

LIFE HISTORY EVOLUTION IN EVENING PRIMROSES (*OENOTHERA*):
COLE'S PARADOX REVISITED

by

Margaret Eleanor Katharine Evans

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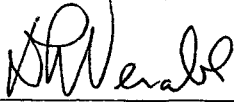
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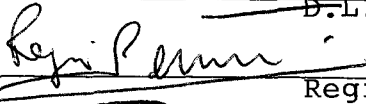
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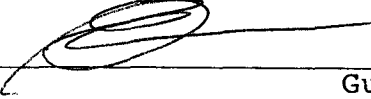
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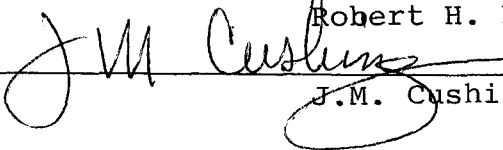
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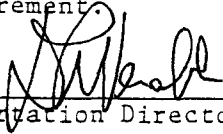


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TABLE OF CONTENTS

LIST OF ILLUSTRATIONS.....	6
LIST OF TABLES.....	7
ABSTRACT.....	8
CHAPTER 1: INTRODUCTION.....	10
<i>Cole's Paradox and its Resolution</i>	10
<i>After Charnov and Schaffer (1973)</i>	12
<i>Focal Models</i>	16
<i>Testing These Ideas</i>	19
CHAPTER 2: PRESENT STUDY.....	22
<i>Summary</i>	22
<i>Significance</i>	26
REFERENCES.....	28
APPENDIX A: EVOLUTION OF THE ANNUAL VS. PERENNIAL HABIT IN EVENING PRIMROSES (<i>OENOTHERA</i> , ONAGRACEAE): A PHYLOGENETIC COMPARATIVE ANALYSIS.....	34
APPENDIX B: A BET-HEDGING VIEW ON COLE'S PARADOX: DEMOGRAPHIC AND CLIMATIC EVIDENCE FROM TWO DESERT SPECIES OF EVENING PRIMROSE (<i>OENOTHERA</i> , ONAGRACEAE).....	78
APPENDIX C: WHY BE ANNUAL VS. PERENNIAL? EVIDENCE FROM TWO DESERT EVENING PRIMROSES (<i>OENOTHERA</i> , ONAGRACEAE) IN A RECIPROCAL COMMON GARDEN EXPERIMENT.....	155

LIST OF FIGURES

Figure 1.1 Concept map of theoretical papers most relevant to the question of why organisms should be semelparous (annual) vs. iteroparous (perennial).

Figure 1.2 Graphical comparison among three sets of reproductive effort models.

LIST OF TABLES

Table 1.1 Comparison of the factors favoring iteroparity vs. semelparity and relevant citations.

ABSTRACT

Why some organisms reproduce just once in their lifetime (semelparity), while others reproduce more than once (iteroparity), has been a central question of life history theory since it was posed by Cole (1954). I used comparative studies at large (phylogenetic) and small (demographic) scales to address this question in a group of evening primroses (the Sections *Anogra* and *Kleinia*, genus *Oenothera*, Onagraceae) found in the arid and semiarid region west of the 100th meridian in North America. In the phylogenetic study, I found that changes in habit were not associated with the changes in aridity that I expected, based on the classic demographic model of Charnov and Schaffer (1973). Instead, this study suggested that changes to the annual habit were associated with increased temperature. I propose that temperature is an important factor influencing the favorability of the annual habit via the effect that temperature has on growth rate. The remaining two studies, comparing the performance of a closely-related desert annual and desert perennial in natural and experimental settings, also indicated that temperature correlated with habit. Using demographic data from natural populations, I evaluated seed banking and iteroparity as alternative means of bet hedging. I found evidence that bet hedging occurs via seed banking in both populations, and may occur via post-reproductive survival in the perennial populations. The demographic data did not clearly show the patterns expected to favor one form of bet hedging over the other. Based on an analysis of climate data, I suggest that cold temperatures are unfavorable to the annual habit. I compared the performance of the same species pair directly in two common

environments. In this reciprocal common garden experiment, the annual outperformed the perennial when conditions were good, and when conditions became stressful relatively early. The annual, with lower leaf mass per area, more rapid above ground growth, and accelerated phenology, exhibits the classic stress-avoiding strategy of desert annuals, explaining the conditions under which it excelled. Relative to the annual, I describe the perennial as a stress-tolerator, and discuss water and temperature stress as two forms of stress it may excel at tolerating.

CHAPTER 1

INTRODUCTION

A fundamental axis of life history variation describes the number of reproductive bouts per lifetime. Some organisms reproduce just once per lifetime (semelparity), while others reproduce repeatedly (iteroparity). Fisher (1930) stated: “It would be instructive to know...what circumstances in the life history and environment would render profitable the diversion of a greater or lesser share of the available resources towards reproduction.” Cole (1954) expressed the problem in terms of annual (semelparous) vs. perennial (iteroparous) plant life histories. His formulation suggested that all plants should be annual, when, in fact, they are not (see below). The problem was subsequently dubbed “Cole’s Paradox.” In their introduction to Cole’s 1954 paper, Real and Levin (1991) go so far as to state “Almost all contemporary research on the evolution of life-history phenomena is rooted in the resolution of [Cole’s] paradox.” In my dissertation research I have focused on the reasons for evolutionary transitions between the perennial and annual habit in a group of evening primroses (*Oenothera*, Onagraceae) found in arid and semiarid areas in western North America.

Cole’s Paradox and its Resolution

Cole (1954) sought to understand why organisms would reduce or delay reproduction. He compared two life histories, one perennial (and iteroparous), and the other annual (and semelparous). Cole’s perennial was iteroparous in the extreme, in that

reproductive plants survived indefinitely. Further, Cole assumed that all offspring would survive to reproduce. Given these assumptions:

“For an annual species, the absolute gain in intrinsic population growth which could be achieved by changing to the perennial reproductive habit would be exactly equivalent to adding one individual to the average litter size.”

Cole (1954)

That is, an annual would have to make just one additional seed to have population growth equal to the perennial. The relative increase in the population growth rate gained by becoming perennial diminishes rapidly with increasing litter size (number of seeds produced). The thinking behind the paradox is that for organisms with large litter size, making one additional seed would be less costly, or easier to evolve, than having extended reproductive lifespan. Cole’s construction of the argument led to the conclusion that the conditions under which iteroparity is favored are narrow, and “arouse[d] curiosity as to why iteroparity exists at all” (Cole 1954).

Cole’s Paradox was resolved by recognizing that not all offspring survive to reproduce, nor do reproductive plants survive indefinitely (Roff 1992, Stearns 1992). This seemingly obvious resolution came in pieces (Murdoch 1966, Gadgil and Bossert 1970, Bryant 1971), and was most definitively composed by Charnov and Schaffer (1973). Charnov and Schaffer (1973) provided explicit terms for pre-reproductive (juvenile) and post-reproductive (adult) survival. Their model suggested that the annual habit would be favored under the condition that the absolute difference between annual and perennial fecundity is greater than the ratio of adult and juvenile survival. If the condition is reversed, the perennial habit would be favored. In addition to the explicit

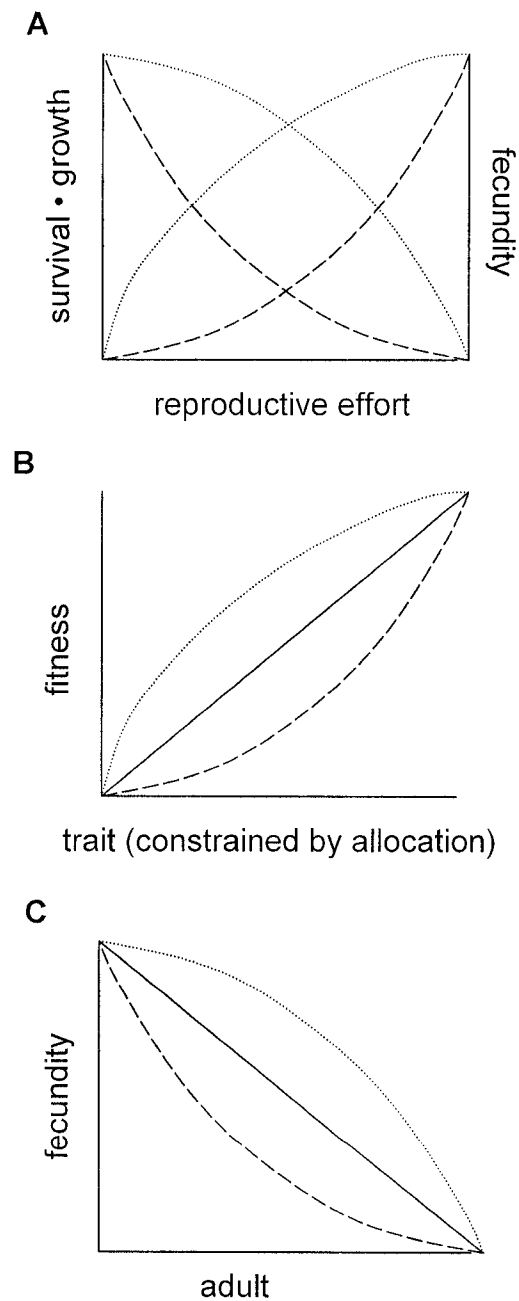
terms for juvenile vs. adult survival, the Charnov and Schaffer (1973) model implicitly assumes a trade-off between fecundity and adult survival.

After Charnov and Schaffer (1973)

The list of factors that have been examined in the years following Charnov and Schaffer's (1973) resolution of Cole's Paradox, with respect to the problem of annual vs. perennial, or semelparous vs. iteroparous life histories, is comprehensive. Many of the models can be categorized with respect to two dimensions: whether demographic parameters are constant (deterministic) or variable (stochastic), and whether they are density-dependent or density-independent (Figure 1). Related to the stochastic models are a group of bet-hedging models that are discussed in more detail below (Figure 1). Another group of models examines the effect of selection on reproductive effort (Figure 1), or nonlinear relationships between fitness (or fitness components) and reproductive effort (or components thereof). Some of these models include stochasticity (Lacey et al. 1983, Real and Ellner 1992) or density-dependence (Takada and Nakajima 1992, Takada 1995). Most incorporate a trade-off between fecundity and subsequent survival, and all obtain similar results (Figure 2). A number of recent models have considered the effect of spatial structure on the coexistence of semelparous vs. iteroparous (annual vs. perennial) life histories (Ronce & Olivieri 1997, Ranta et al. 2000b, Ranta et al. 2001, Tesar et al. 2001; Figure 1).

Given this diversity of models, and the complexity of some individual models, there are no "rules" about the conditions that favor the annual vs. perennial, or

Figure 2. Graphical comparison among three models. I refer to these as reproductive effort models, after Young and Augspurger (1991) and the earliest work by Schaffer (1974a). The dotted lines show the functions favoring iteroparity. The dashed and solid lines show the functions favoring semelparity. Panel A is modified from Shaffer (1974a) and Schaffer and Gadgil (1975), panel B is modified from Lacey et al. (1983) and Real and Ellner (1992), and panel C is modified from Takada and Nakajima (1992) and Takada (1995). Both Real and Ellner (1992) and Takada (1995) found that the concave function (dotted line) favoring iteroparity is conditional upon other parameters.



semelparous vs. iteroparous habit, that are without exception. The modeling exercise of Bell (1976) illustrates this point. Bell (1976) sought to create a series of increasingly realistic and hence complex demographic models, based on those of Cole (1954) and Charnov and Schaffer (1973). He explicitly parameterized age-dependent survival and fecundity and age at first reproduction, with the result that his “general formulation of Cole’s result leads to no very neat generalization” (Bell 1976). In a parameter-rich model, the conditions under which the two strategies are equivalent depends upon the combination of values for all the parameters, which does not lead to a few simple rules about those conditions.

Nonetheless, certain generalizations have arisen from the rich theoretical literature on the conditions that favor semelparity vs. iteroparity. Among the factors that favor the evolution of iteroparity are high adult survival, long reproductive lifespan, low or variable pre-reproductive survival, density-dependence in pre-reproductive survival, and fitness (or a fitness component) that is a decelerating function of reproductive effort (Table 1). Under some conditions and criteria, delayed maturity favors the evolution of iteroparity (see the results of Young 1981 compared to Cole 1954 and Bell 1976). Factors that favor the evolution of semelparity include high pre-reproductive survival, high population growth rate or increasing population size, high fecundity or a large (absolute or relative) difference between semelparous and iteroparous fecundity, low or variable adult survival, density-dependence of adult survival, and fitness (or a fitness component) that is an accelerating function of reproductive effort (Table 1). Several of

these generalizations boil down to restatements of the results of Charnov and Schaffer (1973).

Table 1. Comparison of the factors favoring iteroparity vs. semelparity and relevant citations.

Factors favoring iteroparity (perennial habit)	
High adult survival, long reproductive lifespan	Charnov and Schaffer 1973, Schaffer and Gadgil 1975, Young 1981, Roff 1992, Stearns 1992, Charlesworth 1994
Variability in pre-reproductive survival or “reproductive success”	Murphy 1968, Hairston et al. 1970, Schaffer 1974b, Schaffer and Gadgil 1975, Goodman 1984, Charlesworth 1994
Variability in general	Goodman 1984, Bulmer 1985, Orzack & Tuljapurkar 1989, Stearns 1992, Benton & Grant 1999
Density-dependence in pre-reproductive survival	Goodman 1984, Bulmer 1985
Fitness or a fitness component is a decelerating function of reproductive effort	Schaffer 1974a, Schaffer & Gadgil 1975, Lacey et al. 1983, Real & Ellner 1992, Takada & Nakajima 1992, Takada 1995, Charlesworth 1994, Roff 2002
Factors favoring semelparity (annual habit)	
High pre-reproductive survival	Charnov and Schaffer 1973, Schaffer and Gadgil 1975, Stearns 1992, Charlesworth 1994
High growth rate, growing population	Roff 1992, Charlesworth 1994
High fecundity, large difference in fecundity between strategies	Cole 1954, Charnov and Schaffer 1973, Stearns 1992, Charlesworth 1994
Variability in adult survival	Schaffer 1974b, Schaffer and Gadgil 1975, Charlesworth 1994
Density-dependence in adult survival	Bulmer 1985, Charlesworth 1994
Fitness or a fitness component is an accelerating function of reproductive effort	Schaffer 1974a, Schaffer & Gadgil 1975, Lacey et al. 1983, Real & Ellner 1992, Takada & Nakajima 1992, Takada 1995, Charlesworth 1994

Focal Models

My dissertation research focuses on the predictions of two major groups of models regarding the evolution of the annual vs. perennial, or semelparous vs. iteroparous habit. These two groups are “demographic” and bet-hedging models (sensu Young and Augspurger 1991). The demographic models include a series of deterministic, density-independent models with increasingly complex demographic structure, as discussed above and illustrated in Figure 1. They are best encapsulated by the Charnov and Schaffer (1973) model, which many regard as “the” resolution of Cole’s

Paradox (Roff 1992, 2002, Stearns 1992, Gurevitch et al. 2002). Generally speaking, the predictions of these models reflect those of the Charnov and Schaffer (1973) model: low adult survival and high juvenile survival, and substantially higher annual than perennial fecundity, should favor evolution towards the annual habit. The opposite conditions should favor evolution towards the perennial (iteroparous) habit, as discussed above. These predictions remain fundamental ideas about the reasons for evolutionary changes between the annual and perennial, or semelparous and iteroparous habit (Young and Augspurger 1991, Stearns 1992, Charlesworth 1994).

The second group of models that I addressed is bet-hedging models. These models are particularly relevant for studying the evolution of an important and sizeable class of annual plants: desert annuals. Annuals make up a significant component of desert floras, more so than in any other terrestrial plant biome (Raunkiaer 1934, Daubenmire 1968, 1978, Gurevitch et al. 2002). It is thought that desert annuals have evolved repeatedly from perennials in nearby, semiarid habitats (Johnson 1968, Stebbins 1974, Axelrod 1979). Water is variably available in deserts, among seasons and within seasons among years (Noy-Meir 1973, Ehleringer and Mooney 1983). This variation in the availability of a major limiting resource causes variation in desert plant demography (Beatley 1974, Kadmon and Schmida 1990, Nobel 1992, Watson et al. 1997, Clauss 1999, Venable and Pake 1999). In deserts then, the stage is set for the evolution of traits that reduce variation in fitness.

Bet hedging, when used as an adjective, refers to traits that have the effect of reducing variation in fitness and hence increase the long-term average of fitness. Since

Lewontin and Cohen (1969), it has been understood that the geometric mean of population growth rates provides a more appropriate measure of average fitness in a variable environment than the arithmetic mean. The small-noise approximation for the geometric mean is a function of the arithmetic mean, discounted by a factor proportional to the variance. Bet hedging can be thought of as a trade-off between these two terms: the arithmetic mean and variance of population growth rates (Seger and Brockman 1987, Philippi and Seger 1989). A bet-hedging trait has the effect of reducing fitness variation (a benefit) at the expense of arithmetic mean fitness (a cost). Goodman (1984) pointed out that iteroparity has the potential to function in a bet-hedging, or “risk-spreading” manner. A number of other studies concluded that variance tends to favor iteroparity (Bulmer 1985, Orzack and Tuljapurkar 1989, Fox 1993, Benton and Grant 1999). But these studies did not recognize that many annual plants also have means of reducing variation in fitness, via seed banking. In fact, seed banking in annual plants is well known as a bet-hedging strategy for persistence in variable environments (Cohen 1966, Ellner 1985, Venable & Pake 1999).

More recently, a number of theorists have recognized that seed dormancy and iteroparity, among other phenomena that temporally mix cohorts, are alternative means of reducing variance in fitness (Tuljapurkar 1990, Rees 1994, Tuljapurkar 1994, Orzack 1997, Ellner et al. 1998, Tuljapurkar & Wiener 2000). These operate much as seed dormancy, dispersal, and size, and specialization of adult traits to year-types do as alternative means of reducing variance in fitness (Venable & Lawlor 1980, Brown & Venable 1986, Venable & Brown 1988, Wiener & Tuljapurkar 1994, Venable and Pake

1999). The question of annual vs. perennial life histories then becomes, under what conditions is bet hedging via seed dormancy vs. iteroparity favored? Work by Rees (1994) and Tuljapurkar & Wiener (2000) suggest that the favored form of bet hedging is that which is less risky. Increasing the average or variance of seed or juvenile mortality makes the seed-banking annual habit riskier, whereas increasing the average or variance of adult mortality makes the iteroparous perennial habit riskier. Thus bet hedging via a seed-banking annual life history might evolve if adult survival becomes too improbable or too variable. Though this bet-hedging view on the annual vs. perennial problem may be viewed as more sophisticated, its predictions are essentially the same as those of Charnov and Schaffer (1973) and Schaffer (1974b), and others (see Table 1).

Testing These Ideas

The rich theoretical literature on the annual vs. perennial problem contrasts with the paucity of empirical tests of these ideas. Very few studies have collected the appropriate data from related annuals and perennials, or semelparous and iteroparous plant taxa. Among the best demographic studies are those of annual and perennial varieties of *Oryza perennis* (Oka 1976) and *Poa annua* (Law et al. 1977), of annual and perennial species of *Hypochoeris* (Fone 1989), of semelparous vs. iteroparous lobelias on Mt. Kenya (Young 1990), and of the proportion of plants with axillary vs. terminal inflorescences in *Arabis fecunda* (Lesica and Shelley 1995). Boutin and Harper (1991) gave comparative demographic data for two perennial and three annual species of *Veronica*, but did not analyze or interpret their data in terms of the life history evolution

question of being annual vs. perennial. None of these studies involved desert annuals and perennials. Schaffer and Schaffer (1979) tested ideas about the evolution of reproductive effort (“reproductive effort” models, Figures 1 and 2) using *Agave*. They found that pollinators preferentially visited taller inflorescences, and percent fruit set was positively correlated with inflorescence height in semelparous species (which were actually clonally iteroparous). However subsequent studies found that fruit or seed set in *Agave*, *Yucca*, and *Lobelia* was typically limited by resources, not by pollinators (Young and Augspurger 1991). An even smaller number of studies have examined the evolution of the annual vs. perennial (or semelparous vs. iteroparous) habit in a phylogenetic context. These two studies (Bena et al. 1998, Conti et al. 1999) were pattern-oriented, with causal explanations relegated to speculation rather than analysis.

In my dissertation research, I chose to address the demographic and bet-hedging models discussed above via comparative studies at large (phylogenetic) and small (demographic) scales. Two studies addressed the demographic models, using a phylogenetically-framed test of the association between climate and habit, and a reciprocal common garden experiment, respectively. A third study addressed the bet-hedging models, using demographic data from natural populations of two species, one perennial and the other annual. Together, these studies allowed me to examine the evolutionary pattern of change between the perennial and annual habit, the demographic patterns that may be responsible for these evolutionary patterns, and differences in strategy and environment driving these demographic patterns. These studies are presented as Appendices.

The phylogenetic study, Appendix A, was conducted in collaboration with David Hearn (Ph. D. candidate, Department of Ecology and Evolutionary Biology, University of Arizona), Dr. William Hahn (Columbia University), Jennifer Spangle (undergraduate, University of Arizona), and Dr. D. L. Venable. My own contribution to this study included the theoretical framing and climatic translation of the Charnov and Schaffer (1973) model, the propagation of and genomic extraction from the ingroup taxa, mapping herbarium specimen collection localities, locating and choosing appropriate nearby weather stations for climatic data, and the compilation, manipulation, and analysis of the large climatic data set used in this study. Bill Hahn performed most of the sequencing. Jennifer Spangle assisted with the sequencing, databasing of herbarium specimen collection localities, and compilation of the climatic data set. David Hearn wrote several Perl scripts that made it possible to calculate contrasts on large samples ($n=1,000$) of trees from the phylogenetic analyses in an automated fashion. David and I came to our method of handling phylogenetic uncertainty in a collaborative manner. In addition, David helped me perform the sequence alignment and phylogenetic analyses.

The two demographic studies, Appendices B and C, were not collaborative, but were facilitated by undergraduate assistance, and advice and feedback from committee members and colleagues (see Acknowledgements). The methods, results, and conclusions of these three studies are summarized in Chapter 2.

CHAPTER 2

PRESENT STUDY

Summary

The methods, results, and conclusions of this study are presented in the papers appended to this dissertation. The following is a summary of the most important findings of this study.

In Appendix A, my collaborators and I used a phylogenetic comparative approach to test ideas about the demographic conditions under which the annual vs. perennial habit is favored. We translated the demographic predictions of the Charnov and Schaffer (1973) model into climatic terms, and tested for an association between these climatic patterns and habit in the context of phylogenetic hypotheses for a monophyletic group of evening primroses (*Oenothera*, Onagraceae) including the Sections *Anogra* and *Kleinia*. This group includes 21 taxa that are distributed throughout the semiarid and arid region west of the 100th meridian in North America, mostly in the United States. These plants are winter annuals and perennials, with germination occurring some time between September and March and reproduction occurring in the spring or early summer. We predicted that increased summer aridity (June through August) should cause post-reproductive survival to decline, and decreased aridity from fall through spring (October through March) should cause pre-reproductive survival to increase, favoring the annual habit. This is the first study to explicitly test the predictions from a model of the evolution of the annual vs. perennial habit in a phylogenetic context. In the process, we

developed a novel method that explicitly incorporates phylogenetic uncertainty into our test.

Our results contradicted both of the climatic predictions that we made based on the model of Charnov and Schaffer (1973). Analysis of phylogenetically independent contrasts calculated on a large sample ($n=1,000$) of plausible evolutionary histories indicated that changes to the annual habit were associated with decreased aridity in the summer and with increased aridity in the period from October through March. Contrasts of average scores per species on principal components of climate indicated that changes to the annual habit were also associated with increased temperature. We suggest that warm temperatures favor the annual habit because they allow for the high growth rates necessary for the annual strategy to be successful. Comparative data on the prevalence of annuals in plant communities across the globe (life form spectra) support this idea. Few annuals are found in cold deserts relative to warm deserts, or in cold, open environments such as arctic or alpine biomes. Though annuals have been associated with aridity by many (Crawley 1997, Smith et al. 1997, Dimmitt 2000, Silvertown and Charlesworth 2001), we suggest that it is two factors correlated with aridity, warm temperatures and open space, which favor the annual habit.

In Appendix B, I addressed the reasons for bet hedging via seed banking in annuals vs. iteroparity in perennials, by collecting demographic data from natural populations of a species pair in the Section *Anogra*, one perennial and the other annual. These were *O. californica* ssp. *avita*, a perennial native to the Mojave and southern Great Basin Deserts, and *O. arizonica*, an annual native to the Sonoran Desert. I present data

on survival and fecundity in three natural populations of the perennial and two natural populations of the annual in three years (2000-2003). I also present observational and experimental data on the seed stage. I sampled soil seed density to estimate germination fraction and soil seed bank survival in the natural populations, and conducted a series of experiments to elucidate the factors that affect these parameters. The literature on seed banking in annuals and iteroparity in perennials as alternative means of bet hedging suggest that low or variable survival after the first reproductive bout should favor bet hedging via seed banking, and that low or variable seed or seedling survival should favor bet hedging via iteroparity (Rees 1994, Tuljapurkar & Wiener 2000).

I used these demographic data to address two questions. First, is there evidence that bet hedging occurs via seed banking and iteroparity? Second, are the demographic data consistent with the patterns expected to favor one form of bet hedging over the other? To address the first question, I constructed models of the population dynamics in the perennial vs. annual populations that reflected their life histories and the data that I had collected. Sensitivity analysis of these models indicated that seed banking limited population decline in a dry year and limited population growth in a wet year, both in the annual and the perennial populations. Via these two effects, seed banking reduces variation in population growth rates, and functions in a bet-hedging manner. There were two cases where survival after the first reproductive bout limited decline in perennial populations. If post-reproductive survival comes at a cost in terms of seed production, there may be conditions under which such survival limits population growth.

The demographic data alone did not provide a strong pattern indicating which form of bet hedging (seed banking vs. iteroparity) should be favored. Estimation of survival after the first reproductive bout was complicated by clonality in the perennial, but is probably low, which would act against the favorability of bet hedging via iteroparity. I did not find clear, species-level differences in seed or seedling survival, which would affect the favorability of bet hedging via seed banking. Instead, the differences in demography between these two taxa, which were until recently both considered subspecies of *O. californica*, are subtle, at least in natural, allopatrically-occurring populations. A comparison of climatic across the range of each species showed that cold winter temperatures are associated with the perennial habit. I suggest that the negative effect of cold temperatures on growth rates, both on ecological and evolutionary time scales, make the annual habit less favorable where the perennial is found in the Mojave and southern Great Basin Deserts.

In Appendix C, I examined the predictions of the Charnov and Schaffer (1973) model in a reciprocal common garden experiment, using the same pair of species whose demography I studied in natural populations (*O. californica* ssp. *avita* and *O. arizonica*). This experiment complemented both the comparative phylogenetic study in Appendix A and the comparative study of demography in natural populations in Appendix B. I grew both species in two common gardens, each garden reflecting the climate of origin of one species. The annual was predicted to outperform the perennial in the annual's climate and the perennial was predicted to outperform the annual in the analog of the perennial's climate. I ran two trials of this experiment, and manipulated water and nutrient levels. I

used additional data from the second trial to compare above ground growth rate, phenology, and leaf-level traits between the two species.

Instead of one strategy consistently outperforming the other in the garden reflecting its climate of origin, the direction and magnitude of the difference between annual and perennial fitness depended on the conditions experienced by the plants. The annual outperformed the perennial under the best conditions (both gardens of the first trial) and the worst conditions (the low water treatment of the second trial) experienced by the plants. The data on growth rate, phenology, and leaf mass per area lent insight into these demographic patterns. The annual rosettes grew faster, reproduced earlier, and had lower leaf mass per area (less dense leaves), indicating that they have higher photosynthetic capacity. These traits suggest the annual has the stress-avoiding strategy typical of desert annuals (Solbrig and Orians 1977, Smith et al. 1997). Hence the annual outperformed the perennial under the benign conditions of the first trial, and in the low water treatment of the more stressful trial, where its accelerated phenology allowed it to avoid stress. Unlike previous studies that have related differences between annuals and perennials to the r vs. K spectrum of life histories (Oka 197, Law et al. 197), the data from this experiment with a desert annual vs. perennial suggested that the relevant axis of life history variation is one from stress-avoidance to stress-tolerance.

Significance

The question of why plants should reproduce once vs. more than once per lifetime is a fundamental one that has received generous attention, mostly theoretical, in the last

fifty years. I see my work as having made three contributions to the topic. First, my research has suggested that temperature and open space are two important factors governing the favorability of the annual habit. Regarding temperature, I have suggested that growth rates covary positively with temperature on both ecological and evolutionary time scales. Articulated in this manner, these ideas are ripe for further testing. Second, I have emphasized a bet-hedging perspective on the annual vs. perennial question. Annuals make up a greater proportion of desert floras than any other biome, and environmentally-driven variation in demography is prominent in deserts. Bet hedging is an anticipated solution to the problem of variable fitness presented to deserts plants. If we wish to explain the evolution of a large class of annual species, a bet-hedging perspective is likely to be useful. The idea of seed banking in annuals and iteroparity in perennials as alternative means of bet hedging has been around for about ten years, in the literature of stochastic demography (Tuljapurkar 1990, Rees 1994, Tuljapurkar 1994, Orzack 1997, Ellner et al. 1998, Tuljapurkar & Wiener 2000), but has had little discernable impact in the empirical realm. My hope is that my own work will bring attention to this idea. Also to this end, I am collaborating with Regis Ferriere in a modeling exercise exploring these ideas. Third, I have suggested that a relevant axis for life history variation among desert annuals and perennials is one from stress-avoidance to stress-tolerance. This is a novel way of viewing the difference between annuals and perennials.

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APPENDIX A: EVOLUTION OF THE ANNUAL VS. PERENNIAL HABIT IN
EVENING PRIMROSES (*OENOTHERA*, ONAGRACEAE): A PHYLOGENETIC
COMPARATIVE ANALYSIS

Evolution of the annual vs. perennial habit in evening primroses
(*Oenothera*, Onagraceae): a phylogenetic comparative analysis

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ABSTRACT

Evolutionary ecologists have long sought to understand the conditions under which perennial (iteroparous) vs. annual (semelparous) plant life histories are favored. Translating the classic demographic model of Charnov and Schaffer (1973) into climatic terms, we predicted that increased summer aridity (June through August) should cause post-reproductive survival to decline and decreased fall-spring aridity (October through March) should cause pre-reproductive survival to increase in our study group of winter annuals and perennials (Sections *Anogra* and *Kleinia* of the genus *Oenothera*, Onagraceae), favoring the annual habit. We tested for these associations between aridity and annuality in the context of phylogenetic hypotheses resulting from Bayesian and parsimony analyses of DNA sequence data from three gene regions (2,888 base pairs). Aridity was quantified via descriptive statistics summarizing long-term records of temperature and precipitation from weather stations near herbarium specimen collection localities throughout the range of each taxon. We also conducted a principal components analysis of our climate data set (103 variables). Phylogenetically-independent contrasts of aridity and scores on the first three principal components were calculated on 1,000 of the trees resulting from Bayesian and parsimony analysis. We evaluate the results of our test in terms of the distribution of average contrasts across this plausible set of evolutionary histories, with the null expectation that the average contrast on each tree should be zero. Neither of the predictions regarding aridity were supported by our results. There was a trend for summer aridity to decrease with changes to the annual habit, rather than increase as we had predicted. Changes to the annual habit were

associated with increased rather than decreased fall-spring aridity; this pattern was robust to phylogenetic uncertainty. The contrasts of scores on the principal components recovered these same results, but also indicated that changes to the annual habit were associated with increased temperature throughout the year. We hypothesize that warmer temperatures favor the annual strategy because the high growth rates needed to move through the life cycle and gain large size rapidly are more easily achieved in warmer environments. Our study suggests that among three correlated factors, aridity, warm temperatures, and open space, it is the latter two that favor the annual habit, rather than aridity per se.

Keywords: aridity, Bayesian analysis, iteroparity, life history evolution, phylogenetic uncertainty, semelparity, temperature

INTRODUCTION

A fundamental axis of life history variation concerns the number of reproductive bouts per lifetime, or biomass allocation to reproduction per bout. Some organisms reproduce just once in their lifetime, allocating so much biomass to reproduction that subsequent chances of survival are nil (known as semelparity or monocarpy). Others reproduce more than once per lifetime, and allocate less to offspring production per bout (known as iteroparity or polycarpy).

Evolutionary ecologists have long sought to understand the conditions under which one of these reproductive strategies should be favored over the other. Cole (1954) was the first to address this question quantitatively, but his formulation led to the non-intuitive conclusion that an annual (which is semelparous) should need to produce just more than one additional seed compared to a perennial (which is iteroparous) to be favored (Cole's Paradox). Charnov and Schaffer (1973) did much to resolve Cole's Paradox by focusing on pre-reproductive (juvenile) vs. post-reproductive (adult) survival. Their model predicts that the annual habit should be favored when the ratio of adult and juvenile survival is less than the absolute difference between annual and perennial fecundity. This prediction is particularly intuitive with respect to adult survival: when adults are unlikely to survive to reproduce again, natural selection is predicted to favor putting more effort into current reproduction, leading to the annual habit. More detailed demographic models were subsequently explored by Bell (1976) and Young (1981), including factors such as age-dependent fecundity and mortality, age at maturity, time between reproductive bouts, and population growth rate. In general, changes that

increase the value of juveniles or reduce the value of adults cause semelparity to be favored over iteroparity; for example, increased adult mortality or decreased juvenile mortality are predicted to favor semelparity (Stearns 1992). In addition to these “demographic” explanations (as they are described by Young and Augspurger [1991]), theorists have sought explanations for the evolution of semelparity vs. iteroparity in nonlinear trade-offs (Schaffer 1974a; Schaffer & Gadgil 1975; Lacey et al. 1983; Real & Ellner 1992), selection on reproductive effort via pollinators (Schaffer & Rosensweig 1977; Schaffer & Schaffer 1979; Young 1990) or floral herbivores or pathogens (Klinkhamer et al. 1997), variance in demographic parameters (Murphy 1968; Schaffer 1974b; Orzack & Tuljapurkar 1989; Fox 1993), density dependence of demographic parameters (Ranta et al. 2000a), spatial structuring (Ronce and Olivieri 1997; Ranta et al. 2000b; Ranta et al. 2001; Tesar et al. 2001) or combinations thereof (Goodman 1984; Bulmer 1985; Takada & Nakajima 1992; Takada 1995; Benton & Grant 1999; Ranta et al. 2002).

