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LIFE HISTORY STRATEGIES IN VARIABLE ENVIRONMENTS:
DEMOGRAPHY, DELAYED GERMINATION AND BET-HEDGING IN A DESERT
ANNUAL PLANTAGO

by

Maria Johanna Clauss

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A Dissertation Submitted to the Faculty of the
DEPARTMENT OF ECOLOGY AND EVOLUTIONARY BIOLOGY

In Partial Fulfillment of the Requirements
For the Degree of

DOCTOR OF PHILOSOPHY

In the Graduate College

THE UNIVERSITY OF ARIZONA

1999

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As members of the Final Examination Committee, we certify that we have read the dissertation prepared by Maria J. Clauss

entitled Life history strategies in variable environments:

Demography, delayed germination and bet-hedging

in a desert annual Plantago

and recommend that it be accepted as fulfilling the dissertation requirement for the Degree of Doctor of Philosophy



D. Lawrence Venable

12 April 99
Date



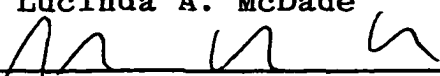
Nancy A. Moran

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Date



J. Bruce Walsh

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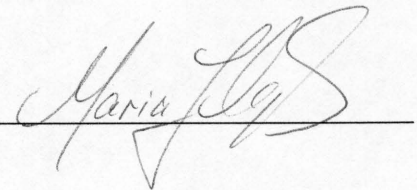
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A handwritten signature in cursive script, appearing to read "Maria Lopez", written over a horizontal line.

ACKNOWLEDGMENTS

I am indebted to the many people who have contributed to this project. For their assistance and insights, I thank my committee: Larry Venable, Lucinda McDade, Nancy Moran, Rob Robichaux and Bruce Walsh. Larry Venable has shared with me his broad knowledge of plant evolutionary ecology, enthusiasm for desert annuals, and his dedication to the perfect analysis. I have also greatly enjoyed the diversity of interests and academic stimulation centered around the weekly meetings of the McDade and Bronstein lab groups. The camaraderie, support and intellectual contributions of a large number of present and past graduate students at the University of Arizona have made lasting and treasured impressions. Much appreciated assistance in the greenhouse, lab and field was provided by Robert Bellsey, Andrew Gardner, Jennifer McGilton, Ken Moriuchi, Caroline Van Hemert and Michael Wagenheim. I thank Organ Pipe Cactus National Monument and Luke Air Force Base for access to the Organ Pipe and Gila Bend sites, respectively. My research could not have been completed without the generous financial assistance of the Department of Ecology and Evolutionary Biology, the Research Training Group in the Analysis of Biological Diversification at the University of Arizona, the Graduate College, the National Science Foundation and the National Science and Engineering Council of Canada.

DEDICATION

To the Sonoran Desert landscape, may it persist in spite of the ravages of civilization.

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ABSTRACT

Temporal variability in the environment can affect population dynamics and life history strategies. Annual plants in desert environments are subject to large fluctuations in precipitation, both within and among years. I used a combination of field and laboratory studies to characterize variability in the populations dynamics and life history of a desert winter annual plant. I conducted demographic studies over four seasons in four populations of Plantago insularis Eastw. [Plantaginaceae] located along a precipitation gradient in the Sonoran Desert. I quantified the fates of germinated and non-germinated individuals by monitoring permanent quadrats and repeatedly sampling the soil seed bank. A fraction of seeds in all populations delayed germination and formed a persistent seed bank. Populations with more among-year variation in precipitation had greater variability in reproductive success for germinated seedlings, and the population in the most xeric environment was the most variable. Survival of non-germinated seeds was less variable than reproductive success of germinated seeds in all populations. Thus, non-germinating seeds reduced temporal variation in population dynamics by increasing population growth in dry years and decreasing growth in wet years. In this field study, populations in historically more xeric environments had lower mean germination fractions. Using geometric mean growth rate as an estimate of fitness, I demonstrate that germination fractions less than one were adaptive in three of four populations. Results of

experimental studies with up to twelve populations of *P. insularis*, suggest that field germination responses emerged from a combination of two processes. Lower water availability during germination resulted in lower germination fractions. When water was amply available, all populations could express high germination fractions. A pattern of delayed germination consistent with bet-hedging as an adaptation to temporal variability in reproductive success arose in the field, in part, because frequencies of wet and dry germination conditions differed among populations. Phenotypic plasticity in germination response for seeds in the most xeric environment conferred greater fitness than would have been possible with any one constant germination fraction.

CHAPTER 1

INTRODUCTION

Temporal variability in population growth rates can lower geometric mean population size and increase the risk of extinction. Selection for variance-reducing life history strategies is predicted to be greater in more variable environments, and deserts are among the most temporally variable ecosystems. Accordingly, a classic theoretical example of a life history strategy evolved to reduce temporal variance in individual fitness is embodied in desert annual plants possessing delayed seed germination. The effect of temporal variance on life history evolution and population dynamics has received extensive attention in the theoretical literature. Fewer empirical studies have addressed the resultant evolutionary predictions and their underlying assumptions. Even predictions concerning delayed seed germination in desert annuals that have been in the literature for over thirty years have yet to be tested rigorously. In this dissertation, I present empirical data on life history and demographic variability in several populations of the desert annual, Plantago insularis, within the context of theoretical predictions for life history evolution in variable environments.

Temporal variability

Population growth is multiplicative and the long-term growth rate of a population, estimated by the geometric mean, is sensitive to variance among years (Cohen 1966; Tuljapurjar and Orzack 1980; Freckleton and Watkinson 1998). Similarly, the fitness of a

genotype through time is a function of its geometric mean fitness, which can be thought of as the arithmetic mean discounted by the variance. Incorporating the effect of temporal variance in population growth rates (λ), and in fitness, into models of population dynamics and life history evolution has been an important aspect of population biology during the past thirty years (Cohen 1966; Gillespie 1977; Tuljapurkar 1990; Stearns 1992; Benton and Grant 1996; Sibly 1996; Tulapurkar and Caswell 1997). Large temporal fluctuations in some components of fitness can select for variance-reducing life histories (Cohen 1966; Venable and Lawlor 1980; Tuljapurkar 1990; Orzack 1997). When these temporal fluctuations are unpredictable and have coefficients of variation above one, models predict that life history strategies with multiple reproductive events, each of which is relatively small in magnitude (e.g., iteroparous perennials, annuals with delayed germination) will have maximal long-term growth rates (Tuljapurkar 1990; Orzack 1997). Anecdotal evidence supporting these predictions can be found in the community composition of variable ecosystems such as deserts (Noy-Meir 1973; McGinnies 1981; Schmida et al. 1986). Annual plants with persistent seed banks comprise a large fraction of the flora in hot deserts, this fraction tends to increase with aridity (Venable et al. 1993), and most desert taxa are thought to be recently derived from perennial ancestors (Gleason and Cronquist 1964; Johnson 1968; Schaffer and Gadgil 1975; Axelrod 1979).

