledas in 2007 where mean values among treatments were very similar (Figure

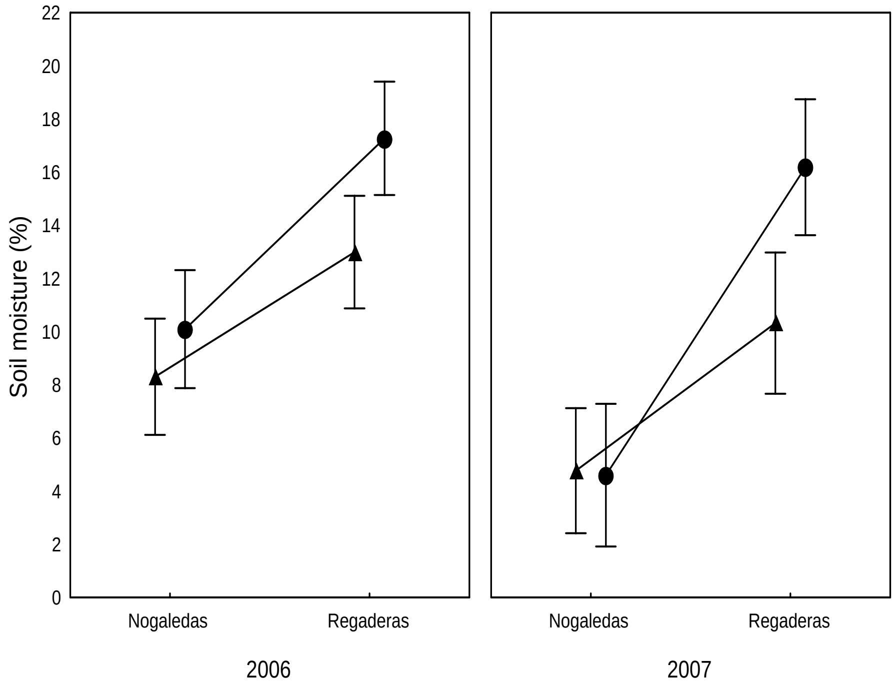

Figure 1. Soil moisture (measurement in mid-summer) means in two populations, microhabitats and years. (circle: grassland and triangle: shrubs).

