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Physiological bases of plant shrinkage

and its demographic implications

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PHYSIOLOGICAL BASES OF PLANT SHRINKAGE

AND ITS DEMOGRAPHIC IMPLICATIONS

Roberto Salguero-Gómez

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Physiological bases of plant shrinkage and its demographic implications

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Roberto Salguero-Gómez

Bonum ex integra causa, malum ex quocumque defectu

Dedication

This doctoral dissertation is dedicated to my parents.

Without their discipline, as well as unconditional support, I would still be trying to figure out what I want in life and how to get there.

Dedicación

Dedico esta disertación doctoral a mis padres.

Sin su disciplina, así como su apoyo incondicional, aún estaría intentando buscar formas de dar de comer a los pájaros que tenía (y aún tengo) en mi cabeza. Ya tenéis un doctor en la familia... aunque no sea de medicina, sino de "plantas con pinchos".

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Life is an ever-growing snowball

Let me be clear: I don't believe in destiny; however, I find it extremely fortuitous that looking retrospectively –matrix analytical jokes aside– it suddenly seems to me that every step I've taken has inexorably led me to the next one. I am most grateful to everybody who has had an impact in my life thus far and has helped me along in my decisions, including my family, friends, teachers, colleagues and advisors. Science (at least my science) is not a lonely pathway, and I have counted on the expertise of a wide array of researchers in the last years. The pages that follow are the result of their wise advice, solid infrastructure, and immeasurable patience and support... now, any potential mistakes in this document are mine alone, of course.

Clearly, I owe a lot to my family. My parents have always been supportive of whatever I was interested in... be that minerals and rocks, kayaking, or succulent plants. They have instilled in me essential values such as respect, tolerance, comradeship, hard work and friendship. The aforementioned snowball reached a critical mass when my parents supported me to go to London for my Master's degree. Being exposed to the international community and doing fieldwork in remote regions awakened my desire to explore and grow as a person and as a scientist. My siblings have been great role models in regards to setting goals and achieving them. In addition, my sister has been a bastion for "going abroad". Thanks a lot of hosting me in Vienna!

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Penn has nurtured me with a learning environment that strives for excellence. Everybody whom I have had the pleasure of interacting with is overwhelmingly bright and hardworking. I have been inspired by lab mates and "annexed satellites" (Richard Lucas, Baoming Ji, Jennifer Doherty, Lori Spindler, Pierre Liancourt, Erin Wiley, Aurora MacRae-Crerar, Daniel Song, Chris Graves, Camilo Khatchikian, Leeanne McGurk, Emma Aronson, Xin Song, Jeff Klemens, Laura Fox, Godefroy Devevey, Haihan Zhang, Katie Vazquez...), staff members (Colleen Gasiorowski, Tracylea Byford, Vannesa Jerolmack, Linda Robinson, Melanie Cedrone...) and faculty members (Warren Ewens, Kim Gallagher, Scott Poethig, Doris Wagner, Bruce Lenthall, Catherine Turner...) to (try to) pursue excellence in research, teaching, mentoring and eco-service.

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La vida es una bola de nieve que no para de crecer

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ABSTRACT

Physiological bases of plant shrinkage and its demographic implications Roberto Salguero-Gómez

Brenda B. Casper

Perennial plants are plastic organisms and can vary greatly in size within and between years. While much attention has been paid to the factors that maximize plant growth, *plant shrinkage* has been bluntly overlooked. Here we study anatomy, physiology, demography and comparative biology to understand how often plants shrink, mechanisms by which plants may internally regulate their architecture to shrink, and shrinkage's demographic implications. We explored belowground resource uptake, hydraulic transport and demographic contributions of shrinkage of individuals of *Cryptantha flava* (Boraginaceae) in the Great Basin desert. We used a database with >700 species to explore shrinkage's frequency and ecological consequences by examining demographic parameters such as population growth rate, longevity and reproductive output for species with and without shrinkage.

We show that *C. flava* can forage the heterogeneous desert space by uptaking via some roots but not others, and that individuals become sectored with age (*i.e.*, individual roots transport resources only to specific canopy regions). The switch in hydraulic design with ontogeny may explain why large individuals are more likely to shrink after droughts than juveniles. Perturbation analyses demonstrated that large individuals contribute very

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little to the population growth rate (λ) and that growth to large classes can negatively affect λ in *C. flava*. The comparative analyses indicated that shrinkage correlates positively with lifespan, survival, fecundity and growth. Finally, we found a significant number of candidate herbaceous species where shrinkage might be under selection because in them shrinking increases λ .

We have linked anatomical traits, physiological mechanisms and population dynamics to offer a mechanistic explanation of how and why plants shrink. We argue that sectoriality in *Cryptantha flava* may allow individuals to minimize respiratory demands during harsh conditions by shedding sectors. Thus shrinkage, being preferable over mortality, is a survival mechanism that helps individuals buffer stochasticity. The finding that large individuals of *C. flava* contribute very little to λ in comparison to medium-sized individuals and that positive shrinkage vital-rate sensitivities occur frequently in the plant kingdom, together with recent demographic analytical developments, make exploring plant shrinkage a very promising venue of ecological and evolutionary research.

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Chapter I

Introduction: plant shrinkage happens... and it matters

Roberto Salguero-Gómez

"The more the division of labor and the application of machinery extend,

the more does competition extend among the workers, the more do their wages shrink together"

Karl Marx (1818-1883)

I.1. Why study plant size?

Size plays a crucial role in plants' survival and productivity; hence, the study of the factors that determine plant size is at the very core of plant ecology and evolution. My dissertation investigates the mechanisms and implications of an overlooked phenomenon that influences plant size: their ability to drastically decrease in size (*plant shrinkage*, hereafter). To understand how, why and how often plants shrink, as well as the demographic implications of shrinkage, I have undertaken a multi-disciplinary approach that includes anatomical descriptions, physiological experiments, long-term field demographic censuses involving the effects of expected climate change and literature surveys of demographic data (Fig. I.1).

While much is known about the requirements for plant growth at cellular (Wilkinson and Davies 2008), physiological (Enquist et al. 2007a), demographic (Harper 1977) and environmental (Enquist et al. 2007b) levels, knowledge is scant regarding the mechanisms that result in the opposite phenomenon, plant shrinkage. Although plants may shrink due to external agents such as fire (Quintana-Ascencio et al. 2003) or herbivory (Lesica 1995), shrinkage resulting from the potential ability to regulate internally size has tremendous ecological and evolutionary implications; this type of plant shrinkage is the primary focus of my doctoral dissertation.

Size –not age, as it is with most non-sessile organisms– is the most important determinant of fitness in plants (Harper 1977, Silvertown and Charlesworth 2001). This is especially the case in long-lived species, where the alternative approach to measure fitness and predict productivity, determining the age, is methodologically complicated (but see Garcia and Antor 1995). The main challenge for size-based studies with long-lived species is appropriately classifying individuals. For instance, herbaceous perennial plant species are characterized by a large annual turn-over of tissue, *i.e.*, aboveground biomass is renewed at the beginning of every growing season, and they can exhibit dramatic changes in size, both positive and negative, within and between years. Without acknowledging the possibility of shrinkage, two individuals with the same size would be treated as identical using classical demographic approaches (Caswell 2001), while they could represent a growing juvenile and a shrinking adult with distinctive present and future performances and contributions to their population (Ehrlen 2000, Roach et al. 2009).

Why deserts and why this study system?

The experimental component of the present thesis (Chapters II, III and IV) was carried out on a natural population of the desert perennial *Cryptantha flava* L. (Boraginaceae), in the Great Basin Desert. The inception of the thesis came about with the field observation that individuals of *C. flava* display a dichotomous behavior in response to natural droughts: while most small individuals keep growing, large individuals, regardless of being in the same cohort (Casper 1996) or not –as I show in chapter IV– are more likely to shrink. Furthermore, shrinkage occurs preferentially through the death of entire spatially aggregated patches of rosettes (Salguero-Gómez & Casper, unpublished), but previous physiological approaches dealing with whole-plant respiration and assimilation do not satisfactorily explain this size-specific phenomenon (Casper 1996, Casper et al. 2005, 2006).

Cryptantha flava is an excellent model organism with which to explore the mechanisms of plant shrinkage and its demographic consequences because much is already known regarding its biology. Published research on *C. flava* covers almost all levels of biological organization: belowground foraging (Peek and Forseth 2005), pollination biology (Casper 1981, 1985, 1988, 1994), physiology (Forseth et al. 2001, Casper et al. 2005), demography (Casper 1996, Casper et al. 2001, Lucas et al. 2008, Peek and Forseth 2009) and even community ecology (Gebauer and Ehleringer 2000, Maestre et al. 2005).

Deserts are excellent ecosystems to explore plant shrinkage because desert plants commonly shed a significant amount of their aboveground biomass every year (Kozlowksi 1973), and because plant-water relations are of particular interest given that water is the primary limiting factor in deserts (Noy-Meir 1973, Gallardo and Schlesinger 1992). Consequently, simulating pulses of precipitation can help us decipher the effects of plant growth and shrinkage on population growth rates. But the relevance of studying desert ecology does not cease there: deserts cover over one third of the Earth's land surface (Noy-Meir 1973) and rank among the top three ecosystems at risk of species

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extinction because of their direct connections to shifts in temperature and precipitation (Giorgi et al. 1994, Easterling et al. 2000a, IPCC 2007). Specifically, both historical records (<u>http://www.wrcc.dri.edu</u>) and climatic models (Easterling et al. 2000a) for the Great Basin Desert project increases in precipitation at the end of the natural growing season, in August-September (Fig. IV.1).

In addition to the perils brought about by shifts in precipitation, one more challenge pushes the existence of the desert biota to the edge: the great spatial heterogeneity of aridlands. Spatial variation of resources in deserts can be as large within the rooting area of an individual plant as the variation in the entire community (Jackson and Caldwell 1993). One of the hypothesized mechanisms to cope with spatial heterogeneity is to develop vasculature redundancy so that cavitated vessels (the inevitable result of the negative pressures under which most perennial desert plants operate in order to uptake belowground resources, and that can halt the soil-water-atmosphere continuum that is necessary for photosynthesis to take place; Tyree and Zimmermann 2002) can be bypassed (Ewers et al. 2007, Pratt et al. 2008, Schenk et al. 2008) and even refilled (Hacke et al. 2001).

In Chapter II, I explore the ability of individuals of *C. flava* to uptake belowground resources in space and time. First I described histologically a previously undescribed root structure, the *short root*, where no root elongation is necessary prior to the development of fine roots in response to rains. Then I simulated pulses of precipitation of various intensities at the end of the growing season and around different regions of the plants. This research highlights the ability of *C. flava* to benefit from pulses of precipitation at the end of its growing season and to induce the growth of fine roots only in those patches of soil that were watered.

In Chapter III, I test whether the ability for spatial resource uptake described above also translates in spatial transport within the individual plant; in other words, whether individuals of *C*. *flava* are hydraulically integrated or sectored. I performed a battery of complementary anatomical and physiological experiments to test whether preferential vascular pathways develop with ontogeny such that the cavitation of a specific vessel could be refilled by integrated juveniles, but not by sectored adults, thus resulting in the preferential shrinkage of large plants under hydraulic stress. The results indicate that while juveniles are able to compensate the hydraulic loss of a lateral root and to transport dye and water from any lateral root to the entire canopy, hydraulic sectoriality develops within the lateral roots as plants grow older, even though the whole system remains integrated to the taproot. Histological sections of the caudex, the underground stem, revealed that anatomical traits directly related to hydraulic design, such as xylem lumen, heartwood area, and distance between neighboring xylem vessels, explain how individuals of *C*. *flava* become sectored.

In Chapter IV, I explore the role of plant shrinkage in buffering climate change at the population level in *C. flava*. Previous research has already shown that *C. flava* creates new leaves (Casper et al. 2001) and roots (Chapter II) in response to late summer rains. By following a natural population of *C. flava* for five years, replicating simulated intense pulses of precipitation at the end of each growing season in separate sets of permanent plots, and constructing integral projection models (Easterling et al. 2000b), I was able to show long-term positive effects of late-summer rains on the population growth rate of *C. flava*. However, different aspects of the life cycle were affected differently: individuals that were watered the previous year produced more flowers and underwent less ovule abortion, a common characteristic of control plants (Casper 1981), while recruitment was

not affected. As a consequence the role that reproduction played in the population dynamics was virtually nil. In contrast, size fluctuations (growth and shrinkage) governed the population dynamics: watered individuals had greater survival and a higher chance of either staying the same size, in years after drought, or growing, in relatively wet years, when compared to the control plants. Plant shrinkage occurred profusely the year after natural droughts. The LTRE analyses (Caswell 2001) revealed the important role of natural variation in precipitation, as well as the simulated pulses, on the overall population fitness. Perhaps the most shocking result is that large individuals (>40 rosettes), in spite of being common at the field site, do not contribute much to the population growth rate.

I.3. Is shrinkage universal?

To determine the importance of plant shrinkage beyond the demographics of a single species (*i.e.*, *C. flava*) I extended my studies into a representative portion of the plant kingdom. I utilized the database COMPADRE II, which contains ecological, phylogenetic and demographic (population projection matrix) information for over 700 plant species. In Chapters V and VI, I explore how often plant species undergo shrinkage and how shrinkage correlates with other demographic processes. In addition, an exhaustive review of the literature associated to the published projection matrix studies of COMPADRE II allowed me to report that shrinkage has indeed been overlooked; the reasons for this are presented in Chapter VI.

As a first approach to understanding the demographic implications of shrinkage from a comparative perspective, I analyzed the matrix models of 80 herbaceous perennial species (Chapter V), previous standardization of their matrix dimensions (Salguero-Gómez & Plotkin 2010; Chapter VII). The results indicate that shrinkage correlates with a different set of demographic parameters than either stasis or growth do, and thus lumping shrinkage with stasis or with growth, as has been done in the past (Silvertown et al. 1993, Pfister 1998, Franco and Silvertown 2004), is not justified. In a second step, I compared the relative importance (de Kroon et al. 1986) of all demographic processes (e.g., clonal growth, sexual reproduction, dormancy, etc) for species with and without shrinkage. The results indicate that shrinkage is biologically linked to reproduction, growth and survival, and it positively correlates with lifespan and resilience. Then I used loop analyses (van Groenendael et al. 1994) to explore the importance of shrinkage integrated with growth in the ability of "phenotypic size plasticity". This approach led to the realization that high population growth rates can be achieved not only through high reproduction, but also through the persistence of phenotypically plastic individuals.

I.4. Can shrinkage ever be adaptive?

Motivated by the fact that shrinkage had positive effects on the population growth rate of *C. flava* in over 50% of the examined period × treatment interactions (Chapter IV), I then looked for evidence of positive vital rate sensitivities of shrinkage in a larger set of herbaceous perennials and found that 33 out of 123 species show this phenomenon (Salguero-Gómez, Burns & Casper, unpublished). That shrinkage could ever have positive effects on the population growth rate has important implications for plant ecology and evolution, and it begs for a re-evaluation of how we use plant size to study plant demography. It is commonly assumed that in plants *bigger* means *better* because typically survival and reproduction, the two components of fitness, scale monotonically with size (Harper 1977, White 1979, Watkinson and White 1986). Because vital rate sensitivities are analogous to Lande's selection gradients (van Tienderen 2000), positive vital rate sensitivities of shrinkage imply that there is a selection gradient that favors decrease in size of those individuals because shrinking results in greater individual fitness. Hence, bigger may not always be better.

How, mechanistically, could shrinkage be adaptive? *Cryptantha flava* offers an excellent study system to further explore this question. As previously described (Chapter III), *C. flava*'s hydraulic architecture of lateral roots shifts from integrated in juveniles to sectorial in adults, while the taproot remains integral to the whole individual regardless of ontogeny. Consequently, the death of a module (group of rosettes connected to the same stem within an individual) should result in an increase of survival and/or fecundity (= greater fitness) of the remaining modules. Recent research has pointed out the potential adaptive value of sectoriality in arid environments (Zanne et al. 2006, Schenk et al. 2008), where the respiratory demands fluctuate largely depending on the temperatures and amount of water available intra- and inter-annually. Schenk (1999) highlighted the fact that in deserts, sectorial plants achieve longer lifespans than integrated species. This parallels the observation that species with shrinkage achieve longer life spans than species without shrinkage (Chapter IV). I argue that sectoriality facilitates the independence of modules, and thus the death of one module results in plant shrinkage,
which in turn may not only allow the whole individual to survive, but also may increase its overall fitness. Although not a part of the present document, there is evidence that when a module of *C. flava* dies naturally, both the survival and fecundity of the remaining modules increase significantly (Salguero-Gómez & Casper, unpublished), and that the probability of shrinkage correlates negatively with the demographic rate of senescence of over 100 herbaceous species (Salguero-Gómez, Burns & Casper, unpublished). Obviously, correlations do not prove causality, but when taking all these lines of evidence together, it seems reasonable to argue that shrinkage may allow plants to escape senescence, produce longer lifespans, and provide a greater competitive ability in contrast to species that are not sectored. Plants can occlude xylem vessels in response to injury or as protection from fungi (tylosis sensu Tyree and Zimmermann 2002) and further research should address whether tyloses can result in plant shrinkage. This will ultimately prove that plants can indeed internally regulate size.

The field of plant demography has undertaken colossal steps in the past few decades and now there exists a massive arsenal of robust statistical procedures to disentangle the implications of shrinkage (Chapter VI). Showing that shrinkage happens frequently, pointing out that the way size is measured may not be optimal for modeling population dynamics and reporting the effects of shrinkage and its ecological correlates represent just the tip of the iceberg. I hope that the present doctoral research will motivate other scientists to further pursue a better understanding of the role of size in plant ecology and evolution.

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Figure I.1. Multidisciplinary "T"-shaped approach undertaken to study the importance of plant shrinkage: by studying the anatomical features, physiological processes and demographic dynamics within and among individuals for the study species *Cryptantha flava* I have gained a basic understanding of how plants may shrink. By comparing demographic information of over 700 plant species, I have explored the frequency and importance of shrinkage across the plant kingdom.

Chapter II

Introducing short roots in a desert perennial: anatomy and

spatio-temporal foraging responses to increased precipitation

Roberto Salguero-Gómez

in collaboration with Brenda B. Casper

II.1. Summary

- The desert flora possesses diverse root architectures that result in fast growth in response to precipitation. We introduce the *short root*, a previously undescribed third-order root in the aridland chamaephyte *Cryptantha flava*, and explore fine root production.
- We describe the *short root* anatomy and associated fine roots, correlate standing fine root crop with soil moisture, and explore the architectural level –the short root, second order lateral roots, or the whole root system– at which fine roots are induced by watering and the amount of water required.
- We show that (i) short roots are borne at intervals on lateral roots and produce fine roots at their tips, (ii) new fine roots are white and have root hairs, while brown and black fine roots are apparently dead, and (iii) fine root production is triggered at the level of lateral roots and with relatively low precipitation (≤ 2 cm).
- Short roots are suberized thus not capable of water uptake themselves, but serve as initiation sites for fine roots that grow rapidly in response to rainfall. Thus, C. flava should be a beneficiary of projected precipitation increases in habitats where rainfall is pulsed.

Key words: *Cryptantha flava*; fine root; Great Basin desert; hydraulic sectoriality; pulse-reserve paradigm; short root; soil water content; threshold.

"Sometimes you have to go back to the root to solve the (above-ground) problem"

P. Liancourt, 2009

II.2. Introduction

Life in arid ecosystems is primarily limited by the overall low, yet temporarily and spatially variable water availability. Water modulates microbial decomposition and nutrient cycling (Steinberger *et al.*, 1995; 2008), facilitates nutrient uptake and transport (Holbrook & Zwieniecki, 2005), and enables photosynthesis. In cold deserts, water is made available by the melting of snow accumulated during the winter and via precipitation pulses during the growing season, which vary greatly in intensity and frequency (Dobrowolski *et al.*, 1990). In addition, the spatial variation of resources –including soil moisture– in deserts may be as large within the rooting area of a plant as the variation in the entire community (Jackson & Caldwell, 1993).

Desert plant species posses a wide array of strategies to cope with such temporal and spatial water variability. Some examples include tolerance to long drought periods via extensive root systems that tap into a large soil volume (Mooney *et al.*, 1980; Canadell *et al.*, 1996), roots that store water (Graham & Nobel, 1999), and spatio-temporal partitioning of the soil moisture by precipitation intensity via differential root depth and seasonal root activation (Lin *et al.*, 1996; Schwinning *et al.*, 2003; Ogle & Reynolds, 2004). Furthermore desert plants are extremely phenotypically plastic and can quickly produce new roots when it rains (Nobel & Sanderson, 1984; Jackson & Caldwell, 1989) and abscise them when the soil dries out (North *et al.*, 1993).

General circulation models project a 25-50% increase in summer precipitation in the next decades in the southwest of the United States (Arritt *et al.*, 2000; Easterling *et al.*, 2000). However, regional climatic models for the Great Basin desert currently differ on whether this increase in precipitation will take place in the form of more frequent, smaller pulses (Sala & Lauenroth, 1982; Field *et al.*, 1999), or fewer, more intense pulses (Groisman *et al.*, 1999; TNAS, 2000). These different pulse intensities may vary in infiltration and runoff (Wainwright *et al.*, 1999) and thus may have consequences for the physiology, demography and community composition of the native flora (Schwinning *et al.*, 2003; Huxman *et al.*, 2004).

Although much work has been devoted to the study of aboveground responses of desert plants to precipitation (Lin *et al.*, 1996; BassiriRad *et al.*, 1999; Gebauer & Ehleringer, 2000; Huxman *et al.*, 2004; Schwinning *et al.*, 2004), we still lack a full understanding of their belowground responses. This knowledge is critical in the light of climate change because root responses typically precede aboveground changes (Fernandez & Caldwell, 1975), because of a large proportion of desert plant biomass is belowground (Canadell *et al.*, 1996), and because the desert flora often operates close to hydraulic failure under the current climatic conditions (Davis *et al.*, 2002; Ackerly, 2004).

In the present study, we explore belowground responses of the aridland species *Cryptantha flava* to spatial and temporal variation in precipitation intensity. Previous studies have shown that *C. flava* can respond to late-summer rainfall by creating new sets of leaves (Casper *et al.*, 2001), that the carbon thus assimilated carries over to the following spring (Casper *et al.*, 2005), and that naturally occurring large fall precipitation augments seedling establishment and contributes to population growth (Lucas *et al.*, 2008). Here, we first offer an anatomical description of a unique root type found in *C. flava*, the *short root* and its associated fine roots. We then examine the abundance of fine roots in relation to natural soil water conditions throughout the growing season and under an experimentally prolonged

growing season, where we simulated pulses of various intensities to explore thresholds of fine root production. Finally we examine the ability of *C. flava* to forage under spatial heterogeneity by watering different soil sectors around a plant and recording its root responses.

II.3. Materials and Methods

Study species and field site

Cryptantha flava (A. Nels.) Payson (Boraginaceae) is a chamaephyte (herbaceoussubshrub; Raunkiaer, 1934) species common throughout the Colorado Plateau, USA (McLaughlin, 1986). Leaves are normally present from late March through early August unless extended by late season rains (Casper *et al.*, 2001). Flowering occurs May-June, and seeds mature by mid-July. Most seeds germinate either in September-October or at the beginning of the following growing season (B. Casper, pers. obs.). Leaf rosettes are grouped into *modules*, each connected to a different branch of the caudex (Fig. II.1.a), the underground stem. There is a single taproot, extending at least 1.5 m deep, from which several lateral roots branch off at depths of 20-40 cm. Lateral roots spread horizontally up to ~0.9 m in juveniles and ~1 m in adults (Peek & Forseth, 2005) before turning downwards at the ends. Fine roots are produced in clusters along the lateral roots.

The hydraulic design of *C. flava* changes with ontogeny. In juveniles, belowground resources gathered by all lateral roots and the taproot are shared throughout the entire individual, but as plants grow they become internally fragmented, resulting in several "integrated hydraulic units" (*sensu* Schenk, 1999); soil resources taken up by a specific lateral root travel to a specific

rosette module (Salguero-Gómez & Casper, 2011; see chapter III). The roots of adults also differ in having a thicker covering of suberin, a hydrophobic protein, which likely reduces water loss during droughts (R. Salguero-Gómez, pers. obs.).

Experiments were conducted and material for histological examination collected at a site managed by the Bureau of Land Management near the Redfleet State Park (40° 30'N, 109° 22'30'' W, 1730 m a.s.l., NE Utah). The vegetation is dominated by woody species (*Juniperus osteosperma, Artemisia tridentata* and *Chrysothamnus nauseosus*); *C. flava* is the dominant chamaephyte. The soil is an Aridisol, and *C. flava* thrives where a discontinuous, thin hardpan (10-15 cm deep) is not present.

Root histology

For histological examination of fine root clusters, we collected segments of lateral roots during Summer 2007 and fixed them *in situ* with FPA (30% ethanol, 5% propionic acid, 5% formaldehyde, 50% distilled H_2O , with an additional 10% glycerol to soften tissue for later sectioning). Samples were dehydrated in a graded ethanol series, embedded in histological resin (Technovit 7100; Heraeus Kulzer, Frankfurt, Germany), sectioned at 10 µm using a rotary microtome with a Tungsten blade (Reichert-Jung, D-profile; Leica, Bannockburn, IL, USA), and stained with Toluidine blue (0.5%, v/w). Longitudinal and cross sections were photographed (Olympus BX51; Olympus, Allentown, NJ, USA) at 10X and 40X magnification.

Climatic data

To compare the timing and amount of our experimental watering to natural patterns of precipitation, we obtained records (1931-2008) from a permanent meteorological station, "Maeser 9 NW," located 18 km away, at 1950 m a.s.l. (Western Regional Climate Center, <u>http://wrcc.dri.edu</u>). Because in cold deserts the buildup of soil moisture from snow can be important the following growing season (Ogle & Reynolds, 2004), we compared annual precipitation from September of the preceding year to August of the studied year (2006-2007 or 2007-2008) to the long-term mean (1931-2008). We also estimated from the long-term climatic data the probability that a precipitation event equal in intensity to each of our experimental watering treatments would occur within each calendar month.

Experimental design

Toward understanding the ecology of fine roots, we measured the standing number of fine roots under natural levels of soil moisture and also fine root production in response to experimental watering treatments. We were interested both in the quantity of water needed to induce fine roots and whether induction is controlled at the level of the whole plant, the entire lateral root or the specific site of a fine root cluster.

Standing fine root crop during the growing season

We collected lateral root segments throughout the growing season and compared the number of live fine roots to soil moisture content. We removed ~5 cm long segments of lateral roots from eight arbitrarily chosen individuals on 13 different days at ~7 day intervals beginning the last week of May until the last week of August, both in 2007 and 2008. Roots were obtained at approximately 25 cm depth and 20-30 cm away from the caudex and preserved immediately in 50% ethanol. We never re-sampled individuals. We quantified the standing fine root crop as the total length of white, apparently live and functional, fine roots (Fig. II.1) on each lateral root segment, normalized by the actual length of the sampled lateral root (mm fine root 'mm⁻¹ lateral root). Each fine root was measured to the nearest 0.1 mm with a caliper under a dissecting microscope (Olympus MV Plapo 2XC). We also collected soil surrounding the sampled lateral root segment to calculate the gravimetric soil water content (*SWC* hereafter; Pearcy *et al.*, 1989). We counted the total number of leaf rosettes, which correlates strongly with aboveground biomass (Salguero-Gómez & Casper, 2011; chapter III), and classified individuals as juveniles (non-flowering, < 25 rosettes individuals without evidence of having shrunk from a larger size) or adults (\geq 25 rosettes) to test whether ontogenetic stage and SWC affected standing fine root crop using a 2-way ANOVA.

We tested whether precipitation affects fine root production by carrying out three analyses (ANCOVA) for each year with plant size as covariate, standing fine root crop as the response variable, and either (i) SWC, (ii) monthly precipitation registered the calendar month of root collection, or (iii) monthly precipitation registered the calendar month immediately preceding root collection date as the explanatory variable. Data met normality assumptions. We then fitted linear and polynomial regressions to describe changes in standing fine root and SWC over the 2007 and 2008 growing seasons separately and used adjusted R^{2} 's to determine the best model.

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Moisture threshold for producing fine root growth

We examined fine root production in response to simulated pulses of precipitation in August, both in 2007 and 2008. We chose three locations, 100 m apart, and supplied no water (0 cm), or a one-time pulse of precipitation of 2, 4.5 or 7 cm evenly distributed over the 1m radius of a circle center on each individual (*homogeneous watering treatment*, hereafter). Long-term data show these amounts occur naturally with probabilities of 0.7-0.015 in August (Fig. II.2). To ensure accurate deliveries of water pulses, we place small rain gauges within the watered area. Each arbitrarily selected plant ($n_{Total} = 72$) was watered once between 17:00 h and 18:00 h. All watering took place over three days during the second week of August, when natural monsoonal precipitation might occur. No natural precipitation occurred during or two weeks prior to water in 2008, but a light rain (< 0.3 cm) occurred during the first week of August 2007. Prior to watering, for each individual, we counted the number of rosettes and collected ~100 g of soil 1.5 m south at 25 cm depth between 16:00 h and 18:00 h in order to obtain pre-treatment gravimetric soil water content (SWC_{Pre-watering}).

Between 16:00 h and 18:00 h on the seventh day after watering an individual, we collected one 5-cm lateral root segment from its east side and one from its west side at a depth of ~ 25 cm and 20-30 cm from the caudex. We counted white fine roots and measured the standing fine root crop as previously described. At the time of root collection, we also collected ~100 g of soil neighboring the lateral root in order to measure post-treatment soil water content (SWC_{Post-watering}). We calculated the net change in soil water content caused by our watering treatment as Δ SWC = SWC_{Post-watering} - SWC_{Pre-watering}.

We used linear regressions to examine the effect of pulse intensity on standing fine root crop and on Δ SWC. We tested significant differences among pulse intensities in standing fine root crop and in Δ SWC using the Tukey-Kramer HSD tests (Sokal & Rohlf, 1995). Since date of sample collection, plant size (regression analyses), and whether the root segment came from the east or west side of the plant (paired t-test) did not significantly affect either fine root crop or Δ SWC, we excluded them from posterior analyses.

Degree of independence of fine root growth

Because we were interested in a plant's response to soil water heterogeneity, given the species fragmented architecture (Salguero-Gómez & Casper, 2011; chapter III), we supplied pulses of precipitation to different portions of the root system to determine the spatial scale at which water induces fine root production.

First, we tested whether fine roots are produced in response to water applied to a cluster of fine roots. We arbitrarily chose 16 individuals in late May 2007, carefully excavated one live lateral root, and recorded the number and measured the cumulative length of live fine roots within a single cluster using a caliper. For eight individuals, we carefully placed beneath the lateral root a 30 mL plastic cup filled with water and used a sponge to wick water to that single cluster of fine roots. One end of the sponge was placed in the water and the other wrapped around the lateral root and fine root cluster and covered with plastic wrap to prevent conduction of water to neighboring portions of the root. In the remaining eight individuals, we tagged a targeted cluster of fine roots with tape on the lateral root and measured the number and cumulative length of white fine roots. In both cases, watered and unwatered, we replaced the soil and re-measured the number and cumulative length of white fine roots within the targeted fine root clusters seven days later. No natural precipitation occurred during this experiment. We used repeated measures ANOVA (Sokal & Rohlf, 1995), with watering treatment and time of measurement as explanatory variables, to examine cumulative live fine root length at day 0 and 7. Because six of the 16 targeted fine root clusters had no live fine roots, data were not normally distributed. We excluded these from the analyses, but we report their responses here.

Failing to induce fine roots at the level of the fine root cluster, we then tested whether fine roots are induced along lateral roots when the soil around them is watered. We arbitrarily selected individuals in each location used for the homogeneous watering treatment and watered a 60° sector of a 1-m radius circle centered on each plant (heterogeneous watering treatment, hereafter). We simulated precipitation pulses of 2 cm, 4.5 cm and 7 cm on 15, 15 and 10 individuals per location and year, respectively ($n_{Total} = 240$ plants). Watering took place at the same time as the homogeneous watering treatment, and seven days later we collected two lateral root segments per individual, one from the watered sector and the other 180° away in the unwatered sector. We counted the number of live fine roots on each sample and measured their standing fine root crops. We collected soil 1.5 m south from each individual at the onset of the experiment and at the time of root collection immediately adjacent to each sampled lateral root in order to calculate Δ SWC. For each year, we carried out 2-way ANOVAs with pulse intensity and sector (watered or unwatered, paired by individual as a random variable) and as explanatory variables and standing fine root crop or Δ SWC as response variables. Location, plant size and date of water application were not significant effects.

To determine whether fine root growth on lateral roots in watered sectors is the same as when the whole root system is watered, we compared standing fine root crop and Δ SWC between the heterogeneous and homogeneous watering treatments each year. First, we made comparisons between the 0 cm pulse of the homogeneous watering treatment and the unwatered sector of the heterogeneous treatment using t-tests. Next, we made comparisons between the homogeneous watering treatment and the watered sectors of the heterogeneous watering treatment using 2-way ANOVAs with treatment and pulse intensity (2, 4.5 and 7 cm) as explanatory variables.

Finally, we determined whether the standing fine root crop induced by each of our watering treatments at the end of the growing season differed from the standing fine root crop under a comparable level of SWC during the growing season. To do so, we tested whether the slope of the relationship between SWC and standing fine root crop differed for natural levels of precipitation and our experimentally manipulated pulses. We used a two-way ANOVA with standing fine root crop as the response variable and SWC and pulse intensity (natural levels or pulses intensities of 2, 4.5, or 7 cm) as explanatory variables. Because in both years, the SWC x pulse intensity interaction was not significant, we carried out ANCOVAs with SWC as main effect and pulse intensity as the covariate to compare the relationship between SWC and fine root crop among pulse intensities. We used JMP 8.0 (SAS Institute) for all statistical analyses.

II.4. Results

Histology of short roots

In *C. flava*, fine roots, first-order roots are produced exclusively on second-order short branch roots, which in turn are borne on the third-order lateral roots. We call these

second-order roots "*short roots*"¹ because their lack of elongation and their production of fine roots are analogous in function to non-elongating short shoots in many woody species (Fig. II.1.e, g). Our histological investigations reveal that short roots develop from the pericycle of the lateral root, rupturing the cortex as they emerge (Fig. II.1.f,g), and they connect the vasculature of the lateral and fine roots (Fig. II.1g). Most of the short root, is covered by the waxy protein suberin (Fig. II.1.f). Short roots average 2.2 \pm 0.4 (S.E.) mm in width and 2.7 \pm 0.3 (S.E.) mm in length.

Fine roots exist in three color-classes: white –the only ones apparently alive, brown and black. These differ in their cellular integrity and spatial positioning on the short root: white fine roots are found at the apex, brown fine roots lie immediately posterior to the white ones, and black fine roots occur at the base of the short root (Fig. II.1.e,g). Unicellular root hairs are only present on white fine roots (Fig. II.1.c,d), which have a one to two cell epidermis, a cortex two to three cells thick, and a typical onecelled endodermis and stele (Fig. II.1.d). Neither subcellular components nor vascular tissues are identifiable in brown and black fine roots, which are significantly more fragile and ~3-fold thinner than white fine roots, and withered. At any one time, a short root typically supports either none or just one white fine root and 1-6 brown or black fine roots total. Short roots contain a significant proportion of cortical cells (Fig II.1.f,g), considerably more than the lateral root.

¹ The structure *short root* described here is not to be confounded with the SHORT-ROOT gene (*SHR*), which controls asymmetric cell division and formation of root endodermis and cortex (Helariutta *et al.*, 2000).

Climate patterns

The long-term (1930-2008) annual mean precipitation at the Maeser meteorological station is 25.11 cm, but the amount of precipitation has increased significantly during the past 78 years (Annual precipitation: t = 43.76, df = 76, P < 0.001), with the greatest monthly increase in August (Online supporting information, table II.1). Annual precipitation was below the mean in 2006-2007 (28.11 cm) and above the mean in 2007-2008 (36.34 cm). In 2006-2007, winter precipitation was above the mean but the growing season was drier. Precipitation in 2007-2008 was more evenly distributed throughout the year (Fig. II.3.a). The probability of a precipitation event comparable to intensities used in our experiment occurring within the span of a week varies monthly. The baseline probability for no precipitation is rather constant throughout the year (pulse intensity = 0 cm; average probability $p = 0.67 \pm 0.02$, S.E.); large precipitation events are more likely in May, August and October (Fig. II.2).

Standing fine root crop relates to soil water content

Under natural precipitation, the standing fine root crop of *C. flava* was significantly less during the 2007 growing season (0.17 ± 0.02; $x \pm S.E.$) than in 2008 (0.24 ± 0.02; t = 6.32, df = 377, P = 0.01). The standing fine root crop of an individual was positively correlated with local SWC both years (2007: t = 5.81, df = 190, P = 0.01; 2008: t = 9.27, df = 185, P < 0.001; Fig. II.3.b) but not with ontogenetic stage (juvenile or adult) or its interaction with SWC. Furthermore, soil sample SWC and standing fine root crop were both positively correlated with the amount of precipitation received during the calendar month of each sample collection (SWC, 2007: t = 7.30, df = 190, P < 0.001; 2008: t = 5.92, df = 185, P < 0.001; fine root crop, 2007: t = 1.89, df = 190, P = 0.06; 2008: t = 4.02, df = 185, P < 0.001) but not with precipitation in the previous month. In both years, SWC and standing fine root crop decreased during the growing season, but then increased in mid August, coinciding with the arrival of monsoonal rainfall events (Fig. II.3.b). Such responses were satisfactorily described by second-degree polynomial regressions; for the standing fine root crop (SFRC) in 2007: SFRC = $0.58 - 2.45 \cdot 10^{-3}$ ·d + $3.61 \cdot 10^{-5}$ ·(d - 189.19)² (adjusted $R^2 = 0.75$, P < 0.001) and in 2008: SFRC = $1.31 - 6.25 \cdot 10^{-3}$ ·d + $9.85 \cdot 10^{-5}$ ·(d - 186.08)² (adjusted $R^2 = 0.83$, P < 0.001); and for the soil water content (SWC) in 2007: SWC = $0.02 - 7.25 \cdot 10^{-5}$ ·d + $3.27 \cdot 10^{-6}$ · (d - 188.85)² (adjusted R^2 =0.51, P = 0.011) and in 2008: SWC = $0.11 - 5.31 \cdot 10^{-4}$ ·d + $1.07 \cdot 10^{-5}$ · (d - 186.07)² (adjusted R^2 =0.94, P < 0.001), where d = day of year.

Threshold for fine root growth

Standing fine root crop in *C. flava* increased with the application of water of any intensity (2, 4.5 and 7 cm) both years (Fig. II.4.a). The increase was driven both by the production of new white fine roots and the elongation of existing fine roots; fine roots were present on 14% (2007) and 35% (2008) of the sampled short roots in all watering treatments combined (2, 4.5 and 7 cm), while white fine roots were present only in 4% (2007) and 17% (2008) in controls (0 cm). The average length of white fine roots in the watering treatments was 11.41 ± 2.75 (S.E.) mm (2007) and 9.65 \pm 2.32 mm (2008) and in control plants 0.88 \pm 0.19 mm (2007) and 3.97 \pm 2.12 mm (2008).