The micro-evolutionary predictions of these models can be tested by comparing populations, within a species, that experience different amounts of temporal variability in survivorship or reproduction. Because long-term data on variation in life history parameters are rarely available for multiple populations, variability in abiotic

characteristics of the environment is generally used to define the selective gradient (Philippi 1993; Appendix B). If the environmental factor being measured is a limiting resource and exhibits large fluctuations that are unpredictable, then this may be a reasonable assumption. Precipitation in desert environments can be both variable and unpredictable among years (Noy-Meir 1973; Sellers and Hill 1974; Schmida et al. 1986; Davidowitz 1998). Within the desert, locations differ greatly in the degree of temporal variability in rainfall among years (Davidowitz 1998). The survival and reproduction of annual plants in the desert is positively correlated with the amount of rainfall they receive during the growing season (Beatley 1974; Polis et al. 1997; Venable & Pake 1999; Appendix A). As a result, we expect unpredictable variability in reproductive success among years for desert annual plants. Furthermore, within a species, populations are predicted to vary in the strength of selection for variance-reducing life histories.

Bet-hedging strategies and delayed seed germination

Bet-hedging is the term used for strategies that reduce temporal variance in fitness, and also reduce arithmetic mean fitness. Bet-hedging is adaptive when this trade-off between mean and variance results in a greater geometric mean than alternative strategies. Since the formulation of a bet-hedging model in 1966 by Dan Cohen, the concept has been integrated into many aspects of evolutionary theory (for review see Seger and Brockmann 1987). One of the hypothetical examples of adaptive bet-hedging

in the original 1966 paper pertains to desert annual plants with delayed seed germination. Because of high variance in the survival and reproduction of germinated seeds among years, the maximum geometric mean growth rate is attained by maternal genotypes that delay germination of a fraction of their offspring to a subsequent year. Whereas offspring that do not germinate in a favorable year represent a missed opportunity for reproductive success (lowering the arithmetic mean fitness of the genotype), offspring that do not germinate in a poor year, yet survive as seeds, reduce the variance in fitness of the genotype. Conditions under which geometric mean fitness (\bar{W}) is maximized by bet-hedging via delayed seed germination in unpredictably variable environments were formalized by Cohen (1966) with the equation,

$$\bar{W} = \prod_i [s(1-G) + Y_i G]^{P_i},$$

where s is the survival rate to the following year of non-germinated seeds, G is the fraction of seeds germinating in any given year, Y_i is the average seed yield per germinated seed in type i years and P_i is the probability of a type i year. When s is held constant and there are only two year types, good years (g), where $Y_g \gg 0$, and poor years (p), where $Y_p=0$, the germination fraction that maximizes fitness is approximately equal to the probability a year will be good for survivorship and reproduction (P_g). In environments in which P_g is low, the optimal strategy is for a genotype to spread its offspring out over many years by having a low germination fraction in any one year. Thus, all else being equal, this model can be used to predict the optimal germination

fractions for populations differing in the probability of a good year. Variability in the historical precipitation record suggests that populations of a single desert annual species can differ widely in the probability of a good year (Philippi 1993; Appendix B). Consequently, desert annuals are a model study system in which to test micro-evolutionary predictions of adaptive bet-hedging.

This study

For my dissertation research, I examined among-year temporal variation in demographic and life history characteristics in several populations located along a precipitation gradient. In a series of experiments I tested for differentiation among populations in germination strategies and compared these empirical data to predictions arising from bet-hedging theory. I conducted these studies in a desert annual plant endemic to the Sonoran and Mohave Deserts. Plantago insularis occurs at high densities on low elevation creosote flats throughout the desert Southwest. Previous studies in the relatively mesic desert annual plant community at Tumamoc Hill in Tucson, Arizona have reported that P. insularis is subject to less temporal variability in reproductive success than many other species (Venable et al. 1993). The populations chosen for the current study span a range of environments, from a mesic location, similar to the Tucson site, at which the probability of a good year for reproductive success in P. insularis is estimated as 0.78, to much more xeric environments where the probability of a good year is as low as 0.10 (Appendix B).

Appendix A (“Temporal variability in demographic parameters: implications for

life history strategies in four populations of a desert annual Plantago”) reports the results of a four-year study monitoring the dynamics of seeds and seedlings in four populations of Plantago insularis. As predicted by models of life history evolution in variable environments, in each year, all four populations consisted of individuals that germinated, and individuals that did not germinate, yet remained as viable seeds in the soil seed bank. Coefficients of variation among years were greater than one for reproductive success of germinated individuals, and populations experiencing more among-year variation in precipitation had greater variability in reproductive success. The survival of non-germinated seeds was less variable than the reproductive success of germinated seeds. As a result, non-germinated seeds decreased λ in wet years and increased λ in dry years, thus reducing temporal variation in population dynamics and lowering the risk of local extinction.

Appendix B (“Life history evolution in variable environments: a study of bet-hedging and delayed seed germination in populations of the desert annual Plantago insularis”) reports the results of three studies of variation in seed germination fractions among populations. In each population, empirical germination fractions were compared to the optimal germination fraction predicted as a bet-hedging adaptation to unpredictable temporal variability. In addition to delayed seed germination as a bet-hedging strategy, seed germination fractions exhibited phenotypic plasticity in response to environmental conditions during germination. These data have implications for understanding the ecology and evolution of germination strategies in desert annuals.

CHAPTER 2

PRESENT STUDY

My interests center on the ecology and evolution of life history strategies in temporally variable environments. For the reasons detailed above, desert annuals are well suited as a study system for this type of investigation. In the Sonoran and Mohave Deserts, winter annuals such as Plantago insularis germinate in response to large frontal systems that bring rain from the Pacific Ocean between September and March. Growth and reproduction of germinated individuals is positively correlated with the amount of subsequent precipitation. Years differ in the number and magnitude of storm fronts that pass over the Southwestern deserts. During the course of the study, average seasonal precipitation across populations differed by up to 250% among years. Although storm fronts generally result in rainfall throughout the entire region, populations differ significantly in the amounts of precipitation they receive. The average winter season precipitation at the most mesic population in this study was 182mm, whereas the most xeric population received on average only 72mm. The community of desert winter annuals at the four populations differed both in species diversity and species composition (Table 1) and P. insularis is one of a few annual species found in high densities over this wide range of environments.