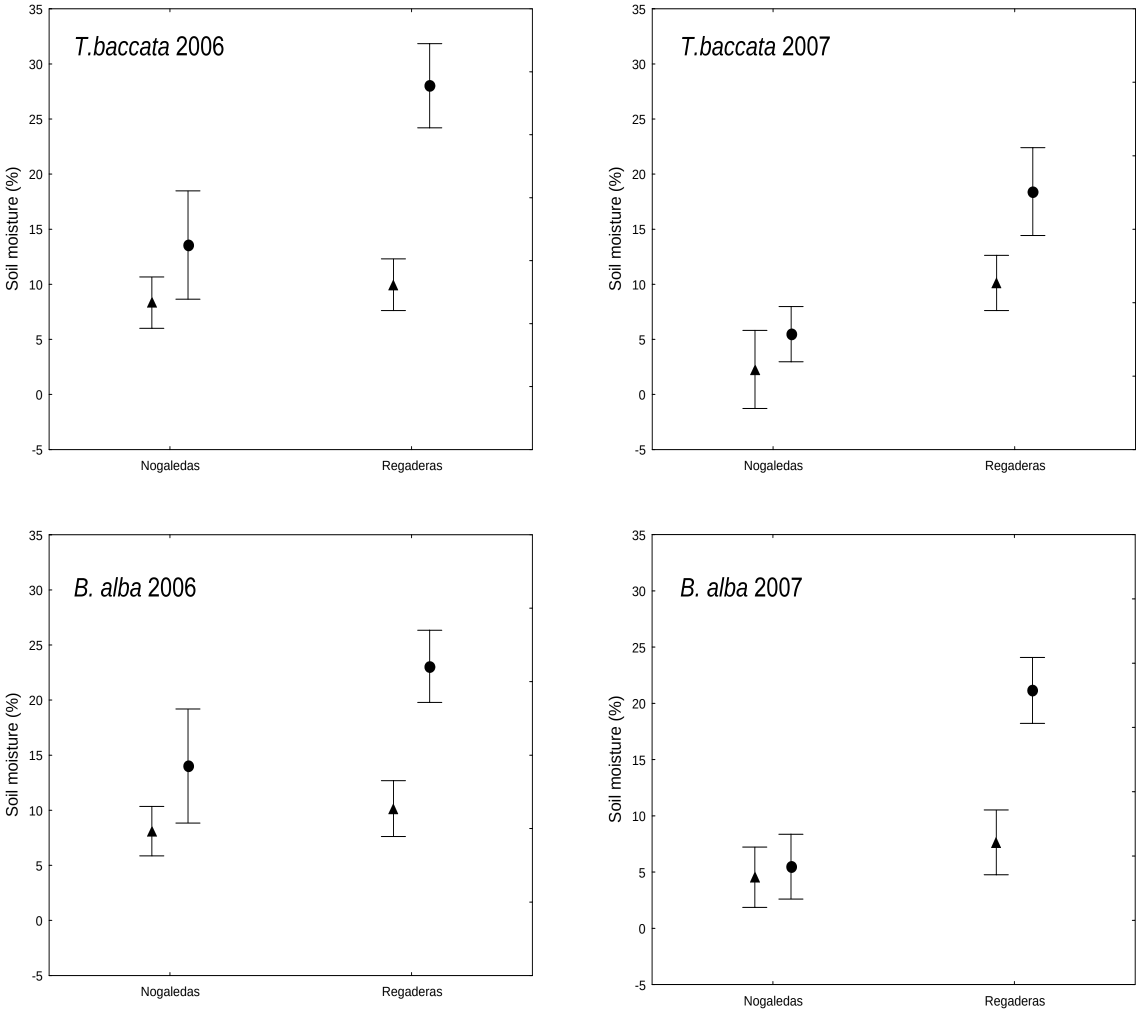

Figure 2: Soil moisture mean values in post-summer dead seedlings (triangles) and alive seedlings (circles) for both species, years and populations.

1). Values in the open treatment ranged from 4.6 to 10.1% in Nogaledas and from 16.2 to 17.3% in Regaderas across the two study years. In the shrub treatment values ranged from 4.8 to 8.3% in Nogaledas and from 10.3 to 12.9% in Regaderas.

Irradiance values in 2006 were different in both populations (F = 223.479, df = 1.299, $p < 0.001$) and treatments (F = 125.532, df = 1.299, $p < 0.001$). Besides, we noted an interaction between populations and microhabitat (F = 82.681, df = 1.299, $p < 0.001$). Light availability was greater in the open grassland than beneath shrubs in both populations.

Seedling survival

GLM modelling (main effects ANOVA design) performed with the two-year dataset showed a significant effect of soil moisture, year (higher in 2006), and population (higher in Nogaledas) on yew seedling survival (Tabla 1a). For birch seedlings there were significant effects of soil moisture and year (higher in 2007). Since the effect of block was non-significant in all analyses, we conducted a factorial analysis without the "block" factor to account for factor interactions. In this case, there where significant interactions between population and year (p = 0.008), whereas the effect of treatment did not reach statistical significance (p = 0.077) in the analysis of yew seedlings (results not shown). Similarly, no effect of treatment was noted for birch seedlings (p = 0.962), while a significant three-way interaction between population, year, and treatment was found (p = 0.010). When irradiance was included in the models besides moisture (2006 dataset), we found no significant effect of light availability on the survival of yew (F = 0.063, df = 1,158, p = 0.808) and birch (F= 0.307, df= 1,158, p = 0.595).

Table 1. Main effects GLM models (ANCOVA design) testing for the effects of population, and soil moisture (covariate) on seedling survival in 2006 and 2007. The upper and lower table corresponds to yew and birch, respectively.

Effect	df	F	p
a) Yew			
Population	1	13.296	0.001
Year	1	19.547	<0.001
Treatment	1	2.574	0.121
Block	3	0.565	0.643
Soil moisture (covariate)	1	9.694	0.004
b) Birch			
Population	1	1.852	0.186
Year	1	23.547	<0.001
Treatment	1	0.008	0.927
Block	3	1.063	0.383
Soil moisture (covariate)	1	20.843	0.001

Figure 2 depicts mean values of soil moisture according to the fate of seedlings after the first summer in each treatment, population, and year. Moisture values were higher for surviving seedlings in all cases. Interestingly, the difference in moisture between seedlings that died and survived was much greater in Regaderas in both species and years.