Although Δ SWC was positively and linearly affected by the pulse intensities used (2007: t = 3.95, df = 62, P < 0.001; 2008: t = 2.81, df = 56, P < 0.001; fig. I.4.b), the standing fine root crop did not exhibit a monotonic increase as a function of pulse intensity; there was a significant increase in live (white) fine root abundance between 0 to 2 cm of precipitation (P < 0.005 for both years), but standing fine root crop did not differ among pulses of 2, 4.5 and 7 cm either year (Fig. II.4.a).

Degree of independence in fine root growth

Fine root number and cumulative length had not increased by seven days after the application of water to individual fine root clusters (short roots) of *C. flava* (Table II.2). Furthermore, short roots that did not support live fine roots prior to watering them individually had not developed new life fine roots seven days later. In contrast, in the heterogeneous watering experiment, the standing fine root crop was significantly higher in the root sector that received water than in the unwatered sector, regardless of pulse intensity (Fig. II.5; table II.3).

The standing fine root crop for sectors that did not receive water in the heterogeneous treatment $(0.013 \pm 0.003 \text{ mm} \text{ mm}^{-1} \text{ in } 2007, 0.072 \pm 0.0337 \text{ mm} \text{ mm}^{-1} \text{ in } 2008)$ was not different from roots in the homogeneous watering experiment where no water was delivered to the plant at all $(0.004 \pm 0.007 \text{ mm} \text{ mm}^{-1} \text{ in } 2007, 0.007 \pm 0.087 \text{ mm} \text{ mm}^{-1} \text{ in } 2008$; table II.4.a). Likewise, the standing fine root crop for plants receiving water in the homogeneous treatment and for watered sectors of the heterogeneous watering treatment did not differ for any pulse intensity (Table II.4.b). Across all

watering intensities, the standing fine root crop in watered sectors of the heterogeneous treatment was 0.17 ± 0.03 mm⁻¹ in 2007 and 0.22 ± 0.03 mm⁻¹ in 2008 and in watered plants of the homogeneous treatment 0.17 ± 0.04 mm⁻¹ in 2007 and 0.22 ± 0.04 mm⁻¹ in 2007 and 0.22 ± 0.04 mm⁻¹ in 2008.

No detectable amount of water moved from watered to unwatered soil sectors in the heterogeneous watering experiment. SWC in the unwatered soil sector of the heterogeneous watering experiment remained constant regardless of pulse intensity in 2007 and decreased slightly in 2008 (Fig. II.5.b; table II.3). Furthermore, the Δ SWC of the unwatered soil sectors of the heterogeneous watering treatment and the soils of 0 cm intensity in the homogeneous watering treatment did not differ (Table II.4.a).

Retrospective comparison on the production of fine roots

The relationship between SWC and standing fine root crop (Fig. II.6) was the same in the watering treatments (2, 4.5 and 7 cm) at the end of the growing season as under natural levels of precipitation throughout the growing season. While the overall 2-way ANOVA model comparing root standing crop among water treatments and natural levels of precipitation was significant (2007: $F_{7, 229} = 8.26$, P = 0.03; 2008: $F_{7, 226} = 12.41$, P < 0.001), neither pulse intensity alone nor its interaction with SWC had a significant effect. The ANCOVA tests with SWC as a main effect and pulse intensity as covariate revealed a significant effect of the former on standing fine root crop (2007: P = 0.02; 2008: P < 0.001), but pulse intensity, including natural levels of precipitation, was not significant.

II.5. Discussion

An undescribed root type: the short root

To our knowledge the root type introduced in this study, the *short root*, has not been previously described. This structure is at least present in a congener (*Cryptantha flavoculata*; R. Salguero-Gómez, pers. obs), and there exists photographic evidence for another desert perennial in a different family (*Franseria deltoidea*, Compositae; Cannon, 1911. P. 73), although those roots were not examined histologically. The name "short root" was chosen because of its analogous design to short shoots in taxa such as *Ginkgo biloba* (Gunckel & Wetmore, 1946).

We suggest that the short root anatomy in *C. flava* is advantageous in a waterlimited environment for at least three reasons: (i) It enables the rapid production of fine roots in response to sufficient precipitation just as short shoots of some desert shrubs quickly produce new leaves (Edwards & Diaz, 2006). In both short shoots and short roots, little growth of the apical meristem is necessary in order to generate lower rank structures (leaves or fine roots). We found fine roots two days after a simulated rainfall of 4.5 cm (R. Salguero-Gómez, unpublished). (ii) The clustering of fine root production on short roots, and thus in discrete locations, minimizes the exposure of more permeable root surface to dry soils because the remainder of the lateral root is suberized, although the taproot of *C. flava* is less suberized with increasing depth. (iii) The short root serves as a short connector pathway between fine roots and lateral roots, which with their high proportion of conducting tissue are suited for long distance transport. However, lateral roots of *C. flava* do have some cortex, which is lacking in second-order roots of trees (Guo *et al.*, 2008).

Because of their rapid response, fine roots in *C. flava* perform analogously to "rectifier roots" of some succulents in response to water (Nobel & Sanderson, 1984), proteoid roots in response to rich P and Fe microsites (Watt & Evans, 1999), or pad adventitious roots in climbing vines (Shishkova *et al.*, 2007). However, the branching architecture of *C. flava* differs structurally from these other examples. Fine "rain roots" of succulents are mostly found on thin lateral roots several branching orders removed from the taproot; these lateral roots are not as well suberized (Gibson & Nobel, 1990), and the rain roots themselves are more ephemeral (Snyman, 2006) than the fine roots *C. flava* that may continue growing at least four days after watering (Salguero-Gómez, pers. obs.). In addition, lateral roots of cacti are usually closer to the soil surface than those of *C. flava*, and so precipitation pulses of very low intensity can activate their fine root production (Dougherty *et al.*, 1996.).

Although we do not have direct evidence, we suspect that increased coloration of fine roots correlates with age, based on the fact that only white roots possess root hairs, the darkest fine roots are located farthest from the short root apex, and dark roots show a general degradation in internal structure. Thus fine root coloration matches a chronological sequence if fine roots are always produced near the apex of the short root. Additionally, mycorrhizal vesicles, which may resist unfavorable environmental conditions (Harrier, 2001), are primarily found in brown and black fine roots, while hyphae and arbuscules are visible in white ones (Fig. II.7). While fine roots in other species may become more pigmented with age (Van Rees *et al.*, 1990), the extent to which they lose function is debated; in some species, dead fine roots are still able to absorb water (Eissenstat & Yanai, 1997; Comas *et al.*, 2000). The function of brown and black fine roots in *C. flava* deserves further attention.

Spatial heterogeneity and resource foraging

While fine roots are confined to short roots, our watering experiments show their production occurs in response to soil moisture cues received at a higher level of root architecture, though still at a level below the whole root system. This ability should position *C. flava* as an effective forager for spatially heterogeneous soil resources typical of deserts (Forseth *et al.*, 2001; Maestre *et al.*, 2005).

Our results here enable us to link the activity of individual lateral roots in *C. flava* to the spatial distribution of soil resources within the plant as determined in a prior study. In adult plants, but not in juveniles, the movement of water between lateral roots and clusters of leaf rosettes is highly sectored whereby a single lateral root supplies a particular portion of the canopy (Salguero-Gómez & Casper, 2011; chapter III), a condition known as *hydraulic sectoriality* (Orians *et al.*, 2005). While the single lateral root of a juvenile might supply the entire plant with water or even, we hypothesize, allow horizontal hydraulic redistribution through the root system from a wet patch of soil to a dry one (Bauerle *et al.*, 2008), an adult's lateral root located in a particularly dry microsite and the particular rosette modules to which it is connected could experience severe water stress without the possibility of augmentation by the remainder of the root system. Indeed, following drought, larger individuals (Casper, 1996; Lucas *et al.*, 2008).

Juveniles are also less reliant on lateral roots and depend more on the taproot than adults (Salguero-Gómez & Casper, 2011; chapter III). Thus root anatomy and development are linked to whole plant physiology and, in turn, to demography. A full understanding of fine root development in *C. flava* in response to water would include information on genetic and developmental mechanisms, including relevant signal transduction pathways.

Temporal variability and climate change

The appearance of new white fine roots in response to watering in August and September suggests that C. flava will exploit end of growing season increases in precipitation projected by some climate change models (Schlesinger and Mitchell 1987, Mitchell et al. 1990 in Lin 1996). Above average precipitation those months has induced new cohorts of leaf rosettes in C. flava at our field site, prolonging the growing season by over a month (Casper et al., 2001). Lin and colleagues (1996) suggest that herbaceous species are better equipped to profit from late season increases in precipitation than woody species due to their shallower root architecture and greater phenotypic plasticity. As a chamaephyte, C. flava has a woody caudex with secondary growth and a deep taproot, but it resembles herbaceous species in its ability to respond rapidly to rainfall events. Our finding some white fine roots throughout the growing season provides morphological confirmation that C. *flava* is capable of taking up water and other soil resources throughout the summer even though it responds strongly to punctual rainfall events, particularly at the end of the growing season (Gebauer & Ehleringer, 2000). The advantages of perennating woody tissue together with the ability to exploit shallow,

temporally available soil resources may help explain the commonness of the chamaephyte growth form throughout much of the cold and arid Colorado Plateau (McLaughlin, 1986).

Thresholds and climate change: small vs. large pulses

Identifying thresholds of soil moisture responses in different species is critical to understanding how changes in the intensity and frequency of rainfall events, as predicted by climate change models, will impact community composition. Intense pulses can recharge the water table, and thus are expected to benefit deep-rooted woody species, whereas small pulses reach limited soil depths, where typically herbaceous forage (Sala & Lauenroth, 1982). Biological responses may not scale linearly with water availability, as suggested by the 'pulse-reserve' paradigm (Noy-Meir, 1973), but exhibit a threshold of activation (Reynolds et al., 2004; Schwinning et al., 2004). Here, we show that C. flava has a relatively low threshold for activation of fine root growth (≤ 2 cm) and that pulses of higher intensity do not result in greater root production. We can think of several explanations for this asymptotic scaling: (i) fine root production may be limited by the plant's carbon budget or physically limited by the number of existing short roots, (ii) additional water uptake might take place through the suberized root layer under very high soil water content, as reported for Atriplex confertifolia (Caldwell & Camp, 1974); and/or (iii) regardless of the permeability of lateral roots, additional fine roots might not further increase water uptake rate. We can reject the possibility that 2 cm pulses are enough to saturate the soil (Sala & Lauenroth, 1982) because increasing pulse intensities resulted in

wetter soils (Fig. II.4.b). Leaf water potentials and/or the use of isotopically labeled water might reveal whether water uptake increases with pulse size even without additional fine roots.

Final remarks

Our description of short roots in *C. flava* and their ability to produce fine roots rapidly in response to soil water adds to the documented repertoire of strategies plants use to cope with spatio-temporal resource variability characteristic of arid ecosystems. Our finding that fine root production can be induced at a scale smaller than the whole root system means an individual can utilize spatially heterogeneous soil resources. The continued production of fine roots in response to late season water causes us to predict benefits for this species, as well as others of similar morphology, from increased late season precipitation forecasted for the Great Basin desert by climate change models.

II.6. Acknowledgements

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Table II.1. Monthly, seasonal and annual patterns of precipitation at the field site. Italics,underlined: P < 0.05; bold: P < 0.001.

Period	df	t-value
January	77	4.24
February	77	<u>7.50</u>
March	76	<u>6.75</u>
April	75	1.62
May	77	10.31
June	76	1.9455
July	76	6.59
August	76	15.13
September October November		2.52
		<u>10.23</u>
		<u>7.63</u>
December		0.189
Annual	78	43.76
Growing season (March- August)	78	20.86
Winter dormant season (September-February)	78	31.48

Table II.2. Summary of the repeated measures analysis of variance for the responses of the live fine roots of *Cryptantha flava* to the water treatment on individual short roots. Italics, underlined: P < 0.05; bold: P < 0.001.

Effect	df	F-ratio
Between-subjects		
Treatment	1	0.02
Treatment(Individuals)	8	0.02
Within-subjects		
Time	1	2.79
Time × Treatment	1	1.07

Table II.3. Summary of the two-way analysis of variance for the responses of the fine root growth and net change in soil water content in the heterogeneous watering treatment, where one sector of the plant was watered with pulses of different intensity (2, 4.5 and 7 cm) and the remaining sector of the plant was unwatered (0 cm). Italics, underlined: P < 0.05; bold: P < 0.001.

		Standing fine root		Net change soil	
		crop		water content	
Effects	df	SS	F-ratio	SS	F-ratio
2007					
Sector	1	1.10	23.46	0.001	<u>9.51</u>
Pulse	1	0.000	0.000	0.001	<u>8.68</u>
Sector × Pulse	1	0.002	0.04	0.010	2.12
<u>2008</u>					
Sector	1	0.749	<u>8.69</u>	0.000	<u>7.57</u>
Pulse	1	0.295	2.61	0.000	0.04
Sector × Pulse	1	0.010	0.17	0.000	0.12

Table II.4. a. Summary of *t*-tests for fine root production and net change in soil water content in soils that did not receive water, from the 0 cm pulse in the homogeneous watering treatment and from the non-watered sectors of the heterogeneous watering treatment. b. Summary of two-way analysis of variance for the responses of the fine root growth and net change in soil water content where plants were either watered in one sector or in its entire surrounding surface with watering pulses of various intensities (2, 4.5 and 7 cm).

		Standing fine	Net change soil
		root crop	water content
Effect	df	F-ratio	F-ratio
a. Unwatered soil			
<u>2007</u>			
Treatment	1	1.223	0.024
<u>2008</u>			
Treatment	1	0.482	0.20
b. Watered soil			
<u>2007</u>			
Treatment	1	0.002	0.131
Pulse	1	0.094	26.113
Treatment × Pulse	1	0.1885	0.314
<u>2008</u>			
Treatment	1	0.083	0.716
Pulse	1	2.598	0.298
Treatment × Pulse	1	0.094	0.931



Figure II.1. Architecture of an adult of *Cryptantha flava* and its root system. a. Groups of leaf rosettes develop from different shoots (modules), but they all branch off from the same caudex, the central, underground stem. The root system consists of a deep tap root and a discrete number of lateral roots that spread laterally. b. Lateral roots (*LR*) have *short roots* (*SR*), from which fine roots of different colorations develop: white (*WFR*,

white arrow), brown (*BrFR*, brown arrow) and black (*BlFR*, black arrow) fine roots. c. Portion of lateral root containing white, brown and black fine roots. Note that only the white fine root possesses root hairs (*RH*), while the brown and black fine roots are thin and seemingly not functional. d. Unstained 30 μ m cross-section of a white fine root with its epidermal cells (*Ep*), cortex (*CX*), endodermal cells (*En*), and the stele (*S*), which contains the xylem (*X*) and phloem vessels (*P*). e & f. Toluidine-blue stained 8 μ m longitudinal and cross section, respectively, of the vasculature of the lateral root and its connection with the short root from the pericycle (*PC*) of the lateral root. g. Stained 5 μ m longitudinal section of a short root, showcasing the development of a white fine root from the apex of the short root, and the connections of brown and black fine roots at the base of the short root.



Figure II.2. The probability that a cumulative precipitation of various intensities $(0, \ge 2, \ge 4.5 \text{ or } \ge 7 \text{ cm})$ will take place within the span of a week varies throughout the year and is particularly greater in May, August and November. Note logarithmic response axis.



Figure II.3. Precipitation and root responses during the study. a. Monthly mean precipitation in relation to the 1930-2009 record. b. Gravimetric soil water content (black dots) and amount of fine roots (white dots) of *C. flava* as a function of the collection time during the growing seasons of 2007 and 2008. Black and gray lines indicate polynomial regressions fitted to the soil water content and standing fine root crop, respectively.



Figure II.4. Effect of the homogeneous watering treatment with different pulse intensities on (a) the fine roots and (b) soil water content in August of 2007 and 2008. Bars with the same uppercase letters did not differ significantly in Tukey's HSD adjusted comparisons for each panel separately. Bars represent standard errors. Sample sizes are described in the methods section.



Figure II.5. Effect of the heterogeneous watering treatment, where one sector of the plant was watered with different pulse intensities (gray) but another was not (white) on (a) the fine roots and (b) soil water content in August of 2007 and 2008. Bars with the same uppercase letters did not differ significantly in Tukey's HSD adjusted comparisons for each panel separately. Bars represent standard errors. Sample sizes are described in the methods section.


Figure II.6. Comparison of the paired soil water content (SWC) - standing fine root crop (mm live fine root 'mm⁻¹ lateral root) measured throughout the growing season under natural precipitation, and during the first week of August of 2007 and 2008, when pulses of various intensities were simulated (2, 4.5 and 7 cm).



Figure II.7. Association of arbuscular mycorrhizal fungi (AMF) in the fine roots and short roots of *Cryptantha flava*. a. White fine root (*WFR*, white arrow) stained with trypan blue stain (for a detailed methodology see Phillips & Hayman, 1970), which highlights entities of mycorrhizal nature found outside the root stele (*S*): arbuscule (*AR*) and hyphae (*H*) (*RH*: root hair). b. Stained brown fine root (*BrFR*, brown arrow) with mycorrhizal vesicles (*V*). c. Connection of a white fine root and the short root (*SR*); mycorrhizal fungi are found in both the fine root and the short root (see also figure II.1.f).
d. Portion of short root containing vesicles, arbuscules and hyphae of arbuscular mycorrhizal fungi.

Chapter III

A hydraulic explanation for size-specific plant shrinkage: developmental hydraulic sectoriality

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in collaboration with Brenda B. Casper

III.1. Summary

- While great attention has been paid to the mechanisms controlling plant growth, much less is known about why and how plants shrink. Plant's modular design may facilitate the independence of modules if the xylem vasculature is hydraulically sectored. We examined the hydraulic connectivity of modules comprising juveniles and adults of the aridland, chamaephyte *Cryptantha flava* (Boraginaceae), motivated by the observation that rosette mortality is spatially aggregated in adults, but not in juveniles.
- We explored spatial patterns of leaf wilting after clipping a single lateral root, tracked physiological dyes taken up by a single root, and measured within-plant variation in leaf water potentials after watering a portion of the root system. We then measured xylem anatomical features related to hydraulic connectivity.
- Our approaches reveal hydraulic integration in juveniles but hydraulic sectoriality in adults. We attribute the developmental changes to increasing distances between xylem bundles, and larger xylem lumen and heartwood areas as plants age.
- We demonstrate *functional* sectoriality in a desert chamaephyte, and report the mechanism by which sectoriality occurs, offering a hydraulic explanation for the death of whole plant portions resulting in shrinkage of large plants, and for the high occurrence of this design in deserts.

Key-words: *Cryptantha flava*, distance-to-xylem, dye tracking, fragmentation, Great Basin desert, hydraulic integration/sectoriality, leaf water potential.

"Let the gentle bush dig its root deep and spread upward to split the boulder" Carl Sandburgh (1878-1967)

III.2. Introduction

Plants' modular design and indeterminate growth allow them to display large fluctuations in size between years, both growing and shrinking. Understanding the mechanisms that control plant size is important because size is commonly used as a proxy to individual fitness (Harper 1977). Consequently, the ecological, evolutionary and agricultural literature has paid much attention to the factors that promote and limit growth, both at the cellular (Wilkinson & Davis 2008), anatomical (Hsaio 1973; Enquist et al. 2007a), physiological (Enquist et al. 2007b; Niklas 2007) and demographic level (Caswell 2001). However, the ability of perennial plants to decrease in size has been overlooked. This is surprising because plant shrinkage is a frequent phenomenon, occurring in published population projection matrices of over 90% of perennial plant species (n = 199 species; Salguero-Gómez, unpublished; see also chapters V and VI).

In woody plants, portions of the shoot and the associated root may die during drought because the negative pressures of the xylem water column may precipitate dissolved air, resulting in runaway embolism, which may disrupt water flow (Tyree & Dixon 1986; Tyree & Zimmerman 2002). It is commonly assumed that plants evenly distribute belowground resources among all modules of their architecture, a condition known as *hydraulic integration* (Horwath et al. 1992). However, there is increasing evidence that some species are composed of independent hydraulic units (IHUs *sensu*

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Schenck 1999), and that in them, water and nutrient transfer is limited, a condition known as *hydraulic sectoriality* (Orians et al. 2005).

Hydraulic sectoriality is a trait with likely adaptive value in water-limited environments because it may allow the individual plant to (i) avoid runaway embolism (Orians et al. 2005), (ii) optimize resource usage by failing to support other, less fortunate modules foraging in low-resource soil patches, which in turn may increase the probability of whole-plant survival (Ginsburg 1961), and (iii) suppress or slow down whole plant senescence (Silvertown et al. 2001). All of these possibilities are relevant for desert plants because they operate close to hydraulic failure (Tyree & Dixon 1986; Sperry et al. 2008) and must forage for scarce soil resources that are heterogeneously distributed on fine scales (Jackson & Caldwell, 1993).

In the present study, we explore whether the aridland chamaephyte *Cryptantha flava* (A. Nels.) Payson (Boraginaceae; figure III.1) exhibits hydraulic sectoriality. In this species, shrinkage during or following a particularly dry year is specific to larger individuals (Casper 1996) and occurs through the death of spatially aggregated rosettes. Past measurements of leaf water gas exchange in this species—transpiration and photosynthesis—and leaf water potentials do not explain why larger individuals are more severely affected during drought (Casper et al. 2006).

Here, we undertake a multi-disciplinary approach to study the functional hydraulic design and underlying anatomy of *C. flava*. Specifically, we examined functional hydraulic connections between roots and aboveground modules using three complementary approaches: (i) severing an individual root and looking for evidence of localized wilting in clusters of leaf rosettes, (ii) using dyes to track the pathway of water

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movement from a particular root through the shoot, and (iii) measuring within canopy variation in leaf water potentials when only part of the root system was watered. We carried out these experiments on both juveniles and adults. Finally, we investigate whether underlying changes in xylem anatomical traits, such as the distance between neighboring xylem vessels and the area of viable xylem, occur with plant ontogeny and we argue that these traits are ultimately responsible for the shifts we find in the hydraulic architecture in *C. flava*.

III.3. Materials and Methods

Description of study species and field site

Cryptantha flava is a long-lived, aridland plant species with large scattered populations throughout the Colorado Plateau. A single plant may consist of one to > 150 basal leaf rosettes, each with a shoot apical meristem and typically 5-13 oblanceolate leaves. Leaves first appear in mid-April, but considerable leaf turnover occurs as the growing season progresses (Casper et al. 2001). New leaf rosettes arise from basal axillary buds. The species is considered a small chamaephyte (its height, not including flowering stalks, averages 10 cm) with characteristics of both herbaceous and woody species. From a demographic point of view, it is herbaceous perennial because its aboveground tissue is herbaceous and completely replaced each year as the plant enters winter dormancy by August; from a purely anatomical point of view, it is woody because it possesses secondary growth in the branched underground stem, the caudex.

We refer to a group of rosettes and the part of the branched stem to which they are connected as a *module* (Fig. III.1). Juveniles typically have 1-3 modules with 1-10

rosettes per module, while large adults may have up to ~6 modules with 5-20 rosettes in each, although wide variation in this arrangement exists. All modules are connected via the caudex to a single root system (Fig III.1), consisting of a taproot and well-defined lateral roots. The laterals emerge from the taproot at a depth of 15-40 cm and extend horizontally out to 1 m (Peek & Forseth 2005), where they bend downward. In adults, the taproot and lateral roots have a suberized, hydrophobic covering; clusters of ephemeral white, fine roots interrupt the waxy covering every 1-3 cm along the lateral roots. Ephemeral roots can be induced independently by the localized application of water (Salguero-Gómez & Casper, unpublished; chapter II).

The field site is located at the Redfleet State Park, Utah (1730 m, 40 30' N, 109 22' 30" W), a cold desert habitat characterized by the woody species *Juniperus osteosperma*, *Artemisia tridentata*, and *Chrysothamnus nauseosus*, where *C. flava* is the dominant chamaephyte. The precipitation is bimodal, with peaks in May and October. Annual precipitation averages 225 mm, but variation is high (C.V. = 41%).

Functional Sectoriality

In order to evaluate the hydraulic connectivity between roots and rosettes of *C*. *flava* we carried out the following physiological techniques on both juveniles and adults. We defined juveniles as small (\leq 15 rosettes), non-reproductive individuals, and adults as flowering individuals of any size, or not currently flowering individuals of large size (> 15 rosettes).

Severing roots

With hydraulic integration, we would expect some compensation among connected modules so that no part above part of the plant would wilt if a single lateral root were severed. With hydraulic sectoriality, on the other hand, we would expect spatially aggregated wilting/mortality of rosettes. To examine these possibilities, we severed a single lateral root in 12 randomly chosen juveniles and 24 adults in July 2007. Additionally, we severed the taproot instead of a lateral root in another three juveniles and three adults. We carefully excavated a lateral root and followed it 30-40 cm away from the caudex, where we removed a 1-cm long portion and measured its diameter. In the case of the taproot, we exposed and cut it at a depth of 1 m, far below any lateral root. We used extreme care in excavations to prevent injury and immediately replaced the sandy soil.

To quantify the amount and spatial location of wilting, we placed a $30 \times 30 \text{ cm}^2$ grid on 30 cm tall legs over the plant and photographed (Sony Cybershot DSC-H2) each individual from a height of 70 cm before severing the root, then 1, 24, 48 and 72 h after the treatment was applied, and again the following year, in June 2008. The high quality of the photos (1200 dpi) allowed us to count the number of wilted rosettes in the hours following the treatment. We used regressions to examine the relationship between the plant's number of rosettes the day before the treatment and the number of wilted rosettes, if any, at 72 h, both with and without the diameter of the severed root as a covariate. We also looked for abrupt changes in the number of wilted rosettes as a function of initial number of rosettes using a piece-wise regression using R (R Developmental Team 2009).

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Such abrupt change, if any, would indicate a size threshold for the response of rosette wilting.

Tracking dyes

We traced the hydraulic pathways of randomly chosen individuals in July 2007 using solutions of acid fuchsin (1% w/v; m.w. = 585.52 umas), fast green FCF (0.5%; 808.84), and Toluidine blue (0.5%; 305.83) supplied to different lateral roots of 8 juveniles and 24 adults. We uncovered a root as described above, cut it under water in order to avoid cavitation and immediately placed it in a 25 ml beaker containing the dye solution. We covered the beaker with plastic wrap and carefully replaced the soil. After 24 h, we quantified the number and specific location of rosettes that had taken up the dye. We tried to implement the same procedure for taproots but we did not succeed in feeding the dye without causing almost immediate wilting of the whole plant.

To determine if dyes would redistribute within the plant if transpiration were impeded, we isolated the dyed rosettes in a water-saturated atmosphere. Such redistribution would suggest that dyes had originally followed the path of least hydraulic resistance but not the only possible pathway from a particular lateral root. We covered them with a plastic bag containing a piece of wet sponge and then surrounded the bag with aluminum foil. Unstained rosettes were checked 24 h later for potential dye transfer.

Within individual variation in water potential

We also followed the pathway of water movement more directly by measuring variation in leaf water potential within the canopy after watering only a portion of the

root system. Because dye particles are much larger (300-1000 g/mol) than water molecules and other naturally occurring molecules that might be transported in the xylem, such as gibberellins (e.g., GA1: 348.4 g/mol), cytokinins (CK: 234 g/mol), and abscisic acid (ABA: 264.32 g/mol), we wanted to make sure that dye movement tracks the same pathway as water. We conducted the experiment in mid June 2008, when plants were still photosynthetically active but the soil was relatively dry (gravimetric soil water content: 0.03 ± 0.01 g water/g soil; Salguero-Gómez & Casper, *in press*; chapter II), so watering would significantly increase leaf water potentials. Lower leaf water potentials reflecting even drier soils later in the growing season would have forced us to use a psychrometer (M. Peek, , pers. comm.), which is much more time-consuming than the pressure chamber we used here (Model 1001, PMS Instrument Co., Corvallis, Oregon). A rosette module on each individual was carefully identified and tagged at the base with thin tape. Individuals where then randomly assigned to one of three treatments: control with no water (2 juveniles and 3 adults), partial watering (6 juveniles and 12 adults) and full watering (2 juveniles and 3 adults). In early evening on a single day (18.30 h), plants in the full watering treatment received 45 mm of water in a 1-m radius circle centered on the plant; plants in the partial watering treatment received 45 mm of water in a 60° sector of the same sized circle. A pulse of similar intensity at the same time of year was previously shown to stimulate fine root production (Salguero-Gómez & Casper, in press; chapter II). We measured leaf water potentials in all rosette modules at 18.00 h and 22.00 h of the day that the plants were watered at 18.30 h, and then again at 04.00 [predawn] and 12.00 h [*midday*] the following day. We sampled 3-6 fully developed leaves per module of each individual, depending on module size.

We analyzed the effect of the watering treatment on leaf water potentials using repeated measures of variance (MANOVA; Huberty & Olejnik 2006), first with developmental stage as an explanatory variable, and then conducting separate MANOVAs for juveniles and adults, since developmental stage was a significant effect (Table III.1). Watering treatment served as a fixed effect, and individuals and modules nested within individuals as random effects, with measurements repeated four times (18.00, 22.00 h, predawn and midday). These analyses were used to determine if partially watered plants developed greater within-individual variation in water potential over time than plants in other treatments. We also calculated variance components among individuals and among modules at each measurement time to examine their relative contributions to total variation in leaf water potential.

We used within-individual variation in leaf water potentials to cross-validate results obtained using dyes. For partially watered plants, we dug up the watered section of the soil in search of lateral roots and tracked their hydraulic connections to rosette modules using dye solutions just as described previously. We always found only one lateral root in the watered soil sector. We then used absence/presence of dye in the different modules 24 hours after dye application as the response variable in a logistic regression with watering-induced changes in leaf water potential among modules at midday as the explanatory variable. We also saturated the atmosphere of the stained modules, as described above, to explore all possible hydraulic connections aboveground.

We then compared leaf water potentials in partially watered plants to those in plants either fully watered or not watered (controls). First we explored whether dyed modules of partially watered plants operated at the same water potential level as modules of fully water plants; second we explored whether undyed modules of partially watered plants operated at the same water potential level as modules of control plants. We employed unpaired t-tests with plant treatment as dependent variable and leaf water potential as response variable.

Vascular anatomy

We examined vascular arrangement in caudexes of several juveniles and adults, including some adults from the dye-tracking experiment described above, by measuring neighboring xylem distances and widths (Dale 1999). We fixed the caudexes in FPA (30% ethanol, 5% propionic acid, 5% formaldehyde, 50% distilled H₂O) with 10% glycerol to soften tissue for cross sectioning. Discs of the caudex (0.5 cm thick) were taken at 3-4 cm below the first shoot branch and used in standard paraffin and plastic embedding procedures.

We used paraffin-mounted samples to compare general changes in vascular structure with plant size and track internal staining by dyes used in the dye tracking experiment. The samples underwent a dehydration gradient to 100% tert-butanol at room temperature then heated at 58°C for 12 h before embedding (Paraplast Plus®, McCormick Scientific, St. Louis, USA). We carefully sliced off paraffin until a full cross-section was exposed and soaked samples in 1% dish detergent for 24 h to further soften the tissue (J. Mauseth, pers. comm.). We obtained 20-50 µm cross sections per sample using a rotary microtome (Jung supercut 2065 automatic, Leica), mounted them with poly-lysine and removed paraffin in a graded xylene series. Because we were interested in locating the dyes used in the dye-tracking experiment, we did not use any

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histological stain. We photographed the cross-sections through a dissecting microscope (Olympus MV Plapo 2XC) using the image program DP Controller v. 3.1.1.267 (Olympus 2006).

We mounted similar sections of caudexes from 10 individuals in plastic media to study xylem and heartwood characteristics in plants differing in caudex size. Samples were dehydrated in a graded ethanol series, embedded in histological resin (Technovit 7100) for four days, sectioned at 3-5 µm using the rotary microtome with a Tungsten blade (Reichert-Jung, D-profile), and stained with Toluidine blue (0.5%, v/w). Cross sections were photographed on an electronic microscope (Olympus BX51). To determine the relative spacing of xylem bundles and individual vessels, we used the point-to-target distance technique (Dale 1999), where we chose 20 random coordinates within the nondecayed parenchyma region of each caudex cross section and measured the distance from each point to its closest xylem vessels using the program IMAGE J (NIH, 2004). Relatively large measurements of point-to-target distance represent great distances among the targeted objects (Dale 1999) –in this case the xylem bundles and vessels. Thus, larger values of point-to-target distance can be interpreted as spatially separated units of vertical water transport and reduced chances of lateral water transport or hydraulic integration. We also measured the lumen diameter of 50 randomly chosen xylem vessels in each individual. Because tracheids are only slightly thinner than the smallest vessel elements in C. *flava*, we are only able to tell them apart in cross section under the electronic microscope; we did not distinguish between them in our analyses.

Because we found great variation in the area occupied by decayed heartwood in the caudexes, we also measured its area to explore if it could explain the degree of integration-sectoriality in *C. flava*. We then correlated xylem distance, xylem lumen diameter, and decayed heartwood area (all log-transformed) with the caudex diameter to determine whether these anatomical features change with plant size in a way that explains developmental sectoriality in *C. flava*. The regressions were carried out against caudex diameter as a measure of plant size, which correlates significantly with the number of leaf rosettes ($t_{50} = 15.23$, P < 0.001, $R^2 = 0.23$), and likely better represents plant age than does canopy size due to the ability of large plants to shrink aboveground.

III.4. Results

Severing roots

Severing the taproot of either juveniles or adults caused the entire aboveground biomass to wilt in a matter of minutes, and the plants eventually died. Severing one lateral root caused spatially aggregated wilting in nine of the 24 adults but no wilting of rosettes in juveniles (Fig. III.2.a). Wilted tissue did not subsequently recover, and that part of the plant was dead the following year in all nine cases. The piece-wise regression revealed a significant size threshold in the wilting response of 20 rosettes ($t_{34} = 11.34$, P= 0.001) below which no wilting occurred and above which over 40 % of the plants showed some wilting. A simple linear regression showed that the initial number of rosettes explained 25 % of the variation in the number of wilted rosettes ($t_{34} = 11.42$, P =0.002; $R^2 = 0.25$), indicating more tissue loss in larger plants; adding the diameter of the clipped lateral root as a covariate did not improve the correlation (ANCOVA: $F_{2,33} =$ 5.57, P = 0.008, adjusted $R^2 = 0.21$).

Tracking dyes

One day after the dye solution was applied to a lateral root, the dye appeared in all rosettes of juveniles, but was aggregated in a specific group of rosettes in adults (Fig. III.3). Posterior examination showed that all stained rosettes in adults belonged to the same rosette module (i.e., the dyed rosettes were all connected to the same branch of the caudex). The staining of all rosettes in juveniles was not driven by the existence of only one module, because several juveniles had two, and both were equally stained. In two large juveniles and two small adults, out of the 32 total, we detected movement of dye to another module when we saturated the atmosphere of the originally stained modules.

Leaf water potentials

Leaf water potentials differed significantly between juveniles and adults and among watering treatments (Table III.1), but not before the watering occurred. At 18.00 h, there was no significant effect of treatment ($F_{2,131} = 0.42$, P = 0.65), developmental stage ($F_{1,133} = 1.85$, P = 0.18) or their interaction ($F_{3,130} = 0.83$, P = 0.48) on leaf water potential. After watering, leaf water potentials were higher –less negative– in the full watering treatment than in the partial watering treatment, which were higher than in controls ($F_{2,532} = 8.68$, P < 0.001; $\psi_{L Full} = -0.78 \pm 0.03$ MPa, $\psi_{L Partial} = -0.76 \pm 0.02$ MPa, $\psi_{L Control} = -0.59 \pm 0.03$ MPa). For juveniles, partially watered plants had higher water potentials than controls only at 22.00 h, whereas partially watered adults also had significantly greater leaf water potentials at midday (Fig III.4.a; Table III.2). Leaf water potentials were elevated in the full watering treatment, compared to controls, at 22.00 h $(t_{14} = 22.65, P < 0.001)$ and predawn $(t_{12} = 7.22, P < 0.02)$ for juveniles, and at 22.00 h $(t_{27} = 20.90, P < 0.001)$, predawn $(t_{27} = 8.70, P = 0.005)$ and midday for adults $t_{29} =$ 69.07, P < 0.001). Two separate repeated measures ANOVA, one for juveniles and one for adults, revealed significant effects of watering treatment and time, as well as their interaction. However, when we considered the variation in leaf water potentials due to the modules nested within individuals, the model was statistically significant for adults but not for juveniles.

Watering only one sector of the plant increased variation in leaf water potential more among modules of adults than among modules of juveniles. In partially watered juveniles, the variance component due to modules (Fig. III.4.b) was 26% before watering, at 18.00 h, 38% at 22.00 h, and 29% the following midday. In contrast, variation in leaf water potential among modules within partially watered adults increased from 6% before watering and 7% at 22.00 h to 28% the following midday. Interestingly, in both partially watered juveniles and adults, the variance component of leaf water potential due to modules was zero before dawn when plants are assumed to be at equilibrium with soil water potential (Sperry et al. 1996).

With subsequent application of dye to the root in the watered sector of partially watered plants with multiple modules, the dye always travelled to the module that had previously experienced the highest leaf water potential at midday ($X_{135}^2 = 46.79$, P < 0.001; Fig. III.5, fig. III.6, fig. III.7). After the surrounding atmosphere of the stained rosette modules was saturated, no dye moved to other regions of the plant, with two exceptions: in juvenile 4 (Fig. III.6), the dye travelled to the only other module, staining the entire plant; in adult 4, dye travelled to one of three previously unstained modules,

which had shown the second highest leaf water potential among all the modules of the plant.

Unstained modules of partially watered plants operated at similar leaf water potential as modules of control plants. For juveniles, this was true regardless of the time of measurement ($t \ge 3.65$, $P \ge 0.08$). In adults, unstained modules of partially watered plants did not differ in water potential from controls ($t \ge 3.47$, $P \ge 0.07$) except at midday when they had higher values than controls ($t_{53} = 13.33$, P < 0.001). There was slightly less concordance between stained modules of partially watered plants and fully watered plants. In juveniles, stained modules had lower water potential than fully watered juveniles at predawn ($t_{12} = 5.33$, P = 0.04). In adults, the same was true at both predawn ($t_{46} = 10.52$, P = 0.002) and midday ($t_{51} = 7.91$, P = 0.007).

