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SPECIAL FEATURE

ADVANCES IN PLANT DEMOGRAPHY USING MATRIX MODELS

Keeping plant shrinkage in the demographic loop

Roberto Salguero-Gómez* and Brenda B. Casper

Department of Biology, University of Pennsylvania, 215 South University Avenue, 321 Leidy Laboratories, Philadelphia, PA 19104, USA

Summary

1. Plant demographers using matrix tools have paid special attention to vital rates of reproduction, growth and survival. The demographic implications of plants regressing in size, or shrinking, have been overlooked. Shrinkage has either been ignored during demographic censuses or lumped with other demographic processes such as stasis or growth under the assumption that they have similar demographic effects.

2. We carried out a comparative prospective analysis using classical vital rate elasticities in size-based projection matrices of 80 herbaceous perennial species. We analysed the correlations of the elasticities of each demographic vital rate with the demographic life-history traits (life span, population growth rate, etc.).

3. We also conducted a comparative loop analysis to understand the effects of shrinkage on demographic parameters linked to size plasticity. We classified loops into 'recruitment' (growth that contributes to reproduction), 'size plasticity' (where individuals fluctuate in size) and 'size rigidity' (no change in size class), and used them as the basis to explain ecological characteristics of the species.

4. Our results with classical vital rates demonstrate that considering shrinkage as a separate vital rate increases our understanding of factors that contribute to demographic equilibrium (e.g. minimized departure from population growth rate at equilibrium) and buffering (e.g. higher speed of recovery after disturbance), and to reproductive strategies (e.g. mean age of parents of offspring).

5. The loop analysis results support the findings with vital rate analyses and also reveal new patterns: high growth rates are not exclusively dominated by high elasticities of recruitment, but also by size-plastic loops, and long-lived species experience a marginal increase in the demographic importance of size plasticity.

6. *Synthesis*. This study illustrates the necessity for exploring individual demographic vital rates, as opposed to grouping them, to advance our understanding of how different biological processes affect population dynamics. Shrinkage is demographically important because it aids in demographic buffering, increases survival and is related to maintenance–reproduction trade-offs. However, shrinkage cannot be fully explored only with traditional elasticity approaches; because shrinkage for some species is a fundamental plastic trait, its importance is more appropriately captured with loop analyses.

Key-words: comparative plant demography, damping ratio, life span, matrix dimension, plant shrinkage, population growth rate (λ), projection matrix models, size phenotypic plasticity

> "*To return to the origin is not to regress*"
> Dani Carbonell, 2007

Introduction

Phenotypic plasticity, the ability of an organism to modify its physiology or morphology in response to environmental variation (Schlichting 1986), is an extremely prolific area of ecological research. Such adjustments hold particular importance for plants because of plants' sessile habit and modular, ever-changing architecture (Cook & Johnson 1968; Dodd *et al*. 2002). Although we are still far from a complete understanding of the genetic and environmental controls of phenotypic plasticity in plants, an elegant theoretical framework has been put together concerning its evolutionary implications (Bradshaw 1984; Schlichting 1986; Schmid 1992; Pigliucci,

*Correspondence author. E-mail: salguero@sas.upenn.edu

Murren & Schlichting 2006; Magyar *et al.* 2007). Theoretical considerations of plasticity have also been extended to demography (Caswell 1983; Tuljapurkar 1989; Caswell & Trevisan 1994; McNamara & Houston 1996), but empirical studies linking plasticity with its demographic consequences are still lacking.

One feature of plasticity that is likely to play a crucial role in population dynamics is the ability of individuals to fluctuate in size – through both growth and shrinkage. Such ability is adaptive in a number of animal species (Ebert 1967; Levitan 1988; Marinovic & Mangel 1999; Wikelski & Thom 2000). For plants, its implications would expectedly be greater, given their higher degree of modularity (Kozlowski 1973; White 1979). Especially in perennials, whose life spans can encompass considerable year-to-year environmental variation, shrinkage could have significant demographic ramifications for several reasons. First, shrinkage might affect plant fitness because size, its best predictor (Silvertown & Charlesworth 2001), is often correlated with reproductive output and probability of survival (Harper 1977; but see Aarsen 2008). Secondly, shrinkage, if adaptive, might allow plants to achieve greater longevity (Horvitz & Schemske 1995; Morris & Doak 1998). Thirdly, shrinkage could be an indirect cost of reproduction (Bierzychudek 1982). And finally, shrinkage might reflect a decay of an individual's performance throughout plant senescence (Inghe & Tamm 1985; Roach 2001).

A link between size plasticity and plant demography can be easily instituted using projection matrix approaches, where some of the matrix elements may represent size retrogression probabilities (i.e. shrinkage), and other matrix elements may represent progression probabilities (growth). However, despite the fact that shrinkage is often recorded in size-based projection matrices, its implications are seldom discussed (see survey in Appendix S1 in Supporting Information). Overlooking shrinkage in projection matrices can be attributed to four factors. First, its demographic importance, as estimated with classical prospective analyses (i.e. elasticity *sensu* de Kroon *et al.* 1986; Caswell 2000), ranks among the lowest of all demographic vital rates (Fig. 1). Secondly, ecologists have typically focused only on the factors that increase plant fitness over the short term and, because class-specific survival and reproduction are almost always greater in larger individuals, shrinkage has been regarded as the antithesis of fitness (Caswell 2001, p. 220; Fig. 1). Thirdly, some matrix models merge shrinkage with plant fission, sexual and/or clonal reproduction in the same matrix elements, which makes it difficult to study shrinkage separately (e.g. Dixon & Cook 1990; O'Connor 1993; Freville & Silvertown 2005; Jongejans & de Kroon 2005). Finally, comparative studies utilizing population projection matrices often obscure the demographic effects of shrinkage by combining size retrogression and other matrix elements, such as stasis or positive growth, in the same category.

In their seminal paper, where they used projection matrices for comparative purposes, Silvertown, Franco & McConway (1992) combined the matrix element elasticities of retrogression with stasis (L), fertility (F) and growth (G) for plant demographic dynamics according to Grime's (1977) ecological strategies: stress tolerant ($S = L$), ruderal ($R = F$) and competitor ($C = G$). In later contributions, the matrix element elasticities were decomposed into their underlying vital rate elasticities (Zuidema & Franco 2001; Franco & Silvertown 2004), and negative and positive growth were then combined in the same demographic process (hereby *bi-directional growth*). These approaches have since been successfully implemented in a number of intraspecific (Valverde & Silvertown 1998; Menges & Quintana-Ascencio 2004) and interspecific studies (Silvertown *et al.* 1993; Marcante, Winkler & Erschbamer 2009), but neither the lumping of shrinkage with stasis in matrix element elasticities, nor the addition of shrinkage with growth permits a clear evaluation of the importance of shrinkage *per se* or in the context of size plasticity. The latter is true because a percentage of the growth elasticities lumped with shrinkage do not actually contribute to size plasticity, but to the achievement of the minimum size necessary for reproduction.

