

Modelling the effects of genetics and habitat on the demography of a grassland herb

F. Xavier Picó^{a,b,*}, Pedro F. Quintana-Ascencio^c, Mikael Mildén^d, Johan Ehrlén^d, Ian Pfingsten^c

^aEstación Biológica de Doñana, CSIC, Avda. María Luisa s/n, 41013 Sevilla, Spain

^bCenter for Ecological Research and Forestry Applications (CREAF), Autonomous University of Barcelona, 08193 Bellaterra, Barcelona, Spain

^cDepartment of Biology, University of Central Florida, 4000 Central Florida Boulevard, Orlando, FL 32816-2368, USA

^dDepartment of Botany, Stockholm University, SE-106 91 Stockholm, Sweden

Received 7 June 2007; accepted 20 February 2008

Abstract

There is growing evidence that genetic and ecological factors interact in determining population persistence. The demographic effects of inbreeding depression can largely depend on the ecological milieu. We used demographic data of the perennial herb *Succisa pratensis* from six populations in grazed and ungrazed sites with different soil moisture. We built an individual-based model assessing the demographic consequences of inbreeding depression in populations with different management and habitat. Today this plant has to cope with severe landscape fragmentation, deteriorating habitat conditions in terms of decreasing grazing intensity, and the effects of inbreeding depression. For each population we performed simulations testing two inbreeding depression hypotheses (partial dominance and overdominance) and three epistatic functions among loci. The results indicated stronger inbreeding depression effects for populations in unfavourable sites without grazing or in xeric habitats compared to populations in favourable mesic sites with grazing. Overall, we found stronger effects with overdominance, a result that emphasizes the importance of understanding the genetic mechanisms of inbreeding depression. Hence, management practices can interact with the genetic consequences of inbreeding depression in population dynamics, which may have important implications for plant population ecology and evolutionary dynamics of inbreeding depression.

© 2008 Gesellschaft für Ökologie. Published by Elsevier GmbH. All rights reserved.

Zusammenfassung

Es gibt zunehmend Hinweise darauf, dass genetische und ökologische Faktoren bei der Bestimmung der Persistenz von Populationen zusammenwirken. Die demographischen Effekte von Inzuchtdepressionen hängen in großem Ausmaß von der ökologischen Umwelt ab. Wir nutzten die demographischen Daten des perennierenden Krautes *Succisa pratensis* aus sechs Populationen, die entweder beweidet oder unbeweidet waren und unterschiedliche Bodenfeuchten zeigten. Wir erstellten ein individuenbasiertes Modell um die demographischen Konsequenzen der Inzuchtdepression in verschiedenen Populationen bei verschiedenen Bewirtschaftungen und Habitaten abzuschätzen. Heute muss diese Pflanze mit ernster Landschaftsfragmentierung, sich verschlechternden Habitatbedingungen in Form

*Corresponding author. Tel.: +34 95 423 2340; fax: +34 95 462 1125.

E-mail address: xpico@ebd.csic.es (F.X. Picó).

von abnehmender Beweidungsintensität und den Auswirkungen der Inzuchtdepression zurecht kommen. Für jede Population führten wir Simulationen durch, um zwei Inzuchtdepressions-Hypothesen (teilweise und Überdominanz) und drei epistatische Funktionen über die Loci zu testen. Die Ergebnisse wiesen auf stärkere Auswirkungen der Inzuchtdepression bei Populationen in ungünstigen Habitaten ohne Beweidung oder in xerischen Habitaten im Vergleich zu Populationen in den bevorzugten mesischen Habitaten mit Beweidung hin. Insgesamt fanden wir stärkere Effekte bei Überdominanz, ein Ergebnis, das die Wichtigkeit betont, die genetischen Mechanismen der Inzuchtdepression zu verstehen. Die Bewirtschaftungsweise kann also mit den genetischen Konsequenzen der Inzuchtdepression in der Populationsdynamik interagieren. Dies kann wichtige Implikationen für die Pflanzenpopulationsökologie und die evolutionäre Dynamik der Inzuchtdepression haben.

© 2008 Gesellschaft für Ökologie. Published by Elsevier GmbH. All rights reserved.

Keywords: Extinction risk; Grazing; Inbreeding depression; Individual-based models; Population dynamics; *Succisa pratensis*

Introduction

In the last decades, a growing body of work focusing on the joint roles of ecological and genetic factors on population persistence has accumulated evidence suggesting that extinction risk can be underestimated if genetic factors are not considered (Frankham, 2005; Hedrick & Kalinowski, 2000; Higgins & Lynch, 2001; Lande, 1988, 1994; Lynch, Conery, & Burger, 1995). Inbreeding depression (i.e. the reduction in fitness of selfed progeny compared to outcrossed progeny) is regarded as the main genetic factor affecting population viability (Frankham, 2005; Soulé, 1987). The effects of inbreeding depression on fitness components throughout the entire life cycle have been evidenced for many plant species (Husband & Schemske, 1996).