Vascular anatomy

Xylem vasculature differed between juveniles and adults at three levels (Fig. III.2.b). First, distance from a random point to the closest xylem vessel increased as a function of caudex diameter ($t_{198} = 127.59$, P < 0.0001, $R^2 = 0.39$; fig. III.2.b), being nearly ten-fold greater for adults (144.87 ± 1.74 µm) than for juveniles (15.56 ± 2.12 µm; $t_{119.43}$ = -5.77, P < 0.0001). Juveniles already exhibited some signs of sectoriality because their xylem vessels are grouped in bundles separated by the dense packs of rays of the radial system (Fig. III.1, fig. III.5.b). This packing resulted in large distance among the xylem vasculature of these bundles near the cambium region (Fig. III.5.d). Second, the diameter of the xylem vessels increased linearly with caudex diameter ($t_{501} = 216.83$, P < 0.001, $R^2 = 0.30$), and it was almost twice as large in adults (40.47 ± 0.69 µm) as in

juveniles (22.17 ± 0.84 µm; $t_{500.11}$ = -17.82, P < 0.0001). Within individuals, variation in xylem diameter was very low. Third, the area of decayed heartwood in the central region of the caudex increased linearly with caudex diameter (t_8 = 35.00, P = 0.004, R^2 = 0.85, Fig. III.2.b, fig. III.5.a-g). Comparisons across plants of different sizes showed that heartwood decomposition took place from the pith outwards, first following the groups of rays described above (Fig. III.5.c & d). In very large adults, decayed heartwood extended to the surface and resulted in physical fragmentation of the live vasculature (Fig. III.5.e-g & i).

In caudex cross sections from adults used in the dye-tracking experiment, the dye was confined to a specific portion of the xylem, demonstrating sectoriality in the distribution of the dye. Staining occurred only in the newer xylem tissue suggesting that older xylem is not functional (Fig. III.5.h & i).

III.5. Discussion

Physiological evidence for functional hydraulic sectoriality

We have established that the transport of water is integrated throughout the caudex in juveniles of *C. flava* but becomes sectored as plants grow larger. This was demonstrated by three complementary methodologies: (i) in adults, but not in juveniles, severing lateral roots caused wilting and eventual death of a portion of the canopy, (ii) dyes applied to a single lateral root were distributed throughout the rosette modules of juveniles but compartmentalized in adults, and (iii) watering a lateral root of adults caused within plant variation in leaf water potential consistent with hydraulic sectoriality. Such sectoriality was positively correlated with plant size; our study demonstrates that

intermediate developmental stages can still exploit alternative hydraulic pathways to some degree, whereas fully developed adults cannot. These seem to be the first such findings for a chamaephyte. We know of only one example in a woody plant, the desert shrub *Ambrosia dumosa*, where sectorial transport of water-soluble dyes and increased variation in leaf water potential and stomatal conductance have all been linked (Espino & Schenk 2009).

It appears that water still redistributes internally among modules when stomata are closed. We base this on the observation that leaf water potential does not vary among modules at predawn despite such variation at 22.00 h and midday. Assuming that at predawn plants reach equilibrium with the soil water potential where their connected lateral roots forage (Sperry et al. 1996), partially watered adults should show high variance in leaf water potentials among modules. The fact that significant leaf water potential variation does not exist among modules before dawn implies that small amounts of water are redistributed to other modules in the absence of high transpiration rates.

Cross validation of dye-tracking techniques

By coupling dye-tracking techniques with leaf-water potential measurements in partially watered plants, we have proved the validity of using physiological dyes to explore the hydraulic design of *C. flava*. Dyes supplied to roots in the watered region travelled always to the aboveground sectors that experienced a significant increase in leaf water potential as a consequence of partial watering. The concern about dye-tracking experiments is that, despite their common usage to explore hydraulic pathways (Ellmore et al. 2006), the molecular size of dyes may not allow for lateral movement in the xylem and so the dyes might not follow the same pathway as water and minerals (Choat et al. 2003; Sano 2004). Indeed, Hargrave et al. (1994) reported greater distribution of stain in the xylem vessels of the shrub *Salvia menifera* for basic fuchsin (337.86 g/mol) than for the alcian blue, a larger molecule (1298.86 g/mol). Our approach with dyes is valid as long as the possibility of redistribution of dyes to non-preferential hydraulic pathways can be ruled out. Our saturating the atmosphere of the stained rosette module showed such redistribution in some medium-sized individuals. However, because anatomical characteristics that can strongly affect the hydraulic design (e.g., pit vessel number and area) are species-specific (Ellmore et al. 2006; Jacobsen et al. 2008), our success with this method may not necessarily transfer to other species.

Anatomical bases for the switch from hydraulic integration to sectoriality

The changes we observed in three caudex anatomical features (distance among xylem vessels, xylem vessel lumen, and decayed heartwood area) with plant size likely underlie the hydraulic switch from integration to sectoriality as plants grow (Fig. III.2.b). Our findings support hypotheses that implicate discontinuities in the vasculature as factors contributing to functional sectoriality (Kitin et al. 2004; Orians et al. 2005). In at least one species that remains hydraulically integrated, these anatomical features do not change throughout development (Domec et al. 2009).

In *C. flava*, anatomical sectoriality takes place relatively early in development. Primary xylem, however, lacks the reticulation imposed by the radial and ray systems. Consequently, the xylem vessels in juveniles form a single, tight cluster, which likely allows for hydraulic integration. But as secondary growth takes place in the caudex, anatomical fission of the xylem occurs through a combination of changes previously documented either in sectorial desert shrubs or anatomically sectorial temperate herbaceous species. First, the xylem vasculature is re-organized into bundles by the formation of rays that delimit the contact of xylem vessels (Marshall 1996; Price, Hutchings & Marshall 1996). The radial growth increments then translate into greater distance among xylem bundles and a reduced probability of lateral water movement. Second, the hardening and eventual decay of the heartwood (Moss 1940), renders the more closely packed primary xylem vessels, located in the center of the caudex, nonfunctional, which means there may be exaptive value to the formation of heartwood because it may increase the degree of sectoriality as the plant grows (Stewart 1966). The die-tracking experiment shows clearly that water travels preferentially through the outermost vessels (Fig. III.5.h-i). In some very large individuals, the decay of the heartwood in the caudex may extend, in some instances, to the epidermal cork.

The spatial aggregation of dyed vessels in *C. flava* starts to occur at about the time that heartwood decay and xylem bundle formation are first evident. In some species, the vascular system completely fragments, a condition known as axis splitting (Jones & Lord 1982; Espino & Schenk 2009), but even in those species, complete anatomical fragmentation may occur subsequent to functional hydraulic independence of modules (Vasilevskaya & Shokina 1968; Zanne et al. 2006; R. Dickson, personal communication).

Only *partial* axis splitting is evident in *C. flava*. Axis splitting is never complete because regardless of plant size and developmental stage, modules remain connected to a single taproot. The formation of this taproot is a large carbon expense for such a small plant, which, unlike desert trees and shrubs (Horwath et al. 1992; Espino & Schenk

2009), only possesses one such foraging structure to inspect more reliable, deep water reservoirs. Consequently, the vascular organization of its taproot deserves investigation. Our study reveals that the taproot supplies an essential quantity of water, but we have not discerned whether it is anatomically or functionally sectored. We would like to know whether the persistence of the taproot makes more water available to the remaining modules when some modules die during drought (Casper 1996). Such an increase in water availability would occur if the taproot is fully integrated or if sectoring of the taproot little affects total water uptake from the surrounding soil. In other words, sectoriality may not hold the same significance for the vertical taproot as it does for the caudex, whose sectors are connected to different lateral roots that forage over large horizontal distances. Members of two other genera in the family Boraginaceae, *Mertensia* and *Lithospermum*, have taproots that do undergo internal fission (Moss 1940).

Final remarks: plant shrinkage as a survival mechanism

Despite the fact that desert chameaphytes and fully woody species (i.e. shrubs and trees) differ a great deal in foraging strategies (Smith et al. 1997), growth form (Raunkiaer 1934) and overall size (Noy-Meir 1973), the hydraulic sectoriality we demonstrate in *C. flava* is strikingly similar to that in desert shrubs, where it appears to have adaptive significance. The number of species with hydraulically sectored design increases along aridity gradients (Schenk et al. 2008), and sectored desert woody species achieve longer life spans than integrated desert woody species (Schenk 1999). It is sometimes suggested that shoot dieback in woody species increases root:shoot ratio

(Kozlowski 1973; Davis et al. 2002), but in our view this clearly depends on how much of the root system survives and on the pattern and degree of vascular integration.

The hydraulic re-arrangement that occurs with development in *C. flava*, from integration in juveniles to sectoriality in adults, likely explains why drought induces the death of spatially aggregated rosettes only in larger, older individuals (Casper 1996). Plants lacking integration may be unable to rescue a water-stressed segment. Any spatial heterogeneity the root system encounters in soil water or nutrients should be translated to variation within the shoot. Considerable spatial heterogeneity at the scale of the root system has been documented for both water (Salguero-Gómez, unpublished; chapter II) and nitrogen (Peek & Forseth 2009) in this habitat.

Finding smaller vessel lumen in juveniles and overall vascular reorganization with development adds to our understanding of physiological differences between juveniles and adults in *C. flava* (Casper 1996; Casper et al. 2006). When differences occur in basic gas exchange parameters, juveniles have greater stomatal conductance (g_s), lower carbon assimilation (A_{max}) and lower instantaneous (A_{max}/g_s) and integrated (carbon isotopic discrimination rate, Δ) water use efficiency (WUE; Casper et al. 2006). Smaller plants may also show lower midday and/or predawn leaf water potentials (Casper et al. 2006). Their greater transpiration may help juveniles accumulate nutrients or extend carbon gain in dry soils, which could be especially important for the growth and establishment of young plants.

In a previous literature-based meta-analysis of herbaceous perennials, we found that species with the ability to decrease in size experience higher population resilience (i.e. the speed of recovery after a disturbance) and longer life spans (Salguero-Gómez & Casper 2010; chapter V). Thus, it seems likely that plant shrinkage –facilitated in *C. flava* by hydraulic sectoriality, plays a key role as a survival strategy, which may be particularly important in deserts with large temporal variation in water availability (Salguero-Gómez *et al.*, unpublished; chapters IV & VI).

In fact, we suggest that sectoriality may help explain why the particular growth form of *Cryptantha flava* –with a combination of herbaceous and woody habit– is so common in cold deserts (McLaughlin 1986). In general, perennials must be able to tolerate temporal fluctuations in water availability, while annual species, which are more common in warm deserts, can avoid drought through seed dormancy. The perennial growth form allows persistence of the genotype, while sectoriality enables independent foraging, death of only the weakest/less productive modules, and increased foraging efficiency, all advantages ascribed to sectored woody species (Orians et al. 2005; Espino & Schenk 2009).

III.6. Acknowledgements

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Effect	df	Mean squares	F-ratio				
Between subjects:							
Treatment							
	2	1.026	11.294				
Developmental stag	e						
	1	0.475	10.453				
Treatment × Develo	pmental stag	je					
	2	0.067	0.733				
Individual (Treatment × Developmental stage)							
	21	2.158	2.261				
Module (Individual (Treatment × Developmental stage))							
	28	1.832	1.439				
Within subjects:							
Time							
	3	9.040	66.296				
Time × Treatment							
	3	0.079	0.582				
Time × Developmental stage							
	6	1.698	6.227				
Time × Treatment × Developmental stage							
	6	0.456	1.674				
Time × Individual (Treatment × Developmental stage)							
	63	10.537	3.679				

Table III.2. Separate repeated measures ANOVA, for juveniles and adults, for leaf water potentials of modules within individuals exposed to three different watering treatments and followed for four time points. Italics, underlined: P < 0.05; bold: P < 0.001.

	Juveniles				Adults				
Effect	df	Mean squares	F-ratio	df	Mean squares	F-ratio			
Between subjects:									
Treatment									
	2	0.330	<u>6.074</u>	2	0.826	10.046			
Treatment (Individuals)									
	7	0.352	1.849	14	1.800	3.122			
Treatment (Individual (Module))									
	5	0.081	0.597	23	1.683	<u>1.781</u>			
Within subjects:									
Time									
	3	3.166	38.794	3	7.272	58.984			
Time × Treatment									
	6	0.589	<u>3.607</u>	6	1.999	8.111			
Time × Treatment (Individual)									
	21	1.251	<u>2.190</u>	42	9.456	5.479			
Time × Treatment (Individual (Module))									
	15	0.620	1.519	69	5.502	1.941			



Figure III.1. Spatially aggregated mortality of rosettes in an adult of *Cryptantha flava* (left), and its anatomy (right): (a) groups of rosettes branching from the same shoot are clustered into a module. Modules branch off from the caudex (b), the central, underground stem. The root system consists of a deep taproot and a discrete number of lateral roots that spread laterally approximately 1 m.



Figure III.2. Differences in individuals of *C. flava* as a function of plant size. a. Aboveground response to the loss of hydraulic conductivity when a single lateral root was clipped per individual (n = 12 juveniles and 24 adults). Dashed line represents piecewise regression, with a breakpoint for plants of 20 rosettes. b. Xylem vessel lumen (μ m), distance to closest xylem vessel (μ m) and decayed area of heartwood (mm²) increases with caudex diameter and development (n= 4 juveniles and 6 adults). Note different logarithm axes for the anatomical measurements.



Figure III.3. Diagram representing a juvenile (a) and an adult (b) of *C. flava* 24h after a dye solution (acid fuchsin) was fed to one lateral root with a vial. In the case of the juvenile the dye stained all leaf rosettes, but in the adults the dye was concentrated into a specific module, as indicated by the distinctive leaf and flower red coloration. Dashed arrows indicate continuation of root.



Figure III.4. Watering either one sector of the plant or its entirety affects significantly the water status of the modules of the plant. a. Mean (\pm standard error [S.E.]) leaf water potentials of whole individuals of *C. flava* before and after watering treatments were applied as vertical asterisk line (18.30 h). b. Total contribution (number at the bottom of each time point) and percentage (pie-chart) of the variation in leaf water potentials due to individuals, its modules and noise for only the partial watering treatment at each time point. Sample sizes are detailed in the methods section.



Figure III.5. Developmental series of cross sections of the caudex of individuals of *C. flava*. (a-g) 5 μ m plastic sections of juveniles and adults organized by increasing size. Missing heartwood tissue due to putrefaction was photo-edited to black background. As individuals develop secondary grow, the heartwood decays and eventually discontinuities give rise to physically independent modules. (h & i) 40 μ m paraffin cross sections showing stained xylem vessels (arrows) of a small and a large juvenile and a small adult in which dyes (fast green FCF and acid fuchsin, respectively) were tracked from a lateral root. Scale bar = 1 mm.



Figure III.6. Average leaf water potential of modules (± standard error [S.E.]) for juveniles and adults. After all the leaf water potential were measured, the hydraulic conductivities were tracked using green fast FCF (green) or acid fuchsin (red). Dashed line represents the module that exhibited the dye after 24 h while solid lines represent modules that did not receive dye. Dotted line represents the module to which the dye transferred when the atmosphere of the previously stained module (dashed line) was saturated. Complete experimental results in figure III.7. Sample sizes are detailed in the methods section.



Figure III.7. Leaf water potentials of the modules of individuals of *Cryptantha flava* in control, partial watering and full watering treatments. In partially watered individuals, we examined the appropriateness of dye-tracking techniques after the leaf water potentials were measured targeting the roots foraging in the watered sector (green: green fast FCF; red: acid fuchsin; blue: Toluidine blue). Dashed line: module that received the dye within 24 h after it was fed to the lateral root. Dotted line: module to which the dye travelled after the atmosphere of the previously stained module (dashed line) was saturated. None of the trials with Toluidine blue worked, although modules exhibited significantly different hydraulic statuses during the midday following the watering.

Chapter IV

Positive long-term effects of climate change

on the population dynamics of a native desert perennial

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IV.1. Summary

- Climate change is a pervasive agent and the expected leading cause of loss of biodiversity. In much of the Western arid regions of the US, increases in precipitation have been recorded by historical climatic stations and are projected to keep increasing, according to regional climate models. Specifically, in the Great Basin desert, where this work took place, intense pulses of precipitation are expected at the end of the growing season of the native flora.
- We explored the potential effects of increases in precipitation on a natural population of the native *Cryptantha flava*. We simulated pulses of 4.5 cm of precipitation at the end of every year, replicated four times, and followed individual dynamics for five years.
 We built an integral projection model and analyzed the data using elasticity analyses and two separate two-way (period x treatment, and time since watering × treatment) life table response experiment analyses.
- Watering resulted in lower survival of individuals the period that the pulse was simulated, but increased the population growth rate one and two years after watering. Although watered plants produced more flowers and aborted fewer embryos the year after the pulse, recruitment was not enhanced. The elasticity analyses show that recruitment is not a critical process in the dynamics of this population, but the survival and changes in size of small-medium size individuals are. The LTREs show that the overall effect of the simulated pulses of precipitation is not greater than the one resulting from the inter-annual variation in current precipitation.
- Research on the impacts of climate change on native biota typically reports negative effects. Here we presents a positive projection for *C. flava*: although creating more

flowers and seeds did not pay off, individuals survived better on the long-term and were more likely to grow when received a pulse of precipitation at the end of the growing season, when otherwise they would be entering winter dormancy. The periods after a drought, the observed size distribution approximates closely the stable size distribution, where small-intermediate size individuals contribute most to the population growth rate. This phenomenon occurred as a result of greater seedling mortality and large plant shrinkage. The aforementioned finding, the low elasticities of large adults, and positive effects of shrinkage in a large number of periods and treatments, leads us to introduce plant shrinkage as a buffering strategy against droughts in desert ecosystems.

Key words: Climate change, plant demography, growing season, precipitation, integral projection model (IPM), life table response experiment (LTRE) analysis, Cryptantha flava, shrinkage.

"The effect of climate change is not going to be noted in one year to the next"

Robert Zeigler

IV.2. Introduction

Arid regions constitute the most extensive terrestrial biome, with over a third of the Earth's land surface (Noy-Meir 1973, Fischer and Turner 1978). Currently, these regions host 43% of the human population (IPCC 2007), and an even greater percentage is likely to be affected since arid regions are expected to expand 17% during this century (Schlesinger et al. 1990). Furthermore, global climate change models project an increase in the frequency, intensity and unpredictability of precipitation events in deserts (Giorgi et al. 1994, Easterling et al. 2000a). For the Great Basin desert, where this study took place, regional models forecast an increase of up to 100% in rainfall during July-September (Arritt et al. 2000) when most native species normally initiate winter dormancy (Comstock and Ehleringer 1992, Donavan and Ehleringer 1994). Similar precipitation shifts have dramatically affected ecological interactions such as competition and facilitation (Franco and Nobel 1989, Forseth et al. 2001), and could eventually affect population dynamics, ecosystem services, and community composition (Walther et al. 2002, Parmesan 2006). Consequently, studying survival strategies of native desert biota has become a research goal of primary interest (Holmgren et al. 2006, IPCC 2007, Reynolds et al. 2007).

In deserts, water is only available very erratically and typically in the form of intense pulses of precipitation that can saturate biological demands during brief periods

of time, interlaced by long periods of drought (Huxman et al. 2004, Ogle and Reynolds 2004, Reynolds et al. 2004). The availability of water is tightly linked to nutrient cycling and primary productivity because microbes can only free up vital nutrients by decomposing organic matter in the presence of water (Gallardo and Schlesinger 1992, Yahdjian et al. 2006), and plants can only uptake those nutrients when in solution (Peek and Forseth 2009). Consequently, desert plant species have evolved a rich repertoire of ecological strategies to deal with the temporally stochastic nature of precipitation (Comstock and Ehleringer 1992). At the anatomical level, some desert species are able to create fine roots exclusively when it rains (Nobel and Sanderson 1984, Pavon and Briones 2000, chapter II), develop succulence (Smith et al. 1997) or produce large root:shoot ratios (Canadell et al. 1996, Schwinning and Ehleringer 2001). At the physiological level, stomatal conductance is fine-tuned to limit the amount of water loss during photosynthesis (Dodd et al. 2002), and xylem architecture may be replicated to circumvent/refill/repair cavitated vessels resulting from the very negative pressures under which plants operate to extract belowground resources (Orians et al. 2005, Ewers et al. 2007). At the community level, dissimilar growth forms have undergone niche differentiation to avoid competition for resources (Ehleringer et al. 1991, Gebauer and Ehleringer 2000, Schwinning et al. 2003, Ogle and Reynolds 2004).

Despite the remarkable understanding achieved regarding desert plant anatomy, physiology and community ecology, we still lack a basic understanding of how desert plants, at the population level, respond to –and may potentially buffer– natural stochasticity. This knowledge is crucial because natural selection operates on individuals, favoring those whose demographic contributions over their entire lives are greatest. Nonetheless, the exploration of survival strategies of desert plants at the demographic level is inherently challenging due to the logistical limitations associated with following individuals for extended periods of time under harsh conditions and in an environment where predicting precipitation pulses is virtually impossible (Noy-Meir 1973). The few studies of which we know, required very long-term data, where precipitation was a fortuitous element and thus replication with respect to precipitation events was not possible (Goldberg and Turner 1986, Miriti et al. 2001, Stampfli and Zeiter 2004). On the other hand, the studies that deliberately explored survival strategies of desert species, where replication was implemented, did not use demographic, but physiological approaches (Cui and Caldwell 1997, BassiriRad et al. 1999, Huxman et al. 2004; but see Pierson and Turner 1988).

Here we explicitly explore the effects of predicted rainfall increases on the population dynamics of a native perennial species, *Cryptantha flava*, by simulating large pulses of precipitation at the end of the growing season. Our experimental approach, where we replicated pulses in four years and examined the population dynamics during five years, allowed us to ask (i) whether the demographic consequences of predicted increases in precipitation will be greater than the current late summer precipitation at the field site, (ii) whether there are long-term demographics consequences of increased precipitation on the population growth rates, and (iii) the relative importance of reproduction, survival, growth and shrinkage in buffering against such environmental stochasticity.

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IV.3. Materials and Methods

Species description

Cryptantha flava L. (Boraginaceae) is a chamaephyte (herbaceous perenial subshrub; Raunkiaer 1934) that grows in sandy soils from central Wyoming, along the Colorado Plateau in eastern Utah, and into northern Arizona and New Mexico, USA (Fig. IV.1.a). Its average lifespan ranges 10-15 years, and individuals typically consists of 1 to 100 leaf rosettes, although some may be as large as 200 (Casper 1996).

Rosettes are connected to branches of the woody underground stem, the caudex. Leaf rosettes first appear in April, and new rosettes may develop throughout the growing season from axillary meristems of existing rosettes. Vernalization is required for floral induction, whereupon a rosette bolts to ~25 cm and produces 20-70 flowers. Most flowers mature only one, or more rarely two, seeds (nutlets) through embryo abortion (Casper 1981). Flowering rosettes die as the seeds ripen in late July. Seedlings may emerge in September-October, or at the beginning of the next growing season. As the soil dries in late summer, typically at the beginning of August, the remaining leaves on vegetative rosettes senesce and shoot apical meristems become quiescent. However, late summer rainstorms trigger the creation of new fine roots (Salguero-Gómez & Casper, *in press*) and leaves (Casper et al. 2001), effectively prolonging the growing season of *C*. *flava*.

Extreme changes in size, both positive (growth) and negative (*shrinkage* hereafter), can occur in individuals of *C. flava* during the growing season (Salguero-Gómez & Casper, unpublished) as well as over winter (Fig. IV.1.c). Size fluctuations

result from an imbalance between the birth of new rosette and the loss of existing ones through either mortality or semelparous flowering as described above. While plant growth occurs through the birth of rosettes located randomly within the plant's canopy, shrinkage occurs primarily through the death of spatially aggregated rosettes (Salguero-Gómez & Casper, *unpublished*).

Field site description and climatic patterns

The studied population is located near the Red Fleet State Park in Uintah County in northeastern Utah, US (40° 30' N, 109° 22' 30" W, 1730 m a.s.l.; fig. IV.1.b) where the vegetation mainly consists of the shrubs *Artemisia tridentata* Nutt.(Asteraceae) and *Chrysothamnus nauseosus* (Pallas) Britt. (Asteraceae), and the small tree *Juniperus osteosperma* (Torr.) Little (Cupressaceae). *C. flava* is the dominant chamaephyte species.

The field site is arid/semi-arid. The long-term (1931-2010) mean annual precipitation is 25.12 cm (Maeser 7 meteorological station, Western Regional Climate Center, http://www.wrcc.dri.edu; 17 Km away from the field site). This mean precipitation coincides with the 25.00 cm threshold for classification of arid *vs*. semiarid areas (McGinnies et al. 1968). However, annual precipitation is highly variable (C.V. = 41.34%) and so some years are extremely dry (<5 cm) and other years relatively wet (>50 cm). Furthermore, precipitation has increased since 1933 at a rate of 2.7 cm/decade (Appendix A.a).

Seasonal precipitation regime is bimodal, with maxima in April and October. Snowmelt also contributes to soil water availability in spring (Dobrowolski et al. 1990). Consequently, belowground resources are most available to *C. flava* in early spring and following these rainfall episodes. However, August registers as the month with the steepest precipitation increase in the last decades ($t_{76} = 3.83$, P < 0.001; 0.4 cm/decade), potentially extending the growing season for *C. flava*.

Experimental design and censuses

In 2006, we initiated a five-year experiment in which we watered separate parts of the population each August to examine how changes in precipitation patterns may affect the population dynamics of C. flava. Demographic censuses of every permanent plot were conducted at the end of May, concurring with the peak of flowering season, until 2010. We initially selected four locations at the site and established at each location a $5 \times$ 5 m² control plot, receiving natural precipitation (Fig. IV.2.a), and a 5×5 m² watering plot where, in addition to the natural precipitation, a pulse of 4.5 cm of precipitation was simulated the year of its establishment. Every May, we established one more watering plot at each location to accommodate the replication of the treatment. In 2008 and 2009, to increase replication, we increased the sampled locations from four to eight, including new control and watering plots (in total $n_{\text{Control plot}} = 8$, $n_{\text{Watering plot}} = 24$). We applied the simulated pulses always within the first four days of August (Fig. IV.2.b) and used a pumper truck (Vernal BLM office, UT) and nozzle to simulate the impact of raindrops. To avoid run-off, the treatment was split in two smaller pulses of 2.25 cm on two consecutive days, always between 17:00-19:00 h, when monsoonal precipitation is most likely to occur at the site (R. Salguero-Gómez, pers. obs.).

Although plot locations were arbitrarily chosen with the criteria that they be >100 m apart, they were placed close enough to an unimproved road to allow access of the pumper truck. Each permanent plot contained nine $1 \times 1 \text{ m}^2$ quadrats where individuals of *C. flava* were censused, separated by four 0.5 m-wide access corridors to minimize impact on censused quadrats (Appendix B). Each quadrat was delimited at its four corners with 30 cm PVC pipes pounded into the sandy ground. This setup allowed us to re-locate pre-existing individuals year after year. In total, we followed >3500 individuals over 288 m².

We quantified recruitment, survival of established individuals, changes in size and fecundity. We measured size as the total number of rosettes, both vegetative and flowering. To estimate fecundity, we used the number of flowering rosettes per individual and, for the last three periods of the study (2007-08, 2008-09 and 2009-10), we also counted flowers per rosette and mature seeds per flower (0-4) and per rosette. Because calyces with enclosed seeds are deciduous, we netted whole flowering rosettes once all the corollas had wilted, around mid July. We arbitrarily chose one to three flowering rosettes of one to three arbitrarily selected reproductive individuals for 2007, 2008 and 2009, respectively). We collected the nets in August of each year to count flowers and mature seeds, and the seeds were immediately returned nearby their progenitors. We then used a two-way analysis of variance (Sokal and Rohlf 1995) to examine the effect of treatment, year and their interaction on the number of mature seeds per flower, and the total number of flowers and mature seeds per flowering rosette.

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Demographic modeling and analyses

We used Integral Projection Models (IPM; Easterling et al. 2000b) to model the population dynamics of C. flava using pre-existing code (Ellner and Rees 2006). An IPM approach was preferable to classical matrix models, where individuals are grouped in discrete classes (Caswell 2001), because we found no evidence of natural breaks in the scaling of survival, changes in size and fecundity with size (Salguero-Gómez, unpublished). Additionally, IPMs are more robust to small sample sizes than classical approaches (Ramula et al. 2009). Briefly, an IPM describes changes in the population structure *n* using a (quasi-)continuous state variable –in this case, number of rosettes– that changes in discrete time, during the period t to t+1 (equation 1; Hesse et al. 2008). The IPM produces a kernel k that describes the probability p with which individuals survive and transition to a lower/same/higher state along the continuous variable, and the per-capita contribution f of established individuals to new recruits (equation 2, where L and U are the minimum and maximum states over which transitions and per-capita contributions are possible/observed). In our study, L = 1 and U = 100 (equations 1, 2), but individuals of larger size were implicitly included because they were considered in the vital rate regressions (see below).

$$n(y,t+1) = \int_{L}^{U} k(y,x) n(x,t) dx$$
(1)

$$n(y,t+1) = \int_{L}^{U} [p(x,y) + f(x,y)] n(x,t) dx$$
(2)

To parameterize the vital rate functions that integrate the IPM, we used data for each period (2006-07, 2007-08, 2008-09, 2009-10) and treatment (control and watering;

see figure IV.2.b-c) separately. This resulted in 13 different period × treatment combination IPMs, and we used six vital rates for each (Appendix C). The first two define the p kernel (changes in size conditional on survival): survival during the period t to t+1 (σ), and change in size from t to t+1 (γ) together with its associated variance (equation 3). The remaining vital rates define the f kernel (sexual per-capita contribution to new offspring): probability of flowering in year t (φ), number of flowering rosettes produced per individual that year (χ), number of fully developed seeds produced per flowering rosette that year (ψ), and size distribution of seedlings the following year t+1 (\Box) (equation 4). Survival (σ) and flowering probabilities (ϕ) were modeled using logistic regressions. The size distribution of seedlings (\Box) was modeled with a negative Poisson exponential regression. Because the number of fully developed seeds produced per flowering rosette was not size dependent (not shown), we used the average value (thus ψ is not a function of size x at time t in equation 4). Data on number of fully developed seeds was not available for 2006 and 2007, but we assumed their production for control or watered plots of 2006 and 2007 to be the average of the control or the watering plots in 2008, 2009 and 2010, respectively (Appendix C). The remaining vital rates (γ and χ) were analyzed using linear regressions, which fit better than polynomial regressions (i.e., lowest AIC; Sakamoto et al. 1986).

$$p(x,y) = \sigma(x) \gamma(x,y) \tag{3}$$

$$f(x, y) = \varphi(x) \chi(x) \psi \vartheta(y)$$
(4)

Finally we tested whether the vital rates of survival (σ), changes in size (γ), and flowering probability (φ) varied significantly among plots as a function of spatial heterogeneity, and whether our 13 period × treatment IPMs differed significantly from

one another. To test the effect of the spatial heterogeneity on the IPMs, we calculated the Tukey's HSD indexes from the least squares resulting from the two-way ANOVAs with size at time *t*, site (random variable) and their combination as effects, and σ , γ and φ as response variables, separately. Because in the majority of cases the least squares were not statistically different, we lumped all plots belonging to the same period × treatment combination IPM (Appendix D). Likewise, to test the differences among the 13 IPMs, we again used two-way ANOVAs with size at time *t*, period × treatment IPM model and their interaction as effect variables, and σ , γ and φ as response variables separately. Tukey's HSD tests reported significant differences among most period × treatment IPM models (Appendix E).

Population growth rate, elasticities and LTRE

The kernel k(y,x) obtained from each individual IPM can be readily transformed into a classical projection matrix $\mathbf{K}(y,x)$ of large dimensions, providing the same battery of outputs available for a classical matrix model, including the population growth rate λ , stable size distribution w, reproductive value v, sensitivities and elasticities (Ellner and Rees 2006). The transformation from the IPM to a classical projection matrix requires imposing a mesh, an analog of the projection matrix dimension. We discretized each of our IPMs with 49 x 49, 99 x 99 and 149 x 149 mesh points over the state variable size, resulting in discrete categories in increments of 2, 1 and 0.66 rosettes, respectively. We then calculated λ , w and v, the expected per-capita sexual contributions to the population, under each of the three mesh scenarios. Because λ , w and v stayed fairly constant regardless of mesh size (Appendix F), we opted for the 99×99 mesh, which allows for a straightforward interpretation of results because each mesh point equals one rosette increment.

To examine the departure of the observed size distribution from the stable size distribution w for each period and treatment, we calculated Keyfitz's Δ (Caswell 2001, p. 101). This index ranges between 0 and 1, indicating maximum similarity or difference, respectively. We then used this index to explore how our watering treatments and interannual variation pushed the population structure away from its equilibrium.

We calculated λ to quantify the effect of watering treatments on population-level fitness. To obtain 95% confidence intervals, sets of censused individuals for each period and treatment were bootstrapped 1000 times with individual replacement (Rose et al. 2005). To examine variation in λ , we used a two-way ANOVA and Tukey's HSD test with time since watering (0 year, 1 year and 2 years) and treatment (watering 2006, 2007, 2008 or 2009) as effects and the bootstrapped population growth rates as the response variable. Finally, we reported the population-level effects of the watering treatments as $\lambda_{\text{Treatment}} - \lambda_{\text{Control}}$ for each year and treatment separately.

To determine which demographic processes govern the population dynamics under normal conditions and how the watering treatments may affect them, we examined the relative importance of transition elements and their underlying vital-rates to λ by conducting elasticity analyses (de Kroon et al. 1986, de Kroon et al. 2000), first on the matrix elements (Silvertown et al. 1992) and then on each vital rate (fecundity, survival, growth and shrinkage) (Zuidema and Franco 2001). The matrix element elasticities are

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useful to determine the range of sizes that most influence λ , while vital rate elasticities allow for a more in-depth study of the underlying demographic processes such as survival (Caswell 2001). The sensitivity of each vital rate as a function of size can be described as:

Fecundity:

$$S_{\Psi_{ij}} = \frac{\delta\lambda}{\delta\Psi_j} = \sum_i \frac{\delta\lambda}{\delta F_j} \frac{\delta F_j}{\delta\Psi_j} = \sum_i s_{ij} \sigma_j$$
(5)

Survival:

$$S_{\sigma_{j}} = \frac{\delta\lambda}{\delta\sigma_{j}} = \frac{\delta\lambda}{\delta P_{j}} \frac{\delta P_{j}}{\delta\sigma_{j}} + \sum_{i} \frac{\delta\lambda}{\delta G_{ij}} \frac{\delta G_{ij}}{\delta\sigma_{j}} + \sum_{i} \frac{\delta\lambda}{\delta R_{ij}} \frac{\delta R_{ij}}{\delta\sigma_{j}} + \sum_{i} \frac{\delta\lambda}{\delta F_{j}} \frac{\delta F_{j}}{\delta\sigma_{j}} =$$
$$= S_{jj} \left(1 - \sum_{i} \gamma_{ij} - \sum_{i} \rho_{ij} \right) + \sum_{i} s_{ij} \gamma_{ij} + \sum_{i} s_{ij} \rho_{ij} + \sum_{i} s_{ij} \Psi_{j}$$
(6)

Growth (size *j* at time *t* < size *i* at time *t*+1):

$$S_{\gamma_{ij}} = \frac{\delta\lambda}{\delta\gamma_{ij}} = \sum_{i} \left(\frac{\delta\lambda}{\delta P_j} \frac{\delta P_j}{\delta\gamma_{ij}} + \frac{\delta\lambda}{\delta G_{ij}} \frac{\delta G_{ij}}{\delta\gamma_{ij}} \right) = \sum_{i} \left(s_{jj} \left(-\sigma_j \right) + s_{ij} \sigma_j \right)$$
(7)

Shrinkage (size *j* at time t > size *i* at time t+1):

$$S_{\rho_{ij}} = \frac{\delta\lambda}{\delta\rho_{ij}} = \sum_{i} \left(\frac{\delta\lambda}{\delta P_j} \frac{\delta P_j}{\delta\rho_{ij}} + \frac{\delta\lambda}{\delta R_{ij}} \frac{\delta R_{ij}}{\delta\rho_{ij}} \right) = \sum_{i} \left(s_{jj} \left(-\sigma_j \right) + s_{ij} \sigma_j \right)$$
(8)

where the vital rates of fecundity (Ψ_j) , survival (σ_j) , growth (γ_{ij}) and shrinkage (ρ_{ij}) are functions of the probabilities of reproduction (F_j) , stasis (P_j) , progression (G_{ij}) and retrogression (Rij; see Zuidema and Franco 2001 for a more in-depth description). It is important to note (from equations 7 and 8) it follows that if the sensitivity of stasis for a given size is greater than the sensitivity of progression/retrogression, the vital rate sensitivities of growth/shrinkage will be negative/positive, respectively. The elasticity of a given vital rate, vr_{ij} , corresponds to its sensitivity normalized by the value of the vital rate at a given size over the population growth rate:

$$E_{\nu r_{ij}} = \frac{\delta \log \lambda}{\delta \log \nu r_{ij}} = \frac{\delta \lambda / \lambda}{\delta \nu r_{ij} / r \nu_{ij}} = \frac{r \nu_{ij}}{\lambda} S_{\nu r_{ij}}$$
(9)

Differences in population growth rates among treatments, periods or the time elapsed since the watering treatment took place may be caused by variation in vital rates across the employed treatments, periods and times since watering. We used two separate Life Table Response Experiments (LTRE; fig. IV.2.c) analyses to quantify such vital rate contributions to the differences in population growth rate (Caswell 2001, Jongejans and de Kroon 2005). The first LTRE tested period (α) and treatment (τ) effects, and the second LTRE we examined the effects of time since watering (β) and treatment (τ).

The two-factor LTRE analysis for treatment and period is as follows:

$$\lambda^{(mn)} = \lambda^{(..)} + \alpha^{(m)} + \tau^{(n)} + (\alpha\tau)^{(mn)}$$
(10)

where λ of period *m* (*i.e.*, 2006-07, 2007-08, 2008-09, 2009-10) and treatment *n* (*i.e.*, control, watering 2006, watering 2007, watering 2008 or watering 2009) is calculated as the sum of λ for the overall mean IPM, $\lambda^{(..)}$ (*i.e.*, the element-by-element average 100 × 100 matrix from all 13 IPMs), the effect of period *m*, $\alpha^{(m)}$, the effect of treatment *n*, $\tau^{(n)}$, and the interaction term ($\alpha \tau$)^(*mn*). We first calculated the main effects as:

$$\tilde{\alpha}^{(m)} = \sum \left(\nu r_{ij}^{(m.)} - \nu r_{ij}^{(..)} \right) \frac{\delta \lambda}{\delta \nu r_{ij}} \Big|_{\boldsymbol{K}^{(..)}}$$
(11)

$$\tilde{\tau}^{(n)} = \sum \left(v r_{ij}^{(.n)} - v r_{ij}^{(..)} \right) \frac{\delta \lambda}{\delta v r_{ij}} \Big|_{\boldsymbol{K}^{(..)}}$$
(12)

where the differences between the value of a particular vital rate $vr_{ij}^{(m.)}$ of the meanperiod matrix $\mathbf{K}^{(m.)}$ or $vr_{ij}^{(.n)}$ of the mean-treatment matrix $\mathbf{K}^{(.n)}$ and the overall mean vital rate of the matrix $\mathbf{K}^{(..)}$ were multiplied by the sensitivity values of the overall mean matrix (Caswell 2001, Yamada et al. 2007).