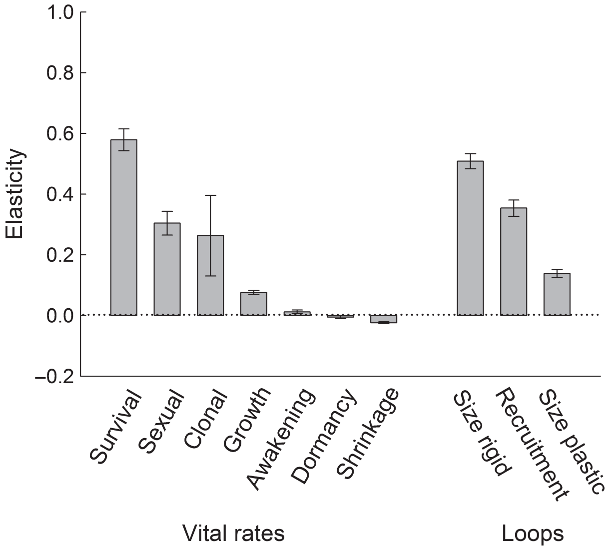

Fig. 1. Averaged ($\bar{x} \pm$ SE) ranked vital rate elasticities and loop elasticities for the 80 herbaceous perennial species studied, including sexual and clonal reproduction. Note that not all species had sexual reproduction ($n = 77$), clonal reproduction ($n = 7$) or vegetative dormancy-awakening ($n = 8$).

In this study, we use size-based population projection matrices of 80 herbaceous perennial species to explore the implications of plant shrinkage on plant demographic dynamics in general and on size plasticity in particular. We employ classical elasticity analysis (de Kroon *et al.* 1986) as well as loop analysis (van Groenendael *et al.* 1994), where the contributions to the population are integrated into full life-history pathways (de Kroon, van Groenendael & Ehrlen 2000), to ask: (i) do the components of bi-directional growth (growth and shrinkage) have demographically similar effects, and can they, therefore, be lumped? (ii) how do population-level demographic parameters and other vital rates relate to shrinkage? and (iii) what is the demographic importance of fluctuations in size?

Materials and methods

DATA BASE ACQUISITION AND STANDARDIZATION

We assembled a data base of published projection matrices and associated relevant ecological information for herbaceous perennial plant species. We focused solely on non-succulent herbaceous perennials to compare plants of similar growth forms and life histories, and because we expected higher incidence of documented plant shrinkage and greater size plasticity in demographic traits among herbaceous compared to woody plants. We systematically searched the plant demography literature from 1980 to 2009 using BIOSIS, ISI Web of Science, AGRICOLA and SCOPUS (keywords: 'plant population', 'projection OR transition AND matrix', 'life table response analysis OR LTRE', 'population viability analysis OR PVA', 'population growth rate', and 'elasticity') for manuscripts containing projection matrices on herbaceous plant species' populations, or life tables from which projection matrices could be constructed. We obtained matrices for additional species from a pre-existing data base (M. Franco, pers. comm.) and from unpublished studies (see Acknowledgements). We calculated the element-by-element arithmetic average projection matrix for each species for all its field sites and years of census (see Appendix S1), which has been identified as the best approach to characterize species demographically (Tuljapurkar & Caswell 1996). We only considered those matrices constructed from populations under natural conditions, without experimental manipulations such as grazing or artificial climate treatments. When multiple studies reported matrix models for the same species, we used the one with the highest number of size-based classes, spatial replication and sampling length (e.g. Ehrlén *et al.* 2005; Lehtilä *et al.* 2006). In some study species, the class-specific mortalities were negative, which is biologically impossible, and we learned from the authors that expedited sexual reproduction (where some new recruits grow to advanced classes within the year of recruitment) and/or clonal reproduction and shrinkage events had been added and modelled together. Therefore, we only included the species in which we were able to separate clearly each demographic process, which for some species involved acquiring additional unpublished data from the investigators.

We reduced the initial number of identified herbaceous perennial species from 211 to 80, belonging to 29 taxonomic families (Appendix S1) to meet necessary requirements for our comparative demographic approach. First, we considered only models based on size or size combined with age and/or developmental stage so that progression and retrogression probabilities would represent individual plant growth and shrinkage, respectively. Secondly, because matrix dimensions affect elasticities (Silvertown *et al.* 1993; Enright, Franco & Silvertown 1995; Benton & Grant 1999), we collapsed all matrices into the same dimensions to assure the posterior comparability of their elasticities with other associated demographic parameters. We chose a threshold matrix dimension of 5×5, because it is the mode of the projection matrix dimensions published for herbaceous plant species, and because this allows the matrix to include all of the possible demographic processes that can be involved in a population without having to merge any two in a single matrix element (i.e. sexual reproduction, clonal reproduction, growth, stasis, shrinkage, vegetative dormancy and awakening from dormancy; see Appendix S3.A). There were 35 species with matrices of this exact dimension, and 48 species with larger matrices that we collapsed to 5×5. We ignored three species with complex life cycles for which we could not collapse matrices without merging transition probabilities for stasis, progression and/or retrogression $p_{ij} \in \{0, 1\}$ with sexual and/or clonal reproduction $a_i \in \{0, \infty\}$.

The ideal algorithm to standardize matrix dimensionality allows collapsing matrices in the absence of raw data while maintaining their associated eigenvalues and eigenvectors almost unaltered (Hooley 2000). The criteria we used to collapse matrix classes met the preceding goal with the least effects on the associated elasticity values (R. Salguero-Gomez & J.B. Plotkin, unpubl. data). Briefly, these criteria consist of leaving early classes of the life cycle unmodified (e.g. seedling, juvenile) and collapsing larger size classes without necessarily preserving the overall class-specific residence time or keeping reproductive versus non-reproductive classes separated, unlike the procedure suggested by Enright, Franco & Silvertown (1995). For those matrices with more than one class representing seed bank or vegetative dormancy (see Appendix S1), we merged the multiple classes within each matrix to allow for a greater resolution of size fluctuation transition probabilities.

DEMOGRAPHIC IMPORTANCE OF SHRINKAGE

Because a frequent phenomenon is not necessarily an important phenomenon, the overall importance of a specific vital rate on population dynamics cannot simply be evaluated by determining its frequency, as reflected by its corresponding transition probabilities in the matrices (Aberg *et al.* 2009). Rather, its demographic importance is indicated by its elasticity, a measure of the proportional effect that an infinitesimally small change in any of the elements or group of elements of the matrix would have on the population growth rate λ (de Kroon *et al.* 1986). We opted for vital rate elasticities, as opposed to matrix element elasticities (Silvertown *et al.* 1993), since vital rates describe more accurately the fundamental demographic processes. Vital rate elasticities, which are widely applied in comparative studies (Franco & Silvertown 2004; Burns *et al.* 2010), describe the importance of underlying demographic processes ascribed to each element of a projection matrix (Zuidema & Franco 2001; Franco & Silvertown 2004). For instance, each matrix element contains a component of survival in addition to the particular demographic process it represents (e.g. growth, stasis, shrinkage, etc.). Consequently, the study of elasticities on vital rates allows us to evaluate (i) the importance (magnitude) of shrinkage, independent of the survival associated with its retrogression probabilities, (ii) its effect on other vital rate elasticities, including survival; this can be done without obtaining spurious correlations because vital rate elasticities need not all add to 1 (Zuidema & Franco 2001), and also to explore (iii) whether the magnitude of shrinkage correlates positively or negatively with the population growth rate λ (see Future Directions). Negative vital rate elasticities can happen because a small increase in the chance of shrinkage will affect not only the retrogression transition probability (increasing it) but also the stasis transition probability (decreasing it), and this leads to a reduction in λ (see Zuidema & Franco 2001). We carried out the calculations of vital rate elasticities with MatLab version 7.1 (Mathworks 2001).