Land use affects vital rate variation and most likely interacts with inbreeding depression determining demographic performance. For example, several plant species occurring in European semi-natural grasslands benefit from traditional low-intensity mowing or grazing regimes for persistence, and abandonment has negative consequences (Bühler & Schmid, 2001). These plants increasingly occur in highly fragmented landscapes (Hooftman, van Kleunen, & Diemer, 2003; Picó & van Groenendael, 2007; Vergeer, Sonderer, & Ouborg, 2004), and there is ample evidence that fragmentation provokes isolation and reduces population sizes increasing inbreeding rates and inbreeding depression (Oostermeijer, 2000). Hence, these concurrent ecological and genetic factors could jeopardize the persistence of plant populations.

A comprehensive analysis of the effects of inbreeding depression on fitness will require the consideration of its genetic basis. Studies involving the comparison of the demographic performance of populations differing in their level of inbreeding, support the hypothesis that inbreeding depression is caused by the expression of deleterious recessive mutations, i.e. the partial dominance hypothesis (Carr & Dudash, 2003; Charlesworth & Charlesworth, 1999). Alternatively, studies using

molecular markers to study quantitative trait loci support the hypothesis that the fitness of heterozygotes is higher than that of homozygotes, i.e. the overdominance hypothesis (Carr & Dudash, 2003; Charlesworth & Charlesworth, 1999). It is also necessary to take into account the epistatic relationships among loci that tell us how individual fitness changes with increasing homozygosity to assess the demographic implications of inbreeding depression (Carr & Dudash, 2003).

We analysed the joint effect of inbreeding depression and habitat on population performance. We developed a stochastic individual-based model parameterized with empirical data to evaluate the demographic implications of inbreeding depression in populations of the perennial herb *Succisa pratensis* under different management. Recent demographic and genetic data made *S. pratensis* a particularly suitable model species. Our individual-based model allowed us to tackle the effects of inbreeding depression at the individual level. We compared populations with contrasting grazing and soil moisture, two hypotheses of inbreeding depression (partial dominance and overdominance) and three epistatic functions relating individual fitness to homozygosity (diminishing, linear and reinforcing epistasis).

Materials and methods

Study species and study site

S. pratensis Moench. (Dipsacaceae) is a long-lived, iteroparous herb widely distributed in semi-natural European grasslands. It is relatively drought-resistant but reaches higher abundance in moist habitats. This plant has a mixed-mating system (Picó, Mix, Ouborg, & van Groenendael, 2007; Vergeer et al., 2004). Further details can be found in Mix, Picó, van Groenendael, and Ouborg (2006).

The study populations were located in the northern part of the Nynäs Nature Reserve (Sweden; 58° 50' N, 17° 24' E). Due to abandonment, semi-natural grasslands

Table 1. Characteristics of the six *S. pratensis* study populations including management regime (regime), soil moisture (soil), approximate population size, number of sampled plants in the first study year (sample), average plant survival, average growth (proportion of plants growing in size), and average fecundity (seed production) among years, and average seedling production rate (seedlings)

Variable	Population					
	A	B	C	D	E	F
Regime	Grazed	Grazed	Grazed	Abandoned	Abandoned	Abandoned
Soil	Moist	Moist	Xeric	Road verge	Moist	Moist
Pop. size	20,000	4,000	600	600	900	900
Sample	281	260	268	260	263	257
Survival ^a	0.75	0.71	0.61	0.54	0.51	0.66
Growth ^a	0.47	0.46	0.33	0.21	0.25	0.43
Fecundity ^a	11.38	2.93	10.29	32.18	37.01	7.28
Seedlings	3.084	0.866	1.078	1.514	2.625	0.904

See Appendix A1 for more information on model parameters.

^aData from Mildén (2005).

are turning to forests, whereas many former fields are now grazed (Cousins & Eriksson, 2001). Abandoned sites have lower population sizes than grazed sites (Herben et al., 2006). Six *S. pratensis* populations were selected representing different management regimes, soil moisture conditions, population sizes, and overall demographic attributes (Table 1). Three of the sites are currently grazed (A, B and C), two have been abandoned for 40–70 years (E–F), and one is situated on a road verge (D). All sites are mesic or moist except site C, which is more xeric. Hence, our populations represent a gradient of suitability from very favourable sites housing large populations (e.g. A and B) to poor sites with small populations (e.g. C and D).

Demographic data

Data on fecundity, growth and survivorship were obtained from a minimum of 250 individuals including at least 50 flowering plants in each population and study year (2000–2003). Between six and 14 permanent plots (0.25–1 m²) were established at each study site and all individuals within plots mapped and measured. At each census, all new seedlings that appeared in the plots were also mapped and included in the study. The total number of individuals recorded during the entire study in each population ranged from 416 to 737 plants.

The status (dead/alive, reproductive/vegetative) of each plant was recorded at each census. Plant size was estimated as the area defined by an ellipse using the two longest perpendicular diameters of the leaf rosette. The reproductive output of each flowering plant (e.g. seed production) was calculated as the product of the number of flowering heads and the mean number of filled seeds per flower head (recorded from a sample of 8–30 heads per population per year). For each population and year, seed germination data were obtained from a seed sowing

experiment including six additional plots (10 × 10 cm²) with 50 seeds each. Seedling fate was recorded until the end of the study in 2003.