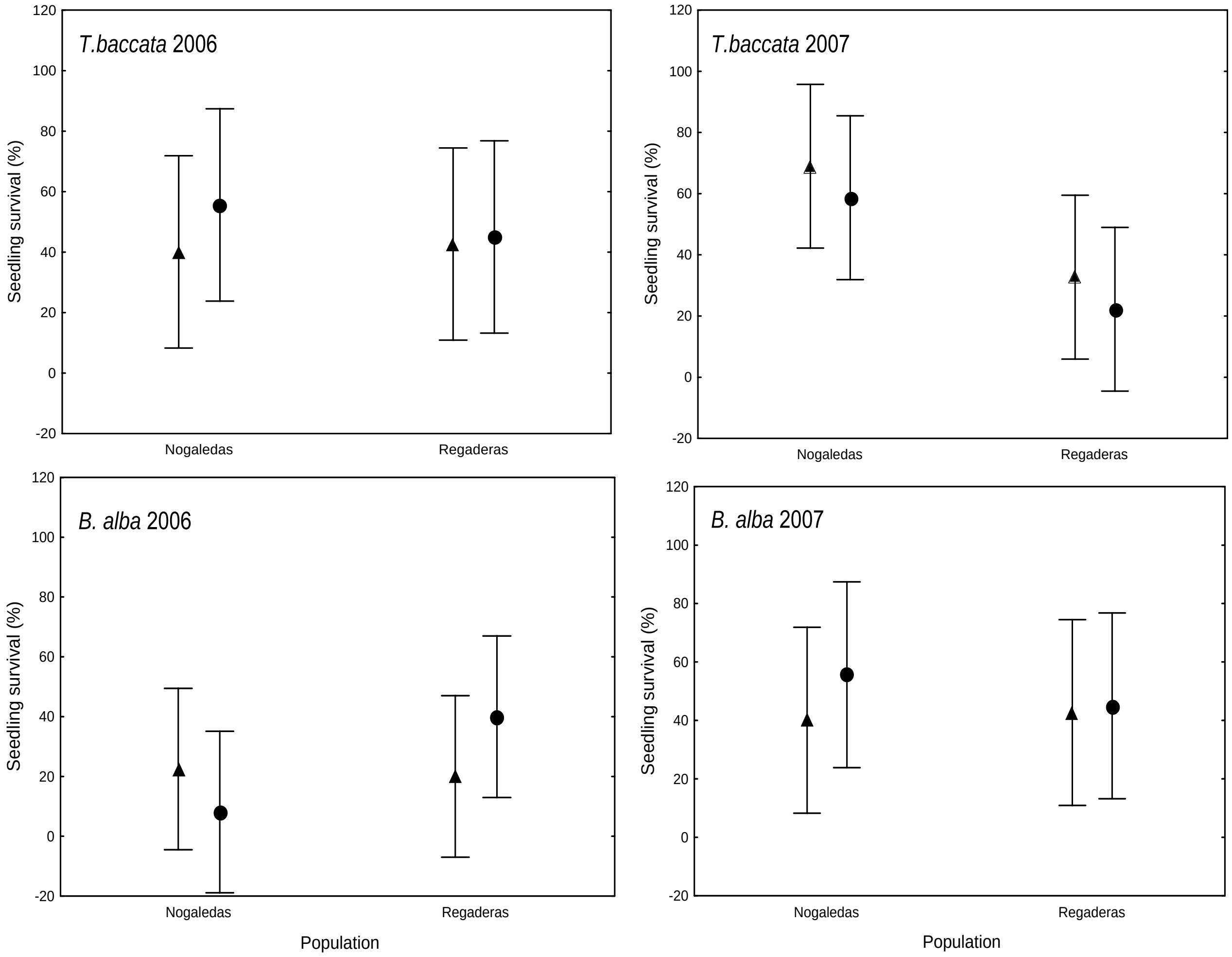

Figure 3. Seedling survival in the two years studied in two different microhabitats and two populations (triangle: shrubs and circle: open grassland).

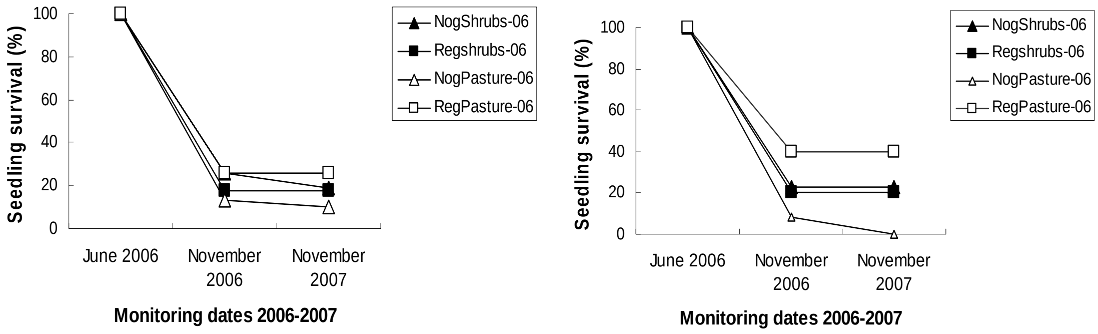

Figure 4. Seedling survival in *Taxus baccata* (left graft) and *Betula alba* (right graft) in two different microhabitats (shrubs and pasture) and two populations (Regaderas and Nogaledas).

For *T. baccata* survival at the end of the first summer increased from 2006 to 2007 in the driest site (Nogaledas) while it decreased in the humid site (Regaderas; Figure 3). For *B. alba* survival increased from 2006 to 2007 at both sites (Figure 3). When survival after the second summer was considered, no noticeable changes were noted with respect to the survival rates found after the first summer in either species (Figure 4).