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 in these papers.

Appendix A reports that in four seasons, four natural populations of the desert annual Plantago insularis exhibited large temporal fluctuations in population size, population growth rate and reproductive success. This variation was positively correlated with, and greater than, among-year variability in total winter precipitation. The population closest to the center of the species' range and in the most xeric environment had the largest total seed population size. This population also had the greatest variability in population size, growth rate, reproductive success and precipitation as measured by coefficients of variation. Yearly population growth rates as low as $\lambda=0.03$ were observed and are among the lowest reported in the literature. Nonetheless, geometric mean growth rates over the four-year period were fairly close to one, suggesting that these populations are persistent. As predicted by models of life history evolution in variable environments, each population had a fraction of seeds that did not germinate. I calculated the elasticity of population growth with respect to each demographic parameter. Elasticities enabled me to quantify the degree to which non-germinated seeds decreased λ in wet years and increased λ in dry years, and thus reduced temporal variation in population dynamics. The potential effect of non-germinated seeds on population dynamics was greater in more xeric populations and in drier years. This is the first study to assess the demographic consequences of delayed seed germination and seed banks in populations demonstrated to differ in their levels of temporal variability of reproductive success.

In Appendix B, I demonstrate that seeds of Plantago insularis exhibited germination fractions of less than one under several field and experiment conditions, and

that this delayed germination can function as a bet-hedging strategy. I used the historical precipitation record to characterize the selective regime associated with temporal variability in reproductive success at each population. In the field study, I found that populations in more xeric environments, with a lower probability of a good year, had lower mean germination fractions, as is predicted if delayed germination is a bet-hedging adaptation to temporal variability. This is the first study to measure germination fractions in the field for more than one population in multiple years. Further analysis of the field data together with the results of the germination experiments demonstrated that mean response was composed of two different elements. First, more xeric populations exhibited greater phenotypic plasticity in germination fractions in response to water availability. Second, more xeric populations had a wider range of germination dates within the season. A synthesis of these results suggests that the pattern of delayed germination among populations may reflect a bet-hedging adaptation, but not as a result of constant and optimal germination fractions. Rather, the mean germination response was attained through an interaction between the distribution of germination environments in mesic and xeric populations, and plasticity in the germination response. Populations in mesic environments generally received more rainfall, had seeds with intermediate germination fractions and had a narrow germination season. In contrast, populations in more xeric environments received less rainfall, had higher germination fractions when water was available and had a longer germination season. This study illustrates the need to consider the ecological expression of characteristics in studies of life history evolution in variable environments.

Table 1. Winter annual species composition at four locations in Southern Arizona. Listed species were found within 10m of permanent quadrats in 1997-98. The average number of unique species (standard deviation; $n=20$) within quadrats was 2.8 (1.2), 8.2(1.8), 7.9 (2.5) and 3.4 (1.2) at Sentinel (SE), Gila Bend (GB), Organ Pipe (OP) and Florence (FL), respectively.

		SE	GB	OP	FL
Apiaceae					
<u>Bowlesia</u>	<u>incana</u> Ruiz & Pav.			x	
<u>Daucus</u>	<u>pusillus</u> Michx.			x	
Asteraceae					
<u>Calycoseris</u>	<u>wrightii</u> A. Gray			x	
<u>Chaenactis</u>	<u>carphoclinia</u> A. Gray		x		
<u>Eriophyllum</u>	<u>lanosum</u> (A. Gray) A. Gray		x	x	
<u>Gaillardia</u>	<u>arizonica</u> A. Gray			x	
<u>Lasthenia</u>	<u>chrysostoma</u>				x
<u>Geraea</u>	<u>canescens</u> Torr. & A. Gray			x	
<u>Rafinesquia</u>	<u>neomexicana</u> A. Gray			x	
<u>Malacothrix</u>	<u>fendleri</u> A. Gray			x	
<u>Monoptilon</u>	<u>bellioides</u> (A. Gray) Hall		x	x	
Brassicaceae					
<u>Eruca</u>	<u>vesicaria</u> subsp. <u>sativa</u>	x			
<u>Caulanthus</u>	<u>lasiophyllus</u> (Hook & Arn.) Payson var. <u>lasiophyllus</u>		x		
<u>Lepidium</u>	<u>lasiocarpum</u> Nutt.	x	x	x	x
<u>Lesquerella</u>	<u>gordonii</u> A. Gray		x	x	
<u>Thlaspi</u>	<u>arvense</u> L.		x	x	
Boraginaceae					
<u>Amsinckia</u>	<u>intermedia</u> Fisch & Meyer		x	x	x

		SE	GB	OP	FL
<u>Lappula</u>	<u>redowskii</u> (Hornem.)Greene			x	
<u>Pectocarya</u>	<u>recurvata</u> I.M. Johnst.	x	x	x	x
Chenopodiaceae					
<u>Monolepis</u>	<u>nuttalliana</u> (Schult.) Greene				x
Euphorbiaceae					
<u>Euphorbia</u>	<u>albomarginata</u> Torr. & A. Gray	x			
<u>Euphorbia</u>	<u>polycarpa</u> Benth.	x			
Fabaceae					
<u>Astragalus</u>	<u>nuttallianus</u> DC.		x	x	
<u>Dalea</u>	<u>mollis</u> Benth.	x			
<u>Lotus</u>	<u>humistratus</u> Greene		x	x	
<u>Lupinus</u>	<u>sparsiflorus</u> Benth.		x	x	
Geraniaceae					
<u>Erodium</u>	<u>cicutarium</u> (L.) L'Her.			x	x
<u>Erodium</u>	<u>texanum</u> A. Gray		x	x	x
Hydrophyllaceae					
<u>Nama</u>	<u>hispidum</u> A. Gray	x			
<u>Phacelia</u>	<u>distans</u> Benth.			x	
<u>Phacelia</u>	<u>pedicellata</u> A. Gray		x	x	
Linaceae					
<u>Linum</u>	<u>lewisii</u> Pursh			x	
Malvaceae					
<u>Sphaeralcea</u>	<u>coulteri</u> S. Watson	x			
Nyctaginaceae					
<u>Allionia</u>	<u>incarnata</u> L.	x			
Onagraceae					