Inbreeding depression data

The effects of inbreeding depression on *S. pratensis* life-cycle traits have been reported elsewhere (Vergeer et al., 2004: performance of selfed and crossed progeny in field conditions, Picó et al., 2007: multigenerational inbreeding effects on life-cycle traits). Although the partial dominance hypothesis accounted for inbreeding depression, the overdominance hypothesis could not be ruled out completely (Picó et al., 2007). These experiments were conducted on Dutch populations, but we assume that Swedish populations responded similarly to inbreeding depression. Overall, these studies indicated that several life-cycle traits (e.g. plant fecundity, seed germination, juvenile growth and survival) were affected by inbreeding depression to varying degrees.

The demographic model

We built an individual-based model for *S. pratensis* using empirical functions fitted to the data and theoretical distributions based on sampled data (Appendix A1). We used our estimate of plant size as a predictor of vital rates and calculated all parameters separately for each population and year. We used logistic regression models to predict the association between plant size at time t and survival probability at time $t+1$, and plant size and reproduction probability both at time t . We used a logarithmic function to predict individual growth rate between time t and $t+1$. We estimated the number of flower heads per plant using Poisson distributions whose means equalled the average

number of flowers produced per plant in each population per year (see Appendix A2). Seed number per flower was modelled following normal distributions with observed mean and variance from each population and year. Seed production was calculated as the product of the number of flower heads and the number of seeds per flower head. We used seed germination estimates from the seed sowing experiment for each population and year. Due to additional sources of seed mortality (e.g. predispersal seed predation; Ehrlén, 1996), estimates of recruitment based on seed production and germination experiments are generally overestimated. We estimated this component of mortality (Appendix A3) by comparing our predicted values to the actual seedling production. Other studies have indicated the low importance of the seed bank and clonal reproduction in *S. pratensis* (Mildén, 2005), so our model did not include these processes.

We ran the stochastic individual-based model separately for each study population by randomly selecting model parameters for each year and estimating plant fates using the above functions and distributions predicting survival, growth, and reproduction. We used mean values of the model parameters for those years when vital rates did not have significant associations with plant size (four cases only). We included density-dependent reproduction using an arbitrary threshold that stops recruitment when populations reached 3000 individuals.

Modelling the effects of inbreeding depression

We simulated the effects of inbreeding depression on *S. pratensis* demographic traits under the partial dominance and overdominance hypotheses. The model takes into account the proportion of homozygous deleterious recessive loci for the former and the proportion of heterozygous loci for the latter. Each simulated individual was provided with a genome represented by an array of 500 diploid loci. Each locus has a dominant (1) and a recessive (0) allele. The proportion of homozygous dominant (11), recessive (00) and heterozygous (01 and 10) loci were known for each simulated individual at each time t of the simulation.

Three epistatic functions related the genetic characteristics of individuals with their fitness components. As the proportion of homozygous recessive loci increases or the proportion of heterozygous loci decreases, fitness components decrease. On a logarithmic scale these relationships can be concave (diminishing epistasis), linear (no epistasis), or convex (reinforcing epistasis) (Carr & Dudash, 2003; Appendix A4). On average, individuals with a 50% homozygosity exhibit reductions ca. 20% in fitness components (Appendix A4), which was consistent with the low/moderate inbreeding de-

pression in *S. pratensis* reported elsewhere (Picó et al., 2007; Vergeer et al., 2004).

In our model, reproduction, growth and survival were affected by inbreeding depression. Randomly selected life-cycle traits were multiplied by a genetic factor that depended on the genetic characteristics of simulated individuals given by the inbreeding depression hypothesis and the epistatic function selected. In each generation, genomes of all new individuals experience free recombination at all loci (no linkage) and a random mutation rate of 0.025 per generation. For the sake of simplicity we assumed no linkage among loci, which may be overestimating the effects of recombination. Our model randomly selects up to 20% of the genome and a position in the diploid genome to produce genetic recombination when a new individual is produced. The diploid genome of new individuals is produced by uniting gametes from the two parents.

Simulation procedure

A scheme of the simulation procedure is shown in Appendix A5. We performed 1000 simulations for each population combining two inbreeding depression hypotheses and three epistatic functions (six scenarios). We also performed 1000 baseline simulations for each population with no inbreeding depression effects. To start the simulations we used the number and initial population structure of plants observed in the 2000 census (257–281 individuals and > 50 reproductive individuals per population). Each individual was randomly assigned a 500-loci diploid genome. We stochastically projected each population for 10 years as described above. For each population and scenario, we estimated: (1) extinction probability, as the ratio between number of extinct runs (e.g. when population size drops below 1 individual) and total number of runs, (2) mean ratio between final and initial population sizes, which is an estimate of population growth rate over 10 years, (3) mean genetic variability, as the average of final number of unique genotypes (individuals bearing unique loci combinations) between final number of individuals at year 10, (4) mean proportion of homozygous deleterious recessive loci (for partial dominance only), as the average of final proportion of homozygous recessive loci at year 10, and (5) mean proportion of heterozygous loci (for overdominance only), as the average of final proportion of heterozygous loci at year 10. We used MATLAB (v.6) to run our computations. Code is available upon request.