Discussion

Effects of soil moisture on seedling survival

Seedling survival was strongly related with water availability as found in other marginal populations of woody plant species in Mediterranean mountain environments exposed to summer drought (García 2001, Castro et al. 2004, 2005). Soil moisture consistently affected the survival of both species, and its effect was much greater than those of other factors. Furthermore, clear differences were noted in soil moisture according to the final fate of seedlings in both species, years, and populations. Hence, it can be concluded that, despite growing close to riverbeds, seedlings of yew and birch may experience water stress, presumably because of the decrease of the water level as the dry season proceeds. This suggests that the location of our relict species in refuge habitats does not imply the absence of high levels of water stress (Hampe & Arroyo 2002, Pulido et al. 2008).

Microhabitat effects on seedling survival

Our results confirmed that microhabitat influenced soil water content as found in previous studies in Mediterranean mountains, where soil moisture was higher beneath shrubs than in open areas without vegetation (Castro et al. 2002, Castro et al.

2004, Gómez-Aparicio et al. 2005b). Other studies in similar environments showed no significant differences in soil moisture (Gómez-Aparicio et al. 2005a, Gómez-Aparicio et al. 2008). In our study sites, soil water content was higher in open microhabitats than beneath shrubs, which suggests that shrubs are more efficient than herbaceous plants in depleting soil water resources (Nobel 1989). Under these conditions we failed to confirm any significant effect of shrubs (either positive or negative). Given the limiting role of water for our experimental seedlings, the fact that higher moisture did not enhanced survival in the open suggests that other factors could be compensating for the water effect. Among these factors, it is unlikely that excess irradiance was responsible for seedling mortality, as we found no effect of this factor using data for one year. It can be then speculated that high temperatures during summer could be very harmful for seedlings of several species (Brooker et al. 2008)

Species-specific responses

Our results showed a similar behaviour of both tree species despite different responses were predicted in view of the differences in the strategies of light use previously documented for yew (shade tolerant) and birch (light demanding). The findings of this study suggest that the labelling of both species, mostly established from studies carried out in central populations at temperate latitudes (Miles & Kinnaird 1979a, Taylor & Davies 1985 for birch and Dovciak 2002, Iszkulo & Boratynski 2006 for yew), could be useless when applied in a different ecological context. Thus, in our marginal populations both yew and birch seedlings and saplings are usually found, above all, in permanently watered places no matter the light environment they actually experience (see chapters 1 and 2 in this volume).

Summarizing, the survival of tree seedlings growing in refuge habitats of relict species closely depended on water availability, whose microhabitat variation was not influential for recruitment. On the other hand, light heterogeneity did not result in differential survival of seedlings, and this was true of species that were presumed to differ in light preferences. Thus, the behaviour of both species in marginal habitats seemed to depart from that found in central ones. This poses some caution on the use of models of range dynamics that uniformly treat populations throughout the entire range of species (Pearson & Dawson 2003).

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Capítulo 7

Discusión general

Discusión general

Los trabajos realizados en la presente tesis doctoral abordan diferentes limitaciones de la regeneración de dos especies relictas que mantienen un número reducido de poblaciones en la periferia sur de su área de distribución. En concreto, se estudió el efecto de diferentes factores involucrados en la regeneración natural a lo largo de las distintas etapas demográficas que determinan el ciclo reproductivo. Mediante diferentes aproximaciones metodológicas se han podido identificar procesos ecológicos característicos de las poblaciones marginales y que son infrecuentes en el centro de su área de distribución. Así, se ha obtenido información demográfica novedosa sobre poblaciones enclavadas en hábitat refugio. En concreto, se utilizó el tejo como modelo de estudio para discutir hipótesis generales a múltiples escalas, desde la local a la geográfica pasando por la regional.

La regeneración natural de una población de plantas depende de la acción de múltiples factores acaecidos durante las distintas fases del ciclo de regeneración de la especie. En la fase predispersiva y en el caso del tejo, el estudio de la producción de flores, semillas y las tasas de aborto, junto con el estudio de la polinización, permitieron observar la importancia de la estructura espacial de las poblaciones sobre el éxito reproductivo de los individuos.

Una vez que los propágulos se han diseminado, es preciso conocer la magnitud del efecto de los factores que controlaran la germinación, emergencia y establecimiento de una nueva plántula o el efecto de los depredadores de semillas, puesto que cada uno de ellos puede suponer un cuello de botella para la regeneración. Así, para el abedul se puso mayor énfasis en la fase posdispersiva, estudiándose desde la producción y dispersión de semillas hasta la germinación, encontrándose resultados que pueden ser extrapolables a otros núcleos de población con similares características a los aquí estudiados.

