
Demographic Viability of a Relict Population of the Critically Endangered Plant *Borderea chouardii*

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Abstract: *In addition to human-caused changes in the environment, natural stochasticity may threaten species persistence, and its impact must be taken into account when priorities are established and management plans are designed. Borderea chouardii is a Tertiary relict at risk of extinction that occurs in only one location in the world, where the probability of human disturbance is low. Its persistence, therefore, is mainly linked to its response to natural threats such as stochasticity. Over 8 years I monitored up to 25% of this rupicolous small geophyte. The population had an unbalanced size structure and 90% failure in seed arrival at appropriate microhabitats, which suggests a problem with recruitment. I used matrix models to describe its population dynamics, conducted hand sowings, and performed stochastic simulations to investigate the effect of environmental stochasticity on population trend and viability. I modeled several scenarios to represent a variety of ecological situations, such as population reduction, episodic or persistent disease, and enhancement or decrease of recruitment. Population growth rate (λ) was never significantly different from unity over the study period. The risk of extinction was null over the next five centuries under current conditions. Increase of mortality and decrease of recruitment reduced stochastic population growth rate, but no factor except a persistent increase of 10% mortality resulted in extinction. These results are the consequence of the plant's extremely long life span (over 300 years) and low temporal variability of key vital rates. Even though hand sowing significantly increased the stochastic population growth rate, other approaches may be more important for the persistence of this species. The extremely slow capacity for recovery following disturbances renders habitat preservation essential. In addition, the founding of new populations would reduce the risk associated with habitat destruction.*

Viabilidad Demográfica de una Población Relicta de la Planta en Peligro Crítico *Borderea chouardii*

Resumen: *Además de los cambios ambientales antropogénicos, la estocacidad natural puede amenazar la persistencia de especies, y su impacto debe tomarse en cuenta cuando se establecen prioridades y se diseñan planes de manejo. Borderea chouardii es un relicto del Terciario en riesgo de extinción que ocurre sólo en una localidad en el mundo donde la probabilidad de perturbación humana es baja. Por tanto, su persistencia está ligada principalmente a su respuesta a amenazas naturales como la estocasticidad. Durante 8 años monitoricé hasta el 25% de este pequeño geófito rupícola. La población tenía una estructura demográfica desequilibrada y un 90% de fracaso en la dispersión de semillas a microhábitats adecuados, lo que sugiere un problema de reclutamiento. Utilicé modelos matriciales para describir su dinámica poblacional, efectué siembras manuales y realicé simulaciones estocásticas para investigar el efecto de la estocacidad ambiental sobre las tendencias y la viabilidad de la población. Se modelaron varios escenarios para representar la variedad de situaciones ecológicas, tales como la reducción de la población, enfermedades episódicas o persistentes y el incremento o reducción de reclutamiento. La tasa de crecimiento poblacional nunca fue*

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significativamente diferente de la unidad durante el período de estudio. Bajo las condiciones actuales, el riesgo de extinción fue nulo para los próximos cinco siglos. El incremento de la mortalidad y el decremento del reclutamiento redujeron la tasa de crecimiento poblacional estocástico, pero ningún factor resultó en la extinción excepto el incremento persistente de 10% en la mortalidad. Estos resultados son consecuencia del ciclo de vida extremadamente largo de la planta (más de 300 años) y la escasa fluctuación interanual de las tasas vitales clave. Aunque la tasa de crecimiento poblacional estocástico incrementó significativamente con la siembra manual, otras aproximaciones pueden ser más importantes para la persistencia de esta especie. La preservación del hábitat es esencial debido a la capacidad de recuperación extremadamente lenta después de perturbaciones. Además la fundación de nuevas poblaciones podría reducir el riesgo asociado a la destrucción del hábitat.

Introduction

An increasing number of species face risk of extinction because they occur in very specific or highly fragmented areas, have a reduced number of populations or individuals, or are declining (World Conservation Union 1994). Currently, habitat loss is the agent most destructive of plant biodiversity (Wilcove et al. 1998). Besides human-caused changes in the environment, however, natural stochasticity may also pose an additional threat to species persistence (Nakaoka 1996; Menges 1997; Holsinger 2000; Vucetich et al. 2000). The large variety of life histories that plants exhibit also plays an important role in the way they are affected by these factors and must be taken into account when priorities are established and management plans are designed (Higgins et al. 2000).