We compared the frequency with which shrinkage occurs in natural populations to its elasticity ($E_{\mathrm{Shrinkage}}$ from now on). We considered shrinkage to take place in a species only when all the retrogression transition probabilities in that species' mean matrix surpassed a threshold, $\sum \sigma_j \rho_{ij} > 0.05$, where j is the class of an individual at time t before it survives (σ) and retrogresses (ρ) to class i at $t+1$, with $i < j$. On the other hand, the importance of shrinkage was evaluated in two quantitative ways. First, exploring its absolute effect alone, we established a threshold above which its elasticity was considered to be significant ($|E_{\mathrm{Shrinkage}}| > 0.05$). Secondly, we evaluated $E_{\mathrm{Shrinkage}}$ in relation to the elasticities of other vital rates for each species (E_{Survival}, E_{Growth}, E_{Dormancy} (vegetative dormancy), $E_{\mathrm{Awakening}}$ (awakening from vegetative dormancy), $E_{\mathrm{Sexual\ reprodution}}$ and $E_{\mathrm{Clonal\ reproduction}}$). For each of these vital rate elasticities, we determined the percentage of species in which the absolute effects of $E_{\mathrm{Shrinkage}}$ were significantly greater than the effects of the above-mentioned vital rates of interest ($|E_{\mathrm{Shrinkage}}|-|E_{\mathrm{Vital\ rate\ of\ interest}}| > 0$).

MATRIX ANALYSIS

For each average matrix, we calculated the main set of population-level parameters that characterize demographic dynamics. The main goal was to compare whether and how $E_{\mathrm{Shrinkage}}$ and E_{Growth}, examined separately, correlate with these population parameters: the deterministic population growth rate (λ, the dominant eigenvector of the matrix), the net reproductive rate (R_0, expected number of replacements), the generation time (T, time necessary for an increase of the population by R_0-fold), and the mean age of parents of offspring produced by a cohort over its lifetime (μ_1) (see Appendix S2). We computed these parameters using STAGECOACH version 2.3 (Cochran & Ellner 1992) and POPTOOLS version 3.0 (Hood 2003). We also examined how $E_{\mathrm{Shrinkage}}$ and E_{Growth} correlate with the main parameters of transient behaviour: the speed (ρ[1], damping ratio: the ratio of the dominant eigenvalue λ_1 to the modulus of the subdominant eigenvalue λ_2), and the period of oscillation (P_i, for the ith highest possible complex eigenvalue; Caswell 2001) with which a perturbed system returns to its dynamic equilibrium. Finally, we examined how $E_{\mathrm{Shrinkage}}$ and E_{Growth} correlate with life span, which we calculated as the number of years elapsed in order for the population to reach an unsustainable size. We did this by setting the sexual and clonal reproduction elements of the matrix to zero and cyclically multiplying up to 1000 times the projection matrix by the population vector after introducing one initial individual in the first not-seed class of the life cycle. The life span was determined by the number of cycles (years) elapsed before the total number of individuals in the resulting population vector was lower than 0.01 (Forbis & Doak 2004). Only in one case was the algorithm not able to provide a deterministic life span value (*Succisa pratensis*; Jongejans & de Kroon 2005), which we excluded from the life span analyses. Transient dynamic parameters and life span were calculated with MATLAB.

Two additional aspects must be noted regarding our calculation of vital rate elasticities. First, although the elasticities of growth and awakening from dormancy on the one hand, and of shrinkage and vegetative dormancy on the other hand, are typically lumped, respectively (Oostermeijer *et al.* 1996), we treated them independently to tease apart exclusive effects of shrinkage versus those of growth. Secondly, while we were most interested in the relationships that life span has with $E_{\mathrm{Shrinkage}}$ and with E_{Growth}, we also extended the comparisons of population-level demographic traits to the rest of vital rate elasticities (E_{Dormancy}, $E_{\mathrm{Awakening}}$, $E_{\mathrm{Sexual\ reproduction}}$ and $E_{\mathrm{Clonal\ reproduction}}$), because doing so allowed us to contrast our results with those of other comparative studies that included a variety of life-forms such as annuals, biennials, succulents, shrubs and trees (Franco & Silvertown 2004; Morris *et al.* 2008).

We also asked whether life span correlated differently with population-level parameters (λ, T, R_0, μ_1, ρ and P_i) for species with shrinkage ($\sum \sigma_j \rho_{ij} > 0.05$, where the ρ_{ij}s are retrogression transition probabilities) and species without shrinkage by comparing the slopes and intercepts of linear regressions. Similarly, we examined the correlation between life span and the deviation of the population growth rate from equilibrium, expressed as the absolute value of the difference of each growth rate from $\lambda = 1$ (i.e. $|1-\lambda|$).

We evaluated the appropriateness of lumping $E_{\mathrm{Shrinkage}}$ with E_{Growth} by comparing the direction (positive/negative) and significance of Spearman rank correlation coefficients of these vital rate elasticities first separately and then lumped into $E_{\mathrm{Bi\text{-}directional\ growth}}$ ($= |E_{\mathrm{Growth}}| + |E_{\mathrm{Shrinkage}}|$) when regressed against each of the previously calculated population-level parameters. This method identifies which demographic parameters correlate significantly with $E_{\mathrm{Shrinkage}}$ and with E_{Growth}. We used absolute values of $E_{\mathrm{Shrinkage}}$ because it normally has a negative value (see Results), which would complicate comparisons to correlations with E_{Growth}.

LOOP ANALYSIS

In our second approach, we used loop analysis to examine the demographic implications of plant size plasticity (both positive and negative growth) for the same herbaceous perennial species. Loop analysis is emerging as a useful complementary approach to the perturbation analysis of individual matrix elements, because the latter do not fully describe the life-history traits of a population (van Groenendael *et al.* 1994; de Kroon, van Groenendael & Ehrlen 2000). Instead, loop analysis recognizes that the life cycle of any population is composed of a number of simpler abstract life cycles, or loops, which individuals in the population undergo (e.g. some individuals reproduce the year after they are recruited, while others may take longer to do so). Each loop is characterized by a transition that no other loop contains, and the total contribution of a particular loop to the population growth rate can be calculated as the elasticity of that transition (i.e. the characteristic elasticity of the loop) times the number of transitions involved in the loop.

