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POPULATION ECOLOGY - ORIGINAL PAPER

Linking environmental and demographic data to predict future population viability of a perennial herb

Per Toräng · Johan Ehrlén · Jon Ågren

Abstract Recent advances in stochastic demography provide tools to examine the importance of random and periodic variation in vital rates for population dynamics. In this study, we explore with simulations the effect of disturbance regime on population dynamics and viability. We collected 7 years of demographic data in three populations of the perennial herb *Primula farinosa*, and used these data to examine how variation in vital rates affected population viability parameters (stochastic growth rate, λ_S), and how vital rates were related to weather conditions. Elasticity analysis indicated that the stochastic growth rate was very sensitive to changes in regeneration, quantified as the production, survival, and germination of seeds. In one of the study years, all seedlings and mature plants in the demography plots died. This extinction coincided with the driest summer during the study period. Simulations suggested that a future increase in the frequency of high-mortality years due to climate change would result in reduced population growth rate, and an increased importance of survival in the seed bank for population viability. The results illustrate how the limited demographic data

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typically available for many natural systems can be used in simulation models to assess how environmental change will affect population viability.

Introduction

Populations of many species decline and risk going extinct because of changes in the environment induced by human activities. A major challenge facing ecologists is therefore to identify the factors governing population dynamics and to develop methods to forecast the effect of environmental change on population viability (Lindenmayer et al. 2008). Because all natural populations experience stochastic variation in vital rates, stochastic demography models (Tuljapurkar et al. 2003; Horvitz et al. 2005; Boyce et al. 2006; Gotelli and Ellison 2006) provide an appropriate framework for analyzing the effects of directional changes in environmental conditions and of changes in the disturbance regime on population dynamics.

In plants, environmental conditions may influence the establishment of new individuals, and the growth, survival, and reproductive success of established individuals in several ways. For example, severe weather-induced disturbances such as drought, fire and flooding are often associated with high density-independent mortality, and are typically followed by improved conditions for establishment due to released competition (e.g., Gross et al. 1998; Horvitz et al. 1998; Hubbell et al. 1999; Smith et al. 2005). As a result, vital rates may shift periodically as a function of the cycle of disturbance and recovery transitions following disturbance (between-phase variability, sensu Morris et al. 2006).

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To accommodate such shifts in vital rates, information about disturbance regime and rates of recovery after disturbance should be combined with data on the correlation between vital rates and environmental state in analysis of population dynamics (Horvitz et al. 2005). Models based on correlations between vital rates and environmental conditions, and stochastic variation or directional change in environmental conditions can be used to examine a wide range of scenarios by simulation models. Such analyses should be useful in the evaluation of the effect of environmental changes on the dynamics and viability of populations (Morris et al. 2006).

Climatic trends that influence the length of the growing season and the frequency of disturbance events are important for the dynamics of many species (Mouillot et al. 2002; Sitch et al. 2003; Beckage et al. 2006). Consequently, the threat of climate change to various species has, of late, become a growing concern (McCarty 2001; Thomas et al. 2004; Maschinski et al. 2006; Parmesan 2006; Thuiller et al. 2008; Adler and HilleRisLambers 2008; Morris et al. 2008). In this study, we employ a recently proposed method to predict population viability in environments that undergo directional change (Horvitz et al. 2005), based on the limited demographic and environmental data typically available for natural systems.

We examined how temporal variation in vital rates affects population dynamics of the perennial herb *Primula farinosa* using a combination of population and habitat transition matrices. We collected demographic data over 7 years in permanent plots in three populations to document interannual variability in vital rates, and the relationship between vital rates and summer precipitation. The study was conducted in moist seminatural alvar grasslands on Öland island, southern Sweden. This is a habitat that in some years is affected by severe drought that strongly affects the dynamics of local plant populations (Rosén 1982; Sterner and Lundqvist 1986). Examining the effects of drought-induced disturbances is particularly relevant as scenarios of global warming indicate that the frequency of very dry and very wet years is likely to increase in northern Europe (Kjellström et al. 2005; Rowell 2005). The present study included one very dry summer, which was associated with complete mortality of seedlings and mature plants in the study plots. Our specific aims were (1) to document current population dynamics of *P. farinosa* in habitats known to be subject to intermittent severe disturbance, (2) to assess the relative importance of survival, growth and regeneration for overall plant fitness under different disturbance regimes, (3) to examine the relationship between summer precipitation expressed as the rainfall anomaly index (RAI) and estimates of population vital rates, and (4) to predict by simulations how an altered disturbance frequency, e.g., due to climate change, would affect population dynamics.

Materials and methods

Study species

Primula farinosa L. (Primulaceae) is a hermaphroditic, self-incompatible, distylous perennial herb with a disjunct distribution across most of Europe (Hambler and Dixon 2003). It is favored by grazing, and in Sweden many populations have declined or become extinct due to ceased or changed management practices during the last century (Lindborg and Ehrlén 2002). Flowering individuals typically produce a single inflorescence, which develops from the leaf rosette. The flowers are arranged in an umbel. Flowering takes place in May. In the study area, butterflies (especially *Pyrgus malvae*) and solitary bees (especially *Osmia bicolor*) are the main pollinators. The fruit is a multi-seeded capsule that matures in late June–July. Seeds germinate in spring, and seedlings form a small leaf rosette in the 1st year. Populations on the large islands of Öland and Gotland in the Baltic Sea are dimorphic for scape-length (Lagerberg 1948). The lifespan of established individuals is more than 21 years under low disturbance (Ehrlén and Lehtilä 2002).

Study sites and climate

The present study examined population dynamics of *P. farinosa* at three sites located in the northern part of Stora Alvaret (the Great Alvar) on Öland island off the southeast coast of Sweden (distances between sites ranged from 0.6 to 2 km; Appendix A in the Electronic Supplementary Material). The sites occur on alvars—habitats characterized by shallow soils on limestone rock. The flat topography results in a mosaic of temporal wetlands and pools in a matrix of dry grassland (Rosén and Borgegård 1999). Two populations, Tranekärr and Dröstorp 1, were located on very thin soils that are usually flooded in early May and dry up completely later in the season. Vegetation was sparse and restricted mainly to rock fissures in a matrix of bare soils. Disturbance was intense due to repeated flooding and drought, and freezing and thawing. The third population, Dröstorp 2, was located in closed vegetation on somewhat deeper soil with expected more stable water availability. All sites were exposed to wind and sun, and to some disturbance caused by trampling and grazing by domestic grazers (cattle and sheep).