		SE	GB	OP	FL
<u>Camissonia</u>	<u>boothii</u> (Douglas) R.H. Raven subsp. condensata (Munz) P.H. Raven		x		
<u>Camissonia</u>	<u>californica</u> (Torr. & A. Gray) P. H. Raven		x		
<u>Camissonia</u>	<u>claviformis</u> subsp. <u>rubescens</u> (P.H. Raven) P.H. Raven		x		
Papaveraceae					
<u>Argemone</u>	<u>pleiakantha</u> subsp. <u>ambigua</u>	x			
<u>Eschscholzia</u>	<u>californica</u> Cham. subsp. <u>mexicana</u> (Greene) C. Clark		x	x	
Plantaginaceae					
<u>Plantago</u>	<u>insularis</u> Eastw.	x	x	x	x
<u>Plantago</u>	<u>patagonica</u> Jacq.			x	
Poaceae					
<u>Schismus</u>	<u>barbatus</u> (L.) Thell.		x	x	x
<u>Vulpia</u>	<u>octoflora</u> (Walt.)		x	x	
Polemoniaceae					
<u>Eriastrum</u>	<u>diffusum</u> (A. Gray) Mason	x	x		
<u>Linanthus</u>	<u>bigelovii</u> (A. Gray) Greene			x	
Polygonaceae					
<u>Chorizanthe</u>	<u>brevicornu</u> Torr. subsp. <u>brevicornu</u>		x	x	
<u>Chorizanthe</u>	<u>rigida</u> (Torr.) Torr. & A. Gray	x	x	x	
<u>Eriogonum</u>	<u>thomasii</u> Torr.			x	
<u>Eriogonum</u>	<u>trichopes</u> Torr. var. <u>trichopes</u>		x	x	
Resedaceae					
<u>Oligomeris</u>	<u>linifolia</u> (Vahl) Macbr.			x	
Scrophulariaceae					
<u>Castilleja</u>	<u>exserta</u> (Hell.) Chuang & Heckard		x	x	

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Venable, D. L., C. E. Pake, and A. C. Caprio. 1993. Diversity and coexistence of Sonoran Desert winter annuals. *Plant Species Biology*. 8:207-216.

APPENDIX A**TEMPORAL VARIABILITY IN DEMOGRAPHIC PARAMETERS: IMPLICATIONS
FOR LIFE HISTORY STRATEGIES IN FOUR POPULATIONS OF A DESERT
ANNUAL PLANTAGO**

***Running head:* Population dynamics in desert annuals**

**Temporal variability in demographic parameters: implications for life history strategies
in four populations of a desert annual Plantago**

Maria J. Clauss

Department of Ecology and Evolutionary Biology

University of Arizona, Tucson, AZ 85721 USA

Tel. 520-621-5956

FAX. 520-621-9190

clauss@u.arizona.edu

ABSTRACT

Temporal variability in the environment can affect population dynamics and life history strategies. Annual plants in desert environments are subject to large fluctuations in precipitation among years. I conducted demographic studies over four seasons in four populations of Plantago insularis Eastw. located along a precipitation gradient in the Sonoran Desert. I quantified the fates of germinated and non-germinated individuals by monitoring permanent quadrats and repeatedly sampling the soil seed bank. In two wet years, population growth rates were positive ($\lambda > 1$), reflecting the high reproductive success of germinated seedlings. In two dry years, λ was as low as 0.03 and most populations were declining as a result of low survivorship for germinated seedlings. Populations experiencing more among-year variation in precipitation had greater variability in reproductive success of germinated individuals. In all years some viable seeds remained in the soil seed bank and seed survivorship and germination fractions varied less across years than the survivorship and reproduction of germinated individuals. Thus, non-germinating seeds reduced temporal variation in population dynamics by increasing λ in dry years and decreasing λ in wet years, and lowered the risk of local extinction. The contribution of the persistent seed bank to population growth, quantified by the elasticity of the germination fraction, was greater the more xeric the environment.

INTRODUCTION

Temporal variation in life history parameters significantly affects population dynamics and life history evolution (Cohen 1966; Gillespie 1977; Tuljapukar 1990; Stearns 1992; Benton and Grant 1996; Sibly 1996; Tulapurkar and Caswell 1997; Pfister 1998). Unpredictable temporal fluctuations in some components of fitness can select for variance-reducing life histories that incorporate delayed reproduction, iteroparity or delayed germination (Cohen 1966; Venable and Lawlor 1980; Tuljapukar 1990; Orzack 1997). When a reduction in the variance of fitness is adaptive and is associated with a decline in arithmetic mean of fitness, the result is an adaptive bet-hedging strategy (Seeger and Brockman 1987). In annual plants, temporal variability in survivorship and reproduction of germinated individuals is predicted to select for maternal genotypes that delay the germination of a fraction of their seeds to subsequent years as a bet-hedging strategy (Cohen 1966, 1967; MacArthur 1972; Venable and Lawlor 1980; Bulmer 1984; Cohen and Levin 1985; Ellner 1985, 1986, 1987; Leon 1985; Brown and Venable 1986; Klinkhamer et al. 1987; Venable and Brown 1988; Venable 1989). A related body of literature modeling the dynamics of annual plant populations makes a similar prediction: populations with high among-year variation in survivorship and reproduction can persist longer with a multi-year seed bank (MacDonald and Watkinson 1981 ; Kalisz and McPeck 1993; Jarry et al. 1995). The importance of delayed germination and seed banks

in annual plant population dynamics has been demonstrated in a small number of empirical studies conducted in one season (Watkinson 1978; Leverich and Levin 1979) and over multiple years (e.g., Mack and Pyke 1983; Kelly 1989; Kalisz and McPeck 1992; Wagner and Spira 1994; Jarry et al. 1995; Pake and Venable 1996; Venable and Pake 1999).

A life cycle diagram for a winter annual plant with delayed seed germination illustrates the two possible fates of individuals during the winter months (Fig. 1). Seeds germinating with the probability G in the winter, survive to reproduction with the probability L , and have fecundity (B). The product of survival times reproduction is the reproductive success (LB) of germinated individuals. Seeds not germinating, with the probability $1-G$, survive the winter season with the probability R . All seeds survive the summer with the probability S . The population growth model based on this life cycle is

$$\lambda = (1-G)RS + GLBS, \quad \text{eqn. 1}$$

where λ is the finite rate of increase. This model has two stages, germinated and non-germinated individuals, no age-specific effects and assumes no migration (see MacDonald and Watkinson 1981; Schmidt and Lawlor 1983 for similar models). When population growth is estimated from the parameters in eqn. 1, the proportional effect on λ of proportional changes in each parameter can be evaluated using elasticities (de Kroon et al. 1986; Caswell 1989). The change in population size from one year to the next can also be used to calculate $\lambda (=N_{t+1}/N_t)$, where N is measured at the seed stage.