Patterns of birth and death ultimately determine population size and can vary drastically among and within species (e.g., Roff 1992). The persistence of a population depends on a numerical equilibrium over time, whatever the schedules of fecundity, recruitment, and survival, and the integration of such parameters in simulation models allows exploration of their relative importance (Schemske et al. 1994; Horvitz & Schemske 1995; Caswell 2001). Understanding the mechanisms that govern population dynamics and their temporal variability is therefore essential for estimating extinction probabilities for endangered species (Schemske et al. 1994; Menges 2000).

Population viability analysis (PVA) is the most comprehensive tool with which to estimate the future size and risk of extinction for populations, but its predictive accuracy depends on the quality and quantity of data (Bierzychudek 1999; Higgins et al. 2000; Coulson et al. 2001). There is little doubt, however, that PVAs are useful for comparing effects of different factors or management options (Beissinger & Westphal 1998; Menges 2000). Stochastic simulations have been used widely to test and compare how populations would respond under current or hypothetical ecological scenarios where threats (e.g., predation, diseases, inbreeding, population reduction) and management actions are suspected to negatively or positively affect population growth rate (Groenendael

& Slim 1988; Ehrlén 1995; Nantel et al. 1996; Menges 1997; Menges & Dolan 1998; Pfab & Witkowski 2000; Lennartsson & Oostermeijer 2001). Exploring the response to particular external factors and natural stochasticity can, therefore, be of great aid in designing actions for population persistence or recovery.

I examined the population dynamics of *Borderea chouardii* Gaussen (Heslot) (Dioscoreaceae), a plant species with a singular life history. It is an endemic species with only one location in the world; thus, its threat category is critically endangered (World Conservation Union 1994), and it is a priority species according to the European Union Habitats Directive. It is considered at risk of extinction because of its restriction to one population with 300–500 individuals growing on <1 km² of rocky walls. A recovery plan was approved in 1995 by the government of the region where it occurs (Aragón). After an intensive search through its potential habitat and recent detailed censuses, population size was estimated at about 1300 reproductive plants (males plus females; García et al. 2002). This case represents a striking example of an ancient species persisting despite the combined effect of various threat factors: limitation to a single locality, population size reduction, high habitat specificity, extremely low recruitment, and almost no opportunities for successful long-distance dispersal.

I present descriptive parameters—population structure and reproductive success—of the only known population, that illustrate low recruitment because of an important failure in the dispersal mechanism. Over eight growing seasons, I monitored up to one-quarter of the entire population and conducted experimental seed sowings. I also set up matrix population models to explore the following questions: (1) Is the population declining? (2) To which life-history components is population growth most and least sensitive? (3) Which are the key traits for the persistence of this ancient species? (4) To what extent might threat factors (environmental stochasticity, reduction in population size, recruitment, or survival rates) and management actions (enhancement of recruitment) affect population viability in the long run?

Methods

Natural History of the Species

Borderea (Fam. Dioscoreaceae) is a paleorelict genus of dioecious geophytes that is composed of two species: *B. pyrenaica* Miégevillé, endemic to the screes of the Pyrenees but not threatened, and *B. chouardii* (Gaussen) Heslot (Gaussen 1952), growing on shaded crevices of north-facing limestone walls and overhangs. Both share the same unusual feature that the annual aerial stem leaves a permanent scar on the tuber, which allows one to determine the plant's age (García & Antor 1995a) when the tuber is removed.

The small tubers of *B. chouardii* are <10 cm long, grow in crevices, and may be covered by a calcium carbonate layer. Males produce several racemose terminal inflorescences, whereas females bear only a few flowers. Flies and ants have occasionally been observed visiting the small flowers. Ovaries contain six ovules, and pedicels of female flowers move toward the rocky substratum once they have been fertilized, sometimes entering a crevice and developing inside, where they release the seeds (hereafter called autosowing). Plants do not propagate vegetatively, although some tubers might produce more than one aerial stem without splitting.