Sensitivity analysis

We analysed the sensitivity of the individual-based model to changes in demographic rates under the two

inbreeding depression hypotheses for each population of study. For the sake of simplicity, we only used the linear epistasis given the consistency of results among the epistatic functions (see below). We only present results reporting the effects of changes in demographic rates on population growth rate, as this parameter was the most informative. The sensitivity analysis was conducted by changing (10% reduction) each demographic trait at a time (i.e. survival, growth and fecundity) and running the model again (500 simulations) for the baseline model with no inbreeding depression and for the two inbreeding depression hypotheses. The percentage difference between the baseline population growth rate and each new population growth rate represents the sensitivity of that demographic trait and inbreeding depression scenario.

Results

Simulations of *S. pratensis* populations without inbreeding depression exhibited low or nil extinction probabilities (Table 2). When inbreeding depression was included, simulated populations showed an increase in extinction probabilities but results depended on habitat and the genetic basis of inbreeding depression. For example, with partial dominance, only the road verge population (D) showed increased extinction probability with increasing effects of inbreeding depression (from no inbreeding depression to reinforcing epistasis; Table 2). With overdominance, all populations increased their extinction probabilities with increasing effects of inbreeding depression (Table 2). It is remarkable to observe that in this case two of the three abandoned

populations (D and E) plus the xeric grazed population (C) were the ones most affected by inbreeding depression (Table 2).

In the absence of inbreeding depression, five of the six populations exhibited positive estimates of population growth (Fig. 1). Only the population on the road verge (D) showed a negative population growth rate. Inbreeding depression affected population growth rates and reversed growth rates from positive to negative under many scenarios and in many populations. The effects were more pronounced with overdominance than with partial dominance (Fig. 1). Again, two of the abandoned populations (D and E) and the xeric grazed population (C) were the populations that exhibited the most severe reductions in population growth rate due to inbreeding depression under both hypotheses (Fig. 1).

Inbreeding depression influenced genetic diversity only under more specific conditions. The road verge population (D) had lower genetic variability than the remaining populations. Only with overdominance and either no epistasis or reinforcing epistasis the populations showed markedly reduced genetic variability (Table 3). Inbreeding depression had minor effects on the final proportion of deleterious recessive loci in homozygosis and the final proportion of loci in heterozygosis (Table 4). No clear differences were found between grazed and abandoned populations for these parameters (Table 4).

Sensitivity analyses in baseline populations consistently suggested that survival had the largest effects on population growth rate (range of absolute proportional changes = 8.5–57.2%; Fig. 2), whereas changes in growth and fecundity hardly changed population growth rates (1.6–13.4%; Fig. 2). Survival also had the largest effects also in the two inbreeding depression scenarios, and here changes were much larger with overdominance than with partial dominance (Fig. 2).

Table 2. Extinction probability (%) for *S. pratensis* populations affected by inbreeding depression

Function	Population					
	A	B	C	D	E	F
<i>(A)</i>						
No ID	0	4.0	0	10.7	0.1	0
Diminishing	0	4.6	0	30.1	3.2	0
No epistasis	0	3.3	0	35.6	3.4	0.2
Reinforcing	0	6.0	0	37.4	3.4	0
<i>(B)</i>						
No ID	0	3.5	0	10.4	0	0
Diminishing	0.1	5.7	0.2	66.8	25.1	1.4
No epistasis	0.9	10.6	14.2	85.1	57.5	5.4
Reinforcing	27.7	30.2	77.1	88.2	63.3	27.7

The partial dominance (A) and the overdominance (B) hypotheses and three epistatic functions (diminishing epistasis, no epistasis, reinforcing epistasis) were tested. Results for the baseline simulation with no inbreeding depression (ID) are also shown.

Discussion

Our results illustrate how genetic and ecological factors interactively determine population dynamics. In our simulations, inbreeding depression reduced population growth and increased extinction risk, but the strength of its effect depended on habitat type. When inbreeding depression was not taken into account, five out of six study populations showed positive population growth. Moreover, the three populations in favourable sites exhibited an extinction risk that was below 11% in all scenarios. Populations with positive population growth and low/nil extinction risks appeared to cope better with the effects of inbreeding depression. The inclusion of inbreeding depression into the model was more important for the two populations in the most