Winter annual plants are a large and diverse component of plant communities in the Sonoran and Mohave Deserts (Venable et al. 1993). Survival and reproduction of desert annuals are sensitive to water availability (Klikoff 1966; Pake and Venable 1995) and increased precipitation increases the probability of seedling survival, plant size and fecundity (Beatley 1974; Polis et al. 1997; Venable and Pake 1999). Desert environments exhibit large amounts of temporal variability in abiotic environmental factors, especially in precipitation (Noy-Meir 1973; Sellers and Hill 1974; Schmida et al. 1986; Davidowitz 1998). Within desert ecosystems, more xeric locations are predicted to experience more temporal variability in rainfall among years than more mesic locations (Davidowitz 1998). Therefore, populations of desert annuals in xeric locations with more variable precipitation regimes should experience more temporal variability in reproductive success, though this has not been demonstrated empirically. It is widely assumed that the survivorship of non-germinated seeds has a lower mean and variability than reproductive success. If this is so for desert annuals, the contribution of germinated and non-germinated individuals to population growth, and their associated elasticities, should differ systematically with the amount of seasonal precipitation. In wet years and in more mesic environments, the reproductive success of germinated seeds should determine population growth. In contrast, in dry years and in more xeric environments, the elasticity of non-germinated seeds should be large and seed survivorship should determine population growth rates. Differences among years and populations in the relative contributions of life history stages to population growth have been described

previously using elasticities (Bierzychudek 1982; van Groenendael and Slim 1988; Kalisz and McPeck 1992; Bullock et al. 1994; Horvitz and Schemske 1995; Damman and Cain 1998; Menges and Dolan 1998; Valverde and Silvertown 1998).

I conducted a study of population dynamics in the winter annual Plantago insularis. Four populations were chosen along a gradient of precipitation in the Sonoran Desert. Over a four year period, I measured dynamics of both germinated and non-germinated individuals, and determined their relative contributions to population growth. The research was designed to address the following questions: 1) how variable are life history parameters among years, 2) is temporal variability in reproductive success sufficiently large to result in selection for variance-reducing life histories, 3) can variability in reproductive success be predicted by variability in precipitation and 4) what is the role of non-germinated seeds in the dynamics of P. insularis populations in different years?

METHODS & MATERIALS

Study species and populations

Plantago insularis Eastw. [incl var. fastigiata (E. Morris) Jepson; Plantaginaceae] is a scapose winter annual plant that is endemic to the Sonoran and Mohave Deserts of southwestern United States and northwestern Mexico. The plants occur on low elevation desert bajadas and flood plains (0-1000m) in association with other annuals such as

Amsinckia intermedia, Chorizanthe rigida, Erodium texanum, Lepidium lasiocarpum, Pectocarya recurvata, and Schismus barbatus, as well as perennial vegetation (e.g., Ambrosia dumosa, Atriplex canescens, Carnegiea gigantea, Larrea tridentata, and Opuntia spp.). P. insularis is one of the most abundant native annual species of these deserts. Seeds germinate between September and March in response to discrete rainfall events (Appendix B), and plant growth is positively correlated with the amount of rainfall in the several months after germination (Venable and Pake 1999). The wind-pollinated and self-compatible flowers develop in early spring and individuals complete their reproductive life cycle by the onset of the arid foresummer in May. The two ovules per fruit develop into seeds (mean mass =0.725mg; n=200) that disperse by gravity from a dehiscent capsule. P. insularis has a multi-year soil seed bank that is formed when viable seeds remain ungerminated in the soil after the germination season (Appendix B).

I conducted a four-year demographic study of four populations of P. insularis located in the Arizona Upland and Lower Colorado Valley subdivisions of the Sonoran desert in southern Arizona (Fig. 2). The study populations are samples of the contiguous distribution of P. insularis; separated by a minimum of 50 km with the easternmost population situated near the edge of the species range. The populations were chosen to span a range of precipitation regimes during the winter season (September-April). The mean, minimum and maximum of winter precipitation in the historical record decreases by more than half from the most mesic (Florence) to the most xeric environment (Sentinel) (Table 1). In addition to being lower, precipitation at the more xeric locations

is more variable among years, as indicated by greater coefficients of variation (Table 1). In contrast to precipitation, monthly and winter season average temperatures vary little among years and locations (Sellers and Hill 1973).

The mean, minimum and maximum precipitation at each population during the four-year demographic study were representative of the historical climatic differences (Table 1). Populations in more mesic environments (Organ Pipe Cactus National Monument and Florence) received more rainfall than those in historically more xeric locations (Gila Bend on the Barry M. Goldwater Air Force Range and Sentinel). All populations experienced wetter than average seasons in the first and last years, 1994-95 and 1997-98, and a drought during the intervening two years (Fig. 3). Both positive and negative deviations from the historical precipitation mean were greatest in the most xeric environment, Sentinel (Fig. 3). As a result, the coefficient of variation of rainfall in the four years of the study was ca. twice as large at Sentinel as at the remaining locations (Table 1).

Seedling population

The density, survivorship and reproduction of germinated individuals of P. insularis at four populations were studied between September 1994 and May 1998. At each population, five sites with eight quadrats were deployed at 1km intervals, for a total of forty permanent quadrats (Fig. 2). The eight quadrats per site were positioned using stratified random sampling within a 25m X 20m area divided into 5mX5m grid squares

(Fig. 2). Quadrats were located randomly within grid squares with the provision that the minimum distance between two quadrats was 2m and that each quadrat be located >1m from the edge of any shrub. The majority of the habitat is in the open at these locations (Shreve and Wiggins 1964) and the density of P. insularis is higher in the open than under shrubs (Venable and Pake 1999; M. Clauss pers. obs.). Quadrat size was adjusted from 0.0225 to 0.25m² in different years to maintain sample sizes in the face of fluctuating seedling density. Following each rainfall between September and March, I surveyed all quadrats for newly germinated seedlings and mapped individuals of P. insularis on acetate sheets using a clear plexiglass mapping table. The density of germinated seeds (E) each year for each population was estimated as the mean of the number of seedlings per m² in each quadrat. Survivorship was monitored at regular intervals (ca. 3 weeks) following establishment. The number of fruits with mature, fully developed seeds was recorded after each individual had senesced. This was possible because the bottom of the circumscissile capsule remains attached to the infructescence after mature seeds disperse whereas fruits with aborted seeds remain attached and undehisced. For plants with more than 8 infructescences, fruit number was counted on four randomly selected infructescences and total fruit number was estimated by the average number of fruits per infructescence times number of infructescences. Number of seeds was estimated as twice the number of fruits for each individual. Both ovules within a fruit developed into viable seeds on all plants except where infructescences were damaged late in development (<1% of plants; Clauss, pers. obs.).