Quadrat sampling

In July 2000, we mapped and classified all *P. farinosa* individuals in a total of 18 permanent 1 m × 1 m quadrats in the three populations. Plants were classified according to developmental and reproductive status into three

developmental stage classes: seedlings (i.e., new plants not recorded in the previous year), vegetative rosettes, and flowering rosettes. In the following 6 years, during the fruiting period in June, survival and status (vegetative or flowering) was recorded for all plants mapped in the previous year and any new seedlings in each quadrat were recorded and mapped. The number of mature fruits produced by each reproductive plant was noted. These data allowed us to track the fate of individual plants from one year to the next. During the 7-year period 2000–2006, 8,911 individual seedlings, vegetative rosettes and flowering rosettes were followed. In the analysis, short- and long-scaped plants were pooled because a large proportion of individuals never flowered, and there is presently no method to determine scape morph of non-flowering plants. Moreover, scape-morph differences in survival and probability of flowering were small in the present study (χ^2-tests, $P > 0.30$, except for 2001 in the Dröstorp 2 population when a larger proportion of long-scaped than short-scaped plants flowered, $P = 0.033$), as well as in a previous field study (Ågren et al. 2006) and in a common-garden experiment, which included 1,860 plants from eight populations (Toräng et al. 2010). To estimate seed production per fruit, in each population we collected 1–2 fruits from each of 18–110 reproductive plants growing in close vicinity to the study plots in 2000 and 2001. We used records of the number of fruits produced by reproductive plants in the permanent plots in July 1999 to estimate reproductive output in the study populations in the year preceding the start of the demographic study.

Life-history transition matrices

The life cycle of *P. farinosa* can be regarded as consisting of four stages: seeds, seedlings, vegetative rosettes, and flowering rosettes (Fig. 1). To model population dynamics we constructed life-history transition matrices, in which the elements (a_{ij}) describe the probabilities of individuals to transition from one stage class j in year $t - 1$ to stage class i in year t (Caswell 2001). For each population, life-history transition probabilities for established plants were calculated from observations pooled over quadrats. Elements of the life-history transition matrix can be summed to obtain the probability of growth (the probability of survival × the probability of advancing into a higher stage-class), stasis (the probability of survival × the probability of remaining in a stage-class), retrogression (the probability of survival × the probability of retrogressing to a lower stage-class) and fecundity. Vegetative propagation was not observed in the quadrats and is rare in the study area (J.Å., J.E. and P.T., unpublished data).

For each population and year, seed production of flowering individuals was estimated as fruit production for that year multiplied by the population mean seed production per fruit in 2000 and 2001 (mean ± SE based on these two yearly means, 47 ± 6.7 seeds per fruit in Tranekärr ($n_{2000} = 18$, $n_{2001} = 110$), 57 ± 5.1 seeds per fruit in Dröstorp 1 [$n_{2000} = 20$, $n_{2001} = 43$], and 38 ± 3.1 seeds per fruit in Dröstorp 2 ($n_{2000} = 59$, $n_{2001} = 43$)]. Seeds produced in one year may, provided that they survive until the next year, either germinate or enter a transient seed bank. The probability

Fig. 1 Life cycle graph of *Primula farinosa*. Four stage classes were recognized in the models: seeds (stage 1), seedlings (stage 2), vegetative rosettes (stage 3), and flowering rosettes (stage 4). *Arrows* represent possible transitions between stages, and *letter codes with subscripts* depict corresponding matrix entries
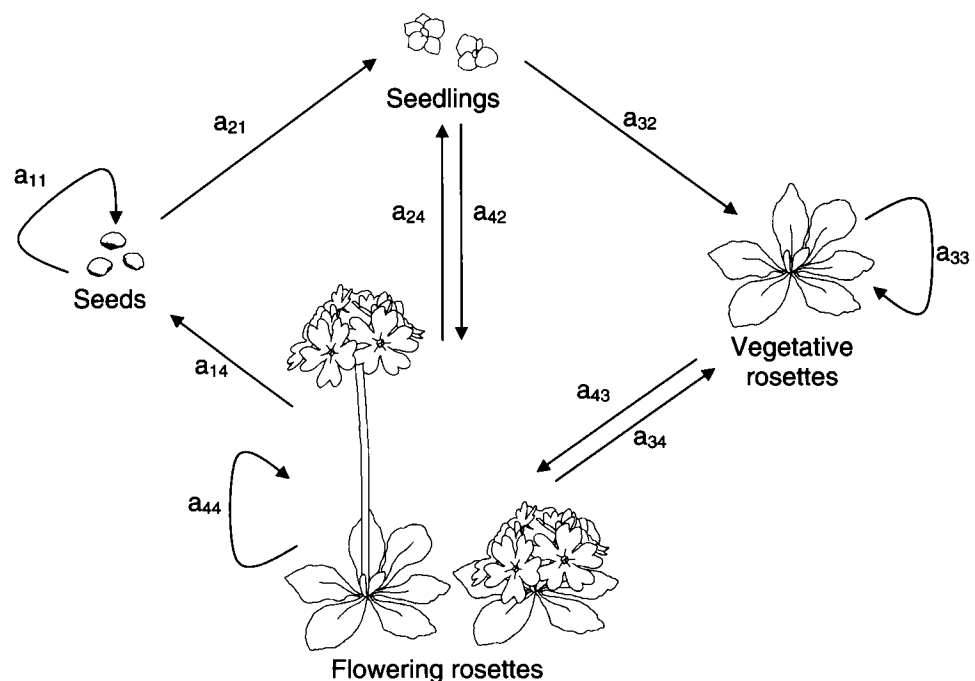
of the former transition is the product of seed survival and germination rate; the probability of the latter transition is the product of seed survival and (1 – germination rate).