We implemented Guneralp's (2007) systematic classification of demographic components of the life cycle of a population in our loop analysis. Similar algorithms exist, but they are too mathematically complex for large data bases (Jones 2007; Sun & Wang 2007; Adams 2008), or do not always identify biologically relevant loops (Wardle 1998) as this one does. Guneralp's algorithm starts by assigning the characteristic elasticity to loops of the shortest length (self-loops). Next, those characteristic elasticities are subtracted from the remaining elasticity pool of the matrix, and increasingly longer loops are identified, to which their elasticities are attributed, until this elasticity pool of the matrix is depleted. For a complete description of the analytical

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[1] Please note that the established terminology (Caswell 2001; Franco & Silvertown 2004) uses 'ρ' to denote both the retrogression vital rate in a projection matrix as well as the damping ratio. Unless otherwise noted explicitly, here we refer to damping ratio as ρ and to the elasticity of shrinkage as $E_{\mathrm{Shrinkage}}$, and not as $E\rho_{ij}$ (but see Appendix S3). Moreover, the Spearman correlation coefficients are typically reported as 'ρ', but we have not referred to them by their Greek letter to avoid confusions.

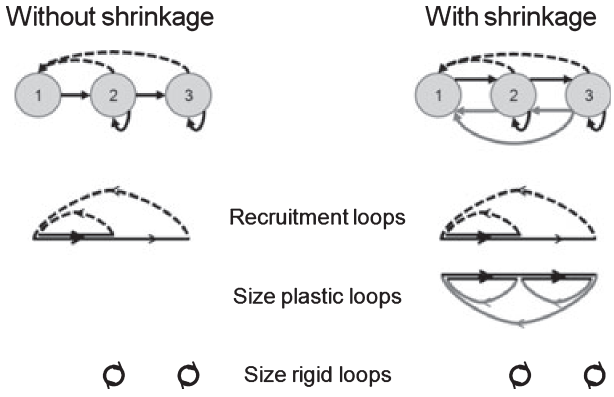


Fig. 2. Three-stage life cycle (top) and loop decomposition for two imaginary plant species that do or do not present retrogression transition probabilities (grey). Dashed lines correspond to reproduction and continuous lines to transitions (growth, stasis and shrinkage). Recruitment loops include individuals that grow to stages where they contribute to recruitment; size-plastic loops include individuals' size fluctuation (both growth and shrinkage); size-rigid loops describe individuals that do not fluctuate in size. Notice that for the species without shrinkage there are no size-plastic loops because there are no retrogression transition probabilities needed to complete these loops.

approach of loops elasticities, see van Groenendael *et al.* (1994) and Wardle (1998).

To examine the importance of size-based phenotypic plasticity in herbaceous perennial populations, we classified the loop elasticities of each species into three different categories: *recruitment loops*, in which individuals grow to a class where they reproduce sexually or clonally; *size-plastic loops*, where the individuals fluctuate in size positively and negatively; and *size-rigid loops*, where individuals do not change in size. It is important to note that all size-plastic loops include elements of both growth and shrinkage, while loops with growth but no shrinkage were classified as recruitment loops (Fig. 2). We then explored how $E_{\text{Recruitment loops}}$, $E_{\text{Size-plastic loops}}$ and $E_{\text{Size-rigid loops}}$ relate to the previously calculated population parameters (life span, λ, R_0, T, μ_1, ρ, P_i) using Spearman rank correlation coefficients.

We used a randomization procedure to determine whether collapsing projection matrices to 5 × 5 dimensions affected vital rate and loop elasticities. Randomizations were necessary because the distribution of the original matrix dimension for the various species was not normal (see Appendix S1). We only included species whose matrices were collapsed to 5 × 5 (n = 45). The permutation tests (Manly 1997) decoupled the elasticity values and matrix dimensions that were paired by species and re-arranged them over 1000 permutations. For each of these permutations, we then obtained a Spearman rank correlation coefficient for the relationship between matrix dimension and a particular elasticity value (e.g. $E_{\text{Shrinkage}}$, E_{Growth}, etc.). Next, 95% confidence intervals were obtained from the distribution obtained and used as a base to examine whether there was a causal effect of matrix dimension on elasticity values. In addition, we extended the permutation tests to the analyses of the population-level parameters.

Despite the relatively large number of statistical tests performed, we did not correct the P-values with a sequential Bonferroni adjustment due to the large size of our data base, as suggested by Moran (2003). Instead, we only ran analyses on parameters that we hypothesized *a priori* could be affected by an individual's ability to decrease in size and which also had a biological meaning – in other words, the data base was not mined for significant relationships. We cautiously evaluated the statistical tests with P-values lower than, but close to, 0.05.

Results

THE DEMOGRAPHIC IMPORTANCE OF SHRINKAGE

Although shrinkage is a common phenomenon among herbaceous perennials (87.5% of the species had significant retrogression transition probabilities), the cases in which shrinkage was demographically relevant *per se*, as measured by its vital rate elasticity $|E_{\text{Shrinkage}}| > 0.05$, were few (13.8%). In contrast, the shrinkage loop elasticities, which are based on shrinkage and growth, were important in a high percentage of species (76.3%; $E_{\text{Size-plastic loops}} \geq 0.05$; Appendix S4). The species characterized by low or no values of $E_{\text{Size-plastic loops}}$ (< 0.05) were always a subset of the species with low or no $E_{\text{Shrinkage}}$ values.

The demographic importance of shrinkage, in absolute value, when compared to other vital rates varied greatly. For instance, $|E_{\text{Shrinkage}}|$ was lower than E_{Survival} in 77.5%, lower