I estimated the probability of surviving to reproduction (\underline{L}) in each year by the proportion of germinated individuals within each quadrat that survived to produce seeds. Per capita fecundity of individuals surviving to reproduction (\underline{B}) was calculated for each quadrat as the mean number of seeds produced by all individuals surviving to set fruit. \underline{L} and \underline{B} were then averaged across all quadrats for population mean estimates. Reproductive success (survivorship(\underline{L})*fecundity (\underline{B})= \underline{LB}) was also calculated for each quadrat, and then averaged across all quadrats in each year. Seed production per m² (\underline{F}) each year for each population was estimated as the population mean of \underline{LB} times seedling density (\underline{E}) in each quadrat. In the first three years of the study, the same 40 quadrats were sampled from each population for a total of 5669, 7003, and 947 individuals in 1994-95, 1995-96 and 1996-97, respectively. After determining that a 50% reduction in sample size did not reduce the power for demographic analyses much, I randomly selected half the quadrats in 1997-98 at each site within populations and monitored a total of 1573 individuals.

Overall variation in survival, reproduction and \underline{LB} among years and populations was analyzed using a random effects analysis of variance (ANOVA). Quadrats were not included in the analysis of \underline{L} and \underline{B} when they had no seedlings or no reproductive plants, respectively. Because the quadrat means of these variables violated both the normality and homoscedasticity assumptions of parametric tests, I tested the significances of the actual Z-statistics against a distribution of Z-statistics derived from the data set in a randomization procedure (Manly 1991). The empirical Z-distributions

were created by randomizing population and year identity 1000 times and analyzing each new dataset using PROC MIXED (SAS Institute 1990). The Z-statistic is an approximation to a normal test statistic and is used for random effects models (SAS Institute 1990). Variance components were calculated for each random effect.

I compared the effect of seasonal precipitation (September-March) on LB using a test for heterogeneity of slopes among populations for the linear relationships between log precipitation and log mean LB from four seasons. As a result of the log transformations, the residuals of the analysis were normally distributed.

The spatially nested sampling design within each population allowed me to estimate the variance associated with different spatial scales. I used a fully nested ANOVA and variance component analysis (PROC NESTED, SAS Institute, 1990) to partition variance in the seed set of individuals surviving to reproduction (B) at four spatial scales: 50-200km (populations), 1-4km (sites), 2-30m (quadrats) and ≈50cm (individuals). I conducted the analysis for each of the two wet years separately (1994-95 and 1997-98). Only the wet years were used because samples size were large and fairly well-balanced, and the residuals for B were normally distributed after log transformation. Fecundity alone was used to examine spatial variation because seed set data for individual plants allowed me to analyze the variance component among individuals, within quadrats. At the remaining three spatial scales, fecundity and survivorship exhibited a similar pattern of variance (results for survival not shown). I calculated the rank correlation of mean B for sites, and for quadrats, across the two wet years within

populations.

Seed population

The density of the seed population in the soil after germination was estimated in each year at each population. Soil samples were taken within 10m of permanent seedling quadrats at each site. Sampling intensity differed among years for a total area of 550, 660, 7680 and 770 cm² from 25, 30, 16 and 35 samples in 1994-95, 1995-96, 1996-97 and 1997-98, respectively, in each population (see Appendix B for details). All samples were taken to a depth of 2cm. Shallow soil cores provide an appropriate estimate of the seed bank because most (>89%) viable seeds lie within the top 2cm of the soil surface in desert sites (Reichman 1984; Pake and Venable 1996) and because P. insularis seeds buried under greater than 1cm of sand do not germinate (Claus unpubl. data). The soil from each sample was sieved, all P. insularis seeds were removed and viable seeds were counted. All seeds were cut or poked through the seed coat to determine viability. Seeds with fleshy endosperm were regarded as viable. This technique for testing seed viability was found superior to tetrazolium chloride because some deeply dormant viable seeds show minimal staining with tetrazolium and because embryos and endosperm in the field usually undergo easily recognizable changes upon death (e.g. desiccation, decay). In 1994-95, 1995-96, and 1997-98, samples were collected in March following the germination season and prior to seed dispersal, and spring seed density per m² (D) was calculated as the mean of all samples within a population. In 1996-97 seed soil samples

were collected in the fall of 1996 prior to germination and \underline{D} was estimated by subtracting the density of subsequently germinating seedlings from the fall seed density.

I estimated the population size of *P. insularis* each year between 1994 and 1998 as the seed density in each fall prior to germination (Fig.1). From 1994 to 1997, fall seed density was estimated by the sum of the density of seeds that germinated (\underline{E}), plus the density of ungerminated seeds in the soil (\underline{D}). For the fall of 1998, after the demographic study had been terminated, seed density was predicted by the sum of the seed production per m^2 (\underline{E}) plus the density of ungerminated seeds per m^2 in the soil (\underline{D}) in the spring of 1998, multiplied by the three-year average summer seed survivorship (\underline{S} : see below). The finite rates of increase (λ) for each population were calculated as the ratio of fall seed population size from one year to that of the previous year ($\lambda_t = \underline{N}_{t+1} / \underline{N}_t$; where t =winter season).

To estimate survival of seeds in the soil, I evaluated the change in seed population size between spring, following seed dehiscence, and the next fall, prior to germination, for three years (1995-1997). Spring density was estimated by the sum of seed production/ m^2 (\underline{F}) and the number of non-germinated seeds per m^2 in the soil (\underline{D}). Thus, seed survival was estimated by the fall seed density ($\underline{D}_{t+1} + \underline{E}_{t+1}$) divided by the previous spring seed density ($\underline{D}_t + \underline{F}_t$) (see Appendix 1).