The transition probabilities of seeds were inferred from data on the number of new seedlings each year. Because the number of seedlings appearing in one year is a function of seed production in several previous years, we constructed a multiple regression model where the emergence of seedlings in year t is a function of seed production in year $t - 1$ and $t - 2$.

$$\text{Seedlings}(t) = a + b_1 \times \text{Seeds}(t - 1) + b_2 \times \text{Seeds}(t - 2)$$
$$(1)$$

where a, b_1 and b_2 are constants. Including estimates of seed production in year $t - 3$ and earlier did not improve the fit of the model, suggesting that survival of seeds for more than two seasons in the seed bank has little impact on population dynamics. To calculate a mean value for seed survival, we made the simplifying assumptions that seed survival and germination were constant across years and did not vary with seed age. We further assumed that the survival rates of seeds and seedlings were equal from the start of germination (usually in early May) until the census in June. Then $b_1 = s \times g$, and $b_2 = s^2 \times g \times (1 - g)$, where s = seed survival and g = proportion of surviving seeds that germinate. Substitution then gives $s = b_1 + (b_2/b_1)$. We fitted this model to pooled data from all three populations and years and obtained a mean value for seed survival of 0.60 ($b_1 = 0.0507$ and $b_2 = 0.0281$). Because we had records of the number of flowering plants and their seed output from 1999 to 2002, and because all plants died between the censuses of 2002 and 2003 and no flowering plants appeared in the quadrats before 2004 or 2005, we could derive an additional estimate of seed survival from the emergence of new seedlings in these years. Assuming no net seed import into the quadrats (i.e., all new seedlings develop from seeds produced in the quadrats in previous years), the proportion of seeds surviving from year to year had to be greater than 0.5. Although the two estimates of seed survival were close, there is still a considerable amount of uncertainty involved in the parameterization. We therefore examined how sensitive model output was to probability of seed survival by examining values from 0.5 to 1.0 in steps of 0.1.

We estimated the seed bank size and the proportion of seeds germinating for each census from values of the number of emerging seedlings and the estimated seed survival. The number of seedlings emerging in year t is the product of the seed pool in year $t - 1$ (i.e., the number of seeds produced in year $t - 1$ and the number of seeds in the seed bank in $t - 1$), seed survival from year $t - 1$ to t, and the proportion of surviving seeds germinating at t. Using this relationship, we could estimate the proportion of seeds germinating from each census to the next. The size of

the seed pool was estimated as the product of seeds produced in previous years, seed survival estimated from Eq. 1, and the proportion of seeds not germinating. The initial number of seeds in the seed bank the first study year (2000) was not known and could not be estimated by simulations. It was instead estimated as the product of seeds produced in 1999 and seed survival estimated from Eq. 1 (0.60), plus the average seed production over all study years (as an estimate of seed production in 1998) multiplied by [0.60 × (1 – germination)]. For the calculation of the initial seed bank, germination was estimated as the average over all study years. The resulting life history transition matrices for each year and population are presented in Appendix B of the Electronic Supplementary Material, and corresponding deterministic lambda values are reported in Table 1.

We examined whether survival of established plants (seedlings and adult plants pooled) was higher in the deep-soil population Dröstorp 2 than in the thin-soil populations Tranekärr and Dröstorp 1 using χ^2-tests. This procedure generated eight tests and the resulting P values were subject to sequential Bonferroni adjustment.

Habitat transition matrices

Demographic transition probabilities are likely to vary among years depending on environmental conditions. In our simulations, we included information on temporal changes in vital rates in the form of habitat states. During

Table 1 Categories of habitat states between demographic censuses, and the deterministic growth rate (λ^{det}) with standard errors in three *Primula farinosa* populations

Population	Year	Habitat category[a]	$\lambda^{\text{det}} \pm$ SE
Tranekärr	2000–2001	Mature	1.46 ± 0.029
	2001–2002	Mature	1.14 ± 0.034
	2002–2003	Disturbance	–
	2003–2004	Recovery	–
	2004–2005	Mature	0.62 ± 0.0071
	2005–2006	Mature	0.63 ± 0.042
Dröstorp 1	2002–2003	Disturbance	–
	2003–2004	Recovery	–
	2004–2005	Recovery	–
	2005–2006	Mature	0.99 ± 0.14
Dröstorp 2	2000–2001	Mature	1.16 ± 0.032
	2001–2002	Mature	0.87 ± 0.055
	2002–2003	Disturbance	–
	2003–2004	Recovery	–
	2004–2005	Recovery	–
	2005–2006	Mature	0.74 ± 0.086

[a] Habitat categories are explained in the text

each census interval, a population is in one of K possible habitat states. The probability that the habitat shifts from state α to state β over one time step is denoted $c_{\beta\alpha}$, and is an element of a habitat transition matrix c. Each habitat state determines a particular life-history transition matrix A_χ. The habitat transition matrix contains the probability rules used to generate a sequence of habitat states over time, and the relative frequency of habitat states is given by its dominant right eigenvector f^*.

We constructed one habitat transition matrix for each study population. We considered each period between two censuses as a unique habitat state and categorized habitat states according to their order after disturbance, and to whether they contained flowering plants at the start of the period or not (Table 1). Our matrices have $K = 6$ possible habitat states corresponding to the six transitions 2000–2006. They were classified into three main categories: (1) disturbance states, habitat states with complete mortality of established plants; (2) recovery states, habitat states that follow disturbance and during which at least some established plants survive; and (3) mature states, habitat states during which demographic transitions from flowering plants were observed. We distinguished between recovery states and mature states because during the former the probability of the transition from seedling to vegetative plant tended to be higher than during mature states (see below) indicating differences in environmental conditions, and because in two populations it took 2 years before any reproductive plants appeared after disturbance. Each category was represented by 1- to 4-year-specific life-history transition matrices obtained from the six transitions from 2000 to 2006, resulting in a 6×6 Markov transition matrix c for each population. Because of small sample sizes, we could not construct reliable life-history transitions matrices for the Dröstorp 1 population in 2000–2001 and 2001–2002. This population is therefore represented by a 4×4 transition matrix corresponding to the four transitions from 2002 to 2006.

In all populations, the habitat state 2002–2003 belonged to the disturbance category (Table 1). If the six transitions observed in this survey is representative of the long-term dynamics of *P. farinosa* in the study area, this gives a frequency of similar catastrophic years of $1/6 \approx 0.17$. To model the long-term effect of intermittent disturbance years, we hence constructed habitat transition matrices where the disturbance state occurred with a probability of 0.17. The remaining habitat transition probabilities were generated based on the number of recovery states (i.e., habitat states that follow disturbance and during which at least some established plants survive) observed before any flowering plants appeared in the population after disturbance.