In this study, we focus on the predictions of the “demographic” models. They remain fundamental ideas about the reasons for evolutionary changes in habit (Young and Augspurger 1991; Roff 1992; Stearns 1992; Charlesworth 1994; Roff 2002), yet there have been few tests of these ideas. We take a phylogenetic comparative approach, using a monophyletic group of about 20 taxa of *Oenothera* (evening primrose), some of which are perennial and others of which are annual. Given the number of taxa and the broad geographic scope of their ranges, we did not collect demographic data from each taxon directly. Instead, we evaluate the demographic predictions, that decreases in adult

survival and increases in seedling survival should favor the annual habit, in climatic terms. Because of their short generation times, we expect that the climate currently occupied by these annuals and herbaceous perennials is not a relict of past distribution or climate. All of the study taxa are native to the generally arid area in the United States west of the 100th meridian (Table 1), where climate is likely to be a strong selective force shaping their life histories. In herbaceous plants without special means of storing water, like these taxa of *Oenothera*, we expect increased aridity to make it more difficult for adults to survive from one year to the next. Specifically, increased aridity after reproduction but before the season of germination, when annuals are dead but perennials persist, should affect the adult survival of perennials without affecting seedling survival of either strategy. Similarly, we can argue that decreased aridity during the time that seedlings are establishing, all else being equal, should allow seedling survival to increase. Our study group consists of winter annuals and perennials in which seedlings recruit in the fall, winter, and spring, and flowering and fruiting occurs in the late spring or early summer. Thus, one set of predictions that follows from the Charnov and Schaffer (1973) and related demographic models is that changes to the annual habit should be associated with increased summer aridity and/or decreased fall-spring aridity in our study group.

Only two previous studies of plants have examined the evolution of the perennial vs. annual habit in a phylogenetic context (Bena et al. 1998; Conti et al. 1999), but neither related changes in habit to a putative causal factor. Here we examine phylogenetically-independent contrasts of climate with respect to habit, to see if changes in habit are associated with changes in summer or fall-spring aridity as predicted above.

We also compiled and analyzed a large climatic data set to explore more generally what aspects of climate variation are associated with changes in habit along a phylogeny. We used principal components analysis to distill this climate variation into a smaller number of dimensions, calculated contrasts of the scores on the principal components, and examined whether changes in habit are associated with changes along these axes. We explicitly incorporated phylogenetic uncertainty into our test by calculating contrasts on large samples of the phylogenetic trees resulting from Bayesian (n=1,000 trees) and parsimony (n=1,000 trees) analysis of our DNA sequence data. We evaluate the results of our test in terms of the distribution of contrasts across these two sets of plausible evolutionary histories.

METHODS

Study System

Our study group includes the Sections *Anogra* and *Kleinia* in the genus *Oenothera* (Onagraceae). This group of 21 taxa is well suited for the study of climate-driven evolution of the perennial vs. annual habit: 7 are annuals, 12 are perennials, and two taxa vary in habit (*O. deltooides* ssp. *cognata* and *O. pallida* ssp. *trichocalyx*; see Table 1). We have included all but one (*O. pallida* ssp. *brevifolia*, a perennial in the predominantly perennial species complex of *O. pallida*) in our study. These plants are found throughout the arid western United States, especially in the southwestern U. S. (Table 1). Three taxa

are endemic to unique dune systems (Table 1). Existing taxonomic and phylogenetic information suggested that this is a monophyletic group with multiple changes in habit. The Section *Anogra*, including the two taxa later placed in Section *Kleinia* by Munz (1931), has long been recognized as a distinct entity: a genus of its own in the past (Spach, 1835). More recently, the monophyly of *Anogra*+*Kleinia* was supported in a phylogenetic study focusing on the Tribe Onagreae (Levin et al., in press). Klein's (1970) hypothesis about the relationships among nine of the taxa in Section *Anogra*, based on ecological, biogeographical, cytogenetic, and artificial hybridization data, suggested that at least three changes in habit had occurred.

We included ten outgroup taxa in our study, in addition to the twenty ingroup taxa. These were species from seven other Sections of the genus *Oenothera*, including species from the four Sections most closely related to our ingroup, according to the study of Levin et al (in press): *O. primiveris* from Section *Eremia*, *O. xylocarpa* from Section *Contortae*, *O. tubifera* from Section *Ravenia*, and *O. elata* ssp. *hookeri*, *O. stubbei*, *O. organensis*, and *O. magellanica* from Section *Oenothera*. Three other Sections represented in our outgroup are Section *Lauvaxia* (by *O. flava* ssp. *taraxacoides*), Section *Xylopleurum* (by *O. speciosa*) and Section *Hartmannia* (by *O. tetraptera*).

Climate data

We characterized the climate of each taxon using long-term weather records. Weather stations were chosen from throughout the range of each taxon, using herbarium specimens to identify stations near collection localities. We began with range maps

created by Warren Wagner at the Smithsonian Institution, which were based on specimens in the U. S. National Herbarium. To these we added localities from loan material from another six herbaria: Rancho Santa Ana Botanic Garden, University of Nevada at Las Vegas, University of California at San Diego, University of New Mexico, University of California at Berkeley, and University of Arizona. In some cases many more localities were mapped (>50), in other cases the loan material did not add very many localities (<20). In a few cases, we simply relied on the Wagner maps, which we found through our own intensive mapping exercises to be quite reliable.

We then added all weather stations near plant localities to the range maps, and chose the best stations. These were stations that were closest to plant localities geographically and in elevation, and with the longest record of weather. In those few cases where more than one equally good station was available, we used a random number to choose a station. Our final choices were spatially stratified with respect to the range of each taxon. The total number of stations chosen per taxon ranged from one (i. e. unique dune endemics) to 16 (see Table 1).

We compiled summary statistics calculated from each station's period of record for several climate variables. These statistics were obtained, for weather stations in their regions, from web pages maintained by the Western Regional Climate Center (WRCC) and High Plains Regional Climate Center of the National Oceanic and Atmospheric Administration. Statistics for stations in the United States outside of these regions were obtained by request from the WRCC. Details of how the statistics are calculated can be found on the web pages (see <http://www.wrcc.dri.edu/summary/>). The climate variables

for which we gathered historical summary statistics included the average high and low temperatures for each month (January through December) and most extreme high and low temperatures recorded each month, as well as average annual precipitation, average annual snowfall, skew of annual precipitation, minimum recorded annual precipitation, the coefficient of variation of annual precipitation, and the average and coefficient of variation of precipitation for every month (January through December). One species, *O. wigginsii*, is found only in Baja California Norte, Mexico. We obtained summary statistics for the five stations chosen for this species from three sources: average high and low temperatures per month from Miranda et al. (1991), extreme high and low temperatures per month, and average temperature per day (for calculating potential evapotranspiration, see Appendix 1) from Quintas (2000), and precipitation data from technical report number BOO.00.R02.07.4.- 02. 4 3 9, from the Comisión Nacional del Agua.

We also calculated potential evapotranspiration (PET), per month and per year, for each station. Potential evapotranspiration is a measure of the drying power at a particular location. In theory, it is “the amount of water...transpired by a short green crop, completely shading the ground, of uniform height and never short of water” (Penman 1956). We used the Hargreaves equation (Hargreaves and Samani 1982) to estimate potential evapotranspiration (Appendix 1). We then calculated an aridity index, per month and per year, for each weather station. This aridity index is simply the potential evapotranspiration divided by the average amount of precipitation for a given time period. Because it integrates the drying power of the environment and the actual

precipitation at a site, the aridity index should correlate with the level of water stress that plants experience. For example, an area with an aridity index above three is considered semiarid (Dimmitt 2000): there is the potential to lose three times as much water via evaporation and transpiration as is received in precipitation. There were some cases in which the denominator of the aridity index (average precipitation) was either zero or a very small number, leading to very large values of the aridity index. We replaced zeros with the smallest amount of precipitation observed at another weather station in that month. We then \log_{10} -transformed the aridity data for each month, and found the average \log_{10} -transformed aridity among the summer months of June through August and among the winter and spring months of October through March, for each weather station. Subsequent analyses were conducted on the average per taxon of log-transformed summer and fall-spring aridity.

We used principal components analysis to find a lower-dimension description of the climate data set, which had 103 variables. This analysis was performed on the correlation matrix (i.e. the data were centered and standardized), since temperature and precipitation variables have different scales (PROC PRINCOMP, SAS Institute 1989).

DNA sequence data

Total genomic DNA was extracted from the sources shown in Table 2 using the extraction protocol of Taylor and Powell (1982) or a modified CTAB protocol (Doyle and Doyle 1987). One nuclear and two plastid non-coding regions were sampled for this study: the Internal Transcribed Spacer (ITS) of the nuclear ribosomal RNA cistron

(Baldwin 1992; Baldwin et al. 1995), and the plastid intergenic spacers between *trnL-trnF* (Taberlet et al. 1991) and *trnH-trnK* (Demesure et al. 1995). Standard PCR protocols were used to amplify these regions and the PCR products were cleaned with PEG/NaCl precipitation (Kusakawa et al. 1990). Cycle sequencing of the PCR products used ABI Big Dye chemistry (Applied Biosystems, Foster City, CA) and all reactions were run on an ABI 377 automated sequencer.

Amplifications of the ITS region were conducted using primers “ITS4’ (5’-TCC TCC GCT TAT TGA TAT GC-3’; White et al., 1990) and “ITS5HP” (5’-GGA AGG AGA AGT CGT AAC AAG G-3’; Hershkovitz and Zimmer 1996). Sequencing of the region used these primers and ITS2 (5’-CGT AGC TAC TTC TTG CAT CG-3’; White et al. 1990), ITS3B (5’-GCA TCG ATG AAG AAC GTA GC-3’; White et al. 1990), and C5.8S (5’-TGC GTT CAA AGA CTC GAT-3’; Suh et al. 1993). Amplification and sequencing of the *trnL-trnF* intergenic spacer used primers “e” (5’-GGT TCA AGT CCC TCT ATC CC-3’) and “f” (5’-ATT TGA ACT GGT GAC ACG AG-3’) of Taberlet et al. (1991). Amplification of the *trnH-trnK* intergenic spacer used primers “trnH(GUG)” (5’-ACG GGA ATT GAA CCC GCG CA-3’) and “trnK(UUU)” (5’-CCG ACT AGT TCC GGG TTC GA-3’) of Demesure et al. (1995). We created new designs of “trnH” (5’-GAA CGA CGG GAA TTG AAC-3’) and “trnK” (5’-TTA TCT ACT CCA TCC GAC T-3’) for a few taxa that we had difficulty amplifying. Additional internal sequencing primers were designed for Onagreae and were used with the two PCR primers: "H400" (5’-TAC GCT CGT GCA TAA CTT CC-3’), "H400R" (5’-GGA AGT TAT GCA CGA GCA TC-3’), "KR400" (5’-GCT CAT AAG GAC CAC CGT TG-3’), and "KR400R"

(5'-GTT GCC ACC AGG AAT ACT CG-3'). Sequence fragments were edited and contiguous sequences generated using Sequencher version 3.1 (Gene Codes Corp., Ann Arbor, Michigan). We used ClustalX (version 1.8) to align the sequences. This alignment employed the multiple sequences alignment mode, with the factory settings, with the exception of the gap opening cost set at 15. Each gene region was aligned separately, then the aligned sequences were concatenated for subsequent analyses.

Phylogenetic Analyses

Phylogenetic analyses were performed on the aligned sequences using PAUP*4.0b10 (Swofford 2002) and MrBayes (Huelsenbeck and Ronquist 2000). In the parsimony analysis, all characters were given equal weight and gaps were treated as missing data. We used a heuristic search with 500 stepwise random addition sequence replicates with tree-bisection reconnection branch-swapping. In the Bayesian analysis, we used the general time reversible model of nucleotide evolution, with site-specific rate heterogeneity estimated by the gamma distribution (GTR + Γ ; Yang 1993; Yang 1994), and the priors set to the defaults in MrBayes. We ran the Markov-chain Monte Carlo simulation for one million generations, sampling every 50th generation. We saved the sampled trees after the log-likelihood score converged for subsequent analyses.

Changes in Habit and Climate: "PIC's" Analyses

We used CAIC (Comparative Analysis by Independent Contrasts; Purvis and Rambaut 1995) to calculate phylogenetically-independent contrasts (PIC's) of climate

variables with respect to habit. The Brunch algorithm in CAIC calculates independent contrasts for combinations of categorical and continuous data. We made habit a dichotomous variable by grouping the species that are plastically capable of more than one habit (*O. deltooides* ssp. *cognata* and *O. pallida* ssp. *trichocalyx*) with the perennials. As such, our habit categories are best described as “potentially iteroparous” vs. “obligately semelparous”. The contrasts can be either positive or negative, depending on how the values of the categorical variable are assigned. More importantly, the null expectation is that the average of the contrasts on a given tree is zero. To explicitly incorporate phylogenetic uncertainty into our test, we calculated contrasts on a random sample (n=1,000) of the Bayesian trees sampled from the posterior distribution after the log-likelihood score had converged, as well as on a random sample (n=1,000) of the most parsimonious trees. We present the distribution of average contrasts for this set of plausible phylogenies and compare it to the distribution of average contrasts calculated from these same trees, but with the habit and climate data randomized in the ingroup. Any pattern in the latter distribution results simply from the structure of the phylogenies. To randomly assign habit, we found the frequency of habit (potentially iteroparous vs. obligately semelparous) in the ingroup, then obtained a random number between 0 and 1 for each taxon, and reassigned habit to that taxon based on whether the random number fell above or below the observed frequency of habit. The actual values of the climate variables were sampled without replacement, and assigned to the ingroup taxa. Perl scripts to create and manage the tens of thousands of files involved in this type of analysis are available upon request.

We calculated contrasts between habit and five climate variables. The first two variables allow us to test the predictions developed above: that summer aridity should be higher, and fall-spring aridity should be lower, where annuals are found. Contrasts were calculated based on average log-transformed aridity per taxon in each season. The remaining three climate variables were the average scores per taxon on the first three axes generated by the principal components analysis.

Habit and Climate: "TIP's" Analyses

We chose to compare the results of an analysis that treats taxa as independent data points (TIP's) to the results from the phylogenetically-independent contrasts (PIC's). We used a t-test to evaluate whether (log-transformed) summer or fall-spring aridity or scores on the first three principal components differed between contrasting habits (potentially iteroparous vs. obligately semelparous).

RESULTS

DNA and phylogenies

Our final sequence data set included 2,888 aligned characters, compiled from ITS (701 base pairs), trnL-trnF (458 bp) and trnH-trnK (1729 bp). Of these 2,888 sites, 2,533 were constant, 221 were variable but not parsimony informative, and 134 (4.6%) were parsimony informative. Parsimony analysis produced 1,937 most parsimonious trees with score 493. In the Markov-chain Monte Carlo simulation, the log-likelihood scores

converged after about 60,000 generations. The sampled tree with the lowest log-likelihood score was at generation 821,300. Sections *Anogra* + *Kleinia* were recovered as a monophyletic group in all of the most parsimonious trees, and in all of the trees sampled from the posterior distribution of the Bayesian analysis. Using the Brunch algorithm, CAIC found five contrasts in habit on 74% of the 1,000 Bayesian trees, four contrasts in habit on 25% of these trees, and three contrasts on 1% of these trees. Given the sample of 1,000 most parsimonious trees, CAIC found five contrasts in habit on 91% of the trees and six contrasts in habit on 9% of the trees.

Climate data

Though the climate data set consisted of 103 variables, 75% of the variation among weather stations was explained by the first three principal components (57%, 11%, and 7%, respectively). The first axis (PCA1) indexes both temperature and potential evapotranspiration (the drying power of the environment). All but 3 of the 48 variables describing temperature load with similar, positive magnitude, as do 11 of the 13 potential evapotranspiration variables (Table 3). The estimates of PET were calculated from temperature and latitude, which are correlated. Thus the first principal component can be interpreted as an axis of increasing temperature and decreasing latitude. Sites with high scores on the second axis (PCA2) receive on average more precipitation and are less arid in the winter (Nov-Mar); they also receive on average less summer precipitation, less reliable summer precipitation, and are more arid in the summer (Jul-Sept; Table 3). Along the third axis (PCA3), precipitation increases and aridity decreases in spring

(March, April), fall (September, October), and on an annual basis. Average precipitation in each month loads on the third axis to some degree (Table 3), though the winter months of December, January, and February load most weakly. More subtle aspects of the interpretation of the first three principal components are detailed in Table 3.

Changes in Habit and Climate: “PIC’s” Analyses

The random contrasts (open bars, Figures 1-2) were distributed in a similar manner for all five climate variables. In each case, about half the averages were positive and half were negative (Table 4). Thus we can say that any positive or negative trend in the averages of the true contrasts is not due to the structure of the trees themselves.

The contrasts of summer and fall-spring aridity did not show the patterns that we predicted. The trend in the averages of contrasts indicated that summer aridity actually decreased with changes to the annual habit, rather than increased. This was the pattern on 100% of the trees reconstructed by parsimony analysis, and on 85.6% of the trees generated by the Bayesian analysis (Figure 1a, Table 4). With respect to the remaining four climate variables, we focus on the results from the Bayesian trees, since the results from the parsimony trees were essentially the same (Table 4). On all 1,000 of the Bayesian trees, changes to the annual habit were associated with increased fall-spring aridity (Table 4), the opposite of what we predicted.

Contrasts of the first principal component indicated that changes to the annual habit were associated with increased temperature and evapotranspiration throughout the year (Figure 2a). This pattern was consistent in the face of phylogenetic uncertainty:

averages of the contrasts from 999 of the 1,000 Bayesian trees showed this pattern (Table 4). As discussed above, the first principal component also may be viewed as an axis of decreasing latitude, so these contrasts also can be interpreted to show that changes to the annual habit are associated with decreased latitude in our study group. Average contrasts of the second principal component indicated that changes to the annual habit were associated with decreased winter precipitation (Figure 2b), which is entirely consistent with the above pattern that changes to the annual habit are associated with increased fall-spring aridity. The contrasts of PCA2 also indicate that changes to the annual habit are associated with decreased summer aridity, increased summer precipitation, and more reliable summer precipitation, which is consistent with the above contrasts of summer aridity. This pattern was robust to phylogenetic uncertainty (Table 4). Contrasts of scores on the third principal component, which indexes spring, fall, and annual precipitation, did not show a consistent pattern across the plausible set of evolutionary histories of our study group: 76.9% of trees indicated changes to the annual habit were associated with decreased spring, fall, and annual precipitation, whereas another 23.1% of trees indicated changes to the annual habit were associated with increased spring, fall, and annual precipitation (Figure 2c, Table 4).

Changes in Habit and Climate: “TIP’s” Analyses

The results of t-tests of the climate data indicated weaker patterns than we found in the phylogenetically independent contrasts, but generally corresponded to the PIC’s results. Average summer aridity per taxon did not differ between taxa that are potentially

iteroparous vs. obligately semelparous ($F_{1, 19}=0.249$, $p=0.624$), in contrast to the trend that we found in the PIC's analysis. But the t-test, like the phylogenetically-independent contrasts, showed that obligate annuals occur in places that are significantly more arid in the winter and spring months ($F_{1, 19}=4.956$, $p=0.039$). Among the principal components, only the scores on the first axis were significantly different between potentially iteroparous vs. obligately semelparous plants ($F_{1, 19}=5.765$, $p=0.027$). Just as indicated by the phylogenetically independent contrasts, the annuals in our group are found where it is warmer and potential evapotranspiration is higher. While there was a clear trend in the averages of contrasts of PCA2, which indexes winter and summer aridity, the t-test did not reveal that scores on PCA2 differed between our two categories of habit ($F_{1, 19}=0.596$, $p=0.451$). Scores on the third principal component did not differ between the two categories of habit ($F_{1, 19}=0.000$, $p=0.990$).

In the climate space defined by the first vs. second principal component, the average scores per taxon show some clustering with respect to our two categories of habit (Figure 3). Annuals are found where it is warmer throughout the year, drier in the winter months and wetter in the summer months, whereas the perennials and potentially iteroparous taxa are found where it is cooler throughout the year, wetter in the winter months and drier in the summer months. The exceptions are one perennial, *O. pallida* ssp. *gypsophyla*, found in the annual climate space, and one annual, *O. deltoides* ssp. *piperi*, found in the perennial climate space. Additionally, two annuals, *O. albicaulis* and *O. wigginsii*, and three perennials, *O. pallida* ssp. *runcinata*, *O. californica* ssp. *avita*, and *O. californica* ssp. *eurekaensis*, are found very close to the boundary that we have drawn.

No such clustering with respect to habit is found in other pairings of principal components.

DISCUSSION

Associations between climate and habit

Neither of the predictions that we constructed, based on the Charnov and Schaffer (1973) and related demographic models, were supported by the results. We expected increased summer aridity to reduce adult survival of perennials and favor the annual habit. Instead, the trend was the opposite of what we expected. Many of the Bayesian trees and all of the parsimony trees showed that changes to the annual habit were actually associated with decreased summer aridity, while only a minority of the Bayesian trees showed that changes to the annual habit were associated with increased summer aridity. We also expected decreased aridity in the winter and spring months to increase seedling survival and favor the annual habit. In fact, the annuals in our study group are found in places that are more arid in the winter and spring months, counter to this prediction. This pattern was robust to the phylogenetic uncertainty, and differed clearly from the distribution of average contrasts that results simply from the structure of the trees.

Why were our predictions not met? It could be that the Charnov and Schaffer (1973) model does not capture the important causes of life history evolution in this group. Or it may be that the biological features of this model do explain the evolutionary

patterns in our system, but our operationalization of the predictions in terms of climate somehow provided inadequate tests. We suspect both reasons. We predicted that increased summer aridity would reduce adult survival and favor the annual habit. But the trade-off between perennial adult survival and annual fecundity that is implied in the Charnov and Schaffer (1973) model may not be actualized in the face of increased summer aridity, or it may be complicated by additional dimensions of fitness or additional trade-offs not in the model. Our data indicate that some of the perennials in our study group (*O. deltoides* ssp. *howellii*, *O. californica* ssp. *avita*, *O. californica* ssp. *californica*, and *O. californica* ssp. *eurekaensis*) are persisting in places that are comparably or more arid in the summer months than the places where annuals are persisting. And some of the annuals (*O. engelmannii* and *O. albicaulis*) are found in places that are not particularly arid in the summer.

We also predicted that decreased aridity in the period that seedlings are establishing should increase seedling survival. But seedling survival may be low in more mesic, closed-canopy environments because of competition (Silvertown and Charlesworth 2001). One interpretation of the pattern that we found, that changes to the annual habit were associated with increased fall-spring aridity and decreased winter precipitation, is that increased aridity in the period of seedling recruitment is associated with more open space, making it possible for seedling survival to be high via the classic drought-avoiding mechanisms of desert annuals: plastic germination in response to rain (Beatley 1974; Ehleringer 1985; Clauss and Venable 2000) and high photosynthetic rates (Solbrig and Orians 1977; Smith et al. 1997). However, the plants in our study group are

found in the loose, coarse-grained soils of dunes, sandhills, washes, or roadsides (Klein 1970, and other citations in Table 1), which all tend to be relatively open habitats. An evaluation of the role of competition in shaping the life histories of these plants would require, at least, data on percent cover where the annuals vs. perennials are found.

The analysis of phylogenetic trends in principal components of climate showed that changes to the annual habit were associated with increased winter aridity and decreased summer aridity (PCA2), as discussed above, but also with increased temperature and potential evapotranspiration throughout the year (PCA1). The latter is an axis of climatic variation that we did not predict to have an evolutionary correlation with habit. Temperature may be an important general factor determining the favorability of the annual vs. perennial strategy. Growth rates are temperature dependent in plants. An annual must progress from seed germination to seed set in a short period of time, and to be favored over a perennial strategy, exceed the lifetime seed production of a perennial in one season, which may be difficult to achieve in a cold environment (Comstock and Ehleringer 1992; Evans 2003). Cold temperatures not only suppress plant growth, they can also act as a form of stress. Adaptation to cold may result in a chronically lower growth rate; that is, there may be a trade-off between cold-tolerance and growth rate. We suspect that higher fall-spring aridity where annuals are found is another indication that annuals are found where it is warmer, rather than an indication that annuals are found where it is drier, at that time of year.

The role of temperature in favoring annual vs. perennial life histories has left a strong signature in floristic life-form spectra. Few annuals are found in cold deserts or in

cold, open environments in general (Comstock and Ehleringer 1992; Dimmitt 2000; Gurevitch et al. 2002). Among the four North American deserts, the Chihuahuan, Sonoran, Mohave, and Great Basin Deserts, the latter is considered a cold desert, or a steppe or shrub-steppe (Daubenmire 1978; Smith et al. 1997; Dimmitt 2000).

Daubenmire (1978) reports that in steppe regions, including the area known as the Great Basin “Desert”, about 20% of plant species are annuals, whereas annuals make up about 50% of plant species in warm deserts, including the Mojave, Sonoran, and Chihuahuan Deserts. Comparing life form spectra across biomes, the data of Raunkiaer (1934), shown in Daubenmire (1968), illustrate that annuals make up the greatest fraction of floras in desert and chaparral biomes, and the smallest fraction of floras in tundra (arctic and alpine) biomes, despite the availability of open space in many parts of the latter biome.

That few annuals are found in cold deserts highlights the need to parse the effects of aridity, temperature, and open space on the favorability of the annual habit. Extreme aridity is often associated with high temperatures, resulting in less plant cover and more open space. Annuals have been associated with aridity (Venable et al. 1993; Crawley 1997; Smith et al. 1997; Dimmitt 2000; Silvertown and Charlesworth 2001), while aridity is associated with warm temperatures and open space. Our results suggest that it is the latter two factors that may actually be favoring annuals, rather than aridity per se. The plants in our study group all occur in relatively arid, open habitats, and are physiologically active in the fall through spring. In this group, it seems to be temperature

that most clearly differentiates between the places where annuals vs. perennials are found.

Phylogenetic uncertainty and testing ideas in a phylogenetic context

Phylogenetic uncertainty is pervasive in uncontrolled evolutionary data sets. Our sequence data set, though sizeable (2,888 base pairs) in the context of current technology, led to 1,937 most parsimonious trees. Thirteen of the 21 taxa in our ingroup are subspecies of just three species, so the low level of parsimony-informative sequence variation (4.6%) is not surprising. But this does not preclude testing ecological ideas in a historical framework. Evolutionary biologists have expressed the need to develop methods that explicitly account for phylogenetic uncertainty when testing ideas in a historical framework (Harvey and Pagel 1991; Donoghue and Ackerly 1996; Huelsenbeck et al. 2000). Several studies in the last decade have, in one way or another, accounted for phylogenetic uncertainty (Debry 1992; Ackerly and Reich 1999; Joseph et al 1999; Weiblen et al. 2000; Fishbein 2001; Lutzoni et al. 2001; Sanderson and Doyle 2001; Aanen et al 2002; Belshaw and Quicke 2002; Huelsenbeck and Imennov 2002; Miller and Venable 2003). Given the nature of our question, the association between a dichotomous life history trait and a continuous predictor variable, there is a straightforward null expectation for a single statistic from each tree: The average of the contrasts of the continuous variable with respect to the dichotomous variable should be zero. Rather than estimating the strength and direction of the association on a single “best” tree, and then evaluating the sensitivity of that pattern to phylogenetic uncertainty,

we have examined the distribution of this statistic across a set of plausible evolutionary histories. We do not treat phylogenetic uncertainty as a nuisance variable; rather, our approach explicitly incorporates that uncertainty into the estimation of the pattern. This sort of approach to phylogenetic uncertainty has been championed by Huelsenbeck and other Bayesians (Huelsenbeck et al. 2000; Huelsenbeck et al. 2001; Lutzoni et al. 2001; Huelsenbeck and Imennov 2002; Huelsenbeck and Rannala 2003). We have applied this approach both to trees generated by Bayesian and parsimony analyses. The distribution of Bayesian trees reflects their posterior probabilities, so that the result from each tree is weighted by the probability of that topology given the sequence data, the model of nucleotide evolution, and the prior probabilities. The parsimony trees have no associated likelihood; they are equally parsimonious. In our study, the patterns indicated by these two types of trees corresponded quite well.

There are alternatives to the method presented here. We chose to randomize both the habit and climate data on each phylogeny. This disrupts not only any correlation present between the habit and climate data, but also any correlation present between each variable and the phylogenies. An alternative would be to randomly evolve habit and climate on each phylogeny. That would have the advantage of disrupting only the correlation between the two variables on the tree, the pattern in which we are interested. However, this would involve specifying a model of character evolution (e.g. specifying whether the transition probabilities between the perennial and annual habit are weighted equally or not), which we chose to avoid. Huelsenbeck and Rannala (2003) recently presented a method and example of testing for a correlation between two or more

continuous characters in a Bayesian framework. In their method, the covariance between the variables of interest is another parameter estimated in the Monte Carlo simulation. The result of their method and ours is a distribution of a parameter that describes the association between two variables of interest. Our method is simply the multi-tree extension of what evolutionary biologists have done for some time now.

Significance

In the process of testing for the demographic patterns predicted by the classic model of Charnov and Schaffer (1973) regarding the favorability of the annual (semelparous) vs. perennial (iteroparous) habit, we uncovered a different, unexpected pattern. In our study group, the evolution of the annual habit is associated with increased temperature. This is consistent with the global observation for plant communities that few annuals are found in cold environments, even those with little plant cover, where open space is readily available for recruitment. The annual habit is probably not favored in cold environments because cold temperatures suppress growth rates, making it difficult for annuals to rapidly capitalize on good conditions. If it cannot rapidly capitalize on good conditions, a plant may be favored to have a longer lifespan, so that it can build up body mass over time and integrate fitness over multiple opportunities for reproduction.

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TABLE 1. Ecological information for taxa in the Sections *Anogra* and *Kleinia* of the genus *Oenothera* (Onagraceae). Standard abbreviations are used for state names in the United States (BCN refers to Baja California Norte in Mexico); lower case letters before such abbreviations indicate ordinate directions. Habit is either annual (A), perennial (P), or biennial (B). The citations for habit (in superscript) are: (1) Klein 1970, (2) Pavlik and Barbour 1988, (3) Wiggins 1980, (4) Wagner 1998, (5) Klein 1962, (6) Martins and Hutchins 1981, (7) Welsh et al. 1987, (8) Munz 1931, (9) McGregor and Barkley 1986, (10) Correll and Johnston (1970), and (11) Hickman (1993). In the last column (weather data), is the number of weather stations chosen for each species, followed by the mean number of years of data at those stations.

Taxon	Distribution	Elevation (m)	Habit	weather data
Section <i>Anogra</i>				
<i>Oenothera arizonica</i>	Sonoran Desert in sAZ, nwSonora	210-600	A ^{1,4}	9, 81
<i>O. californica</i> ssp. <i>avita</i>	Mohave Desert in seCA, sNV, nwAZ, swUT	600-2,250	P ^{1,11}	12, 64
<i>O. californica</i> ssp. <i>californica</i>	sCA, nBCN	300-2,250	P ^{1,11}	12, 53
<i>O. californica</i> ssp. <i>eurekaensis</i>	Endemic to the Eureka Dunes, northwest of Death Valley, CA	~1,020	P ^{1,2,11}	1, 45
<i>O. deltooides</i> ssp. <i>ambigua</i>	sNV, swUT, nwAZ	300-900	A ¹	5, 68
<i>O. deltooides</i> ssp. <i>cognata</i>	San Joaquin Valley, CA	30-810	A/P ^{1,11}	9, 58
<i>O. deltooides</i> ssp. <i>deltooides</i>	sCA, wAZ, nSonora, nBCN	-30-750	A ^{1,3,11}	11, 61
<i>O. deltooides</i> ssp. <i>howellii</i>	Endemic to the Antioch dunes, CA	~30	P ^{1,11}	2, 30
<i>O. deltooides</i> ssp. <i>piperi</i>	Great Basin Desert in wNV, neCA, seOR	1,200-1,950	A ^{1,1}	12, 69
<i>O. engelmannii</i>	nwTX, wNM, and OK panhandle	1,500-1,950	A ^{6,9,10}	9, 71
<i>O. latifolia</i>	CO, SD, NE, KS, OK, UT, WY, NM	1,500-1,950	P ^{6,9}	13, 67
<i>O. neomexicana</i>	sNM, eAZ (+Sedona, AZ);	1,800-2,700	P ⁶	11, 58
<i>O. nuttallii</i>	MT, WY, CO, ND, SD, NE, KS, MN, WI, Alberta, Saskatchewan	1,050-2,400	P ⁹	13, 64
* <i>O. pallida</i> ssp. <i>brevifolia</i>	AZ, NM, TX, Chihuahua	-----	P ⁸	-----
<i>O. pallida</i> ssp. <i>gypsophylla</i>	Endemic to White Sands, NM	~1,200	P ⁸	1, 62
<i>O. pallida</i> ssp. <i>pallida</i>	WA, OR, ID, WY, UT, NV, AZ, NM	1,200-1,500	P ⁶	13, 65
<i>O. pallida</i> ssp. <i>runcinata</i>	NM, AZ, CO, TX, Chihuahua	1,050-2,100	P ^{6,10}	12, 64
<i>O. pallida</i> ssp. <i>trichocalyx</i>	WY, CO, UT	1,500-2,400	P/B/A ⁶	12, 66
<i>O. wigginsii</i>	Coastal BCN	0-30	A ^{1,3,5}	5, 46
Section <i>Kleinia</i>				
<i>O. albicaulis</i>	ND, SD, MT, WY, CO, NE, KS, OK, TX, NM, AZ, UT, Sonora, Chihuahua	1,200-2,250	A ^{7,9,10}	16, 82
<i>O. coronopifolia</i>	SD, NE, KS, WY, CO, UT, NM, AZ	1,500-2,400	P ^{7,9}	13, 77

*Not included in the study.

TABLE 2. Ingroup and outgroup taxa used in our study of the Sections *Anogra* and *Kleinia* (*Oenothera*), the vouchers for the DNA material, and the herbarium where vouchers are deposited.