The interaction effect was then calculated as:

$$\widetilde{\alpha}\widetilde{\tau}^{(mn)} = \sum \left(v r_{ij}^{(mn)} - v r_{ij}^{(..)} \right) \frac{\delta\lambda}{\delta v r_{ij}} \Big|_{\boldsymbol{K}^{(..)}} - \widetilde{\alpha}^{(m)} - \widetilde{\tau}^{(n)}$$
(13)

In the second LTRE (LTRE $\beta \times \tau$ in figure IV.2.c), we examined the effect of time since watering ^(m) (*i.e.*, 0 years, 1 year after watering and 2 years after watering), treatment $\tau^{(n)}$ (*i.e.*, watering 2006, watering 2007, watering 2008 and watering 2009), and the interaction term $(\beta \tau)^{(mn)}$. Because this LTRE focuses explicitly on watering, no control matrices were included in the overall mean matrix $\mathbf{K}^{(..)}$.

For both LTRE analyses, we tested that the vital rate contributions that give rise to the population growth rates for each specific model obtained with equations 11, 12 and 13 approximated the observed population growth rates. We also calculated the coefficients of variation on the LTRE vital rate effects as a function of size in order to explore the mechanistic effects of period α , time since watering β and treatment τ on λ . We used R 2.12.0 (R development core Team 2010) to perform all modeling and statistical analyses. The vital rate linear model decomposition (equation 13) provided good estimates of the effects of α , β and τ on λ , since the deviations between expected λ s and observed λ s were only 6% (LTRE $\alpha \times \tau$) and 8% (LTRE $\beta \times \tau$).

IV.4. Results

Climatic patterns

Monthly precipitation was relatively constant in years when the amount of precipitation (from September of year *t* to August of year t + 1) was much greater than the long-term mean (P₂₀₀₅₋₀₆ = 32.61 cm, P₂₀₀₇₋₀₈ = 36.35 cm, P₂₀₀₈₋₀₉ = 35.13 cm), but precipitation was highly seasonal in years with closer to mean precipitation. For instance, in 2006 (P₂₀₀₆₋₀₇ = 28.12 cm) a surplus of 10.25 cm occurred during September-October 2006 compared to the mean of that period, when the temperatures do not yet allow for water storage in the form of snow for the next growing season; the precipitation in the remainder of the year experienced a surplus of 5.17 cm with respect to the mean. A similar seasonal pattern occurred in 2009-10, but it was preceded by a surplus of precipitation of 9.92 cm on April to August 2009, when individuals of *C. flava* are photosynthetically active (Fig. IV.2.a).

Variation in vital rates as a function of size, treatment and period of study

Fecundity (Ψ_j), survival (σ_j), growth (γ_{ij}) and shrinkage (ρ_{ij}) varied greatly during the experiment, both as a function of period and watering treatment. Fecundity and survival were positively correlated with size. Fecundity ranged from zero for individuals with one rosette to 0.15 ± 0.08 (S.E.) new recruits per capita for large individuals (\geq 50 rosettes; appendix C). Survival ranged from an average of 0.66 ± 0.04 for individuals with one rosette to 0.99 ± 0.01 for plants of \geq 50 rosettes. Individual's changes in size, both growth and shrinkage, were usually size-specific: small plants normally had a greater probability to grow than large plants in most treatment × period combinations; the intercept of the relationship between size of individuals at time *t* and *t*+1 (γ in equation 3) was always significantly greater than zero, but the slopes were significantly < 1 – implying preferential shrinkage for adults– in seven of the 13 scenarios (controls 2006-07, 2007-08 and 2009-10; watering 2006 in 2007-08; watering 2007 in 2007-08 and 2009-10; watering 2006 in 2007-08; watering 2007 in 2007-08 and 2009-10; watering 2006 in 2006-07; watering 2008 in 2009-10). The slope was not significantly ≠ 1 in three scenarios (control in 2008-09; watering 2006 in 2006-07; watering 2008 in 2009-10) and significantly > 1 in two scenarios (watering 2006 in 2008-09 and watering 2007 in 2007-08.

Following the intense drought of the summer 2007, included in the 2006-08 period (Fig. IV.2.a), the IPMs of the control, watering 2006 and watering 2007 treatments reported the lowest values for the survival (0.52 ± 0.06) and most extreme shrinkage during that interval (slope of changes in size = 0.57 ± 0.02 , γ in equation 2) in comparison to other periods (Appendix C). This phenomenon is depicted in figure IV.3, where drastic shrinkage is shown in the kernels corresponding to the 2007-08 period. In contrast, the overwinter drought in 2009-10 did not significantly affect survival or the slope of the relationship between size in year *t* and size in year *t* + *1*.

Our experimental manipulations of precipitation at the end of the growing season had strong effects on the survival and changes in size. All watering treatments reduced the survival during the period waster was applied compared to controls (Appendix C), but survival was significantly lower only for the watering 2006 treatment. Interestingly, the watering treatments also resulted in significantly greater survival the periods following the watering, particularly for the watering 2006 treatment (Appendix E.1). Watering also improved growth in most periods compared to the controls, with the exception of the watering 2007 treatment in the 2007-08 period, where γ was not statistically different from its control (Appendix E.2).

Watering also affected reproduction in *C. flava.* Watering treatments and controls did not differ in reproductive probability and output in the summer that watering was applied in August, but there were differences the following year. Plants watered the preceding period showed a higher probability of flowering for all periods (Appendix E.3), and more flowers per rosette in 2010 and more mature seeds per rosette in 2009 and 2010 compared to the respective controls (Table IV.1; fig. IV.4.a). Watering also affected the rates of embryo abortion in period t + 1: plants watered in August 2007 produced fewer flower with no mature seeds (t = 4.93, P = 0.03) and more flowers with one mature seed (t = 9.51, P = 0.01; table IV.1; fig. IV.4.b) in 2008; plants watered in August 2008 produced more flowers with two mature seeds than the controls in 2009 (t = 12.23, P = 0.004), and plants watered in 2009 produced more flowers with one (t = 6.11, P = 0.02) and two mature seeds (t = 5.30, P = 0.03) than the controls in 2010.

Population growth rates and stable size structure

The population growth rates (λ) varied greatly across the studied periods and our watering treatments increased λ over time. The population growth rate of the control plots was drastically affected by the 2007 drought: it transitioned from a situation of demographic growth in 2006-07 ($\lambda_{2006-07} = 1.09 \pm 0.001$) to demographic decline ($\lambda < 1$)

during the 2007-08 and 2008-09 periods, and λ did not recover its original value during the span of our censuses (Fig. IV.5.a; Appendix F.3). For watered plots that we followed for three periods (watering 2006 and 2007), there was no or negative effect on λ the first period, followed by a positive effect the next two periods compared to the controls (Fig. IV.5.b). The long-term effect of watering remained positive even when we included treatments for which we only had two (watering 2008) or one periods (watering 2009; t =3710.012, P < 0.001), or when we averaged the effect of the watering treatment ($\lambda = 1.05 \pm 0.002$) vs. the controls across years ($\lambda = 1.00 \pm 0.003$; t = 15.05, P < 0.001).

The observed population size structure differed strongly from the calculated stable size structure, but more so in the 2006-07 (Keyfitz's $\Delta = 0.75$) and 2008-09 ($\Delta = 0.64$) periods, characterized by above-mean annual precipitation, than in the dry periods of 2007-08 ($\Delta = 0.45$) and 2009-10 ($\Delta = 0.52$). While the stable size structure of *C. flava* averaged for all periods contained a high frequency of small-medium size (5-25 rosettes) individuals, the observed size structure was slightly deviated towards both ends of the size continuum: more seedlings (1-5 rosettes) and a significant frequency of large (>25) individuals (Appendix F.1 & 2)

Importance of demographic processes

The matrix element elasticity kernels of all IPMs systematically indicate that large (>50 rosettes) plants did not contribute much to the population growth rate λ (Fig. IV.5); this finding is revealing because individuals of even >200 rosettes are common in our field site. Individuals of up to ~30-40 rosettes had most effect on λ via their staying in the

same size (stasis) and changing sizes through progression and retrogression, but recruitment was unimportant, regardless of size. The intense 2007 summer drought, which resulted in drastic shrinkage of large individuals in the 2007-08 period, translated in λ being affected exclusively by even smaller plants (< 25 rosettes). This indicates that matrix element elasticity of retrogression either had a small or no effect whatsoever on λ .

Our vital rate elasticity analyses reported relatively high values of fecundity and growth in the small-intermediate (5-40 rosettes; appendix G) sizes but low importance of survival and shrinkage for λ of our IPMs. While the matrix element elasticity of recruitment is very low, the vital rate elasticity of fecundity seems to be driving the demographic dynamics. The two measures are fundamentally different: (i) matrix element elasticities are mathematically constrained to one (Mesterton-Gibbons 1993), while vital rate elasticities are not, and (ii) matrix element elasticity of recruitment contains the vital rate of seedling survival, while the vital rate elasticity of fecundity does not. The vital rate elasticity of survival was very low across all treatment × period kernels studied here, and we attribute the differences between fecundity and recruitment elasticities to such a phenomenon.

In most scenarios, the effect of changes in size fluctuated between positive and negative values as a function of size. The elasticities of the vital rate of growth were always positive for small sizes, but in eight of the 13 IPMs this vital rate turned to negative values with increasing size (Fig. IV.a; Appendix G). Likewise, the vital rate elasticity of shrinkage increased from negative values to positive in 6 out of the 13 cases studied. The size at which both vital rates, growth and shrinkage, switched in the direction of their effects was always lower for the former than for the latter (Fig. IV.b). Demographic effects of projected increases in precipitation: LTREs

Our two-way LTRE analyses showed that our watering treatments (τ) did not affect λ as much as the natural precipitation (). However, there was an important delayed effect of watering treatment on λ , expressed by the large contribution of the time since watering effect (), since the absolute mean effect was as large as that of period (; Table IV.2). Nonetheless, the interactions period × treatment and time since watering × treatment had very strong effects on λ .

The watering treatments most affected the vital rate of growth. In the two-way LTRE with period () and treatment (τ) as the main effects, most variation in λ was explained by differences in growth alone (CV : 82.35 %, CV_r: 29.77 %), followed by shrinkage (CV : 7.72 %, CV_r: 19.92 %), survival (CV : 7.25 %, CV_r: 23.33 %) and fecundity (CV : 2.68 %, CV_r: 26.97 %). In our second two-way LTRE analysis, where we tested the effects of time since watering () and treatment (τ) the pattern was similar too; differences in λ were driven mostly by variation in growth (CV : 44.67 %, CV_r: 31.96 %), followed by shrinkage (CV : 17.11 %, CV_r: 32.59 %), survival (CV : 28.56 %, CV_r: 7.53 %) and fecundity (CV : 9.56 %, CV_r: 27.93 %).

IV.5. Discussion

Our work, where we simulated predicted shifts in the precipitation regime in the Great Basin at a time when the native flora normally enters winter dormancy (Comstock and Ehleringer 1992), highlights the ability of the native chamaephyte *Cryptantha flava* to benefit from the resources made available by the rains at that time, its faculty to store

them and profit from them several years later, and the crucial role that size fluctuations play in dealing with environmental stochasticity.

Prolonged growing seasons

Despite the imminent challenges associated with climate change, we know surprisingly little about the demographic effects of prolonged growing seasons. Furthermore, the few existing investigations are limited to alpine ecosystems (Saavedra et al. 2003, Ladinig and Wagner 2007) and their results are case-specific (Earle 1993, Aitken and Hannerz 2001, KSLA 2001). Consequently, there is no general consensus for deserts, although intuitively we would expect longer growing seasons, with more water, to result in higher primary productivity. Cryptantha flava can create new leaves (Casper et al. 2001) and fine roots (Salguero-Gómez & Casper, in press; chapter II) in response to late-summer rains, and the present work links root dynamics, leaf photosynthesis and demography because we have found that the population growth rate the year after the pulse was simulated increased in comparison to control plants. Clearly, C. flava must be able to store the carbohydrates fixed at the end of the growing season so they can be used the following growing season. However, C. flava's well defined root system makes us wonder where storage actually takes place. A likely candidate is the caudex, the underground stem, since the lateral roots and taproot possess very little cortex (chapter II). However, the caudex undergoes internal heartwood decay with ontogeny (Salguero-Gómez and Casper 2011; chapter III), and so resources stored in the center of the caudex

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are likely not retrievable (Stewart 1966). The storage of resources overwinter in *C. flava* deserves further attention.

The role of plant growth and shrinkage in buffering stochasticity: bigger is not always better

Although our matrix element elasticity analyses indicate that the population dynamics of of *C.flava* are predominantly governed by small-medium size individuals, large individuals (*e.g.*, >100 rosettes) are not uncommon. How and why do individuals achieve such large sizes? We hypothesize that those individuals germinated in rich pockets found in the otherwise poor soil matrix. Indeed, high spatial heterogeneity for soil resources is an intrinsic characteristic of arid ecosystems (Jackson and Caldwell 1993, Aguiar and Sala 1999) and has been reported to control individual size in desert species (Kadmon 1993). Our field site too is spatially heterogeneous: we have observed intense rains delivered by isolated convective clouds within small areas (*ca.* 100 m²; R. Salguero Gómez, pers. obs.), frequent outcrops of highly fractured conglomerate sandstone that form pockets of moisture (R. Salguero-Gómez, unpublished), and nutrient-islands formed by shrubs (Forseth et al. 2001).

Our results contrast with commonly held assumptions on the role of growth and shrinkage in plant population dynamics. The components of fitness –survival and reproduction– are believed to increase with plant size (Watkinson and White 1986), and so elasticities of growth should systematically be positive, while those of shrinkage, negative. In over half of the period × treatment IPMs, growth to large sizes affected

negatively the population growth rate λ (*i.e.*, elasticity of growth became negative and elasticity of shrinkage positive for larger sizes). To our knowledge, Morris & Doak (1998) were the first to report positive vital rate elasticity of shrinkage, but this phenomenon is rather common, with 33 out of 123 herbaceous perennials having at least one size category in their projection matrices where the vital rate elasticity of shrinkage is positive (Salguero-Gómez, Burns & Casper, unpublished).

Here we offer evidence that plant shrinkage plays a critical role in the maintenance of a natural population in a highly stochastic environment. The greatest vital rate contributions to the observed differences in population growth rates due to natural and simulated precipitation were consistently those of size changes (growth and shrinkage). Historically, plant shrinkage has been overlooked due to numerous field census limitations and methodological misuses (chapter VI). However, a recent comparative demographic investigation has demonstrated that shrinkage is an important demographic phenomenon since it correlates positively with lifespan, resilience, fecundity, growth and survival (Salguero-Gómez and Casper 2010; chapter V). The average observed size distribution of C. flava at the field site during above-mean precipitation periods follows an exponential decay, with a high frequency of seedlings and relatively low frequency of medium and large individuals (Fig. IV.8). However, after periods of drought, the observed size distribution "retreats" to closely resemble the stable size distribution, where the frequency of individuals that most contribute to the population, 5-25 rosette individuals, is highest (Caswell 2001). We suggest that favorable environmental conditions allow C. flava to explore extreme ecological strategies along the slow-fast continuum (Franco and Silvertown 1996) by recruiting many seedlings (r-strategy) and sustaining large, long-lived individuals (k-strategy; Pianka 1970). However, under harsh conditions performance at either extreme of the size continuum is

sacrificed via high seedling mortality and frequent adult shrinkage so as to optimizing the population-level fitness (λ) halfway along the slow-fast continuum.

Linking anatomy, physiology, demography and natural selection

The plant shrinkage that we have observed in C. flava is likely a result of the plant's ability to explore the spatial heterogeneity of this ecosystem. Previous investigations have shown that individuals of C. flava become more sectored with ontogeny, that is, in juveniles all belowground resources are shared across the whole individual, but in adults lateral roots transport water and nutrients to specific regions of the canopy, what we have before referred to as rosette modules (Salguero-Gómez and Casper 2011; chapter III). We now also know that C. flava can activate the growth of fine roots on different lateral roots independently, depending on which region of the soil is wet (chapter II). Consequently if an adult individual of C. flava has only one lateral root in a rich soil patch, likely only the module associated with that root will survive and the whole-plant will shrink. The shedding of entire branches -and possibly entire sections of the root connected to those branches- in desert woody species has special incidence during or immediately after droughts (Kozlowksi 1973), and shrinkage in C. flava happens predominantly through the death of entire rosette modules (Salguero-Gómez & Casper, unpublished).

Li *et al.* (2011) have recently shown that the desert shrub *Artemisia ordosica* can also undergo drastic shrinkage, particularly in large size classes and in association with time periods and habitats characterized by low water availability. Just as in *C. flava*, *A*.

ordosica is also hydraulically sectored (Schenk et al. 2008). However, in *A. ordosica* the contributions of the vital rates to the differences in periods and habitats were not as strong as the ones reported here for *C. flava*, and in *A. ordosica* positive vital rate elasticities of shrinkage were not reported. We suspect that these differences may be driven by the way size was measured: counting rosettes in *C. flava* clearly allows for the exploration of how its modular architecture affects size fluctuations, whereas measuring height, as in the IPMs of *A. ordosica*, does not fully capture the dynamic nature of sectored organisms (chapter VI).

Strengths of our modeling approach

The modeling approach taken in the present study to explore the population dynamics of *C. flava* with integral projection models, where size was treated as a continuous variable (Easterling et al. 2000b), offers higher resolution than classical projection models (Caswell 2001). Conveniently, classical matrix models have been applied to the same natural population of *C. flava*. Lucas et al. (2008) explored the effects of early-summer droughts by using rainout shelters and categorized individual into seven size categories. Our integral projection model offers numerous advantages over this classical matrix approach. First, 49 parameters were necessary to construct the matrix, while here we have used only 13 (Appendix C), consequently decreasing the error propagation associated with model construction (Ellner and Rees 2006). Second, exploring the values of the vital rates in gross size classes likely explains why the classical approach did not report positive elasticities of shrinkage in dry years, as we have

done here. Moreover, such class lumping does not allow for the close-up LTRE decomposition offered by our IPMs: indeed, the contributions of growth and shrinkage to the differences in λ detailed in our LTREs varied greatly for individuals whose size differed in just a few rosettes (Appendix H). Finally, IPMs have been reported to perform better than classical matrix models with small sample sizes as in the studied population (Ramula et al. 2009).

Final remarks: will climate change have only positive effects?

The effects of climate change have been focus of much attention by plant demographers and these studies generally report negative effects of increased environmental stochasticity on the population growth rate (λ) (Inouye et al. 2002, Morris et al. 2008, Bremer and Jongejans 2010, Dalgleish et al. 2010, Jongejans et al. 2010). Water is the limiting factor in xeric environments (Noy-Meir 1973) and thus it should not be shocking that additional precipitation favored survival, growth and reproduction of *C*. *flava*. Nonetheless, while climate models for the Great Basin desert predict increases in precipitation, they also forecast more erratic rain distribution (Schlesinger et al. 1990, Arritt et al. 2000, Easterling et al. 2000a). In reality, desert populations are likely to encounter years of extreme drought intertwined with years of intense rains (Noy-Meir 1973). Here we have shown that *C. flava* produces more flowers and seeds the year after being watered, but that recruitment is not enhanced. Moreover, our watering treatments affected negatively λ during the period of the pulse, mostly via increased mortality of seedlings and young established individuals; we believe that soil runoff –intrinsic characteristics of the precipitation at such high elevations (Comstock and Ehleringer 1992)– is responsible. Consequently, we hypothesize that (i) a battery of rainy years might in fact be negative for the population dynamics of this species by means of decreasing its recruitment and increasing aging of the population, but that (ii) late-summer rains (in year *t*) coupled with significant snow accumulation during the winter of that would follow the next growing season (year t + 1 to t + 2), right before seeds are to be recruited, will have positive effects on the population growth rate λ .

The present work suggests that timing of delivery of resources associated with pulses is of crucial importance for long-term population dynamics. While here we have reported long-term positive effects on λ , the opposite pattern has also been found for the same population. Peek and Forseth (2009) simulated pulses of nitrogen in early spring and followed the vital rates of individuals of *C. flava* for three years. They found that treated plants outperformed control plants the first year, but then treated plants became more likely to die, shrink and less likely to reproduce in the following years. Great basin desert native plant species, *C. flava* among them, can use resources differently depending on the time of the year (Gebauer and Ehleringer 2000) and we suspect that the radically different results are due to the timing of the pulse. However, it is also entirely possible that *C. flava* responds differently to different resources, as it has been shown in other species (Chapin et al. 1990).

In the present study we have explored the effects of shifts in precipitation, but the reality of climate change is more complex than just changes in one variable. Climate models also predict increases in temperature in the Great Basin desert (Team 2000, IPCC 2007), and a significant rise of 0.2° C per decade has already been recorded at our field

site (Appendix A.b; Western Regional Climate Center, <u>http://www.wrcc.dri.edu</u>). Increases in winter temperature will likely affect negatively the population dynamics of *C. flava* because less snow will be stored and thus be available when individuals resume growth the following growing season (Comstock and Ehleringer 1992), and because reproduction, dependent on meristem vernalization (Casper 1985), may be diminished. Future research will focus on incorporating the dual (temperature and precipitation) stochastic nature of this ecosystem using integral projection model to evaluate the role of variable environments and size fluctuations of individuals within the population.

IV.6. Acknowledgements

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Table IV.1. *F*-ratios from the two-way analyses of variance examining the effect of watering (τ) in period (α) *t* on the flower and mature seed production in period *t* + *1*, replicated for three years (2007, 2008 and 2009), in comparison to control plots, which only received natural precipitation. Italics and underlined: *P* < 0.05; bold: *P* < 0.001.

			Total	Total					
			flowers	mature		Mature seeds per flower			
			per	seeds per					
			rosette	rosette					
		df			0	1	2	3	4
Period ((α)	2	14.716	20.883	0.367	50.903	1.260	1.364	<u>3.482</u>
Treatment ((τ)	1	<u>1.240</u>	<u>3.386</u>	<u>3.765</u>	<u>4.177</u>	<u>2.418</u>	0.189	2.110
$\alpha \times \tau$		2	<u>0.717</u>	<u>0.431</u>	0.931	1.076	1.036	1.518	<u>3.830</u>

Table IV.2. Main effects and interactions of the two LTRE analyses depicted in the experimental design (Fig. IV.2.c): (left) period × treatment and (right) time since watering x treatment.

LTRE ×		LTRE ×	
Period ()		Time since watering ()	
2006-07	0.015	t = 0	-0.064
2007-08	-0.065	t = 1	-0.007
2008-09	0.138	t = 2	0.139
2009-10	0.004		
	$0.055 \pm$		$0.052 \pm$
Mean ± S.E.	0.031	Mean ± S.E.	0.032
Treatment (<i>t</i>)		Treatment (<i>t</i>)	
Watering 2006	0.050	Watering 2006	0.029
Watering 2007	0.053	Watering 2007	-0.009
Watering 2008	0.040	Watering 2008	-0.006
Watering 2009	0.016	Watering 2009	-0.046
	$0.040 \pm$		$0.023 \pm$
Mean ± S.E.	0.008	Mean ± S.E.	0.009
Period x Treatment ($\times \tau$)		Time since watering x Trea	tment ($\times \tau$)
Watering 2006 × 2006-07	-0.090	Watering $2006 \times t = 0$	-0.110
Watering 2006 × 2007-08	-0.002	Watering $2006 \times t = 1$	-0.039
Watering 2006 × 2008-09	0.194	Watering $2006 \times t = 2$	0.236
Watering 2007 × 2007-08	-0.090	Watering $2007 \times t = 0$	-0.191
Watering 2007 × 2008-09	0.169	Watering $2007 \times t = 1$	0.120
Watering 2007 × 2009-10	0.079	Watering $2007 \times t = 2$	0.043
Watering 2008 × 2008-09	0.115	Watering $2008 \times t = 0$	0.090
Watering 2008 × 2009-10	-0.036	Watering $2009 \times t = 1$	-0.102
Watering 2009 × 2009-10	0.016	Watering $2009 \times t = 0$	-0.046
	$0.088 \pm$		$0.108 \pm$
Mean \pm S.E. $\times \tau$	0.022	Mean \pm S.E. $ \times \tau $	0.022



Figure IV.1. a. Distribution of *Cryptantha flava* along the Colorado Plateau (red), and studied population in Utah, USA (star). b. A permanent plot used to census individuals of *C. flava* at the field site during the five years of the study. The measuring sticks are 1 m in length. c. An adult of *C. flava* showing drastic shrinkage: 44% decrease in aboveground biomass in 2007-2008, following the intense 2007 drought (see figure III.2.b). Size in 2007: 123 rosettes; size in 2008: 54 rosettes. The dead rosettes are still visible on the right side of the individual (dashed, white polygon). Photo credits: R. Salguero-Gómez.



Figure IV.2. a. Monthly precipitation during the length of the study showing deviations from the long-term (1931-2010) mean precipitation (\pm S. E). b. Experimental design: a pulse of precipitation of 4.5 cm of intensity, represented by a cloud in this diagram, was simulated in early August of each year for a separate set of plots (gray tones). The control

plots (white) received only the naturally occurring precipitation (panel *a*). The population dynamics of individuals of *C. flava* in each plot were then monitored every May from 2006 to 2010. The light gray background regions indicate the growing season of *C. flava*. The growing season during the year of a watering treatment is extended (chapter II). The experimental design contains three effects: period (*a*), time since watering (β) and treatment (τ). C. Scheme for the 2 two-way Life Table Response Experiment (LTRE) analyses used to explore the effects of period (hatched) and treatment (white and gray gradient), and time since watering (0 years since watering: black, 1 year since watering: dark gray; 3 years since watering: light gray) and treatment (gray gradient). Note that in the second LTRE no control plots were included in the analysis.


Figure IV.3. Integral projection model (IPM) kernels for each of the periods under the experimental design depicted in figure III.2.b. Colored areas above the 1:1 dotted line represents growth from time *t* to t+1, while colored areas below represent shrinkage. Colored areas at the bottom of each panel represent recruitment (individuals in time *t* contribute to the population with seedlings in t+1).



Figure IV.4. Watering increased in some years the number of flowers and mature seeds produced, as well as decreased the rate of seed embryo abortion per flower. a. Production of flowers and mature seeds a given year for the control and plots that had been watered the previous year. b. Number of mature seeds produced per flower in each flowering rosette. Three- and four-seeded flowers were re-scaled to ×10 for graphical display purposes. * P < 0.05, ** P < 0.005.



Figure IV.5. Watering treatment effects on the population growth rates (λ). a. Population growth rates (\pm 95% confidence intervals) for the control and watering treatments for each year of the demographic census; letters were obtained through Tukey HSD significance test and represent significant differences in population growth rates among period × treatment combinations. The dashed, horizontal line represents $\lambda = 1$, where the population is neither increasing nor declining. b. Treatment effects (Population growth rate differences in treatment and control plots for the same year: $\lambda_{\text{Watering}} - \lambda_{\text{Control}}$) 0, 1 and 2 years since pulses of 4.5 cm of precipitation were simulated in August of 2006, 2007, 2008 and 2009. * *P* < 0.05, ** *P* < 0.005, *** *P* < 0.001.



Figure IV.6. The demographic performance of large individuals (>~40 rosettes) of *C*. *flava* did not contribute much to the population growth rates, as shown in the IPM matrix element elasticities for the control and watering treatments. 1:1 dotted line represents stasis in size time *t* to t+1. See experimental design described in figure 1.B for guidance.



Figure IV.7. a. Vital rate elasticities of fecundity (, dashed, gray line), survival (, solid, gray line), growth (, dotted, black line) and shrinkage (, dot-dashed, black line) as a function of size (number of rosettes) for the control and watered plots of 2009-10. Arrows indicate the size at which the effect of the vital rate of growth/shrinkage on the population growth rates turns from positive/negative to negative/positive as size increases (see appendix G). b. Seven scenario IPMs showed switches from positive to negative values in the vital rate elasticities of growth and shrinkage; the switch occurred at smaller sizes for growth than for shrinkage. Dotted line represents the 1:1 size ratio.



Figure IV.8. The observed size structure of *Cryptantha flava* after wet periods (2006-07, 2008-09) describes an exponential decay with many seedlings and a significant number of large plants. The population is re-structured following drought periods (2007-08, 2009-10) by means of high seedling mortality and large plant shrinkage, which results in an observed size structure closer to the stable size distribution.

Chapter V

Keeping plant shrinkage in the demographic loop

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in collaboration with Brenda B. Casper

V.1. Summary

- 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.
- 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.).
- We also conducted a comparative loop analysis in order 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.
- 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).
- 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.

• 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, matrix dimension, life span, plant shrinkage, population growth rate (λ), projection matrix models, size phenotypic plasticity

"To return to the origin is not to regress"

Dani Carbonell, 2007

V.2. 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 *et al.* 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). Second, shrinkage, if adaptive, might allow plants to achieve greater longevity (Horvitz & Schemske 1995; Morris & Doak 1998). Third, 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 A). 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. V.1). Second, ecologists have typically focused only on the factors that increase plant fitness over the short term and, because classspecific survival and reproduction are almost always greater in larger individuals, shrinkage has been regarded as the antithesis of fitness (Caswell 2001: 220; Fig. V.1). Third, 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 and co-workers (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 et al. 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.

In this paper, 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 *et al.* 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?

V.3. Materials and methods

Database acquisition and standardization

We assembled a database of published projection matrices and associated relevant ecological information for herbaceous perennial plant species. We focused solely on nonsucculent herbaceous perennials in order 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 A), 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 clearly separate 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 A) in order 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. Second, because matrix dimensions affect elasticities (Silvertown *et al.* 1993; Enright *et al.* 1995; Benton & Grant 1999), we collapsed all matrices into the same dimensions in order to assure the posterior comparability of their elasticities with other associated demographic parameters. We chose a threshold matrix dimension of $5 \times$

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 C). 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 $p_{ij} \square \{0, 1\}$ with sexual and/or clonal reproduction $a_i \square \{0, \infty\}$.

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 (Salguero-Gómez & Plotkin, 2010; chapter VII). 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 vs. non-reproductive classes separated, unlike the procedure suggested by Enright *et al.* (1995). For those matrices with more than one class representing seed bank or vegetative dormancy (see Appendix A), we merged the multiple classes within each matrix in order 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 not only affect 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 (The MathWorks, Inc., Natick, MA, USA).

We compared the frequency with which shrinkage occurs in natural populations to its elasticity ($E_{Shrinkage}$ 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 ($|E_{Shrinkage}| > 0.05$). Second, we evaluated $E_{Shrinkage}$ in relation to the elasticities of other vital rates for each species ($E_{Survival}$, E_{Growth} , $E_{Dormancy}$ (vegetative dormancy), $E_{Awakening}$ (awakening from vegetative dormancy), $E_{Sexual reproduction}$ and $E_{Clonal reproduction}$). For each of these vital rate elasticities, we determined the percentage of species in which the absolute effects of $E_{Shrinkage}$ were significantly greater than the effects of the above-mentioned vital rates of interest ($|E_{Shrinkage}| - |E_{Vital rate of interest}|$ > 0).

Matrix analyses

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 $E_{Shrinkage}$ 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 average age of parents of offspring produced by a cohort over its lifetime (μ_l) (see Appendix B). We computed these parameters using STAGECOACH version 2.3 (Cochran & Ellner 1992) and PopTools version 3.0 (Hood 2003). We also examined how $E_{Shrinkage}$ and E_{Growth} correlate with the main parameters of transient behaviour: the speed (ρ^2 , damping ratio: the ratio of the dominant eigenvalue λ_I to the modulus of the subdominant eigenvalue λ_2), and the period of oscillation (P_i , for the i^{th} highest possible complex eigenvalue; Caswell 2001) with which a perturbed system returns to its dynamic equilibrium. Finally, we examined how $E_{Shrinkage}$ 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.

² 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 $E_{Shrinkage}$, and not as $E\rho_{ij}$ (but see Appendix C). Moreover, the Spearman correlation coefficients are typically reported as ' ρ ', but we have not referred to them by their Greek letter to avoid confusions.

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 1996), we treated them independently in order to tease apart exclusive effects of shrinkage versus those of growth. Second, while we were most interested in the relationships that life span has with $E_{Shrinkage}$ and with E_{Growth} , we also extended the comparisons of population-level demographic traits to the rest of vital rate elasticities ($E_{Dormancy}$, $E_{Awakening}$, $E_{Sexual Reproduction}$ and $E_{Clonal Reproduction}$), 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 (Morris *et al.*, 2008, Franco and Silvertown, 2004).

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 $E_{Shrinkage}$ 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 $E_{Bi-directional}$ growth (= $|E_{Growth}|$ + $|E_{Shrinkage}|$) when regressed against each of the previously calculated population-level parameters. This method identifies which demographic parameters correlate significantly with $E_{Shrinkage}$ and with E_{Growth} . We used absolute values of $E_{Shrinkage}$ 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 *et al.* 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 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. V.2). We then explored how $E_{Recruitment loops}$, $E_{Size-plastic loops}$ and $E_{Size-rigid loops}$ 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 A). 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*_{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.

In spite of 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 $P \leq 0.05$.

V.4. 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 $|E_{Shrinkage}| > 0.05$, 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%; $E_{Size-plastic loops} \ge 0.05$; Appendix D). The species characterized by low or no values of $E_{Size-plastic loops}$ (<0.05) were always a subset of the species with low or no $E_{Shrinkage}$ values.

The demographic importance of shrinkage, in absolute value, when compared to other vital rates varied greatly. For instance, $|E_{Shrinkage}|$ was lower than $E_{Survival}$ in 77.5%, lower than E_{Growth} in 95%, lower than $E_{Sexual reproduction}$ in 76.9% and lower than E_{Clonal} reproduction in 87.5% of the species, respectively. Nevertheless, $|E_{Shrinkage}|$ was higher than $|E_{Dormancy}|$ and $|E_{Awakening}|$ in 87.5% and 75% of the species with such processes, respectively. In a reduced number of species, $E_{Shrinkage}$ was positive (*Cynoglossum virginianum, Erythronium japonicum, Lobularia maritima,* and *Tillandsia deppeana*; but for the latter two species $E_{Shrinkage}$ 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. V.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 ($t = 4.99, P < 10^{-10}$ 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 $E_{Shrinkage}$ did not vary significantly as a function of life span, the former was always positive and the latter almost always negative (Fig. V.4). E_{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*_{Sexual reproduction} decreased rapidly with life span. In regards to the 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 $|E_{Shrinkage}|$ only correlated (positively) with the damping ratio (Table V.1.a). In contrast, when shrinkage and growth were lumped, $E_{Bi-directional growth}$ 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 $E_{Shrinkage}$, the values of $E_{Bi-directional growth}$ were negatively affected (Table V.1.a).

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_{Sexual} reproduction than those species without shrinkage (Fig. V.5).

Insights from loop analysis

In loop analysis, herbaceous perennials were characterized by high values of $E_{Size-rigid \ loops}$ and by a wide range of values for $E_{Recruitment \ loops}$ (Fig. V.1). The values for the $E_{Size-plastic \ loops}$ 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, $E_{Recruitment loops}$ correlated with the same demographic parameters and in the same direction as $E_{Sexual reproduction}$ (negatively: life span, matrix dimension, T and μ_I ; positively: λ , R_0 , ρ and P_i) (Fig. V.4, Table V.1.b), and $E_{Recruitment loops}$ and $E_{Sexual reproduction}$ also correlated significantly with each other (Table V.2). Nevertheless, while $E_{Sexual reproduction}$ was negatively affected by having collapsed matrix dimensions, $E_{Recruitment loops}$ was not affected. $E_{Size-plastic loop}$, which incorporates both E_{Growth} and $E_{Shrinkage}$ (but also $E_{Dormancy}$ and $E_{Awakening}$, 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 $E_{Size-plastic loop}$ correlated positively with $E_{Survival}$, E_{Growth} and $E_{Shrinkage}$. As for $E_{Size-rigid loops}$, it correlated significantly and in the same direction as $E_{Survival}$: positively with life span, T and μ_I , and negatively with ρ and P_i . The correlation between $E_{Size-rigid loops}$ 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 $E_{Recruitment loops}$ and

 $E_{Size-rigid \ loops}$ were similar, and obviously $E_{Size-plastic \ loops} \approx 0$ (Fig. V.5). Species with shrinkage had, on average, high values of $E_{Size-rigid \ loops}$, intermediate values of $E_{Recruitment}$ loops and relatively low values of $E_{Size-plastic \ loops}$.

V.5. 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 V.1.a). 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). Second, 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 sizeplastically to the new conditions. Second, 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 figure IV.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_{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. V.2). However, the consequent finding, that the existing $E_{Size-plastic loop}$ values in species with shrinkage are subtracted from the $E_{Recruitment loop}$ values in species without shrinkage, while $E_{Size-rigid loops}$ 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 A). 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. Second, 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 et al. 2006), stem length (Liu et al. 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 and collaborators (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. Second, the application of periodic projection matrices (Caswell & Trevisan 1994; Le Corff & Horvitz 2005; Smith et al. 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; Claessen 2005; Aberg et al. 2009; Caswell 2010; 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 life time 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 longlived 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 (*c.f.* 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 classspecific survival and class-specific reproductive output increase with plant size (Silvertown *et al.* 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 (Salguero-Gómez & Casper, unpublished; chapter V). For instance, because the survivorship of small individuals of Tillandsia deppeana (Bromeliaceae), Lobularia maritima (Brassicaceae) and Fritillaria meleagris (Liliaceae; citations in Appendix A) 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. V.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.

V.6. Acknowledgements

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Table V.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-underlined are significant at P < 0.05 and in bold at P < 0.001. 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[†]. $E_{Bi-directional} = |E_{Growth}| + |E_{Shrinkage}|$

Elasticities		Matrix	λ	R_0	Т	μ_{I}	ρ	P_i
		dimension						
		$n=45^{\dagger}$	n=79	n=79	n=77	n=79	n=79	n=70
(a)	E _{Survival}	<u>0.33</u>	<u>-0.37</u>	<u>-0.34</u>	0.63	0.48	-0.34	<u>-0.33</u>
	E _{Growth}	-0.03	<u>0.32</u>	<u>0.32</u>	-0.10	-0.04	<u>0.35</u>	<u>0.29</u>
	$ \mathbf{E}_{\mathrm{Shrinkage}} $	-0.13	-0.06	-0.14	0.16	0.11	<u>0.23</u>	0.02
	E _{Domancy}	-0.01	-0.06	-0.07	-0.03	-0.09	-0.06	0.06
	$E_{Awakening}$	0.03	0.22	0.17	-0.15	-0.15	<u>0.24</u>	-0.06
	$E_{Bi-directional}$	<u>-0.23</u>	0.19	0.15	0.03	0.01	<u>0.27</u>	<u>0.26</u>
	E _{Sexual reproduction}	<u>-0.32</u>	<u>0.35</u>	<u>0.36</u>	-0.49	<u>-0.32</u>	<u>0.22</u>	<u>0.22</u>
	$E_{Clonal reproduction}$	-0.01	0.06	0.06	-0.20	-0.19	0.12	<u>0.26</u>
(b)	E _{Recruitment} loops	-0.37	0.39	0.39	-0.80	-0.52	0.47	0.67
	$E_{Size-plastic\ loops}$	0.38	<u>-0.25</u>	<u>-0.34</u>	0.18	0.06	<u>0.30</u>	0.10
	$E_{\it Size-rigid\ loops}$	0.01	-0.21	-0.17	0.78	0.56	-0.65	-0.70
Table V.2. Spearman rank correlation coefficients between vital rate elasticities and loopelasticities. Coefficients in italics-underlined are significant at P < 0.05 and in bold at P < 0.001.