The populations varied in terms of the number of years it took until flowering plants appeared after the disturbance in 2002–2003 (Table 1). The habitat transition matrices are therefore specific for each population (Appendix C in the Electronic Supplementary Material). In the Tranekärr population, the disturbance in 2002–2003 was followed by a recovery state during which reproductive plants appeared, while in the Dröstorp 1 and 2 populations, reproductive plants did not appear until 2 years after this disturbance. Four different mature transitions were recorded in the Tranekärr population, one in the Dröstorp 1 population, and three in the Dröstorp 2 population (Table 1).

Stochastic models of population dynamics

To model stochastic population dynamics we used MAT-LAB-scripts (adjusted from C.C. Horvitz, personal communication) and followed the methods suggested by Tuljapurkar et al. (2003) and Horvitz et al. (2005). The population size by stage at time t is enumerated in a vector, $N(t)$, and is governed by the following equation (Tulja-purkar et al. 2003):

$$N(t) = X(t)N(t-1) \tag{2}$$

where the random life-history transition matrix $X(t)$ takes on values determined by the habitat state between time $t-1$ and time t. The total population size $P(t)$ is the sum of the elements of vector $N(t)$ and depends on previous habitat states in the population. The stochastic growth rate is obtained from the following equation (Tuljapurkar et al. 2003):

$$\log \lambda_S = \lim_{t \to \infty} (1/t) \log[P(t)/P(0)] \tag{3}$$

We obtained mean stochastic growth rates from simulations with 100,000 time steps (Caswell 2001; Tuljapurkar et al. 2003). We also quantified deterministic growth rate for mature habitat states.

We further examined the sensitivity of fitness to changes in life-history transitions for different habitat states. The effects of perturbations of a given life-history transition on the stochastic growth rate, λ_S, may vary among habitat states (Tuljapurkar et al. 2003) as described by the matrices of habitat-stage elasticities, E_β^S, where β is a habitat state. Stochastic elasticity, E^S is the sum of habitat-stage elasticities, E_β^S, over habitats, and quantifies the importance of individual life-history transitions for population growth rate (Caswell 2001; Horvitz et al. 2005). Habitat elasticity is the sum of all E_β^S for a given habitat, and reflects its relative frequency (Horvitz et al. 2005). The magnitude of a given habitat-stage elasticity is a function of the habitat elasticity, and the relative contribution of individual life-history transition rates to the habitat elasticity (Horvitz et al. 2005). In our study, we had four to six different habitat states for each population and hence four to six

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different matrices of habitat-stage elasticities, E_β^S. Habitat-stage elasticities were estimated from numerical simulations of 2,000 time steps.

Plant survival, weather and climate change

To assess the effect of weather-induced environmental conditions on variation in survival, we correlated plant survival with summer precipitation (June–August) in the previous year. The habitats of *P. farinosa* on Öland may dry out towards the end of the summer and this is likely to expose the plants to drought stress. The rate at which the soil dries out should be a function of the cumulative precipitation during the summer months (June–August), and low precipitation during this period may reduce survival in many local plant species in late summer (Sterner and Lundqvist 1986; Andersson 1988; Bengtsson 1993; Rosén 1995). Hence, cumulative precipitation during June–August in year t is important for survival until the next year, which is recorded at census $t + 1$. Precipitation was expressed as the rainfall anomaly index based on data recorded by the Swedish Meteorological and Hydrological Institute's (SMHI) weather station at the southern tip of the island, about 45 km south of the study sites. This index makes use of a ranking procedure to assign magnitudes to precipitation anomalies (van Rooy 1965; Keyantash and Dracup 2002). One estimate of survival was removed from the analysis because it was based on very few observations (survival 2000–2001 at Dröstorp 1, $n = 12$).

To document the historical frequency of years with a RAI as low or lower than in 2002, data on monthly total precipitation for the years 1950–2005 were obtained from the SMHI weather station.

To explore how an altered disturbance frequency, e.g., due to climate change, would affect population dynamics, we obtained stochastic growth rates for each population for scenarios in which the catastrophic year frequency was decreased by 50%, to 0.085, or doubled, to 0.34. We then compared the results of these simulations with those based on the observed frequency of catastrophic years (=0.17, see above).

Results

Population dynamics under current conditions

Survival of established plants varied among years and deterministic population growth rates varied among mature habitat transitions. In the disturbance year 2002, all seedlings, vegetative rosettes, and flowering rosettes died in all populations after the census in June, i.e., only newly emerged seedlings were observed at the census in June

2003. In the other years, survival varied among populations and life-history stages (Appendix B in the Electronic Supplementary Material). Survival was higher in the deep-soil population Dröstorp 2 than in the thin-soil population Tranekärr following the summer with the second lowest precipitation (2005), and also following the summers 2001 and 2004 (χ^2-tests, $P < 0.05$ after sequential Bonferroni adjustment; Fig. 2). Following the summer 2001, survival in Dröstorp 2 was also higher than in the Dröstorp 1 population (χ^2-tests, $P < 0.05$ after sequential Bonferroni adjustment; Fig. 2).

In all models, the stochastic growth rate λ_S was less than 1, indicating that population sizes are likely to decline under current conditions. In models with the observed disturbance year frequency (0.17), the stochastic growth rate was very similar among populations and varied from 0.81 in the Dröstorp 1 and Tranekärr populations to 0.78 in the Dröstorp 2 population (Table 2).

According to the simulation models, seeds made up the major proportion of individuals present in all populations. On average, 93% of all individuals were seeds at a given time in the Tranekärr population, whereas the corresponding figures in the Dröstorp 1 and Dröstorp 2 populations were 68 and 96%, respectively.