Taxon	collection	herb
ingroup		
<i>Oenothera albicaulis</i>	RAR98-52	ARIZ
<i>O. arizonica</i>	MEKE03-4	ARIZ
<i>O. californica</i> ssp. <i>avita</i>	MEKE03-10	ARIZ
<i>O. californica</i> ssp. <i>californica</i>	Wagner <i>s. n.</i>	US
<i>O. californica</i> ssp. <i>eurekaensis</i>	Pavlik 41	DAV
<i>O. coronopifolia</i>	Wagner <i>s. n.</i>	US
<i>O. deltooides</i> ssp. <i>ambigua</i>	RAR99-06	ARIZ
<i>O. deltooides</i> ssp. <i>cognata</i>	RAR99-48	ARIZ
<i>O. deltooides</i> ssp. <i>deltooides</i>	RAR99-01	ARIZ
<i>O. deltooides</i> ssp. <i>howellii</i>	None*	-----
<i>O. deltooides</i> ssp. <i>piperi</i>	RAR99-47	ARIZ
<i>O. engelmannii</i>	MEKE03-6	ARIZ
<i>O. latifolia</i>	MEKE03-7	ARIZ
<i>O. neomexicana</i>	RAR98-167	ARIZ
<i>O. nuttallii</i>	RAR99-72	ARIZ
<i>O. pallida</i> ssp. <i>gypsophyla</i>	MEKE00-1	ARIZ
<i>O. pallida</i> ssp. <i>pallida</i>	RAR98-87	ARIZ
<i>O. pallida</i> ssp. <i>runcinata</i>	RAR96-05	ARIZ
<i>O. pallida</i> ssp. <i>trichocalyx</i>	RAR98-92	ARIZ
<i>O. wigginsii</i>	RAR98-09	ARIZ
outgroup		
<i>O. elata</i> ssp. <i>hookeri</i>	Cult. DUSS 91-313 (Cleland <i>s. n.</i>)	MO
<i>O. flava</i> ssp. <i>taraxacoides</i>	MEKE00-2	ARIZ
<i>O. magellanica</i>	Wagner <i>s. n.</i>	US
<i>O. organensis</i>	Cult. DUSS 76-0334 (Emerson <i>s. n.</i>)	MO
<i>O. primiveris</i>	Wagner and Mill 4565	MO
<i>O. speciosa</i>	Zimmer 48-86	LSU
<i>O. stubbei</i>	Cult. DUSS 791 (Sanders et al. 1203)	MO
<i>O. tetraptera</i>	Rzedowski <i>s. n.</i> in 1986, no voucher	
<i>O. tubifera</i>	Cult. DUSS 0305, Stubbe <i>s. n.</i> seeds (Breedlove 14321)	MO
<i>O. xylocarpa</i>	No voucher, same population as DeDecker <i>s. n.</i>	MO

*This material was collected by Bruce Pavlik (Mills College) and confirmed by Warren Wagner (Smithsonian Institution).

TABLE 3. Summary of variables that load within specified ranges on the first three principal components. All variables not listed had loading values less than 0.08. Months are indicated by standard three (or four) letter abbreviations. CV is the coefficient of variation and PET is potential evapotranspiration. Loadings are positive unless otherwise noted.

Axis	0.3>loading>0.2	0.2>loading>0.15	0.15>loading>0.1	0.1>loading>0.08
1			<ul style="list-style-type: none"> • average high and low temperatures: Jan-Dec • extreme low temperatures: Jan-Dec • extreme high temperatures: Sept-Apr, Jun • PET: annual, Sept-May • annual snowfall (-) • CV of precipitation: Apr-Jun, Oct • Aridity: Oct 	<ul style="list-style-type: none"> • extreme high temperatures: May, July, Aug • PET: Jun, Aug • CV of precipitation: annual, Sept, Nov, Jan-Mar • Aridity: annual, Apr, May, Nov
2	<ul style="list-style-type: none"> • average precipitation: Nov-Mar • aridity: Jan, Feb (-) 	<ul style="list-style-type: none"> • CV of precipitation: Jul-Sept • aridity: Dec, Mar (-); Jul, Sept (+) 	<ul style="list-style-type: none"> • Average precipitation: May-Sep (-) • CV of precipitation: Jun • Average high temperature: Jun (-) • Average low temperature: Dec-Jan • Extreme low temperatures: Nov-Mar • Aridity: Aug (+), Nov (-) 	<ul style="list-style-type: none"> • Average low temperature: Nov, Feb • CV of precipitation: Mar (-) • Extreme high temperature: Jun (-) • Extreme low temperatures: Oct • Aridity: Apr (-) • PET: May, Jun (-)
3	<ul style="list-style-type: none"> • average precipitation: annual, Mar, Apr, Sept, Oct • minimum annual precipitation 	<ul style="list-style-type: none"> • average precipitation: May, Jul, Aug, Nov • aridity: annual, Oct (-) 	<ul style="list-style-type: none"> • average precipitation: Dec-Feb, Jun • aridity: Apr-Jun, Nov (-) • extreme high temperature: Dec-Mar • CV of precipitation: annual, Oct (-) 	<ul style="list-style-type: none"> • CV of precipitation: annual, Apr-Jun (-) • extreme high temperature: Nov, Apr, May • aridity: Mar, Sept (-)

TABLE 4. Statistics describing the distributions of average contrasts per tree, given the climate and habit data as they are observed with respect to the study taxa (“true” contrasts) vs. randomized with respect to the study taxa (“random” contrasts). Also shown is the distribution of the differences (“diff”) between true and random averages, which are paired by phylogeny. The statistics include the number of trees (N), the mean and standard deviation of the distribution (std dev), and the percent of averages that were positive (%+).

		N		mean		std dev		% +	
		Bayes	Pars	Bayes	Pars	Bayes	Pars	Bayes	Pars
Summer Aridity	True	1000	1000	-2.699	-0.071	2.5272	0.018	14.4	0
	Rnd	1000	997	-0.057	0.005	6.506	0.107	49.6	52.8
	Diff	1000	997	-2.643	-0.076	7.006	0.109	34.9	23.2
Winter aridity	True	1000	1000	3.712	0.0606	0.7371	0.0043	100	100
	Rnd	997	996	-0.014	0.0006	2.197	0.0376	50.7	49.8
	Diff	997	996	3.729	0.0600	2.30	0.0378	94.5	94.4
PCA1	True	1000	1000	70.42	0.932	20.4805	0.185	99.9	100
	Rnd	997	998	4.573	0.034	72.704	1.238	52.2	51.8
	Diff	997	998	65.80	0.898	76.707	1.252	81.2	76.5
PCA2	True	1000	1000	-51.07	-0.955	15.2051	0.073	0	0
	Rnd	993	997	0.862	-0.018	37.010	0.641	49.8	48.7
	Diff	993	997	-51.92	-0.937	39.808	0.642	8.9	6.4
PCA3	True	1000	1000	-6.515	-0.049	9.4297	0.069	23.1	25.7
	Rnd	1000	999	-0.727	0.002	21.636	0.411	48.0	51.1
	Diff	1000	999	-5.788	-0.051	23.408	0.414	34.9	44.9

FIGURE 1. Frequency histograms of average contrasts of (a) summer aridity and (b) fall-spring aridity with respect to habit in Sections *Anogra* and *Kleinia* (*Oenothera*, Onagraceae). The data shown are the average contrasts per tree calculated on 1,000 trees resulting from the Bayesian analysis of sequence data. The open bars are the average contrasts with climate and habit data randomized with respect to the ingroup taxa. The filled bars are the actual average contrasts.

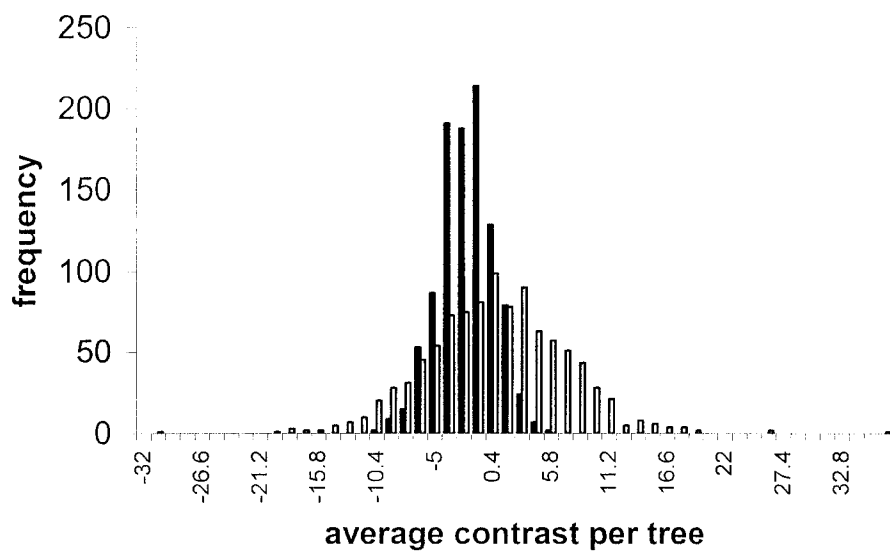
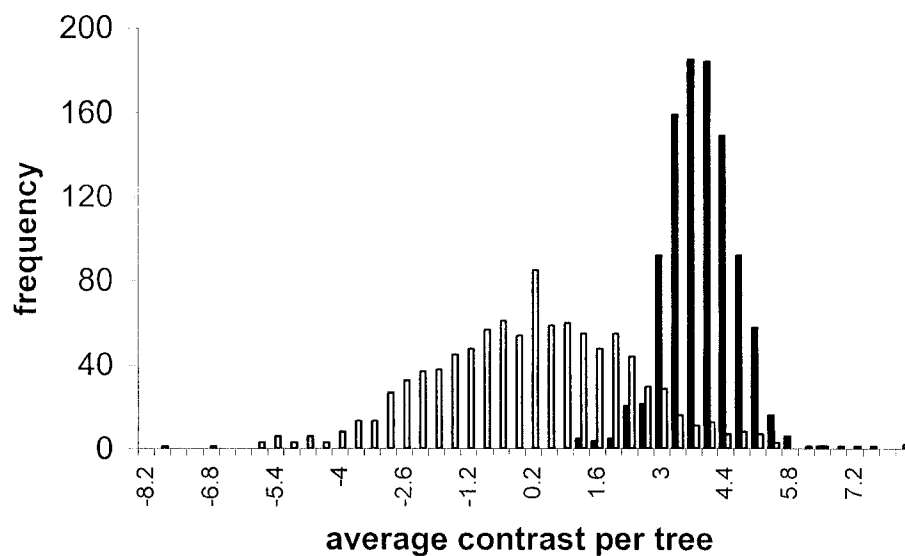
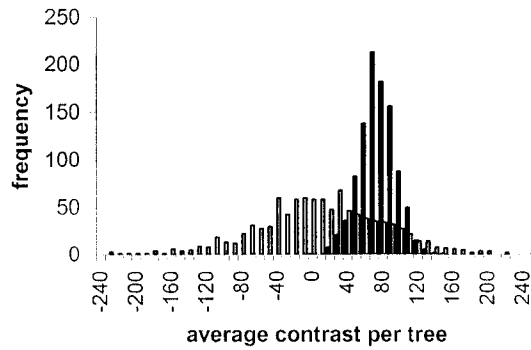
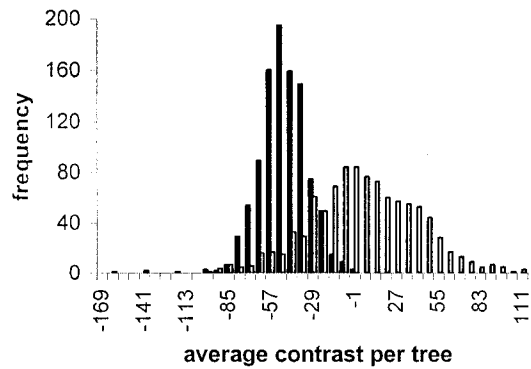
a**b**

FIGURE 2. Frequency histograms of average contrasts of scores on the (a) first, (b) second, and (c) third principal components of climate with respect to habit in Sections *Anogra* and *Kleinia* (*Oenothera*, Onagraceae). The data shown are the average contrasts per tree calculated on 1,000 trees resulting from the Bayesian analysis of sequence data. The open bars are the average contrasts with climate and habit data randomized with respect to the ingroup taxa. The filled bars are the actual average contrasts.

a



b



c

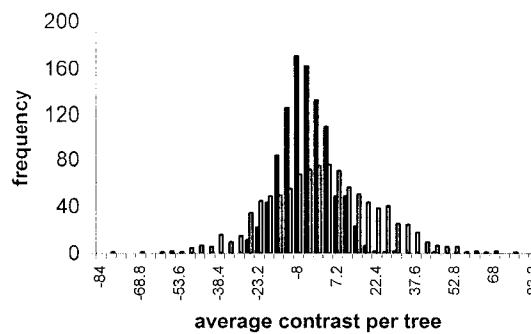
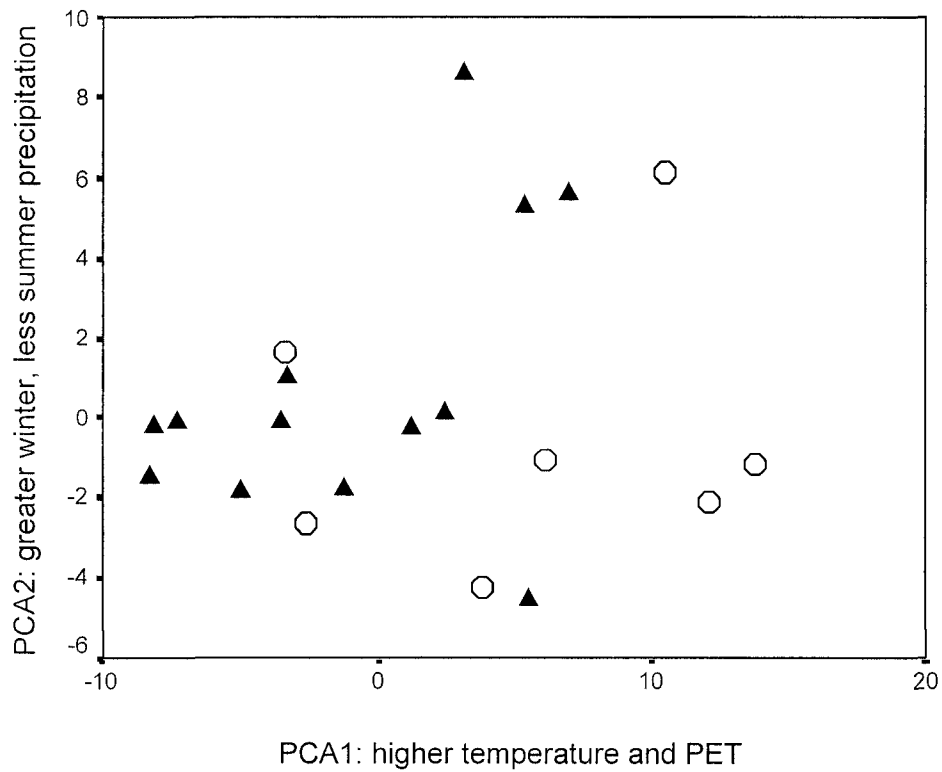


FIGURE 3. Average scores per taxon on the first vs. second principal components of climate in the Sections *Anogra* and *Kleinia* (*Oenothera*, Onagraceae). Clustering with respect to habit in the PCA1 vs. PCA2 space is emphasized by the arbitrary placement of a dashed line.



APPENDIX 1.

We used the Hargreaves equation (Hargreaves and Samani 1982) to calculate potential evapotranspiration (PET):

$$PET = 0.0075 * R_a * C_t * \delta_t^{(1/2)} * T_{avg}$$

Where R_a is an estimate of incoming solar energy, calculated for each time step, from the relative distance between the sun and earth (d_r), solar declination in radians (δ), and the sunset hour angle in radians (w_s):

$$R_a = 15.392 (d_r (w_s * \sin\phi * \sin\delta + \cos\phi * \cos\delta * \sin w_s))$$

where

$$d_r = 1 + 0.033 * \cos((2\pi J)/365)$$

$$\delta = 0.4093 * \sin(((2\pi J)/365) - 1.405)$$

$$w_s = \arccos(-\tan\phi * \tan\delta)$$

and J is Julian date and ϕ is latitude in degrees. The parameter C_t is the estimated temperature reduction coefficient:

$$C_t = 0.035 (100 - w_a)^{(1/3)} \quad \text{when } w_a > 54\%$$

$$C_t = 0.125 \quad \text{when } w_a < 54\%$$

where w_a is relative humidity. Because relative humidity data were not available, and because the areas we studied are generally arid, we made the simplifying assumption of setting C_t to 0.125. The parameter δ_t is the mean monthly maximum temperature ($^{\circ}\text{F}$) minus the mean monthly minimum temperature ($^{\circ}\text{F}$), and T_{avg} is simply the mean temperature ($^{\circ}\text{F}$) in the time step. We chose day as a time step. Hence PET (in mm) was calculated for each day. We then summed daily PET numbers to get monthly values and an annual value for each weather station.

APPENDIX B: A BET-HEDGING VIEW ON COLE'S PARADOX: DEMOGRAPHIC
AND CLIMATIC EVIDENCE FROM TWO DESERT SPECIES OF EVENING
PRIMROSE (*OENOTHERA*, ONAGRACEAE)

A bet-hedging view on Cole's Paradox: demographic and climatic evidence from two
desert species of evening primrose (*Oenothera*, Onagraceae)

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Abstract

Why some organisms reproduce just once in their lifetime (semelparity), whereas others reproduce more than once (iteroparity), has been a central question of life history theory since it was posed by Cole (1954). We examined the role of environmentally driven variation in demography in favoring the annual (semelparous) vs. perennial (iteroparous) habit in a pair of closely related, allopatrically occurring desert plants. In particular, we ask why bet hedging via seed banking vs. iteroparity should be favored. The study species were *O. arizonica*, a winter annual found in the Sonoran Desert, and *O. californica* ssp. *avita*, a winter perennial in the Mojave and southern Great Basin Deserts. We present three years of demographic data from two populations of the annual and three populations of the perennial, including observational and experimental data on the seed stage. Based on these data, we constructed models of annual and perennial population dynamics that explicitly parameterize the seed stage. Sensitivity analysis showed that bet hedging via seed banking occurs in both the annual and perennial populations. Seed banking limited population decline in a dry year, and limited population growth in a wet year. Our data suggest that bet hedging via iteroparity may also occur in the perennial populations, if survival after the first reproductive bout comes at a cost in terms of fecundity. The demographic patterns in the annual vs. perennial populations did not clearly match those predicted to favor bet hedging via seed banking vs. iteroparity, respectively. Estimation of survival after the first reproductive bout in the perennial was complicated by clonality, but was probably low, which would act against the favorability of bet hedging via iteroparity. Seed and seedling survival did not differ consistently

between the two species. Analysis of climatic data throughout the range of each species suggested that temperature plays an important role in shaping the favorability of the annual vs. perennial habit. In the colder winter temperatures of the Mojave and southern Great Basin Deserts, the rapid growth rates needed to make the annual habit a successful strategy are probably difficult to achieve.

1. Introduction

Why some organisms reproduce just once in their lifetime (semelparity), whereas others reproduce more than once (iteroparity), has been a central question of life history theory since it was posed by Cole (1954). Cole (1954) suggested that an annual plant would have equal fitness (finite rate of increase) to a (iteroparous) perennial plant if it produced just one additional offspring relative to the perennial. This result suggested that all plants should be annual, which they are not. Cole's Paradox, as it came to be known, inspired many life history theorists in the following decades. Initial responses elucidated the effect of more complex demographic structure than Cole's model (Charnov and Schaffer 1973, Bell 1976, Young 1981). In addition, nonlinear trade-offs (Schaffer 1974a, Schaffer & Gadgil 1975, Lacey et al. 1983, Real & Ellner 1992, Takada & Nakajima 1992, Takada 1995), selection on reproductive effort via pollinators (Schaffer & Rosensweig 1977, Schaffer & Schaffer 1979, Young 1990) or floral herbivores or pathogens (Klinkhamer et al. 1997), variation in demographic parameters (Murphy 1968, Schaffer 1974b, Goodman 1984, Bulmer 1985, Orzack & Tuljapurkar 1989, Benton & Grant 1999, Ranta et al 2002), density dependence of demographic parameters (Goodman 1984, Bulmer 1985, Takada & Nakajima 1992, Takada 1995, Benton & Grant 1999, Ranta et al. 2000a), and spatial structuring (Ronce and Olivieri 1997, Ranta et al 2000b, Ranta et al 2001, Tesar et al 2001) have all been explored as factors influencing evolution of the annual vs. perennial (or semelparous vs. iteroparous) habit.

In this study, we focus on the role of environmentally driven variation in demography for two reasons. First, annuals reach their highest component of florals in

deserts (Raunkiaer 1934, Daubenmire 1978, Gurevitch et al. 2002), where water is variably available (Noy-Meir 1973, Ehleringer and Mooney 1983, Schmida et al. 1986). This variation in water availability drives variation in desert plant demography (Beatley 1974, Goldberg and Turner 1986, Kadmon and Schmida 1990, Turner 1990, Nobel 1992, Watson et al. 1997, Pierson and Turner 1998, Clauss 1999, Venable and Pake 1999), and is thought to shape plant life histories in deserts (Schaffer and Gadgil 1975, Ehleringer 1985, Comstock and Ehleringer 1992). Second, a critical ingredient has been missing from most analyses of annual vs. perennial life histories in temporally varying environments: seed dormancy (e.g. the studies of Schaffer 1974b, Goodman 1984, Bulmer 1985, Orzack & Tuljapurkar 1989, Fox 1993, and Benton & Grant 1999).

In fact, seed banking in annual plants is well known as a bet-hedging strategy for persistence in variable environments (Cohen 1966, Ellner 1985, Venable & Pake 1999). More recently, a number of theorists have recognized that seed dormancy and iteroparity, among other phenomena that temporally mix cohorts, are alternative means of reducing variance in fitness (Tuljapurkar 1990, Rees 1994, Tuljapurkar 1994, Orzack 1997, Ellner et al. 1998, Tuljapurkar & Wiener 2000). These traits operate much as seed dormancy, dispersal, and size, and specialization of adult traits to year-types do as alternative means of reducing variance in fitness (Venable & Lawlor 1980, Brown & Venable 1986, Venable & Brown 1988, Wiener & Tuljapurkar 1994, Venable and Pake 1999). With the addition of a dormant seed stage, a new view of the question of annual vs. perennial life histories emerges: Under what conditions is bet hedging via seed dormancy vs. iteroparity favored? Work by Rees (1994) and Tuljapurkar & Wiener (2000) suggests

that the favored form of bet hedging is that which is less risky. Increasing the mean or variance of seed or seedling mortality makes the seed-banking annual habit riskier, whereas increasing the mean or variance of adult mortality makes the iteroparous perennial habit riskier. Thus bet hedging via a seed-banking annual life history might evolve if adult survival becomes too improbable or too variable.

We evaluate this bet-hedging literature with data from two closely related, allopatrically occurring desert plants, one of which is perennial and the other annual. We present three years of demographic data from two populations of the annual and three populations of the perennial, including observational and experimental data on the seed stage. Based on these data, we construct models of annual and perennial population dynamics that explicitly parameterize the seed stage. These models allow us to quantify the sensitivity of population growth to changes in the life history parameters of each strategy. We use the sensitivities to evaluate whether bet hedging via seed banking vs. extended reproductive lifespan (iteroparity) occurs in the annual and perennial populations. We use these data and analyses, along with climatic information from throughout the range of each species, to address the reasons for bet hedging via iteroparity vs. seed banking.

2. Methods

2.1 Study species

Oenothera californica ssp. *avita* is a perennial occurring in the Mohave Desert and the southern Great Basin Desert in Nevada, California, Arizona, and Utah, U. S. A. (Klein 1970). *Oenothera arizonica* is an annual occurring in the Lower Colorado River Valley and Arizona Upland subdivisions of the Sonoran desert in southern Arizona, U. S. A., as well as in a few disjunct dune populations in northwestern Sonora, Mexico (Klein 1970, Wagner 1998). In the past, both have been considered subspecies of either *O. californica* or *O. avita*, based on cytogenetic data and the pollen fertility of experimental hybrids (Klein 1962, 1964, 1965, 1970; Wagner 1993, 1998), indicating that they are very closely related. More recently, *O. arizonica* was given species status, partly because it was the only annual subspecies of *O. californica*, among three other perennial subspecies (Wagner 1998). This suggests that the direction of change in habit was from perennial to annual. Both species occur in scattered populations in loose, sandy or gravelly soils (Klein 1970), typically where such soils have accumulated because of water or wind or alternatively in roadsides.

Both species are winter-active plants. Mass germination typically occurs in response to rainfall of ≥ 25 mm in the autumn; alternatively, germination can occur in response to heavy rain in the spring, especially if the autumn rains failed (M. Evans, personal observation; as described by Beatley 1974). Seedlings occur in a rosette form until, some time in the spring, as temperatures rise, they switch from vegetative to

reproductive growth. A central stem and side branches develop, with reproductive structures. Flowering occurs in the spring in both species, with the timing and duration variable, depending on the timing of germination, on temperatures, and on soil moisture availability. In general though, *O. arizonica* flowers earlier (February through May) and *O. californica* ssp. *avita* later (March through June). Both species have “one night” flowers: the flowers open at dusk and wilt the following morning. These flowers are white and are primarily visited by hawkmoths (Sphingidae, e. g. *Hyles lineata*) in the crepuscular hours, but can also be visited by bees in the morning. Plants of *O. arizonica* may senesce and disperse seeds between late March and early June, whereas plants of *O. californica* ssp. *avita* typically senesce and disperse seeds in May or June. Plants of *O. californica* ssp. *avita* may survive through the summer, typically with little or no vegetation, and may resprout, even flower and fruit again, if summer rain is sufficient. Surviving plants can sprout from the base or produce rosettes from underground horizontal rhizomes. Three herbivores can cause significant damage to these species: larvae of *Hyles lineata* and larvae and adults of two species of Chrysomelid beetles (*Phaedon purpurata* and *Altica torquata*) consume leaves, and rodents sometimes sever branches or entire plants at the base. In addition, it is likely that rodents, ants, and seed bugs (e.g. *Nysius raphanus*, Lygaeidae) consume the seeds of both species (M. Evans, personal observation).

2.2 Study sites

We censused survival and fertility in three naturally occurring populations of *O. californica* ssp. *avita* (hereafter, the perennial) and in two populations of *O. arizonica* (hereafter, the annual). Our study populations of the perennial were in the southeastern part of its range, on the eastern slopes of three mountain ranges surrounding Kingman, Arizona. They are designated by the type of land ownership: in order of increasing elevation they are the Private site (35° 17' N 114° 03' W, elevation 1,150 m), the State site (35° 15' N 113° 40' W, elevation 1,210 m), and the Bureau of Land Management site (BLM; 35° 01' N 113° 49' W, elevation 1,300 m). Elevation and local topography cause differences in temperature and precipitation among these sites, such that the plant association at each is semidesert grassland, Mohave desertscrub, and interior chaparral, respectively (Brown 1994). The State and BLM populations are found along arroyos, whereas the Private population is located in a disturbed area adjacent to a road, but also near a small drainage. Our study populations of the annual were central in its range, west of Phoenix, Arizona. They are designated the Buckeye site (33° 20' N 112° 38' W) and the Hassayampa site (33° 29' N 112° 45' W). These two sites are more similar to one another, and closer geographically, than the three sites of the perennial. The Buckeye and Hassayampa sites are at 270 m and 300 m, on sandy banks of the Gila and Hassayampa rivers, respectively. Both occur in the Lower Colorado River Valley subdivision of the Sonoran Desert (Brown 1994, Dimmitt 2000).

2.3 Weather and Climate

We recorded precipitation at each study site with a Tru-Chek rain gauge. Each gauge was mounted on a post about 1.5 m above the ground. At each visit to a site, the rain in the gauge was recorded, the gauge was emptied, and an approximately 3 mm layer of vegetable oil was replaced in the gauge. Hence the vegetable oil prevented rain from evaporating between visits. We kept a layer of wire mesh in the top of the gauge, which prevented insects from getting in the water or oil, but did not interfere with the interception of rain by the gauge. We also present data collected at weather stations nearest the study sites. The station nearest the annual study populations was the National Weather Service's Buckeye station ($33^{\circ} 22' N 112^{\circ} 35' W$, elevation 300 m). Two weather stations in the Kingman area bracket the range of elevation of the perennial study populations: one at the Kingman airport ($35^{\circ} 16' N 113^{\circ} 56' W$, elevation 1050 m) is about 12 km from the Private site and about 100 m lower in elevation, and a second station maintained by the Bureau of Land Management is about 7.2 km from our BLM site, though at about 530 m higher elevation ($35^{\circ} 2' N 113^{\circ} 53' W$, elevation 1830 m). Data taken at the Kingman airport are probably more representative of the weather at the Private and State sites; the BLM weather station represents an upper limit on precipitation experienced by the BLM site.

To get a broader sense of climatic differences between localities of the two study species, we conducted a multivariate analysis of long-term weather statistics from stations throughout each species' range. To choose these weather stations, we mapped herbarium localities of each species, and then located weather stations nearest to these

plant localities. We started with range maps created by Warren Wagner at the Smithsonian Institution, which were based on specimens in the U. S. National Herbarium. To these we added localities from loan material from another six herbaria: Rancho Santa Ana Botanic Garden, University of Nevada at Las Vegas, University of California at San Diego, University of New Mexico, University of California at Berkeley, and the University of Arizona. Weather stations were considered acceptable options if they were in close proximity (within ~24 km) and close in elevation (within ~150 m) to a collection locality, and if the station's period of record included at least 50 years of data. The final selection of stations, among all the stations considered acceptable, was spatially stratified with respect to each species' range. Twelve stations were chosen for the perennial: Austin, Caliente, Desert Game Range, Searchlight, and Smokey Valley in Nevada; Independence, Deep Springs College, and Bishop in California; Kingman and Wickieup in Arizona; and Milford and New Harmony in Utah. Nine stations, all in Arizona, were chosen for the annual: Granite Reef Dam, Florence, Sacaton, Buckeye, Laveen, Tucson, Casa Grande, Ajo, and Bouse.

We collected summary statistics for each station from the Western Regional Climate Center's Historical Summary web pages (<http://www.wrcc.dri.edu/summary/>). These summary statistics included mean annual snowfall, mean annual precipitation, the coefficient of variation, skew, and minimum of annual precipitation, mean and extreme high and low temperatures per month, and the mean and coefficient of variation of precipitation per month. In addition, we calculated potential evapotranspiration (PET) on an annual basis and for each month for each station, using the Hargreaves equation

(Hargreaves and Samani 1982; Appendix 1). Finally, we calculated an aridity index, on an annual basis and for each month, for each weather station. This aridity index is simply potential evapotranspiration divided by mean precipitation for a given time period. Because it integrates the drying power of the environment and the actual precipitation at a site, the aridity index should correlate with the level of water stress that plants experience. Areas with an aridity index above three are considered semiarid (Dimmitt 2000): there is the potential to lose three times as much water, through evaporation and transpiration, as is received in precipitation. We conducted principal components analysis on the correlation matrix (i. e. the data were centered and standardized, since temperature and precipitation variables have different scales) using PROC PRINCOMP in SAS (SAS Institute 1989). We also used t-tests to detect differences between the weather stations chosen to represent annual vs. perennial localities with respect to certain climate variables. The aridity data were \log_{10} -transformed to approximate normality before using t-tests.

2.4 Plant studies

We recorded survival and estimated seed output per plant in four seasons (1999-2000, 2000-2001, 2001-2002, 2002-2003). Plants were censused after the first significant autumn rain (>25 mm) and approximately every eight weeks thereafter, until flowering had ended the following spring. Annual populations only had two types of plants: seedlings in the autumn, winter, and spring, and reproductive plants (adults) at the end of the season, none of which persisted through summer. In the perennial populations, we

distinguished three types of plants: seedlings, adults, and clones. Seedlings were identified by the presence of distinctively shaped cotyledons, which typically remained detectable over the census interval of eight weeks. Newly observed plants that lacked cotyledons were partially excavated to inspect below-ground structures. Seedlings have a true root, whereas the vertical structure supporting a clonal rosette is a stem. The roots of seedlings are typically narrow, brown or yellow-brown, and have fine root hairs extending horizontally, whereas the stems below clonal rosettes are larger in diameter, pink-purple to white, and have scales instead of root hairs. Clones typically emerged in the spring, after temperatures warmed. In the first year of our study (1999-2000), we had not yet identified these characters distinguishing seedlings from clones. Our attempts to handle this problem led to a sampling design that we consider sufficiently problematic that we do not present those data. The distinction between clones and adults was a practical one. Adults included first-year adults, i. e. plants known to be seedlings that survived to produce at least one fruit, and adults greater than one year old. The latter were plants that sprouted from the base of an existing, previously recorded adult. We were able to identify adults in the first year of our study based on the presence of persistent, woody reproductive branches from the previous season. Clones also sprouted from a previous year's plant, but from rhizomes, such that we were unable to identify the adult to which the rosettes belong. We were also unable to identify genetic individuals (genets) of clones, not without extensive and harmful excavation, so we treated clones on a ramet basis. However, we did not treat every single clonal rosette as a separate individual. Our designation of clonal individuals was subjective: we grouped together

clonal rosettes that were tightly clustered. Clonal rosettes separated by a gap somewhere between 5 and 10 cm were considered separate individuals, and survival and fecundity data were recorded separately. It is likely that this criterion overestimates the number of clonal genets, since we know from excavations that clonal rosettes almost a meter apart can be connected (M. Evans, personal observation).

We recorded data from as many plants as possible at each study site, under the constraint that each site was censused in one day. Since plant densities varied from year to year, the area sampled also varied, from less in the wet years to more in the dry years. Individuals were relocated by their coordinates within marked quadrats or belt transects. In the annual populations in the first year of the study, quadrats were located arbitrarily rather than randomly, and were biased toward high-density patches as a matter of convenience. In the remaining three years, we used a 60-m baseline transect on one side of each population; belt transects 0.25 m or 0.50 m wide perpendicular to this baseline were chosen in a stratified random manner each year. At the two sites of the perennial on public land, study areas were fenced or caged to exclude cattle. At the State site, there were two fenced areas, $\sim 140 \text{ m}^2$ and $\sim 30 \text{ m}^2$, respectively, and ten cages ranging from 1.95 m^2 to 3.42 m^2 . The cages were built of concrete reinforcement mesh and secured to the ground with rebar stakes. At the BLM site, there were two fenced areas, $\sim 320 \text{ m}^2$ and $\sim 140 \text{ m}^2$, respectively. At the Private site, we established two study areas, one 112 m^2 and another 91 m^2 . In all of these study areas but the largest at the BLM site, we censused either the entire area or a new stratified random sample of 1-m^2 quadrats each year, or, in the cages, a random fraction of the cage with respect to its x axis, as plant

densities and time constraints allowed. In the large study area at the BLM site, we marked the corners of a stratified random sample of 1-m² quadrats with rebar, and relocated these quadrats, or a stratified random sample of them, for censusing each year.