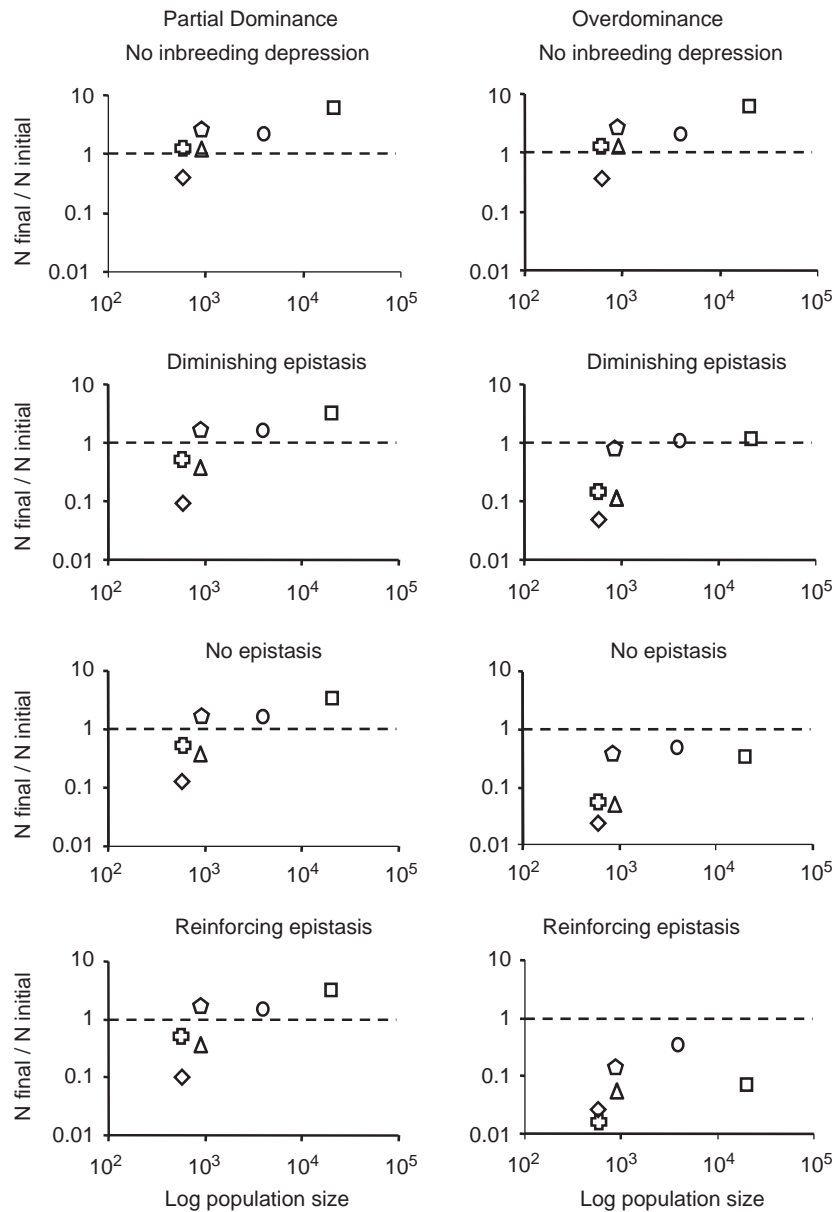


Fig. 1. Mean ratios between final and initial population sizes for *S. pratensis* populations affected by inbreeding depression. Population stability is indicated by the dotted line. Grazed populations: A (square), B (circle); grazed xeric population: C (cross); abandoned road verge population: D (diamond); abandoned populations: E (triangle), and F (pentagon).

stressful environments. The populations on the road verge and in the xeric habitat had the lowest population numbers, the most negative population growth, and the highest inbreeding depression effect. This dependence of effect size of inbreeding depression on the environment has also been documented in natural experiments (Hedrick & Kalinowski, 2000) and simulation studies (Lande, 1994; Mills & Smouse, 1994; Wang, Hill, Charlesworth, & Charlesworth, 1999). Regardless the lack of replicates for each type of population in this study, the results suggest that populations with a poor performance have higher probabilities of going extinct

as a result of genetic factors acting in concert with demographic processes (Soulé, 1987).

Our model allowed us to test the effect of different hypotheses and epistatic functions that account for the basis of inbreeding depression. A general pattern that emerged from the results was that the demographic effects of inbreeding depression on extinction risk and population growth were more severe when (1) inbreeding depression was accounted for by overdominance than by partial dominance, and (2) the epistatic relationship among loci became more intense. With partial dominance *S. pratensis* populations survived well

despite inbreeding depression, whereas with overdominance all populations showed higher extinction probabilities, reaching 25% in combination with reinforcing epistasis. A plausible explanation for this pattern could be that plant fitness is more sensitive to changes in heterozygosity than to the expression of deleterious recessive alleles. With respect to the effects of epistasis, the results met our expectations because increasing epistatic relationship among loci implies a decrease in plant fitness. Sensitivity analyses also supported this notion: population growth was most sensitive to

survival changes with overdominance. It is also worth noting that survival was the most important demographic trait for maintaining population growth, as is the case in many other long-lived perennial plants (Picó & Riba, 2002; Pino, Picó, & de Roa, 2007).