Antes de la germinación de una semilla dispersada, ésta se enfrenta al riesgo de ser consumida por diferentes depredadores. Aquí se exploró el efecto de la depredación de semillas por parte de ratones sobre la regeneración del tejo, la magnitud de este efecto y el papel de los distintos microhábitats y la distancia a la planta fuente de semillas como determinantes del tránsito de semilla a plántula.

Si las semillas pudieron ser dispersadas a un lugar adecuado para germinar y escaparon a la acción de los depredadores, es muy probable que emerja una nueva plántula. De ahí que se estudiaran los patrones de emergencia y supervivencia de plántulas de ambas especies y la relación de estas con la disponibilidad hídrica y la presencia de micrositios y microhábitats favorables.

Estructura demográfica: poblaciones centrales y poblaciones periféricas

Las poblaciones marginales de tejo y abedul son de reducido tamaño y presentan tasas de reclutamiento extremadamente bajas. La clase de edad mejor representada es la clase "adultos", compuesta por ejemplares reproductores muy frecuentemente añosos. En general, se observó una escasa presencia de brinzales e individuos juveniles a pesar de que las poblaciones objeto de estudio se escogían por presentar regeneración constatada.

Según la hipótesis del centro-periferia, las poblaciones de especies leñosas que habitan en áreas marginales dentro de su área de distribución suelen presentar baja viabilidad debido principalmente a su pequeño tamaño y una acusada fragmentación, directa o indirectamente relacionadas con el estrés climático (Brown et al. 1996, Gaston 2003, Vucetich & Waite 2003). Se puede predecir así que estas poblaciones serán más vulnerables frente a alteraciones genéticas o cambios demograficos y ambientales (Wilcox 1986, Lawton 1993, Vucetich & Waite 2003). El estudio sobre variación geográfica de la estructura poblacional objeto del capítulo 1 demuestra que las poblaciones marginales de tejo, tanto del borde norte como del borde sur, presentan menor índice de regeneración que las poblaciones centroeuropeas, como habían constatado otros autores para poblaciones de *Juniperus communis* (D. García et al. 1999). En todo caso, debe apuntarse que esta regla también presenta excepciones y que existen trabajos con evidencias contrarias a ella (Sagarin & Gaines 2002, M. B. García 2006). En cualquier caso, el capítulo 1 muestra la existencia de tendencias geográficas significativas cuyos mecanismos subyacentes se analizan en los capítulos subsiguientes.

Polinización y producción de semillas

En poblaciones periféricas de tejo, de reducido tamaño y muy aisladas entre si, la unión de dioecia y anemofilia puede suponer una fuerte barrera para la reproducción. El éxito reproductivo dependerá al menos de la cantidad de polen producida por las flores masculinas y la distancia entre árboles de distinto sexo (Regal 1982, Whitehead 1983, Charleswoth 1993). A estas variables, habrá que añadir otras de carácter abiótico implicadas en la emergencia, desarrollo y maduración de las flores. En las regiones templadas, los árboles dioicos son fundamentalmente anemófilos pero, sin embargo, son escasos los estudios con este tipo de especies, en aparente desventaja frente a grupos de plantas con otras estrategias reproductivas (Seltmann et al. 2007, Wesselingh 2007). En el caso de las poblaciones marginales de tejo presentes en ambientes mediterráneos la producción de frutos mostró variaciones significativas entre poblaciones y entre años. Se constató una acusada limitación en la llegada de polen a las flores de los árboles hembra, como se había comprobado para otras especies del género (Allison 1990, Di Fazio 1998) y para poblaciones aisladas y de reducido tamaño de otros árboles anemófilos (Holm 1994, Knapp 2001). Por otra parte, de la distribución espacial de los árboles de diferente sexo se derivan importantes consecuencias, puesto que el efecto de la distancia a los donadores de polen sobre la fertilización fue muy significativo en ambos años estudiados. Similares resultados han sido obtenidos con otras especies arbóreas (Allison 1990, Knapp 2001, Sork et al. 2002, Steven & Waller 2007) de tal forma que el aislamiento de una hembra con respecto a los machos es considerado como el principal factor para explicar la baja tasa de fertilización natural de la población. Además el espaciamiento entre los árboles de distinto sexo, unido al reducido tamaño poblacional, comporta la aparición de fenómenos de estocasticidad demográfica y ambiental (Sagarin & Gaines 2002, Yakimowski & Eckert 2007, Crawford 2008), que se reflejan en una contribución desigual de los genotipos a la producción poblacional de propágulos (Wagenius et al. 2007).

En cuanto a las poblaciones de abedul, presentan valores en la producción de semillas comprendidos entre los rangos que se dan para otras poblaciones ibéricas y europeas (Miles & Kinnaird 1979, Reyes & Casal 2003), de tal modo que este evento no constituiría una fuente de limitación del reclutamiento para la especie. Por otra parte, se constataron diferencias en la producción en las diferentes poblaciones y en menor grado entre los dos años estudiados, como de hecho ocurre en estudios realizados con otras especies del género *Betula* (Holm 1994, Houle 1999, Reyes & Casal 2000).