Seed output was estimated after the end of the flowering season, when the great majority of plants were senescent. We counted the number of fruits on every plant in census areas. Fruits were collected from a subset of these plants, and we counted the number of seeds in each fruit. Seed output per plant was estimated by multiplying the number of fruits per plant by the mean number of seeds per fruit for a given population. We did not quantify seed output in response to summer rains in the perennial populations, which involved very few individuals.

2.5 Seed studies

Seed demography— In order to model the annual and perennial populations, and address ideas about bet hedging via seeds vs. post-reproductive survival, we needed demographic information on seeds. Estimates of the density of ungerminated, viable seeds in the soil allow us to calculate both germination fraction and seed-bank survival. We collected soil samples after germination had ended but before new seeds were dispersed. We used a 7 cm x 4.5 cm (diameter x depth) soil tin, hence the surface area per sample was ~38.48 cm². In the spring of 2000 we collected samples just from the two sites of the annual, with the samples (n=100) located arbitrarily and immediately adjacent to the plots where the plant studies occurred. We collected 100 soil samples in a spatially stratified random manner at each of the five study sites, three perennial and two

annual, in the spring of 2001 and 2002, and about 66 samples per site in the spring of 2003. Seeds were sorted from a spatially stratified random subset of the soil samples collected in 2000, 2001, and 2002, totaling about 66 samples per site. We used the flotation method described in Pake and Venable (1996) to sort seeds from soil samples. The viability of seeds was assessed by visual criteria, and in the case of seeds of questionable viability, by dissecting seeds. We calculated germination fraction by dividing seedling density (sampled above in the plant studies) by the sum of seedling density and viable, ungerminated seed density (in soil samples).

We calculated the survival of seeds in the soil based on the above estimates of soil seed density, seedling density, and seed rain density. The density of ungerminated, viable seeds from one year to the next (D_{t-1} and D_t , respectively) changes according to the equation

$$D_t = ((D_{t-1} \cdot r_{t-1} + F_{t-1}) \cdot s_{t-1} - E_t) \cdot q_t$$

where F_{t-1} and E_t are estimates of seed rain density and seedling density, respectively, the gains and losses to soil seed density. Seed survival in three intervals enter in this equation: from the time of soil seed sampling to the time of seed rain (r_{t-1}), from the time of seed rain to the time of germination (s_{t-1}), and from the time of germination to soil seed sampling (q_t). The parameters D_{t-1} , D_t , F_{t-1} , and E_t are known. To solve the equation for the seasonal seed-bank survival rates, r_{t-1} , s_{t-1} , and q_t , we expressed two of the unknowns in terms of the third. For lack of more specific information, we assumed a constant rate

of seed survival, and calculated the relationship among these survivals by using the time in each interval. We then found (by numerical simulation) the value of the relevant seed survival parameter that solved the above equation. In the two annual populations, soil seed samples were collected at the same time seed rain was estimated (i. e. mature but indehiscent fruits were counted and sampled). Therefore, we assumed that no time passed between soil seed sampling and seed rain, permitting no seed mortality in this interval ($r=1$). In some populations and years, most of the germination occurred in a narrow window of time, such that we could easily define germination date, and hence the number of days in s vs. q . In other situations, germination was spread out over a longer period of time. We defined the time of germination as the time by which approximately half of all observed seedlings had been recorded. Total annual seed survival from the time of a post-reproductive census in one year to the next was calculated as $s_{t-1} * q_t * r_t$.

Germination trials—To better understand germination behavior in the wild, we evaluated the germination fraction of annual vs. perennial seeds under various laboratory conditions. In one study, seeds were put in petri dishes on filter paper, covered with a thin layer of sand, and kept moist in one of two temperature regimes. The warm temperature regime recreated the mean high and low temperatures in September in Kingman, Arizona (30°/13°C day/night), while the cool temperature regime mimicked November in Buckeye, Arizona (21°/4°C day/night). This reflected our ideas about the ideal timing of germination in perennial vs. annual populations, respectively. All the seeds included in the experiment had passed a float test for viability (viable seeds sink;

see Intrinsic seed survival, Methods and Results). This study was done in two trials, using seeds collected in late May or early June, 2001 for the seed survival study (2001-2002) described below. The first trial began in February of 2002, after these seeds had been stored in the lab at room temperature for about nine months. The second trial ran from November, 2002 to February, 2003, using seeds that had been buried in the wild from June of 2001 to June of 2002, then stored in the lab for about five months. Each petri dish contained 20 seeds (Trial 1) or 15 seeds (Trial 2) from either the State, Private, Buckeye, or Hassayampa population. There were 8 replicates (petri dishes) of each population per temperature treatment. After each census of germination, petri dishes were arbitrarily rearranged within a growth chamber. In the first trial, temperature treatments were conducted at the same time but in different growth chambers, and germination was recorded for 24 days. In the second trial we had only one functional growth chamber available to us, so the temperature treatments had to be conducted one after another. To control for the effect of passing time between temperature treatments, we ran two replicates of each temperature treatment, starting with the warm and ending with the cool treatment each time. In the second trial we recorded germination for 12 days. The germination data were analyzed with a general linear mixed model (PROC GLIMMIX in SAS; Littell et al. 1996). We assumed that the response variable, the number of germinated seeds as a proportion of the number of viable seeds at the beginning of the trial, was binomially distributed. We used the logit link to linearize the data, and corrected test statistics for overdispersion. Temperature, species, and their interaction were treated as fixed effects, and population was treated as a random effect

nested within species. In the second trial, we also treated temperature replicate, and the interactions between temperature, temperature replicate, and species as fixed effects.

In a second test of germination, we simply left seeds submerged in water for four days. We used seeds that were produced in the spring of 2000 and had been used in the seed survival study described below. We tested germination of seeds that remained viable after 12 vs. 24 months in the soil in their population of origin. We tested 45 and 31 groups of perennial seeds, and 20 and 21 groups of annual seeds, that had been in the soil 12 vs. 24 months, respectively, reflecting the number of packages recovered from the seed survival study that began in 2000 (see below, and Results). On average, there were 10 annual seeds and 30 perennial seeds tested for germination per group. The germination data were tested with a general linear mixed model (PROC GLIMMIX in SAS; Littell et al. 1996) as above. The response variable was the number of germinated seeds as a proportion of the number of viable seeds. We treated the species, the number of months in soil, and their interaction as fixed effects, and treated population as a random effect nested within species.

Intrinsic seed survival—To evaluate the relative roles of intrinsic vs. extrinsic factors in soil seed mortality, we conducted two trials designed to test the rate at which seeds protected from predation survive in the soil. In the first trial, seeds produced in the spring of 2000 were sewn into packages made of organza cloth and buried in their population of origin in June, 2000. Seeds were sorted for viability according to visual criteria before they were sewn in groups of 20 seeds (the annual) or in groups of 40 seeds (the

perennial). These packages were buried approximately 1 to 4 cm below the soil surface in marked arrays that were placed in a stratified random manner at each site. There were 6 arrays of 6 packages at the Buckeye and Hassayampa sites of the annual, and 9 arrays of 6 packages at the State and Private sites of the perennial. Approximately half of the packages per array were exhumed in late June, 2001 and the other half in late June, 2002. In a second trial, we sought to evaluate whether seed survival might differ at the perennial vs. annual localities, so we performed a reciprocal transplant experiment. Seeds produced in 2001 were sewn into packages, and buried in June, 2001, and exhumed in late June, 2002. The details of this trial were similar to the first trial, but each array included three packages from each of the four sites (two sites of each species), and there were nine arrays at each site. The packages in the second trial all contained 30 seeds.

The contents of packages exhumed in 2001 were tested for viability according to four different criteria. First was a visual determination of viability, identical to the criteria for inclusion in the package at the beginning of the study. Second, seeds were put in a petri dish with water and the number floating (nonviable) vs. sinking (viable) was recorded after approximately 24-36 hours. Third, ten seeds that sank were arbitrarily chosen for dissection, and the presence (or absence) of a viable embryo was recorded. Fourth, these embryos were removed from the seed coat and placed in a petri dish on moist filter paper. These embryos either turned green and started developing or did not. The seed lots used for the packages buried in 2001 were tested for viability using these same four criteria, but the contents of all packages exhumed in 2002 were tested using

just the first two criteria (since the “float” test proved to be very accurate; see Results). We tested the data from the first trial using a generalized linear mixed model as above with the germination data. The response variable, the number of viable seeds over the number of non-germinated recovered seeds per package, was assumed to be binomially distributed. We used the logit link to linearize the data, and test statistics were corrected for overdispersion. We treated the species (either the species identity of seeds, or the species found where the seeds were placed) and the number of months seeds were in soil as fixed effects, and population as a random effect nested within species. These tests were performed using PROC GLIMMIX in SAS (Littell et al. 1996). The data from the second trial were corrected for the proportion of seeds that were viable at the start of the experiment, such that the data were no longer integers. We used proportional seed viability per package as the response variable (these data were approximately normally distributed). We tested these data with a mixed model (PROC MIXED in SAS; Littell et al. 1996), treating the species identity of seeds (annual vs. perennial) and the species (annual vs. perennial) occupying the site where seeds were placed as fixed effects. We treated the source population of seeds as a random effect nested within seed species identity, and the population where seeds were placed as a random effect nested within the identity of the species (annual vs. perennial) found at those sites.

2.6 Fitness and Sensitivities

Annual Populations—Following Charnov and Schaffer (1973; and many others), we use the finite rate of increase to quantify fitness. Assuming no age structure in the seed bank,

we can project just one class of individuals in the annual populations: the number of seeds immediately after the time of reproduction (S). Their numbers are governed by the scalar equation

$$S_t = S_{t-1} \{ [s^*(1-g)*q*r] + (s*g*c*B_A) \}$$

where s , q , and r are defined as above, g is the fraction of seeds that germinate, c is the fraction of seedlings that survive to produce at least one fruit, and B_A is the mean number of seeds produced by plants that make at least one fruit. This is very similar to the model of an annual plant with a seed bank presented by Schmidt and Lawlor (1983; Figure 1a).

The finite rate of increase, λ , is

$$\lambda = [s^*(1-g)*q*r] + (s*g*c*B_A)$$

The first term on the right hand side of this expression quantifies the fitness achieved by dormant seeds in the soil seed bank. The second term quantifies the fitness achieved by seeds that germinate. The sensitivity of the finite rate of increase to changes in each parameter in the life history (c , B_A , g , s , and q) is found by taking the derivative of this function with respect to each parameter in turn. The resulting formulas are presented in Table 1. These sensitivities are related to the selection gradients measured by population geneticists (van Tienderen 2000).

Perennial Populations—To evaluate fitness and sensitivities in the perennial populations, we constructed a matrix model with three life stages: seeds, adults, and clones. As in the annual model, the perennial model is constructed to reflect a post-reproductive census, so seedlings are not found as a class in the model. The choice of two classes of reproductive plants reflects the data that we collected. The adult stage includes both first-year adults (seedlings that survived to produce at least one fruit), and plants after their first year that sprouted from a previously identified adult. Clones also sprouted from a previous year's plant, but from rhizomes, such that we were unable to identify the adult to which the rosettes belong. Clones are treated on a ramet basis in this model. The life cycle diagram of this model is shown in Figure 1b. The parameters include those in the model of the annual with a seed bank, as above (Figure 1a); in addition, there is a term describing the rate of adult survival (p), a term describing mean seed production per clone (B_c), and two terms describing the rate of clone production (R_1 and R_2). The latter are two parameters for which we have only indirect data. We know the number of clones in each year of the study. Based on these data, we can attribute some fraction of the number of clones in a given year to the survival of clones from the previous year (R_2) and the remaining fraction to the production of new clones from adults (R_1). What fraction of clones we choose to attribute to the clone vs. adult stage of the previous year is an arbitrary decision, but it is also one whose effects we can easily examine, by manipulating this number.

The dynamics of the perennial populations are governed by the following equation:

$$\mathbf{n}(t+1) = \mathbf{A} * \mathbf{n}(t)$$

In this equation, \mathbf{n} refers to a vector of the abundances of the three classes of individuals (seeds, adults, and clones), and \mathbf{A} refers to the transition matrix

$$\mathbf{A} = \begin{vmatrix} s*(1-g)*q*r + s*g*c*B_p & p*B_p + R_1*B_c & R_2*B_c \\ s*g*c & p & 0 \\ 0 & R_1 & R_2 \end{vmatrix}$$

which follows from the life cycle diagram in Figure 1b. The entire model for the annual populations is contained in the upper left position of this matrix: the seed to seed transition. The matrix element in the second column of the first row, which describes the transition from adult to seed, also contains two terms. The first ($p*B_p$), is the probability of surviving as an adult multiplied by the mean fecundity of adults. The second term (R_1*B_c) is the rate of clonal rosette production by adults multiplied by the mean fecundity of clonal rosettes. The remaining matrix elements are straightforward. We constructed such matrices for each pair of years of data from each of the three perennial study populations, and used simulations of population growth to find the asymptotic population growth rate for each matrix. We also calculated the sensitivity of the

asymptotic population growth rate of each matrix to changes in each matrix element. The general formulation for sensitivities is

$$s_{ij} = d\lambda/da_{ij} = v_i * w_j / \langle \mathbf{w}, \mathbf{v} \rangle$$

where a_{ij} indicates the matrix element in the i th row and j th column, v_i is the reproductive value of the i th class of individuals, w_j is the fraction of the population in the j th class after the stage distribution has stabilized, and $\langle \mathbf{w}, \mathbf{v} \rangle$ is the scalar product of the stable stage distribution (\mathbf{w}) and the vector of reproductive values (\mathbf{v} ; Caswell 1978). We also examined the sensitivity of the asymptotic growth rate to changes in the lower-level parameters that are found in the matrix elements. These include the parameters whose sensitivities we calculated above in the annual model (c , B_p , g , s , q , and r) as well as the parameters unique to the perennial model (p , B_c , R_1 , and R_2). The general formula for calculating sensitivities of lower-level parameters is

$$d\lambda/dx = \sum_{ij} s_{ij} (da_{ij}/dx)$$

where x is the lower-level parameter (van Tienderen 2000, Caswell 2001, Morris and Doak 2002). The formulas for the sensitivities of all ten parameters in the perennial model are shown in Table 1.

3. Results

3.1 Climate

The annual is found in places that are warmer throughout the year than the perennial (Figure 4; $p < 0.001$). The perennial vs. annual weather stations differed significantly with respect to scores on the first principal component ($t = -5.854$, $df = 19$, $p = 0.000$; Figure 3), which primarily represents a gradient from cooler to warmer sites (Table 2). Accordingly, places occupied by the perennial are more likely to experience freezing temperatures in the winter (Table 3).

Places where the annual is found are more arid in most months (Figure 5), largely because these sites are warmer, but seasonal differences in precipitation between the Mojave and Great Basin vs. Sonoran Deserts make log-transformed annual aridity no different between localities of these two species ($t = -0.918$, $df = 19$, $p = 0.370$). Potential evapotranspiration is significantly higher, in every month and on an annual basis, where the annual is found ($0.027 > p > 0.000$). Our estimates of potential evapotranspiration are based on temperature and latitude data; the difference between the species in potential evapotranspiration reflects the results described above for temperature, and is accentuated by the fact that the annual is found at lower latitudes. Mean precipitation at perennial vs. annual sites does not differ from September through March ($0.871 > p > 0.106$), the period during which germination and seedling growth occur in both species. Nor does mean annual precipitation differ between the perennial vs. annual sites ($t = -0.110$, $df = 19$,

$p=0.914$). But annual sites receive significantly less rain than perennial sites in April through June ($0.040 > p > 0.016$), and significantly more rain than perennial sites in July and August ($p=0.004$ and $p=0.006$, respectively). The arid “foresummer” in May and June and the monsoon season in July and August are well-known climatic features of the Sonoran Desert that distinguish it from the Mohave and Great Basin Deserts.

Precipitation is significantly less reliable at annual sites than at perennial sites at the time of the arid foresummer (coefficient of variation of precipitation in April and May, $p=0.017$ and $p=0.000$, respectively) and significantly more reliable at the time of the monsoon (coefficient of variation of precipitation in July and August, $p=0.027$ and $p=0.021$, respectively). The signature of the arid foresummer is also found on the first principal component: the mean and coefficient of variation of precipitation in April, May, and June loaded between -0.09 and -0.11 on the first axis (Table 2). The result of these patterns (of potential evapotranspiration and precipitation) is that log-transformed aridity is significantly higher where the annual is found in most months (January-June and November; $0.032 > p > 0.000$), but is significantly lower in July and August ($p=0.030$ and $p=0.035$, respectively; Figure 5).

Perennial vs. annual sites did not differ in their scores on the second or third principal components ($t=-1.541$, $df=19$, $p=0.140$ and $t=0.769$, $df=19$, $p=0.452$, respectively). The interpretation of these axes are detailed in Table 2. The first three axes explained, cumulatively, 64%, 82% and 87% of the variation in the data. The principal components analysis also revealed much tighter clustering (greater similarity) of annual sites with respect to climate than perennial sites (Figure 3).

3.2 Plant Demography and Weather

The most striking pattern in the statistics of plant demography is the variation among years (Table 4). The four years of our study encompassed two dry years (1999-2000 and 2001-2002) and two wet years (2000-2001 and 2002-2003) at both the annual and perennial study sites (Figure 2a-c). Weighted mean seedling survival and seed output were much lower in the two dry years than in the two wet years in both annual and perennial populations (Table 4). The mean fraction of seedlings that survived to produce at least one fruit varied from 0.00 to 0.56 among four years of study in the annual populations, and from 0.00 to 0.45 among three years of study in the perennial populations. Mean seed output of reproductive plants ranged from 0 to 451 in the annual populations and from 68 to 486 in the perennial populations in these same periods.

Compared to the differences among years, seedling survival and per capita seed output were comparable between the two species. The dry year in which we can compare their demography, 2001-2002, was disastrous for both perennials and annuals. At the annual sites, germination rain was meager and came at a cold time of year (Figure 2c), so that few seeds germinated and seedling density was very low (Table 5). None of the seeds that did germinate produced a single seed (Table 4), which is not surprising given that no rain was recorded between January and June of 2002 (Figure 2c). The perennial populations experienced good germination rains in the autumn of 2001 (Figure 2a,b), but between January and June of 2002, only 4.75 mm was recorded at the Kingman airport (Figure 2a) and precipitation totaled only 5.00 mm in the upper Moss Wash basin (Figure

2b), explaining why only 4 plants (all adults) out of the 1045 perennials monitored that year produced even a single fruit.

In contrast, the two wet years, 2000-2001 and 2002-2003, were generally favorable for both annual and perennial populations. Precipitation near the annual and perennial study populations was relatively gradual and generally followed the average pattern of precipitation (Figure 2a-c), totaling 14.38 cm and 13.95 cm at the Kingman airport between October and May in the 2000-2001 and 2002-2003 seasons, and 15.00 cm and 12.98 cm at the Buckeye weather station in the same two periods. In the 2000-2001 season, mean seedling survival in the annual vs. perennial populations was 0.44 vs. 0.19, and mean seed output was 304 vs. 486 seeds, respectively (Table 4). In the 2002-2003 season, mean seedling survival was 0.56 vs. 0.45, and mean seed output was 451 vs. 81 in annual vs. perennial populations, respectively (Table 4). Lower mean perennial seedling survival in the 2000-2001 season was partly due to the low rate of seedling survival (0.07) and large sample size (538 seedlings) at the BLM site (Table 4). Many seeds germinated in response to ample rains in the autumn of 2000 at the BLM site (14.38 cm in August and 8.18 cm in October, 2000 at the BLM weather station; Figure 2b); we suspect that their low rate of survival resulted from hard freezes in the following months. The other two sites of the perennial also had lower survival than the annual populations in the same year (0.28 each, Table 4). This was partly due to damage caused by rodents: many plants were destroyed by rodent activity (knawed off at ground level, buried by rodent excavations). If these plants are excluded from the calculations, rates of

seedling survival at these two populations are much more comparable to those at the two annual populations (0.37 and 0.40 vs. 0.48 and 0.40, respectively).

The roles played by three types of plants, seedlings (or first-year adults), adults past their first reproductive bout, and clones, varied among years and populations, but in general, seedlings were the most numerous and first-year adults produced the most seeds. Considering the composition of populations some time immediately before reproduction, seedlings comprised more than 90% of individuals in five out of nine combinations of population and year (Figure 6). Adults that had reproduced at least once already were the least numerous type of individual: they comprised less than 5% of individuals in seven combinations of population and year (Figure 6). Clones varied the most in their numbers, both among populations and years. The Private site never had many clones, which we suspect had to do with its relatively compacted soil. Clones were most prevalent in the dry year, 2001-2002. First-year adults produced most of the fruits: more than 80% in four out of seven combinations of population and year (Figure 7). Clones produced disproportionately few fruits, compared to their numbers, but the criterion that we used to identify clonal individuals surely inflates their numbers. In contrast, adults that had reproduced at least once already produced disproportionately many fruits relative to their numbers (Figure 7). We note that at the State site in 2001-2002, all seeds were produced by adults past their first reproductive bout, but this was the seed production of only four individuals in a dry year when all seedlings died before reproduction.

In six of nine combinations of site and year-pair, adult survival (non-clonal survival after at least one reproductive bout) was 5.3% or less (Table 4). Mean adult

survival (among sites) was ~4% in the 2000-2001 and 2001-2002 seasons. In the last year of the study, adult survival was 50% at one site, but this was 50% out of only two reproductive plants that had survived the drought of 2002. At the highest elevation (BLM) site, adult survival was 10% and 13% in the second and third years of the study, respectively (Table 4).

3.3 Seed Demography

We used estimates of soil seed-bank and seedling densities to calculate natural field germination fractions (Table 5). Estimates of in situ germination fraction were generally lower in dry than wet years for both species. In the dry year of 2001-2002, less than 3% of seeds germinated in any of the study populations, perennial or annual (Table 5). Germination fraction varied more widely in the two wet years (2000-2001 and 2002-2003): between 5% and 68% (Table 5). Local differences in temperature and precipitation probably drive some of this variation in germination. Estimates of germination fraction were very high (>85%) in the annual populations in the first year of the study, a dry year. However, the scope of inference for these estimates is limited, since the samples of both seedling and soil seed-bank densities were arbitrarily located in patches of high seedling density.

Estimates of seed-bank survival varied even more than the estimates of germination fraction. Seed-bank survival per year ranged from 2.5% to 100% in just one population in two years (the annual population at the Buckeye site; Table 6). The value 100% results from a higher estimate of soil seed density in 2003 than in 2002, with no

new seeds produced in the interim. Yearly seed-bank survival was low (<5%) in the annual populations in 2001-2002, compared to values ranging from 14% to 64% among the perennial populations in the same year. The following year (2002-2003), the pattern was reversed: seed-bank survival was lower in the perennial populations (1% to 14%) than in the annual populations (19% to 100%).

3.4 Seed Experiments

Germination Trials-- The two germination studies, using seeds produced in two different years that had experienced different experimental conditions, revealed a consistent ranking of germination fraction among the four populations studied. In descending order of mean germination fraction, this ranking was: State, Private (the two perennial populations), Buckeye, and then Hassayampa (the two annual populations). These studies showed that warmer temperature significantly increased the rate of germination, but that mean germination fraction did not clearly differ at the species level. In the first trial of the growth chamber experiment, using seeds that had been stored on the lab for about nine months, 80% of perennial and 66% of annual seeds germinated in the warmer temperature regime, whereas 3% of perennial and 1% of annual seeds germinated in the cooler temperature regime (Figure 8a). The difference between species in the warm treatment was largely because of less germination of seeds from one annual population (the Hassayampa site, see Figure 8a). As a result, perennial vs. annual seeds did not differ significantly in germination fraction ($F_{1,2}=2.10$, $p=0.2847$), but seeds in the warmer temperature regime were significantly more likely to germinate ($F_{1,58}=141.27$,

$p < 0.0001$). The interaction of species and temperature did not have a significant effect ($F_{1, 58} = 0.00$, $p = 0.9904$).

Seeds were much more likely to germinate in the warm temperature regime in the second trial as well ($F_{1, 117} = 318.27$, $p < 0.0001$; Figure 8b). Averaging across other factors, 93% of perennial and 66% of annual seeds germinated in the warmer temperature regime, whereas 35% of perennial and 4% of annual seeds germinated in the cooler temperature regime (Figure 8b). The seeds used in the second trial had been stored in the soil in the wild for 12 months. These seeds germinated at equal or higher rates than in the first trial, even though we ran the second trial for half the length of time (12 instead of 24 days), suggesting that time spent in the soil made the seeds more germinable. There was a trend for germination fraction to vary between species in the second trial ($F_{1, 2} = 9.09$, $p = 0.0946$; Figure 8b). Two patterns contributed to this trend. Annual seeds germinated at a lower rate in the second replicate of the warm temperature regime (data not shown), leading to a significant effect of the interaction between replicate and species ($F_{1, 117} = 12.38$, $p = 0.0006$), and a significant three-way interaction between replicate, species, and temperature ($F_{1, 117} = 4.37$, $p = 0.0387$). The germination behavior of seeds from the State site in the cool temperature regime of the second trial also contributed to the species effect: they germinated at a relatively high rate (Figure 8b). This pattern was consistent in both replicates of the cool temperature regime. It seems that seeds from the State site were relatively insensitive to the temperature treatment, at least after they had spent a year buried in soil in the wild.

Similarly, perennial and annual seeds produced in 2000 and buried in their population of origin for 12 or 24 months did not differ in the rate at which they germinated after four days in water ($F_{1,2}=2.03$, $p=0.2903$). Of seeds buried for 12 months, 60% of perennial seeds vs. 31% of annual seeds germinated. Of seeds buried for 24 months, 76% of perennial seeds vs. 48% of annual seeds germinated. Again, the difference between species in mean germination fraction was largely caused by very low germination of seeds from the Hassayampa site (Figure 9). Seeds that had been buried in the wild longer were significantly more likely to germinate ($F_{1,111}=5.85$, $p=0.0172$), but the interactive effect of species and the number of months spent in soil was not significant ($F_{1,111}=0.14$, $p=0.7054$).

Intrinsic Seed Survival-- Perennial and annual seeds buried in packages survived at high rates (Figure 10). The four tests of seed viability used in 2001 all gave similarly high values; we report only the estimate of seed survival after both visual inspection and the “float” test, since these were used to test seed viability in 2002 as well. After 12 months buried in their population of origin, 93% of annual seeds and 94% of perennial seeds produced in 2000 were viable. After 24 months in their population of origin, 84% of annual seeds and 90% of perennial seeds were viable. The general linear model indicated that the species effect was not significant ($F_{1,2}=0.64$, $p=0.5072$), nor was the interaction between species and the number of months spent in soil ($F_{1,113}=0.99$, $p=0.3216$), but that the number of months in soil did affect seed viability ($F_{1,113}=16.71$, $p<0.0001$).

Seeds produced in 2001 and buried in a reciprocal transplant design also had high viability after 12 months in the soil, although this result must be viewed with some caution. Tests of viability of the seed lots used in this experiment showed that just over half of the perennial seeds were viable at the beginning of the experiment (53% and 55% of seeds from the Private and State sites, respectively; $N=100$). Initial viability of annual seeds was much greater: 94% and 97% of seeds from the Buckeye and Hassayampa sites were viable at the start of the experiment. After correcting for initial seed viability, some packages had viability greater than 1.0 after 12 months in the soil. This result is reasonable: the fraction of seeds initially viable in any given sample of 30 seeds could have been greater than the values cited above. However, mean seed viability of some groups of perennial seeds was significantly greater than 1.0 (Figure 11), suggesting that the initial values of seed viability were underestimates. Mean viability after 12 months in the soil was 115% and 99% among seeds from the two perennial populations (Private and State, respectively) and 91% and 81% among seeds from the two annual populations (Buckeye and Hassayampa, respectively). Though these values must be viewed with some caution, the pattern is similar to that in the first trial: seed survival after 12 months in the soil was high. As in the first trial, there was a non-significant trend for perennial seed survival to exceed annual seed survival ($F_{1,2}=4.57$, $p=0.1660$). Whatever error there may be associated with the correction for initial viability is constant, for each seed source, across the four locations where those seeds were placed. Survival did not differ significantly between seeds placed at sites occupied by the annual vs. the perennial ($F_{1,2}=0.16$, $p=0.7314$). The effect of the interaction between seed identity (annual vs.

perennial) and the species (annual vs. perennial) occupying the site where seeds were placed was significant ($F_{1, 385}=9.04$, $p=0.0028$). This pattern seems to be limited to perennial seeds from the Private site, which had greater viability after 12 months at sites occupied by the annual than at sites occupied by the perennial (Figure 12). This significant interaction effect, also, must be viewed with some caution.

3.4 Fitness and Sensitivities

In the annual populations, the finite rates of increase and their sensitivities to changes in life history parameters were similar within a year, but very different between years (Figure 12). In the dry year (2001-2002), both populations declined: the growth rates were 0.025 and 0.045 at the Buckeye and Hassayampa sites, respectively. Seed production failed in both populations, because no seedlings survived to produce fruit ($c = 0$). Under these conditions, the finite rates of increase (λ) were most sensitive to changes in the rate of seed survival, especially s , survival from the time of seed production to the time of germination (Figure 12a). Increased seed survival would cause the finite rate of increase to increase. The sensitivity of the finite rate of increase to germination fraction was negative, indicating that increased seed banking would increase population growth. In the wet year (2002-2003), both populations grew: the finite rates of increase were 2.62 and 246.38 at the Buckeye and Hassayampa sites, respectively. As a result, the finite rates of increase were strongly positively sensitive to changes in germination fraction, indicating that higher germination fractions would increase population growth. This was especially so at the Hassayampa site, where population growth was two orders of

magnitude greater (Figure 12b). The finite rates of increase were also positively sensitive to changes in seedling survival and seed survival from the time of seed production to the time of germination (s ; Figure 12b).

In the perennial populations, asymptotic finite rates of increase and sensitivities varied both within and between years (Table 7, Figure 13). In the dry year (2001-2002), recruitment from the seed stage to the adult stage failed in all three perennial populations ($c = 0$), as in the annual populations. In addition, plants already in reproductive classes failed to produce any seeds in two of three populations, and at the Private site, production of clonal rosettes failed as well. Given these failures, the asymptotic population growth rates, or rather, the rates of decline, were governed by either the rate of self-looping in the seed stage (seed-bank survival) or the rate of self-looping in the clone stage (clone survival), whichever was greater (Table 7). At the Private site, where clone survival was zero, the population growth rate was 0.14, the rate of seed-bank survival (Table 7). At the State and BLM sites, how many clones we choose to attribute to clone survival vs. production of new clones by adults causes the population growth to be determined by the rate of clone survival or the rate of seed-bank survival. In any case, the rate of self-looping in one or the other of these two stages sets an upper limit on the rate at which the population declines. The rate of self-looping in the adult stage, adult survival, did not influence the population growth rate in any of the study populations in the dry year, because adult survival was lower than seed-bank survival (where clone survival was zero) or lower than both seed-bank survival and clone survival, and the only pathway into the adult stage failed in all three populations. The sensitivity and elasticity matrices reflect

these patterns (Table 7): either seed-bank survival or clone survival had a sensitivity and elasticity of one, depending on which of the two of these survival rates was higher.

Where seed-bank survival set the upper limit on population decline, the sensitivities to lower-level parameters were similar to those in the annual populations in 2001-2002: the finite rates of increase were positively sensitive to seed-bank survival parameters (s , q , and r) and negatively sensitive to change in the germination fraction (g ; Figure 13a).

Where clone survival limited population decline, the finite rate of increase was positively sensitive to clone survival, and insensitive to changes in all other life history parameters (Figure 13a).

In the wet year (2002-2003), the populations at the State and BLM sites grew, but the population at the Private site declined (asymptotic finite rates of increase were 2.46, 9.51, and 0.50, respectively; Table 7). In all three populations, the asymptotic finite rates of increase were most sensitive to changes in recruitment to the adult stage, i.e. the term $s*g*c$ (Table 7). In the growing populations, recruitment to the adult stage also had the highest elasticity (Table 7). In the declining population, where adult survival was 50% at the same time that all pathways in or out of the clone stage failed, recruitment to the adult stage was low, and fecundity was low, the elasticity of adult survival was greatest (Table 7). That is, a 1% increase in adult survival would lead to a greater proportional change in the population growth rate than a 1% change in any other transition. The sensitivity of the asymptotic population growth rate to life history parameters also differed between the growing vs. declining populations. In the growing populations, the sensitivities were similar to those in the annual populations in 2002-2003: the finite rates of increase were

strongly positively sensitive to change in the germination fraction and seedling and seed-bank survival, all three of the parameters in the term $s*g*c$ (Figure 13b). In the declining population, the growth rate was most sensitive to changes in adult survival.

Using these models of the perennial populations, we can ask how much mean fecundity would have to increase to make up for the lost fitness if there was no post-reproductive survival. In other words, how much would fecundity have to increase for the annual habit to be an equivalent strategy in these perennial populations? There would be no change in the asymptotic rate of population growth in response to the loss of post-reproductive survival in the two perennial populations where all pathways into or out of the reproductive classes failed, and population decline was limited by seed-bank survival (the Private and BLM sites in 2001-2002). Given the data from the State site in 2001-2002, loss of post-reproductive survival would cause the asymptotic growth rate to decline from 0.37 (the rate of clonal survival) to 0.20 (the rate of seed-bank survival). Pre-reproductive survival failed in all three of these populations, and in that sense, increased fecundity cannot change the asymptotic growth rate. Alternatively, we can set pre-reproductive survival to a value lower than the sampling zero that we obtained: given seedling survival of 0/228 at the State site in 2001-2002, we can choose a value $<1/228$, such as 0.001. Given this low rate of seedling survival, mean fecundity would have to increase by 13,622 seeds to recover the asymptotic population growth rate obtained with the observed values of post-reproductive survival at the State site in 2001-2002. Given the 2002-2003 data, mean fecundity would have to increase by 58, 236, and 2,442 seeds

at the State, BLM, and Private sites, respectively, for the annual habit to be an equivalent strategy.