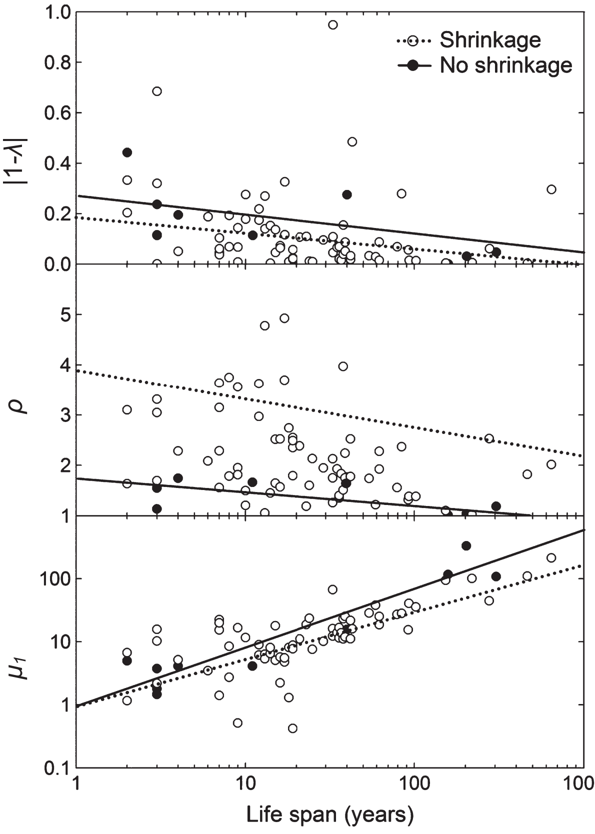


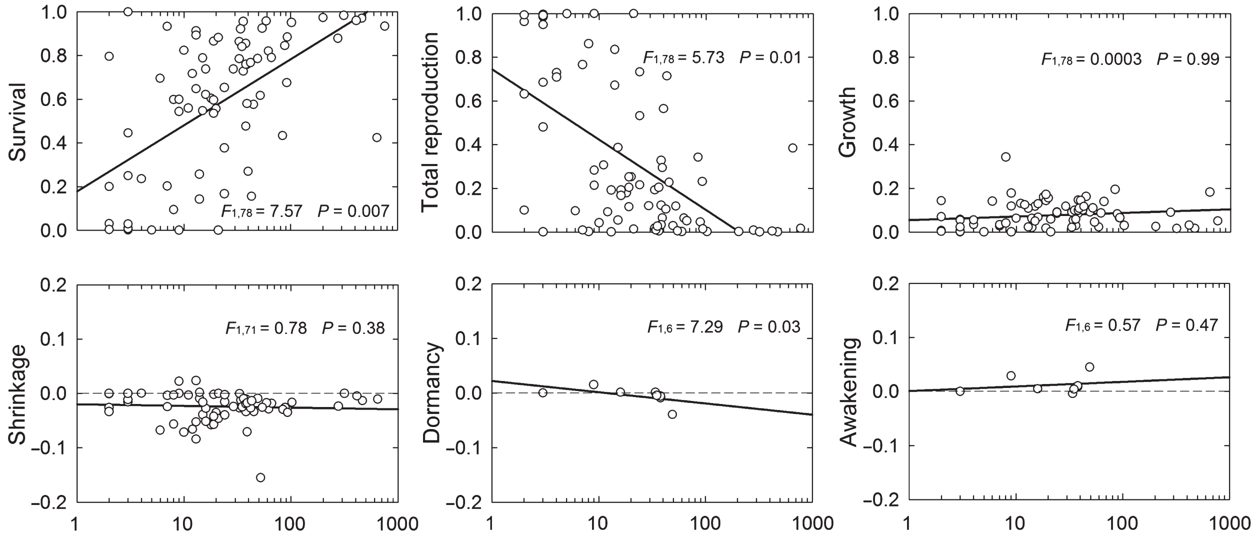
Fig. 3. Relationship between the life span of 80 herbaceous perennial plant species that shrink and do not shrink, and (top) their deviation from the population growth rate at equilibrium (λ = 1), (middle) their damping ratios (ρ), and (bottom) mean age of parents of offspring of a cohort (μ_1; log-scaled). Some damping ratios of species with shrinkage are not shown here because they were off the scale. They were, however, included in the regression analyses (Appendix S2).

than E_{Growth} in 95%, lower than $E_{\text{Sexual reproduction}}$ in 76.9% and lower than $E_{\text{Clonal reproduction}}$ in 87.5% of the species. Nevertheless, $|E_{\text{Shrinkage}}|$ was higher than $|E_{\text{Dormancy}}|$ and $|E_{\text{Awakening}}|$ in 87.5% and 75% of the species with such processes, respectively. In a reduced number of species, $E_{\text{Shrinkage}}$ was positive (*Cynoglossum virginianum*, *Erythronium japonicum*, *Lobularia maritima* and *Tillandsia deppeana*; but for the latter two species $E_{\text{Shrinkage}}$ was very low (< 0.002)).

The populations of species exhibiting shrinkage were in greater demographic equilibrium than those without shrinkage. The deviation of the population growth from $\lambda = 1$, $|\lambda{-}1|$, as a function of life span did not differ significantly for species with and without shrinkage ($F_{1,79} = 0.71$, $P = 0.86$; Fig. 3), but species with shrinkage had, on average, λ values closer to 1 (ANCOVA test for intercept: $t = 5.12$, $P < 0.0012$) than species without shrinkage. This does not mean that populations of individuals that are able to shrink have lower λ values on average; some of those populations without shrinkage have greater λ values and some have lower λ values than those with shrinkage so that λ values of populations with and without shrinkage do not differ statistically ($t = -1.19$, $P = 0.20$). A similar pattern was true for the speed of recovery after disturbance (measured by the damping ratio, ρ) as a function of life span. Populations with shrinkage had higher ρ values based on the intercept than those without shrinkage ($t = 4.99$, $P < 0.001$), although the slopes of the linear regressions between life span and ρ for species with and without shrinkage were not significantly different ($F_{1,72} = 3.26$, $P = 0.08$). ANCOVA tests also revealed that proportional correlation between life span and μ_1 ($t = 3.20$, $P = 0.002$) was greater for species without shrinkage than with shrinkage ($F_{1,76} = 8.07, P = 0.006$).

There were striking differences among the vital rate elasticities in their relationships with population-level parameters. For instance, although the values of E_{Growth} and $E_{\text{Shrinkage}}$ did not vary significantly as a function of life span, the former was always positive and the latter almost always negative (Fig. 4). $E_{\text{Awakening}}$ followed a very similar trend to that of E_{Growth}, while E_{Dormancy} decreased with life span, transitioning from positive values for short-lived to negative values for long-lived species. E_{Survival} increased steadily with life span, while $E_{\text{Sexual reproduction}}$ decreased rapidly with life span. In regards to the

(a)
Vital rate elasticities



(b)
Loop elasticities

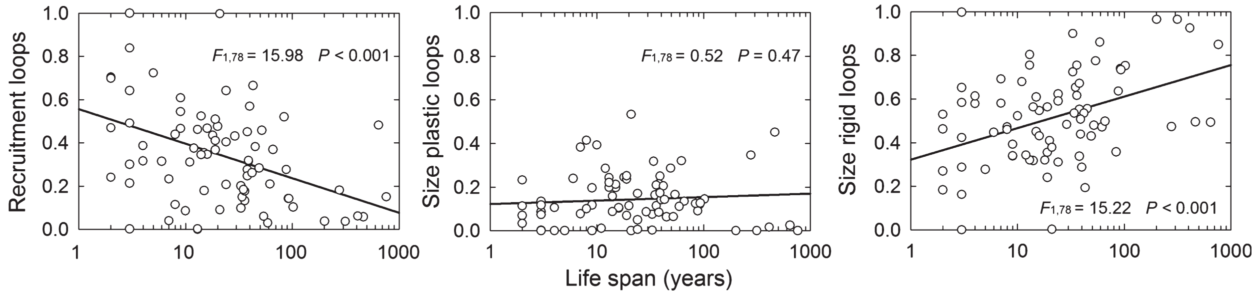


Fig. 4. Linear correlations between the life spans of 79* herbaceous perennial plant species and (a) the vital rate elasticities of the demographic processes involved in their population dynamics and (b) their corresponding loop elasticities. Not all matrix models incorporated vegetative dormancy and awakening. Total reproduction includes sexual and clonal reproduction. Note the different axis scaling for the elasticities of shrinkage, vegetative dormancy and awakening. *We were not able to determine life span for one species of the 80 in our study.