The life cycle of winter annuals is comprised of two periods of survivorship for seeds: summer-fall survival (which applies to all seeds) and winter-spring survival (which applies only to non-germinated seeds) (Fig. 1). There was no separate empirical

estimate of \underline{R} . In summer 1995 and 1997 estimates of \underline{S} above include the seed mortality of non-germinated seeds during the following winter (\underline{R} in 1995-96 and 1997-98, respectively). \underline{S} in the summer of 1996 does not include \underline{R} because viable seed densities were measured in the fall of 1996. Because seeds generally experience less predation with increasing time after dispersal (Sarukhan 1974; Carey and Watkinson 1993), I assumed that the among-year variation in true winter seed survivorship is less than, or at most equal to, the variation of \underline{S} as estimated above.

The proportion of viable seeds in the population that germinate during a winter annual season is the germination fraction (\underline{G}). The germination fraction was estimated by $\underline{G} = \underline{E}/(\underline{D} + \underline{E})$ for each population in each season. $1 - \underline{G}$ is the fraction of the population that delays germination.

Decomposition of population growth

In order to assess the role of each life history stage in the observed fluctuations in overall population size, I used estimates of the population mean reproductive success of germinated individuals (\underline{LB}), summer survivorship of seeds (\underline{S}), and germination fraction (\underline{G}) to calculate the population growth each year according to eqn. 1 (Fig. 1; Appendix 1). The average population \underline{S} for three years was used as an estimate for 1997-98 because seed densities were not measured in the winter of 1998-99. I evaluated population growth over a range of values for \underline{R} from 0.1 to 0.9. When not otherwise stated, results were given for $\underline{R} = 0.5$. Variation in life history parameters among years

was described by the ranges and coefficients of variation of population means across years. Correlations among life history parameters were calculated for population means across all years and populations.

The proportional sensitivity, or elasticity, of lambda to different life history stages, was evaluated by the partial derivatives of lambda with respect to each of the six parameters for the log population growth equation,

$$\ln\lambda = \ln S + \ln[(1-G)R + GLB] : \quad \text{eqn. 2}$$

$$\frac{\partial \ln\lambda}{\partial \ln R} = \frac{(1-G)R}{(1-G)R + GLB} \quad \text{eqn. 3}$$

$$\frac{\partial \ln\lambda}{\partial \ln L} = \frac{\partial \ln\lambda}{\partial \ln B} = \frac{\partial \ln\lambda}{\partial \ln LB} = \frac{GLB}{(1-G)R + GLB} \quad \text{eqn. 4}$$

$$\frac{\partial \ln\lambda}{\partial \ln S} = 1 \quad \text{eqn. 5}$$

$$\frac{\partial \ln\lambda}{\partial \ln G} = \frac{G(LB - R)}{(1-G)R + GLB} \quad \text{eqn. 6}$$

$$\frac{\partial \ln\lambda}{\partial \ln(1-G)} = \frac{(1-G)(R - LB)}{(1-G)R + GLB} . \quad \text{eqn. 7}$$

Elasticities were evaluated according to eqns 3-7 for each year and population using the observed parameter estimates. The elasticities represent the proportional change in

lambda resulting from a proportional change in the parameter of interest and are generally used to compare the relative impact of parameters on population growth (de Kroon et al. 1986). Elasticities are directly comparable among parameters, even when the scales of measurement differ (e.g., seed survivorship and reproductive success). Whereas the elasticities of all elements in a matrix model of population growth sum to one, this is not a property of elasticities in general (de Kroon et al. 1986). For eqn. 2, $\epsilon_{\underline{L}} = \epsilon_{\underline{B}} = \epsilon_{\underline{LB}}$, which means that a 10% change in either fecundity or survival, or a 5% change in each, will all have equivalent effects on lambda. $\epsilon_{\underline{LB}}$ plus $\epsilon_{\underline{R}}$ equals one. Because \underline{S} had a multiplicative effect on population growth (eqn. 1), the derivative of lambda with respect to \underline{S} for the logged equation was independent of the remaining parameters and a proportional increase or decrease in \underline{S} will have an equal effect on lambda (eqn.5).

The effects on lambda of changes in the proportion of individuals that germinate (\underline{G}) and that delay germination ($1-\underline{G}$) are not independent (Fig. 1), and are opposite in sign in this model of population growth. For example, when $\underline{G}=0.5=(1-\underline{G})$, $\epsilon_{\underline{G}} = -\epsilon_{(1-\underline{G})}$. For all other values of \underline{G} , $\epsilon_{\underline{G}}$ and $-\epsilon_{(1-\underline{G})}$ result in an effect on lambda that is equal in magnitude and opposite in sign but the elasticities are not equal and opposite. This is because a 10% increase in \underline{G} when $\underline{G}=0.2$ is not equal to a 10% decrease in $1-\underline{G}$. When elasticities for \underline{G} and $(1-\underline{G})$ are scaled by the values of \underline{G} and $(1-\underline{G})$, respectively, $\epsilon_{\underline{G}}/\underline{G} = -\epsilon_{(1-\underline{G})}/(1-\underline{G})$, and this is equivalent to

$$\frac{\partial \ln \lambda}{\partial \underline{G}} = - \frac{\partial \ln \lambda}{\partial (1-\underline{G})} . \quad \text{eqn. 8}$$

For ease of interpretation, I report these scaled effects of \underline{G} and $1-\underline{G}$ on lambda which are equal in magnitude and opposite in sign (and are referred to as $\epsilon' \underline{G}$ and $\epsilon'(1-\underline{G})$, respectively). A similar relationship between elasticities has been noted in a population dynamical model that included the effect of the probability of infection by a fungus (van Tienderen 1995). Population dynamical consequences of the two pathways ($\underline{G}*\underline{L}*\underline{B}*\underline{S}$ and $(1-\underline{G})*\underline{R}*\underline{S}$; Fig. 1) can be fully described by the elasticities of \underline{G} and $1-\underline{G}$ because $\epsilon(\underline{G})=\epsilon(\underline{G}*\underline{L}*\underline{B}*\underline{S})$ and $\epsilon(1-\underline{G})=\epsilon((1-\underline{G})*\underline{R}*\underline{S})$.

RESULTS

Population size

The population sizes of *P. insularis*, as estimated by the density/m² of seeds in the fall prior to germination, varied over two orders of magnitude in a five year period (Fig. 4). All populations exhibited large fluctuations in density among years that mirrored the pattern of precipitation during the study period with a lag of one year. Mean population size varied between 1000 to 6600 seeds/m², with the population in the most xeric environment having the largest size in four of five years (Fig. 4). Population size was more variable in the two more xeric populations than in the mesic populations as measured by the coefficients of variation in population size among years (Fig. 4). For each population, the finite rate of increase (λ), as calculated from the change in fall seed density from one year to the next, was greater during the two wet years than during the two drought years (Table 2). In general, populations grew ($\lambda > 1$) during the two wet

years and declined ($\lambda < 1$) during the two drought years (Table 2). Although the maximum yearly growth rates indicated the potential for all populations to grow rapidly ($12 < \lambda < 44$), the geometric mean of λ , which is sensitive to the low values observed at all populations, was close to one (Table 2). The range in λ among years was at least two times greater for the xeric Sentinel population than for the remaining populations (Table 2).