4. Discussion

A striking pattern in our plant demography data is the variation among years in seedling survival and mean seed production per reproductive plant. In one particularly dry season (2001-2002), no seedlings survived to produce fruit in either annual or perennial study populations. In the wetter years, mean seedling survival was high, ranging from ~20% to ~55%. This variation is not unexpected; the aboveground demography of desert annuals is known to be dramatically variable among years (Beatley 1974, Kadmon 1993, Clauss 1999, Venable and Pake 1999). There was also considerable within-year, among-site variation in plant demography, especially among populations of the perennial. Compared to this variation, seedling survival and seed output were comparable between the two species. It may be that seedling survival tended to be lower in the perennial populations than in the annual populations in the three years that we can compare them, which is consistent with the idea that the annual habit is favored where seedling survival is higher. But it is difficult to make a strong statement about this pattern with only three years of data, given the strong variation among years. The data do not support the idea that annual seed output is greater than perennial seed output, as the Charnov and Schaffer (1973) model, and other models, would have us expect. Data from

a common garden experiment with these two species (Chapter 3) illustrated that the magnitude and direction of the difference between annual and perennial seed output depended upon the conditions that plants experience.

Of particular interest is the rate of post-reproductive survival in the perennial life history. The estimation of post-reproductive survival was complicated by an asexual stage: clonal rosettes sprouted from underground rhizomes. We were unable to identify the individuals from which these rosettes had originated, or attribute survival to those individuals. Mean post-reproductive survival that excludes survival via clonal rosettes was around 4%. This is the same value that Pavlik and Barbour (1988) reported for non-clonal survival of *O. californica* ssp. *eurekaensis*, a close relative of the perennial that we studied, *O. californica* ssp. *avita*. Our estimates of non-clonal post-reproductive survival were rarely >5%, and the highest values involved the smallest sample sizes. The value 4% surely underestimates post-reproductive survival, but if the true number were much greater, we should have seen many more clonal rosettes than we did (often less than 10% of plants, with clones treated on a ramet basis).

Estimates of germination fraction and seed-bank survival in natural populations did not differ consistently between the two species. These estimates varied considerably, whereas intrinsic seed survival and germination fractions under ideal conditions were consistently high. The germination trials in growth chambers showed that most of annual and perennial seeds will germinate, given ideal conditions. For both annual and perennial seeds, ideal conditions involved, beyond moisture and light, warmer rather than cooler ambient temperatures. This pattern was observed previously for members of the

Onagraceae in the Mojave Desert (Went 1948, Beatley 1974, Mulroy and Rundel 1977, Brown 1994). In contrast, germination fractions were low (<5%) in the dry year of 2001-2002, and variably higher (5% to 68%) in the wetter years of 2000-2001 and 2002-2003. These data suggest that most viable seeds are germinable in a given year, but that seeds in the wild may or may not experience conditions sufficient for germination, either in terms of moisture, temperature, or both. In other words, germination is plastic in response to environmental conditions (as shown by Clauss and Venable 2000). In situ and experimental seed-bank survival contrasted as well. Annual and perennial seeds placed in packages and buried in the soil in wild populations survived at high rates after 12 or 24 months, often >90%. In situ seed-bank survival, on the other hand, was quite variable, ranging from 2.5% to 100%. The difference between experimental and in situ seed-bank survival suggests that much seed mortality occurs through extrinsic factors (e.g. seed predation), rather than intrinsic properties of the seeds.

We synthesize these results, along with the climate data, into a more qualitative description of the two life histories, contrasting their phenologies, and the stresses and resources they face with respect to temperature and precipitation. We begin with germination. Both species are intrinsically more likely to germinate in response to rain before or after the coldest part of the winter, in the autumn or spring. We observed germination of the perennial earlier than the annual: in August, September, or October rather than in October, November, or later months. Mean temperatures decline earlier where the perennial is found, but there are also selective reasons for the perennials to germinate earlier. In an ideal year, perennial seeds would germinate early in the autumn,

so that seedlings reach a reasonably large size before cold temperatures set in. The larger seedlings are, the better chance they have of surviving the stresses of winter: freezing, drought, and their combination. Larger seedlings also are better positioned for rapid growth in the potentially narrow window of opportunity for growth in spring in the Mojave and southern Great Basin Deserts. Where the perennial is found, there is only about a two-month period (from the second half of March through the first half of May) that is reliably free of hard freezes but is not so arid that soil moisture availability becomes a source of stress. Germination in the spring is unlikely to lead to reproductive success because of these constraints, and we observed little spring germination of the perennial. These are the same reasons that Beatley (1974) concluded that the success of winter annuals in the Mojave Desert depends critically upon rains sufficient for germination in the autumn.

The phenology of the annual is less limited by cold temperatures. We observed significant germination cohorts of the annual in October, November, February, and March. In the milder temperatures of the Sonoran desert, the annual can grow essentially throughout the autumn, winter, and spring (late October through April), as long as soil moisture is available. Even in the coldest months, hard freezes (-2°C) are uncommon where the annual grows. Compared to the perennial then, the annual's growth is not so severely interrupted by cold temperatures, nor does it experience cold as a source of stress. Both species experience stressful aridity in the late spring and early summer, and both can experience drought in the season of recruitment and growth (autumn, winter, and spring). But layered upon these two common sources of stress is one unique to the

perennial both in its nature and timing: cold winter temperatures. Cold winter temperatures are likely to suppress growth in the perennial, and impose mortality (and hence selection) in some places and years, and this in the middle of the season of recruitment and growth. In the milder Sonoran Desert winter temperatures, the annual can avoid the stress of the most arid season as best it can with the combination of (1) plastic germination in response to rain, (2) a high enough growth rate to produce seeds with only a germination rain and (3) seed dormancy. This is the drought-evading strategy of desert annuals described by others (Solbrig and Orians 1977, Smith et al. 1997, Clausen and Venable 2000).

We turn now to some of the more synthetic aspects of demography, including the population growth rates and sensitivities. In the dry year, the annual population growth rates were 0.025 and 0.045; that is, the populations declined by 97.5% and 95.5%, respectively. In the same year, the asymptotic rates of decline of the perennial populations ranged between 37% and 86%. In the annual populations, survival in the seed bank set an upper limit on the rate at which the population declined, whereas in the perennial populations, either seed-bank survival or clone survival set an upper limit on the rate of population decline, whichever was higher. In populations, either perennial or annual, where the rate of decline was limited by seed-bank survival, an increase in germination fraction would cause population decline to accelerate; that is, the sensitivity of population growth to germination fraction was negative. In contrast, in the wet year, four of the five study populations grew ($\lambda > 1$). The asymptotic population growth rates ranged from 0.50 to 9.51 among the perennial populations, and the annual population

growth rates ranged from 2.62 to 246.38. In all of these populations, the sensitivity of population growth rates to change in germination fraction was positive rather than negative. In the growing populations ($\lambda > 1$), the sensitivity of population growth to changes in germination fraction was greater than sensitivity to change in any other life history parameter. The impact of germination fraction on population growth changed in sign and magnitude dramatically in just two years. Increased seed banking was favorable in a dry year, when it set an upper limit on population decline. Increased seed banking was unfavorable in a wet year, with increasing magnitude in populations with increasing growth rates. This pattern is the essence of bet hedging: a trait is disadvantageous in a good year, because it prevents the population growth rate from being higher, but is advantageous in a bad year, because it prevents the population growth rate from being lower (Seeger and Brockman 1987). Together, these actions should allow seed banking to lower the variance and the arithmetic mean population growth rate, while increasing geometric mean population growth rate.

What about bet hedging via extended reproductive lifespan, i.e. iteroparity? Post-reproductive survival of perennials contributed significantly to the asymptotic rate of population growth in two cases. One of these was at the State site in 2001-2002, where the estimated value of clone survival was greater than the value of seed-bank survival. This, combined with the fact that pre-reproductive survival failed, made the population growth rate equal to the rate of clone survival, and more sensitive to change in clone survival than in any other transition or life history parameter. However, as we noted, we have no data on the true rate of clone survival. In this case, we arrived at a value of clone

survival by assuming that half of the clones observed in 2002 were the result of survival of clones from the previous year and the other half were new clones produced by adults in 2001. This led to a value of 0.37 for clone survival. We view this value as high for mean clone survival across space and time, but not unreasonable for a particular time and place. The second case in which post-reproductive survival contributed significantly to the asymptotic rate of population growth was at the Private site in 2002-2003. Adult survival was 50% at the same time that all pathways in or out of the clone stage failed, recruitment to the adult stage was low, and fecundity was low. Under these conditions, the asymptotic growth rate was more sensitive to adult survival than any other life history parameter.

In these two cases, perennial population decline apparently was limited by post-reproductive survival (adult survival or clone survival). This is part of the task of demonstrating that extended reproductive lifespan functions in a bet-hedging manner. The sensitivity of the asymptotic growth rate to change in the post-reproductive survival terms (p , R_1 , and R_2) cannot be negative, so it is not possible to demonstrate that bet hedging occurs via post-reproductive survival in the same way that we have with respect to germination fraction. However, the sensitivity of the asymptotic growth rate to p , R_1 , and R_2 could be negative if these terms were negatively correlated with another, significant aspect of fitness. Perturbation of the perennial models indicated that mean fecundity would have to increase by 34, 98, 2,442, or 13,622 seeds (at the State, BLM, and Private sites in 2002-2003, and at the State site in 2001-2002, respectively) for the asymptotic growth rate to recover from the loss of post-reproductive survival. The

exchange rates between post-reproductive survival and fecundity would have to be greater than these values for a decline in post-reproductive survival to increase the asymptotic growth rate in these times and places. We do not have measurements of the rate at which post-reproductive survival can be transformed into seeds, but it seems likely that the ability of plants to exceed these critical exchange rates, like the critical values themselves, probably also changes over time and space. When plants can exceed the critical exchange rate, post-reproductive survival limits population growth.

More generally, the data from the perennial populations suggest that the three types of individuals that we distinguished, seeds, adults, and clones, may play different roles in different times and places. Each may set a limit on the rate at which a population declines in different year types, and each may limit population growth in other year types. In this sense, the perennial life history structure itself may be viewed as a diversified bet-hedging strategy, with fitness primarily achieved by different types of individuals under different conditions. Seed banking, adult survival, and clonality each may buffer environmental variation, but different kinds of variation.

This still leaves us with the question: why bet hedge via seed banking, adult survival, and clonality, and be perennial, vs. bet hedge via seed banking alone, and be annual? The bet-hedging literature suggests that bet hedging via iteroparity should be a less successful strategy than bet hedging via seeds if post-reproductive survival is low and variable, relative to seed-bank and seedling survival (Rees 1994, Tuljapurkar & Wiener 2000). There is uncertainty in our estimates, but it seems likely that post-reproductive survival is low in the perennial that we studied, suggesting that bet hedging

via iteroparity would not be favored. But it also appears that post-reproductive survival may be less variable than seed or seedling survival, which would act in favor of bet hedging via iteroparity. The considerable variation in seed and seedling survival that we found did not differ in a consistent way between the annual vs. perennial. Our sensitivity analysis suggested that seed banking may be the most important form of bet hedging in the perennial life cycle. We found stronger evidence for bet hedging via seeds in the perennial populations, and this in more times and places. Further, we documented complete failure of adult survival, clone survival, and clone production at certain times and places, but not failure of seed-bank survival ($s*(1-g)*q*r$). The demographic data alone do not suggest a clear answer as to why one plant should bet hedge via seeds, and the other via seeds and post-reproductive survival.

The climate data lend insight into this question. We suspect that warmer winter temperatures in the Sonoran Desert tip the balance against the perennial habit there, and that colder winter temperatures in the Mojave and southern Great Basin Deserts tip the balance against the favorability of the annual habit there. The essence of the desert annual strategy, as discussed above, is to take advantage of good conditions when they occur, progressing from seed germination to seed set in a short period of time. Growth rates are temperature dependent in plants. The rapid growth rates needed to build up biomass from seed, and transform that biomass into a greater number of seeds than a perennial can produce in its lifetime, may be difficult to achieve in a cold environment. Cold temperatures not only suppress plant growth on an ecological time scale, they can cause mortality. Adaptation to cold may result in a chronically lower growth rate; that is,

there may be a trade-off between cold-tolerance and growth rate. Cold-tolerant seedling traits in the perennial may act as a conservative bet-hedging strategy, buffering yet a different kind of life-threatening environmental variation. An annual mutant could trade off some of this cold-tolerance for higher growth rate, with the consequence that some fraction of annual seedlings (larger than the fraction of perennial seedlings) would die. Among the survivors, cold temperatures would suppress growth, limiting the advantage that a higher growth rate would otherwise confer. In the long run, the seed output of the surviving annual seedlings may not make up for the additional seedling mortality, the potential difference between annual and perennial lifetime seed output, and the bet-hedging value of extended reproductive life span. In the Sonoran Desert, where it is considerably warmer in the winter, the annual is freed from selection for cold-tolerant traits, and can achieve the high growth rates that make the annual strategy successful. In more general terms, we suggest that the “exchange rate” between fecundity and survival is temperature sensitive: achieving equal or greater fitness in the currency of fecundity in exchange for a given amount of fitness in the currency of survival is difficult in a cold environment, because of the temperature-sensitivity of growth, and the size dependency of fecundity, in plants.

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Table 1. Formulas for sensitivities of the finite rate of increase to changes in each life history parameter ($d\lambda/dx$) in annual vs. perennial populations, based on the life history models of Figure 1. Parameters are described in the text.

	Annual	Perennial
$d\lambda/dc$	$s^*g^*B_A$	$s_{11}(s^*g^*B_P) + s_{21}(s^*g)$
$d\lambda/dB$	s^*g^*c	$s_{11}(s^*g^*c) + s_{12}(p)$
$d\lambda/dg$	$(s^*c^*B_A) - (s^*q^*r)$	$s_{11}(s^*c^*B_P - s^*q^*r) + s_{21}(s^*c)$
$d\lambda/ds$	$(1-g)^*q^*r + (g^*c^*B_A)$	$s_{11}(q^*r - g^*q^*r + g^*c^*B_P) + s_{21}(g^*c)$
$d\lambda/dq$	$s^*(1-g)^*r$	$s_{11}(s^*(1-g)^*r)$
$d\lambda/dr$		$s_{11}(s^*(1-g)^*q)$
$d\lambda/dp$		$s_{12}B_P + s_{22}$
$d\lambda/dR_1$		$s_{12}B_c + s_{32}$
$d\lambda/dR_2$		$s_{13}B_c + s_{33}$
$d\lambda/dB_c$		$s_{12}R_1 + s_{13}R_2$

Table 2. Loading of climate variables on the first, second, and third principal components axes. Loadings are positive unless noted otherwise. The coefficient of variation is abbreviated here as “CV”, standard deviation is abbreviated as “SD”, and potential evapotranspiration as “PET”.

	>0.20	±0.19-0.15	±0.14-0.09
Axis 1			<ul style="list-style-type: none"> • Ave and extreme high and low temperatures: Jan-Dec • PET: annual, Jan-Dec • aridity: Jan, Feb, Apr-Jun, Nov • Ave annual snowfall (-) • Ave precip (-): Apr-Jun • CV of precip: Apr-Jun
Axis 2	<ul style="list-style-type: none"> • Ave precip: Sep, Oct, annual • aridity (-): Sept, Oct • CV of precip (-): Jul, Aug 	<ul style="list-style-type: none"> • Ave precip: Mar, Jul, Aug, Nov, Dec • aridity (-): Jul, Aug, annual • CV of precip (-): Jan-Mar, Oct, Dec, annual • minimum annual precip 	<ul style="list-style-type: none"> • Ave precip: Jan, Feb, Apr • aridity (-): Mar, Nov, Dec • CV precip (-): Sep, Nov
Axis 3	<ul style="list-style-type: none"> • Ave precip: Dec-Feb 	<ul style="list-style-type: none"> • Ave precip: Nov • aridity (-): Dec-Feb • CV of precip: Mar, Sep-Nov, annual • Extreme low temperature: Oct 	<ul style="list-style-type: none"> • skew of annual precip • CV of precip: Jan, Feb, Aug • aridity: Jul-Sep • PET (-): Jul-Sept • Ave precip: Mar, annual • Ave low temperature: Nov-Jan • Extreme high temperature (-): Mar • Extreme low temperature: Nov-Mar

Table 3. Autumn and spring freeze probabilities in Kingman, Arizona, near the study sites of the perennial *O. californica* ssp. *avita*, and in Buckeye, Arizona, near the study sites of the annual *O. arizonica*. The values given are the probability of the specified temperature (in degrees Celsius) occurring before the given date (for November and December) or after the given date (for January, February, and March). Data can be found on the web site of the Western Regional Climate Center (see <http://www.wrcc.dri.edu/summary/>).

	-6.7 °C		-4.4 °C		-2.2 °C		0 °C		2.2 °C	
	King	Buck	King	Buck	King	Buck	King	Buck	King	Buck
Nov 1	<10	<10	<10	<10	<10	<10	15	<10	52	24
Dec 1	10	<10	32	15	75	7	>90	76	>90	>90
Jan 1	45	25	75	62	>90	>90	>90	>90	>90	>90
Feb 1	34	<10	64	23	82	60	>90	>90	>90	>90
Mar 1	12	<10	33	<10	62	24	>90	63	>90	>90

Table 4. Pre-reproductive (seedling) survival, fecundity (seed output per plant), and non-clonal post-reproductive (adult) survival in natural populations of the Sonoran desert annual *Oenothera arizonica* and the Mohave desert perennial *O. californica* ssp. *avita*. In parentheses is the number of plants censused. Weighted means (in bold) are shown for each species and year.

	ANNUAL			PERENNIAL			
	Seedling survival (c)			Seedling survival (c)			
	BUCK	HASS	ave	PRIV	STATE	BLM	ave
99-00	0.06 (340)	0.02 (402)	0.04 (742)	-----	-----	-----	-----
00-01	0.48 (410)	0.40 (420)	0.44 (830)	0.28 (425)	0.29 (300)	0.07 (538)	0.19 (1263)
01-02	0 (84)	0 (7)	0 (91)	0 (255)	0 (228)	0 (213)	0 (696)
02-03	0.50 (896)	0.75 (283)	0.56 (1179)	0.12 (43)	0.47 (610)	0.45 (654)	0.45 (1307)
	Fecundity (B _A)			Fecundity (B _P)			
	BUCK	HASS	ave	PRIV	STATE	BLM	ave
99-00	31 (17)	9 (7)	25 (24)	-----	-----	-----	-----
00-01	346 (198)	254 (167)	304 (365)	876 (120)	183 (108)	149 (42)	486 (270)
01-02	NA	NA	NA	NA	68 (4)	NA	68 (4)
02-03	112 (452)	1,174 (212)	451 (664)	4 (6)	24 (287)	138 (294)	81 (587)
				Adult survival (p)			
				PRIV	STATE	BLM	ave
99-00				-----	-----	-----	-----
00-01				0.004 (249)	0.053 (399)	0.10 (40)	0.038 (688)
01-02				0.017 (121)	0.037 (108)	0.133 (45)	0.044 (274)
02-03				0.500 (2)	0 (4)	0 (6)	0.083 (12)

Table 5. The total number of seeds found in soil samples, estimated seed and seedling density, and germination fraction in natural populations of the Sonoran desert annual *Oenothera arizonica* and the Mohave desert perennial *O. californica* ssp. *avita*. Soil samples were collected after germination had concluded, and before new seed rain occurred. In parentheses is the number of soil samples processed per site and year. Germination fraction was calculated by dividing seedling density by the sum of seedling and seed density, as they are reported here.

	Annual Populations		Perennial Populations		
	Total # of Seeds (N)		Total # of Seeds (N)		
	BUCK	HASS	PRIV	STATE	BLM
99-00	1 (69)	2 (65)	---	---	---
00-01	5 (62)	17 (64)	23 (68)	18 (65)	22 (64)
01-02	7 (65)	7 (63)	125 (66)	24 (67)	36 (66)
02-03	7 (57)	1 (58)	1 (66)	0 (67)	3 (46)
	Soil Seed Density (per m ²)		Soil Seed Density (per m ²)		
	BUCK	HASS	PRIV	STATE	BLM
99-00	3.77	8.00	---	---	---
00-01	20.96	69.03	87.90	71.97	89.33
01-02	27.99	28.88	492.12	93.09	141.75
02-03	31.91	4.48	3.94	3.00 ²	16.95
	Seedling Density (per m ²)		Seedling Density (per m ²)		
	BUCK	HASS	PRIV	STATE	BLM
99-00	22.89 ¹	306.3 ¹	---	---	---
00-01	6.50	5.66	7.59	3.41	9.78
01-02	0.76	0.03	1.26	2.56	1.68
02-03	5.03	1.73	0.21	6.36	5.19
	Germination Fraction (g)		Germination Fraction (g)		
	BUCK	HASS	PRIV	STATE	BLM
99-00	0.859 ¹	0.975 ¹	---	---	---
00-01	0.237	0.076	0.080	0.045	0.099
01-02	0.026	0.001	0.003	0.027	0.012
02-03	0.136	0.279	0.051	0.679	0.234

1. The plots sampling the BUCK and HASS populations in 1999-2000 were arbitrarily placed. They were biased towards high-density patches, so the estimates of seedling density shown here are probably higher than they would be for each population as a whole. The estimates of germination fraction also may not be representative of the entire populations.

2. No seeds were found in the 67 soil samples collected at the State site in 2003, hence the upper limit of soil seed density is 3.87 seeds per m². We take soil seed density to be a value (3.00) that is arbitrarily lower than this upper limit.

Table 6. Realized seed-bank survival for three intervals, from the time of soil seed-bank sampling to the time of seed rain (r), from the time of seed rain to the time of germination decision (s), and from the time of germination decision to the time of soil seed-bank sampling (q). Seed-bank survival per year is also presented ($r*s*q$). These were calculated in two populations of the annual, *Oenothera arizonica*, and in two populations of the perennial, *Oenothera californica* ssp. *avita*, in the seasons shown.

		Annual populations		Perennial populations		
		Buck	Hass	Private	State	BLM
2001-2002	r	(1.0)	(1.0)	0.755	0.813	0.939
	s	0.054	0.085	0.397	0.411	0.807
	q	0.469	0.527	0.468	0.622	0.840
	per year	0.025	0.045	0.140	0.208	0.637
2002-2003	r	(1.0)	(1.0)	0.510	0.645	0.763
	s	1.0	0.323	0.033	0.344	0.414
	q	1.0	0.589	0.484	0.208	0.428
	per year	1.0	0.190	0.008	0.046	0.135

Table 7. Transition matrices, finite rates of increase (λ), sensitivity matrices, and elasticity matrices for three populations of the perennial *O. californica* ssp. *avita* in 2001-2002 and 2002-2003.

Private 01-02

Transition matrix			λ	Sensitivity matrix			Elasticity matrix		
0.14	0	0	0.14	1	~0	0	1	0	0
0	0.017	0		~0	~0	0	0	~0	0
0	0	0		0	0	0	0	0	0

State 01-02

Transition matrix			λ	Sensitivity matrix			Elasticity matrix		
0.202	2.52	0	0.37	~0	~0	~0	~0	~0	0
0	0.037	0		~0	~0	105	0	~0	0
0	35	0.37		~0	~0	1	0	~0	1

BLM 01-02

Transition matrix			λ	Sensitivity matrix			Elasticity matrix		
0.63	0	0	0.63	1	~0	~0	1	0	0
0	0.13	0		~0	~0	~0	0	~0	0
0	208	0.5		~0	~0	~0	0	~0	~0

Private 02-03

Transition matrix			λ	Sensitivity matrix			Elasticity matrix		
0.0085	2	0	0.50	0.002	0.0004	0	~0	0.002	0
0.0002	0.5	0		4.06	0.999	0	0.002	0.997	0
0	0	0		0	0	0	0	0	0

State 02-03

Transition matrix			λ	Sensitivity matrix			Elasticity matrix		
2.62	202	2.88	6.28	0.620	0.011	0.038	0.259	0.344	0.017
0.109	0	0		20.9	0.362	1.27	0.362	0	0
0	21	0.3		0.299	0.005	0.018	0	0.017	0.001

BLM 02-03

Transition matrix			λ	Sensitivity matrix			Elasticity matrix		
6.12	993	4.53	10.41	0.702	0.003	0.020	0.413	0.281	0.009
0.044	0	0		69.0	0.289	1.95	0.289	0	0
0	68	0.31		0.315	0.001	0.009	0	0.009	0.0003

Figure 1. Life cycle diagrams of the models used for populations of the Sonoran Desert winter annual *Oenothera arizonica* and the Mohave and southern Great Basin Desert perennial *O. californica* ssp. *avita*. Three classes of individuals are possible: seeds (“sd”), adults (“ad”), and clones (“cl”). Definitions of these classes and the parameters are in the text.

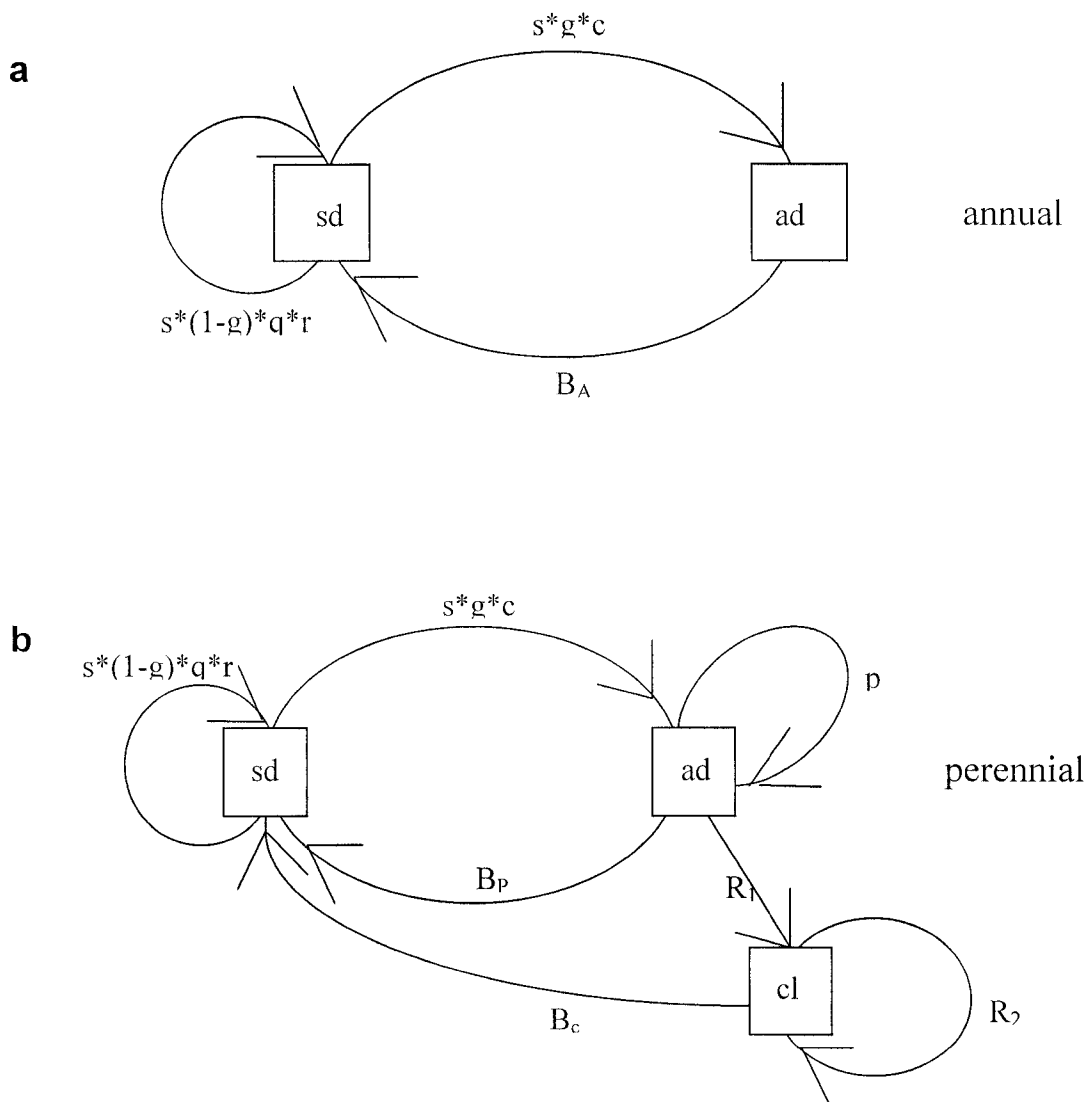


Figure 2. Cumulative precipitation in the four years of the study and on average at weather stations nearest our perennial (a and b) and annual (c) study sites, respectively. The data in (a) were recorded at the Kingman airport, and the data in (b) were recorded at a remote station maintained by the Bureau of Land Management. Average precipitation data shown in (a) are from the Kingman and Kingman No2 weather stations near the Kingman airport (NCDC co-op numbers 024639 and 024645, respectively). The data in (b) were collected at the Buckeye weather station (NCDC co-op number 021026).

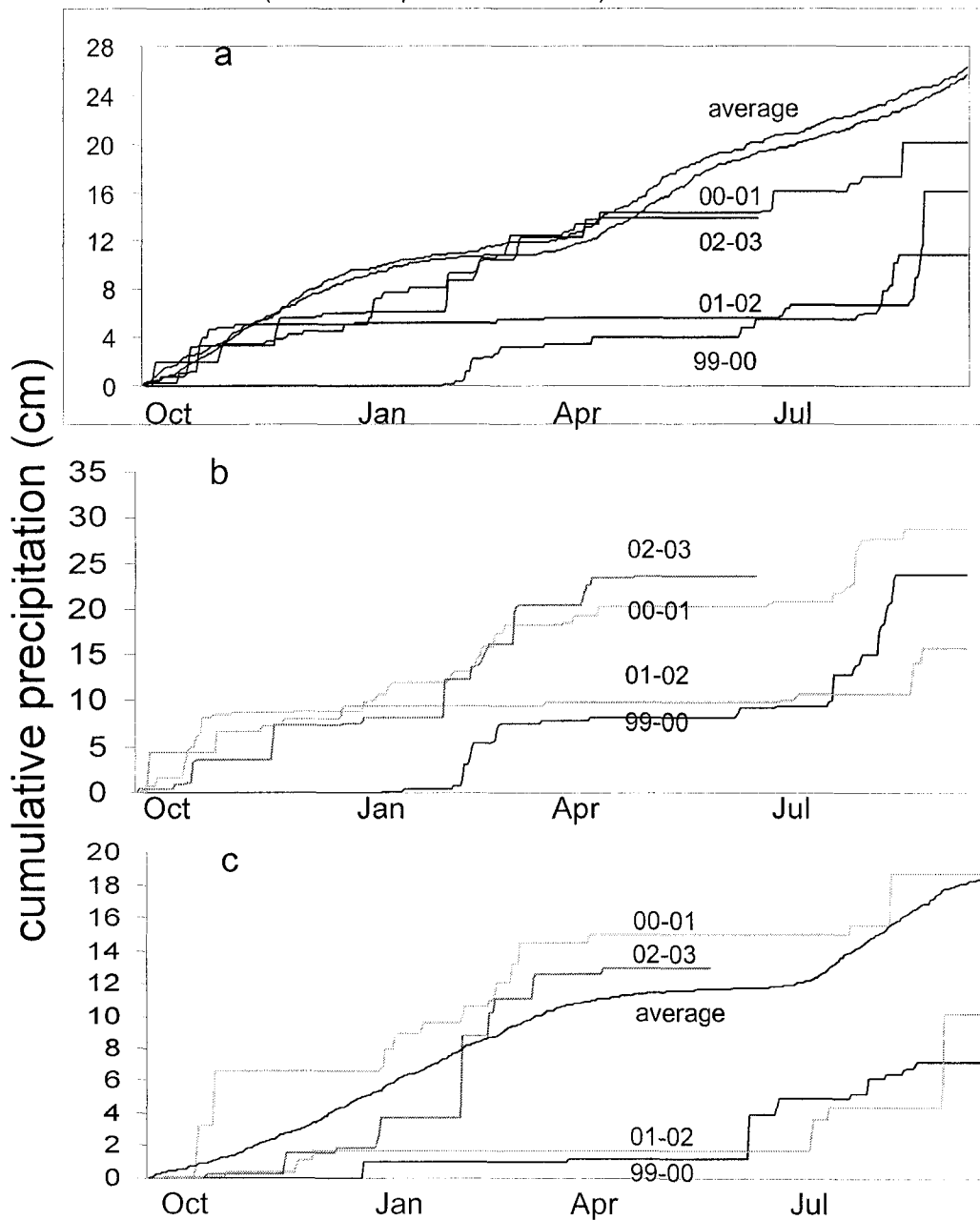


Figure 3. Scores along axis 2 vs. axis 1 generated by the principal components analysis of summary statistics from long-term weather data collected at 12 locations where the perennial *O. californica* ssp. *avita* (▲) is found vs. 9 locations where the annual *O. arizonica* (○) is found.

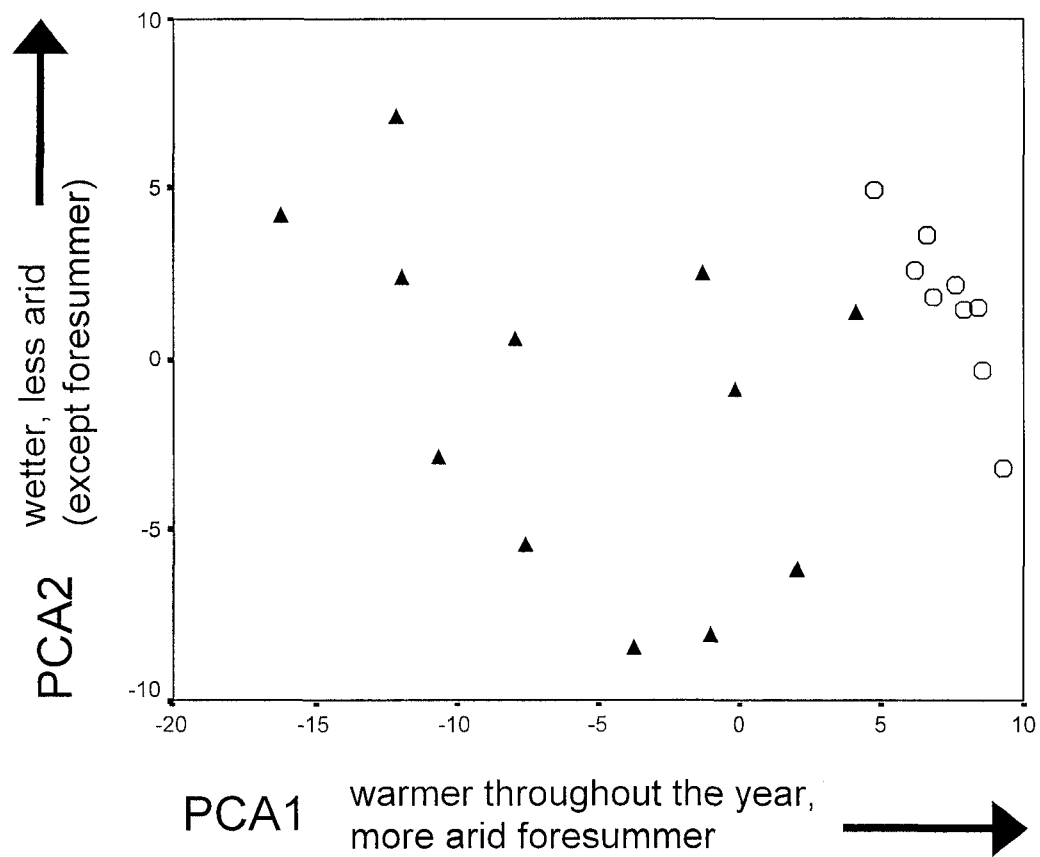


Figure 4. Mean high (a) and low (b) temperatures per month at 12 locations throughout its range where the perennial *O. californica* ssp. *avita* is found vs. 9 locations throughout its range where the annual *O. arizonica* is found. The months are arranged from January to December. The error bars are 95% confidence intervals.