Table 1. Spearman rank correlation coefficients between demographic parameters (see Materials and methods for description) and (a) vital rate elasticities and (b) loop elasticities. Coefficients in italics are significant at $P < 0.05$ and in bold at $P < 0.001$. $E_{\text{Bi-directional}} = |E_{\text{Growth}}| + |E_{\text{Shrinkage}}|$

Elasticities	Matrix dimension (n = 45)*	λ (n = 79	R_0 (n = 79)	T (n = 77)	μ_1 (n = 79)	ρ (n = 79)	P_i (n = 70)
(a)							
E_{Survival}	*0.33*	*−0.37*	*−0.34*	**0.63**	**0.48**	−0.34	*−0.33*
E_{Growth}	−0.03	*0.32*	*0.32*	−0.10	−0.04	*0.35*	*0.29*
$\lvert E_{\text{Shrinkage}}\rvert$	−0.13	−0.06	−0.14	0.16	0.11	*0.23*	0.02
$\text{E}_{\text{Domancy}}$	−0.01	−0.06	−0.07	−0.03	−0.09	−0.06	0.06
$E_{\text{Awakening}}$	0.03	0.22	0.17	−0.15	−0.15	*0.24*	−0.06
$E_{\text{Bi-directional}}$	*−0.23*	0.19	0.15	0.03	0.01	*0.27*	*0.26*
$E_{\text{Sexual reproduction}}$	*−0.32*	*0.35*	*0.36*	**−0.49**	*−0.32*	*0.22*	*0.22*
$E_{\text{Clonal reproduction}}$	−0.01	0.06	0.06	−0.20	−0.19	0.12	*0.26*
(b)							
$E_{\text{Recruitment loops}}$	−0.37	**0.39**	**0.39**	**−0.80**	**−0.52**	**0.47**	**0.67**
$E_{\text{Size-plastic loops}}$	0.38	*−0.25*	*−0.34*	0.18	0.06	*0.30*	0.10
$E_{\text{Size-rigid loops}}$	0.01	−0.21	−0.17	**0.78**	**0.56**	**−0.65**	**−0.70**

*We measured the effect of the original matrix dimension on the elasticities obtained after having collapsed them to 5 × 5 using permutation tests, and only on those matrices that were collapsed.

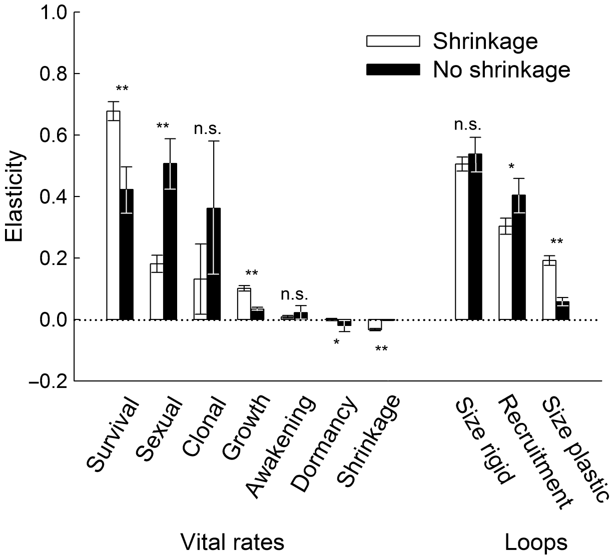


Fig. 5. Elasticity values ($\bar{x}$ ± SE) of vital rates and loops for 80 herbaceous perennial species with and without shrinkage (defined as summation of retrogression probabilities in the matrix < 0.05). *Statistically significant at $P < 0.05$; **statistically significant at $P < 0.001$.

rest of the population-level parameters, E_{Growth} correlated positively with λ, with R_0, with the damping ratio (ρ) and with P_i, while $|E_{\text{Shrinkage}}|$ only correlated (positively) with the damping ratio (Table 1a). In contrast, when shrinkage and growth were lumped, $E_{\text{Bi-directional growth}}$ acted as an intermediate of both processes, since it correlated positively with the damping ratio and P_i, but not with λ and R_0. Furthermore, although the initial dimension of those matrices that were collapsed to 5 × 5 did not affect E_{Growth} and $E_{\text{Shrinkage}}$, the values of $E_{\text{Bi-directional growth}}$ were negatively affected (Table 1a).

The population dynamics of species with shrinkage differed markedly from dynamics of species without shrinkage. Species with shrinkage had higher E_{Survival}, E_{Growth} and higher – but negative values of – E_{Dormancy}, as well as lower values of $E_{\text{Sexual reproduction}}$ than those species without shrinkage (Fig. 5).

Table 2. Spearman rank correlation coefficients between vital rate elasticities and loop elasticities. Coefficients in italics are significant at $P < 0.05$ and in bold at $P < 0.001$

Elasticities	$E_{\text{Recruitment loops}}$	$E_{\text{Size-plastic loops}}$	$E_{\text{Size-rigid loops}}$
E_{Survival}	**−0.82**	*0.27*	**0.67**
E_{Growth}	*0.25*	*0.33*	*−0.28*
$\lvert E_{\text{Shrinkage}}\rvert$	−0.02	**0.53**	−0.21
E_{Dormancy}	0.35	−0.48	−0.14
$E_{\text{Awakening}}$	0.26	0.14	−0.24
$E_{\text{Bi-directional}}$	*0.31*	0.15	*−0.24*
$E_{\text{Sexual reproduction}}$	**0.75**	*−0.35*	**−0.54**
$E_{\text{Clonal reproduction}}$	0.75	−0.43	−0.64

INSIGHTS FROM LOOP ANALYSIS

In loop analysis, herbaceous perennials were characterized by high values of $E_{\text{Size-rigid loops}}$ and by a wide range of values for $E_{\text{Recruitment loops}}$ (Fig. 1). The values for the $E_{\text{Size-plastic loops}}$ were always lower than 0.5, with the exception of one species (*Sanicula europaea*).