The species' habitat is naturally fragmented. Despite intensive searching over 4 years at suitable habitat patches across the Pyrenean range, additional populations were not found (Guzmán et al. 2000). On the other hand, its habitat specificity could be linked to its incapacity to grow in other substrata. Attempts to cultivate it in standard soil have failed, and there have been difficulties with *ex vitro* acclimatization in pots after *in vitro* culture, despite >90% seed germination (M.B.G., unpublished data; J. M. Iriondo, personal communication). Given the long time *B. chouardii* has had to spread, its current extremely reduced distribution might be interpreted as resulting from high stenochory with almost no possibilities for new colonizations or as the last redoubt of a formerly more widespread distribution in a completely different climate regime (it belongs to a tropical family).

Population Sampling

I monitored two areas: (1) the rocky wall of a cliff (3 × 6 m) from 1995 until 2002 and (2) the ceiling of a wide-open cave (3 × 10 m) from 1997 until 2002. I surveyed the areas at the end of August, when vegetative development was over and just before seed release. To map all the plants growing in the monitoring areas (including all emerging seedlings) I stood on scaffolding up to 6 m high. A total of 180 to 545 individuals (before and after 1997, respectively) was monitored over the eight seasons, up to 25% of the estimated total population. At each census, I noted the reproductive status and sex of each plant,

the number of leaves, and the length and width of the largest one. The number of flowers, fruits, and seeds per fruit were counted in all females. The success of natural autosowing in crevices by females was estimated as the ratio between fruits developing in crevices and the total number of fruits produced every year. Determining the age of individual plants was not possible because it entails taking out tubers from crevices (and therefore killing plants); however, some dead tubers were removed for age recording.

I determined the seed-germination rate from the ratio of the number of seedlings in year t to the number of autosown seeds in year $t - 1$ (number of fruits inside crevices × average number of seeds per fruit). Survival in the seed bank was estimated from germinations following 69 hand sowings (1138 seeds) from the second year onward. Hand sowings were carried out annually from 1996 and increased by three the proportion of autosown seeds in the monitoring areas.

Data Analysis for Deterministic Models

Finite population growth rates were calculated from matrix models. Given the difficulty of estimating male fertility and the impossibility of determining the age of individuals in a nondestructive manner (except for 1-year seedlings, which appeared between two consecutive censuses), I used a female, size-based model. Sex ratio is male-biased in this species, the fruit and seed set is high, and mortality is similar or slightly lower for males. So, although the possibility of pollen limitation has not been tested experimentally, population dynamics may be assumed to be governed by the availability and reproductive success of females, therefore allowing for the use of this single-sex model (Brook et al. 2000; Caswell 2001). All small plants that never produced flowers were included in the model in accordance with a 1:1 sex ratio, although their sex was unknown, because there is no reason to expect a different performance before the onset of reproduction.

I examined the number and length of leaves and reproductive status—to find biological criteria with which to structure the population into a number of numerically balanced (avoiding reduced sample sizes) and biologically homogeneous (similar fate) classes. Size-frequency distributions and logistic regression were used to estimate the probability of flowering according to size, and mortality rates were also examined. The number of leaves was the only significant variable in a stepwise regression, with biomass as the dependent variable and other field measures (and combinations) as independent variables ($p < 0.0001$, $n = 17$), accounting for 98% of variance. Biomass was obtained from broken stems caused by the setting up of the scaffolds or manipulation for plant identification over the 8 years (all these individuals reappeared in the following year).

I established six classes: (1) seeds in the seed bank (S, could be viable for 3 years or more); (2) seedlings (F0, plants younger than 1 year, highest mortality); (3) juveniles (F1, older than 1 year, 1 leaf, no reproduction); (4) small females (F2, 2–5 leaves, <50% produce flowers every year); (5) medium females (F3; 6–10 leaves, 75% reproduce yearly); and (6) large females (F4, >10 leaves, 95% reproduce yearly). Plant dormancy may occur in this species, although it is infrequent. Only five individuals became dormant for only 1 year over 8 years, and I assigned them to the size class of their previous record. In the last transition (2001–2002), however, dormant and dead individuals were impossible to distinguish. To overcome this problem, I estimated dormancy rate from the rate calculated over 1995–2001.

For each pair of years, I constructed a 6×6 Lefkovich matrix by assembling rates of fecundity and survival for each class. Seven projection matrices were created in this way, in which each element, a_{ij} , represents the probability of an individual in the j th category to contribute to the i th category in year $t + 1$. A mean matrix was also constructed.