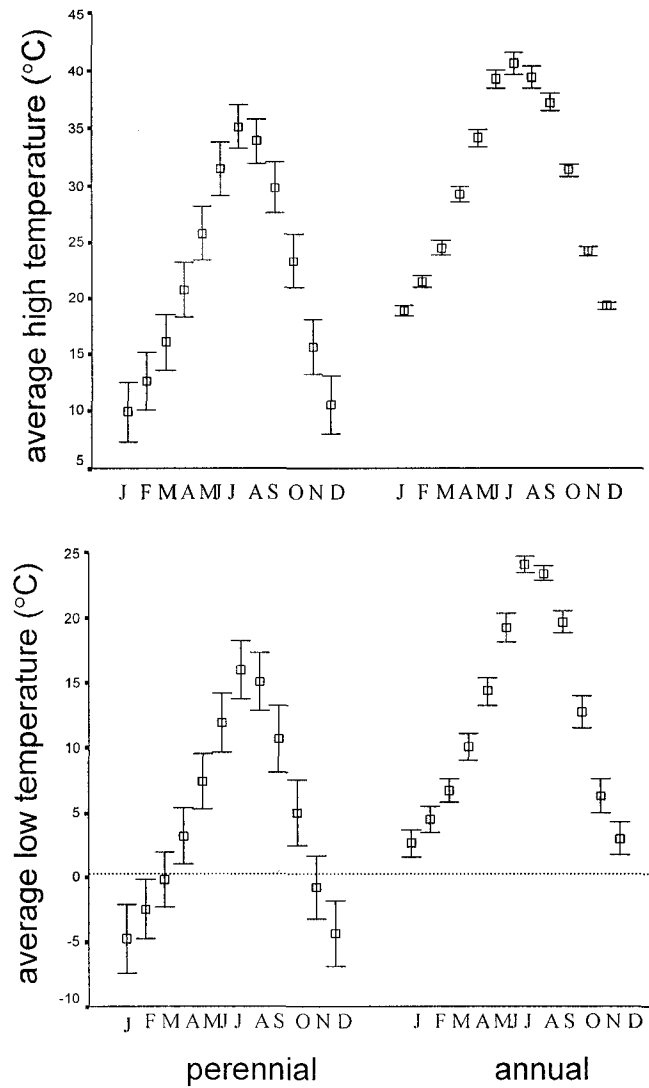


Figure 5. \log_{10} -transformed aridity per month at 12 locations throughout its range where the perennial *O. californica* ssp. *avita* is found vs. 9 locations throughout its range where the annual *O. arizonica* is found. The months are arranged from January to December. The error bars are 95% confidence intervals.

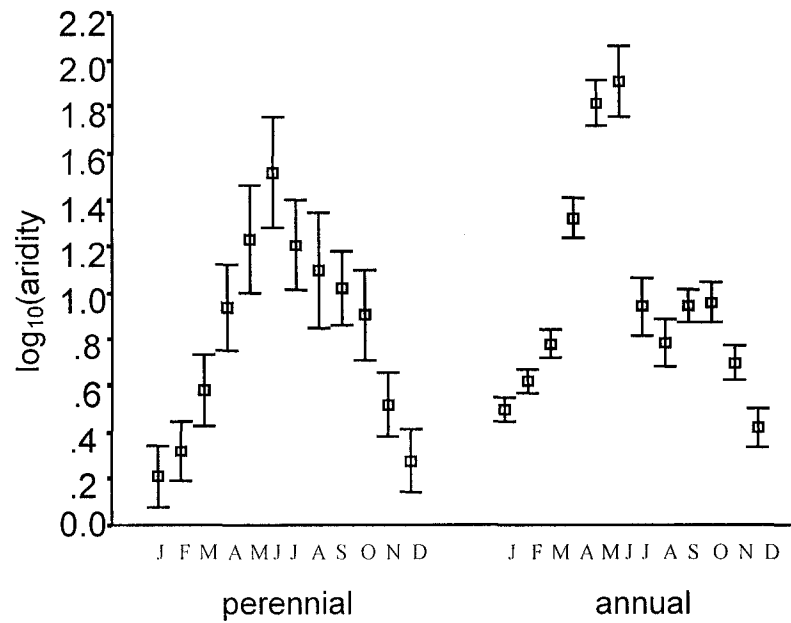


Figure 6. Composition of three study populations of the perennial *O. californica* ssp. *avita* in three years: the percent of individuals that were seedlings (shaded) vs. clones (white) vs. adults past their first reproductive bout (black). These numbers include all the seedlings and clonal “individuals” observed, but the number of adults after their first reproductive bout shown is the number that survived to the time of reproduction in the following year. The great majority of mortality of adults after their first reproductive bout immediately follows reproduction, so that the numbers of adults shown are very similar to the numbers when seedlings and clones emerged. Above the bars are the total numbers of individuals.

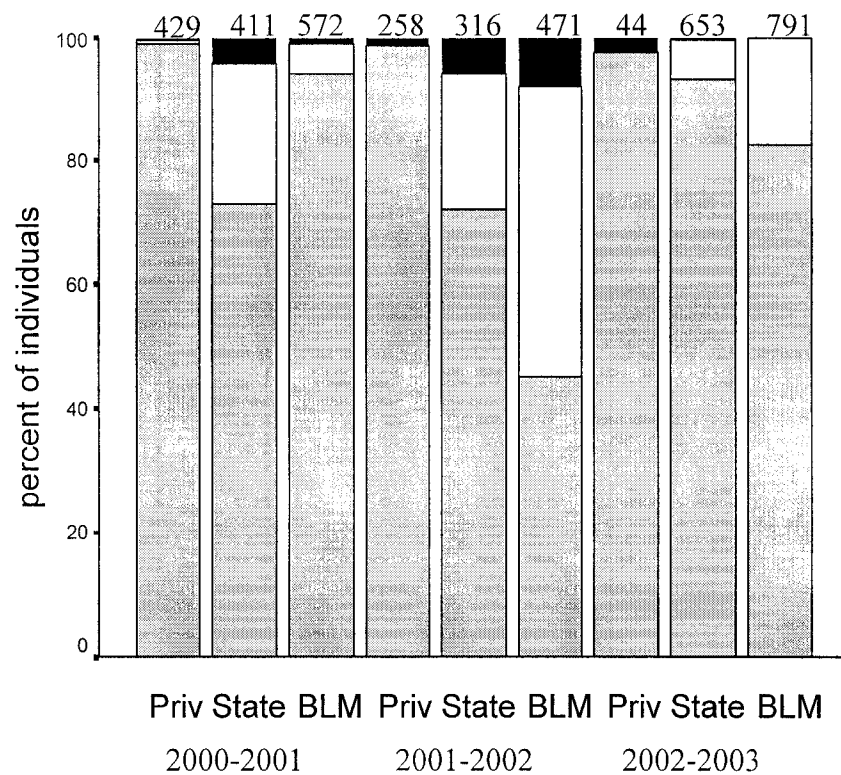


Figure 7. Percent of fruits produced by 1st-year adults (shaded), >1st-year adults (black), and clones (white) in three populations of the perennial *O. californica* ssp. *avita* in three years. Above the bars are the total numbers of fruits.

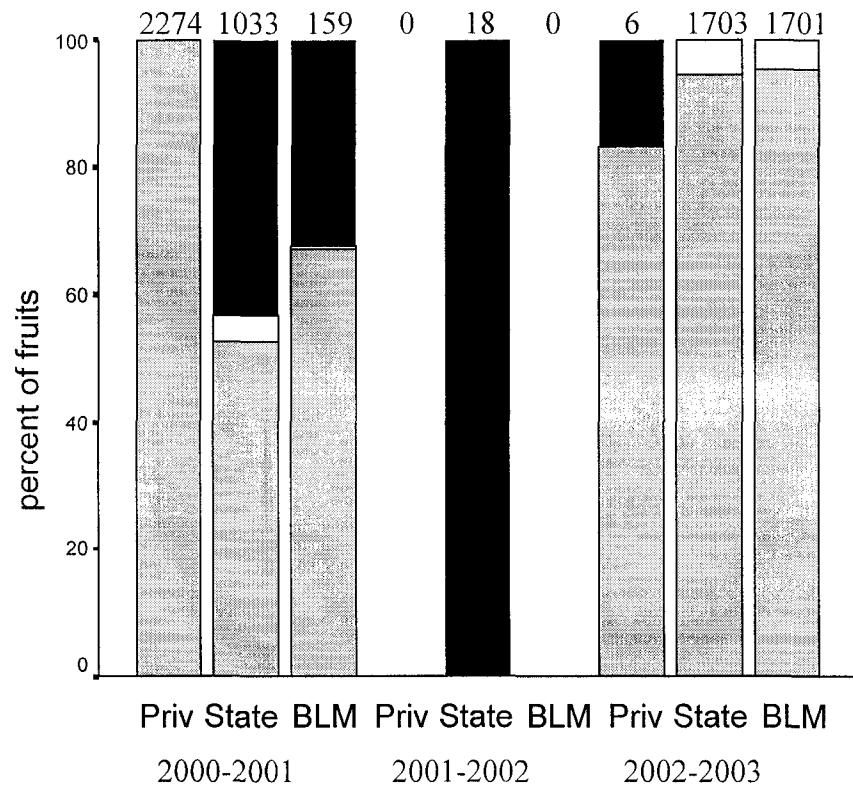


Figure 8. Germination of seeds from two populations of the perennial *O. californica* ssp. *avita* (Private and State sites, ▲ and ■, respectively) vs. two populations of the annual *O. arizonica* (Buckeye and Hassayampa sites, ○ and ▽, respectively) in two temperature treatments. Seeds in (a) Trial 1 were stored in the laboratory for nine months and were given 24 days to germinate. Seeds in (b) Trial 2 had spent one year buried in the wild, followed by laboratory storage for five months, and were given 12 days to germinate. Data from the two replicates of the second trial were combined to produce (b). The error bars are 95% confidence intervals.

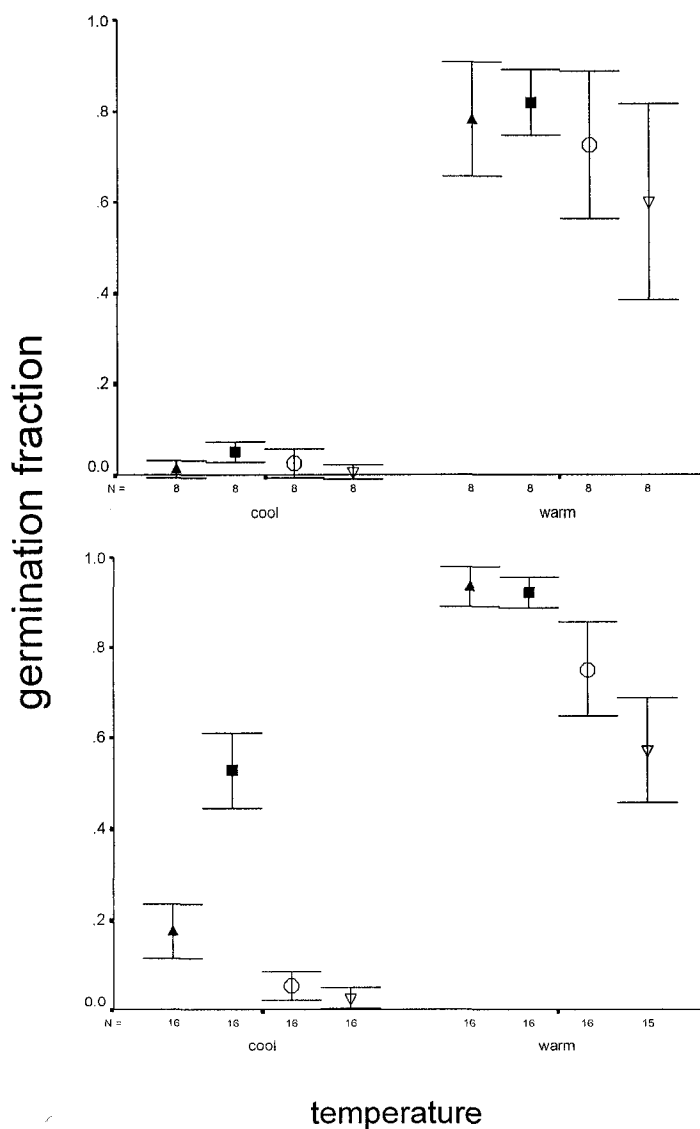


Figure 9. Germination of seeds from two populations of the perennial *O. californica* ssp. *avita* vs. two populations of the annual *O. arizonica* after 12 (▲) vs. 24 (○) months spent buried in soil in the wild. Seeds were submerged in water and given 4 days to germinate.

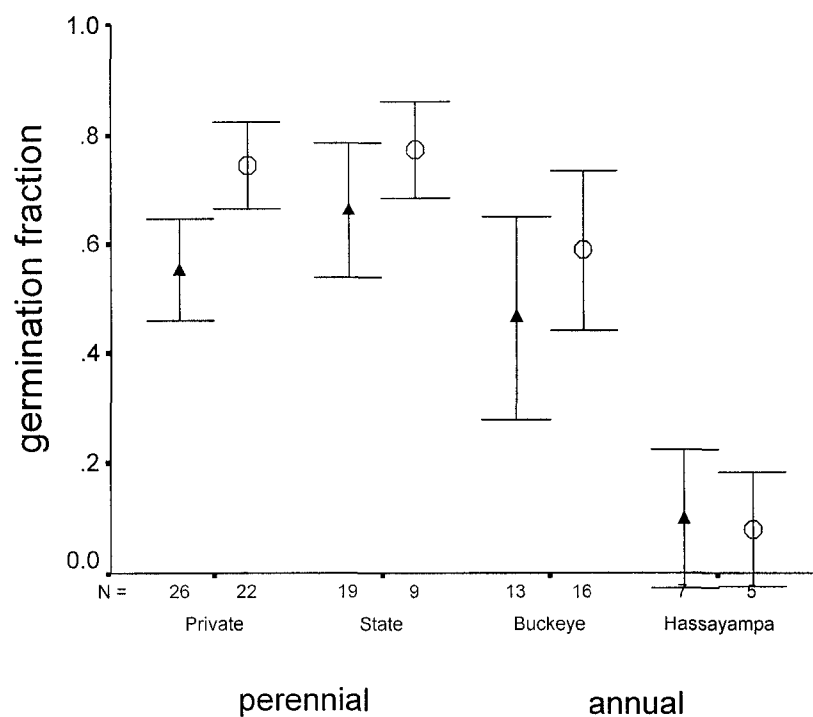


Figure 10. Survival of seeds of the perennial *O. californica* ssp. *avita* vs. the annual *O. arizonica* after 12 (▲) vs. 24 months (○) in soil. Seeds were buried in their population of origin sewn into packages of organza cloth. The error bars are 95% confidence intervals. The number of packages recovered is shown immediately below the x-axis.

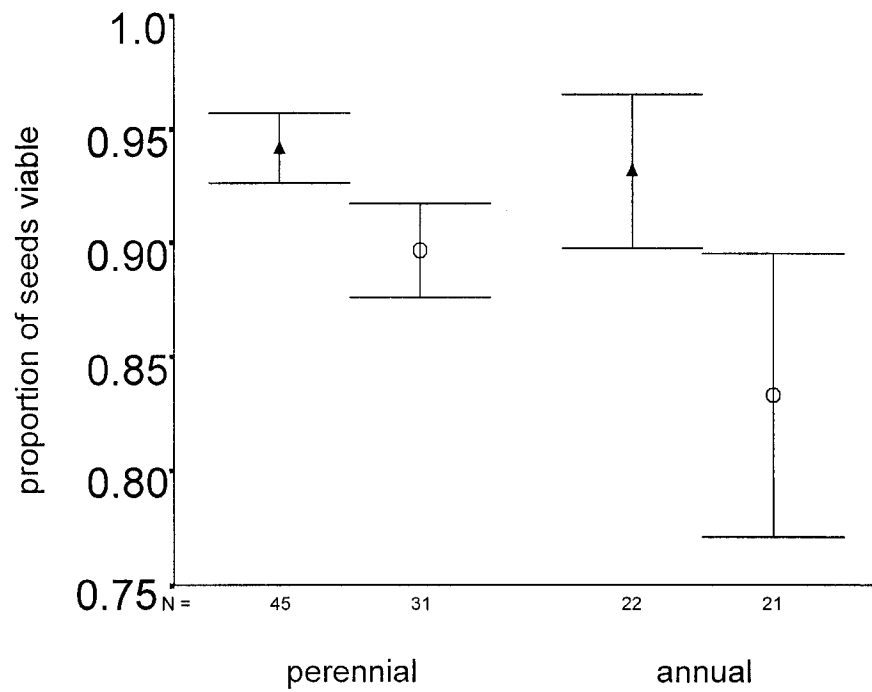


Figure 11. Survival of seeds from two populations of the perennial *O. californica* ssp. *avita* (Private, State) and two populations of the annual *O. arizonica* (Buck, Hass) after burial for 12 months in a reciprocal transplant design. Packages of seeds were buried at either the Private (\blacktriangle), State (\blacksquare), Buck (\circ), or Hass (∇) site. The error bars are 95% confidence intervals. The number of packages recovered is shown immediately below the x-axis. The reason for proportions greater than one is discussed in the text.

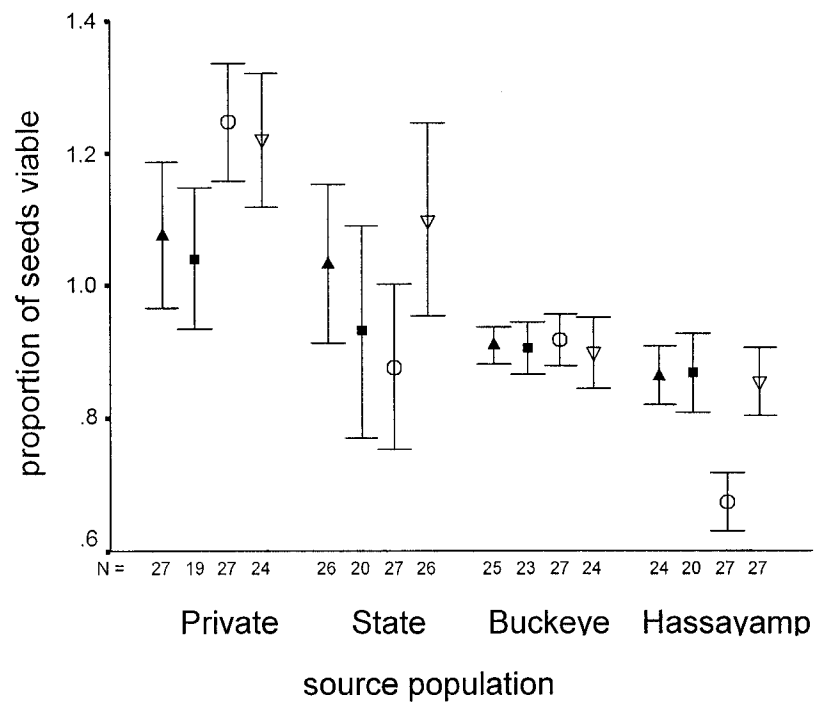


Figure 13. Sensitivity of the finite rate of increase (λ) to changes in life history parameters in two populations of the annual *Oenothera arizonica* in (a) 2001-2002 and in (b) 2002-2003. The parameters are described in the text. The shaded bars are data from the Buckeye site; the open bars are data from the Hassayampa site.

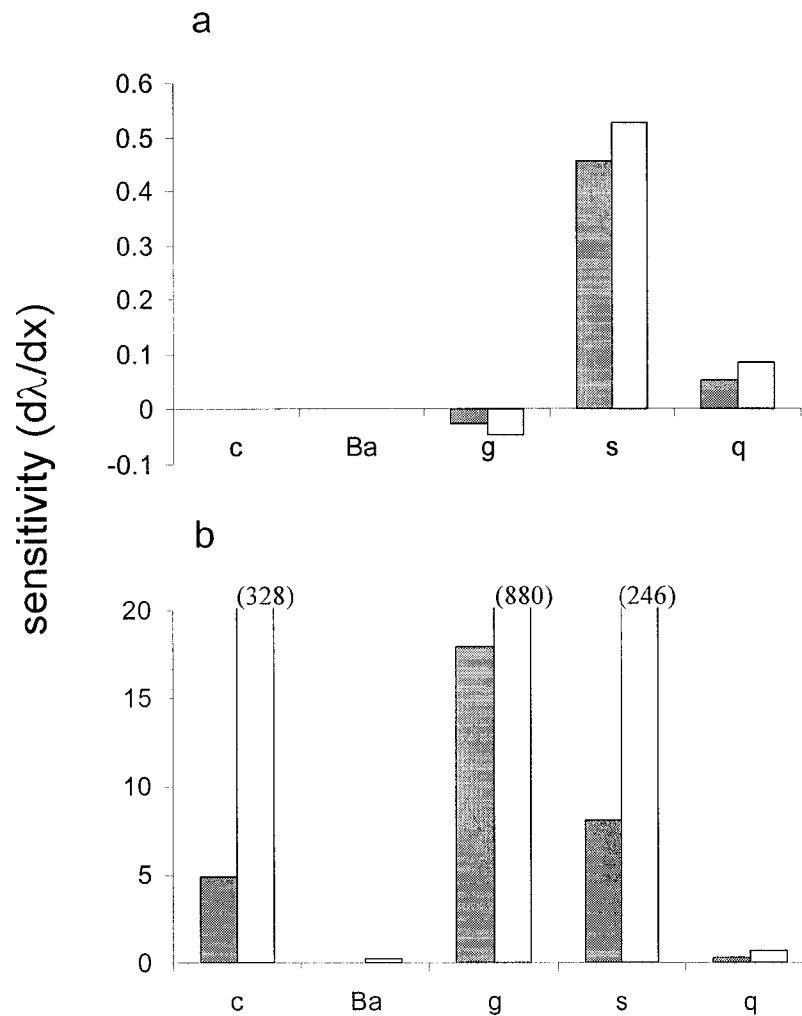
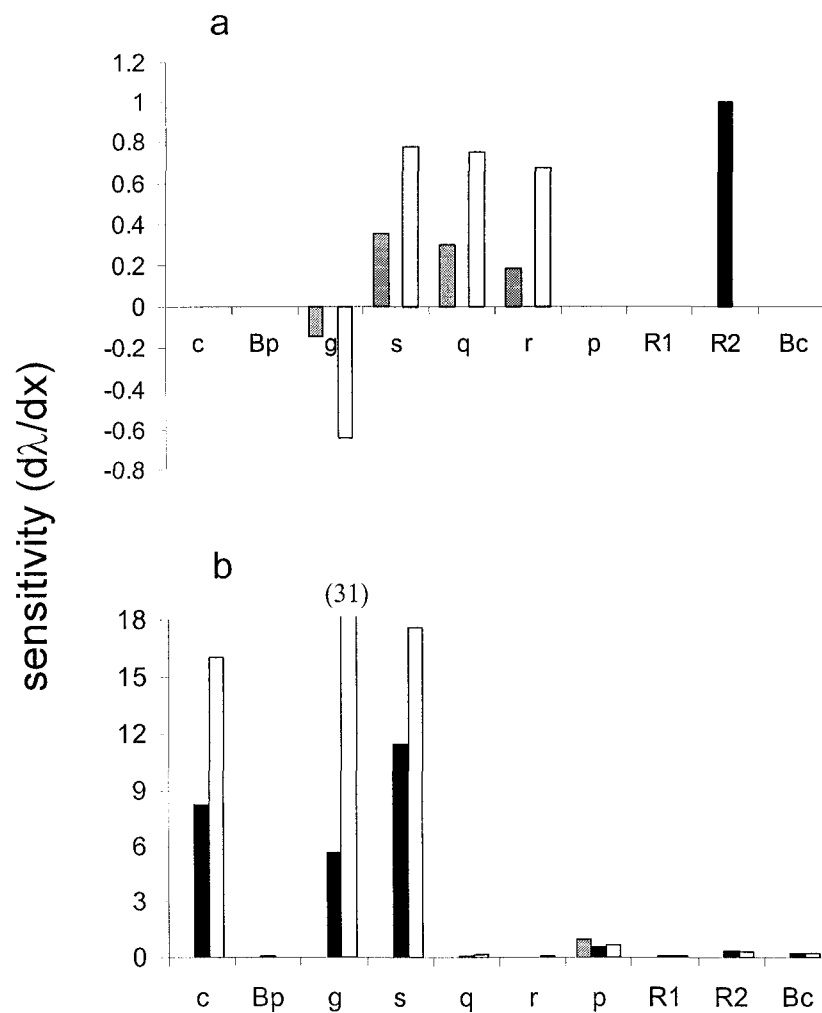


Figure 14. Sensitivity of the finite rate of increase (λ) to changes in life history parameters in three populations of the perennial *Oenothera californica* ssp. *avita* in (a) 2001-2002 and in (b) 2002-2003. The parameters are described in the text. The black bars are data from the State site, grey bars are data from the Private site, and open bars are data from the BLM site.



Appendix 1.

We used the Hargreaves equation (Hargreaves and Samani 1982) to calculate potential evapotranspiration (PET):

$$PET = 0.0075 * R_a * C_t * \delta_t^{(1/2)} * T_{avg}$$

Where R_a is an estimate of incoming solar energy, calculated for each time step, from the relative distance between the sun and earth (d_r), solar declination in radians (δ), and the sunset hour angle in radians (w_s):

$$R_a = 15.392 (d_r (w_s * \sin\phi * \sin\delta + \cos\phi * \cos\delta * \sin w_s))$$

where

$$d_r = 1 + 0.033 * \cos((2\pi J)/365)$$

$$\delta = 0.4093 * \sin(((2\pi J)/365) - 1.405)$$

$$w_s = \arccos(-\tan\phi * \tan\delta)$$

and J is Julian date and ϕ is latitude in degrees. The parameter C_t is the estimated temperature reduction coefficient:

$$C_t = 0.035 (100 - w_a)^{(1/3)} \quad \text{when } w_a > 54\%$$

$$C_t = 0.125 \quad \text{when } w_a < 54\%$$

where w_a is relative humidity. Because relative humidity data were not available, and because the areas we studied are generally arid, we made the simplifying assumption of setting C_t to 0.125. The parameter δ_t is the mean monthly maximum temperature ($^{\circ}\text{F}$) minus the mean monthly minimum temperature ($^{\circ}\text{F}$), and T_{avg} is simply the mean temperature ($^{\circ}\text{F}$) in the time step. We chose day as a time step. Hence PET (in mm) was calculated for each day. We then summed daily PET numbers to get monthly values and an annual value for each weather station.

APPENDIX C: WHY BE ANNUAL VS. PERENNIAL? EVIDENCE FROM TWO
DESERT EVENING PRIMROSES (*OENOTHERA*, ONAGRACEAE) IN A
RECIPROCAL COMMON GARDEN EXPERIMENT

Why be annual vs. perennial? Evidence from two desert evening primroses
(*Oenothera*, Onagraceae) in a reciprocal common garden experiment

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Abstract

Evolutionary ecologists have long sought to understand the conditions under which one vs. more than one reproductive bout per lifetime (semelparity vs. iteroparity, respectively) should be favored. The demographic solution given by Charnov and Schaffer (1973) is often cited, but has rarely been evaluated in an experimental setting. We collected demographic, size, phenological, and leaf-level physiological data from two closely-related species of evening primrose, one of which is an iteroparous perennial (*Oenothera californica* ssp. *avita*; Onagraceae) and the other a semelparous annual (*O. arizonica*), in a reciprocal common garden experiment. The two gardens differed in temperature and precipitation in a manner reflecting the climate of origin of the perennial vs. annual species. We ran two trials of this experiment. Water and nutrients were provided generously in the first trial, and less generously in the second trial. In addition, we manipulated soil moisture via drip irrigation at three levels. The direction and magnitude of the difference between the fitness (finite rate of increase) of annuals vs. perennials depended upon the conditions experienced by the plants. In the first trial, the annual outperformed the perennial in both gardens. In the more stressful conditions of the second trial, perennial fitness was equal to or exceeded annual fitness in the two higher water treatments, but annuals outperformed perennials in the low water treatment. Analysis of above-ground size and phenological data showed that the annual grew faster and reproduced earlier than the perennial. Perennial leaves had 27% more mass per area than leaves of the annual, but their leaves did not differ in percent nitrogen, percent carbon, carbon nitrogen ratio, or $\delta^{13}\text{C}$, a proxy for water use efficiency. The higher

growth rate and accelerated phenology of the annual suggest that it excels at rapidly capitalizing on good conditions, building up biomass and transforming that biomass into seeds. This made the annual successful in the first trial when conditions were good, and in the low water treatment of the second trial, where it was able to avoid stress. The lower growth rate and higher leaf mass per area of the perennial suggest that it is more of a stress-tolerator. We discuss two forms of stress that the perennial may excel at tolerating: water stress and cold stress.

1. Introduction

A central focus in the study of life histories has been to understand the conditions that favor different reproductive schedules (Fisher 1958). Cole (1954) expressed this problem in terms of annual vs. perennial plant life cycles. In his model, annuals reproduce just once in their lifetime and subsequently die, whereas perennials reproduce repeatedly. Cole's formulation of the problem suggested that all plants should be annual (Cole's Paradox), stimulating much theoretical research. Charnov and Schaffer (1973) published a model that many regard as the resolution of Cole's Paradox (Stearns 1992, Gurevitch et al. 2002, Roff 2002). Their model predicted that the perennial habit should be favored if the ratio of adult and juvenile survival (survival after vs. before the first reproductive bout) is greater than the absolute difference between annual and perennial fecundity, and vice versa (Charnov and Schaffer 1973; Figure 1). Since then, several factors have been implicated in driving changes between the annual and perennial habit (or semelparity and iteroparity), or in allowing the coexistence of contrasting strategies. This includes trade-offs (especially nonlinear trade-offs, e.g. Schaffer 1974a, Schaffer & Gadgil 1975, Lacey et al. 1983, Real & Ellner 1992, Takada & Nakajima 1992, Takada 1995), fitness nonlinearities generated by biotic interactions (e.g. pollination, flower predation or disease; Schaffer & Rosensweig 1977, Schaffer & Schaffer 1979, Young 1990, Klinkhamer et al. 1997), density-dependence (e.g. Goodman 1984, Bulmer 1985, Takada & Nakajima 1992, Takada 1995, Benton & Grant 1999, Ranta et al. 2000a), environmental variation (e.g. Murphy 1968, Schaffer 1974b, Goodman 1984, Bulmer 1985, Orzack & Tuljapurkar 1989, Benton & Grant 1999, Ranta et al 2002), and spatial

structuring (e.g. Ronce and Olivieri 1997, Ranta et al 2000b, Ranta et al 2001, Tesar et al 2001). Given this diversity of models, and the complexity of some individual models, none of the “rules” about the conditions that favor semelparity over iteroparity (or the annual over the perennial habit) are without exception. Still, the predictions of the Charnov and Schaffer (1973) model have essentially stood the test of time and are found in many textbooks of life history evolution (Roff 1992, 2002, Charlesworth 1994), plant ecology (Gurevitch et al. 2002, Crawley 1997), and population biology (Silvertown and Charlesworth 2001).

Empirical tests of this theoretical literature are much less numerous. Few studies provide the data necessary to evaluate the Charnov and Schaffer (1973) model (estimates of juvenile survival, adult survival, and fecundity in annual and perennial organisms) let alone more complex models. Among studies of plants, these few include the comparative studies of Fone (1989), Young (1990), Boutin and Harper (1991), Lesica and Shelley (1995), and Evans et al. (Appendix B). In most of these studies the contrasting life histories are allopatric, thus the performance of each strategy is evaluated under different conditions. In two studies (Fone 1989, Boutin and Harper 1991) the annuals and perennials occur sympatrically, but in both cases the evolutionary distance between them is not clear. Two studies have evaluated the performance of contrasting, intraspecific life history variants in a common garden: Oka (1976) and Law et al. (1977). In both cases the single common environment favored one life history over the other. We suggest that a strong test of the Charnov and Schaffer (1973) model would have these three elements: it would (1) evaluate demography throughout the life cycle, (2) use closely-related

annuals and perennials, and (3) evaluate the performance of each life history with respect to the other in the habitat of each, or along a gradient of some characteristic of the habitat.

In this study we set out to perform such a test of the Charnov and Schaffer (1973) model. We evaluated seedling survival, fecundity, and adult survival of two closely related species, one of which is annual and the other perennial, in two trials of a reciprocal common garden experiment. The two gardens differed in temperature and precipitation in a manner reflecting the climate of origin of the perennial vs. the annual species. The gardens received natural precipitation. In addition, we manipulated soil moisture by applying water via drip irrigation at three levels, to try to capture the range of possible year types with respect to water availability experienced by each species in the wild within a single year. In the first trial of the experiment, we also attempted to quantify the trade-off between fecundity and subsequent survival by experimentally manipulating reproduction. Using these data we evaluated two predictions that follow from the Charnov and Schaffer (1973) model: first, that perennial fitness should be greater than annual fitness in the garden reflecting the perennial's climate, in the manner shown in Equation 1 in Figure 1. Second, we evaluated whether annual fitness was greater than perennial fitness in the annual's climate, in the manner set forth in Equation 2 in Figure 1.