In all populations and for all habitats, the stochastic growth rate was very sensitive to changes in regeneration, quantified as the production, survival, and germination of seeds. In the Tranekärr population, regeneration elasticity summed across habitat transitions accounted for 72.6% of total elasticity (regeneration elasticity defined as the sum of the elasticities of seed production, seed survival, and seed germination; Fig. 3; Appendix D in the Electronic Supplementary Material). In the Dröstorp 1 and Dröstorp 2 populations, the corresponding figures were 63.1 and 77.3%, respectively (elasticities for individual transitions not shown).
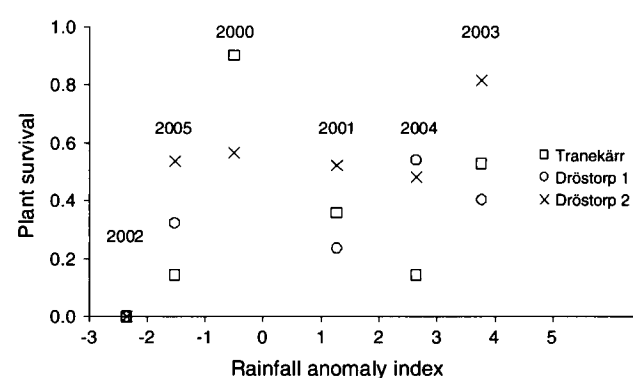

Fig. 2 The proportion of established plants (seedlings and adult plants pooled) that survived to the next census in *P. farinosa* populations Tranekärr (*open squares*), Dröstorp 1 (*open circles*), and Dröstorp 2 (*crosses*) as a function of the rainfall anomaly index based on summer (June–August) precipitation ($n = 77$–2,469)

Table 2 Stochastic growth rate, λ_S, of three *P. farinosa* populations estimated with simulations based on the observed, 50% of the observed and 200% of the observed frequency of disturbance years during the study period

Drought year frequency	Population		
	Tranekärr	Dröstorp 1	Dröstorp 2
50% of observed	0.85	0.89	0.86
Observed	0.81	0.81	0.78
200% of observed	0.74	0.67	0.68

Mean stochastic growth rates were calculated from 100,000 time steps

In all habitats, seed survival contributed most to regeneration elasticity, and its contribution increased with increasing frequency of disturbance years (Appendix D in the Electronic Supplementary Material), and remained high for all modelled values of seed bank survival (Appendix E in the Electronic Supplementary Material). In the Tranekärr and Dröstorp 2 populations, the transition from seedling to reproductive adult (a_{42}, Fig. 1) also had high elasticity (13.1 and 11.1%, respectively). In the Dröstorp 1 population, the transition from vegetative to reproductive adult (a_{43}, Fig. 1) had high elasticity (14.2%). Variation in habitat-stage regeneration elasticities among modeled disturbance-year frequencies was due mainly to variation in the relative magnitude of habitat elasticities, i.e., the relative frequency of the different habitat transitions (Fig. 3).

Plant survival, weather and climate change

The regression of plant survival on rainfall anomaly index in the previous year was not statistically significant (generalized linear model with binomial error distribution, separate for each study site, $P > 0.1$ in all cases). However, the massive mortality of seedlings and mature plants between the censuses of 2002 and 2003 (Fig. 2) coincided with the driest summer during the study period (Fig. 4). In 2002, only 77 mm rain was recorded during the 3 months of summer, corresponding to an index value of -2.34, and the little rain that did come was recorded in June and July (June 26 mm, July 50 mm, August 0 mm). For years with a summer precipitation greater than that observed in 2002, no trend towards an increase in survival with increasing precipitation was observed (Fig. 2).

Simulations showed that the stochastic growth rate decreased strongly with increased frequency of disturbance years in all populations (Table 2). They further indicated that λ_S was affected more strongly by the frequency of disturbance years in the Dröstorp 1 and 2 populations than in the Tranekärr population.

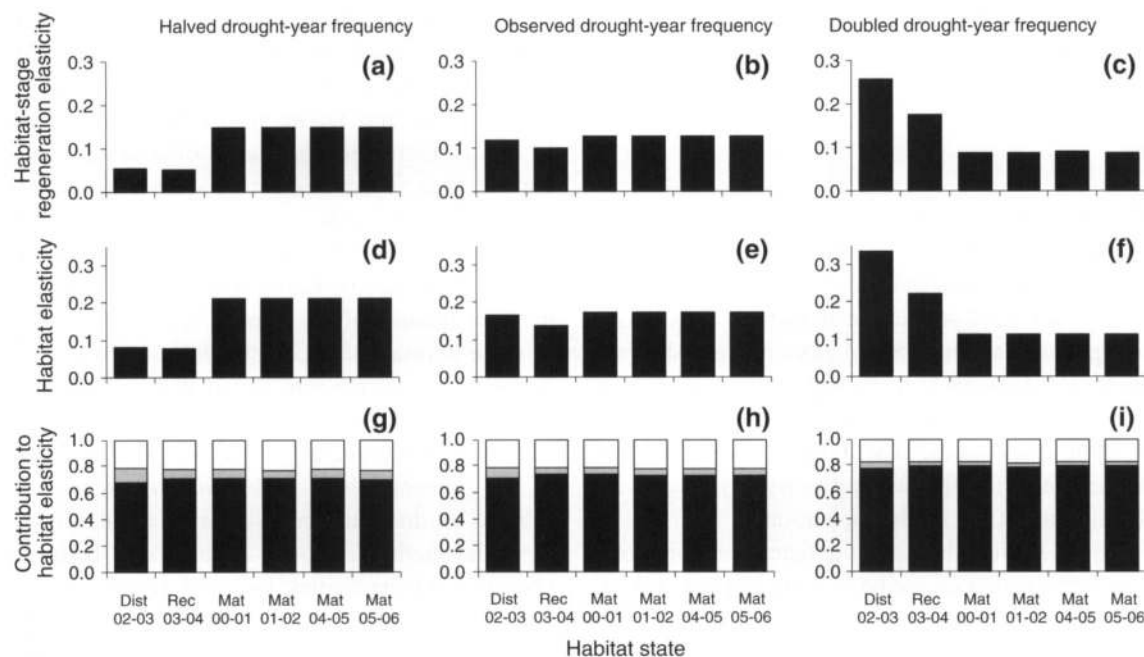**Fig. 3 a–i** Habitat-stage elasticity for regeneration (summed across all relevant life stages: fecundity, seed survival in the seed bank, and germination) and its two components for the Tranekärr population. Graphs illustrate results of simulations based on **a, d, g** halved disturbance frequency (0.085); **b, e, h** the frequency of disturbance observed during the study years (0.17); and **c, f, i** doubled disturbance frequency (0.34). *Top panels* Habitat-stage regeneration elasticity, *middle panels* habitat elasticity, *bottom panels* proportional contribution to habitat elasticity from regeneration (*black*), stasis (*grey*), growth (*white*), and retrogression (too small to be visible in **a–f**). Habitat transitions are named according to category (disturbance, recovery or mature) and the year in which they were observed. In all habitats, regeneration contributes most to total elasticity as seen in the bottom graphs, and its relative contribution increases with increasing frequency of disturbance years. The relationships among habitat-stage elasticities were similar in the two other study populations
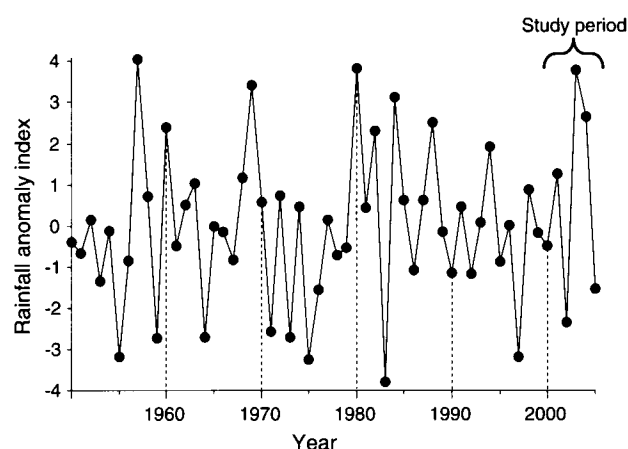
Fig. 4 The rainfall anomaly index based on summer precipitation (June–August) at the southern tip of Öland in 1950–2005. The period of the present study is indicated