The *Recruitment–Size-plastic–Size-rigid* loop elasticity approach produced some similar results to the findings described above with classical vital rate elasticities. For instance, $E_{\text{Recruitment loops}}$ correlated with the same demographic parameters and in the same direction as $E_{\text{Sexual reproduction}}$ (negatively: life span, matrix dimension, T and μ_1; positively: λ, R_0, ρ and P_i) (Fig. 4, Table 1b), and $E_{\text{Recruitment loops}}$ and $E_{\text{Sexual reproduction}}$ also correlated significantly with each other (Table 2). Nevertheless, while $E_{\text{Sexual reproduction}}$ was negatively affected by having collapsed matrix dimensions, $E_{\text{Recruitment loops}}$ was not affected. $E_{\text{Size-plastic loops}}$, which incorporates both E_{Growth} and $E_{\text{Shrinkage}}$ (but also E_{Dormancy} and $E_{\text{Awakening}}$, and of course E_{Survival}), more closely matched how

E_{Survival} correlated with population-level parameters than how any other involved vital rate elasticity correlated with these same parameters, although $E_{\text{Size-plastic loops}}$ correlated positively with $E_{\text{Survival,}}$ E_{Growth} and $E_{\text{Shrinkage}}$. As for $E_{\text{Size-rigid loops}}$, it correlated significantly and in the same direction as E_{Survival}: positively with life span, T and μ_1, and negatively with ρ and P_i. The correlation between $E_{\text{Size-rigid loops}}$ and E_{Survival} was highly positively significant.

Species with shrinkage and those without shrinkage also differed in the relative magnitudes of the elasticity values for the three types of loops – recruitment, size-plastic and size-rigid loops. For species without shrinkage, the mean values of $E_{\text{Recruitment loops}}$ and $E_{\text{Size-rigid loops}}$ were similar, and obviously $E_{\text{Size-plastic loops}} \approx 0$ (Fig. 5). Species with shrinkage had, on average, high values of $E_{\text{Size-rigid loops}}$, intermediate values of $E_{\text{Recruitment loops}}$ and relatively low values of $E_{\text{Size-plastic loops}}$.

Discussion

Explicitly incorporating shrinkage, as we have done here, reveals previously unreported links between demographic processes and size fluctuations. When shrinkage is regarded as a demographic process separate from growth, our findings suggest that shrinkage causes demographic buffering. For instance, the population dynamics of species exhibiting shrinkage are in greater equilibrium (population growth rates λ closer to 1) and are characterized by higher speed of recovery after disturbance than those without shrinkage, as measured by their damping ratios. Our results suggest that shrinkage benefits the individuals by enabling them to decrease in size in the light of a stressful event – as opposed to die. The stable class distribution and reproductive contributions may be reached quicker when supplemented by already existing individuals than by other mechanisms such as recruitment. Growth, awakening from vegetative dormancy and sexual reproduction, together with shrinkage, increase such speed of population recovery (Table 1a). Furthermore, this study also reports a trade-off, based on our vital rate elasticity results, between maintenance and reproduction, of which shrinkage seems to be an outcome; species with shrinkage have higher demographic importance (elasticity) of survival and growth, but lower importance of sexual reproduction. Thus, treating shrinkage as a vital rate *per se*, instead of lumping it with other processes of strikingly different nature, as has been done previously, is extremely informative.

The second approach, using loop analysis, holds some advantages over the classical prospective analysis for two reasons. First, loop analysis allows for the identification and careful assessment of complete demographic pathways in a complex life cycle, as opposed to single annual demographic steps that may not be necessarily linked demographically, such as the artificial merging of shrinkage and growth events (e.g. Zuidema & Franco 2001; Franco & Silvertown 2004). Secondly, our classification of loops into three categories, namely contributions to recruitment, size plasticity and size rigidity, also allows for the exploration of population-level parameters of interest as a response to individuals' *complete* ecological strategies. In this context, loop analysis reveals three striking findings. First, the speed of post-disturbance demographic recovery (ρ) does not rely entirely on recruitment, but also on individuals' ability to respond size-plastically to the new conditions. Secondly, although *a priori* our analyses show that the control exerted on population dynamics by size plasticity is on average the same for all species, regardless of life span, omitting four very long-lived species as outliers of the linear correlation analyses in Fig. 4 (*Heliconia acuminata*, *Minuartia obtusiloba*, *Molina caerulea* and *Paronychia pulvinata*) produced a different result. With such omission, the correlation between life span and elasticity of size-plastic loops became significantly positive ($F_{1,74} = 7.84$, $P = 0.006$), while the correlation of life span with elasticity of size-rigid loops and with recruitment loops remained significant ($F_{1,74} = 5.66$, $P = 0.02$ and $F_{1,74} = 12.66$, $P < 0.001$, respectively). This indicates a marginal increase in the importance of size plasticity as longevity increases. Finally, that the value of $E_{\text{Size-plastic loops}}$ is almost zero for species without or with very low shrinkage is obvious, since these species lack the retrogression transitions to complete the size-plastic loops (Fig. 2). However, the consequent finding, that the existing $E_{\text{Size-plastic loop}}$-values in species with shrinkage are subtracted from the $E_{\text{Recruitment loop}}$-values in species without shrinkage, while $E_{\text{Size-rigid loops}}$ stay unaltered for species with and without shrinkage, is of special interest because the existence of size-plastic loops in species with shrinkage accounts for – and affects – approximately one quarter of the usual importance of recruitment loops in herbaceous perennial species. Examples of plant shrinkage following a year of high reproductive investment clearly exist (Bierzychudek 1982; Meagher 1982), and our findings are further supported by the results of another manuscript of this special feature (Davison *et al.* 2010), and by our own classical vital rate elasticity results: when a species lacks shrinkage, its demographic dynamics are controlled by higher vital rate elasticities of sexual reproduction, while both survival and growth (basic parameters that constitute the recruitment loop too) decrease.

Our conclusions about the importance of shrinkage and size plasticity are likely conservative since the percentages of shrinkage reported in our data base might have been underestimated by the published studies *per se* and perhaps also by our own analyses. There are two main reasons for the underestimation of shrinkage from published work. First, the extent to which the published projection matrices are representative of the typical population dynamics is limiting (Jongejans *et al.* 2010), especially given the poor spatial (3 ± 3 sites) and temporal (4 ± 3 years) replication in demographic studies for herbaceous perennial species (Appendix S1). This is a concern because shrinkage might play a critical role in the population's recovery after intense, but infrequenty events (e.g. droughts, pests) and with such poor replication, plant shrinkage may just not be encountered by the demographer. Secondly, the likelihood of reporting shrinkage may depend on the variables used in the size-based matrix (i.e. tuft circumference (O'Connor 1993), storage structure length (Zotz & Schmidt 2006), number of tillers (Fowler, Overath & Pease 2006), stem length (Liu, Menges & Quintana-Ascencio 2005), etc.). Although our collapsing of matrices to the same dimension (5 × 5) did neither affect calculation of the vital rate elasticity of shrinkage nor the loop elasticity of size plasticity, it is still possible that the alternative approach of Enright, Franco & Silvertown (1995) to compare demographic dynamics, namely making matrix dimensions a linear function of the species' longevities, might be a more biologically meaningful approach. Nevertheless, we must point out that their second approach is incompatible with our data base due to our comparative purposes: for our 80 species, the linear – or any directly proportional – correlation between matrix dimension and life span simply does not exist ($t_{1,78} = 2.70$, $P = 0.10$). Additionally, it is possible that the algorithm used to identify and characterize the loop elasticities (Guneralp 2007) underestimated the importance of size-plastic loops, since this algorithm operates sequentially from the shortest to the longest loops and stops when there are no more elasticity values left in the matrix, regardless of whether all loops have been covered or not. This order may have left some long-length, phenotypically plastic loops without elasticity values. However, our analyses are robust, as indicated by the positive correlations between the loop elasticities and the vital rate elasticities that are involved in each of the loops classified (e.g. the loop elasticity of size plasticity was positively correlated with survival, growth and shrinkage). Future work should further evaluate the importance of size plasticity by determining the upper and lower bounds of its probability of occurrence (see Adams 2008; Zuidema *et al.* 2009).