The dominant eigenvalue for each projection matrix (λ) corresponded to the asymptotic population growth rate. To assess uncertainty and differences in population growth rate among years, I calculated their 95% confidence interval (CI) (Alvarez-Buylla & Slatkin 1994). The right eigenvector corresponds to the stable-stage distribution, which I compared to the observed one through G tests. Elasticity analyses (de Kroon et al. 1986) were performed to examine the relative importance of survival and recruitment (involving seed survival, seed germination, and transitions from reproductive plants to seedlings) to population growth rate (Silvertown et al. 1993; Horvitz et al. 1997; Caswell 2000). I calculated elasticity values from the mean matrix and correlated them to the variability of vital rates (estimated as the coefficient of variation, CV).

Population Trend and Viability under Different Ecological Scenarios

I assessed the impact of factors that might affect population viability in the long run by using stochastic models. I modified initial population size or elements of original matrices to examine population trend and risk of extinction under five different ecological scenarios.

Scenario 1: reduction of population size. The initial number of females (1100 supposing a 1:1 sex ratio at the seedling stage and balanced mortality rate between males and females) was reduced by 25%, 50%, and 75% to estimate the minimum viable population (MVP) under environmental stochasticity. This situation is representative of strong harvesting without habitat destruction or a drastic disease.

Scenario 2: higher frequency of years of negative population growth. Four out of the seven deterministic models provided population growth rates slightly below 1 (hereafter, “bad years”). Simulations were performed under the premise that bad years were actually much more frequent (90% of the years) than good years (10% of the years) over a long temporal series.

Scenario 3: drastic reduction of recruitment. The vital rates corresponding to seed production, survival, and germination were set to zero in four of the seven matrices (bad years) or all of the matrices (no recruitment at all). This situation might be the result of reduced seed production (caused, for example, by a lack of pollinators or extremely unbalanced sex ratios), higher failure of autosowing, sporadic or persistent seed disease, or predation.

Scenario 4: increase in the annual mortality of established plants. The mortality rate of every class was increased both lightly (1%) and moderately (10%). Also, the effect of stochastic events leading to an increase of mortality by 20% every 20 years was explored. These situations could be the result of different factors such as disease or extreme climatic conditions.

Scenario 5: increase of recruitment. Hand sowings were carried out over 7 years in selected places by introducing two to four fruits (about 12–20 seeds) in 69 crevices. This increased natural sowing in the monitoring areas by threefold. For the total population, this enhanced fertility was similar to multiplying the sowing probability by 1.4. The low number of seeds produced by female plants, the scarcity of available crevices, and the inaccessibility of most parts of the habitat make hand sowing at this intensity or slightly higher almost the only in situ active-management technique possible.

The current total population size of *B. chouardii* is 2200 individuals (including seedlings), large enough to expect that demographic stochasticity will not play an important role. Therefore, I considered only environmental stochasticity. To estimate the effect of threat factors and enhanced recruitment, I used the current population size (or the different initial population sizes for scenario 1, keeping the current stage structure) and performed simulations by multiplying the initial population vector by a random sequence of matrices modified according to the factor examined. A specific “visual basic” program was written for that purpose (K. Lehtilä, X. Picó). For the scenario of a higher frequency of bad years, the random sequence was defined so that 90% of the matrices chosen produced a λ of <1 .

Iterations were performed for 500 years or until the population was extinct, and 1000 replicates for each simulation were run. I used 500 years because this plant can live for over 300 years. The stochastic growth rate was analytically calculated as $\log \lambda_s = (\log N_0 - \log N_t)/t$ (seeds excluded; Caswell 2001). The proportion of runs that resulted in population extinction