Our results indicate that inbreeding depression slightly decreased genetic variability but this decrease depended on the genetic basis of inbreeding depression. The genetic impoverishment, predicted as a result of inbreeding depression (Charlesworth, 2003), was more severe with overdominance than with partial dominance. In the case of overdominance, the loss of genetic variability also tended to increase with increasing epistasis among loci. The link between demography and genetics could explain such a difference between inbreeding depression hypotheses. With overdominance and reinforcing epistasis, population size is reduced more severely than with partial dominance. Hence, the probability of ending up with individuals sharing identical genotypes is higher with overdominance than with partial dominance. Overall, our results indicate that inbreeding depression increases extinction risk of *S. pratensis* populations but has little effect on genetic variability. Experimental studies with other species have also shown that plant population persistence seems to be more affected by inbreeding depression than by genetic variability per se (Vilas, Miguel, Amaro, & García, 2006).

Finally, our model also computed the genetic composition of extant individuals but results in this respect were less clear. Inbreeding depression had few effects on the final proportion of deleterious recessive loci in homozygosity and the final proportion of loci in heterozygosity, which were relevant for the partial

Table 3. Mean values for genetic variability for *S. pratensis* populations affected by inbreeding depression

Function	Population					
	A	B	C	D	E	F
<i>(A)</i>						
No ID	0.65	0.56	0.63	0.42	0.54	0.60
Diminishing	0.61	0.52	0.57	0.37	0.43	0.55
No epistasis	0.61	0.53	0.57	0.37	0.42	0.55
Reinforcing	0.61	0.53	0.56	0.38	0.42	0.55
<i>(B)</i>						
No ID	0.66	0.57	0.63	0.47	0.57	0.60
Diminishing	0.54	0.51	0.46	0.37	0.36	0.49
No epistasis	0.45	0.47	0.42	0.40	0.40	0.44
Reinforcing	0.34	0.43	0.48	0.41	0.41	0.39

Genetic variability values of 1 mean that all final individuals had unique genotypes. The partial dominance (A) and the overdominance (B) hypotheses and three epistatic functions (diminishing epistasis, no epistasis, reinforcing epistasis) were tested. Results for the baseline simulation with no inbreeding depression (ID) are also shown.

Table 4. Mean (\pm SE) values for (A) the final proportion of deleterious recessive loci in homozygosity and (B) the final proportion of loci in heterozygosity for the six *S. pratensis* study populations when populations were affected by different epistatic relationships among loci (see text for details)

Function	Population					
	A	B	C	D	E	F
<i>(A)</i>						
No ID	25.5 \pm 0.01	27.0 \pm 0.11	25.6 \pm 0.01	29.2 \pm 0.19	26.8 \pm 0.15	26.2 \pm 0.04
Diminishing	25.6 \pm 0.01	27.2 \pm 0.13	25.9 \pm 0.03	30.4 \pm 0.27	28.6 \pm 0.15	26.5 \pm 0.07
No epistasis	25.6 \pm 0.02	27.1 \pm 0.13	25.8 \pm 0.03	30.0 \pm 0.28	28.0 \pm 0.13	26.4 \pm 0.06
Reinforcing	25.5 \pm 0.02	26.9 \pm 0.12	25.7 \pm 0.03	29.0 \pm 0.26	27.8 \pm 0.13	26.3 \pm 0.06
<i>(B)</i>						
No ID	51.0 \pm 0.01	54.2 \pm 0.23	51.2 \pm 0.02	57.7 \pm 0.35	53.3 \pm 0.12	52.3 \pm 0.07
Diminishing	52.8 \pm 0.08	55.3 \pm 0.27	56.8 \pm 0.23	65.9 \pm 1.04	64.7 \pm 0.58	55.3 \pm 0.23
No epistasis	54.1 \pm 0.18	53.6 \pm 0.25	59.4 \pm 0.41	58.2 \pm 1.23	60.7 \pm 0.71	54.4 \pm 0.25
Reinforcing	57.9 \pm 0.48	54.9 \pm 0.40	62.4 \pm 1.23	56.4 \pm 1.24	61.8 \pm 0.82	56.8 \pm 0.41

The baseline simulation (no inbreeding depression) is also given. The proportion of deleterious recessive loci (A) and the proportion of loci in heterozygosity (B) are obtained when inbreeding depression is assumed to be explained by the partial dominance and overdominance hypotheses, respectively.