ADDITIONAL APPROACHES FOR THE INCORPORATION OF SHRINKAGE IN DEMOGRAPHIC STUDIES

Changes in the methodological approaches to matrix modelling could also improve our understanding of the biological significance of shrinkage. For example, complex life cycles can be partitioned into two matrices that separate transitions of surviving individuals (stasis, growth, shrinkage and dormancy) and the contribution of new individuals via sexual and clonal reproduction (Caswell 2001, p. 110), or by including additional classes in the life cycle to distinguish between sexual and clonal reproductions. Secondly, the application of periodic projection matrices (Caswell & Trevisan 1994; Le Corff & Horvitz 2005; Smith, Caswell & Mettler-Cherry 2005), which evaluate the dynamics of a population at a much finer temporal scale (e.g. months, within growing seasons, etc.), can allow us to pinpoint exactly when fluctuations in size occur within a year, and consequently suggest their underlying cause. Finally, the incorporation of stochastic variation into elasticity analyses (Caswell 2005, 2010; Claessen 2005; Aberg *et al.* 2009; Davison *et al.* 2010) will allow us to assess the long-term impacts of demographic processes with low elasticity value, such as size phenotypically plastic loops and shrinkage. Vital rates characterized by low elasticities typically exhibit greater variation than vital rates with high elasticities (Zuidema & Franco 2001; Davison *et al.* 2010). Although this result has been used to suggest that natural selection promotes population stability by reducing variability only in the life-history traits that matter the most (Pfister 1998; Morris & Doak 2004; Morris *et al.* 2008), another equally valid interpretation may be that processes that have been overlooked because of their low elasticity values provide important raw material for natural selection over the long term.

FUTURE DIRECTIONS

Demonstrating the actual advantage of any plastic trait or behaviour can be challenging (Schlichting 1986). More studies are needed to determine if – and in what taxonomic groups, growth forms and ecosystems – shrinkage, as a form of phenotypic plasticity, is an adaptive behaviour that increases plant longevity or lifetime reproductive output and to what extent it represents a decline in vigour that follows high reproductive output or is due to environmental stressors or advanced plant age. That the elasticity of shrinkage alone is consistently low for herbaceous species while the demographic importance of size changes is much higher suggests that in most species of our study shrinkage is not a by-product of senescence, but represents 50% of a buffering strategy – the other 50% being re-growth after disturbance. This is further supported by the fact that the importance of survival and growth for species with shrinkage is significantly higher than for species without shrinkage. Nevertheless, more longitudinal cohort studies (Harper 1977) tracking the fates of individuals before and after shrinkage are needed to tackle this question.

It is also possible that shrinkage has different implications for short- and long-lived species just as it is the case for vegetative dormancy. We found that vegetative dormancy has a positive effect on plant fitness for short-lived species, but a negative one for long-lived species (cf. Shefferson 2009). Furthermore, because the absolute effect of vegetative dormancy was significantly higher for species without shrinkage than for species with shrinkage, we suggest that shrinkage may be a temperate, supplementary form of dormancy. Careful demographic research following the performance of closely related species with different life spans exposed to the same environmental variation may help understand the implications of shrinkage in relation to plant longevity and its relationship with plant vegetative dormancy.

Then there is the question: does shrinkage at the *whole* plant level ever occur? Most demographic studies focus on above-ground structures, and plant shrinkage could simply represent reallocation of resources to below-ground structures. Studies that incorporate above- and below-ground biomass might be achieved by combining traditional above-ground censuses with rhizotron observations (Milchunas *et al.* 2005). More work is also needed at the interface between ecophysiology and demography because virtually nothing is known about the internal processes that can result in plant shrinkage.

Future work must determine the set of conditions necessary for shrinkage to affect fitness *positively*, as well as how frequently these conditions occur in natural settings. The sign of the shrinkage vital rate elasticity is generally negative because the class-specific survival and class-specific reproductive output increase with plant size (Silvertown, Franco & Perez-Ishiwara 2001), although this increase is not necessarily monotonic. Consequently, a size decrease places individuals of these species in a class where chances of surviving and/or reproducing are low, and where fitness is comparatively lower. Still, some species do not conform to this rule (R. Salguero-Gomez, unpubl. data). For instance, because the survivorship of small individuals of *Tillandsia deppeana* (Bromeliaceae), *Lobularia maritima* (Brassicaceae) and *Fritillaria meleagris* (Liliaceae; citations in Appendix S1) is higher than that of their respective larger individuals, the vital rate elasticity of shrinkage is positive in some or all of the matrix cells associated with retrogression. Shrinkage elasticities can be positive if shrinkage causes individuals to transition to classes where their reproductive output is higher, as in *Pinguicula villosa* (Lentibulariaceae). The notion that large individuals contribute more to the future population dynamics with their reproductive output due to asymmetric competition, especially in crowded ecosystems, has been recently challenged (Chambers & Aarsen 2009). One example is 'emergency flowering' (*sensu* Larcher 2003), where small, not-reproductive individual plants immediately induce flowering meristematic pathways when stressed by abiotic factors. Another example has to do with the relationship between a plant and its nurse plants; when survival is higher under nurse plants, surpassing the size of the nurse plant translates into losing the benefits of such facilitation (Sans *et al*. 2002).

FINAL REMARKS

The failure to acknowledge shrinkage in natural plant populations has to date impeded the establishment of an intellectual framework with which to explore its demographic implications. Perhaps, the main reason for this fact resides in the typically low, negative vital rate elasticities of shrinkage, yet for some species vital rates of similar or even lower elasticity values (e.g. clonal reproduction or vegetative dormancy; Fig. 1) have been the focus of much attention. Our study finds that significant levels of size plasticity occur in a majority of herbaceous species. Our explicit treatment of shrinkage as a separate vital rate and its posterior incorporation through loop analysis demonstrates that faster post-disturbance recovery speeds, higher survival, trade-offs with sexual reproduction and vegetative dormancy and, marginally, an increase in life span, are all correlated with the ability to shrink and fluctuate in size. However, continued research is needed to elucidate the advantages and disadvantages of shrinkage. In our opinion, ecologists need not ask whether shrinkage is important, but what would happen to plant populations if individuals were not able to shrink.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Description of study species and survey of individual plant shrinkage.

Appendix S2. Demographic parameters.

Appendix S3. Vital rate elasticity calculation and data.

Appendix S4. Loop elasticity data.