2. Methods

2.1 Species

This investigation was conducted with two species in the Section *Anogra* of the genus *Oenothera* (Onagraceae): a perennial (*O. californica* ssp. *avita*) found in the Mojave and the southern Great Basin Deserts, and an annual (*O. arizonica*) found in the Sonoran Desert. These two are very closely related and, based on cytogenetic data and the pollen fertility of experimental hybrids (Klein 1962, 1964, 1970; Wagner 1993, 1998), were both considered subspecies of either *O. californica* or *O. avita* until recently. The annual was given species status by Wagner (1998) in part because it was the only annual subspecies of *O. californica*. This suggests that the direction of the evolutionary transition was from perennial to annual. Hereafter we will refer to *O. arizonica* as “the annual” and to *O. californica* ssp. *avita* as “the perennial”.

In the wild, both species are winter-active plants. Seeds typically germinate in the fall, between September and November (Appendix B). Seedlings grow in a rosette form until some time in the spring, when stems elongate and reproductive structures develop (January-March). Flowering and fruiting occur some time in spring or early summer (January-June), depending on soil moisture availability and the timing of germination (Appendix B). The annual does not survive past June in a vegetative state. The perennial can, but individuals that do so typically have little or no green, aboveground biomass (Appendix B). If summer rains are sufficient, the perennial may revive and even flower and fruit again. More often, individuals of the perennial surviving after their first

reproductive bout resprout from the base or produce new rosettes via underground rhizomes in the following fall or spring (Appendix B). Both species have seed banks: viable seeds are found in the soil after germination has concluded but before new seed rain (Appendix B).

2.2 Experimental design and execution (Trial 1)

We conducted two trials of the experiment, to obtain balanced data on three life stages: seedling survival, fecundity, and adult survival. In the first trial our primary goal was to gather balanced data on the two later life stages, fecundity and adult survival, whereas in the second trial our primary interest was in gathering data on pre-reproductive survival (though all three types of data were collected from each trial). The two common gardens were located at the University of Arizona's Campus Agricultural Center in Tucson, Arizona (which we refer to as the Farm) and at Columbia University's Biosphere II Center near Oracle, Arizona. The Farm is adjacent to the Rillito River, where *O. arizonica* was found in the past, hence this location accurately reflects the climate where the annual is found. The Biosphere II Center, though outside of the perennial's range, is similar climatically to the place where the perennial seeds were collected. Based on long-term records from the nearest weather stations, the Biosphere has a very similar temperature regime to Kingman, Arizona, near the perennial seed sources (Figure 2a), but receives more rain on average (Figure 2b). The actual amount of precipitation at the Biosphere during this study was, in most months, less than or comparable to the average amount of precipitation near the perennial seed sources (Figure 2b).

Three raised beds were constructed at each common garden location (Figure 3). Each bed contained a 9:1 mixture of commercial mortar sand and field soil, bordered by concrete blocks. This soil mixture approximated the loose sandy or gravelly soils in which *O. arizonica* and *O. californica* ssp. *avita* are found (Klein 1970). The interior edges of the concrete blocks created a bed space 150 cm wide by 480 cm long. The soil was 35 cm deep. The beds were divided into thirds using sheets of plexiglass to separate water treatments. These plexiglass barriers were inserted after the plants were in the beds (between May 14 and 22, 2001), without any obvious effect on the plants. We constructed a fence around the beds to exclude vertebrate herbivores.

Seeds were collected from two natural populations of each species in the spring of 2000. The two perennial source populations are on the eastern slopes of the Cerbat and Peacock mountains, respectively, near Kingman, Arizona. They are found at 35° 17' N 114° 03' W (elevation 1,150 m) and 35° 15' N 113° 40' W (elevation 1,210 m). The two annual source populations are on the banks of the Gila and Hassayampa Rivers, respectively, at 33° 20' N 112° 38' W (elevation 270 m) and 33° 29' N 112° 45' W (elevation 300 m). These sites are described in more detail in Appendix B. At each site, seeds were collected from four plants, so that we had four groups of seeds per population related at least as maternal half-sibs. Seeds within the annual sibships may have been related even more closely, since the annual is self-compatible (Klein 1970). Plants were propagated from these seeds in December of 2000. Though we kept track of the sibship identity of plants, ultimately we were unable to analyze sibship as a factor in the experiment because seeds from the Hassayampa site (of the annual) germinated at such a

low rate that there were enough plants of only one Hassayampa sibship for a fully replicated design with respect to other factors in the experiment. All other populations were represented by four sibships.

Plants were raised in a greenhouse in 10-cm² pots until they were transplanted into the common gardens in the first week of March, 2001. The plants were relatively large at the time of planting (see Results) and some of the annuals were already flowering. Plants from each sibship were planted into the gardens in a balanced fashion with respect to bed, water treatment, and garden location. In total, 77 vs. 70 plants of the perennial vs. annual were planted at the Biosphere, and 85 vs. 62 plants of the perennial vs. annual were planted at the Farm, respectively. Plants were planted at a density of one per 900 cm², with a 15-cm buffer along the edge of each bed (Figure 3). Individual plants were randomly assigned one of twenty possible 900-cm² areas within each third of a bed (Figure 3).

To ensure pre-reproductive survival (and hence that we would obtain balanced fecundity data), both water and nutrients were provided generously in the first 11 weeks after transplanting. Immediately after planting into the gardens, plants were given approximately 250 mL of a fertilizer solution (3.24 g/L of Miracle-Gro). This solution was applied once per week for the following four weeks. We used a drip irrigation system on an automatic timer to supply water to the plants. All plants received the same amount of water before the plexiglass barriers separating water treatments were in place. Initially this was 15 minutes once per day, then 15 minutes once every three days. After the plexiglass barriers were in place, at the time of the first reproductive census (May 22

and 23, 2001), a water treatment with three levels was applied in a randomized complete blocks design, with each bed a block (Figure 3). These three levels were 15 minutes of water once every three, five, and seven days, respectively. On June 11, 2001, the medium and low water treatments were adjusted to 15 minutes of water once every seven days, and no supplemental water, respectively. These final water levels were applied to the Trial 1 plants for the remainder of the experiment.

In addition to the water treatments, we also applied a reproductive effort treatment at three levels: suppression, augmentation, and a control. These treatments were applied to the perennials in each garden between April 21 and 24, 2001, in an attempt to augment the trade-off between fecundity and subsequent survival. We suppressed reproductive effort by clipping 2 out of every 3 flower buds present on the plants at that time. Following the method used by Reekie and Reekie (1991), we applied a 1M solution of gibberellic acid to plants to augment reproductive effort. We applied gibberellic acid to individual plants by surrounding a given plant in a large oven bag and then misting the plant inside the bag thoroughly with the gibberellic acid solution. Control plants received neither the gibberellic acid nor had flower buds removed. Perennial plants were randomly assigned to one of these three treatments in a balanced fashion with respect to the other factors in the experiment (garden location, garden bed, third of a garden bed, population, and sibship).

2.3 Modifications made in Trial 2

Certain modifications to the design described above were made in the second trial. A new set of beds was constructed for the second trial, but the interior space of these beds measured 150 cm by 300 cm, with room for 12 plants each occupying 900 cm² per third of a bed, rather than 20. There were four such beds in the second trial, rather than three. The plexiglass barriers were inserted as the beds were constructed, rather than after plants had been planted. Seeds collected in the spring (2001) from four plants per population were used to propagate plants, just as in Trial 1, but the seeds from a given population were mixed together before propagation, so that we did not know the sibship identity of seeds. Plants were propagated in December of 2001 but were transplanted into the gardens six weeks earlier (in late January, 2002) than in the previous year. As a result, the plants were smaller at the time they were planted (see Results). Three individuals from each population were planted in each third of a bed (i. e. combination of bed, water treatment, and location). We maintained several of the excess plants propagated for Trial 2 in the greenhouse, and sampled leaves from these plants to test for species-level differences in some physiological traits.

In the gardens, we supplied water and nutrients less generously in the second trial, to create more stressful conditions under which pre-reproductive survival could be evaluated. Plants were given two rather than five applications of a weaker fertilizer solution. These included approximately 250 mL of a 0.50 g/L solution of Miracle-Gro at the time of planting, and a similar volume of a 1.56 g/L solution a week later. Immediately after planting, water was provided uniformly and generously. The

frequency of watering was gradually reduced, and on March 8, 2002 water treatments were first applied. By March 22, 2002 the water treatment levels were identical to the first trial (15 minutes once every three, five, and seven days, respectively), but this was nine weeks earlier than in Trial 1. We continued to increase the interval between watering in the medium and low water treatments to once every seven and once every twelve days, respectively, on March 28, 2002. On April 17, we further increased the interval between watering in the low water treatment, to once every 14 days, and by July 30, 2002 supplemental water was eliminated from the low water treatment. We did not apply the reproductive effort treatments in the second trial.

Though our goal in the second trial was to evaluate seedling survival under more stressful conditions, certain unintended biotic sources of stress became problematic during this trial, and ultimately had to be controlled. Two types of herbivores, ground squirrels (*Spermophilus* sp.) and flea beetles (*Altica torquata*, Chrysomelidae), began eating and killing seedlings five weeks after planting, especially at the Farm. Ground squirrels were present only at the Farm, and the population of flea beetles increased more rapidly at the Farm, where it was warmer. The ground squirrels were controlled via baited mouse traps. We attempted to control the beetles with neem extract (Green Light Neem Concentrate, 70% neem extract, diluted to 7.9 mL/L) and Safer Brand Insecticidal Soap (2% by volume), neither of which proved sufficient. Ultimately, we controlled the beetles manually.

2.4 Data collected

We censused plants in the gardens at variable intervals, from once every week to once every six weeks, according to the level of plant activity. Survival was recorded at every census. We recorded size of plants from the time of planting until the time of the first reproductive census. These measurements included rosette diameter, the length of the longest leaf (Trial 1 only), and, once reproductive stems were initiated, the number of stems. We also recorded phenological data during this time: the presence vs. absence of flower buds, flowers, and fruits on each plant. We quantified fecundity (seeds per plant) by multiplying estimates of fruits per plant and seeds per fruit. On smaller plants we simply counted the number of fruits per plant. On larger plants, we counted the number of fruiting stems per plant and then counted fruits on an arbitrary subset ($n=1$ in Trial 1, $n=3$ in Trial 2) of these stems. Plants that continued to produce flower buds, flowers, or new fruits had fruits counted again at the following reproductive census. The majority of fruits sampled for counting seeds per fruit were collected at the time of the first reproductive census, and a few fruits were collected during subsequent reproductive censuses. We collected two of what appeared to be average-sized fruits per plant (in Trial 1) or two randomly-chosen fruits (in Trial 2). These fruits were opened under a dissecting scope, and the number of viable seeds, based on a simple visual inspection, was tallied.

We define adult survival as survival from the time immediately after one reproductive bout to immediately before the time of reproduction in the following year. To estimate adult survival, we continued to monitor the Trial 1 beds after the fall of 2001

and the Trial 2 beds after the fall of 2002. We visited the gardens periodically and removed all seedlings, which we identified by their cotyledons, so as not to confuse new plants with surviving plants. Adults survived via clonal rosettes rather than by resprouting from the base, making it impossible to know with certainty from which of the individuals that we had planted these clones originated. This was not a problem in the Trial 1 beds, because very few clones appeared and they did so within a very limited area. In the Trial 2 beds, however, many clonal rosettes appeared, especially at the Farm. At each visit to the gardens we mapped the location and relative size of clonal plants. We used these maps as well as the census data on the survival of the plants we had planted to make our best guess as to the number and identity of surviving adults.

We sampled leaves from excess plants propagated for Trial 2, which were maintained in a greenhouse, to measure leaf mass per area (LMA), percent carbon, percent nitrogen, the ratio of carbon and nitrogen, and $\delta^{13}\text{C}$ content. We measured leaf area by placing freshly harvested leaves onto a scanner, scanning in their images, and using the public domain NIH Image program (available at <http://rsb.info.nih.gov/nih-image/>) to find their areas. These same leaves were oven dried and weighed to determine their mass. Leaf mass per unit area (LMA) is simply the ratio of these two. These data were collected from a single leaf from each of about 20 plants per population, except the Hassayampa population, for which we had only 8 samples. We selected a random sample of ten of these leaves (except the Hassayampa leaves, of which we used all 8) for further analysis. The leaves were minced with a razor on a glass surface (all surfaces and tools were cleaned with ethanol between samples) and analyzed for $\delta^{13}\text{C}$ on a continuous flow

stable isotope mass spectrometer (Delta Plus, Finnigan MAT Inc.) at the University of Arizona Department of Geosciences. The concentration of $\delta^{13}\text{C}$, which measures leaf-level gas (CO_2) exchange, is viewed as a proxy for water use efficiency (carbon gain per water use; Francey and Farquhar 1982, Farquhar 1989, Schemske and Bierzychudek 2001, Williams and Ehleringer 2000). At the same time $\delta^{13}\text{C}$ measurements were made, the samples were analyzed for percent carbon (%C), percent nitrogen (%N), and the ratio of carbon and nitrogen (C/N).

2.5 Data analysis

Pre-reproductive (seedling) survival was uniformly high and post-reproductive (adult) survival was uniformly low in Trial 1, making a statistical test of the survival data unnecessary. In Trial 2, we used general linear models (PROC GENMOD, SAS Institute 1989) to test for effects on pre-reproductive and post-reproductive survival. In these general linear models, we assumed that the distribution of the response variable (survival) was binomial. We used the logit link function to linearize the data. We report the results of models with species, garden location, water treatment, and their interactions as predictor variables. Test statistics were adjusted for overdispersion.

We used a three-factor analysis of variance to evaluate the fecundity data. We tested fruits per plant, seeds per fruit, and seeds per plant as response variables, \log_{10} -transforming the first and last of these to approximate normality. Given the balanced fecundity data in Trial 1, we tested these variables using a mixed model (PROC MIXED; Littell et al. 1996), in which species, garden location, water treatment and their

interactions were considered fixed effects, while population (nested within species) and bed (i.e. block) were considered random effects. We tested the fecundity data from the perennial plants in Trial 1 with a similar model that included the reproductive effort treatment, garden location, water treatment, and their interactions as fixed effects, and the random effects as above. The fecundity data in Trial 2 were unbalanced because of pre-reproductive mortality, hence these data were tested with a model that included just the three main factors and their interactions (PROC GLM, SAS Institute 1989). Because the data were unbalanced, we used Type III sums of squares in this analysis (other analyses employed Type I sums of squares).

We compare the fitness of each life history, within and between garden locations, by filling in Equations 1 and 2 in Figure 1 with the observed rates of seedling survival, adult survival, and average fecundity. Taking this approach, Equations 1 and 2 must track the number of reproductive plants from one year to the next (rather than seeds). In contrast, our experiment tracked individuals from seed to seed. By filling in the values of seedling survival, adult survival, and fecundity from our experiment into these equations, we make the implicit assumption that these values are time-invariant, given the conditions of each Trial. In the case of the Trial 1 data, we compare fitness between species at each garden location. Comparing fitness at each level of the water treatment makes little sense in Trial 1, since water treatments were applied after two of the three fitness components had been determined. In Trial 2, where water treatments were applied much earlier, we compare fitness between species in each water treatment at each location.

We analyzed data on plant size at the beginning of each Trial using a mixed model (PROC MIXED; Littell et al. 1996) as above with the fecundity data.

Measurements of rosette diameter one week after planting (Trial 1) or at the time of planting (Trial 2) were tested with a model that included species, garden location, water treatment and their interactions as fixed effects, and population (nested within species) and bed (i.e. block) nested within garden location as random effects. In the data from Trial 2, the variance estimate for bed was zero, causing the G matrix to be not positive definite, so we removed this factor from the model.

We used a repeated-measures analysis of the rosette diameter data to compare growth of rosettes at the Biosphere in Trial 2. This was our best data set for analyzing growth. In Trial 1, the plants were planted late enough that much growth had already occurred, and censuses were infrequent. In Trial 2, the high rate of herbivory at the Farm lowered the sample size there early in the experiment, and led to large decreases in rosette diameter that had little to do with growth per se. We conducted a profile analysis, as described by von Ende (1993), which uses both univariate (ANOVA) and multivariate (MANOVA) tests to evaluate the repeated-measures data. We had 17 weekly measurements of rosette diameter from the time of planting until the time of the first reproductive census. We analyzed a subset of these repeated measures, which included the period of peak growth: from the fifth through the tenth censuses (see Results). After the tenth census, rosette diameters of annuals declined (especially in the low water treatment) as the rosette leaves senesced and resources were presumably shifted to reproduction. We used PROC GLM (SAS Institute 1989), including the REPEATED

statement and the PROFILE option, so that the tests were conducted on the differences in rosette diameter between adjacent censuses (i. e. rosette diameter at census 6 minus rosette diameter at census 5, etc.). The model included two main effects, species and water treatment, and their interaction.

We analyzed the phenological data from Trial 2 using proportional hazards regression analysis (PROC PHREG, Allison 1995), also known as survival analysis. We used a model that included species, garden location, water treatment and the four interactions as factors, to evaluate the “risk” for plants in these groups of developing flower buds, flower, and fruits. We then used a likelihood ratio test to compare the full model with reduced models. We report the results of the simplest model that did not differ significantly from the full model, in terms of log likelihood. Because our data were heavily tied, we used the EXACT method in SAS for handling ties (Allison 1995).

The leaf mass per area, percent carbon, percent nitrogen, carbon to nitrogen ratio, and $\delta^{13}\text{C}$ data were analyzed with either a mixed model or a t-test. The only factors for these samples, which came from plants raised in a greenhouse, were species and population. Where the variance estimate of population was zero (%C, $\delta^{13}\text{C}$), we removed population from the model and used a t-test of the effect of species. Where the variance of population was not estimated to be zero (LMA, %N, C/N), we used a mixed model with species as a fixed effect and population (nested within species) as a random effect (PROC MIXED; Littell et al. 1996).

3. Results

3.1 Survival

In Trial 1, seedling survival was high and adult survival was low (Table 1). All annual seedlings survived to produce fruit, whereas 99% and 87% of perennial seedlings survived to produce fruit at the Biosphere and Farm, respectively. The perennials that did not produce fruit did not die early in the experiment; rather, they developed slowly enough that by the time aridity became stressful at each garden these individuals had not yet produced a single fruit. Conditions arid enough to cause mortality occurred earlier at the Farm, explaining lower perennial seedling survival there.

In contrast, adult survival in Trial 1 was exceedingly low (~1%). No annuals survived past the end of the summer, and only one perennial at each location resprouted and produced fruits in subsequent seasons. At the Biosphere, a single perennial, out of 76 alive at the time of reproduction in 2001, resprouted in the low water treatment of one bed in the spring of 2002. We attribute survival to just one individual because the number of clonal rosettes that appeared was small and these rosettes occupied a small area. Similarly, we estimate that at the Farm, a single perennial survived, out of 74 alive at the time of reproduction in 2001. Clonal rosettes appeared in the high water treatment of a single bed in the spring of 2003. Initially, there were few rosettes in a small area, but by the end of the spring, that third of a bed was entirely covered with rosettes. Because adult survival was so low, we were unable to detect any effect of the reproductive effort treatments applied in Trial 1.

Seedling survival was lower in Trial 2 than in Trial 1, as intended (Table 2). But the major difference in pre-reproductive survival occurred between garden locations: 72% of seedlings survived at the Biosphere, whereas only 31% survived at the Farm (out of 144 plants at each location). This was largely due to severe herbivory at the Farm. The results of the general linear model indicate that garden location had a highly significant effect on seedling survival ($p < 0.001$). Perennial seedlings survived at a higher rate than annuals at the Farm (36% vs. 25%, respectively; $n = 72$ plants of each species), and a weaker, opposite pattern was found at the Biosphere (69% vs. 75%, respectively). But these effects were not significant: Species did not significantly affect seedling survival ($p = 0.9603$), nor did the interaction of species and garden ($p = 0.3988$). Water did affect seedling survival significantly ($p = 0.0072$): 44% and 46% of seedlings in the low and medium water treatments survived to reproduce, whereas 65% of seedlings in the high water treatment survived to reproduce. Both interactions involving water also significantly affected seedling survival: the interaction between water and garden location ($p = 0.0039$) and the interaction between water and species ($p = 0.0207$). At the Farm, seedling survival was highest in the high water treatment (40%) and lowest in the low water treatment (15%), whereas at the Biosphere, seedling survival was highest in the high water treatment (90%) but lowest in the medium water treatment (54%). Perennial seedling survival was highest in the high water treatment (73%) and lowest in the low water treatment (33%), whereas annual seedling survival was highest in the high water treatment (56%) but lowest in the medium water treatment (40%). The three-way interaction of water, garden, and species was not significant ($p = 0.9642$).

Adult survival was considerably higher in Trial 2 than in Trial 1. Annuals did not survive past the end of the summer, but a fraction of perennials did. Contrary to what we expected, adult survival (of perennials) was higher at the Farm (88%) than at the Biosphere (26%). The results of the general linear model testing post-reproductive survival (of perennials) indicated that garden location significantly affected adult survival ($p < 0.001$). Adult survival was lowest in the low water treatment, across gardens and within each garden, but the effect of water was not significant ($p = 0.8998$), nor was the effect of the interaction between water and garden location ($p = 0.1443$).

3.2 Fecundity

Average seed output per plant was high in Trial 1: on the order of 10^3 or 10^4 (Table 1). Species and garden location each had a marginally significant effect on seed output ($p = 0.05$ and $p = 0.07$, respectively; Table 3). Annuals produced more seeds than perennials at both locations, and, averaging across species, more seeds were produced at the Biosphere than at the Farm (Figure 4a). The interaction between garden location and species had a very significant effect on seed output (Table 3). Each species produced more seeds in the garden reflecting its climate of origin (Figure 4a). The interaction of species and water treatment also significantly affected seed output (Table 3). Because water treatments were applied after most fruit were set, especially on the annual plants, we consider this result to not be meaningful. The reproductive effort treatment did not affect the production of fruits ($p = 0.4507$), seeds per fruit ($p = 0.7512$), or seeds per plant ($p = 0.7151$) on perennial plants. Nor were any of the interactions terms involving the

reproductive effort treatment significant ($p > 0.3324$). The gibberellic acid probably would have been more effective had it been applied earlier, and clipping flowers would have been more effective had we clipped weekly instead of just once. Because the reproductive effort treatment had no effect, we do not discuss it further.

We decompose the fact that annuals produced more seeds than perennials in both gardens into two lower-level variables: fruits per plant and seeds per fruit. When we examine the final estimate of fruits per plant, we find that perennials produced as many fruits as annuals at the Biosphere (Figure 4b). By the end of the summer, species did not significantly affect fruit production (Table 3), although annuals produced more fruits than perennials early in the season at the Biosphere (data not shown). Summer fruit production by perennials at the Biosphere was critical for them to match annual fruit production there. However, annuals produced more seeds per fruit than perennials in both gardens (Figure 4c). Species had a marginally significant effect on the number of seeds per fruit, whereas garden location and the interaction between species and garden location were not significant effects (Table 3). As a result, annuals produced more seeds per plant than perennials, even at the Biosphere, where perennials and annuals had produced comparable numbers of fruits.

In Trial 2, where conditions were more stressful, average seed output per plant varied in the range of 10^2 or 10^3 (Table 2), an order of magnitude less than in the first trial. Also in contrast to the first trial, annuals and perennials produced comparable numbers of seeds per plant; species did not significantly affect seed output (Fig 5a; Table 4). This was true in both gardens, so the effect of the interaction between species and

garden location was not significant (Fig 5a; Table 4). There was a trend for plants at the Farm to make more seeds than plants at the Biosphere: average seed output was 3,619 vs. 1,873 seeds in the two gardens, respectively. But there was considerable variation in seed output at the Farm, probably because of herbivory, so that the effect of garden was not significant (Figure 5a; Table 4). The water treatments, which were applied earlier and were more extreme than in Trial 1, significantly affected seed output (Table 4). In general, plants that received more water produced more seeds (Figure 5b). No other effects were significant (Table 4).

While perennials and annuals produced indistinguishable numbers of fruits per plant in Trial 2 (Figure 5c; Table 4), annuals again produced significantly more seeds per fruit than perennials (Figure 5e; Table 4). Garden location significantly affected the number of fruits per plant and seeds per fruit (Table 4), but in opposite directions: plants at the Farm made more fruits (Figure 5c), whereas plants at the Biosphere produced more seeds per fruit (Figure 5e). Water affected fruit production (Figure 5d), but not seed production per fruit (Figure 5f; Table 4).

3.3 Fitness

Annuals outperformed perennials in both gardens in the first Trial (Table 1), but the pattern was reversed in the medium and high water treatments in the second Trial (Table 2). Substituting the values of seedling survival, adult survival, and fecundity estimated in Trial 1 into the Charnov and Schaffer (1973) models (Eq. 1 and 2, Figure 1), fitness (the finite rate of increase) was 6.9 times greater among annuals than among

perennials in the annual's climate (the Farm), and 1.9 times greater in the analog of the perennial's climate (the Biosphere; Table 1). Fecundity and seedling survival, which contributed most to fitness, were higher among annuals than perennials. The remaining fitness component in the Charnov and Schaffer (1973) model, adult survival, was greater among perennials than annuals, but had little impact on the finite rate of increase.

Using the Trial 2 data, we compare annuals vs. perennials in each water treatment at each garden location (Table 2). Seedling survival, fecundity, and the finite rate of increase of annuals were greater than those of perennials in the low water treatment (Table 2). Perennial seedling survival was higher than annual seedling survival in the medium and high water treatments in both gardens, and perennial fecundity was higher than annual fecundity in the high water treatment at the Biosphere (the "perennial" garden), and in the medium water treatment at the Farm (the annual garden). Perennials exceeded annuals in terms of adult survival again, by much more than in Trial 1, but this parameter still contributed little to fitness compared to fecundity and seedling survival. The net result was that annual fitness was 8.6 times greater than perennial fitness in the low water treatment at the Farm, and 2.6 times greater in the low water treatment at the Biosphere. In the medium water treatment, perennial fitness was 2.6 times greater than annual fitness at the Farm, and about equal to annual fitness at the Biosphere. In the high water treatment, perennial fitness was about 53% greater than annual fitness at the Farm and about 6% greater at the Biosphere.

3.4 Size and Growth

The plants were much larger at the beginning of Trial 1 than they were at the beginning of Trial 2, and in Trial 1 the annuals were significantly larger than the perennials. Average rosette diameter was 14.1 cm among perennials and 18.9 cm among annuals one week after planting in Trial 1. This difference between species was significant ($F_{1,2}=17.28$, $p=0.053$). No other fixed effects in the model that tested these data were significant (garden location, water, or the four interactions; $0.780 \geq p \geq 0.095$). In contrast, in Trial 2, the two species did not differ in rosette diameter at the time of planting ($F_{1,2}=0.00$, $p=0.971$). Average rosette diameter was 4.31 cm among perennials and 4.29 cm among annuals. No other fixed effects in the model testing the initial rosette diameter data from Trial 2 were significant (garden location, water, or the four interactions; $0.852 \geq p \geq 0.104$).

The rosette diameter data from Trial 2 at the Biosphere, the subject of the repeated-measures analysis, illustrate that annual rosettes grew faster than perennial rosettes (Figure 6). The MANOVA test indicated that time significantly affected rosette diameter (Table 5); that is, the slopes of the lines in Figure 6a are significantly different from zero. These tests also indicated that the slopes of the lines in Figure 7a are not parallel with respect to either species or water treatment; that is, the time \times species and time \times water treatment effects were significant (Table 5). Average change in rosette diameter per week was greater among annuals than perennials (Figure 6b). The effect of water on growth between census 5 and census 10 does not make sense. Among both annuals and perennials, plants grew most rapidly in the high and low water treatments,

and grew less rapidly in the medium water treatment (Figure 6b). However, later censuses show that in both species, plants in the low water treatment were smallest (Figure 6a). Peak sizes were shifted left in the low water treatment relative to the medium and high water treatments, as we would expect (Figure 6a). These data suggest that water stress had not yet occurred between census 5 and census 10, the period in which we analyzed growth. The three-way interaction, time \times species \times water, did not significantly affect rosette diameter (Table 5). In other words, the slopes of the lines in Figure 6a (i. e. growth) responded similarly to the different levels of the water treatment in both species. The repeated-measures ANOVA indicated that species and water treatment each significantly affected rosette diameter, but that their interaction did not (Table 6). This test, which evaluates the elevation or height of the lines in Figure 6a, confirms that the annual plants were significantly larger than perennial plants, and that the rosette diameters of plants in different water treatments differed significantly, in the pattern shown in Figure 6a.

3.5 Phenology

Data on presence vs. absence of flower buds, flowers, and fruits from Trial 2 show that reproductive phenology is shifted earlier in the annual than in the perennial (Figure 7). This pattern was evident in the temperature regimes of both gardens. At the time of the first census of flower buds, ten weeks after planting, 74% of annuals at the Biosphere and 39% of annuals at the Farm had flower buds. At that same point in time, 5% of perennials at the Biosphere and 3% of perennials at the Farm had flower buds.

Similar patterns are evident with respect to flowering and fruiting in Figure 7b and c. The survival analysis of the phenological data indicated that species significantly affected the development of flower buds, flowers, and fruits ($p < 0.0001$). The water treatment also significantly affected the development of flower buds ($p = 0.0022$), flowers ($p = 0.0008$), and fruits ($p = 0.0011$). A priori, one would expect the plants at the Farm to flower and fruit earlier, simply because the environment there is warmer, but this was not the case. Delayed reproduction in plants at the Farm relative to the Biosphere (Figure 7) was probably the result of widespread damage due to herbivory. The survival analysis indicated that garden location significantly affected the development of flower buds and fruits ($p < 0.0001$), but did not affect the development of flowers ($p = 0.5294$). The interaction of species and garden location significantly affected the development of flowers ($p = 0.0057$), and the interaction of species and water treatment significantly affected the development of flower buds and fruits ($p = 0.0658$ and $p = 0.0264$, respectively).

3.6 Leaf-level physiological measurements

Leaf mass per area differed significantly between the annual and the perennial ($F_{1, 2.16} = 43.41$, $p = 0.018$; Figure 8), but none of the other leaf-level traits that we measured did. Average leaf mass per area was 4.12 mg/cm^2 for perennial leaves and 3.24 mg/cm^2 for annual leaves. On average, annual leaves were 21% less dense than perennial leaves. In a subset of the same leaves, we found no difference between the species in %C ($t = 0.786$, $df = 36$, $p = 0.437$), %N ($F_{1, 2.02} = 1.08$, $p = 0.408$), C/N ($F_{1, 2.02} = 0.94$, $p = 0.434$), or

$\delta^{13}\text{C}$ ($t=0.162$, $df=36$, $p=0.873$). The trends in the carbon and nitrogen data are as we would expect, given that the annual leaves grow more rapidly and are less dense: percent carbon was higher in the perennials than the annuals (40.11% vs. 39.79%), percent nitrogen was higher in the annuals than the perennials (4.77% vs. 4.08%), and the carbon to nitrogen ratio was higher in the perennials than in the annuals (10.35 vs. 8.69). Average $\delta^{13}\text{C}$ in the perennial leaves was slightly more positive than in the annual leaves (-31.16 vs. -31.19). More positive values for $\delta^{13}\text{C}$ are indicative of higher water use efficiency (Francey and Farquhar 1982, Farquhar 1989).

4. Discussion

Contrary to the predictions of the Charnov and Schaffer (1973) model, annual fitness (finite rate of increase) was not always greater than perennial fitness in the annual's climate, nor was perennial fitness always greater than annual fitness in the garden reflecting the perennial's climate. Instead, the direction and magnitude of the difference between the finite rates of increase of annuals vs. perennials depended upon the conditions experienced by the plants. In Trial 1, where nutrients and water were provided generously, fitness was greater among annuals than perennials in both gardens. Substituting in estimates for the parameters in the Charnov and Schaffer (1973) model, annuals outperformed perennials by a factor of 6.9 to 1 in the garden in the annual's climate (the Farm) and 1.9 to 1 in the garden reflecting the perennial's climate (the Biosphere). We made sure that seedling survivorship was high in Trial 1. As a result, the

finite rates of increase were dominated by seed output. Seed production was greater among annuals than perennials in both gardens, even though perennial fruit production caught up to annual fruit production by late summer at the Biosphere, because annuals produced more seeds per fruit in both gardens.

In Trial 2, where conditions were more stressful than in Trial 1, the gap between annual and perennial fitness closed, especially in the higher water treatments. The plants were planted six weeks earlier and were about one-fourth the size at the time of planting than in Trial 1 (4.3 cm vs. 14 to 19 cm), they received two rather than five applications of a nutrient-rich solution, and water treatments were applied nine weeks earlier. In addition, herbivory was a major source of damage, even mortality, in the second trial. Accordingly, seed output was about an order of magnitude less in the second trial. In the low water treatment, fitness of annuals was 8.6 times greater than fitness of perennials in the annual's climate (the Farm) and 2.6 times greater in the garden reflecting the perennial's climate (the Biosphere). Fitness of perennials was equal to or greater than fitness of annuals in the medium and high water treatments of each garden.

While the second trial was more stressful than the first, the finite rates of increase that we obtained were large (from 51 to 2,707), suggesting the conditions were still relatively good for growth and reproduction of these species. These numbers are not quite as unrealistic as they may seem, since we did not account for mortality in the seed stage in this study. In a separate study of these two species, seed survival in two wild populations of the annual and three of the perennial in two years ranged from 2.5% to 64% among seeds that spent a year in the seed bank, and from 3.3% to 81% among seeds

that germinated in the same year of their production, without differing in a consistent way between the species (see Appendix B). Finite rates of increase in these wild populations in four years, not accounting for seed mortality, ranged from zero to 881 (see Appendix B). Compared to numbers obtained from wild populations, the conditions of the second trial were comparable to or better than the best years that we documented in wild populations.