Elasticities	$E_{Recruitment\ loops}$	$E_{\it Size-plastic\ loops}$	$E_{Size-rigid\ loops}$
E _{Survival}	-0.82	<u>0.27</u>	0.67
E_{Growth}	<u>0.25</u>	<u>0.33</u>	<u>-0.28</u>
$ E_{Shrinkage} $	-0.02	0.53	-0.21
<i>E</i> _{Dormancy}	0.35	-0.48	-0.14
$E_{Awakening}$	0.26	0.14	-0.24
$E_{Bi-directional}$	<u>0.31</u>	0.15	<u>-0.24</u>
$E_{\it Sexual}$ reproduction	0.75	<u>-0.35</u>	-0.54
E_{Clonal} reproduction	0.75	-0.43	-0.64



Figure V.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).



Figure V.2. Three-stage life cycle (top) and loop decomposition for two imaginary plant species that do or do not present retrogression transition probabilities (gray). 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.



Figure V.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 are found out of the scale. They were, however, included in the regression analyses (Appendix B).



Figure V.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.



Figure V.5. Elasticity values ($\bar{x} \pm SE$) 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.

Chapter VI

Plant shrinkage: the big unknown demographic phenomenon,

and its potential adaptive value

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in collaboration with Brenda B. Casper

VI.1. Summary

- Plants' design is highly modular, and consequently plants can display modular gain (growth) as well as loss (plant *shrinkage*). Historically, most emphasis on demography has been placed on understanding the factors that maximize fitness survival, growth and reproduction– but plant shrinkage has been bluntly overlooked.
- Here, we draw from a database of 542 plant species and their respective population matrix models to explore the frequency with which plant shrinkage occurs in natural populations, how often it is object of study, and to summarize its ecological implications. In reviewing the associated literature, we pinpoint the main limitations of the methodological approaches employed to report plant shrinkage and suggest alternative protocols to ensure a more objective identification. We also introduce a theoretical framework that details the necessary conditions for shrinkage to be adaptive.
- While shrinkage occurs very frequently (56%) in natural populations, it is more common among succulents (80%), herbaceous perennials (74%), and shrubs (66%) than in annuals (0%), palms (20%) and trees (30%). We identify three primary areas contributing to our limited understanding of why and how plants decrease in size: field census protocols, model construction, and interpretation of results. When sensitivity values of survival and fecundity change non-monotonically as a function of size, a selective pressure emerges favoring shrinkage, and thus establishing an optimum size that is smaller than the maximum plant size.

 Plant shrinkage is a common phenomenon that has passed unnoticed in demographic research, likely due to the common assumption that larger plants have greater fitness. The use of new methods, including higher temporal and spatial resolution in field censuses and matrix construction, the implementation of stochastic analyses, and a more careful interpretation of elasticities will allow us to better understand the implications of plant shrinkage. Several questions make the study of plant shrinkage a promising venue of research: Why and under what circumstances can shrinkage be adaptive?, Is plant shrinkage a sign of senescence or a buffering mechanism against environmental stochasticity? Does plant shrinkage, through its linkage to plant modularity, have a phylogenetic basis, or is it the product of environmental filtering?

Key-words: comparative plant demography, elasticity, optimum size, plant shrinkage, population growth rate (), population projection matrix models, selection gradients, sensitivity.

"Life shrinks or expands in proportion to one's courage"

Anais Nin (The Diary of Anais Nin, volume 3, 1939-1944)

VI.2. Introduction

Higher plants are extremely plastic organisms; they can exhibit great variation in the physiology and morphology of their individual organs and architecture, both below and aboveground (Watkinson & White 1986). Overall plant size is an important plastic trait because it typically correlates strongly with the plant's competitive ability, survival probability, and/or reproductive output (Werner & Caswell 1977; Metcalf & Pavard 2007). Thus, plant size is often used as a proxy for fitness, serving as an integrative measure of plant response to both environmental variation and selection pressures over generations (Silvertown & Charlesworth 2001).

While many phenotypically plastic morphological and physiological traits (e.g. defense mechanisms, leaf size and shape, vegetative and seed dormancy) have been broadly explored, the capability of individual plants to decrease in size (*shrinkage* hereafter) remains surprisingly unexplored. Leaf senescence and shedding have received a great deal of attention (Osborne 1959; Gan 2007), but the demographic implications of the shedding of larger plant parts, such as entire branches (Orshan 1963; Kozlowksi 1973) that inherently results in shrinkage of the whole plant, remains a big unknown in plant demography.

Plant shrinkage may have important implications for demography because it can alter the size hierarchy of populations, effectively decoupling size from age (Casper

1996). For instance, the widely-used developmental stage-/size-based projection matrix models (Lefkovitch matrix; Lefkovitch 1965) are based on the assumption that individuals within a given class are identical with respect to their future demographic fate (Caswell 2001), *i.e*, that they have the same average probability of transitioning to larger/more developed or smaller/less developed stages of the species' life cycle. This assumption may be violated when individuals can decrease in size because, at any intermediate-size class within the projection matrix, there can be young individuals that have grown from smaller classes and old individuals that have shrunk from larger ones. These two distinct individual trajectories can vary significantly (Ehrlén 2000), especially if adults undergo demographic senescence (i.e. a decline in survival and or reproduction with age; Roach 2004) and exhibit ever-decreasing size until death, as it apparently happens with Aconitum noveboracense (P. Dixon, pers. comm.) and Plantago lanceolata (Roach et al. 2009). Furthermore, the inclusion of shrinkage in projection matrices may affect the estimation of important demographic parameters such as lifespan or age to first reproductive event (Cochran & Ellner 1992); retrogression probabilities (shrinkage in size-based models) are averaged over the entire population into discrete size classes, and so individuals that shrink may be interpreted as "immortal" individuals, who fluctuate indefinitely between retrogression and progression (Silvertown, Franco & Perez-Ishiwara 2001).

Here we draw from a database containing population projection matrix models for 542 plant species to (i) determine how often shrinkage is reported for natural populations and (ii) consider whether plant demographers have underestimated the occurrence of shrinkage, (iii) inspect the published literature and applied models in order to understand

why demographers have not focused more on its importance, and (iv) propose means, using demographic methods, to explore whether shrinkage is an adaptive trait.

VI.3. Database analyses

We compiled a database, COMPADRE II (COMPArative Demographic REsearch), of published projection matrix models and associated relevant ecological and taxonomic information for plant species, obtained as described in Salguero-Gómez & Casper (2010; chapter IV); additional unpublished information was obtained through personal communications with some authors (See acknowledgements). The total sample size of COMPADRE II is 702 plant species, but here we focus only on those species containing size-based matrices (n = 542) so that retrogression transition probabilities would translate into frequency of shrinkage. These include 17 algae, 57 annuals, two mosses, three ferns, 338 herbaceous perennials, one liana, 41 palm trees, 67 shrubs, 33 succulents and 141 tree species. We then systematically looked for evidence of shrinkage in the life cycle and/or projection matrix of these species. To determine whether significant shrinkage occurred, we summed the matrix cell values that corresponded to shrinkage, ρ_{ij} , and normalized it by the number of classes (*n*, or matrix dimension) of the life cycle, a characteristic that is known to affect the estimation of demographic parameters such as the population growth rate (λ) or the elasticities (the proportional effect of a demographic process on λ ; de Kroon *et al.* 1986) (Enright, Franco & Silvertown 1995). We considered the occurrence of shrinkage to be significant, i.e. not likely a measuring error, when its normalized probability $\sum_{ij} \rho_{ij}/n > 0.05$. We then

carefully examined each paper to determine whether the authors acknowledged the existence of this phenomenon when it did occur ($\sum_{ij} \rho_{ij}/n > 0.05$) and whether they discussed its potential ecological implications. In doing so, we noted data collection and matrix construction issues that hampered the detection and reporting of shrinkage.

Survey

The survey of shrinkage in the 542 plant species for which size-based matrix models are available in COMPADRE II revealed that shrinkage occurs very frequently: 56% (n = 305) of these species contained normalized probability $\sum_{ij} \rho_{ij}/n > 0.05$. Certain growth forms drove this percentage: succulents (80%, n_{Total} = 25 species), herbaceous perennials (74%, n_{Total} = 212 species) and shrubs (66%, n_{Total} = 50 species). Other growth forms, such as trees (30%, n_{Total} = 115 species), palms (20%, n_{Total} = 30 species) and annuals (0%, n_{Total} = 34 species), did not experience plant shrinkage as frequently. Statements about lianas (n =1) and ferns (n = 1) are limited due to their low sample sizes.

Despite the frequency with which shrinkage happens in individuals of natural populations, shrinkage has truly passed unnoticed in the literature. In 35% (n = 107 species) of the cases in which $\sum_{ij} \rho_{ij}/n > 0.05$ the authors failed to acknowledge the process by explicitly mentioning the term "shrinkage", "retrogression", or a synonym in the corresponding manuscript. Furthermore, only 0.02% of those studies (n = 4 species) offer a (brief) discussion of the potential ecological value of shrinkage. For instance, Horvitz and Schemske (1995) mentioned upfront that the ability of plants to shrink, rather

than die, during adverse environmental conditions may be common among large herbaceous perennial species. García (2003) highlighted the importance of stasis, growth and shrinkage in the population growth rate of extremely long-lived *Borderea chouardii*. In a case study of *Hilarica mutica*, Vega and Montana (2004) highlighted the greater relevance of stasis and shrinkage over other demographic process such as growth and reproduction. Finally, Morris and Doak (2005) reported positive vital rate elasticities for shrinkage in the alpine cushion *Silene acaulis* (Fig VI.1.b), implying that shrinking large plants increase the population-level fitness.

Is shrinkage reported accurately?

In reviewing population projection matrices from published studies, we realized that shrinkage is likely to be even more common than it is currently reported due to limitations in methodological procedures used in the collection of field data, construction of matrix models and interpretation of their outputs. Here we identify such limitations and suggest ways to circumvent them (Table VI.1).

Collection of field data

The low temporal and spatial replication typical of field studies may not accurately capture demographic traits, especially considering the great potential for phenotypic plasticity among sites (Morris & Doak 2005). The studies collected in COMPADRE II show low spatial (2.74 \pm 0.27 [S.E.] sites) and temporal replications (4.48 \pm 0.27 years). The issue is that poor replication may not satisfactorily describe shrinkage –or any other demographic process– if that process results from temporal and spatial environmental fluctuations or if the process is naturally rare, *e.g.* masting. The implications are far reaching since comparative demographic research assumes that the characteristics of a species observed in a few populations or in a few census periods are representative of that species as a distinct unit (Silvertown, Franco & McConway 1992; Franco & Silvertown 2004). Shrinkage may occur frequently in some populations, but not in others (Jongejans *et al.* 2010) and vary spatially even within the same population. For instance, in arid land patches of vegetation, the dynamics of *Hilaria mutica* are dominated by stasis and shrinkage both in the center and periphery of the patch, but in years of high precipitation, growth and reproduction become more important in the periphery while the center's dynamics do not change (Vega & Montana 2004).

We cannot emphasize enough the importance of following multiple sites for the same species simultaneously for as long as possibly sustained by available funding. Importantly, many herbaceous perennial species have life spans as long as or longer than the researcher investigating them (*e.g., Borderea pyrenaica* = 100-300 years, fig. VI.1.a, García & Antor 1995; *Silene acaulis* >300 years, fig. VI.1.b, Morris & Doak 2005), and so studying their populations for 4-5 years may not be tremendously informative. We know of only a handful of on-going, long-term studies with herbaceous perennials (*e.g. Carduus nutans*, de Kroon; *Dicerandra frutescens* and *Eryngium cuneifolium*, E. Menges; *Frasera speciosa*, D. Inouye; *Plantago lanceolata*, D. Roach; *Trillium grandifolium*, T. Knight; *Cryptantha flava*, R. Salguero-Gómez & B. Casper). We argue

that the low number of species with long-term demographic data limits our current understanding of processes that may correlate with age, such as senescence. Senescence is of particular interest here because shrinkage may be a consequence (Salguero-Gómez & Casper 2010; chapter IV).

Multiple censuses per year would also help us understand the causes of shrinkage, when it occurs, by providing information on the demographic fates of shoot apical meristems over an annual cycle. Are plants smaller when they begin growth than they were the preceding year or does shrinkage occur during the growing season? Is plant size reduced following a year of heavy investment in reproduction or due to the death of semelparous meristems—when apical vegetative meristems are converted to flowering meristems? Does shrinkage coincide with or follow adverse environmental conditions? A multi-seasonal sampling effort would help narrow down these possibilities and underlying environmental factors. Most demographic censuses of perennial species in COMPADRE II were carried out on annual visits to the field, coinciding with the flowering peak and resulting in *annual* projection matrices, which may not offer the temporal resolution needed to understand the role of shrinkage in the life cycle of the species.

The inclusion of *seasonal* demography in perennial studies is feasible. For instance, Goodman matrices (Le Corff & Horvitz 2005) can be used to incorporate seasonal sub-matrices into a larger annual matrix. In addition, periodic projection matrices, a standard tool in annual and biennial plant demography (Caswell & Trevisan 1994), can model seasonal dynamics in a battery of matrices that, when back-multiplied, generates the annual projection matrix. Both tools allow for the same eigen-analyses

employed for annual projection matrices (Ramula, Rees & Buckley 2008; Bacaer 2009). Nonetheless, we know of only three cases in which periodic matrices have been employed in long-lived herbaceous species; these reveal different seasonal timings of shrinkage, and suggest different underlying mechanisms: during spring in *Taraxacum officinale* (Vavrek, McGraw & Yang 1997), in late winter in *Lobularia maritima* (Picó, de Kroon & Retana 2002) and both during the growing and during the dormant seasons in *Cryptantha flava* (Salguero-Gómez & Casper, unpublished).

But perhaps the most important field-based limitation to the true understanding of the effect of size on plant fitness in demographic studies, and the role of shrinkage in such a relationship, is how size is measured. Size-based matrix models vary a great deal in the state variable that is measured in the field and consequently used in the matrix models: number of tillers (Guardia, Raventos & Caswell 2000), shoot height (Fröborg & Eriksson 2003), total leaf area (Fiedler 1985), height (Olmsted & Alvarez-Buylla 1995), stem length (Esparza-Olguin 2005), rhizome diameter (Pino, Sans & Masalles 1998), tuft circumference or area (O'Connor 1993), number of rosettes (Lucas, Forseth & Casper 2008), trunk diameter in trees, making inter-specific demographic comparisons tricky. That no annual species in our database exhibits shrinkage is not surprising, since their optimal life history strategy is to maximize fecundity, not survival. However, we would expect shrinkage to be more frequent in larger, longer-lived growth forms, such as trees and palms, a hypothesis that is not supported by our results when compared to intermediate growth forms like herbaceous perennials and succulents.

We think the problem lies in how woody plants are typically measured. Tree and palm demography is typically based on DBH (diameter at breast height; Zuidema et al.

2010; see critiques by Hernandez-Apolinar *et al.* 2006). Although significant trunk shrinkage has been reported in palm and tree species of tropical dry forests (Lieberman 1982; Baker *et al.* 2002), the fact remains that the majority of the trunk of a palm/tree is dead tissue, which does not reflect gain and loss of live tissue. Thus, we argue that woody plant demography should be carried out using canopy volume as the biometric state variable, for which there exist appropriate forestry biomass scaling equations (Chojnacky 2002) or GPS approaches. For instance, Lamar and McGraw (2005) constructed and contrasted two matrix models for the same population of *Tsuga canadensis*, first using ground-based DBH information, and then using low-elevation GPS imagery. While their estimates of population growth rates were similar with both models, the stable stage distribution, reproductive values, and elasticities differed significantly. In the GPS-based matrix model, retrogression probabilities corresponding to sub-lethal crown disturbance events that resulted from an ice storm were depicted, while their DBH-based matrix model failed to do so.

For herbaceous plants, the number of modules would be a better measure of plant size than canopy diameter or height particularly because of its potential for helping us understand the anatomy of plant shrinkage. Plant shrinkage can occur when plants in emerging after the dormant season produce less biomass than the biomass they formed the previous year (Fig. VI.1.a-b), but shrinkage can be facilitated by the physiological or hydraulic independence of the modules that compose the individual (Fig. VI.1.d-f); death of a module would translate in whole-plant shrinkage. Marking and following individual modules would provide even greater resolution as we would learn about module turnover and whether module death is spatially aggregated. Demographic studies could treat modules of non-clonal plants using methodologies and theoretical frameworks applied as

ramets within genets (White 1979; de Kroon & van Groenendael 1997; de Kroon *et al.* 2005). In COMPADRE II, only three such studies have used –and benefitted from– modeling modules (Butler & Briske 1988; Colling & Matthies 2006; Salguero-Gómez & Casper, unpublished). Colling and Matthies (2006) reported relatively stable dynamics for whole individuals of *Scorzonera humilis* but found significant year-to-year variation in rosette turnover. They argued that whole-plant size does not provide a good understanding of how plants respond to environmental conditions. Module-level demography can also help us evaluate how energy is allocated within the plant. In the case of species whose modules operate independently for uptake of belowground resources (Independent Hydraulic Units, IHUs *sensu* Schenk 1999; Salguero-Gómez & Casper 2011; chapters I & II) and/or for distribution of carbohydrates (Independent Physiological Units, IPUs *sensu* Watson & Casper 1984), the demographic dynamics of modules within a plant can be decoupled, as in the case of *Cryptantha flava* (Salguero-Gómez & Casper, unpublished).

Model construction

In the COMPADRE II database, even if field data contained a level of resolution appropriate to detecting shrinkage, retrogression transition probabilities were frequently obscured in matrix construction. A single matrix cell, for instance, might contain percapita contributions (e.g. sexual or clonal reproduction) and transition probabilities (e.g.

shrinkage). Because per-capita contributions are not theoretically constrained (i.e. an individual plant can produce many new recruits), but transitions are constrained to (0, 1), adding these two very different elements is neither mathematically nor biologically sound. Nevertheless, this happens quite often in plant population matrix models, particularly in perennial, modular species that can grow and shrink in increments that may skip several size-classes. In some cases, dramatic shrinkage events place individuals in the first size class, which is typically "reserved" for seedlings (e.g., Boutela rigidiseta, Fowler, Overath & Pease 2006). In some species, new recruits grow in their first year to intermediate sizes and are grouped with mid-size, shrunken individuals (e.g., Astragalus scaphoides, Lesica 1995; Carduus nutants, Jongejans, Sheppard & Shea 2006). Further complications arise when clonal reproduction (e.g., Saxifraga cotyledon, Dinnetz & Nilsson 2002) or fission (e.g., Allium tricoccum, Nault & Gagnon 1993; Primula veris, Ehrlén 2000) occur. In one extreme case, where shrinkage and clonal reproduction were both present in the life cycle of *Helianthus divaricatus*, Nantel and Gagnon (1999) simply assumed that all matrix elements above the main diagonal corresponded to clonal reproduction. This practice of merging shrinkage with other demographic processes even occurs in other kingdoms as well (e.g., the soft coral Alcyonium sp., Caswell & Trevisan 1994). The problem can be solved by constructing two matrices, one containing transition probabilities (T matrix, Caswell 2001: 110), but in the COMPADRE II database, only in 15% of the cases where shrinkage would be obscured by other demographic processes did the authors reported T and F matrices separately. Alternatively, more detailed life cycles with higher matrix dimensions could be used to assure that individuals of different origin are not lumped mistakenly (Ehrlén 2000).

A vast number of published plant projection matrices use developmental stages and thus ignore size-based transitions. In fact, COMPADRE II contains 121 and 39 plant species with developmental stage-based and aged-based models, respectively, in addition to the 542 species with size-based models used in the present work. While stage- and agebased approached may have been appropriate to answer the specific questions posed for those species, size is almost always a better predictor of individual fitness than developmental stage or age (Silvertown & Charlesworth 2001), and size-based matrices allow more direct comparisons among species (Silvertown, Franco & Perez-Ishiwara, 2001). Further separating developmental/age stages into different size classes (Solbrig *et al.* 1988; Eckstein, Danihelka & Otte, 2009) and increasing matrix dimensions would allow for greater demographic resolution and demonstration of shrinkage if/when it occurs.

There is, however, a trade-off between the census effort and the resolution of the matrix model because one needs to make sure that each class contains significant numbers of individuals. The number of stages of the life cycle, and thus matrix dimensions, affects the probabilities of transitioning to other classes, including that of retrogression (Enright, Franco & Silvertown, 1995). Specifically, the probability of detecting biologically meaningful shrinkage events decreases with lower matrix dimensions (Salguero-Gómez & Plotkin, 2010; chapter VII). Thus, choosing a number of size classes to represent a species' life cycle is not a trivial matter, and doing so when size is a continuous variable may be particularly challenging. Some algorithms are available to determine the cut-off points in size-based classes that minimize the distribution errors associated with the distribution of individuals in the population

(Vandermeer 1978; Moloney 1986; Shimatani *et al.* 2007), but these do not offer recommendations on how many classes a model should have.

In a previous investigation, we found that matrices with dimensions of at least 5 × 5 for species with complex life cycles (e.g. containing clonal reproduction, vegetative dormancy, expedited sexual reproduction), or matrices of 4 × 4 dimensions for species with simpler life cycles, offer room for modeling shrinkage, if it happens (Salguero-Gómez & Plotkin, 2010; chapter VII). With limited sampling effort for small population sizes, integral projection matrices (IPMs, Easterling, Ellner & Dixon 2000) can offer a very useful alternative (Ramula *et al.* 2009). An IPM is a high-resolution projection matrix (~100 classes and above) where changes in size –both growth and shrinkage– survival and fecundity vital rates are analyzed as functions of a (quasi-) continuous size state variable. Whenever possible, IPM modeling exercises are preferred over classical matrix approaches because IPM estimates are less biased by their meshes (=high resolution dimension) than classical projection matrices are affected by their matrix dimensions (Ramula, Rees & Buckley 2009; Zuidema *et al.* 2010).

Analysis and interpretation

The third main limitation that we found towards a more explicit study of the relationship between plant size and population fitness –and thus the role of shrinkage– is based on the analytical tools used and the interpretation that is given to outputs obtained. Population matrix model have become so popular because they are able to compile complex field data that can then be easily analyzed through relatively simple mathematical procedures. Here we argue that all too often a disconnection exists between the math and the biology involved in these analyses, which has partially resulted in the overlooking of plant shrinkage.

Evaluating the importance of particular demographic traits to the growth or stability of populations is typically carried out using perturbation analyses (Caswell 2001), which consist on perturbing a compartment of a complex system (*e.g.*, time spent by a worker) and examining its effect on a parameter important to the system (*e.g.*, productivity of a factory). Classical perturbation analyses are deterministic and asymptotic, meaning that they report the normalized effect of a demographic process of interest on the long-term population growth rate () in constant environments. The most commonly used measurement is elasticity (de Kroon *et al.* 1986). We think that the broad application of perturbation analysis, without careful consideration, is also partly responsible for overlooking plant shrinkage.

Because the original goal of plant demography was to –and still is, to a large extent– determine environmental conditions that result in maximum crop yield (Nault & Gagnon 1993; Valverde, Hernandez-Apolinar & Mendoza-Amarom 2006; van der Voort & McGraw 2006; Winkler, Hulber & Hietz 2007) and because fecundity and survival are assumed to increase monotonically with plant size (Harper 1977; Fig. VI.2.a), decreases in size that inexorably lower fitness have been regarded as maladaptive (Caswell 2001). However, shrinkage can also have a positive effect on population growth rate if maximum plant fitness occurs at some intermediate size. To our knowledge, Morris & Doak (2005) were the first to point out positive elasticities of shrinkage (for *Silene* *acaulis*). It appears that this is not an isolated phenomenon, since we found positive shrinkage vital rate elasticity values in the projection matrices of 33 out of 123 herbaceous species in COMPADRE II (Salguero-Gómez, Burns & Casper, unpublished). The study of these species' size-specific survival and fecundity output sensitivities (an analog to selection pressure gradients, *sensu* van Tienderen 2000) shows that plant fitness does not always increase monotonically with size. The vital rate elasticity analyses on the integral projection models of *Cryptantha flava* show that intermediate-size individuals contribute far more to the population growth rate () than large individuals, thereby selecting for shrinkage of large individuals (Fig. VI.2.b).

Even when the effect of shrinkage on is negative and very small, the frequency of shrinkage might also be biologically linked to trade-offs with other life history traits (Salguero-Gómez & Casper 2010; chapter IV). For example, species that shrink frequently ($\sum_{ij} \rho_{ij}/n > 0.05$) have greater elasticities of survival than those that shrink infrequently ($\sum_{ij} \rho_{ij}/n \le 0.05$). Thus, we fully agree with researchers who have previously called for a more careful interpretation of perturbation analyses (de Kroon, van Groenendael & Ehrlén 2000) and admonish that even demographic processes with small elasticity values can be biologically meaningful.

The field of plant demography has clearly shifted gears from determinism to stochasticity in the last decade (see Salguero-Gómez & de Kroon 2010) in recognition that natural populations live in environments where stochasticity is the rule, not the exception. Classically, elasticities and sensitivities are calculated as the effect of an infinitesimally small relative or absolute change, respectively, of a given matrix element or demographic process on the asymptotic (i.e. predicted long-term value), deterministic (i.e. not stochastic) population growth rate, . But populations very rarely achieve asymptotic dynamic equilibria (Silvertown & Charlesworth 2001). Fortunately, recent advancements include stochastic perturbation analyses for not only asymptotic (Horvitz & Schemske 1995; Davison *et al.* 2010; Horvitz, Ehrlén & Matlaga 2010) but also transient (short-term) dynamics (Caswell 2007; Haridas & Tuljapurkar 2007; Stott *et al.* 2010). The application of these tools to explore the value of vital rates such as shrinkage, that otherwise have small deterministic elasticities, is a promising venue of research.

Another likely reason why shrinkage has been overlooked has to do with established comparative demography protocols that normally lump its occurrence with other phenomena. For example, one common approach in comparative plant demography is to graph species by their elasticity values on a ternary plot, which means reducing all elasticity values to three axes. This usually means grouping shrinkage with stasis (Silvertown et al. 1993) or growth (Franco & Silvertown 2004) to create one axis. The approach originated with the goal of using demographic features to place species on ternary space relative to the three ecological strategies suggested by Grime (1977). The simplicity of this approach caused many plant demographers to adopt it *ipso facto* (Pfister 1998), but its appropriateness was not evaluated until recently. Specifically, this approach assumes that the demographic processes that are lumped together correlate with the same life history traits, in this case shrinkage and stasis or shrinkage and growth, but now we know they do not (Salguero-Gómez & Casper 2010; chapter IV).

Classical elasticity analysis is also limited in that it only evaluates the importance of "one-time" transitions (*e.g.*, a_{ij} , from class *j* at time *t* to class *i* at time *t*+1), and we recognize that shrinkage of plants in a particular year may be linked to performance in

the preceding year –such as increased reproduction– or have unique consequences for those same individuals in subsequent years. A promising, and potentially more biologically meaningful alternative is elasticity loop analysis (van Groenendael *et al.* 1994), which recognizes that an individual's performance is integrated into loops throughout the life cycle of the species (Wardle 1998). For example, a recent application of loop analysis allowed disentangling the relative contributions to the population growth rate of fast-growing vs. slow-growing juvenile plants (Zuidema *et al.* 2009). Loop analysis can also be used to evaluate the importance of plasticity in size (fluctuations between growth and shrinkage) *vs.* its absence (Salguero-Gómez & Casper 2010; chapter IV). Furthermore, loop analyses can importantly overcome one violation of the assumptions underlying matrix models described above: that individuals in the same life cycle stage at a given time will not differ in future performances because of their different past histories (Ehrlén 2000).

We suggest using loop analyses for two additional approaches: (1) to explore the demographic contribution of individuals in a given class (e.g. intermediate size) of the life cycle after having arrived there from different pathways such as ever-growing juveniles vs. shrunken adults, and (2) to discern the relative contribution to of individuals that may be constantly declining in size before dying (*i.e.*, shrinkage being a sign of senescence; Partridge & Gems 2002) *vs.* individuals fluctuating in size in response to abiotic conditions (*i.e.*, shrinkage as a buffering mechanism).

V.4. Future directions

We present evidence that shrinkage of individual plants is a common phenomenon in natural populations, probably even more than it is reported here due to underestimation resulting from suboptimal implementation of demographic approaches (see table V.1). However, that a phenomenon occurs frequently does not suffice to its biological importance. The most promising venue of research on plant shrinkage, in our opinion, is yet to be fully explored: whether it has adaptive value.

Partial evidence already exists for the adaptive role of plant shrinkage at the population level. Shrinkage correlates with important demographic processes such as reproduction and survival (Salguero-Gómez & Casper 2010; chapter IV), and shrinkage is also indirectly linked to two important bet-hedging strategies: populations whose individuals undergo shrinkage are less likely to ever become vegetatively dormant or create seedbank than those without this ability (Salguero-Gómez, Burns & Casper, unpublished). Furthermore, the probability of shrinkage correlates negatively with the demographic rate of senescence (; Silvertown, Franco & Perez-Ishiwara 2001), implying that shrinkage may allow species to escape demographic senescence. These are just too many coincidences for shrinkage to be regarded as an "unimportant" demographic process any more.

Comparative studies may offer a robust framework for the understanding of the potential adaptive role of plant shrinkage. An exhaustive sensitivity analysis of shrinkage vital rates for species for which projection matrix data is available (> 700 plant species) will help determine how many of them show positive –adaptive (van Tienderen, 2000)– values, implying that in those species shrinkage enhances population-level fitness and consequently shrinking individuals are favored by selection gradients (Fig. VI.2.a.ii-iv).

Thus far, positive shrinkage vital rate sensitivities have been found in 27% of herbaceous perennials ($n_{Total} = 123$ species; Salguero-Gómez, Burns & Casper, unpublished). However, the adaptive role of shrinkage in other growth forms such as succulents, shrubs, palms and trees remains unexplored because, as we explained, we believe their size has been measured incorrectly (Table V.1).

At the same comparative scale, statistical approaches that account for phylogenetic relatedness among species (and a large toolbox is available to this end; Harvey & Pagel 1991; Silvertown, Franco & Harper 1997) will show whether there is a heritable basis for adaptive shrinkage, in which case species with positive sensitivities of shrinkage should cluster in the same clade(s), and/or whether plant species with adaptive shrinkage have undergone environmental filtering, in which case species with positive sensitivities of shrinkage should be linked to a specific environment/s, regardless of ancestry. Both common ancestry and environmental filtering could well explain the incidence and effects of shrinkage. On the one hand, phyllotaxis (the arrangement of the leaf vasculature within an individual plant) has been shown to have a strong phylogenetic signal (Marquis 1996), and we would expect shrinkage to be more common in more modular organisms, which have a less intertwined phyllotaxis. On the other hand, the incidence of plant hydraulic sectoriality, which can explain the ability of a plant to shrink by means of shedding entire modules (Fig. VI.1.c-f; chapter II), is greater in arid regions than in temperate ecosystems (Zanne et al. 2006; Schenk et al. 2008). New mathematical developments to quantify selection gradients in stochastic environments will surely prove useful in tackling these questions (Horvitz *et al.* 2010).

The sensitivity of size as a state variable to the population dynamics of the species (something that to our knowledge has not been explored) can also show which plant

characteristics are most useful in studying shrinkage. We anticipate that the way plant size is measured may affect the model's eigen-structure, and thus the elasticities and population growth rate (). After all, the number of classes used in a model has a great impact on the demographic output obtained from such models (Enright *et al.* 1995; Salguero-Gómez & Plotkin, 2010; chapter VII), and clearly some measures of size such as number of modules are more likely to have more natural cut-offs (*i.e.*, dimensions) than others such as volume.

The coupling of above- and below-ground population dynamics will allow us to understand the contribution of plant shrinkage to individual persistence and resource allocation. The specific question here is: what happens to an individual belowground when it shrinks aboveground? Evidence exists that the root system can affect the amount of aboveground tissue exposed under harsh conditions (Garret, Huynh & North, 2010) and also that plants are able to drastically shrink belowground (North, Huang & Nobel, 1993). We believe that the use of *phytotron* facilities (see Mommer *et al.*, 2010), where above- and below-ground demography can be easily studied simultaneously, will provide us with a holistic understanding of the role of true plant size on demographic dynamics and the importance of whole-plant shrinkage. For instance, if a plant is proactively arresting growth aboveground when faced with harsh conditions belowground such as drought, the canopy will shrink but not the belowground storage organ. On the contrary, if shrinkage is mostly the result of environmental pressures and there is no plant regulation on size, we would expect both above- and below-ground shrink in proportion to the degree of environmental harshness.

Even when shrinkage does not contribute positively to the population growth rate () as quantified with standard (*i.e.*, deterministic, asymptotic) sensitivity analyses, some

authors have already recognized the value of shrinkage as an alternative to immediate death (Horvitz and Schemske, 1995; Li et al., 2011). Existing demographic tools can explore the long-term demographic role of shrinkage in opposition to death. Van Tienderen's integrated elasticities and sensitivities (1995), where correlations among vital rates are taken into account (e.g., shrinkage is correlated with survival, growth and reproduction; see Salguero-Gómez & Casper 2010), can be used to establish the relative contribution of plants decreasing in size as opposed to dying; for shrinkage to be adaptive, integrated elasticities should result in increases in population growth rate (), through positive correlations with shrinkage and survival and/or reproduction. But shrinkage is likely to lead to decreases in fitness if survival and fitness scale monotonically with size (Fig. VI.2.a.i), or at least on the short term. Shrinkage, even when having negative sensitivities on the short term, will be adaptive on the long term if sensitivity analyses of individuals' transitions from time t to t+2, t+3, etc, as opposed to t+1 (Ehrlén 2000), are positive. Similarly, if loop analyses (van Groenendael et al., 1994), where demographic phenomena are included in longer than one-step transitions (e.g., size fluctuations, rather than growth or shrinkage separately; see Salguero-Gómez & Casper 2010; chapter IV), can be useful in determine the role of shrinkage on the long term. Specifically, greater elasticity values for loops that represent size fluctuations (growth-shrinkage) than for loops representing lack of phenotypic size plasticity (individuals stay in the same class) will highlight the value of decreasing in size as one side of a buffering strategy against stochasticity.

Shrinkage may be a phenomenon that allows "*plants strive to maintain the functions most important to fitness*" (Ehrlén 2003) such as survival (Crone 2001) and reproduction. We hope that our suggestions for future research will awaken the curiosity

of more plant ecologists and evolutionary biologists regarding how and why plants shrink, as well as whether and under what circumstances plant shrinkage may be adaptive.

VI.5. Acknowledgements

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Category	Limitation	Alternative approach
a. Collection of	a.1. Temporal and spatial replications of field studies	a.1.1. Increase sampling effort within and among
field data	are too low to appropriately capture a/biotic events	populations (Jongejans et al. 2010).
	under which plant's size may fluctuate significantly.	a.1.2. Long-term censuses (Menges et al. 2006).
		a.1.3. Intra-annual sampling and periodic
		matrices applied to perennials (Caswell &
		Trevisan 1994; Ramula et al. 2008; Bacaer 2009).
		a.1.4. Goodman matrices (Le Corff & Horvitz
		2005).
	a.2. There is a lack of knowledge on intra-individual	a.2.1. Ramet/genet framework (White 1979; de
	demographic dynamics that can result in shrinkage.	Kroon & van Groenendael 1997; Colling &
		Matthies 2006).
b. Model	b.1. Shrinkage is often lumped in matrix models with	b.1.1. Greater matrix dimension (Enright, Franco
construction	other processes (e.g. fission, clonal growth, stasis).	& Silvertown 1995; Salguero-Gómez & Plotkin

		2010).
		b.1.2. Integral Projection Models (Easterling,
		Ellner & Dixon 2000; Ramula, Rees & Buckley
		2009; Zuidema et al. 2010).
		b.1.3. Differentiating T and F matrices (Caswell
		2001).
	b.2. Age or stage-based models do not inform on the	b.2.1. Mixed development/age-size based models
	relationship between size and fitness because st/age	(Gregg 1991).
	and size are often times decoupled in plants.	
c. Analysis and	c.1. Deterministic, long-term analyses do not reflect	c.1.1. Stochastic, transient analyses (Horvitz &
interpretation	the stochastic nature to which natural populations are	Schemske 1995; Caswell 2007; Tuljapurkar 2007;
	exerted, and thus the true role of shrinkage.	Davison et al. 2010; Haridas & Horvitz et al.
		2010; Stott et al. 2010).
	c.2. The vox populi interpretation of elasticity (i.e.,	c.2.1. Awareness that small elasticities do not
	small = unimportant) leads to a very simplistic view	necessarily translate in unimportant processes (de
	of the role of shrinkage.	Kroon, van Groenendael & Ehrlén 2000;
		Salguero-Gómez & Casper 2010).

c.3. Lumping of demographic processes for	c.3.1. Loop analyses (van Groenendael et al.
demographic comparisons does not allow to explore	1994; Wardle 1998; Salguero-Gómez & Casper
the role of shrinkage as a separate demographic	2010).
process	



Photo credit: A: M.B. García. B: M.C. Stensvold; C-F: R. Salguero-Gómez.

Figure VI.1. Plant shrinkage, whereby individuals undergo drastic decreases in size from one year to the next, is a very common demographic phenomenon in higher plants. Shrinkage can happen when herbaceous perennial species such as the alpine species *Borderea pyrenaica* (a. Dioscoreaceae) and *Silene acaulis* (b. Caryophyllaceae) awake after the dormant season and form less biomass than in the previous growing season. Yellow arrows on the tuber of *B. pyrenaica* indicate annual leaf abscission marks. Another mechanism leading to shrinkage is the hydraulic failure of entire portions of the shoot (dashed line), as in the desert chamaephyte *Cryptantha flava* (c. Boraginaceae), the succulent *Opuntia rastrera* (d. Cactaceae), the Mediterranean shrub *Rhamnus lycioides* (e. Rhamnaceae) or the aridland tree *Juniperus osteosperma* (f. Cupressaceae).


Figure VI.2. a. In demographic studies, fitness (black, solid line) is frequently assumed to increase with plant size because the effects (vital rate sensitivity) of fecundity (red, dashed line) and survival (gray, solid line; top left panel) are typically greater in larger plants; in such a scenario, a selective pressure emerges promoting growth (green, dotted arrow), as in the case of (i) *Haplopappus radiatus* [Kaye & Pyke 2003]. However, selective pressures for shrinkage (orange, dot-dashed arrow) can also occur when the

effects of fecundity (ii. *Silene acaulis* [Morris & Doak 2005]), survival (iii. *Heteropogon contortus* [O'Connor 1993]) or both (iv. *Ipomoea leptophylla* [Keeler 1991]) do not display monotonic increases, resulting in an intermediate optimum plant size where fitness is greatest. b. In the case of a long-term demographic study of the aridland chamaephyte *Cryptantha flava* (Fig. VI.1.c), intermediate sizes (# leaf rosettes) of plants contribute more to the population growth rate () than larger individuals. In fact, in some years the effect of growth is negative and the effect of shrinkage is positive on for large plants. The vertical dark dotted line for growth and dot-dashed line indicate the sizes at which this switch in effect occurs for growth and shrinkage, respectively.