Dispersión de semillas

En las poblaciones estudiadas de abedul, la dispersión de semillas se concentró fundamentalmente debajo de la planta madre. Así pues, la sombra de semillas es fuertemente contagiosa, concentrándose fundamentalmente bajo los árboles productores de semillas y hasta unas decenas de metros alejadas de la población. Esto, facilita la llegada de la semilla a un sitio seguro, caracterizado por la humedad, para la supervivencia durante el primer año, puesto que un porcentaje elevado de plántulas mueren por desecación durante el primer verano de vida. Pero el establecimiento exitoso a largo plazo es más complicado y, de hecho, son pocos los brinzales y matas que se observan en el subvuelo del abedular, muy posiblemente por efecto de los herbívoros. Sin embargo se observan ejemplares jóvenes a distancias cortas y medias de la población (10-30 m) bajo el vuelo protector de los brezos.

Un alto porcentaje de las semillas fue detectado entre los 0 y 50 metros de las poblaciones estudiadas. La reducida proporción de eventos de dispersión a larga distancia (más de 100 m) compromete la colonización de refugios idóneos para el establecimiento de nuevas poblaciones puesto que es muy baja la probabilidad de llegada de semillas a los arroyos cercanos que, por lo general, se encuentran a distancias mayores de los 100 metros. Por tanto, el reclutamiento en el abedul se ve favorecido a cortas distancias de los rodales existentes, quedando impedido a mayores distancias por la discontinuidad de los hábitats riparios que le son favorables.

En el caso del abedul, los valores de germinación fueron bajos para todas las poblaciones estudiadas, presentando valores por debajo de los observados para poblaciones centrales (Sarvas 1948, Holm 1994, Reyes & Casal 2003). En este sentido, Holm (1994) observó que las poblaciones de abedul que vegetaban en áreas de montaña presentaban baja calidad de las semillas debido a problemas o fallos en la polinización, maduración incompleta de embriones e infecciones causadas por patógenos. Esto significa que un alto porcentaje de las semillas dispersadas por el viento a potenciales sitios seguros no son viables.

Depredación posdispersiva de semillas de tejo por roedores

En general, los trabajos previos que han estudiado la fase de depredación posdispersiva en ambientes de montaña mediterráneos, revelan que la pérdida de semillas por consumo de roedores presenta valores elevados (Hulme 1997, Castro et al. 1999), como también ocurrió en las poblaciones de estudio. Sólo en algunas situaciones, relacionadas probablemente con la disminución en la densidad de las poblaciones de ratones en zonas por encima del límite altitudinal del bosque, como ocurre en el caso de *Juniperus communis* (D. García 2001), las tasas de depredación son pequeñas.

En determinadas ocasiones el consumo de semillas se manifiesta como dependiente del microhábitat (Hulme 1997) pero en otras se manifiesta de manera independiente (Castro et al. 1999). En las poblaciones de estudio, de reducido tamaño y enclavadas en el seno de paisajes fragmentados por la acción de incendios y prácticas ganaderas seculares (Pulido et al. 2007), las tasas de depredación pueden elevarse debido a esta situación de alta fragmentación (D. García & Chacoff 2007), lo que unido a lo fragmentado de las propias poblaciones, aumenta las tasas de depredación en estos ambientes (Santos et al. 1994, 1997). La fuerte depredación registrada bajo los arbustos debe hacer disminuir la emergencia de nuevas plántulas en los posibles sitios seguros. Por otra parte, recientes estudios han comprobado que las tasas de depredación son más elevadas en las montañas del sur de España que en áreas montañosas de Suiza (García-Castaño et al. 2006). Así, las tasas de depredación obtenidas en nuestro trabajo son más elevadas que las registradas en trabajos similares realizados en zonas no marginales dentro del área de distribución de la especie (Hulme 1996, Hulme & Borelli 1999, García et al. 2005), lo que redundaría en una mayor presión por parte de los ratones sobre las semillas de tejo en poblaciones periféricas.

Marginalidad y reclutamiento: supervivencia temprana y establecimiento de las plántulas

La disponibilidad de agua es un factor que condiciona la regeneración de las poblaciones de plantas y se ha invocado como factor limitante en la regeneración de poblaciones marginales arbóreas sometidas a sequía severa (Pigott & Pigott 1993, Brèda et al. 2006). Sobre este punto se constató que, en el caso del tejo a nivel regional, las poblaciones aparecen en hábitats refugio, gargantas y arroyos estacionales, que aseguran una cierta disponibilidad hídrica a lo largo del año, especialmente durante la fuerte sequía estival característica del clima mediterráneo (Woodward 1987, Pigott & Pigott 1993). Del mismo modo que para el tejo, los lugares donde se desarrollan poblaciones de abedul son ambientes riparios, en general, gargantas umbrosas que constituyen verdaderos hábitats refugio que mantienen poblaciones de pequeño tamaño y con reducida regeneración, como ocurre con otras especies de relictos que habitan en estas galerías riparias (Hampe & Arroyo 2002, Mejías et al. 2002, Pulido et al. 2008).