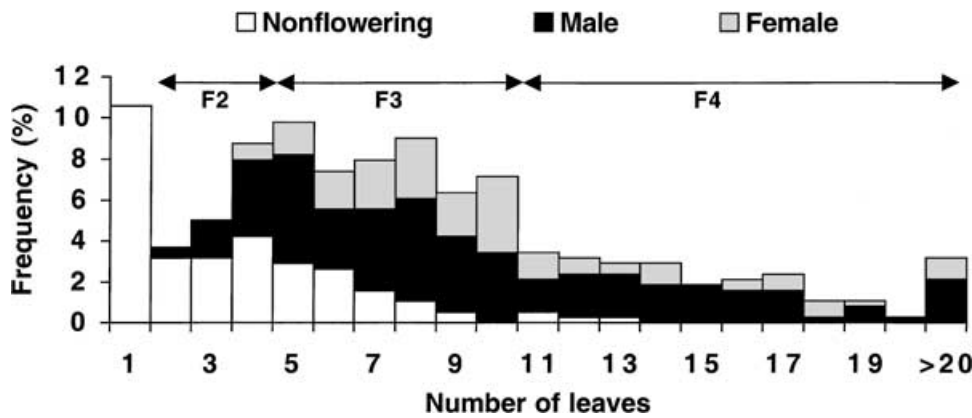


Figure 1. Frequency of individuals of *B. chouardii* according to reproductive status and number of leaves produced in year 2002 ($n = 378$ individuals); F2, small females; F3, medium females; F4, large females.

served to estimate the risk of extinction (extinction threshold = 1).

These density-independent models should be considered a way of comparing situations and stochastic population growth rates as indices of the strength of different factors, rather than a forecast of the future population size (Coulson et al. 2001). Microhabitat availability, which is currently scarce, rather than density, is the most limiting factor.

Results

Population Structure and Reproductive Success

Individuals of intermediate size (F3) were the most abundant in the population, whereas the proportion of smallest plants (F0, F1) was lower (Fig. 1). The sex ratio was calculated on both an annual basis (flowering plants) and a cumulative basis (plants were sexed if they flowered at least once over the study period). In all cases, annual sex ratio was significantly male-biased (from 1.8 to 2.9, all chi-square likelihood ratio tests provided $p < 0.002$, $n = 89-285$; 1.5 from all plants that flowered at least once, $\chi^2 = 7.1$, $p = 0.008$, $n = 339$). Mortality was not

significantly different between males and females over the study period (annual rate, 0.5% and 1% for males and females, respectively; $n = 930$ and 586 records; Fisher exact test $p = 0.217$).

Fruit set (percentage of flowers that set fruit) was between 68.7% and 97.6%, depending on the year ($n = 42-281$; Fig. 2). Seed set (seed:ovule) varied from 43.4% to 81.0% ($n = 41-221$). This notable success in producing seeds contrasted with low success in seed dispersal. Annual autosowing of seeds in crevices varied from 4.4% to 12.2% (Fig. 2). Of the 1316 fruits produced in the monitoring areas over the 8 years, 93% released seeds into the air (Fig. 2); thus, these seeds were lost for recruitment. Natural recruitment was between 0.02 and 0.11 seedlings per reproductive female and year. Hand-sowing resulted in the appearance of seedlings in 35% of the crevices used.

Population Dynamics and Key Life Stages

Survival rate of 1-year-old seedlings was as high as 72% (± 20.3 , $n = 92$), whereas annual mortality rates for juveniles plus adults was between 0 and 3.9%. Population growth rates were between 0.982 and 1.021, and none of them differed significantly from 1 (confidence intervals always included this value; Table 1). There were no significant differences in estimated finite rates of growth among

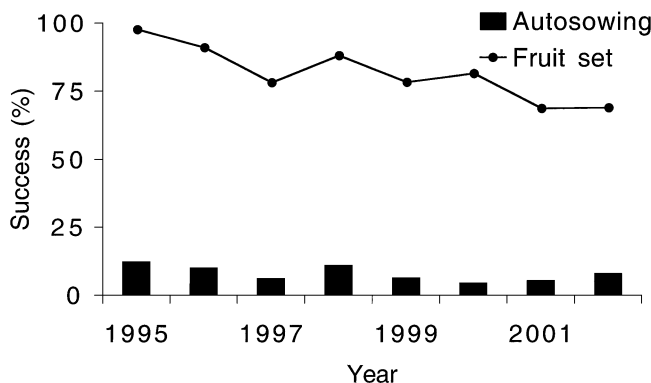


Figure 2. Percentage of female flowers of *B. chouardii* setting fruit over 8 years, and fruits successfully sowed in crevices by mother plants.