Regeneration remained a major determinant of plant fitness at all modelled disturbance year frequencies (Fig. 3; Appendix D in the Electronic Supplementary Material). The relative importance of regeneration compared to other life-history transitions for stochastic growth rate was largest in the models with doubled disturbance year frequency and lowest in the models with halved disturbance year frequency (Fig. 3; Appendix D in the Electronic Supplementary Material). In all scenarios, seed survival contributed most to regeneration elasticity.

Discussion

This 7-year study demonstrates how data on variation in vital rates and environmental conditions summarized in life-history and habitat transition matrices can be combined to explore and simulate population dynamics in variable and changing environments. Simulation models showed that an increased frequency of disturbance years would reduce population growth rate and increase the importance of regeneration from seeds. The results suggest that a predicted increase in the frequency of very dry years will reduce the viability of the study populations.

This study indicates that seed dynamics (formation, survival and germination of seeds) is more important than survival of seedlings and adult plants for population growth of *P. farinosa* at the examined sites, and that seed production thus strongly contributes to plant fitness. Moreover, the habitat-stage regeneration elasticities increased with increasing frequency of disturbance years, indicating that the importance of regeneration for plant fitness would increase in populations subject to more frequent disturbance years. In the Tranekärr and Dröstorp 2 populations, rapid development from seedling to reproductive adult was

also favoured as indicated by the high elasticity of this transition. By comparison, plant survival was higher and the establishment of new plants less important for the dynamics of six populations studied in mainland habitats (Lindborg and Ehrlén 2002). Franco and Silvertown (2004) found that regeneration was less important than survival and growth for population growth rate in a meta-analysis of 102 perennial plant species. Their study was conducted on vital rate elasticities, while we estimated matrix element elasticities. However, Silvertown et al. (1993) similarly concluded that regeneration was less important than survival and growth for population growth rate in a meta-analysis based on matrix element elasticities. In our simulations, the frequency of disturbance years affected habitat-stage regeneration elasticities almost exclusively through its effect on habitat elasticities, i.e., the relative frequency of the different habitat transitions. In all habitats and at all modelled frequencies of disturbance, the production, survival and germination of seeds made the largest contributions to population growth rate. We made the simplifying assumption that survival rates of seeds and seedlings are equal during the period from seedling emergence in spring to the census in June. If survival of seeds is higher than survival of seedlings during this period, then our estimate of the elasticity for seed bank survival may be underestimated and its importance thus somewhat higher.

The increase in habitat-stage regeneration elasticity with increasing frequency of disturbance years was mainly an effect of an increase in stochastic elasticity for seed survival (Appendix D in the Electronic Supplementary Material). Increased importance of seed bank dynamics in the presence of environmental stochasticity has similarly been predicted in other studies (Cohen 1966, 1967; Kalisz and McPeek 1993; Menges and Quintana-Ascencio 2004; Adams et al. 2005). Kalisz and McPeek (1993) predicted that populations of the annual herb *Collinsia verna* that produce dormant seeds can be buffered from extinction in fluctuating environments, but that they also will grow at less than maximal rate in good years. Seed survival was suggested to be crucial for the persistence of a population of the perennial herb *Helenium virginicum*, which was subject to drought stress (Adams et al. 2005). In the perennial herb *Eryngium cuneifolium*, both population viability and elasticities for seed germination were predicted to increase with increasing frequency of fire (Menges and Quintana-Ascencio 2004). Hence, it seems clear that survival in the seed bank is important for the persistence of many populations of herbaceous plants subject to disturbance.

In our study, seed germination and seed survival in the seed bank was not measured directly but inferred from several years of data on seed production and seedling establishment. The parameters could be estimated with a

fairly high accuracy thanks to the lack of seed production in 2003. Moreover, simulations with other values of survival in the seed bank suggested that the conclusions concerning the relative contribution of regeneration for life-time fitness were robust. For most plant species it is very difficult to track the fate of seeds in natural populations and few studies have incorporated seed dynamics in demographic models (Adams et al. 2005). This is problematic, because if omitted life stages are important predictors of population dynamics, the resulting models can provide inaccurate assessments of the questions they are set to address (Doak et al. 2002).

Several observations suggest that the massive mortality observed in 2002–2003 was caused by drought. Many plant species in the area, including *P. farinosa*, showed clear signs of desiccation (J.Å., J.E. and P.T., personal observation). Moreover, between 2002 and 2003, 94% of the *P. farinosa* populations in the area decreased in size, indicating that an environmental factor acting over a large spatial scale was responsible for the high mortality ($n = 77$ populations monitored in a 10 × 4 km large area in the northern part of the Great Alvar; J.Å. and J.E., unpublished data). That *P. farinosa* is negatively affected by extended periods of drought is not surprising given that it thrives in more stable moist soil conditions in other areas (cf. Hambler and Dixon 2003). The study area is characterized by thin soils on weathered limestone bedrock, and precipitation and water availability in summer has been suggested to limit population growth of many local plant species (Sterner and Lundqvist 1986; Andersson 1988; Bengtsson 1993; Rosén 1995). During the period 1950–2005, summers with a rainfall anomaly index lower than 2, i.e., similar to or lower than that of 2002, have occurred nine times in the area (Fig. 3). This means that the frequency of similar drought years, $9/56 \approx 0.16$, is very similar to the observed frequency of disturbance years during the study period, 0.17. If our interpretation is correct and the observed mortality was due to drought, populations are expected to decline in response to predicted future increases in the frequency of very dry years.