A escala local el efecto de la distancia al cauce de agua sobre la supervivencia de plántulas, unido a la presencia de un micrositio favorable (musgo), fue muy significativo, como apuntan otros trabajos en diferentes condiciones ecológicas (Mejías et al. 2002, Dovciak et al. 2008). Por tanto, la presencia de un cauce de agua amortigua el efecto de la sequía estival, etapa crítica para la supervivencia temprana de las plántulas. Estos resultados confirman los obtenidos en diversos estudios llevados a cabo en poblaciones remanentes en diferentes áreas de la montaña mediterránea (Hampe & Arroyo 2002, Castro et al. 2004, 2005, Arrieta & Suárez 2005, 2006, Pulido et al. 2008) que demuestran que la mayor mortalidad de plántulas es debida a la sequía estival.

El estado hídrico de los arroyos y gargantas donde se asientan las poblaciones de tejo y abedul será pues fundamental para su regeneración, máxime cuando es bien conocido que el patrón de precipitaciones es muy variable en el ámbito mediterráneo con las consecuencias propias sobre el patrón de recarga de los cursos de agua (Gasith & Resh 1999). Por otra parte, la disminución en las precipitaciones que auguran las predicciones para la Cuenca Mediterránea (McCarthy et al. 2001) y en especial para las áreas de montaña (Nogués et al. 2008) podrían acentuar, en el futuro, las pérdidas en cuanto al reclutamiento que ocurren en esta fase.

En el caso del abedul, si unimos una baja tasa de germinación a la necesidad de un micrositio favorable para la germinación de las semillas, este evento puede constituir un importante cuello de botella en la regeneración de las poblaciones estudiadas. No obstante, valores de supervivencia extremadamente bajos han sido constatados por estudios realizados en el resto de Europa (Kinnaird 1974, Miles & Kinnaird 1979, Kullman 1986, Skoglund & Verwijst 1989, Laskurain et al. 2003). Este patrón de mortalidad repetido en numerosas localizaciones dentro del área de distribución de la especie invita a prestar especial atención en un futuro al efecto del cambio climático en estos hábitats refugio. Algunos estudios basados en modelización predictiva de nichos climáticos plantean un futuro declive para el abedul debido al aumento de las temperaturas y la disminución en las precipitaciones, que pueden disminuir la capacidad amortiguadora de sus hábitats refugio (Ohlemüller et al 2006).

El efecto del microhábitat sobre la supervivencia de plántulas no presentó diferentes tendencias en función de las especie de estudio, a pesar de las diferencias previstas en función de estudios previos relacionados con el uso de la luz. Sin embargo, el contenido hídrico del suelo estuvo muy relacionado con la supervivencia de las plántulas de ambas especies, como se ha visto en otras especies leñosas presentes en ambientes mediterráneas (Castro et al. 2004, 2005). Los resultados apuntan asimismo que el uso de caracterizaciones ecológicas para las especies derivadas de datos obtenidos en poblaciones centrales es arriesgado a la hora de prever la dinámica del área de distribución, puesto que el comportamiento ecofisiológico de las especies en áreas marginales puede ser muy diferente.

Síntesis y perspectivas de futuro

Como corolario puede decirse que para las dos especies estudiadas se detectaron filtros en diferentes etapas del ciclo de regeneración, que fueron desde la limitación en la producción y las altas tasas de depredación de semillas en el tejo a la reducida dispersión de semillas y baja germinación de las mismas en el abedul. En ambas especies se constató la importancia de la disponibilidad hídrica, así como la presencia de un micrositio y microhábitat favorables para la nascencia de las plántulas y su posterior establecimiento.

Algunos de los procesos ecológicos estudiados en la presente tesis muestran diferencias sustanciales entre diferentes áreas geográficas (disponibilidad hídrica *vs.* estructura demográfica de las poblaciones de tejo), de tal manera que esta memoria puede entenderse como una contribución a los escasos estudios realizados a escala geográfica amplia con poblaciones marginales y centrales de especies leñosas de larga vida (García et al. 1999, García et al. 2000). Del mismo modo, y como denunciaba Hampe (2004), siguen siendo escasos los trabajos sobre poblaciones relictas en el Mediterráneo, ya que, aunque el número de trabajos de campo se ha incrementado, lo ha hecho de una manera leve (Castro et al. 2004, 2005, Arrieta & Suárez 2005, 2006, Pulido et al. 2008) de tal forma que el conocimiento sobre sus problemas de conservación puede considerarse aún rudimentario.