In both trials, perennials outperformed annuals with respect to post-reproductive survival, in the sense that the annuals had no post-reproductive survival. This was expected, but our estimates of perennial adult survival varied in ways that we did not expect. Adult survival was low in the less stressful trial, and high in the more stressful trial. In Trial 1, only ~1% of perennials that reproduced survived to the time of reproduction in the following year. These plants were large at the time of their first reproductive bout, and produced 10^3 or 10^4 seeds, suggesting that they had experienced favorable conditions, but only one individual in each garden survived thereafter. In Trial 2, adult survival was higher, especially in the garden in the annual's climate (the Farm), where herbivory was more severe. Why would adult survival be higher under more stressful conditions? One possibility is that the perennial is plastic in habit. It may behave more like an annual when conditions are good and more like a perennial when conditions are poor. This would be consistent both with the contrast between the two trials and between the two gardens in the second trial. Estimates of non-clonal post-reproductive survival in three natural populations of the perennial in four years were typically around 3% (Appendix B), more like the values in the first trial of this

experiment, but they were sometimes as high as 10% or 13%, and post-reproductive survival that includes survival via clonal rosettes would be higher. In both trials of this experiment, adult survival contributed little to the finite rate of increase, relative to seedling survival and fecundity. In the wild, we found that seedling survival occasionally failed, and either post-reproductive survival or seed bank survival then set an upper limit on the rate at which the population declined (Appendix B).

Other data from Trial 2 point to additional differences between the annual vs. the perennial, lending insight into the conditions that allow one to outperform the other. The repeated measures of rosette diameter at the Biosphere indicated that annual rosettes grew faster than perennial rosettes, even under the cooler temperature regime that reflects the perennial's climate. The phenological data showed that the annuals also developed flower buds, flowered, and fruited earlier than the perennials, and did so in both gardens. That the annuals were significantly larger at the time of planting in Trial 1, and some were flowering, is consistent with both of these patterns. These results, obtained in a common garden setting, suggest that differences in above-ground growth and reproductive phenology between the two species have a genetic basis. The perennial intrinsically grows more slowly, and hence it takes more time to achieve the size necessary for successful reproduction. We also found that, among plants grown together in a greenhouse, leaves of the perennial had 27% more mass per area (LMA) than leaves of the annual. Such a negative correlation between growth rate, or an indicator of growth rate such as net photosynthetic capacity, and LMA has been observed in several comparative studies (Hirose 1988, Reich et al. 1997, Reich et al. 1998, Reich et al. 1999,

Niinemets 1999, Mediavilla et al. 2001, Wright et al. 2001, although see Mediavilla and Escudero 2003).

With its high growth rate, the annual can progress from seed to seed rapidly, and can be viewed as a stress-avoider, in the manner described by Solbrig and Orians (1977) and Smith et al. (1997). The annual excels at rapidly capitalizing on good conditions, building up biomass and transforming that biomass into seeds. In the first trial, conditions were favorable throughout the seedling stage, so the higher above-ground growth rate of annuals allowed them to become larger and hence produce more seeds in both gardens. In the second trial, conditions were initially good, but became stressful, and did so earlier in the low water treatment than in the medium and high water treatments. In the low water treatment, annuals were able to transform initially good conditions into more seeds than the perennial, because their more rapid growth caused them to be larger by the time that conditions deteriorated. The perennial, because of its slower growth rate, is less successful at avoiding stress. In both trials, some perennials survived to the time of reproduction but failed to reproduce. These plants were unable to grow fast enough to reproduce before water and high temperature stress became severe, and among those that managed to produce a few flowers, self-incompatibility may have caused fruit set to fail.

While we have a sense from this experiment of the kinds of conditions that favor the annual, we have less direct or clear evidence of the conditions that favor the perennial. The perennial was able to match or outperform the annual under the generally more stressful conditions of the second trial, but it did so only in the medium and high

levels of the water treatment. These data suggest that while the perennial is less successful than the annual at avoiding stressful conditions, it may be better able to tolerate stress. However, other data on tolerance of water stress from this experiment are equivocal. In general, plants from more arid environments have higher LMA (Abrams 1994, Reich et al. 1999, Wright et al. 2001, Wright et al. 2002). Since the perennial that we studied had higher LMA, we might be led to think, by extension, that it is more drought-adapted. However, a comparison of climatic data from throughout the range of our study species showed that the places where the annual is found are significantly more arid throughout most of the year (the exceptions are July and August; Appendix B). In our case then, higher LMA is associated with lower aridity. We found no difference between the species in $\delta^{13}\text{C}$, a proxy for water use efficiency (carbon gain per unit water). But our $\delta^{13}\text{C}$ data were collected from plants grown in the greenhouse that did not experience water stress.

Another form of stress experienced by the perennial is extreme cold. We have shown elsewhere that plants of the perennial are much more likely to experience a hard freeze, in the Mohave and southern Great Basin Deserts, than plants of the annual, in the Sonoran Desert (Appendix B). There is some indication from other studies that LMA and cold-tolerance are correlated. In a study of winter rape (*Brassica napus* var. *oleifera*; Kacperska and Szaniawski 1993), chilling treatments increased LMA, and in a study of *Polygonum cuspidatum* (Kogami et al. 2001), leaves from populations at 2500 m above sea level had higher LMA than leaves from populations at 10 m above sea level. In a study of seedlings of 52 European woody species, Castro-Diez et al. (2000) found that

leaves with higher LMA had lower water content. High water content has long been known to make leaves more vulnerable to frost damage (Daubenmire 1974, Berry and Bjorkman 1980, Berry and Raison 1981, Long and Woodward 1988). On the other hand, Gurvich et al. (2002) found no significant relationship between leaf resistance to freezing and LMA among 41 Angiosperm species of diverse plant functional types.

There are a number of other differences that we observed between the annual and the perennial, which persisted in the common gardens, which are thought to relate to temperature stress. While both species have a rosette growth form, the perennial leaves press more closely to the ground, and are broad and entire, whereas the annual's leaves lay more loosely on the ground, or not on the ground at all, and are narrow with dissected margins. Mulroy and Rundel (1977) describe broad, entire leaves closely appressed to the soil as an adaptation that maximizes leaf temperature, leaves lifted off the soil surface as an adaptation to avoid extreme high temperatures at the soil surface, and leaf dissection as a trait that decreases boundary layer effects, increasing the exchange of air at the leaf surface and hence the rate of photosynthesis. These differences suggest that the traits selected for in the annual increase its photosynthetic rate and extend its survival in the face of the extreme high temperatures that ultimately terminate reproduction, whereas the traits selected for in the perennial increase its survival in the face of life-threatening cold temperatures that occur in the middle of the season of seedling recruitment and growth.

Whether the perennial excels at tolerating water or cold stress, or both, is unclear from this experiment, but it seems likely that the perennial has a strategy of tolerating

stress, compared to the stress-avoiding strategy of the annual. In this sense, the slower growth rate of the perennial is not adaptive in and of itself; rather, it may be viewed as a constraint resulting from a trade-off between stress-tolerance and high growth rate. This idea could be tested by evaluating the response of the annual vs. the perennial to experimental conditions of cold and water stress. The results of this experiment were similar to those of Oka (1976) and Law et al. (1977), in that the conditions of our gardens tended to favor the annual strategy. However, Oka (1976) and Law et al. (1977) viewed the axis of life history variation that they examined in terms of r- vs. K-strategies. Here we suggest that the relevant axis of life history variation is one between stress-avoidance and stress-tolerance. We suggest that this axis of stress-avoidance vs. stress-tolerance may be more relevant for related desert annuals and perennials, and deserts are where annuals are most numerous (Raunkiaer 1934, Daubenmire 1978, Gurevitch et al. 2002).

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Table 1. Fitness components (seedling survival, fecundity, and adult survival) and fitness of the annual *Oenothera arizonica* and the perennial *O. californica* ssp. *avita* in a reciprocal common garden design. Data are from Trial 1 of this experiment. Comparisons are shaded if the value for perennials is greater than the value for annuals.

Parameter	“Perennial garden”	Annual garden
	Per vs. Ann	Per vs. Ann
seedling surv (c)	0.99 < 1.0	0.87 < 1.0
fecundity (B)	12,226 < 22,468	4,863 < 29,274
adult surv (p)	0.013 > 0	0.014 > 0
λ (finite rate of increase)	12,104 < 22,468	4,231 < 29,274

Table 2. Fitness components (seedling survival, fecundity, and adult survival) and fitness of the annual *Oenothera arizonica* and the perennial *O. californica* ssp. *avita* at three water levels in a reciprocal common garden design. Data are from Trial 2 of this experiment. Comparisons are shaded if the value for perennials is greater than the value for annuals.

Parameter	water treatment	“Perennial garden” Per vs. Ann	Annual garden Per vs. Ann
seedling surv (c)	low	0.58 < 0.88	0.08 < 0.21
	med	0.58 > 0.50	0.46 > 0.29
	high	0.92 > 0.88	0.54 > 0.25
fecundity (B)	low	908 < 1,529	630 < 2,097
	med	1,197 < 1,412	5,882 > 3,533
	high	2,721 > 2,684	2,746 < 3,869
adult surv (p)	low	0.07 > 0	1.0 > 0
	med	0.38 > 0	0.83 > 0
	high	0.32 > 0	0.87 > 0
λ (finite rate of increase)	low	527 < 1,346	51 < 440
	med	695 \approx 706	2,707 > 1,025
	high	2,504 > 2,362	1,484 > 967

Table 3. Results of mixed model analyzing fecundity data of the annual *O. arizonica* vs. the perennial *O. californica* ssp. *avita* in Trial 1 of the reciprocal common garden experiment. Location (or “loc”) refers to the garden location: either the Farm (the annual’s climate) or the Biosphere (“the perennial’s climate”). Significant effects are shaded.

Effect	log₁₀(seeds per plant)		log₁₀(fruits per plant)		seeds per fruit	
location	$F_{1, 4.02}=5.72$	$P=0.07$	$F_{1, 4.02}=6.66$	$P=0.06$	$F_{1, 3.95}=1.87$	$P=0.24$
species	$F_{1, 2.08}=18.69$	$P=0.05$	$F_{1, 2.09}=6.20$	$P=0.13$	$F_{1, 1.96}=10.32$	$P=0.09$
H ₂ Otrt	$F_{2, 268}=0.39$	$P=0.68$	$F_{2, 268}=0.23$	$P=0.79$	$F_{2, 279}=0.51$	$P=0.60$
loc*sp	$F_{1, 267}=35.94$	$P<0.0001$	$F_{1, 267}=38.98$	$P<0.0001$	$F_{1, 279}=2.08$	$P=0.15$
loc*H ₂ Otrt	$F_{2, 268}=2.32$	$P=0.10$	$F_{2, 268}=3.14$	$P=0.05$	$F_{2, 279}=0.61$	$P=0.54$
sp*H ₂ Otrt	$F_{2, 268}=3.47$	$P=0.03$	$F_{2, 268}=2.25$	$P=0.11$	$F_{2, 280}=2.88$	$P=0.06$
loc*sp*H ₂ O	$F_{2, 268}=0.32$	$P=0.73$	$F_{2, 268}=0.24$	$P=0.78$	$F_{2, 279}=0.97$	$P=0.38$

Table 4. Results of mixed model analyzing fecundity data of the annual *O. arizonica* vs. the perennial *O. californica* ssp. *avita* in Trial 2 of the reciprocal common garden experiment. Location (or “loc”) refers to the garden location: either the Farm (the annual’s climate) or the Biosphere (“the perennial’s climate”).

Effect	$\log_{10}(\text{seeds per plant})$		$\log_{10}(\text{fruits per plant})$		seeds per fruit	
location	$F_{1, 134}=2.62$	$P=0.11$	$F_{1, 136}=15.80$	$P=0.0001$	$F_{1, 138}=24.54$	$P<0.0001$
species	$F_{1, 134}=3.05$	$P=0.08$	$F_{1, 136}=2.70$	$P=0.10$	$F_{1, 138}=4.21$	$P=0.04$
H2Otrt	$F_{2, 134}=5.37$	$P=0.006$	$F_{2, 136}=6.37$	$P=0.002$	$F_{2, 138}=0.09$	$P=0.92$
loc*sp	$F_{1, 134}=0.17$	$P=0.68$	$F_{1, 136}=0.14$	$P=0.71$	$F_{1, 138}=0.47$	$P=0.50$
loc*H2Otrt	$F_{2, 134}=0.32$	$P=0.72$	$F_{2, 136}=0.27$	$P=0.76$	$F_{2, 138}=1.30$	$P=0.28$
sp*H2Otrt	$F_{2, 134}=1.02$	$P=0.36$	$F_{2, 136}=1.22$	$P=0.30$	$F_{2, 138}=0.09$	$P=0.91$
loc*sp*H2O	$F_{2, 134}=0.99$	$P=0.38$	$F_{2, 136}=1.37$	$P=0.26$	$F_{2, 138}=0.20$	$P=0.82$

Table 5. Results of MANOVA tests of per plant differences in rosette diameter between adjacent censuses at the Biosphere in Trial 2. The rosette diameter data from censuses 5 through 10 were used.

	Value	F	p
Time			
Wilks' Lambda	0.2451	$F_{5, 110} = 67.76$	<0.0001
Pillai's Trace	0.7549	$F_{5, 110} = 67.76$	<0.0001
Hotelling-Lawley Trace	0.0800	$F_{5, 110} = 67.76$	<0.0001
Roy Greatest Root	0.0800	$F_{5, 110} = 67.76$	<0.0001
Time × Species			
Wilks' Lambda	0.8462	$F_{5, 110} = 4.00$	0.0023
Pillai's Trace	0.1538	$F_{5, 110} = 4.00$	0.0023
Hotelling-Lawley Trace	0.1817	$F_{5, 110} = 4.00$	0.0023
Roy Greatest Root	0.1817	$F_{5, 110} = 4.00$	0.0023
Time × Water			
Wilks' Lambda	0.8368	$F_{10, 220} = 2.05$	0.0297
Pillai's Trace	0.1704	$F_{10, 222} = 2.07$	0.0282
Hotelling-Lawley Trace	0.1864	$F_{10, 162.27} = 2.04$	0.0326
Roy Greatest Root	0.1030	$F_{5, 111} = 2.29$	0.0509
Time × Species × Water			
Wilks' Lambda	0.9266	$F_{10, 220} = 0.86$	0.5761
Pillai's Trace	0.0740	$F_{10, 222} = 0.85$	0.5788
Hotelling-Lawley Trace	0.0787	$F_{10, 162.27} = 0.86$	0.5714
Roy Greatest Root	0.0709	$F_{5, 111} = 1.57$	0.1734

Table 6. Results of repeated-measures ANOVA tests of per plant differences in rosette diameter between adjacent censuses at the Biosphere in Trial 2. The rosette diameter data from censuses 5 through 10 were used.

Source	df	MS	F	p
species	1	176.691	5.77	0.0179
water	2	171.330	5.59	0.0048
species×water	2	14.280	0.47	0.6286
Error	114	30.630		

Figure 2. Comparison of (a) average monthly maximum and minimum temperatures and (b) precipitation recorded at weather stations closest to where the perennial seeds were collected (Kingman: \blacktriangle and \triangle) vs. closest to the common garden at the Biosphere II Center (Oracle: \bullet and \circ). Two weather stations are available at each location: Kingman (1901-1967) and KingmanNo2 (1967-1993), and Oracle (1893-1949) and Oracle2SE (1950-2002). The temperature data in (a) are averages from KingmanNo2 ($35^{\circ} 12' N 114^{\circ} 01' W$ at 1,097m) and Oracle2SE ($32^{\circ} 36' N 110^{\circ} 44' W$ at 1,398m), which are closer in elevation to the perennial seed sources and the Biosphere, respectively. The precipitation data in (b) are compiled from all four stations, including Kingman ($35^{\circ} 11' N 114^{\circ} 03' W$ at 1,037m) and Oracle ($32^{\circ} 36' N 110^{\circ} 47' W$ at 1,426m). Also shown (b) is the actual amount of precipitation recorded at the Biosphere II Center, where the “perennial” common garden is located, in the two years of the study, 2001 (\bullet) and 2002 ($*$).

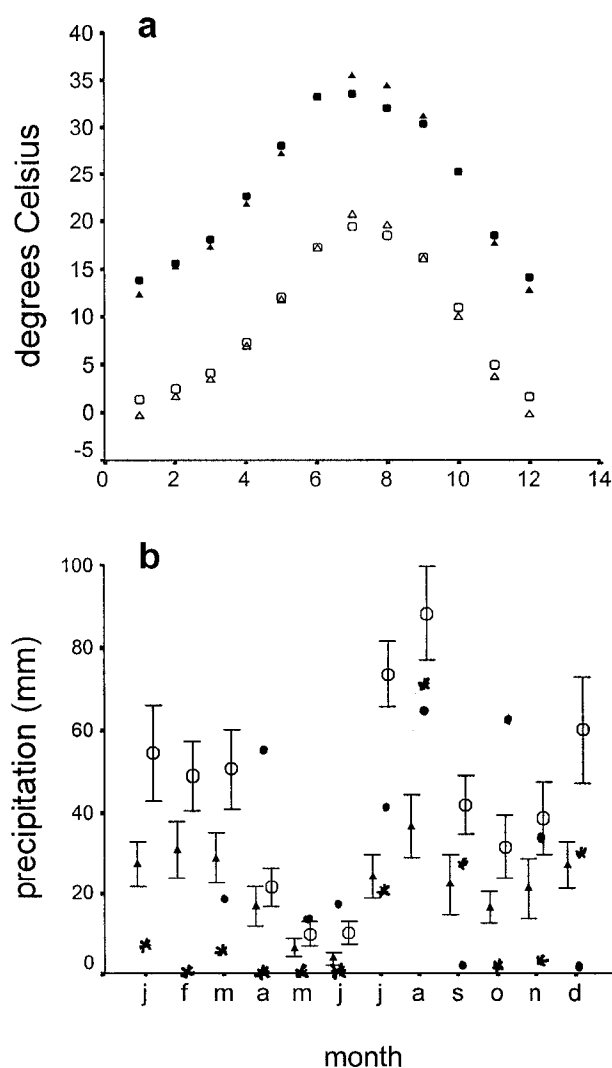


Figure 3. Design of the common garden in the first trial. Each site (Biosphere vs. Farm) had three raised beds, as shown. Each bed was divided in thirds with plexiglass, with room for twenty plants each occupying 900 cm^2 ; each third of a bed received a different water treatment (numbers). Modifications to the garden design in the second trial are described in the text.

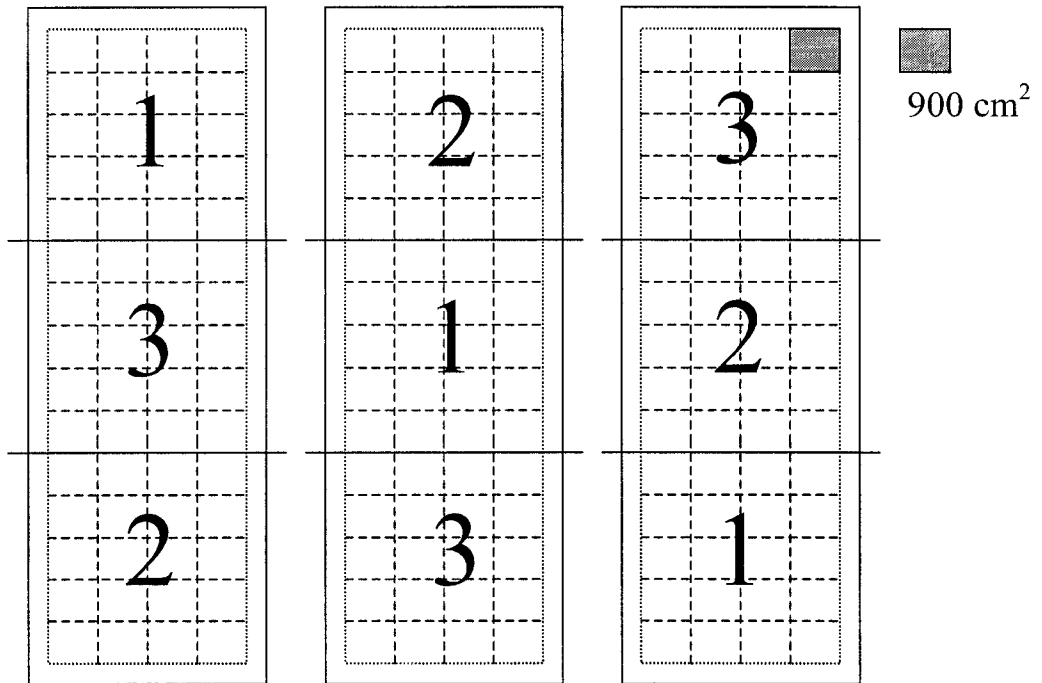


Figure 4. Fecundity of the perennial *O. californica* spp. *avita* (■) and the annual *O. arizonica* (○) in Trial 1 of the reciprocal common garden experiment. One garden is located in the annual's climate (Farm) and the other in a climate reflecting that of the perennial (Biosphere). The three panels are (a) \log_{10} -transformed seeds per plant, (b) \log_{10} -transformed fruits per plant, and (c) seeds per fruit.

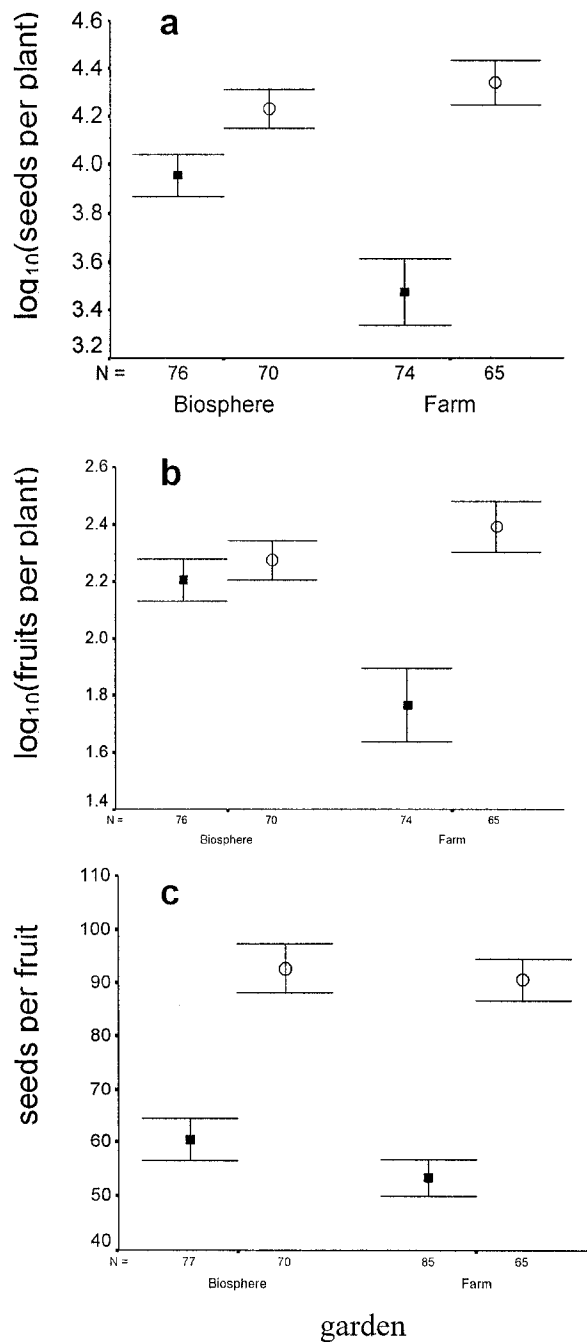


Figure 5. Fecundity of the perennial *O. californica* spp. *avita* and the annual *O. arizonica* in Trial 2 of the reciprocal common garden experiment. One garden is located in the annual's climate (Farm) and the other in a climate reflecting that of the perennial (Biosphere). The data in the six panels are (a, b) \log_{10} -transformed seeds per plant, (c, d) \log_{10} -transformed fruits per plant, and (e, f) seeds per fruit. In panels a, c, and e the data are shown grouped by garden and species (perennial vs. annual, ■ and ○, respectively). In panels b, d, and f the data are shown grouped by species and water treatment level (low, medium, and high, symbolized by Δ , *, and ●, respectively).

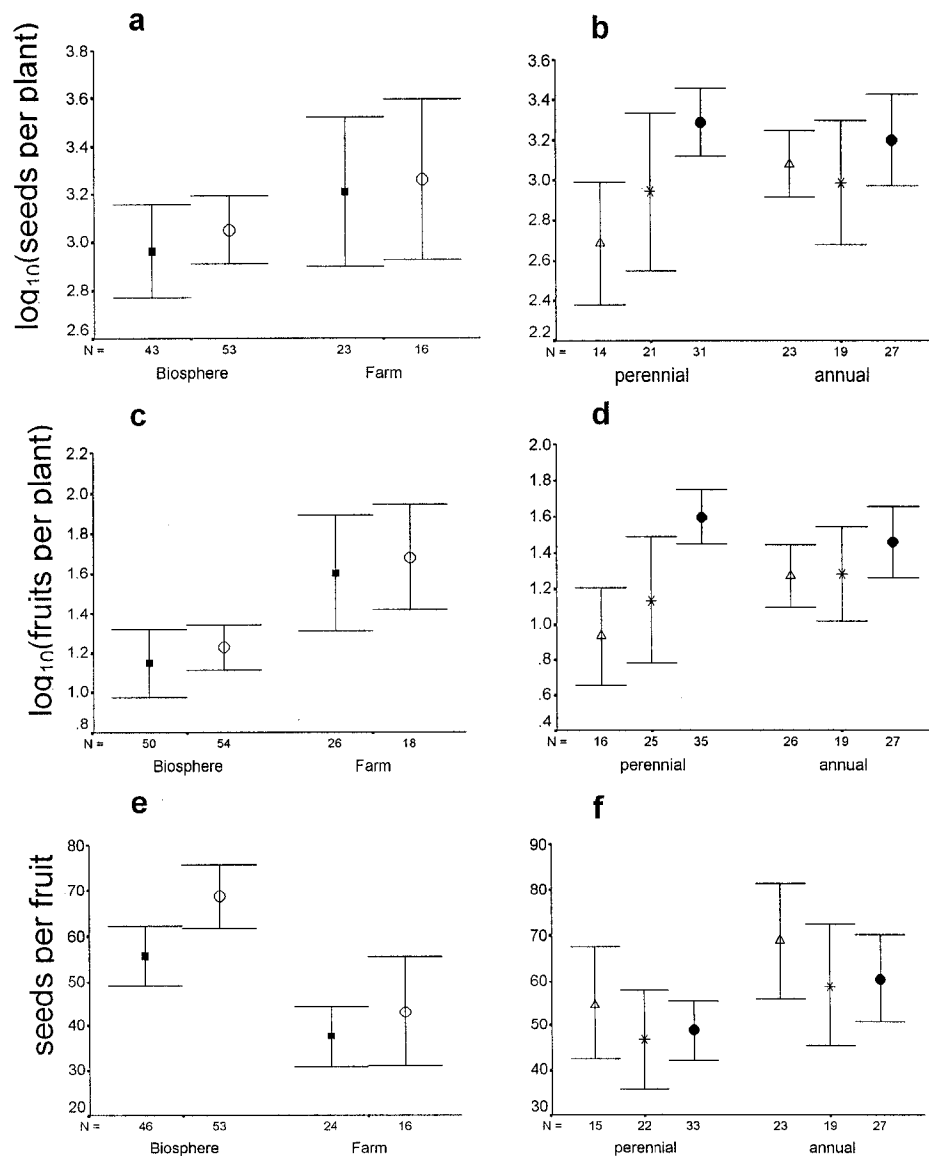


Figure 6. Data from plants of the annual *O. arizonica* (dashed lines) and the perennial *O. californica* ssp. *avita* (solid lines) in the common garden reflecting the perennial's climate (the Biosphere) in Trial 2: (a) average rosette diameter from the time of planting until 14 weeks after planting and (b) average change in rosette diameter per plant per week from four to nine weeks after planting. The vertical dashed lines in (a) indicate the time interval shown in (b). Averages are shown for three levels of a water treatment for each species: the letters H, M, and L at the far right of each panel label the data from the high, medium, and low water treatments, respectively.

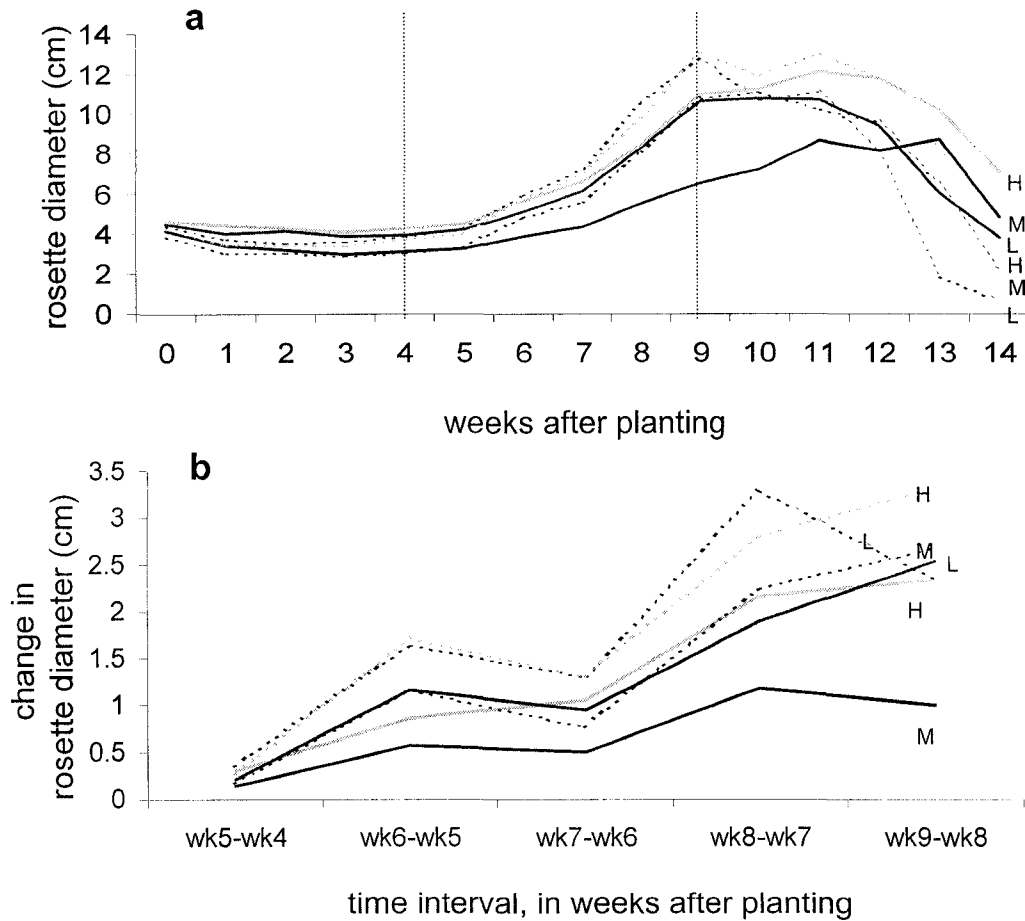


Figure 7. Reproductive phenology of the annual *O. arizonica* (crosses: + and ×) and the perennial *O. californica* ssp. *avita* (squares: □ and ◇) in two gardens, one in the annual's climate (the Farm: + and □) and the other in a climate reflecting that of the perennial (the Biosphere: × and ◇). The fraction of plants with (a) flower buds, (b) flowers, and (c) fruits are shown from Trial 2 of the reciprocal common garden experiment. The plants were planted in the gardens January 25-27, 2002.

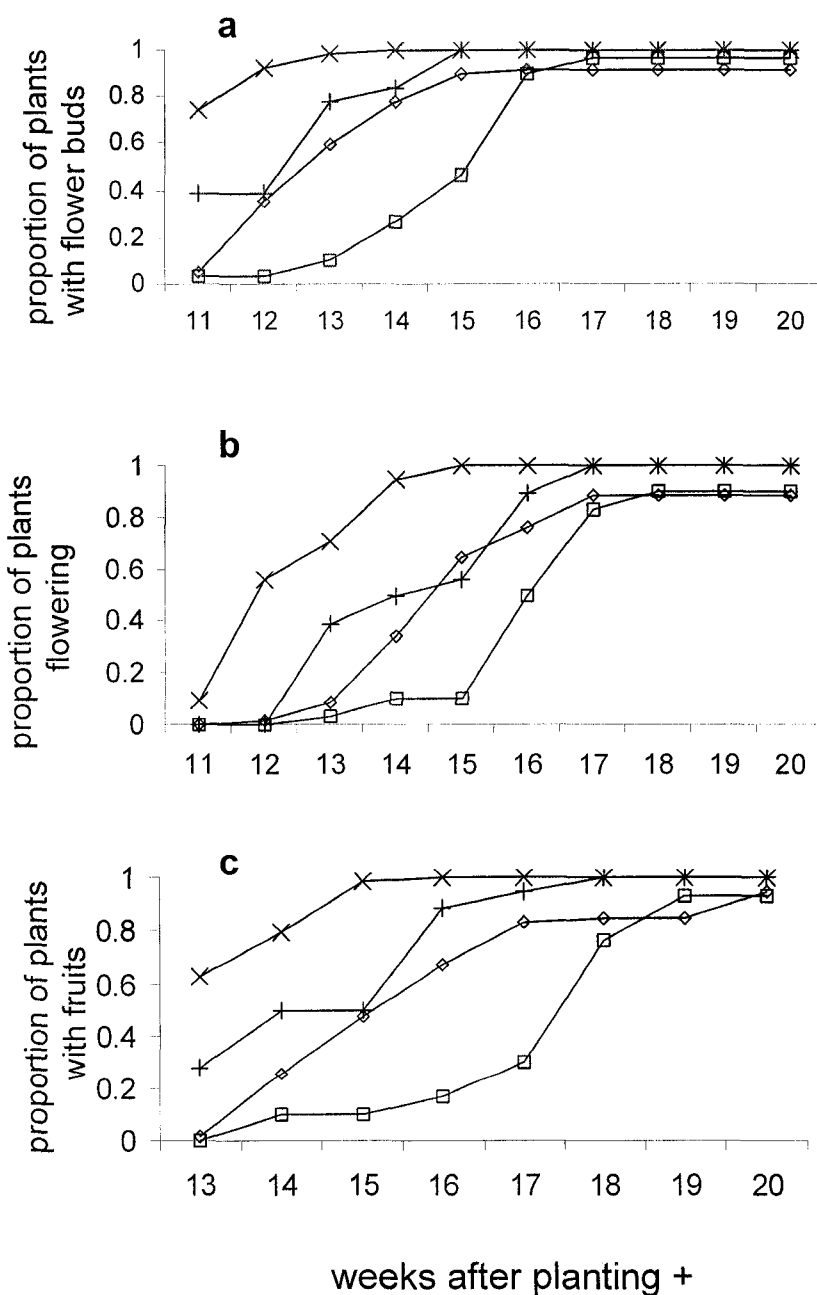


Figure 8. Leaf mass per area of the perennial *O. californica* ssp. *avita* and the annual *O. arizonica*.