Chapter VII

Matrix dimensions bias demographic inferences: implications for comparative plant demography

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in collaboration with Joshua B. Plotkin

VII.1. Summary

- The extensive use of projection matrices in plant demography now permits broad comparative studies. However, such studies are complicated by variation in matrix dimensions across study species. Collapsing matrices to a common dimension may facilitate inter-specific comparisons, but this procedure may bias the inferred demographic parameters.
- Here we study an overlooked algorithm that collapses matrices without altering the asymptotic population growth rate (λ), the stable class distribution, or the reproductive output. We study how matrix dimension affects the inferred demographic elasticities. We analyzed 13 × 13 matrices representing nine plant species with various growth forms and longevities. We collapsed these matrices in two ways: into evenly collapsed 7 × 7, 5 × 5, 4 × 4 and 3 × 3 matrices for each species, and into 5 × 5 matrices using different collapsing criteria.
- The elasticities of stasis and fecundity increased when reducing matrix dimension, whereas the elasticities of progression and retrogression decreased. We suggest a collapsing criterion that minimizes dissimilarities between the elasticities of the original and collapsed matrices. We then applied this criterion to 66 diverse plant species, and studied the influence of life span and growth form on the relationship between matrix dimension and elasticities.
- Our analysis demonstrates that (i) the dimension of a projection matrix has significant effects on inferred demographic parameters, (ii) there are criteria and algorithms for standardizing matrix dimension that perform better than previous suggestions, and (iii) herbaceous perennial projection matrices are particularly

sensitive to changes in matrix dimensionality. For comparative demographic purposes, particularly when dealing with herbaceous perennials, we recommend normalizing matrices to a common dimension by collapsing together the higher classes and leaving the first few classes unaltered.

Key-words: collapsing, comparative plant demography, elasticity, matrix dimension, population growth rate (λ), projection matrix models.

"Your true value depends entirely on what you are compared with"

Bob Wells (1966-present)

VII.2. Introduction

Although most ecologists carry out specific experiments with a limited set of study species, their ultimate goal is to discover general rules, often by compiling and comparing studies. Indeed, most general ecological rules (e.g. exponential growth potential and regulated population growth, the principle of competitive exclusion, robust coexistence, life-history trade-offs, etc) arose and have been confirmed through the extensive application of standardized, comparative methodologies.

In the case of demography, projection matrix models have become a widely used, powerful tool for studying ecological and evolutionary questions. A matrix model classifies individuals in a population according to a discrete range of ages (Leslie 1945), sizes, developmental stages (Lefkovitch 1965), or a mixture of these variables (e.g., Ehrlén et al. 2005, Jacquemyn et al. 2005). The projection matrix quantifies three fundamental processes for each of the classes that together determine the life cycle of the species: (i) the probability of survival of its individuals, (ii) their probability of staying in the same class (stasis) or transition to another class (progression to higher classes, or retrogression to lower classes), and (iii) their contributions with newborns to the population (fecundity). Matrix models have been used to project population growth (e.g., Lefkovitch 1965, Marrero-Gómez *et al.* 2007) and to examine the relative contributions of the different demographic processes to the population growth rate (e.g., Bierzychudek

1999, van Mantgem and Stephenson 2005) using elasticity analysis (de Kroon et al. 1986). Matrix models have also been used to explore the importance of alternative life history strategies (e.g., Moloney 1988, Morris and Doak 1998), to identify the most vulnerable classes of a life cycle for the purposes of population management (Werner and Caswell 1977, Lubben et al. 2008), and to establish exploitation regimes that are compatible with long-term demographic viability (Nault and Gagnon 1993, Freckleton et al. 2003).

A great potential for comparative demographic studies has emerged from the large body of literature based on population projection matrices. Such matrices have now been estimated from data and published for over 475 plant species (Salguero-Gómez, unpublished [but see chapter VI]), whose life spans range four orders of magnitude (e.g., Namkoong and Roberds 1974, Dostal 2007). Because these demographic dynamics are compiled in the same format –that of a matrix– the data can, in principle, be used to examine broad ecological and evolutionary questions about demographic dynamics.

Studies using large numbers of projection matrices have allowed for the linkage between specific demographic processes and stages along ecological succession gradients (Silvertown et al. 1992), for the establishment of methodologies to study the responses of populations to ecotones (Angert 2006), herbivory (Maron and Crone 2006), habitat fragmentation (Bruna et al. 2009), for comparing demographic dynamics of native and invasive plant species (Ramula et al. 2008), phylogenetic relationships of life history strategies (Burns et al. 2010), or relationships between short-term (transient) and longterm (asymptotic) population dynamics (Stott et al. 2010). The number of demographic studies based on projection matrices is growing rapidly (Fig. VII.1). Consequently, matrix models will likely serve an important role in future studies of broad ecological and evolutionary questions.

Using published projection matrices for comparative studies is attractive, but it is complicated by the fact that these matrices vary in the number of classes employed, or matrix dimension (Fig. VII.2). The dimension of projection matrices influences the apparent demographic processes of a specific class, such as per-capita fecundities (de Matos and Matos 1998), as well as other parameters derived from the matrix, such as population growth rates (Lamar and McGraw 2005, Ramula and Lehtila 2005), transient dynamics (Tenhumberg et al. 2009, Stott et al. 2010), elasticities of matrix elements (Silvertown et al. 1993, Enright et al. 1995) and vital rates (Zuidema 2000, Salguero-Gómez and Casper 2010; chapter V), elasticities of demographic pathways (Salguero-Gómez and Casper 2010), as analyzed by loop analysis (van Groenendael et al. 1994), and demographic relationships based on phylogeny (Burns et al. 2010, Stott et al. 2010). This is a non-trivial issue because the matrix dimension varies a great deal: from 2 (Sohn and Policansky 1977) up to 24 (Meagher 1982). Although several algorithms have been proposed to determine optimum criteria to establish cutoffs for classes in constructing the original matrices (Vandermeer 1978, Moloney 1986, Shimatani et al. 2007), thus offering some standardization, most plant demographers still classify systems based on the specific biology of the species and the question being asked (Caswell 2001).

Concerns about matrix dimension were first addressed by Enright et al. (1995), who suggested ways to overcome the problem of variation in dimension among projection matrices. First, they proposed keeping the number of classes proportional to the life span of each species. However, populations of many short-lived herbaceous species are usually classified using many life stages (e.g. 15 classes in *Allium tricoccum* [Nault and Gagnon 1993], or 17 in *Arisaema serratum* [Kakehashi and Kinoshita 1990]) (Fig. VII.2). It would be laborious and probably meaningless from a biological perspective to follow the suggestion of Enright et al. (1995) and enforce a correspondingly higher number of life stages for longer-lived herbaceous, shrub, palm and tree species (Ebert 1999, Caswell 2001). On the other hand, decreasing the number of classes for shorter lived species matrices would blur the study of their demographic dynamics. Alternatively, Enright et al. recommended collapsing matrices to the same dimension for all species of a comparative study. However, we know of no comparative plant demographic study that has adopted this suggestion (but see Salguero-Gómez & Casper 2010), perhaps because this would require raw census data for each species, which are frequently unavailable.

Currently, comparative demographic studies either do not control for varying matrix dimension (Silvertown et al. 2001, Franco and Silvertown 2004, Bruna et al. 2009), or treat dimension as a covariate in the analysis (Ramula et al. 2008, Burns et al. 2010, Stott et al. 2010), which is inappropriate unless the residuals are normally distributed with linear effects on inferred parameters. Integral Projection Models (IPMs, Easterling et al. 2000), on the other hand, offer an appealing alternative for demographic comparisons because they are more robust to life cycle complexity than classical projection matrices (Ramula et al. 2008, Zuidema et al. 2010). However, we know of only a dozen plant species that have been studied with IPMs thus far. For classical projection matrices, Enright et al. suggested specific collapsing criteria to minimize alterations to demographic inferences. These criteria include forming collapsed classes of similar residence time (the average time spent by an individual in a given class), and not merging non-reproductive and reproductive classes because they are biologically different. However, no study has explicitly evaluated whether or not these collapsing criteria minimize associated changes to demographic inferences drawn from the collapsed matrix.

In this manuscript, we explore the inferred demographic parameters associated with matrices of different dimension with the goal of providing rational guidelines for inter-specific comparative studies. Specifically, we evaluate how the relative importance of each demographic parameter (elasticity) varies as a function of matrix dimension. We pay special attention to the population growth rate and elasticities because they are of primary interest in comparative studies (Silvertown et al. 2001). We examine an overlooked algorithm that allows reducing matrix dimensions without using raw data and without altering the inferred population growth rate, reproductive output or stable class distribution (Hooley 2000). We apply this algorithm to the projection matrices of nine plant species with different growth forms and longevities in order to (i) study the dissimilarities in the inferred elasticities of demographic processes in collapsed matrices, and (ii) evaluate Enright's collapsing criteria, as well as (iii) propose alternative collapsing criteria that minimize the differences in elasticity values between the original and the collapsed matrices. We demonstrate that matrix dimension affects the estimation of all parameters of interest, particularly so in herbaceous perennial species, and that such relationships are not always monotonic. We discuss the limitations of Hooley's algorithm regarding stable stage distribution of the population. Finally, we conclude with some

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suggestions for implementing meaningful comparative demographic studies based on projection matrices.

VII.3. Materials and Methods

Implementation of the collapsing algorithm in size and developmental stagebased models

The algorithm of Hooley (2000) describes a method to reduce the dimension of a projection matrix, once it has been decided which classes to collapse. In its original form, Hoooley's algorithm was intended for age-based models. These models provide poor descriptions of plant demographic patterns because plants are often difficult to age and because age is usually not the best predictor of plant demographics (Harper 1977, Werner and Caswell 1977, Ebert 1999). Here, we expand Hooley's algorithm to size- and developmental stage-based matrix models. Such models allow individuals not only to advance several classes per unit time, but also to retrogress (e.g., Bruna and Oli 2005, Lucas et al. 2008).

Briefly, three steps must be taken to reduce a projection matrix of *n* dimensions $A_{n\times n}$ to one of *m* dimensions $C_{m\times m}$: (1) choose classes to collapse according to some specified "collapsing criteria", (2) collapse rows of those classes in the matrix, and (3) collapse the respective columns. Choosing the appropriate classes to collapse (*i.e.* specifying the collapsing criteria) is a non-trivial decision, and we discuss it below. Collapsing rows is performed by a simple element-by-element addition. Collapsing the

columns is the most complex step of the process because, without the raw data, we do not know the proportion of individuals of the original classes that will contribute to forming the matrix elements a_{ii} of the newly collapsed class.

In the simplest case possible, that of collapsing the two classes k and k+1 of an ndimensional matrix $A_{n\times n}$ into a new class k' in the collapsed matrix $C_{(n-1)\times(n-1)}$, we first add the matrix elements $a_{k,j}+a_{k+1,j} \not j$ along the k and k+1 rows. The resulting intermediate matrix $B_{(n-1)\times n}$ is then collapsed for columns k and k+1. For age-based models, determining the entries in column k' of the new collapsed matrix is rather intuitive: simply calculate the proportion of individuals in class k-1 who survive, and consequently age, entering class k after one transition period, as well as the proportion of individuals who survive from class k, who will automatically age into class k+1. Surviving individuals from class k+1 do not represent a challenge for this calculation because they will transition into another class which is not collapsed in this example.

The calculation of the entries of column k' for size- and developmental stagebased models is somewhat challenging, because it involves the calculation of survival for the individuals in the two classes to be collapsed (k and k+1), transition probabilities with which the individuals in either class will *not* leave the collapsed class, and transition probabilities with which the individuals from all other classes (e.g., k-1, k+2, etc) may enter the collapsed class k' –abrupt changes in size and development, typically expressed by some plant species, may lead individuals to leap over several classes over one time interval. For age-, size- or developmental stage-based models, the collapsed vector that can be obtained from the intermediate matrix **B** (n-1)xn will only report the total number of

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individuals in the collapsed class, and not the breakdown in number of individuals coming from each class involved. Thus, in order to collapse the columns, we must assume that the population was close to equilibrium during the field censuses. In this case, it is possible to take the elements of the stable class distribution (w) as the weighting factors to construct the new collapse class. Consequently, we define the weighting factors $r_k = w_k/(w_k + w_{k+1})$ and $r_{k+1} = w_{k+1}/(w_k + w_{k+1})$, which are the proportions of the merged classes that we expect to form from the original class k and class k+1, respectively. Column k' in the collapsed matrix C is made of entries which are the weighted averages, using weighting factors r_k and r_{k+1} , of columns k and k+1 of the partially collapsed matrix **B**. The stable class distribution is an intrinsic parameter of the projection matrix that can be obtained with a two-line command in Matlab: the right eigenvector associated with the dominant eigenvalue. This knowledge regarding the stable class distribution is critical because it can free us from needing the raw field data to be able to quantify matrix entries in collapsed matrices (Appendix A describes whether our techniques are robust when the assumption of stable equilibrium is violated).

Matrix algorithm implementation

Mechanistically, the collapsing algorithm can be applied to almost any (see *Discussion*) projection matrix following the calculation:

$$\boldsymbol{P}_{mxn} \cdot \boldsymbol{A}_{nxn} \cdot \boldsymbol{Q}_{nxm} = \boldsymbol{C}_{mxm} \tag{1}$$

where *P* is a matrix of *mxn* dimensions containing dummy holders ("1") on the elements that are to be collapsed ($a_{k',k}$ and $a_{k',k+1}$), with the rest of the matrix being formed by identity sub-matrices *I*:

$$P = \begin{bmatrix} I_{k-1} & 0 & 0 & 0\\ 0 & 1 & 1 & 0\\ 0 & 0 & 0 & I_{n-k-1} \end{bmatrix}_{mxn}$$
(2)

and where Q is a matrix of *nxm* dimensions that contains the weighting factors for the elements in the columns k and k+1 that are to be collapsed, with the rest of the matrix elements characterized by identity sub-matrices:

$$Q = \begin{bmatrix} I_{k-1} & 0 & 0\\ 0 & r_k & 0\\ 0 & r_{k+1} & 0\\ 0 & 0 & I_{n-k-1} \end{bmatrix}_{nxm}$$
(3)

This algorithm also allows us to collapse multiple classes into a single class or into fewer, separated classes in just one step, which saves a significant amount of time when dealing with projection matrices of high dimensions in large databases. The steps when dealing with multiple collapses are the same: normalize the elements on the merging columns by calculating the weighted average of the appropriate stable class distributions. Illustration of the matrix dimension collapsing algorithm in nine plant species

We applied Hooley's algorithm to population projection matrices of nine different plant species, in order to examine the dissimilarities between the elasticities of demographic processes in matrices of different dimensions, and to establish the optimum collapsing criteria. The elasticity is a widely used measurement of the importance of a demographic process in a population; elasticity reflects the proportional change in population growth rate as a function of a proportional change in a part of the projection matrix (de Kroon et al. 1986). Specifically, we explored (i) how the inferred elasticities are influenced by matrix dimension when using a fixed collapsing criterion ("even collapsing", see below), and (ii) how collapsing a large matrix into a fixed, smaller dimension in different ways (i.e using different collapsing criteria; fig. VII.3) influences the associated elasticities. We refer to the first of these studies as the "matrix dimension test", and the second as the "collapsing criterion test". We then investigated how the elasticities of the collapsed matrices had changed relative to the elasticities of the original, un-collapsed matrices. We used these comparisons to determine guidelines for optimal collapsing (*i.e.* guidelines for both the size of the collapsed matrices and for the collapsing criterion that minimize the dissimilarities between the inferred elasticities).

We chose nine plant species of different growth forms and longevities for which size- or developmental stage-based projection matrices with relatively high dimensions were available in the literature (Table VII.1). These species' matrices differ because the demographic dynamics are strongly influenced by the growth form and life histories of the species (Silvertown and Franco 1993). For instance, herbaceous species display a higher fluctuation in sizes and developmental stages since they may skip over more than one class, both in positive (progression) and negative (retrogression) directions, after one annual transition. By contrast, the dynamics of longer-lived shrubs and trees are "slower" because biomass decreases or dramatic increases occur rarely. We did not include annuals because their matrix dimensions are typically too small for us to implement any reduction with a meaningful outcome (Fig. VII.2).

We chose an original, un-collapsed dimension of 13×13 in order to study the dissimilarities of elasticities in collapsed matrices, starting from a matrix of dimensions that fall within the range typically reported in the literature. For collapsing purposes we treated the original 13×13 matrices as a $(1+12) \times (1+12)$ matrices in which the first class was never merged with other classes so as to avoid mixing the transition probabilities p_{ij} (0, 1) with the per-capita contributions of fecundity $a_{1i} = (0, \infty)$ (Fig. VII.3). Note that in some projection matrix models per-capita contributions such as seed bank, seedling recruitment and clonal reproduction can expand beyond the first row (e.g. Eriksson 1988, Cipollini et al. 1994; but none of the species in table VII.1 do) and that, likewise, these classes should not be merged with those that contain transition probabilities.

Because the matrix dimensions of the chosen species were not identical (Table VII.1), we slightly modified them to produce matrices of initial dimension 13×13 . For those species whose original dimensions were higher than 13×13 (*Ulex minor* and *Araucaria cunninghamii*), we used Hooley's algorithm to collapse the higher classes to form a life cycle of 13 classes. For one species (*Cryptantha flava*), we re-calculated its projection matrix based on a 13-class life cycle using the available raw data (B. Casper,

pers. comm.). The matrix of another species (*Rourea induta*) was already in 13×13 dimensions. All other species had matrix dimensions below 13×13 (*Calathea* ovandensis, Viola frimbriatula, Pterocereus gaumerii, Neobuxbaumia macrocephala, and *Thrinax radiata*) and here we expanded the number of classes by replicating the matrix elements of the last classes, and re-adjusting the transition probabilities and per-capita reproductive contributions to resemble the dynamics described by the original matrices. In all cases, we calculated the primary demographic parameters (life span, population growth rate, stable stage distribution and elasticities) before and after the re-adjustment to make sure that the modification did not alter their demographic traits (Appendix B). Nevertheless, we emphasize that our goal is not to study the precise details of these particular species, but rather to explore the effects of matrix dimensions on the demographic dynamics of realistic exemplars of a range of plant species. Life spans were calculated as described in Forbis and Doak (2004). We calculated the demographic parameters using MatLab version 7.1 (The MathWorks) and PopTools version 3.0 (Hood, 2003).

For every projection matrix, either 13×13 or reduced size, we calculated the population growth rate λ , stable class distribution *w*, reproductive output *v* and elasticities of the demographic processes involved. We calculated two types of elasticities: matrix-element elasticities and vital-rate elasticities. Matrix-element elasticity measures the proportional change in the population growth rate (λ) due to a proportional change in a group of matrix cells corresponding to a demographic process, while vital-rate elasticity measures proportional changes in λ based on proportional changes of the underlying

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demographic processes that correspond to each projection matrix element, such as survival (Franco and Silvertown 2004).

To examine the impact of matrix dimension on the inferred elasticities (Matrix dimension test, hereafter), we collapsed the 13×13 class life cycle into new classes of even size, with the exception of the first class, which was not collapsed. This resulted in matrices of 7×7 , 5×5 , 4×4 and 3×3 dimensions. We then calculated the dissimilarities between the elasticity structure of the original and sequentially collapsed matrices. In order to explore how different ways of collapsing the matrices affects differently the elasticities and to establish an optimum criterion (Collapsing criterion *test*), we collapsed the 13×13 matrices into 5×5 matrices (the median dimension in demographic studies; fig. VII.4), using various collapsing criteria. We then calculated the dissimilarity between the elasticities of the original and its respectively collapsed matrix; the collapsing criterion that resulted in the lowest dissimilarity was then established as the optimum criterion. We performed the matrix dimension test and the collapsing criterion test for both matrix element elasticities and vital rate elasticities. We carried out a principal component analysis (PCA) on the elasticities of survival, stasis, retrogression, progression, and fecundity to calculate elasticity dissimilarities. PCA reveals relationships and measures of proximity based on Euclidean distances (Davidson 1975). The comparisons of elasticities based on Euclidean distances were carried out for both matrix-element elasticities and their underlying vital-rate elasticities.

In the collapsing criterion test, we applied 10 different collapsing criteria to produce collapsed matrix of dimension 5×5 . Briefly, these criteria involved collapsing classes evenly (I), collapsing a large number of classes together but in different positions

of the life cycle (II, III, IV), collapsing irregularly (V, VI, VII), and collapsing so the mean stasis probabilities (VIII), residence times (IX) and mortality rates (X) were as similar as possible for each new class (See figure VII.3 and associated legend for a detailed description of these criteria). For approach IX, the class-specific residence times were calculated according to Caswell (2001:112). The last three collapsing criteria (VIII, IX and X) are species-specific because of the species' different demographic life histories (Appendix B). Similarly, because each species has to pass through different number of classes before attaining maturity, the criteria that separate non-reproductive and reproductive classes, one of the suggestions made by Enright et al (1995), are also species-specific, although there was for each species at least one criterion that fulfilled such condition (Fig. VII.5).

Finally, we also measured the dissimilarity of the elasticity structure before and after collapsing population projection matrices of a large database as a function of their growth form and life span. We applied the optimum collapsing algorithm that was identified from the collapsing criterion test to a set of 66 species' projection matrices. We calculated the Euclidean distance between the elasticities before and after collapsing each original matrix to a 5×5 matrix. We then performed linear regressions to study how life span and growth form correlate with these Euclidean distances using R (R Developmental Team 2009).

VII.4. Results

The collapsed matrices for the matrix dimension and collapsing criterion tests of the nine species had the same or extremely similar asymptotic growth rates and life spans as their respective 13×13 matrices (Appendix B), as guaranteed by the Hooley algorithm. Their stable class distributions and reproductive outputs were also the same, with the exception of the collapsed classes, whose class distribution and reproductive outputs were equal to the sum of the classes that were merged (not shown).

Matrix dimension test: how does matrix dimension affect the estimation of elasticities?

Matrix dimension affected the matrix-element elasticities consistently across all species of our study for matrices collapsed to more than 3 x 3 dimensions. When collapsing evenly to produce 7×7 , 5×5 or 4×4 matrices, the matrix-element elasticities of stasis and fecundity increased, whereas the elasticities of retrogression and progression decreased. The relationships between matrix dimension and inferred elasticities were not always linear (Fig. VII.6). A similar pattern was detected for the vital-rate elasticities, with the exception of *C. ovandensis* (Fig. VII.6.A), *P. gaumeri* and *N. macrocephala* (Appendix C), where the matrix-element elasticities of stasis, after having reached a maximum value at 5×5 dimensions, decreased for the 4×4 matrices.

When the matrices were further collapsed to 3×3 dimensions an unexpected behavior was detected. In the case of the matrix-element elasticities of the herbaceous *C*.

ovandensis and the palm *T. radiata* (Fig. VII.6), the elasticity of stasis decreased drastically in the 3×3 matrices. Nonetheless, this behavior was not consistent across all species. In the case of the vital-rate elasticities, survival decreased from 4×4 matrices to 3×3 matrices, not only in *C. ovandensis* and *T. radiata*, but also in *V. fimbriatula*, *N. macrocephala* and *A. cunninghamii* (Appendix C). In these five species the decreases in the vital-rate elasticity of survival (*C. ovandensis*: -17%; *T. radiata*: -3%; all other species experienced a less drastic decrease of survival, between 0 and -1%) and increases in fecundity (*C. ovandensis*: +435% and +115%; *T. radiata*: +317% and +197%, for element matrix and vital-rate elasticities, respectively) were rather steep.

The effects of collapsing matrix dimension on inferred elasticities were typically smaller for vital-rate elasticities than for matrix-element elasticities. In particular, the Euclidean distances between the collapsed and original elasticities were smaller for vital-rate elasticities than matrix-element elasticities in 29 out of 36 cases (nine species × four matrix dimensions $[7 \times 7, 5 \times 5, 4 \times 4, 3 \times 3]$; *P* < 0.001, binomial test; fig. VII.7).

Collapsing criterion test: What is the best criterion for specifying which classes to collapse?

The collapsing criterion that did not modify the first four classes and collapsed classes k_4 through k_{13} into class k_5 ' (Fig. VII.3, criterion II) resulted in the smallest dissimilarity between the associated elasticities of the 13 × 13 original and 5 × 5 collapsed matrices (Fig. VII.8). This dissimilarity was particularly small for the comparison based on vital-rate elasticities ($\bar{x}_{Criterion II} = 0.07$).

The criteria that formed 5×5 matrices such that the stasis probabilities (VIII), residence time (IX), or mortality probabilities (X) of each collapsed class were similar did not rank among the most optimum collapsing criteria. The Euclidean distances ranked the collapsing criteria as it follows when based on matrix-element elasticities: II (Euclidean distance = 0.16) < V (0.17) < IX (0.20) < III (0.20) < VIII (0.20) < VI (0.20) < I (0.21) < VII (0.23) < X (0.23) < IV (0.27); and when based on vital-rate elasticities: II (0.07) < V (0.13) < VIII (0.16) < X (0.16) < IX (0.16) < I (0.17) < III (0.17) < VI (0.18) < VII (0.19) < IV (0.27; see figure VII.3).

The collapsing criteria that separated non-reproductive and reproductive classes (Fig. VII.5) did not systematically result in lower dissimilarities between the elasticity structure of original and collapsed matrices. For instance, for *C. flava* and *C. ovandensis* all collapsing criteria separated non-reproductive and reproductive classes, but the criterion that collapsed classes k_5 through k_{13} (Fig. VII.3, II) performed the best, in that the dissimilarity between the elasticities of the original and collapsed matrices was lowest. A cursory evaluation of the results in figure VII.8, contrasted with figure VII.5, would suggest that this criterion (Fig. VII.3, II) is the optimum one because it splits non-reproductive and reproductive classes in 5 out of the 9 species of our study. However, the same is true of the criterion where classes k_3 through k_{11} were collapsed (Fig. VII.3, VII), and yet it performed relatively poorly. Furthermore, the criterion that collapsed only the last classes into a new class (Fig. VII.3, II) was the best approach even for those species in which this criterion did not separate reproductive and non-reproductive classes (e.g., *P. gaumerii, N. macrocephala, T. radiata* and *A. curninghamii*).

We found that collapsing matrices had a larger effect on inferred elasticities for shorter-lived species. While the linear regression between life span and dissimilarity measurements of the nine study species was not significant for matrix-element elasticities $(t_{1,8} = 6.14, P = 0.104)$, and border-line significant for vital-rate elasticities $(t_{1,8} = 5.15, P = 0.057)$, this relationship was highly significant when using a more extensive study of 66 species in which their projection matrices had been collapsed to 5 x 5 dimensions using the previously established optimum criterion (Fig. VII.3, II) $(t_{1,64} = 18.49, P < 0.001, R^2 = 22.4\%$; fig. VII.9). Furthermore, the correlation between dissimilarity and life span was growth form specific $(F_{5,60} = 7.45, P < 0.001, \text{ growth form as covariate: } F_{4,60} = 5.02, P < 0.001)$, and it was primarily driven by the significant life span-dissimilarity correlation of herbaceous perennials $(t_{1,36} = 17.95, P < 0.001$ –this correlation was nonsignificant for succulent, shrub, palm or tree species).

VII.5. Discussion

Our study offers insights for how and why the dimension of projection matrices influences the estimation of fundamental demographic parameters. Using an overlooked algorithm (Hooley 2000) for collapsing matrix dimension, without relying on raw field data, we have (i) established better collapsing criteria than previously suggested (Enright et al. 1995), (ii) found that the impact of matrix dimension on the associated elasticity structure is often non-monotonic and not always lower on vital-rate elasticities than on matrix-element elasticities, as previously reported (Zuidema 2000), (iii) observed unexpected behavior for very small matrices (e.g. 3 × 3 dimensions) that allows us to

establish a dimension-threshold for comparative plant demographic studies, and (iv) found a negative relationship between life span and the robustness of elasticities to matrix dimension in herbaceous perennials.

Our results indicate that collapsing a population projection matrix by similar residence time leads to a large difference in elasticities between the original and collapsed matrices, contrary to the suggestion of Enright and co-workers (1995). Specifically, we found that for all species in this study, keeping the first life-cycle classes unaltered (Fig. VII.3, criterion II) resulted in the lowest impact on the inferred elasticities. This likely occurs because individuals of younger/smaller/less developed classes are usually more susceptible to changes in the environment, and thus they typically exhibit distinct class-specific vital rates (Harper 1977). These conclusions are further supported by the fact that while the criterion that grouped the first classes and left the last four classes unaltered (IV, the opposite of II, fig. VII.3) was the worst performer, the criterion where the first classes were collapsed only two at a time, in a very similar form to criterion II, always ranked in the second position. Our results are also supported by a study that suggests ways to save time, resources, and field effort while constructing projection matrices from small populations of threatened species (Ramula and Lehtila 2005).

Our findings suggest that fecundity or age at first reproduction are not the most important biological processes on which to base the classes chosen for matrix construction and collapsing. Enright et al. (1995) recommended against merging nonreproductive and reproductive classes because trade-offs between reproduction, growth and survival would result in distinctive demographic dynamics in both life cycle stages.

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However, we show that collapsing criteria that violate this suggestion can produce more robust elasticities than collapsing criteria that differentiate non-reproductive from reproductive classes.

We also found some inconsistencies with previous works on the robustness of vital-rate vs. matrix-element elasticities to matrix dimension. Zuidema and Zagt (in Zuidema 2000) studied the impact of matrix dimensions on the inferred elasticities and found that progression and retrogression matrix-element elasticities decreased with increasing dimension, consistent with our results. However, they also reported that the vital-rate elasticities were more robust to varying matrix dimension than their matrix-element counterparts. Our results generally agree with theirs, but in 20% of the cases (n = 9 species) in our study vital-rate elasticities were more robust than matrix-element elasticities seem more relevant for the study of ecological patterns because they reflect independent demographic processes, and they allow for the separation of the survival vital-rates (e.g., Bruna et al. 2009).

Although the collapsing algorithm we have analyzed here has the virtue of preserving population growth rates, stable class distributions and reproductive output, this algorithm assumes demographic stability. In an ideal scenario, field censuses would be extensively temporarily replicated so they comprise all biotic and abiotic phenomena that are inherent to the species' life cycle. Doing so would approximate the mean observed class distribution to the stable class distribution. We suggest that class distributions be calculated and compared to the stable class distribution as a prerequisite to decide whether or not to incorporate a given annual transition for later inter-specific comparison.

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Applying methods to do so (Keyfitz's Δ , in Caswell 2001:101), we have found evidence that Hooley's algorithm provides reliable collapsed projection matrices for at least one population subjected to extreme weather events (Appendix A). We also recommend averaging the control transition matrices for as many sites and years as there are data available to reduce the impact of abnormal biotic and abiotic fluctuations.

Intuition behind the impact of matrix dimension on elasticities

Although we cannot provide intuition for all the specific details of our results on the nine plant species, there is a simple intuition for the general effects of collapsing dimension on associated elasticities. The elasticities of fecundity tend to increase as the matrix dimension is reduced because the merging of non-reproductive and reproductive classes inevitably makes reproductive status attainable in a shorter period of time by the faster growing individuals in the population (Enright et al. 1995). Faster demographic processes have been shown to have greater elasticities (Zuidema et al. 2009). Similarly, the elasticity of stasis also increases because, with fewer classes in a collapsed matrix, the amount of stasis is again augmented. Since stasis elasticity increases, while the overall population growth rate \Box is kept constant, the elasticities of retrogression and progression must decrease. Although there is some variation across species and some aberrant behavior at very small dimensions, this simple intuition explains most of the general patterns we have observed. We attribute the unexpected increase in matrix-element progression elasticities in small matrices of some herbaceous perennials and succulent species, and subsequent decrease in stasis elasticity, to the high degree of phenotypic

plasticity of these growth forms and their fast demographic dynamics (Chien & Zuidema 2005). Furthermore, studies of herbaceous perennials often suffer from small sample sizes in large size classes.

Guidelines for comparative demographic studies

Our results on the relationship between matrix dimension and inferred demographic properties have important implications for comparative studies. We have shown that the apparent importance of fecundity, stasis, progression, retrogression and survival is highly sensitive to the dimensions of the projection matrix. Consequently, demographic comparisons of species based on elasticities must carefully account for the varying matrix dimensions.

For comparative work based on published projection matrices, we suggest to alternatives: either account for matrix dimension with a non-linear analysis, or collapse matrices into an equal dimension, at least for the herbaceous perennials, whose elasticities are most sensitive to matrix dimension (Fig. VII.9). Surprisingly, most recent comparative studies using projection matrices have not used matrix dimension as covariate (Franco and Silvertown 2004, Bruna et al. 2009). On the other hand, a trade-off emerges between the matrix dimension cut-off and how many studies to include for comparative purposes because (i) the matrix collapsing will mean that species with fairly dissimilar traits will be treated as equals from a demographic standpoint (e.g. Crouse et al. 1987, Cochran and Ellner 1992), (ii) decreasing dimension, regardless of the collapsing criteria, will tend to artificially promote the apparent importance of stasis and fecundity compared to progression and retrogression, and because (iii) an extreme decrease in the number of classes will not allow for the study of processes such as classspecific mortality rates, time to maturation, senescence, clonal growth or vegetative dormancy. In the extreme, a very small matrix will inevitably merge transition probabilities for stasis, progression and/or retrogression $p_{ij} \square (0, 1)$ with sexual and/or clonal reproduction $a_i \square (0, \infty)$, which makes little biological sense. Based on the results of our matrix dimension test, in which the elasticities exhibited unexpected behaviors for dimensions 4 and smaller, we suggest at least 5 dimensions for comparative studies, despite the fact that this rules out a large number of published projection matrices with smaller dimensions (n = 107; Salguero-Gómez, unpublished) for demographic comparisons. Finally, our results suggest an optimum criterion for choosing which stages to collapse in a projection matrix (Fig. VII.3, criterion II): keeping the first few life-cycle classes unaltered, and collapse all other older/larger/more developed classes, regardless of whether or not that means merging non-reproductive and reproductive classes or keeps the residence times constant in the newly collapsed classes.

VII.6. Acknowledgements

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Table VII.1. Description of species used in this study, ranked by life span. Type represents (H)erbaceous, (S)hrub, (Su)cculent, (P)alm and (T)ree. *Original matrix dimensions in the publication were 7 x 7, but we used the raw data to recalculate the matrix based on a life cycle of 13 stages.

Species	Family	Туре	Life span (yr)	Population growth rate ()	Matrix dimension	Citation
Cryptantha flava	Boraginaceae	Н	14	0.86	13*	Lucas et al 2008
Calathea ovandensis	Marantaceae	Н	20	0.99	8	Horvitz and Schemske 1995
Ulex minor	Fabaceae	S	21	1.31	16	Stokes et al 2004
Viola frimbriatula	Violaceae	Н	23	1.22	11	Solbrig et al 1988
Pterocereus gaumerii	Cactaceae	Su	31	1.00	10	Mendez et al 2004
Neobuxbaumia macrocephala	Cactaceae	Su	41	1.03	10	Esparza-Olguin et al 2005
Rourea induta	Connaraceae	S	52	0.99	13	Hoffmann 1999
Thrinax radiata	Arecaceae	Р	136	1.13	9	Olmsted & Alvarez-Buylla 1995
Araucaria cunninghamii	Araucariaceae	Т	256	1.02	17	Enright & Ogden 1979



Figure VII.1. Histogram with number of plant species with published population projection matrices organized chronologically (n=434). Data collated from ISI Web of Science, Scopus and Google Scholar from 1960 until the end of 2009.



Figure VII.2. Life span (mean \pm S.E., gray) and matrix dimension (mean \pm S.E., white) by growth form, collated from 475 published projection matrices of plant species. Letters indicate significant differences among groups (Tukey-Kramer HSD test).



Classes

Figure VII.3. Collapsing approaches used to reduce the dimensions of 13×13 projection matrices. Adjacent classes represented with the same color were collapsed. The first class was kept unaltered because it contains reproduction probabilities that are not to be merged with transition probabilities. (a) The original 13×13 matrix was collapsed evenly into 7×7 , 5×5 , 4×4 and 3×3 matrices to study the effect of decreasing matrix dimension on its elasticity structure. (b) The original 13×13 matrix was collapsed into 5×5 matrices in different ways to evaluate the effect of several collapsing criteria on the matrix elasticity structure. Criteria are: (I) collapsing an even number of classes, resulting

in the structure {1, 2-4, 5-7, 8-10, 11-13}, (II) leaving unaltered the first three {1, 2, 3, 4, 5-13}, (III) middle two {1,2-6,7,8, 9-13} or (IV) last three classes {1, 2-10, 11, 12, 13}, (V) collapsing every two classes for the first six classes and collapsing the remaining classes in a large class {1, 2-3, 4-5, 6-7, 8-13}, (VI) leaving unaltered the middle and last class and collapsing the remaining {1, 2-6, 7, 8-12, 13}, (VII) collapsing central classes an leaving unaltered the first and last two classes {1, 2, 3-11, 12, 13}, and collapsing so the newly formed classes will keep their respective stasis probabilities (VIII), residence times (IX) and mortality probabilities (X) similar for each new class. Collapsing criteria VIII, IX and X are species-specific (example here presented is for *Cryptantha flava*; appendix B).



Figure VII.4. Stack histogram with number of plant species for which population projection matrices have been published organized by growth form and matrix dimension (n = 475 species).



Figure VII.5. Identification of collapsing criteria that separate non-reproductive and reproductive classes for each study species. Classes where the focal collapsing criterion separated non-reproductive from reproductive stages are represented in white squares. Classes where the non-reproductive and reproductive stages were not separated are represented in black squares. Note that the pattern is species-specific, given the differences in first reproductive class.


Figure VII.6. Effects of matrix dimension on the elasticity of vital rate- and matrix element-based demographic processes for three of the nine species our study: (A) *Calathea ovandensis*, (B) *Ulex minor* and (C) *Thrinax radiata*. In each case, the original 13×13 projection matrix was collapsed by combining 2, 3, 4 or 6 adjacent classes, to produced 7×7 , 5×5 , 4×4 and 3×3 matrices, respectively. Retrogression vital rate elasticities are represented in absolute values to fit in the positive axis, but they are negative.



Figure VII.7. Euclidean distance ($\bar{x}_{Dimension}$) between the elasticities of the original 13 × 13 matrix and the elasticities of its respective 7 × 7, 5 × 5, 4 × 4 and 3 × 3 matrix for each species (using criteria described in figure A.3). Species are ranked from top to bottom by increasing life span.



Vital rates

Figure VII.8. Euclidean distance between the elasticities of the original 13×13 matrix and the elasticities of the 5×5 collapsed matrices obtained with the various collapsing criteria described in figure A.3.b. Overall Euclidean distances are averaged per species $(\bar{x}_{Species})$ and per criteria $(\bar{x}_{Criteria})$.



Figure VII.9. Euclidean distance between the elasticities of the original and the 5×5 collapsed matrices (using collapsing criterion II in figure A.3.b) as a function of life span for 66 plant species – 38 herbaceous perennial, 6 succulent, 6 shrub, 7 palm and 9 tree species.