De cara a la conservación de estas especies se debe poner énfasis en dos puntos principales: la capacidad de colonizar nuevas áreas y su relación con un escenario de cambio climático, y la protección activa de las poblaciones conocidas en base a profundos estudios demográficos, ecológicos y genéticos. En este sentido, los resultados de este trabajo se han plasmado en la elaboración de un plan de recuperación para el caso del tejo y en un plan de conservación para el abedul. La protección *in situ* de ambas especies pasa por la conservación de los hábitats riparios donde se asientan las poblaciones, así como la protección del regenerado más joven y accesible al ganado.

Por otra parte es fundamental la conexión entre los diferentes grupos tanto nacionales como internacionales que trabajan en la conservación de las especies (Serra 2007). Sólo con enfoques multidisciplinares y rigurosos basados en la busqueda de los procesos que pueden limitar la regeneración natural de las especies (Schemske et al. 1994, Zimmerman et al. 2000) se pueden diseñar planes para la gestión de poblaciones de especies amenazadas con una sólida base ecológica (Jordano et al 2004).

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Capítulo 8

Conclusiones

Conclusiones

1. Las poblaciones de tejo y abedul en el área marginal estudiada presentan fuerte especificidad de hábitat, escaso número de individuos y bajas tasas de regeneración.
2. A escala local, el reclutamiento de *T. baccata* está limitado principalmente por la disponibilidad de agua, como consecuencia del efecto que la sequía estival tiene sobre la supervivencia de plántulas durante el primer verano. Del mismo modo la disponibilidad de agua condiciona la presencia de las poblaciones de tejo a escala regional. Las poblaciones aparecen en cauces de agua, con fuerte pendiente y exposiciones nor-noreste principalmente.
3. A escala continental, las poblaciones de tejo se ajustan a la regla biogeográfica del centro-periferia, puesto que las poblaciones tanto del borde norte como del borde sur presentaron menores índices de regeneración que las poblaciones centrales de tejo.
4. Se encontró una relación lineal entre el índice de regeneración de las poblaciones estudiadas de tejo y las precipitaciones medias anuales y estivales. El índice de regeneración aumenta linealmente con el incremento de las precipitaciones.
5. La evaluación del efecto de las restricciones climáticas a diferentes escalas utilizando parámetros clave para la persistencia de las poblaciones, tales como el índice de regeneración, puede facilitar el estudio de los efectos del cambio climático sobre la dinámica del rango.
6. En poblaciones marginales de abedul se observó un fuerte efecto de la sequía estival sobre la supervivencia de plántulas durante el primer verano. Junto a esto, los principales cuellos de botella detectados fueron la baja viabilidad de las semillas y la escasez de micrositios para el reclutamiento dentro de las poblaciones.
7. La dependencia de micrositios húmedos y la escasa capacidad de dispersión de las semillas, hace poco probable la colonización de nuevos hábitats propicios para la creación de nuevas poblaciones de abedul. Los hábitats riparios actúan como refugios topográficos amortiguando el desplazamiento en la distribución de las poblaciones marginales de abedul.
8. La marginalidad impone una alta variabilidad espacio-temporal en la fecundidad del tejo. La gran variación en la fecundidad de los individuos de tejo es consistente en el tiempo. Además, está muy relacionada con la disposición espacial de los

árboles femeninos y masculinos de tejo. Estas características promueven una desigual contribución de los genotipos a la cosecha de semillas y la consiguiente estocasticidad demográfica.

9. Las tasas de depredación de semillas en tejo fueron muy altas, puesto que los ratones consumen la práctica totalidad de las semillas antes de la germinación en todas las poblaciones estudiadas durante dos años diferentes. Por otra parte, se encontraron diferencias en el consumo relacionadas con la variación anual de la cosecha de semillas.
10. Se confirma el efecto positivo de la cobertura vegetal sobre la depredación de semillas en todas las poblaciones y en los dos años de estudio. El efecto del microhábitat pesó más que el efecto de la distancia a la hembra productora de fruto más cercana. Los ratones consumen las semillas más valiosas en términos de reclutamiento (semillas bajo matorral).
11. Los mecanismos que explican el consumo de semillas en poblaciones marginales estuvieron directa o indirectamente relacionados con la fragmentación del hábitat.
12. La supervivencia de plántulas de tejo y abedul dependió exclusivamente de la disponibilidad de agua, sin que existera efecto facilitador del matorral sobre las plántulas, tanto para una especie tolerante a la sombra (tejo) como para una especie teóricamente heliófila (abedul).
13. El efecto del matorral sobre la supervivencia de las plántulas de tejo y abedul en las montañas mediterráneas podría estar amortiguado por condiciones abióticas especiales (humedad del suelo) en los hábitats refugio.