Table 1. Finite growth rates (λ) as predicted by deterministic matrix models, with 95% confidence interval (CI).

Transition years	λ	CI	G^a	λbs^b
1995-1996	0.997	0.941-1.053	12.64*	
1996-1997	1.021	0.923-1.12	11.81*	1.025
1997-1998	0.989	0.934-1.043	3.35 ns	0.991
1998-1999	1.009	0.931-1.088	2.68 ns	1.014
1999-2000	0.999	0.921-1.078	5.52 ns	1.007
2000-2001	0.982	0.936-1.028	1.82 ns	0.985
2001-2001	1.009	0.903-1.115	3.24 ns	1.013

^aComparisons between observed population structures and those expected in stable-stage distribution (ns, $p > 0.05$; *, $0.01 < p < 0.05$).

^bThe λbs are the result, at the population level, of increased fertility after fruits are collected and sowed in the monitoring area.

Table 2. Lefkovich mean matrix for *Borderia chouardii* calculated for 1995–2002 ($\lambda = 1.001$).

	S	F0	F1	F2	F3	F4
S	0.500			0.032	0.220	0.528
F0	0.030			0.002	0.011	0.026
F1		0.772	0.856	0.046	0.002	
F2		0.019	0.095	0.759	0.079	
F3				0.179	0.838	0.151
F4				0.003	0.074	0.845

*Abbreviations: S, seeds in the seed bank; F0, plants younger than 1 year; F1, juveniles; F2, small females; F3, medium females; F4, large females.

years. The mean matrix produced the same lambda as the geometric mean calculated from the seven individual lambdas ($\lambda = 1.00093$) (Tables 1 & 2).

Given the difficulty in estimating the fraction of the seed bank, seeds were excluded before testing for differences between observed and projected stable distributions. Only the 1995 and 1996 structures (obtained from the small monitoring area; sample sizes were three times higher after 1997) differed from the projected distribution based on the mean matrix (Table 1). The two first individual matrices predicted more juveniles and small females (F1 and F2) and fewer medium and large plants (F3 and F4) than the mean matrix.

Prospective analyses showed that the population growth rate was much more sensitive to stasis, growth, or shrinkage of established individuals than to seed or seedling recruitment. Stasis of medium-sized females (F3) showed the maximum elasticity value in six of the seven deterministic models (between 31% and 59%), and the stasis of the largest females was most important in the remaining model (52%). Overall, stasis transitions accounted for 77–91% of the elasticity matrix (81% of the mean matrix), whereas vital rates linked to reproduction accounted only for 0.5–2.7% (2.1% of the mean matrix). Elasticity and temporal variability were inversely correlated because the transitions with the highest elasticity values were the least variable ones (lowest coefficient of variation; Spearman rho = -0.47 , $n = 21$).

Population Trend and Viability under Different Ecological Scenarios

Stochastic models projected a striking population stability (maximum-likelihood estimator of stochastic population growth rate $\lambda_s = 0.99995$; Fig. 3), and simulations resulted in 0% risk of extinction for the next 500 years. The extinction risk after population size reduction was null if the population size was reduced up to 25% of the current size (equivalent of 275 females). Therefore, a population of this species with a few hundred individuals would probably be viable for some centuries under current environmental conditions (greatly reduced temporal variability of the survival rates, no effect of demographic