Beyond the fact that the massive mortality between censuses 2002 and 2003 was associated with the lowest summer precipitation observed during the study period, summer precipitation could not explain a significant portion of the among-year variation in mortality. It is possible that drought-related mortality of *P. farinosa* increases drastically in years when summer precipitation is below a certain threshold value. However, it is also clear that additional factors contribute to among-year variation in mortality in *P. farinosa* and that the importance of drought-related mortality may vary among environments. As expected, survival after the dry summer of 2005 tended to be higher in the deep-soil Dröstorp 2 population than in the

two populations on thin soil (Fig. 2). Vital rates varied considerably among years in the examined populations (Table 1). By comparison, only limited among-year variation in deterministic population growth rate was documented in a 4-year study conducted in six populations on the Swedish mainland (Lindborg and Ehrlén 2002). The relatively stable population dynamics found in that area may at least in part be due to lower among-year variation in water availability because of deeper soils and generally higher precipitation. Future studies should test the prediction that increased among-year variation in precipitation is less important for the population dynamics of *P. farinosa* and other perennial herbs in mesic habitats than in the shallow-soil alvar habitats of the present study. We collected demographic data for 7 years, which is rather long compared to most demographic studies of plants, but still short when it comes to establishing the relationships between environmental variables and vital rates. To determine the causes of mass mortalities such as those observed between 2002 and 2003, it would be necessary to collect demographic data over an even longer period of time and to combine this information with records of local environmental conditions, observations of environmentally induced plant damage, and experimental manipulation of water availability.

The present study adds to the growing number of papers published in recent years that attempt to forecast the effect of global change on plant population dynamics. For example, Adler and HilleRisLambers (2008) showed that increased mean temperatures are likely to influence growth rates of several herbaceous species. Levine et al. (2008) demonstrated that temperatures and timing of major rainfalls may affect population persistence in three annual plants, and Lucas et al. (2008) similarly showed that the seasonal timing of precipitation events may be important for population dynamics in the perennial herb *Cryptantha flava*. At the community level, Keith et al. (2008) modelled extinction risks under stable and changing climate scenarios in the South African fynbos, and Post and Pedersen (2008) demonstrated that herbivores may influence the response of plant communities to climate change. The present study and that of Adler and HilleRisLambers (2008) are unique in that they directly link plant demography to climatic data to predict future scenarios by simulations. Linking climatic factors to demographic parameters may increase our chances of formulating effective measures for the management of plant populations in the face of global change.

To conclude, our study illustrates how the limited demographic and environmental data typically available for natural populations can be combined to examine population viability under environmental change. In the study system, simulations indicated that population growth rate is very sensitive to changes in transition probabilities in the

seed bank. They further indicated that population size would decline and the importance of seed dynamics would increase, with an increased frequency of dry years. The approach undertaken in this study provides a powerful tool to predict population viability in environments that undergo directional change.

References

Adams VM, Marsh DM, Knox JS (2005) Importance of the seed bank for population viability and population monitoring in a threatened wetland herb. Biol Conserv 124:425–436

Adler PB, HilleRisLambers J (2008) The influence of climate and species composition on the population dynamics of ten prairie forbs. Ecology 89:3049–3060

Ågren J, Fortunel C, Ehrlén J (2006) Selection on floral display in insect-pollinated *Primula farinosa*: effects of vegetation height and litter accumulation. Oecologia 150:225–232

Andersson S (1988) Limiting factors on seed production in *Crepis tectorum* ssp. *pumila*. Acta Phytogeogr Suec 76:9–20

Beckage B, Gross LJ, Platt WJ (2006) Modelling responses of pine savannas to climate change and large-scale disturbance. Appl Veg Sci 9:75–82

Bengtsson K (1993) *Fumana procumbens* on Öland—population dynamics of a disjunct species at the northern limit of its range. J Ecol 81:745–758

Boyce MS, Haridas CV, Lee CT, NCEAS Stochastic Demography Working Group (2006) Demography in an increasingly variable world. Trends Ecol Evol 21:141–148

Caswell H (2001) Matrix population models: construction, analysis, and interpretation, 2nd edn. Sinauer, Sunderland

Cohen D (1966) Optimizing reproduction in a randomly varying environment. J Theor Biol 12:119–129

Cohen D (1967) Optimizing reproduction in a randomly varying environment when a correlation may exist between the conditions at the time a choice has to be made and the subsequent outcome. J Theor Biol 16:1–14

Doak DF, Thomson D, Jules ES (2002) Population viability analysis for plants: understanding the demographic consequences of seed banks for population health. In: Beissinger SR, McCullough DR (eds) Population viability analysis. The University of Chicago Press, Chicago

Ehrlén J, Lehtilä K (2002) How perennial are perennial plants? Oikos 98:308–322

Franco M, Silvertown J (2004) A comparative demography of plants based upon elasticities of vital rates. Ecology 85:531–538

Gotelli NJ, Ellison AM (2006) Forecasting extinction risk with nonstationary matrix models. Ecol Appl 16:51–61

Gross K, Lockwood JR III, Frost CC, Morris WF (1998) Modelling controlled burning and trampling reduction for conservation of *Hudsonia montana*. Conserv Biol 12:1291–1301

Hambler DJ, Dixon JM (2003) Biological flora of the British islands: *Primula farinosa* L. J Ecol 91:694–705

Horvitz CC, Pascarella JB, McMann S, Freedman A, Hofstetter RH (1998) Functional roles of invasive, non-indigenous plants in hurricane-affected subtropical hardwood forests. Ecol Appl 8:947–974

Horvitz CC, Tuljapurkar S, Pascarella JB (2005) Plant–animal interactions in random environments: habitat-stage elasticity, seed predators, and hurricanes. Ecology 86:3312–3322

Hubbell SP, Foster RB, O'Brien S, Wechsler B, Condit R, Harms K, Wright SJ, Loo de Lau S (1999) Light gaps, recruitment limitation and tree diversity in a Neotropical forest. Science 283:554–557

Kalisz S, McPeek MA (1993) Extinction dynamics, population growth and seed banks: an example using an age-structured annual. Oecologia 95:314–320