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Appendix

Chapter IV

Appendix A

Long-term (1931-2010) climatic records at the field site (Maeser 7 climatological permanent station; Western Regional Climate Center, <u>http://www.wrcc.dri.edu</u>) for total precipitation and average temperature as functions of season and year.



a. There has been a significant increase in annual precipitation in the last decades (t_{77} = 6.70, P < 0.001). This increase was significant during the season when the study species *Cryptantha flava* is normally dormant (September-February; t_{77} = 4.80, P < 0.001) as well

as photosynthetically active (March-August; $t_{77} = 5.47$, P < 0.001). The month with the steepest increase in precipitation was August, where we simulated pulses of precipitation (See figure IV.2.b). b. Increases in annual mean temperature have also been reported ($t_{77} = 9.82$, P = 0.002), but these were driven by the dormant season ($t_{77} = 4.86$, P < 0.03), not the growing season ($t_{77} = 1.51$, P < 0.22).

Appendix B

Depiction of the permanent experimental plots used in the present demographic study. We used thirty-two $5 \times 5 \text{ m}^2$ plots arranged across eight locations at the field site (near the Redfleet State Park, UT) and followed the demographic dynamics of all individuals of *Cryptantha flava* found in the nine $1 \times 1 \text{ m}^2$ quadrats in each plot from 2006 to 2010. When a watering plot received a simulated pulse of precipitation, the entire $5 \times 5 \text{ m}^2$ area was watered in order to avoid border effects in the quadrats.



Appendix C

Table containing the vital rates modeled in the fixed-effect integral projection model (IPM) to describe the demographic dynamics of *Cryptantha flava*. The state variable *x* is size (number of leaf rosettes) in year *t*. $\Box(\mu, \varepsilon)$ is a normal distribution with mean μ and standard deviation ε ; ε_g is growth variability, ε_r is recruit size variability, and s_0 , s, a_b , b_g , a_{var} , b_{var} , m_0 , ms, a_f , b_f , a_r and b_r are the coefficients of the fitted regressions used in the model for each vital rate. Models were fitted using lm and glm functions in R. The term *t* is present in the intercept (*a*) and/or in the slope (b) of the fitted regression when the main effect of year and/or the time x size interaction were significant, respectively.

Vital rate				Control			
			2006-	2007-	2008-	2009-	
Туре	Model	Parameter	07	08	09	10	
1. Survival (σ)	$\sigma(x) = \text{logit}(s_0(t) + s(t)x)$	s _o	0.22	0.18	1.68	2.14	
			0.44	0.30	0.13	0.07	
2 Size shares and	$\gamma(\mathbf{x}) = \Box(\mathbf{a}_{\mathrm{g}}(t) + \mathbf{b}_{\mathrm{g}}(t)\mathbf{x}, \varepsilon_{\mathrm{g}})$	a _g	3.85	3.77	5.15	5.44	
2. Size change and		Dg	0.83	0.55	1.00	0.71	
variance (γ)	$\varepsilon_{g} = \Box(a_{var} + b_{var}x, \varepsilon_{1})$	a _{var}	1.58	1.48	2.25	2.73	
		b _{var}	0.33	0.23	0.35	0.30	
3. Flowering	$\varphi(x) = \text{logit}(\mathbf{m}_{o}(t) + \mathbf{m}_{s}(t)x)$	m _o	-2.02	-4.55	-3.65	-2.26	
probability (φ)		m _s	0.21	0.31	0.41	0.16	
4. Number of		\mathbf{a}_{f}	1.36	0.61	0.72	0.88	
flowering stalks	$\chi(\mathbf{x}) = \bigsqcup(\mathbf{a}_{\mathbf{f}} + \mathbf{b}_{\mathbf{f}}(t)\mathbf{x}, \varepsilon_2)$	\mathbf{b}_{f}					
(\mathfrak{A})			0.02	0.02	0.03	0.01	
5. Seed production							
per flowering	$\psi(t)^{\dagger}$		0.013	0.010	0.004	0.004	
stalk (ψ)							
6. Recruitment size	$\omega = Pois(a_r(t) + b_r(t)x, \varepsilon_3)$	a _s	6.63	3.41	3.27	2.29	
distribution (ω)		b _s	-1.95	-0.81	-0.45	-0.66	

Watering		Watering			Watering		Watering	
	2006		2007		2008		2009	
2006-	2007-	2008-	2007-	2008-	2009-	2008-	2009-	2009-
07	08	09	08	09	10	09	10	10
-1.11	-1.14	0.18	-0.88	0.66	0.48	0.94	1.32	-0.16
1.08	1.30	0.21	0.63	0.29	0.47	0.52	0.26	0.59
0.61	6.36	9.55	2.67	3.71	4.88	3.46	2.02	3.56
0.97	0.62	1.12	0.54	1.35	0.90	1.05	0.90	0.95
3.43	4.22	7.94	1.76	3.54	2.86	2.27	1.62	2.78
0.23	0.24	0.17	0.16	0.18	0.16	0.28	0.30	0.26
-1.05	-2.93	-3.36	-3.75	-3.20	-3.01	-2.29	-2.92	-2.82
0.15	20.52	0.43	0.33	0.21	0.15	0.25	0.28	0.24
1.38	-0.28	0.15	0.73	0.50	0.44	0.56	0.39	0.81
0.02	0.06	0.04	0.02	0.02	0.02	0.04	0.03	0.02
0.010	0.005	0.005	0.010	0.022	0.009	0.006	0.003	0.004
6.82	1.67	1.22	4.39	4.09	2.25	3.94	2.89	3.01
-3.63	-0.33	-0.10	-0.74	-0.72	-0.28	-0.64	-0.63	-0.55

x is size (total number of leaf rosettes) in year *t* and *y* is size in year t+1. [†]size independent.

^{\Box} Seed production was not quantified this year and we assumed it to be the average from either the control or the watering plots. The averaged values include the seed production of control flowering plants in 2010 (22.23 ± 4.23) or of flowering plants in 2010 that were watered in August of 2009 (36.72 ± 4.23; see figure IV.4).

Appendix D

Tests for spatial heterogeneity for the eight sites sampled (A, B, C, D, W, X, Y and Z). We carried out two-way ANOVAs with size and site (random) as explanatory variables and the vital rate of survival (σ), change in size (γ), and probability of flowering (φ) as separate response variables, for each treatment and year. For all three vital rates, the size × site interaction was always significant (P < 0.05). Values below are least square means for the linear regressions of change in size, and for the logistic regressions of survival and probability of flowering, respectively. Sites not connected by the same letter are significantly different within each treatment-period combination. "-" represents treatment by year combinations that do not exist in our experimental design (See figure IV.2.b).

		Period					
Treatment	Site	Site					
		2006-07	2007-08	2008-09	2009-10		
Control	А	-	-	0.86 ^A	0.66 ^{AB}		
	В	-	-	0.78^{A}	0.90 ^A		
	С	-	-	0.82 ^A	0.60 ^B		
	D	-	-	0.84 ^A	0.06 ^A		
	W	0.58 ^A	0.33 ^A	0.90 ^A	0.06 ^B		
	Х	0.38 ^A	0.26 ^{AB}	0.88 ^A	0.08^{AB}		
	Y	0.46 ^A	0.13 ^B	0.89 ^A	0.07^{AB}		
	Z	0.49 ^A	0.30 ^{AB}	0.86 ^A	0.10 ^{AB}		

1. Survival (σ):

Watering 2006	W	0.59 ^A	0.15 ^A	0.78 ^A	-
	Х	0.09 ^B	0.21 ^A	0.83 ^A	-
	Y	0.34 ^{AB}	0.17 ^A	0.72 ^A	-
	Ζ	0.37 ^{AB}	0.19 ^A	0.67 ^A	-
Watering 2007	W	-	0.30 ^B	0.72 ^A	0.75 ^A
	Х	-	0.30 ^B	0.79 ^A	0.72 ^A
	Y	-	0.56 ^A	0.80^{A}	0.75 ^A
	Ζ	-	0.31 ^B	0.81 ^A	0.83 ^A
Watering 2008	A	_	_	0.92 ^A	0.77 ^A
	В	-	-	0.89 ^A	0.80^{A}
	С	-	-	0.86 ^A	0.63 ^A
	D	-	-	0.88 ^A	0.79 ^A
	W	-	-	0.93 ^A	0.65 ^A
	Х	-	-	0.92 ^A	0.78^{A}
	Y	-	-	0.89 ^A	0.80^{A}
	Z	-	-	0.91 ^A	0.81 ^A
Watering 2009	А	_	_	_	0.80 ^A
	В	-	-	-	0.77^{A}
	С	-	-	-	0.66 ^A
	D	-	-	-	0.73 ^A
	W	-	-	-	0.82^{A}
	Х	-	-	-	0.76 ^A
	Y	-	-	-	0.86 ^A

2. Change in size (γ) :

		Period				
Treatment	Site	2006-07	2007-08	2008-09	2009-10	
Control	А	-	-	19.10 ^A	5.64 ^A	
	В	-	-	15.50 ^A	1.31 ^{BC}	
	С	-	-	15.37 ^A	1.52 ^C	
	D	-	-	15.95 ^A	1.68 ^B	
	W	16.60 ^A	12.11 ^A	11.16 ^A	2.07 ^{BC}	
	Х	15.23 ^A	9.26 ^{AB}	14.38 ^A	3.29 ^{BC}	
	Y	17.47 ^A	5.00 ^B	16.31 ^A	2.47 ^{BC}	
	Ζ	13.14 ^A	9.41 ^{AB}	16.00 ^A	4.57 ^{BC}	
Watering 2006	W	18.83 ^A	19.93 ^A	25.30 ^A	-	
	Х	14.27 ^A	17.32 ^A	27.70 ^A	-	
	Y	13.94 ^A	18.80 ^A	24.72 ^A	-	
	Ζ	14.14 ^A	15.26 ^A	26.74 ^A	-	
Watering 2007	W	-	9.52 ^A	12.09 ^B	14.88 ^A	
	Х	-	8.81 ^A	16.94 ^A	15.18 ^A	
	Y	-	9.95 ^A	12.71 ^{AB}	14.94 ^A	
	Ζ	-	10.15 ^A	13.93 ^{AB}	15.00 ^A	
Watering 2008	А	-	_	20.45 ^{AB}	25.85 ^A	
	В	_	_	18.56 ^B	16.71 ^{AB}	
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	С	-	-	11.39 ^C	9.43 ^C	
	D	-	-	10.64 ^C	14.11 ^{BC}	
	W	-	-	10.55 ^C	9.20 ^C	
	Х	-	-	15.24 ^{ABC}	8.81 ^C	
	Y	-	-	12.81 ^{BC}	8.83 ^C	
	Z	-	-	14.63 ^{ABC}	13.37 ^{BC}	
Watering 2009	Α	-	-	-	21.29 ^{ABC}	
	В	-	-	-	37.77 ^A	
	С	-	-	-	11.59 ^D	
	D	-	-	-	17.40 ^{BCD}	
	W	-	-	-	23.28 ^{AB}	
	Х	-	-	-	20.59 ^B	
	Y	-	-	-	16.62 ^{BCD}	
	Z	-	-	-	12.76 ^{CD}	

3. Probability of flowering (φ):

Treatment	Site	Period					
Treatment	Site	2006-07	2007-08	2008-09	2009-10		
Control	А	-	-	0.47 ^A	0.58 ^{AB}		
	В	-	-	0.39 ^A	0.49 ^{AB}		
	С	-	-	0.39 ^A	0.40^{AB}		
	D	-	-	0.29 ^A	0.27 ^B		

$ \begin{array}{cccccccccccccccccccccccccccccccccccc$		W	0.51 ^A	0.14 ^A	0.47 ^A	0.54 ^A
Y 0.42^A 0.08^A 0.27^A 0.34^{AB} Z 0.44^A 0.09^A 0.30^A 0.47^{AB} Watering 2006W 0.55^A 0.19^A 0.45^A -X 0.60^A 0.14^A 0.52^A -Y 0.57^A 0.24^A 0.52^A -Z 0.62^A 0.31^A 0.55^A -Watering 2007W- 0.28^{AB} 0.11^A 0.33^A X- 0.20^B 0.20^A 0.26^A Y- 0.38^A 0.20^A 0.22^A Z- 0.23^B 0.21^A 0.17^A Watering 2008A 0.60^A 0.40^A B 0.60^A 0.40^A Watering 2008A 0.33^{AB} 0.21^A Watering 2008A 0.51^A 0.48^A D 0.50^A 0.40^A Watering 2009A 0.35^{AB} 0.42^A X 0.48^{AB} 0.36^A Watering 2009A 0.48^{AB} 0.36^A Watering 2009A 0.42^A B0.42^AC 0.42^A		Х	0.39 ^A	0.08^{A}	0.38 ^A	0.53 ^{AB}
Z 0.44^A 0.09^A 0.30^A 0.47^{AB} Watering 2006W 0.55^A 0.19^A 0.45^A $-$ X 0.60^A 0.14^A 0.52^A $-$ Y 0.57^A 0.24^A 0.52^A $-$ Z 0.62^A 0.31^A 0.55^A $-$ Watering 2007W $ 0.28^{AB}$ 0.11^A 0.33^A X $ 0.20^B$ 0.20^A 0.26^A Y $ 0.20^B$ 0.20^A 0.22^A Z $ 0.23^B$ 0.21^A 0.17^A Watering 2008A $ 0.60^A$ 0.40^A B $ 0.33^{AB}$ 0.50^A 0.40^A Watering 2008A $ 0.33^{AB}$ 0.42^A Watering 2008A $ 0.35^{AB}$ 0.42^A Watering 2009A $ 0.35^{AB}$ 0.42^A Watering 2009A $ 0.43^A$ Watering 2009A $ 0.43^A$ Watering 2009A $ 0.43^A$ B $ 0.43^A$ Watering 2009A $ 0.42^A$ Watering 2009A $ 0.42^A$ Watering 2009A $ 0.43^A$		Y	0.42 ^A	0.08 ^A	0.27 ^A	0.34 ^{AB}
Watering 2006 W 0.55^A 0.19^A 0.45^A - X 0.60^A 0.14^A 0.52^A - Y 0.57^A 0.24^A 0.52^A - Z 0.62^A 0.31^A 0.55^A - Watering 2007 W - 0.28^{AB} 0.11^A 0.33^A X - 0.20^{-B} 0.20^A 0.26^A Y - 0.38^A 0.20^A 0.22^A Z - 0.23^{-B} 0.21^A 0.17^A Watering 2008 A - - 0.60^{-A} 0.40^A B - - 0.60^{-A} 0.40^A B - - 0.34^{AB} 0.50^A QUA - - 0.35^{AB} 0.37^A W - - 0.35^{AB} 0.42^A X - - 0.35^{AB} 0.42^A X - - 0.25^{-B} 0.33^A Z - - 0.48^{AB}		Z	0.44 ^A	0.09 ^A	0.30 ^A	0.47 ^{AB}
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	Watering 2006	W	0.55 ^A	0.19 ^A	0.45 ^A	-
Y 0.57^A 0.24^A 0.52^A -Z 0.62^A 0.31^A 0.55^A -Watering 2007W- 0.28^{AB} 0.11^A 0.33^A X- 0.20^{-B} 0.20^A 0.26^A Y- 0.38^A 0.20^A 0.22^A Z- 0.23^{-B} 0.21^A 0.17^A Watering 2008A 0.60^A 0.40^A B 0.60^A 0.40^A D 0.51^A 0.48^A D 0.35^{AB} 0.37^A W 0.35^{AB} 0.42^A X 0.35^{AB} 0.42^A Z 0.35^{AB} 0.42^A B 0.25^{-B} 0.33^A Z 0.48^{AB} 0.36^A Watering 2009A 0.43^A B0.48^{AB} 0.36^A		Х	0.60 ^A	0.14 ^A	0.52 ^A	-
Z 0.62^A 0.31^A 0.55^A -Watering 2007W- 0.28^{AB} 0.11^A 0.33^A X- 0.20^{-B} 0.20^A 0.26^A Y- 0.38^A 0.20^A 0.22^A Z- 0.23^{-B} 0.21^A 0.17^A Watering 2008A 0.60^A 0.40^A B 0.60^A 0.40^A D 0.34^{AB} 0.50^A C 0.35^{AB} 0.37^A W 0.35^{AB} 0.42^A X 0.35^{AB} 0.42^A Z 0.35^{AB} 0.42^A Z 0.35^{AB} 0.42^A W 0.35^{AB} 0.33^A Z 0.48^{AB} 0.36^A Watering 2009AB 0.42^A C 0.42^A		Y	0.57 ^A	0.24 ^A	0.52 ^A	-
Watering 2007 W - 0.28^{AB} 0.11^{A} 0.33^{A} X - 0.20^{-B} 0.20^{A} 0.26^{A} Y - 0.38^{A} 0.20^{A} 0.22^{A} Z - 0.23^{-B} 0.21^{A} 0.17^{A} Watering 2008 A - - 0.60^{-A} 0.40^{A} B - - 0.60^{-A} 0.40^{A} D - - 0.34^{AB} 0.50^{A} C - - 0.31^{A} 0.40^{A} B - - 0.34^{AB} 0.50^{A} C - - 0.31^{A} 0.48^{A} D - - 0.35^{AB} 0.37^{A} W - - 0.35^{AB} 0.42^{A} X - - 0.25^{-B} 0.33^{A} Z - - 0.48^{AB} 0.36^{A} Watering 2009 A - - 0.43^{A} B - - 0.42^{A} <td< td=""><td></td><td>Z</td><td>0.62^A</td><td>0.31^A</td><td>0.55^A</td><td>-</td></td<>		Z	0.62 ^A	0.31 ^A	0.55 ^A	-
X- 0.20^{-B} 0.20^{A} 0.26^{A} Y- 0.38^{A} 0.20^{A} 0.22^{A} Z- 0.23^{-B} 0.21^{A} 0.17^{A} Watering 2008A 0.60^{-A} 0.40^{A} B 0.60^{-A} 0.40^{A} C 0.51^{A} 0.48^{A} D 0.51^{A} 0.48^{A} D 0.35^{AB} 0.37^{A} W 0.35^{AB} 0.42^{A} X 0.55^{AB} 0.45^{A} Y 0.25^{-B} 0.33^{A} Z 0.48^{AB} 0.36^{A} Watering 2009A 0.43^{A} B 0.42^{A} C 0.42^{A}	Watering 2007	W	-	0.28 ^{AB}	0.11 ^A	0.33 ^A
Y- 0.38^A 0.20^A 0.22^A Z- 0.23^{-B} 0.21^A 0.17^A Watering 2008A 0.60^{-A} 0.40^A B 0.34^{AB} 0.50^A C 0.51^A 0.48^A D 0.35^{AB} 0.37^A W 0.35^{AB} 0.42^A X 0.55^{AB} 0.45^A Y 0.25^{-B} 0.33^A Z 0.48^{AB} 0.36^A Watering 2009A 0.43^A B 0.42^A C0.42^A		Х	-	0.20 ^B	0.20^{A}	0.26 ^A
Z- 0.23^{B} 0.21^{A} 0.17^{A} Watering 2008A 0.60^{A} 0.40^{A} B 0.34^{AB} 0.50^{A} C 0.51^{A} 0.48^{A} D 0.35^{AB} 0.37^{A} W 0.35^{AB} 0.42^{A} X 0.55^{AB} 0.42^{A} Y 0.25^{B} 0.33^{A} Z 0.48^{AB} 0.36^{A} Watering 2009A 0.43^{A} B 0.42^{A} C 0.45^{A}		Y	-	0.38 ^A	0.20 ^A	0.22 ^A
Watering 2008 A - - 0.60^{A} 0.40^{A} B - - 0.34^{AB} 0.50^{A} C - - 0.51^{A} 0.48^{A} D - - 0.35^{AB} 0.37^{A} W - - 0.35^{AB} 0.42^{A} X - - 0.35^{AB} 0.42^{A} X - - 0.35^{AB} 0.42^{A} X - - 0.55^{AB} 0.42^{A} X - - 0.55^{AB} 0.45^{A} Y - - 0.25^{-B} 0.33^{A} Z - - 0.48^{AB} 0.36^{A} Watering 2009 A - - 0.43^{A} B - - 0.42^{A} 0.42^{A} C - - 0.42^{A} 0.42^{A}		Z	-	0.23 ^B	0.21 ^A	0.17 ^A
B 0.34^{AB} 0.50^{A} C 0.51^{A} 0.48^{A} D 0.35^{AB} 0.37^{A} W 0.35^{AB} 0.42^{A} X 0.55^{AB} 0.42^{A} Y 0.25^{-B} 0.33^{A} Z 0.48^{AB} 0.36^{A} Watering 2009A 0.43^{A} B 0.42^{A} C- 0.45^{A}	Watering 2008	А	-	-	0.60 ^A	0.40 ^A
C 0.51^A 0.48^A D 0.35^{AB} 0.37^A W 0.35^{AB} 0.42^A X 0.55^{AB} 0.42^A Y 0.25^{-B} 0.33^A Z 0.48^{AB} 0.36^A Watering 2009AB 0.42^A C0.45^A		В	-	-	0.34 ^{AB}	0.50 ^A
$\begin{array}{cccccccccccccccccccccccccccccccccccc$		С	-	-	0.51 ^A	0.48 ^A
W - - 0.35^{AB} 0.42^{A} X - - 0.55^{AB} 0.45^{A} Y - - 0.25^{-B} 0.33^{A} Z - - 0.48^{AB} 0.36^{A} Watering 2009 A - - 0.48^{AB} 0.36^{A} B - - 0.43^{A} - - 0.43^{A} Output A - - 0.42^{A} - - 0.42^{A} Watering 2009 A - - - 0.42^{A} - - 0.42^{A} B - - - 0.42^{A} - - 0.42^{A} C - - - 0.42^{A} - - 0.45^{A}		D	-	-	0.35 ^{AB}	0.37 ^A
$\begin{array}{cccccccccccccccccccccccccccccccccccc$		W	-	-	0.35 ^{AB}	0.42 ^A
Y - - 0.25^{-B} 0.33^{A} Z - - 0.48^{AB} 0.36^{A} Watering 2009 A - - 0.48^{AB} 0.36^{A} B - - - 0.43^{A} C - - 0.42^{A} C - - 0.45^{A}		Х	-	-	0.55 ^{AB}	0.45 ^A
Z - - 0.48^{AB} 0.36^{A} Watering 2009 A - - - 0.43^{A} B - - - 0.42^{A} C - - 0.45^{A}		Y	-	-	0.25 ^B	0.33 ^A
Watering 2009 A - - 0.43 ^A B - - 0.42 ^A C - - 0.45 ^A		Z	-	-	0.48 ^{AB}	0.36 ^A
B 0.42^{A} C 0.45 ^A	Watering 2009	A	-	-	-	0.43 ^A
C 0.45 ^A		В	-	-	-	0.42 ^A
		С	-	-	-	0.45 ^A

D	_	_	-	0.42 ^A
W	-	-	-	0.42 ^A
Х	-	-	-	0.41 ^A
Y	-	-	-	0.43 ^A
Z	-	-	-	0.47 ^A

Appendix E

Tests for differences in the examined vital rates as a function of treatment and period. We carried out two-way ANOVAs with size and all treatment-year combinations as explanatory variables and the vital rate of survival (σ), change in size (γ), and probability of flowering (φ) as separate response variables. For all three vital rates, the size × treatment-period combination was always significant (P < 0.05). Values below are least square means for the linear regressions of change in size, and for the logistic regressions of survival and probability of flowering, respectively. Treatment-period combination. "-" represents treatment by period combinations that do not exist in our experimental design (See figure IV.2.b).

3 Survival (σ):

Treatment		Period				
Treatment	2006-07	2007-08	2008-09	2009-10		
Control	0.47 ^D	0.35 D	0.85 ^{AB}	0.71 ^C		
Watering 2006	0.32 ^{ABC}	0.33 ^D	0.77 ^D	-		
Watering 2007	_	0.37 ^D	0.82 ^{ABC}	0.78 ^{ABC}		
Watering 2008	_	_	0.90 ^A	0.69 ^c		
Watering 2009	_	-	-	0.72 ^{BC}		

2. Change in size (γ) :

Treatment		Per	iod	
Treatment	2006-07	2007-08	2008-09	2009-10
Control	13.56 ^B	10.10 ^D	16.85 ^{AB}	13.75 ^{BCD}
Watering 2006	11.96 BCDE	13.58 ^{ABCDE}	22.68 ^A	-
Watering 2007	-	8.95 ^E	19.45 ^A	15.39 ^{BC}
Watering 2008	-	-	15.70 ^{BC}	12.57 ^{CDE}
Watering 2009	-	-	-	14.67 ^{BCD}

3. Probability of flowering (φ):

Treatment		Period					
Treatment	2006-07	2007-08	2008-09	2009-10			
Control	0.42 ^{AB}	0.21 ^E	0.38 ^{ABC}	0.34 ^{BCD}			
Watering 2006	0.55 ^A	0.35 ^{ABCDE}	0.42 ^{ABCDE}	_			
Watering 2007	-	0.30 ^{CDE}	0.25 DE	0.21 ^E			
Watering 2008	-	-	0.45 ^{AB}	0.38 ^{ABC}			
Watering 2009	-	-	-	0.37 ^{BCD}			

Appendix F

1. Observed size distribution (bars), stable size distribution (blue lines) and reproductive values (red lines) for each period × treatment integral projection model under three mesh resolutions (49 × 49, 99 × 99 and 149 × 149). B. Keyfitz's Δ (Caswell 2001, p. 101) showing the departure of the observed size distribution from the stable size distribution (0 = far from stable equilibrium, 1 = in stable equilibrium). C. Population growth rates (λ) as a function of mesh resolution.



Treatment	Period		5	
		49 × 49	99 x 99	149 × 149
	2006-07	0.443	0.448	0.512
Control	2007-08	0.701	0.729	0.733
Control	2008-09	0.543	0.512	0.502
	2009-10	0.803	0.814	0.804
	2006-07	0.454	0.445	0.438
Watering 2006	2007-08	0.784	0.773	0.801
	2008-09	0.801	0.712	0.745
	2007-08	0.632	0.647	0.649
Watering 2007	2008-09	0.443	0.456	0.435
	2009-10	0.497	0.500	0.459
Watarina 2008	2008-09	0.367	0.380	0.375
watering 2008	2009-10	0.401	0.377	0.379
Watering 2009	2009-10	0.823	0.859	0.901

2. Deviation of the natural population of *C*. *flava* from its stable size equilibrium as a function of mesh:

3. Population growth rate estimates as a function of IPM mesh:

Treatment	Period	Population growth rate ()					
		49 × 49	99 x 99	149 × 149			
	2006-07	1.089	1.090	1.090			
Control	2007-08	0.918	0.920	0.920			
Control	2008-09	0.963	0.964	0.964			
	2009-10	1.023	1.023	1.024			
	2006-07	0.979	0.983	0.982			
Watering 2006	2007-08	1.009	1.011	1.011			
	2008-09	1.374	1.375	1.375			
	2007-08	0.897	0.901	0.900			
Watering 2007	2008-09	1.003	1.006	1.005			
	2009-10	1.179	1.180	1.180			
Watarina 2008	2008-09	1.040	1.042	1.042			
watering 2008	2009-10	1.006	1.007	1.007			
Watering 2009	2009-10	0.983	0.985	0.984			

Appendix G

Vital rate elasticities of fecundity, survival, growth and shrinkage for each period and treatment. Dashed vertical lines indicate when the vital rate elasticity of growth turns from positive to negative values as size increases; dot-dashed vertical lines indicate when the vital rate elasticity of shrinkage turns from negative to positive values as size increases.



Size at time t

Appendix H

Two-way life table response experiment (LTRE) analyses were performed to examine the effect of the watering treatments (Figure IV.2.b) on the demographic dynamics of *Cryptantha flava*. a. First we explored the effects and interactions of the periods of study (α : 2006-07, 2007-08, 2008-09 and 2009-2010) and the four watering pulses delivered at the end of the growing seasons (τ : watering of 2006, 2007, 2008 and 2009). b. Then we explored the effect of the time since watering (β : 0, 1 or 2 years after watering) in conjunction with the watering treatments (τ). The vital rates are fecundity (Ψ : dashed, pink line), survival (σ : solid, gray line), growth (γ : dotted, green line) and shrinkage (ρ : dot-dashed, orange line). 1. Main effects of the two-way LTRE analysis with period (α) and treatment (τ) as explanatory variables:



2. Main effects of the two-way LTRE analysis with time since watering (β) and treatment (τ) as explanatory variables:



Chapter V

Appendix A

Description of the 80 herbaceous perennial species studied in this manuscript. The list details taxonomic families, length of the demographic censuses, number of site replications, and original number of classes before matrices were collapsed to 5x5 dimensions (see Methods).

The last three columns correspond to the survey of plant shrinkage in the literature. In order to gain a basic understanding of the frequency of shrinkage in natural populations, we identified the number of species that underwent individual-level shrinkage as reflected in their average projection matrices (* represents species where $\sum \sigma_i \rho_{ij} > 0.05$; *j* is the class of an individual at time *t* before it survives [σ] and shrinks [ρ] to class *i* at *t*+1, where *i*<*j*). Then we systematically searched each manuscript for the keywords "retrogression", "regression", "shrinkage", "reversion", or "size decrease" to establish, for those species in which shrinkage occurs, whether the author acknowledged it as an independent process. We also looked for discussions about the potential demographic implications of plant shrinkage in each manuscript. Bolded values represent mean ± S.D.

	~ .		Family	Δt	# sites	Classes	Shrinkage	Acknowledges shrinkage	Discusses shrinkage
	Species	Reference	n=29	4±3	3±3	6±2	86% Yes	66% Yes	11% Yes
1	Achnatherum calamagrostis	(Guardia <i>et al.</i> , 2000)	Poaceae	2	4	11	Yes	Yes	No
2	Aconitum noveboracense	(Dixon <i>et al.</i> , 1997, Dixon and Cook, 1990)	Ranunculaceae	4	4	5	Yes	No	No
3	Actaea spicata	(Froborg and Eriksson, 2003)	Ranunculaceae	5	2	6	Yes	No	No
4	Anemone patens	(Williams and Crone, 2006)	Ranunculaceae	6	1	5	Yes	No	No
5	Aspasia principissa	(Zotz and Schmidt, 2006)	Orchidaceae	4	1	7	Yes	No	No
6	Astragalus cremnophylax var. cremnophylax	(Maschinski <i>et al.</i> , 1997)	Fabaceae	3	1	5	Yes	Yes	No
7	Astragalus tyghensis	(Kaye and Pyke, 2003)	Fabaceae	5	5	5	Yes	Yes	No
8	Bouteloua rigidiseta	(Fowler <i>et al.</i> , 2006, Fowler, 1995)	Poaceae	4	1	5	Yes	Yes	No
9	Calathea micans	(Le Corff and Horvitz, 2005)	Orchidaceae	2	1	5	Yes	No	No
10	Calathea ovandensis	(Horvitz and Schemske, 1995)	Orchidaceae	5	1	8	Yes	Yes	Yes
11	Calochortus lyallii	(Miller <i>et al.</i> , 2007)	Liliaceae	4	1	9	Yes	Yes	No
12	Calochortus macrocarpus	(Miller <i>et al.</i> , 2007)	Liliaceae	4	1	9	Yes	Yes	No
13	Catopsis sessiliflora	(Winkler <i>et al.</i> , 2007)	Bromeliaceae	1	1	5	Yes	Yes	No
14	Centaurea maculosa	(Emery and Gross, 2005)	Asteraceae	3	4	5	Yes	Yes	No
15	Chamaecrista keyensis	(Liu et al., 2005)	Fabaceae	2	4	8	Yes	Yes	No

16	Cimicifuga elata	(Kaye and Pyke, 2003)	Ranunculaceae	2	5	5	Yes	Yes	No
17	Cirsium dissectum	(Jongejans <i>et al.</i> , 2008)	Asteraceae	4	3	6	Yes	Yes	No
18	Cryptantha flava	(Salguero-Gómez, unpublished; chapter III; Lucas <i>et</i> <i>al.</i> , 2008)	Boraginaceae	6	2	6	Yes	Yes	No
19	Cynoglossum virginianum	(Cipollini <i>et al.</i> , 1993)	Boraginaceae	5	1	7	Yes	Yes	No
20	Danthonia sericea	(Moloney, 1988, Gross, 2002)	Poaceae	5	1	6	Yes	No	No
21	Dicerandra frutescens	(Menges <i>et al.</i> , 2006, Evans <i>et al.</i> , 2008)	Lamiaceae	9	8	6	Yes	Yes	No
22	Dipsacus sylvestris	(Werner and Caswell, 1977, Caswell, 2001)	Dipsacaceae	_	8	7	No	No	No
23	Encephalartos cycadifolius	(Raimondo and Donaldson, 2003)	Zamiaceae	8	2	9	No*	Yes	No
24	Encephalartos villosus	(Raimondo and Donaldson, 2003)	Zamiaceae	8	2	9	No	No	No
25	Epilobium latifolium	(Doak, 1992)	Onagraceae	2	1	5	Yes	Yes	No
26	Eryngium cuneifolium	(Menges and Quintana-Ascencio, 2004)	Apiaceae	9	1	6	Yes	Yes	No
27	Erythronium japonicum	(Kawano <i>et al.</i> , 1987, Takada <i>et al.</i> , 1998)	Liliaceae	7	1	14	Yes	No	No
28	Fritillaria camtschatcensis	(Yonezawa <i>et al.</i> , 2000)	Liliaceae	2	2	10	Yes	Yes	No
29	Fritillaria meleagris	(Zhang and Hytteborn, 1985)	Liliaceae	2	2	7	Yes	Yes	No
30	Gentiana pneumonanthe	(Oostermeijer <i>et al.</i> , 1996, Chapman <i>et</i> <i>al.</i> , 1989)	Gentianaceae	6	6	5	Yes	Yes	No
31	Gentianella campestris	(Lennartsson and Oostermeijer, 2001)	Gentianaceae	5	1	6	No	No	No

32	Geum reptans	(Weppler <i>et al.</i> , 2006)	Rosaceae	2	2	5	Yes	Yes	No
33	Geum rivale	(Kiviniemi, 2002)	Rosaceae	5	1	5	Yes	No	No
34	Guarianthe aurantiaca	(Mondragon, 2009)	Orchidaceae	2	1	5	Yes	Yes	No
35	Heliconia acuminata	(Bruna, 2002, Bruna, 2003, Bruna and Oli, 2005)	Heliconiaceae	2	1	6	Yes	Yes	No
36	Himantoglossum hircinum	(Pfeifer <i>et al.</i> , 2006)	Orchidaceae	25	1	5	Yes	No	No
37	Hypericum cumulicola	(Quintana-Ascencio et al., 1998, Quintana-Ascencio et al., 2003)	Clusiaceae	5	1	6	Yes	No	No
38	Lathyrus vernus	(Ehrlen, 2000)	Fabaceae	3	1	7	Yes	Yes	No
39	Lespedeza cuneata	(Schutzenhofer and Knight, 2007)	Fabaceae	1	1	6	Yes	No	No
40	Limonium carolinianum	(Baltzer <i>et al.</i> , 2002)	Plumbaginaceae	3	1	7	Yes	No	No
41	Lobularia maritima	(Pico <i>et al.</i> , 2002)	Brassicaceae	5	1	5	Yes	Yes	No
42	Lomatium bradshawii	(Kaye and Pyke, 2003)	Apiaceae	7	7	5	Yes	Yes	No
43	Lomatium cookii	(Kaye and Pyke, 2003)	Apiaceae	5	2	6	Yes	Yes	No
44	Minuartia obtusiloba	(Forbis and Doak, 2004)	Caryophyllaceae	3	3	9	No	Yes	No
45	Molinia caerulea	(Jacquemyn <i>et al.</i> , 2005)	Poaceae	4	1	5	Yes	Yes	No
46	Nardostachys grandiflora	(Ghimire <i>et al.</i> , 2008)	Valerianaceae	3	2	6	Yes	Yes	No
47	Panax quinquefolium	(Charron and Gagnon, 1991, van der Voort and McGraw, 2006)	Araliaceae	2	6	5	Yes	Yes	No
48	Paronychia pulvinata	(Forbis and Doak, 2004)	Caryophyllaceae	3	3	9	No*	Yes	No
49	Pedicularis	(Menges, 1990,	Scrophulariaceae	3	1	6	Yes	No	No

	furbishiae	Gawler <i>et al.</i> , 1987)							
50	Periandra mediterranea	(Hoffmann, 1999)	Fabaceae	3	1	8	Yes	Yes	No
51	Phaseolus lunatus	(Degreef <i>et al.</i> , 1997)	Fabaceae	2	1	6	No	No	No
52	Picris hieracioides	(Klemow and Raynal, 1985, Verkaar and Schenkeveld, 1984)	Asteraceae	3	2	5	No	No	No
53	Pinguicula alpina	(Svensson <i>et al.</i> , 1993)	Lentibulariaceae	6	1	11	Yes	No	No
54	Pinguicula villosa	(Svensson <i>et al.</i> , 1993)	Lentibulariaceae	6	1	7	Yes	No	No
55	Pinguicula vulgaris	(Svensson <i>et al.</i> , 1993)	Lentibulariaceae	6	1	5	Yes	No	No
56	Plantago media	(Eriksson and Eriksson, 2000)	Plantaginaceae	4	2	5	Yes	No	No
57	Potentilla anserina	(Eriksson, 1988, Eriksson, 1986)	Rosaceae	3	1	6	Yes	No	Yes
58	Primula veris	(Lehtila <i>et al.</i> , 2006, Ehrlen <i>et al.</i> , 2005)	Primulaceae	2	1	6	No*	Yes	Yes
59	Primula vulgaris	(Endels <i>et al.</i> , 2007a, Valverde and Silvertown, 1998, Endels <i>et al.</i> , 2007b)	Lentibulariaceae	2	8	5	Yes	Yes	No
60	Ramonda myconi	(Pico and Riba, 2002, Riba <i>et al.</i> , 2002)	Gesneriaceae	5	5	5	Yes	Yes	No
61	Rumex obtusifolius	(Pino <i>et al.</i> , 1998)	Polygonaceae	2	1	6	No	No	No
62	Sanicula europaea	(Gustafsson and Ehrlen, 2003)	Apiaceae	2	1	5	Yes	No	No
63	Saxifraga cotyledon	(Dinnetz and Nilsson, 2002)	Saxifragaceae	4	2	7	Yes	Yes	No
64	Scorzonera humilis	(Colling and Matthies, 2006)	Asteraceae	3	5	5	Yes	Yes	Yes
65	Setaria	(O'Connor, 1993,	Poaceae	4	2	5	Yes	Yes	Yes

	incrassata	O'Connor and Pickett, 1992)							
66	Silene acaulis	(Gross <i>et al.</i> , 2006, Morris and Doak, 1998, Morris and Doak, 2005)	Caryophyllaceae	1	5	12	Yes	Yes	Yes
67	Silene regia	(Menges and Dolan, 1998)	Caryophyllaceae	7	16	6	Yes	Yes	No
68	Succisa pratensis	(Jongejans and de Kroon, 2005)	Dipsacaceae	4	5	6	Yes	Yes	Yes
69	Themeda triandra	(O'Connor, 1993, O'Connor and Pickett, 1992)	Poaceae	4	2	5	Yes	Yes	Yes
70	Tillandsia brachycaulos	(Mondragon <i>et al.</i> , 2004)	Bromeliaceae	3	1	11	Yes	No	No
71	Tillandsia deppeana	(Winkler <i>et al.</i> , 2007)	Bromeliaceae	2	1	5	Yes	Yes	No
72	Tillandsia juncea	(Winkler <i>et al.</i> , 2007)	Bromeliaceae	2	1	5	Yes	Yes	No
73	Tillandsia multicaulis	(Winkler <i>et al.</i> , 2007)	Bromeliaceae	2	1	5	Yes	Yes	No
74	Tillandsia punctulata	(Winkler <i>et al.</i> , 2007)	Bromeliaceae	2	1	5	Yes	Yes	No
75	Trillium grandiflorum	(Knight, 2004)	Liliaceae	2	12	6	Yes	Yes	No
76	Viola elatior	(Eckstein <i>et al.</i> , 2009, Eckstein <i>et al.</i> , 2006, Eckstein and Otte, 2005)	Violaceae	1	11	5	Yes	Yes	No
77	Viola fimbriatula	(Solbrig <i>et al.</i> , 1988)	Violeaceae	5	1	11	Yes	No	No
78	Viola pumila	(Eckstein <i>et al.</i> , 2009, Eckstein <i>et al.</i> , 2006, Eckstein and Otte, 2005)	Violaceae	1	10	5	Yes	Yes	No
79	Viola stagnina	(Eckstein <i>et al.</i> , 2009, Eckstein <i>et al.</i> , 2006, Eckstein and Otte, 2005)	Violaceae	1	6	5	Yes	Yes	No

80Werauhia
sanguinolenta(Zotz et al., 2005)Bromeliaceae725-
317YesYesYes

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Appendix B

List of the 80 herbaceous perennial species with demographic parameters obtained from their control average matrices: life span (yr), population growth rate (λ ; yr⁻¹), net reproductive rate (*Ro*; #individuals/life span progenitor), generation time (*T*; time necessary for population increase of *Ro*-fold, yr), mean age of parents of offspring of a cohort (μ_I ; yr), damping ratio (ρ ; non-dimensional), period of oscillation (*P_i*; yr). References for species can be found in Appendix A. Bolded values represent mean \pm S.D.