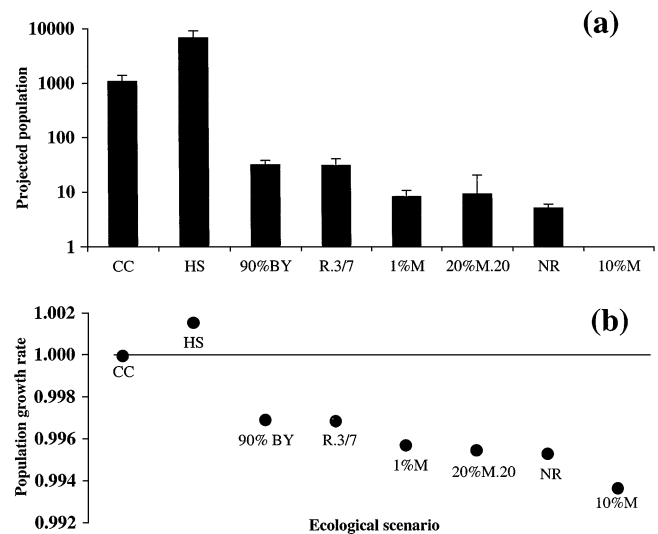


Figure 3. (a) Projected population size and (b) population growth rate (λ) of *B. chouardii* resulting from stochastic models (1000 replicates for each ecological scenario; simulations performed for 500 years). See methods for a detailed explanation of the set of matrices used and probabilities associated with them. Abbreviations: CC, current conditions; HS, hand sowing; 90%BY, 90% of the years with $\lambda < 1$; R.3/7, recruitment in only three of the seven matrices; 1%M, increase of 1% mortality every year; 20% M.20, increase of 20% mortality every 20 years; NR, no recruitment; 10%M, increase of 10% mortality every year.

stochasticity, no alteration of the rocky substrata, high reproductive success, and similar autosowing rate).

The lowest population growth rate resulted when mortality was increased to 10% in a constant way (Fig. 3). Under these conditions, the average population became extinct after 71 ± 12 years (mean \pm SD). No simulation reached 100 years, meaning that the risk of extinction would be 100%. If mortality increased 20% occasionally (once every 20 years), then the population performed similar to that under a constant increase of 1% mortality (Fig. 3); still, no extinction is expected in the next 500 years.

Reduction of seedling recruitment to only 3 out of 7 years had a negative effect on future population trend, similar to a 90% frequency of bad years (Fig. 3). Total absence of recruitment would reduce final population size to a few individuals. No extinction resulted from simulations in any of these scenarios, suggesting that some plants could survive for 500 years.

Hand-sowings in monitoring areas resulted in 27 new seedlings and 51 juveniles currently alive in the population, which increased recruitment from autosowing threefold. The stochastic population growth rate from matrices including enhanced fertility after hand sowing (taking into account that it affected only part of the

population) projected a statistically significant increase of 0.16% in the population growth rate compared with current conditions ($\lambda_s = 1.00153$ and 0.99995, respectively; there was no overlap between the confidence intervals of both estimated values; Fig. 3), despite the fact that individual matrices with enhanced sowing did not significantly increase λ compared with original matrices in deterministic models (Table 1).

Discussion

Few studies have investigated the detailed population dynamics of rupicolous plants (Kephart & Paladino 1997; Picó & Riba 2002). Rocky habitats shelter many endemic and endangered plant species in the Mediterranean basin (Gómez-Campo 1985; Domínguez et al. 1996; Médail & Verlaque 1997) for which little demographic information, if any, is available. *B. chouardii* is an extreme case of long life span in herbs (older than 300 years; García et al. 2002), but longevity, population stability, and remnant dynamics seem to be common characteristics of species occurring in habitats with adverse growth conditions (Eriksson 1996; Morris & Doak 1998; Laberge et al. 2000; Picó & Riba 2002). My results show which life-history traits account for success in the local persistence of a specialist with only one population and almost no possibility for seed germination or seedling settlement after long-distance dispersal.

Demographic Parameters and Life History

At first glance, the population structure of *B. chouardii* seems unbalanced. First, males outnumber females, a common situation among dioecious plants (Delph 1999). Males start to flower when they have two leaves and produce flowers nearly every year, whereas females start flowering when they have four leaves, and even large female plants do not flower every year. Because mortality was not significantly different between sexes, the male-biased sex ratio may be considered a consequence of earlier reproductive onset and higher frequency of flowering in males.

Second, the low frequency of small plants resulted in a size distribution quite different from the typical inverse J of most herbaceous plant species. This fact was formerly interpreted as resulting from the loss of about 90% of seeds produced every year because of failure in the autosowing mechanism. According to matrix models, however, this seed loss is not a threat factor: current size-unbalanced population structure does not differ from the projected stable structure (the mean matrix predicts a low abundance of seedlings of 1.5%), and growth rates from deterministic and stochastic models do not significantly differ from unity despite low reproductive output. Population dynamics in this case are largely inde-

pendent of recruitment, as predicted by elasticity values. *B. chouardii* represents therefore an example of the risk of using static size structures or reproductive parameters alone to assess the dynamics of long-lived species (see also Harper & White 1974; Knowles & Grant 1983; Stewart 1986; Hanzawa & Kalisz 1993; García & Antor 1995b).