Keith DA, Akcakaya HR, Thuiller W, Midgley GF, Pearson RG, Phillips SJ, Regan HM, Araujo MB, Rebelo TG (2008) Predicting extinction risks under climate change: coupling stochastic population models with dynamic bioclimatic habitat models. Biol Lett 4:560–563

Keyantash J, Dracup JA (2002) The quantification of drought: an evaluation of drought indices. Bull Am Meteorol Soc 83:1167–1180

Kjellström E, Bärring L, Hansson U, Jones C, Samuelsson P, Rummukainen M, Ullerstig A, Willén U, Wyser K (2005) A 140-year simulation of European climate with the new version of the Rossby Centre regional atmospheric climate model (RCA3). SMHI Reports Meteorology and Climatology No. 108, SMHI, Norrköping, Sweden

Lagerberg T (1948) Vilda växter i Norden, 2nd edn. Natur och Kultur, Stockholm

Levine JM, McEachern AK, Cowan C (2008) Rainfall effects on rare annual plants. J Ecol 96:795–806

Lindborg R, Ehrlén J (2002) Evaluating the extinction risk of a perennial herb: demographic data versus historical records. Conserv Biol 16:683–690

Lindenmayer D, Hobbs RJ, Montague-Drake R, Alexandra J, Bennett A, Burgman M, Cale P, Calhoun A, Cramer V, Cullen P, Driscoll D, Fahrig L, Fischer J, Franklin J, Haila Y, Hunter M, Gibbons P, Lake S, Luck G, MacGregor C, McIntyre S, Mac Nally R, Manning A, Miller J, Mooney H, Noss R, Possingham H, Saunders D, Schmiegelow F, Scott M, Simberloff D, Sisk T, Tabor G, Walker B, Wiens J, Woinarski J, Zavaleta E (2008) A checklist for ecological management of landscapes for conservation. Ecol Lett 11:78–91

Lucas RW, Forseth IN, Casper BB (2008) Using rainout shelters to evaluate climate change effects on the demography of *Cryptantha flava*. J Ecol 96:514–522

Maschinski J, Baggs JE, Quintana-Ascencio PF, Menges ES (2006) Using population viability analysis to predict the effects of climate change on the extinction risk of an endangered limestone endemic shrub, *Arizona cliffrose*. Conserv Biol 20:218–228

McCarty JP (2001) Ecological consequences of recent climate change. Conserv Biol 15:320–331

Menges ES, Quintana-Ascencio PF (2004) Population viability with fire in *Eryngium cuneifolium*: deciphering a decade of demographic data. Ecol Monographs 74:79–99

Morris WF, Tuljapurkar S, Haridas CV, Menges ES, Horvitz CC, Pfister CA (2006) Sensitivity of the population growth rate to demographic variability within and between phases of the disturbance cycle. Ecol Lett 9:1331–1341

Morris WF, Pfister CA, Tuljapurkar S, Haridas CV, Boggs CL, Boyce MS, Bruna EM, Church DR, Coulson T, Doak DF, Forsyth S, Gaillard J-M, Horvitz CC, Kalisz S, Kendall BE, Knight TM, Lee CT, Menges ES (2008) Longevity can buffer plant and animal populations against changing climatic variability. Ecology 89:19–25

Mouillot F, Rambal S, Joffre R (2002) Simulating climate change impacts on fire frequency and vegetation dynamics in a Mediterranean-type ecosystem. Glob Change Biol 8:423–437

Parmesan C (2006) Ecological and evolutionary responses to recent climate change. Annu Rev Ecol Evol Syst 37:637–669

Post E, Pedersen C (2008) Opposing plant community responses to warming with and without herbivores. Proc Natl Acad Sci USA 105:12353–12358

Rosén E (1982) Vegetation development and sheep grazing in limestone grasslands of south Öland, Sweden. Acta Phytogeogr Suec 72:1–104

Rosén E (1995) Periodic droughts and long-term dynamics of alvar grassland vegetation on Öland, Sweden. Folia Geobot Phytotax 30:131–140

Rosén E, Borgegård S-O (1999) The open cultural landscape. Acta Phytogeogr Suec 84:84–134

Rowell DP (2005) A scenario of European climate change for the late twenty-first century: seasonal means and interannual variability. Clim Dyn 25:837–849

Silvertown J, Franco M, Pisanty I, Medoza A (1993) Comparative plant demography–relative importance of life-cycle components to the finite rate of increase in woody and herbaceous perennials. J Ecol 81:465–476

Sitch S, Smith B, Prentice IC, Arneth A, Bondeau A, Cramer W, Kaplan JO, Levis S, Lucht W, Sykes MT, Thonicke K, Venevsky S (2003) Evaluation of ecosystem dynamics, plant geography and terrestrial carbon cycling in the LPJ dynamic global vegetation model. Glob Change Biol 9:161–185

Smith M, Caswell H, Mettler-Cherry P (2005) Stochastic flood and precipitation regimes and the population dynamics of a threatened floodplain plant. Ecol Appl 15:1036–1052

Sterner R, Lundqvist Å (1986) Ölands kärlväxtflora, 2nd edn. Forskningsrådens förlagstjänst, Stockholm, Sweden

Thomas CD, Cameron A, Green RE, Bakkenes M, Beaumont LJ, Collingham YC, Erasmus BFN, de Siqueira MF, Grainger A, Hannah L, Hughes L, Huntley B, van Jaarsveld AS, Midgley GF, Miles L, Ortega-Huerta MA, Peterson AT, Phillips OL, Williams SE (2004) Extinction risk from climate change. Nature 427:145–148

Thuiller W, Albert C, Araújo MB, Berry PM, Cabeza M, Guisan A, Hickler T, Midgley GF, Paterson J, Schurr FM, Sykes MT, Zimmermann NE (2008) Predicting global change impacts on plant species' distributions: future challenges. Perspect Plant Ecol Evol Syst 9:137–152

Toräng P, Ehrlén J, Ågren J (2010) Habitat quality and among-population differentiation in reproductive effort and flowering phenology in the perennial herb *Primula farinosa*. Evol Ecol. doi:10.1007/s10682-009-9327-z

Tuljapurkar S, Horvitz CC, Pascarella JB (2003) The many growth rates and elasticities of populations in random environments. Am Nat 162:489–502

Van Rooy MP (1965) A rainfall anomaly index independent of time and space. Notos 14:43–48