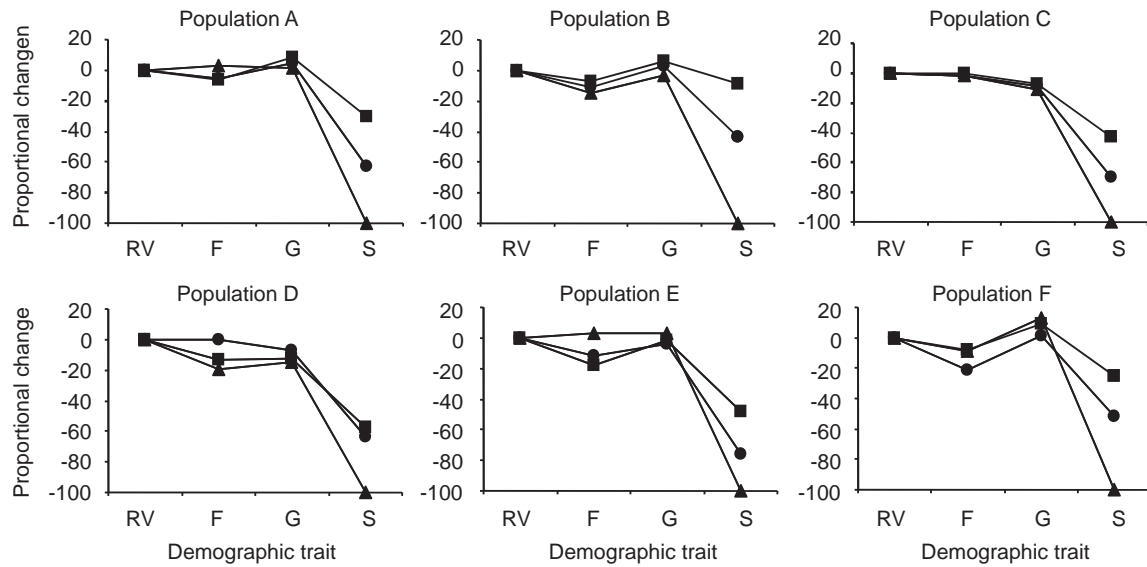


Fig. 2. Proportional changes in population growth rate after changing fecundity (F), growth (G) and survival (S) in *S. pratensis* populations for baseline simulations with no inbreeding depression (quadrats) and with inbreeding depression under partial dominance (circles) and overdominance (triangles). The first value of each panel corresponds to the reference value (RV) obtained with unchanged data.

dominance and the overdominance hypotheses, respectively. Based on these results, we conclude that our model did not purge low fitness individuals due to their genetic composition, which would have been expected from the partial dominance hypothesis (Carr & Dudash, 2003). One of the reasons could be that we did not differentiate between lethal alleles and mutations with small effect. Other simulation studies have shown that populations purge lethal alleles during the initial period of inbreeding (Wang et al., 1999), and that inbreeding depression is mostly caused by mutations of small effect that can be maintained in populations with high inbreeding rates (Carr & Dudash, 2003).

Assessments of the effects of environment and inbreeding depression on simulation-based short-term persistence should be taken with caution. Management effects vary with time and are driven by weather and other vagaries altering vital rates in complex ways, which can change the effects of genetic and environmental factors. For example, current grazing levels within the Nynäs nature reserve result in positive population growth, but more intense grazing can be detrimental for the species and reverse the mitigating effect of this practice on the consequences of inbreeding depression (Bühler & Schmid, 2001). Other studies assessing genetic effects attributable to habitat fragmentation in Europe indicated that differences in *S. pratensis* vital rates were most likely caused by genetic differentiation (Hooftman et al., 2003) or differences in soil conditions (Mix et al., 2006) than by inbreeding depression.

From an applied point of view, our results showed that the demographic consequences of inbreeding depression depend on the ecological and genetic settings, suggesting that ecological and genetic data have to be merged to fully evaluate species performance and extinction risk (Frankham, 2005; Higgins & Lynch, 2001; Oostermeijer, Luijten, & den Nijs, 2003). From a theoretical point of view, our results stress the importance of considering both genetics and ecology in the study of evolutionary dynamics of inbreeding depression in natural populations (Armbruster & Reed, 2005; Cheptou, 2006). Further research should focus on another important aspect excluded in this study: the number of loci involved in inbreeding depression and the distribution of their effects (Carr & Dudash, 2003). Overall, the increasing understanding of the genetic basis of inbreeding depression for different life-cycle traits and the development of demographic models that takes it into account represent a promising research line with multiple basic and applied implications.

Acknowledgements

We thank S. Kalisz, J. Geiger, E. Menges, C. Parkinson, D. Hooftman and two anonymous reviewers for comments on earlier drafts of this manuscript. We were supported by Archbold Expeditions, CREAM, Universidad de Valladolid, EBD-CSIC and funds from the AGAUR and the Ministerio de Educación y Ciencia of Spain (project ref. CGL2006-09792/BOS) to FXP and PFQA.

Appendix A. Supplementary material

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.baae.2008.02.006.