				Ro	Т	μ_{I}		P _i
	Species	53.43	1.029	11.28	21.43	25.64	2.8	11.9
		±	±	±	±	±	±	±
		101.02	0.199	49.660	24.680	48.545	4.76	33.706
1	Achnatherum calamagrostis	33	1.108	3.701	12.740	16.147	1.748	2.060
2	Aconitum noveboracense	39	1.051	1.660	10.249	11.967	2.242	2.593
3	Actaea spicata	7	0.955	0.435	17.924	15.330	1.557	3.660
4	Anemone patens	19	1.019	1.108	5.584	0.423	2.549	-
5	Aspasia principissa	36	0.931	0.270	18.441	11.529	1.352	1.183
6	Astragalus cremnophylax var. cremnophylax	33	0.955	0.515	14.547	12.351	1.260	0.566
7	Astragalus tyghensis	18	1.009	1.074	8.010	8.126	2.741	88.106

8	Bouteloua rigidiseta	8	0.932	0.276	8.865	2.735	3.750	26.809
9	Calathea micans	277	1.061	6.144	30.773	44.748	2.531	-
10	Calathea ovandensis	9	0.992	0.875	17.313	16.692	1.952	3.282
11	Calochortus lyallii	37	0.984	0.794	14.565	13.887	1.834	4.636
12	Calochortus macrocarpus	35	0.934	0.282	18.565	13.923	1.929	2.318
13	Catopsis sessiliflora	10	0.822	0.020	19.915	11.681	1.497	1.078
14	Centaurea maculosa	2	1.332	4.379	5.147	1.163	3.101	16.380
15	Chamaecrista keyensis	7	0.963	0.252	36.973	22.518	3.147	7.471
16	Cimicifuga elata	38	1.154	3.229	8.180	11.132	3.973	5.724
17	Cirsium dissectum	9	1.067	1.165	2.359	0.000	3.561	6.203
18	Cryptantha flava	15	0.864	0.389	6.470	5.092	2.518	2.332
19	Cynoglossum virginianum	7	1.103	1.837	6.196	1.408	3.638	6.581
20	Danthonia sericea	3	0.315	0.000	7.093	2.196	3.312	-
21	Dicerandra frutescens	6	0.813	0.284	6.073	3.484	2.087	22.711
22	Dipsacus sylvestris	2	1.442	5.093	4.449	4.998	15.915	0.902
23	Encephalartos cycadifolius	203	1.031	14.046	87.102	332.942	1.037	-
24	Encephalartos villosus	304	1.047	11.141	52.735	108.199	1.185	1.156
25	Epilobium latifolium	33	1.948	77.245	45.537	67.347	2.131	-
26	Eryngium cuneifolium	2	0.797	0.175	7.658	6.721	1.636	8.861

27	Erythronium japonicum	10	0.724	-	-	-	1.204	-
28	Fritillaria camtschatcensis	36	1.020	1.367	15.675	16.786	1.402	-
29	Fritillaria meleagris	42	1.018	1.210	10.609	11.178	2.524	2.275
30	Gentiana pneumonanthe	16	1.072	1.627	6.961	2.228	2.524	2.275
31	Gentianella campestris	3	0.887	0.736	2.561	1.463	-	15.078
32	Geum reptans	92	1.056	2.719	-	15.468	1.315	0.311
33	Geum rivale	62	1.014	1.387	22.841	25.289	1.924	4.008
34	Guarianthe aurantiaca	102	0.987	0.578	41.451	35.847	1.385	0.842
35	Heliconia acuminata	464	1.004	1.401	93.960	110.222	1.820	6.305
36	Himantoglossum hircinum	3	1.319	5.914	6.413	10.274	3.048	1.380
37	Hypericum cumulicola	17	1.326	4.035	4.946	4.792	3.697	4.911
38	Lathyrus vernus	25	1.009	1.205	19.935	7.574	2.133	2.133
39	Lespedeza cuneata	18	25.029‡	351.389	1.820	1.306	32.692	-
40	Limonium carolinianum	3	1.000	1.003	15.723	15.732	1.697	3.788
41`	Lobularia maritima	4	1.050	1.542	8.854	5.164	2.286	1.382
42	Lomatium bradshawii	19	0.976	0.814	8.510	8.189	2.352	16.423
43	Lomatium cookii	19	1.022	1.202	8.593	8.805	1.794	10.827
44	Minuartia obtusiloba	158	1.000	1.007	116.458	116.880	1.015	10.285
45	Molinia caerulea	644	1.295	267.279	21.585	213.690	2.014	7.457

46	Nardostachys grandiflora	62	1.087	3.095	13.536	18.675	2.278	9.659
47	Panax quinquefolium	38	1.039	2.112	19.576	23.069	1.510	2.223
48	Paronychia pulvinata	219	0.995	0.556	116.043	100.771	1.023	43.260
49	Pedicularis furbishiae	40	1.275	10.330	9.611	15.635	1.767	27.292
50	Periandra mediterranea	79	1.068	3.731	19.923	27.205	1.560	1.936
51	Phaseolus lunatus	3	0.763	0.347	3.927	3.740	1.549	15.966
52	Picris hieracioides	3	0.885	0.606	4.090	1.792	1.137	5.447
53	Pinguicula alpina	42	1.033	1.827	18.692	21.738	1.777	2.738
54	Pinguicula villosa	14	0.997	0.981	6.543	6.522	19.190	7.360
55	Pinguicula vulgaris	39	1.086	4.236	17.440	25.225	1.751	3.723
56	Plantago media	7	0.940	0.081	_	19.917	2.289	2.175
57	Potentilla anserina	17	0.884	0.382	7.795	5.554	4.924	7.303
58	Primula veris	11	1.114	8.956	20.355	4.112	1.665	4.374
59	Primula vulgaris	84	1.279	17.308	11.588	28.209	2.370	49.857
60	Ramonda myconi	93	1.014	1.620	34.163	40.678	1.384	0.738
61	Rumex obtusifolius	4	1.195	8.956	20.355	4.112	1.744	5.407
62	Sanicula europaea	21	0.893	0.114	19.256	11.078	2.384	2.868
63	Saxifraga cotyledon	8	1.193	5.294	9.454	8.483	1.787	13.044
64	Scorzonera humilis	59	0.971	0.141	67.743	38.005	1.220	0.262

65	Setaria incrassata	16	0.936	0.657	6.188	5.714	1.572	-
66	Silene acaulis	153	1.004	1.383	86.200	94.560	1.101	0.285
67	Silene regia	43	1.484	17.365	7.227	16.054	18.676	9.377
68	Succisa pratensis	-	1.176	2.155	52.097	4.911	3.677	6.609
69	Themeda triandra	29	1.095	2.142	8.373	10.152	1.949	2.563
70	Tillandsia brachycaulos	9	0.856	0.605	3.245	0.513	1.813	7.388
71	Tillandsia deppeana	14	0.848	0.181	10.360	8.115	1.451	2.611
72	Tillandsia juncea	24	1.011	1.287	22.097	23.577	1.605	2.358
73	Tillandsia multicaulis	15	0.955	0.361	22.014	18.002	1.646	1.657
74	Tillandsia punctulata	13	0.731	0.001	23.841	6.376	1.056	-
75	Trillium grandiflorum	54	0.967	0.220	45.495	28.674	1.740	1.052
76	Viola elatior	13	0.860	0.399	6.096	5.380	4.779	112.012
77	Viola fimbriatula	12	1.218	3.669	6.583	9.000	3.626	6.086
78	Viola pumila	12	0.826	0.237	7.545	6.163	2.971	15.011
79	Viola stagnina	19	1.057	1.486	7.203	7.765	2.489	0.363
80	Werauhia sanguinolenta	23	1.109	5.354	16.210	18.734	1.188	3.175

‡ Outliers not included in statistical analyses. "-" It was not possible to calculate value.

Appendix C

1. Calculation of vital rate elasticities

The following describes the decomposition of matrix element processes into their underlying vital rate elasticities for a model matrix that contains all possible matrix-element demographic processes:



The matrix-element demographic processes are functions of vital rates described below:

Stasis (as seedbank, active and dormant plant):	$P_j = \sigma_j (1 - \sum \gamma_{ij} - \sum \rho_{ij} - \sum \delta_{ij} - \sum \alpha_{ij})$
Growth: $G_{ij} = \sigma_j \gamma_{ij}$	Shrinkage: $R_{ij} = \sigma_j \rho_{ij}$
Vegetative dormancy: $D_{ij} = \sigma_j \delta_{ij}$	Vegetative awakening: $A_{ij} = \sigma_j \alpha_{ij}$
Sexual reproduction: $F_{ij} = \sigma_j \varphi_{ij}$	Clonal reproduction: $C_{ij} = \sigma_j \kappa_{ij}$

Where σ is the vital rate for survival; γ for growth; ρ for shrinkage; δ and α for plants going dormant and awakening from vegetative dormancy, respectively; φ for sexual reproduction; and κ for clonal reproduction.

The vital rate elasticities were calculated extending the equations described in Caswell (2001), Zuidema & Franco (2001) and Franco & Silvertown (2005) as it follows:

- Survival (σj):

$$E_{\sigma_j} = \frac{\sigma_j}{\lambda} \left[s_{jj} \left(1 - \sum_i \gamma_{ij} - \sum_i \rho_{ij} - \sum_i \delta_{ij} - \sum_i \alpha_{ij} \right) \right] + \sum_i s_{ij} \gamma_{ij} + \sum_i s_{ij} \rho_{ij} + \sum_i s_{ij} \delta_{ij} + \sum_i s_{ij} \alpha_{ij} + \sum_i s_{ij} \phi_{ij} + \sum_i s_{ij$$

- Growth (γ_{ij}) :

$$E_{\gamma_{ij}} = \frac{\gamma_{ij}}{\lambda} [s_{jj}(-\sigma_j) + s_{ij}(-\sigma_j)]$$

- Shrinkage (ρ_{ij}):

$$E_{\rho_{ij}} = \frac{\rho_{ij}}{\lambda} [s_{jj}(-\sigma_j) + s_{ij}(-\sigma_j)]$$

- Vegetative dormancy
$$(\delta_{ij})$$
:

$$E_{\delta_{ij}} = \frac{\delta_{ij}}{\lambda} [s_{jj}(-\sigma_j) + s_{ij}(-\sigma_j)]$$

- Vegetative awakening
$$(\alpha_{ij})$$
:

$$E_{\alpha_{ij}} = \frac{\alpha_{ij}}{\lambda} [s_{jj}(-\sigma_j) + s_{ij}(-\sigma_j)]$$

- Sexual reproduction
$$(\varphi_{ij})$$
:

$$E_{\varphi_{ij}} = \frac{\varphi_{ij}}{\lambda} \left[s_{ij} \sigma_j \right]$$

- Clonal reproduction (κ_{ij}):
$$E_{\kappa_{ij}} = \frac{\kappa_{ij}}{\lambda} \left[s_{ij} \sigma_j \right]$$

2. Vital rate elasticities used in this study

List of the 80 herbaceous perennial species with their corresponding vital rate elasticities obtained from their average control matrices: survival $(E\sigma_j)$, growth $(E\gamma_{ij})$, shrinkage $(E\rho_{ij})$, vegetative dormancy $(E\delta_{ij})$ and vegetative awakening $(E\alpha_{ij})$, sexual reproduction $(E\varphi_{ij})$ and clonal reproduction $(E\kappa_{ij})$. References for species can be found in Appendix A. Bolded values represent mean ± S.D. * indicates $|E\rho| > 0.05$. Values were rounded to the closest third decimal.

	Species		$E\gamma_{ij}$	$E \rho_{ij}$	$E \delta_{ij}$	$E \alpha_{ij}$	$E \phi_{ij}$	$E\kappa_{ij}$
			0.076	-0.021	-0.005	0.012	0.300	0.263
			±	±	±	±	±	±
			0.062	0.027	0.016	0.017	0.342	0.263
1	Achnatherum calamagrostis	0.576	0.163	-0.034	-	-	0.227	-
2	Aconitum noveboracense	0.759	0.106	-0.071*	-	-	0.065	-
3	Actaea spicata	0.203	0.028	-0.004	-	-	0.766	-
4	Anemone patens	0.865	0.018	-0.002	-	-	0.115	-
5	Aspasia principissa	0.956	0.030	-0.010	_	-	0.005	-
6	Astragalus cremnophylax var. cremnophylax	0.864	0.091	-0.027	-	-	0.018	-

7	Astragalus tyghensis	0.604	0.160	-0.058*	-	-	0.179	-
8	Bouteloua rigidiseta	0.598	0.343	-0.057*	-	-	0.002	-
9	Calathea micans	0.878	0.090	-0.024	-	-	0.008	-
10	Calathea ovandensis	0.446	0.058	-0.016	_	_	0.480	_
11	Calochortus lyallii	0.855	0.084	-0.010	-0.009	0.009	0.033	-
12	Calochortus macrocarpus	0.921	0.053	-0.012	0.001	- 0.004	0.008	-
13	Catopsis sessiliflora	0.824	0.063	-0.071*	-	-	0.042	-
14	Centaurea maculosa	0.200	0.143	-0.026	-	-	0.272	0.359
15	Chamaecrista keyensis	0.696	0.140	-0.068*	_	_	0.096	-
16	Cimicifuga elata	0.476	0.146	-0.034	-0.006	0.010	0.328	-
17	Cirsium dissectum	0.000	0.000	0.000	-	-	0.000	1.000
18	Cryptantha flava	0.789	0.117	-0.039	-	_	0.054	-
19	Cynoglossum virginianum	0.543	0.177	0.022	0.015	0.029	0.213	-
20	Danthonia sericea	1.000	0.000	0.000	-	_	0.000	-
21	Dicerandra frutescens	0.249	0.054	-0.012	-	-	0.685	-
22	Dipsacus sylvestris	0.001	0.001	0.000	-	_	0.999	-
23	Encephalartos cycadifolius	0.921	0.042	0.000	-	_	0.036	-
24	Encephalartos villosus	0.933	0.050	0.000	-	-	0.016	-

25	Epilobium latifolium	0.785	0.022	0.000	-	-	0.193	-
26	Eryngium cuneifolium	0.030	0.006	-0.001	-	-	0.963	-
27	Erythronium japonicum	0.912	- 0.064	0.024	-	-	0.000	-
28	Fritillaria camtschatcensis	0.728	0.058	-0.010	-	-	-	0.204
29	Fritillaria meleagris	0.786	0.092	-0.009	-0.039	0.045	0.029	-
30	Gentiana pneumonanthe	0.621	0.129	-0.052*	0.001	0.005	0.191	-
31	Gentianella campestris	0.010	0.006	0.000	-	-	0.984	-
32	Geum reptans	0.675	0.065	-0.028	-	_	0.231	-
33	Geum rivale	0.821	0.087	-0.029	-	_	0.064	_
34	Guarianthe aurantiaca	0.951	0.030	-0.017	-	-	0.002	-
35	Heliconia acuminata	0.970	0.016	-0.013	-	_	_	0.000
36	Himantoglossum hircinum	0.002	0.001	0.000	0.000	0.000	0.996	-
37	Hypericum cumulicola	0.003	0.003	0.000	-	-	0.994	-
38	Lathyrus vernus	0.841	0.099	-0.025	-0.005	0.004	0.027	-
39	Lespedeza cuneata	0.000	0.001	0.000	-	-	0.999	-
40	Limonium carolinianum	0.003	0.001	0.000	-	_	0.997	-
41	Lobularia maritima	0.236	0.034	0.000	-	_	0.729	-
42	Lomatium bradshawii	0.596	0.143	-0.057*	-	_	0.204	_

43	Lomatium cookii	0.556	0.156	-0.035	-	-	0.253	-
44	Minuartia obtusiloba	0.973	0.025	0.000	-	-	0.002	-
45	Molinia caerulea	0.424	0.182	-0.011	-	-	0.384	-
46	Nardostachys grandiflora	0.791	0.140	-0.018	-	_	0.051	_
47	Panax quinquefolium	0.760	0.099	-0.019	-	-	0.122	-
48	Paronychia pulvinata	0.984	0.016	0.000	-	_	0.001	-
49	Pedicularis furbishiae	0.269	0.144	-0.022	-	_	0.565	_
50	Periandra mediterranea	0.845	0.083	-0.026	-	-	0.046	-
51	Phaseolus lunatus	0.007	0.002	0.000	-	-	0.991	-
52	Picris hieracioides	0.029	0.022	0.000	-	_	0.949	_
53	Pinguicula alpina	0.767	0.101	-0.027	-	_	0.105	-
54	Pinguicula villosa	0.257	0.062	-0.009	-	_	0.672	-
55	Pinguicula vulgaris	0.579	0.108	-0.017	-	-	0.295	-
56	Plantago media	0.933	0.034	-0.025	-	_	0.009	-
57	Potentilla anserina	0.796	0.070	-0.034	-	_	0.066	0.035
58	Primula veris	0.559	0.131	-0.003	-	-	0.307	-
59	Primula vulgaris	0.433	0.195	-0.030	-	_	0.342	-
60	Ramonda myconi	0.885	0.066	-0.035	-	_	0.015	-
61	Rumex obtusifolius	0.236	0.055	0.000	-	_	0.709	-

62	Sanicula europaea	0.882	0.058	-0.046	-	-	0.013	-
63	Saxifraga cotyledon	0.095	0.041	-0.003	-	-	0.857	0.004
64	Scorzonera humilis	0.958	0.023	-0.017	-	-	0.002	-
65	Setaria incrassata	0.738	0.068	-0.028	-	_	0.167	-
66	Silene acaulis	0.960	0.031	-0.005	-	-	0.004	-
67	Silene regia	0.155	0.117	-0.014	-	-	0.714	-
68	Succisa pratensis	0.617	0.110	-0.155*	-	-	0.119	-
69	Themeda triandra	0.738	0.118	-0.024	-	-	0.120	-
70	Tillandsia brachycaulos	0.599	0.118	0.000	-	-	0.043	0.240
71	Tillandsia deppeana	0.142	0.020	0.002	-	-	0.835	-
72	Tillandsia juncea	0.653	0.091	-0.040	-	-	0.216	-
73	Tillandsia multicaulis	0.547	0.050	-0.016	-	-	0.387	-
74	Tillandsia punctulata	0.893	0.023	-0.084*	-	-	0.000	-
75	Trillium grandiflorum	0.925	0.045	-0.026	-	-	0.005	-
76	Viola elatior	0.648	0.108	-0.053*	-	-	0.192	-
77	Viola fimbriatula	0.167	0.085	-0.016	-	-	0.732	-
78	Viola pumila	0.717	0.125	-0.066*	-	-	0.092	-
79	Viola stagnina	0.535	0.171	-0.042	-	-	0.251	-
80	Werauhia sanguinolenta	0.376	0.090	-0.002	-	-	0.531	-

Appendix D

List of the 80 herbaceous perennial species with their corresponding loop elasticities organized by loops that contribute to recruitment ($E_{Recruitment loop}$, sexual or clonal reproduction), loops that represent no changes in size class ($E_{Size-rigid loop}$), and loops that represent size fluctuations ($E_{Size-plastic loop}$, including shrinkage and growth, but not reproduction). Loops are organized by length of loop (number of transitions involved in the loop). Not all summations of loop elasticities for each species add up exactly to unity due to rounding only to the third decimal place. References for species can be found in Appendix A. Bolded values represent mean \pm S.D. Loop elasticities were calculated with the matlab routine available in the supplement of Guneralp (2009).

			Contrib recrui	ution to tment)	No				
Spacios			E _{Recruit}	ment loops		E _{Size- rigid}	E E _{Size-plastic loops}			Total
		2	3	4	5	1	2	3	4	
	Species		0.926	0.096	0.087	0.512	0.126	0.013	0.001	1.000
		±	±	±	±	±	±	±	±	±
		0.149	0.129	0.099	0.093	0.222	0.111	0.037	0.006	0.001
1	Achnatherum calamagrostis	0.000	0.097	0.142	0.143	0.556	0.062	0.001	0.000	1.001
2	Aconitum noveboracense	0.115	0.113	0.011	0.075	0.438	0.222	0.028	0.000	1.002
3	Actaea spicata	0.000	0.000	0.000	0.232	0.691	0.077	0.000	0.000	1.000
4	Anemone patens	0.360	0.006	0.001	0.000	0.563	0.069	0.000	0.000	0.999

5	Aspasia principissa	0.012	0.000	0.017	0.103	0.755	0.114	0.000	0.000	1.001
6	Astragalus cremnophylax var. cremnophylax	0.034	0.029	0.062	0.076	0.724	0.075	0.000	0.000	1.000
7	Astragalus tyghensis	0.051	0.120	0.159	0.105	0.319	0.244	0.000	0.000	0.998
8	Bouteloua rigidiseta	0.012	0.022	0.045	0.035	0.471	0.271	0.112	0.031	0.999
9	Calathea micans	0.000	0.152	0.029	0.000	0.473	0.346	0.000	0.000	1.000
10	Calathea ovandensis	0.002	0.083	0.029	0.099	0.652	0.135	0.000	0.000	1.000
11	Calochortus lyallii	0.000	0.000	0.204	0.072	0.552	0.171	0.001	0.000	1.000
12	Calochortus macrocarpus	0.000	0.004	0.137	0.008	0.535	0.306	0.012	0.000	1.002
13	Catopsis sessiliflora	0.000	0.000	0.000	0.085	0.522	0.393	0.000	0.000	1.000
14	Centaurea maculosa	0.162	0.252	0.229	0.061	0.183	0.113	0.000	0.000	1.000
15	Chamaecrista keyensis	0.035	0.179	0.029	0.071	0.447	0.239	0.000	0.000	1.000
16	Cimicifuga elata	0.059	0.354	0.030	0.008	0.337	0.215	0.000	0.000	1.003
17	Cirsium dissectum	0.427	0.000	0.039	0.000	0.338	0.086	0.110	0.000	1.000
18	Cryptantha flava	0.073	0.174	0.005	0.101	0.450	0.197	0.000	0.000	1.000
19	Cynoglossum virginianum	0.254	0.167	0.076	0.047	0.339	0.107	0.010	0.000	1.000
20	Danthonia sericea	0.000	0.000	0.001	0.000	0.998	0.001	0.000	0.000	1.000
21	Dicerandra frutescens	0.073	0.050	0.263	0.105	0.423	0.086	0.000	0.000	1.000
22	Dipsacus sylvestris*	0.075	0.598	0.040	0.010	0.277	0.000	0.000	0.000	1.000
23	Encephalartos cycadifolius*	0.000	0.000	0.082	0.010	0.909	0.000	0.000	0.000	1.001
24	Encephalartos villosus*	0.000	0.000	0.000	0.150	0.850	0.000	0.000	0.000	1.000
25	Epilobium latifolium*	0.078	0.017	0.002	0.001	0.900	0.002	0.000	0.000	1.000
26	Eryngium cuneifolium	0.000	0.017	0.309	0.143	0.462	0.069	0.000	0.000	1.000
27	Erythronium japonicum	0.000	0.000	0.000	0.000	0.803	0.185	0.012	0.001	1.001
28	Fritillaria camtschatcensis	0.088	0.028	0.054	0.006	0.616	0.205	0.004	0.000	1.001
29	Fritillaria meleagris	0.061	0.116	0.088	0.018	0.430	0.278	0.008	0.000	0.999
30	Gentiana pneumonanthe	0.031	0.402	0.003	0.031	0.431	0.103	0.000	0.000	1.001
31	Gentianella campestris*	0.389	0.476	0.136	0.000	0.000	0.000	0.000	0.000	1.001
32	Geum reptans	0.000	0.059	0.045	0.038	0.739	0.115	0.005	0.000	1.001
33	Geum rivale	0.000	0.000	0.130	0.079	0.471	0.320	0.000	0.000	1.000

34 Guarianthe aurantiaca	0.000	0.000	0.004	0.098	0.752	0.145	0.000	0.000	0.999
35 Heliconia acuminate	0.001	0.002	0.009	0.045	0.494	0.406	0.005	0.040	1.002
36 Himantoglossum hircinum	0.064	0.464	0.111	0.002	0.287	0.073	0.000	0.000	1.001
37 Hypericum cumulicola*	0.274	0.075	0.278	0.071	0.269	0.000	0.033	0.000	1.000
38 Lathyrus vernus*	0.000	0.105	0.044	0.034	0.653	0.163	0.000	0.000	0.999
39 Lespedeza cuneata*	0.996	0.002	0.000	0.000	0.002	0.000	0.000	0.000	1.000
40 Limonium carolinianum	0.000	0.009	0.048	0.243	0.583	0.108	0.009	0.000	1.000
41 Lobularia maritime	0.170	0.045	0.092	0.009	0.579	0.106	0.000	0.000	1.001
42 Lomatium bradshawii	0.022	0.170	0.034	0.184	0.355	0.000	0.236	0.000	1.001
43 Lomatium cookie	0.003	0.129	0.118	0.226	0.409	0.114	0.000	0.000	0.999
44 Minuartia obtusiloba*	0.000	0.004	0.018	0.015	0.964	0.000	0.000	0.000	1.001
45 Molinia caerulea*	0.011	0.048	0.168	0.255	0.493	0.025	0.000	0.000	1.000
46 Nardostachys grandiflora	0.013	0.094	0.109	0.153	0.498	0.135	0.000	0.000	1.002
47 Panax quinquefolium	0.012	0.008	0.141	0.085	0.671	0.084	0.000	0.000	1.001
48 Paronychia pulvinata*	0.000	0.000	0.005	0.031	0.964	0.000	0.000	0.000	1.000
49 Pedicularis furbishiae	0.000	0.159	0.154	0.256	0.287	0.139	0.003	0.000	0.998
50 Periandra mediterranea	0.008	0.016	0.103	0.149	0.636	0.065	0.011	0.014	1.002
51 Phaseolus lunatus*	0.035	0.298	0.482	0.024	0.162	0.000	0.000	0.000	1.001
52 Picris hieracioides*	0.000	0.215	0.284	0.501	0.000	0.000	0.000	0.000	1.000
53 Pinguicula alpine	0.000	0.008	0.160	0.093	0.535	0.202	0.003	0.000	1.001
54 Pinguicula villosa	0.023	0.195	0.291	0.015	0.317	0.158	0.000	0.000	0.999
55 Pinguicula vulgaris	0.000	0.023	0.176	0.119	0.507	0.173	0.000	0.000	0.998
56 Plantago media	0.000	0.000	0.000	0.039	0.580	0.306	0.076	0.000	1.001
57 Potentilla anserine	0.039	0.121	0.074	0.006	0.529	0.232	0.000	0.000	1.001
58 Primula veris*	0.000	0.000	0.276	0.034	0.679	0.011	0.000	0.000	1.000
59 Primula vulgaris	0.042	0.159	0.146	0.173	0.357	0.124	0.000	0.000	1.001
60 Ramonda myconi	0.013	0.002	0.044	0.083	0.734	0.116	0.010	0.000	1.002
61 Rumex obtusifolius*	0.007	0.038	0.275	0.067	0.613	0.000	0.000	0.000	1.000
62 Sanicula europaea	0.000	0.000	0.083	0.007	0.378	0.486	0.047	0.000	1.001

63	Saxifraga cotyledon	0.000	0.073	0.045	0.321	0.460	0.100	0.000	0.000	0.999
64	Scorzonera humilis	0.000	0.001	0.009	0.019	0.860	0.095	0.016	0.000	1.000
65	Setaria incrassata	0.229	0.053	0.035	0.029	0.546	0.094	0.012	0.000	0.998
66	Silene acaulis*	0.000	0.001	0.008	0.052	0.925	0.016	0.000	0.000	1.002
67	Silene regia	0.095	0.359	0.154	0.057	0.193	0.143	0.000	0.000	1.001
68	Succisa pratensis	0.264	0.190	0.004	0.000	0.479	0.056	0.006	0.002	1.001
69	Themeda triandra	0.133	0.077	0.116	0.105	0.483	0.052	0.021	0.013	1.000
70	Tillandsia brachycaulos*	0.347	0.000	0.098	0.163	0.392	0.000	0.000	0.000	1.000
71	Tillandsia deppeana	0.000	0.032	0.000	0.313	0.563	0.071	0.016	0.000	0.995
72	Tillandsia juncea	0.000	0.000	0.133	0.074	0.623	0.000	0.170	0.000	1.000
73	Tillandsia multicaulis	0.001	0.000	0.000	0.178	0.609	0.196	0.016	0.000	1.000
74	Tillandsia punctulata	0.000	0.002	0.000	0.000	0.755	0.243	0.000	0.000	1.000
75	Trillium grandiflorum	0.000	0.000	0.000	0.059	0.775	0.166	0.000	0.000	1.000
76	Viola elatior	0.003	0.328	0.092	0.038	0.320	0.220	0.000	0.000	1.001
77	Viola fimbriatula*	0.306	0.068	0.130	0.137	0.310	0.049	0.000	0.000	1.000
78	Viola pumila	0.000	0.117	0.219	0.039	0.343	0.275	0.010	0.000	1.003
79	Viola stagnina	0.029	0.236	0.143	0.101	0.240	0.251	0.000	0.000	1.000
80	Werauhia sanguinolenta*	0.000	0.000	0.115	0.289	0.590	0.005	0.000	0.000	0.999

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Chapter VII

Appendix A

Hooley's collapsing algorithm (2000) assumes that the projection matrix to be collapsed represents the demographic dynamics of a population that is close to stable stage distribution. To test the robustness of this assumption, we used the raw demographic data of a long-term (1997-2000) experiment involving control and experimentally droughted plots of the herbaceous perennial *Cryptantha flava* (Lucas et al. 2008).

For each year and control/treatment, we constructed 13 x 13 projection matrices from the raw data and recorded the respective observed stage distributions and we collapsed each matrix to 5 x 5 dimensions using the collapsing criterion II (see *Results* and figure 2b) We compared the *observed* stage distribution at time t+1 (x) for each 13 x 13 original projection matrix formed from the raw data for times t to t+1, to the stable stage distribution (w) obtained from its corresponding 5 x 5 collapsed projection matrix. We normalized both x and w to 1. We then summed all x_i values from class k_5 to class k_{13} in the observed stage distribution x, in order to obtain a population vector of the same dimensions as the dimensions of the stable stage distribution w from the 5 x 5 collapsed matrix. Finally, we used Keyfitz's Δ to quantify the dissimilarity between the observed x and stable w stage distributions (Caswell 2001:101). Values of Keyfitz's Δ range between 0 and 1, equating to maximum similarity and maximum difference, respectively, between x and w. Populations with Keyfitz's $\Delta < 0.3$ are considered close to stable stage distribution (Keyfitz 1968: 47, Zuidema et al. 2010).

$$\Delta(\bar{x}, \bar{w}) = \frac{1}{2} \sum_{i} |x_i - w_i|$$

The ranges of the Euclidean distances for the elasticities of original-collapsed matrices (0.18-0.72) and the Keyfitz's Δ values (0.04-0.43) were high. Particularly for the latter values, three matrices were close to stable stage distribution (Δ <0.03), and the other three were not. However, we found no significant correlation between the Keyfitz's Δ values and the Euclidean distances ($t_{1,4} = 0.13$, P = 0.74, $R^2 = 0.03$), which implies that, at least for this natural population of *C. flava*, Hooley's collapsing algorithm is relatively robust to the assumption of demographic stable stage distribution.



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Appendix B

This appendix describes the class-specific demographic dynamics (survival, stasis, progression, retrogression and fecundity) of the nine plant species subject of our study at the vital rate and matrix element levels. Because not all the published matrices had 13 x 13 dimensions, we implemented slight modifications to bring them all to the same dimension as a pre-requisite of the goals of our comparative study. For species whose original dimensions were greater than 13 x 13, we used the collapsing algorithm (criterion II, figure 2) to decrease their dimensions to 13 x 13. For species whose original dimensions were lower than 13 x 13, we replicated and modified the values of some higher-classes in additional columns of the expanded 13 x 13 matrix and checked that the fundamental life history characteristics (life span, population growth rate (λ), first reproductive class) were not altered. The correspondence between matrix element and vital rate demographic processes in the following figures is detailed below.

Stasis (as seedbank, active and dormant plant):	$S_j = \sigma_j (1 - \sum \gamma_{ij} - \sum \rho_{ij})$
Progression:	$P_{ij} = \sigma_j \gamma_{ij}$
Retrogression:	$R_{ij} = \sigma_j \rho_{ij}$
Fecundity:	$F_{ij} = \sigma_j \varphi_{ij}$

where σ is the vital rate for survival, γ for progression, ρ for retrogression and φ for fecundity. The vital rate elasticities were calculated according to the equations described in Caswell (2001), Zuidema & Franco (2001) and Franco & Silvertown (2005) as it follows:

- Survival (σj):

$$E_{\sigma_j} = \frac{\sigma_j}{\lambda} \left[s_{jj} \left(1 - \sum_i \gamma_{ij} - \sum_i \rho_{ij} \right) \right] + \sum_i s_{ij} \gamma_{ij} + \sum_i s_{ij} \rho_{ij} + \sum_i s_{ij} \varphi_{ij} + \sum_i s_{ij} k_{ij}$$

- Progression (γ_{ij}):

$$E_{\gamma_{ij}} = \frac{\gamma_{ij}}{\lambda} [s_{ij}(-\sigma_j) + s_{ij}\sigma_j]$$

- Retrogression (ρ_{ij}):

$$E_{\rho_{ij}} = \frac{\rho_{ij}}{\lambda} \left[s_{jj} \left(-\sigma_j \right) + s_{ij} \sigma_j \right]$$

- Fecundity (φ_{ij}) :

$$E_{\varphi_{ij}} = \frac{\varphi_{ij}}{\lambda} [s_{ij}\sigma_j]$$

The matrix-element elasticities were calculated as the sum of the elements that represent fecundity, retrogression, stasis or progression in the elasticity matrix of each species. For instance, for *Cryptantha flava*:



The following graphs show for each study species the class-specific vital rate and matrix element transition probabilities (left axis) as well as the per-capita contributions (fecundity, φ_{ij} , right axis) in the original and transformed matrices:

Cryptantha flava (Boraginaceae)

Original

Dimensions: 7 x 7 ; Life span = 15 years; $\lambda = 0.86$; Adulthood: class 2

Vital rates

Matrix elements



Transformed





Calathea ovandensis (Marantaceae)

Original

Dimensions: 8 x 8; Life span = 20 years; $\lambda = 0.99$; Adulthood: class 3

Vital rates





Transformed





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Ulex minor (Fabaceae)

Original

Dimensions: 16 x 16; Life span = 21 years; $\lambda = 1.31$; Adulthood: class 2



Transformed

Dimensions: 13 x 13; Life span = 21 years; λ = 1.31; Adulthood: class 2





Viola fimbriatula (Violaceae)

Original

Dimensions: 11 x 11; Life span = 24 years; λ = 1.22; Adulthood: class 3

Vital rates





Transformed





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Pterocereus gaumerii (Cactaceae)

Original

Dimensions: 10 x 10; Life span = 31 years; λ = 1.00; Adulthood: class 7

Vital rates

Matrix elements



Transformed

Dimensions: 13 x 13; Life span = 31 years; $\lambda = 1.00$; Adulthood: class 8

Vital rates



Neobuxbaumia macrocephala (Cactaceae)

Original

Dimensions: 10 x 10; Life span = 41 years; $\lambda = 1.03$; Adulthood: class 7

Vital rates





Transformed

Dimensions: 13 x 13; Life span = 41 years; $\lambda = 1.03$; Adulthood: class 8

Vital rates



Rourea induta (Connaraceae)

Original (no need to transform)

Dimensions: 13 x 13; Life span = 52 years; $\lambda = 0.99$; Adulthood: class 3

Vital rates





Thrinax radiata (Arecaceae)

Original

Dimensions: 9 x 9; Life span = 136 years; $\lambda = 1.13$; Adulthood: class 8

Vital rates





Transformed

Dimensions: 13 x 13; Life span = 136 years; $\lambda = 1.13$; Adulthood: class 12





Araucaria cunninghamii (Araucariaceae)

Vital rates

Original

Dimensions: 17 x 17; Life span = 136 years; λ = 1.13; Adulthood: class 12

Vital rates Matrix elements 1 0.9 0.8 0.7 0.6 0.5 0.4 0.3 0.2 0.1 0 10 Per-capita contributions 9 8 7 6 5 4 3 2 1 Per-capita contributions Transition probabilities -0 0 0 10 11 12 13 14 15 16 17 1 2 3 4 5 6 7 89 2 5 8 9 10 11 12 13 14 15 16 17 1 3 4 6 7 Class Class Retrogression Stasis Progression Fecundity -σ -Φ

Transformed

Dimensions: 13 x 13; Life span = 256 years; λ = 1.02; Adulthood: class 11



Appendix C

The projection matrices of nine plant species were collapsed in two different ways in order to (1) explore the effect of matrix dimension on the vital rate and matrix element elasticities, and to (2) establish the optimum way to collapse projection matrices resulting in a minimal perturbation of their elasticity structure. For the first goal, matrices were collapsed in an ever-decreasing order (top graphs) into 7 x7, 5 x 5, 4 x 4 and 3 x 3 matrices. For the second goal, the matrices were collapsed using different collapsing criteria described in figure 2 of the manuscript.









Ulex minor







Pterocereus gaumeri



Neobuxbaumia macrocephala





Thrinax radiata