Despite the herbaceous, nonclonal habit and small size of *B. chouardii* (biomass <5 g of an individual older than 300 years), its vital rates, elasticity values, and low variation in λ match the pattern of shrubs or trees much better than those of small perennial herbaceous species (Bierzychudek 1982; Silvertown et al. 1993; Silvertown et al. 1996), probably because they have a long life span. Life-history theory predicts that low reproductive output, long life span, and slow growth are associated with a stable or slow population growth rate (Caswell 1982), and *B. chouardii* fits this pattern well. The negative relationship between the temporal variance of vital rates and their impact on population growth is widespread and has been interpreted as the result of an evolutionary adaptation that buffers populations from large fluctuations in fitness (Boyce 1977; Ehrlén & van Groenendael 1998; Pfister 1998; Hoffmann 1999; Picó & Riba 2002). On the other hand, it has also been proposed that variance in recruitment instead of survival rates could reduce extinction risk (contrary to theoretical models) for plants that can store reproductive potential over time (Higgins et al. 2000), which is quite likely for this species. The low variance recorded in *B. chouardii* over 8 years, together with its extraordinary longevity, have probably been key to the local persistence of this relict plant.

How Environmental Factors Affect This Long-Lived Plant

Most of the ecological scenarios I simulated have not been observed to date, but they are examples of potential threats in the future, such as those due to climatic change, habitat destruction, or diseases. My results do not give an accurate long-term prediction of population size. Rather, I have emphasized the way the species responds to such factors and the contrast among model projections.

The most remarkable characteristic of the population dynamics of *B. chouardii* is their extraordinary stability, with population growth rates near equilibrium under environmental stochasticity. The persistence of the population was compromised for the next 100 years in only one ecological scenario: a constant increase of mortality (10% every year). If for any reason new seedlings were never produced, the current population would suffer a decline similar to that from sporadic events of higher mortality (increase of 20% every 20 years). Its long life span due to low mortality rates make high recruitment rates unnecessary for population persistence (Gotelli 1991; Higgins et al. 2000). This stability and high independence of recruitment is characteristic of remnant population dynamics (Eriksson 1996).

The same slow dynamics that provide population stability in *B. chouardii* could also prevent the species from recovering after disturbance. Having highly stable dynamics to overcome a certain amount of environmental stochasticity is an obvious advantage because it is the best guarantee for persisting in the long run (Lande & Orzack 1988; Foley 1994; Vucetich et al. 2000), but it also becomes a disadvantage after catastrophic events. Thus, longevity and stability seem to be a perfect combination of traits for species such as *B. chouardii* that live in places with a low probability of perturbation, and this combination is probably one of the main reasons for its persistence from the Tertiary age.

The highly scattered distribution of suitable habitat patches and the extremely low ability of the species to found new populations accentuate the extreme importance of local persistence. Elasticity analyses identify the most effective potential targets for conservation interventions (Benton & Grant 1999; Caswell 2000; de Kroon et al. 2000), but the ecological context and management constraints involve limitations. The highest elasticities corresponded to survival of large females in *B. chouardii*, a common pattern among long-lived organisms (Enright et al. 1995; Heppell et al. 2000; Picó & Riba 2002), but there is not much that can be done to increase this vital rate apart from habitat preservation. My attempt to increase recruitment by hand sowing had a positive effect. However, for a long-lived plant with just one small population, an extremely restricted habitat, low success in seed dispersal, and remnant population dynamics, enhancement of population growth rate might not be as essential as local persistence and founding of new populations, which would reduce the risk associated with habitat destruction.

Conclusions

Two conclusions arise from this study. First, unbalanced size structure or low reproductive success alone do not imply poor population performance for long-lived plants. Size-based demographic structure may differ considerably from age-based structure, and reproduction is only a component of fitness whose importance to population dynamics may be much less than other components. Second, the future viability of *B. chouardii* relies on survival of adults, and population reduction has an enormous impact because of the very slow recovery capacity of the species, which derives from low and highly stable population growth rates. This latter factor stresses the importance of local persistence for conservation of species with remnant dynamics.

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