References

- Armbruster, P., & Reed, D. H. (2005). Inbreeding depression in benign and stressful environments. *Heredity*, *95*, 235–242.
- Bühler, C., & Schmid, B. (2001). The influence of management regime and altitude on the population structure of *Succisa pratensis*: Implications for vegetation monitoring. *Journal of Applied Ecology*, *38*, 689–698.
- Carr, D. E., & Dudash, M. R. (2003). Recent approaches into the genetic basis of inbreeding depression in plants. *Philosophical Transactions of the Royal Society of London, Series B*, *358*, 1071–1084.
- Charlesworth, D. (2003). Effects of inbreeding on the genetic diversity of populations. *Philosophical Transactions of the Royal Society of London, Series B*, *358*, 1051–1070.
- Charlesworth, B., & Charlesworth, D. (1999). The genetic basis of inbreeding depression. *Genetical Research*, *74*, 329–340.
- Cheptou, P.-O. (2006). The ecology of inbreeding depression. *Heredity*, *96*, 110.
- Cousins, S. A., & Eriksson, O. (2001). Plant species occurrences in a rural hemiboreal landscape: Effects of remnant habitats, site history, topography and soil. *Ecography*, *24*, 461–469.
- Ehrlén, J. (1996). Spatiotemporal variation in predispersal seed predation intensity. *Oecologia*, *108*, 708–713.
- Frankham, R. (2005). Genetics and extinction. *Biological Conservation*, *126*, 131–140.
- Hedrick, P. W., & Kalinowski, S. T. (2000). Inbreeding depression in conservation biology. *Annual Review of Ecology and Systematics*, *31*, 139–163.
- Herben, T., Munzbergova, Z., Mildén, M., Ehrlén, J., Cousins, S. A., & Eriksson, O. (2006). Long-term spatial dynamics of *Succisa pratensis* in a changing rural landscape: Linking dynamical modelling with historical maps. *Journal of Ecology*, *94*, 131–143.
- Higgins, K., & Lynch, M. (2001). Metapopulation extinction caused by mutation accumulation. *Proceedings of the National Academy of Sciences USA*, *98*, 2928–2933.
- Hooftman, D. A., van Kleunen, M., & Diemer, M. (2003). Effects of habitat fragmentation on the fitness of two common wetland species, *Carex davalliana* and *Succisa pratensis*. *Oecologia*, *134*, 350–359.
- Husband, B. C., & Schemske, D. W. (1996). Evolution and the magnitude and timing of inbreeding depression in plants. *Evolution*, *50*, 54–70.
- Lande, R. (1988). Genetics and demography in biological conservation. *Science*, *241*, 1455–1460.
- Lande, R. (1994). Risk of population extinction from new deleterious mutations. *Evolution*, *48*, 1460–1469.
- Lynch, M., Conery, J., & Burger, R. (1995). Mutational meltdown in sexual populations. *Evolution*, *49*, 1067–1080.
- Mildén, M. (2005). *Local and regional dynamics of Succisa pratensis*. Doctoral dissertation, Department of Botany, Stockholm University, Sweden.
- Mills, L. S., & Smouse, P. E. (1994). Demographic consequences of inbreeding in remnant populations. *American Naturalist*, *144*, 412–431.
- Mix, C., Picó, F. X., van Groenendael, J. M., & Ouborg, N. J. (2006). Inbreeding and soil conditions affect dispersal and components of performance of two plant species in fragmented landscapes. *Basic and Applied Ecology*, *7*, 59–69.
- Oostermeijer, J. G. B. (2000). Population viability analysis of the rare *Gentiana pneumonanthe*; the importance of genetics, demography and reproductive biology. In A. G. Young, & G. M. Clarke (Eds.), *Genetics, demography and viability of fragmented populations* (pp. 313–334). Cambridge: Cambridge University Press.
- Oostermeijer, J. G. B., Luijten, S. H., & den Nijs, J. C. M. (2003). Integrating demographic and genetic approaches in plant conservation. *Biological Conservation*, *113*, 389–398.
- Picó, F. X., Mix, C., Ouborg, N. J., & van Groenendael, J. M. (2007). Multigenerational inbreeding in *Succisa pratensis*: Effects on fitness components. *Biologia Plantarum*, *51*, 185–188.
- Picó, F. X., & Riba, M. (2002). Spatiotemporal regional scale demography of *Ramonda myconi*: Remnant population dynamics in a preglacial relict species. *Plant Ecology*, *161*, 1–13.
- Picó, F. X., & van Groenendael, J. M. (2007). Large-scale plant conservation in European semi-natural grasslands: A population genetic perspective. *Diversity and Distributions*, *13*, 920–926.
- Pino, J., Picó, F. X., & de Roa, E. (2007). Population dynamics of the rare plant *Kosteletzkya pentacarpos* (Malvaceae): A nine-year study. *Botanical Journal of the Linnean Society*, *153*, 455–462.
- Soulé, M. E. (1987). *Viable populations for conservation*. Cambridge: Cambridge University Press.
- Vergeer, P., Sonderren, E., & Ouborg, N. J. (2004). Introduction strategies put to the test: Local adaptation versus heterosis. *Conservation Biology*, *18*, 812–821.
- Vilas, C., Miguel, E. S., Amaro, R., & García, C. (2006). Relative contribution of inbreeding depression and eroded adaptive diversity to extinction risk in small populations of shore campion. *Conservation Biology*, *20*, 229–238.
- Wang, J., Hill, W. G., Charlesworth, D., & Charlesworth, B. (1999). Dynamics of inbreeding depression due to deleterious mutations in small populations: Mutation parameters and inbreeding rate. *Genetical Research*, *74*, 165–178.