Seed survivorship

Estimates of the proportion of seeds surviving in the soil over the summer and fall varied from 0.09 to 0.98 with a grand mean of 0.38 (Table 3; Appendix 1). In comparison to the other parameters, temporal variation in seed survivorship was lower (c.v. < 1 for each population) and this variability was uncorrelated with other life history parameters and seasonal precipitation (Tables 3,4).

Seed germination fraction

The proportion of viable seeds in the population that germinated during a winter annual season varied from 0.00 to 0.97 with a grand mean of 0.52 (Table 3; Appendix 1). All populations exhibited delayed germination of viable seeds such that the winter (persistent) seed bank varied in size between 13 and 4787 seeds/m². Across all populations and years, germination fraction was significantly positively correlated with the amount of seasonal precipitation but was uncorrelated with other life history

parameters (Table 4).

Seedling survival and reproduction

Survival (L) and reproduction (B) of germinated seedlings showed similar patterns of variation. For both variables and their product (LB), year was highly significant and accounted for the largest component of variation (> 67%; Table 5). Survival to reproduction was on average seven times greater in the wet years of 1994-95 and 1997-98 (0.69-0.90) than in the intervening dry years (<0.00-0.22) (Table 6a). Fecundity followed a similar significant pattern with, on average, fourteen times greater seed set during the two wet years than in the drought years (Table 6b). Temporal variation among years in survival, though less, was significantly and positively correlated with variation in fecundity, and both parameters were positively correlated with seasonal precipitation (Tables 3,4).

Population mean reproductive success (LB) was greater than one in the two wet years (5.93-190.5), indicating the potential for positive growth in all four population (Fig. 5; Appendix 1). In both drought years, LB was < 1, sometimes as low as 0.02, and the populations were declining. In an ANOVA, the main effects for population were not significant for L, B or LB; however, the year*population interactions were significant, indicating that populations differed in their response to years (Table 5). The mesic population in Florence had lower LB than the remaining populations in the two wet years (Fig. 5; Appendix 1). The xeric populations at Gila Bend and Sentinel had the

greatest LB in the first and second wet years, respectively. In the dry years, populations did not differ significantly in LB, although plants in Florence did have a significantly greater probability of surviving to reproduction in 1995-96 (Table 6a). As a result of the differences among populations in their response to years, the range in reproductive success among years was smallest at the mesic Florence population and greatest for the xeric Sentinel population (Table 3).

Assuming that the years differed primarily in the amount of precipitation, I analyzed the relationship between precipitation and LB in each population. Increased precipitation resulted in increased survival and reproduction and the intercepts, but not the slopes, of this relationship varied significantly among populations (Table 7). The more xeric the population, the greater the intercept, indicating that plants in the more xeric populations had higher reproductive success for a given amount of rainfall (Fig. 6).

In nested analyses of variation in B for each of the two wet years, the majority of the variation ($\approx 80\%$) occurred among individuals within quadrats. The remaining three spatial scales (population, site within population and quadrat within site) accounted for a significant, but much smaller percent of the variation in fecundity (Table 8). In both years, populations separated by 50-200km accounted for more variation (6-14%) than sites located at 1km intervals within populations (2-4%). Quadrats accounted for 6-8% of the variation in B in both years, indicating that there was more variation at the scale of 10's of m than among sites (1-4km; Table 8). Mean fecundity of sites and of quadrats

was not significantly correlated among the two years at any population (sites: $r_{\text{spearman}} = -0.100-0.500$; $P > 0.391$; $n=5$; quadrats $r_{\text{spearman}} = -0.068-0.407$; $p > 0.149$; $n=14-20$).

Together, the small amount of variation at the level of quadrats and sites, and the fact that this variation was not correlated among years, suggest relative homogeneity in reproductive output over intermediate spatial scales in open habitats. Thus, for *P. insularis*, quadrats ca. 35x35cm in size represent an appropriate spatial scale at which to replicate population samples, and quadrats can vary independently among years.

Decomposition of population growth

Population growth rates calculated from seed densities as N_{t+1}/N_t and from life cycle components according to eqn. 1 corresponded quite closely (Table 2; Appendix 1). Whereas the life cycle calculation gave lambdas roughly half that of the seed density calculation in Sentinel in 1995-96, and in all populations in 1996-97, there were only two qualitative discrepancies. In 1996-97 at Gila Bend and Florence λ based on life cycle components was less than one and λ based on seed densities was slightly greater than one (Table 2; Appendix 1). These differences were probably due to the assumption that R is constant and equal to 0.5 in the life cycle calculation of lambda.

Differences among years and populations in the effect of each life history parameter on population growth were summarized using elasticities. Proportional changes in parameters had different proportional effects on lambda in wet (1994-95 and 1997-98) versus dry (1995-96 and 1996-97) years and in xeric versus mesic populations

(Table 9). Elasticities are presented for $\underline{R}=0.5$, but the patterns discussed were observed for all values of $0.1 < \underline{R} < 1.0$. The proportional effect on λ of proportionally increasing reproductive success (\underline{LB}) in wet year was positive and large for all populations. Conversely, the elasticity of winter seed survivorship (\underline{R}) in wet years was low. In dry years, $\epsilon \underline{LB}$ was near zero at the most xeric population (Table 9), so increasing \underline{LB} would have had virtually no effect on lambda. Although lower than in wet years, there was some benefit to increasing \underline{LB} even in the dry years at the more mesic populations. Proportional increases in winter seed survival (\underline{R}) had the largest proportional effects on lambda in the xeric populations in dry years (Table 9).

The proportional effect on lambda of increasing the fraction of individuals germinating ($\epsilon' \underline{G}$) was positive and large for all populations in wet years (Table 9). In dry years, $\epsilon' \underline{G}$ at the more mesic populations was negative in 1995-96 but positive in 1996-97, indicating that increasing \underline{G} could decrease lambda in some dry years and increase lambda in others. At the arid Sentinel population, the effects of increasing germination on population growth in dry years were consistently negative (Table 9). The proportional effects of seeds not germinating ($1-\underline{G}$) on lambda were opposite in sign and of the same magnitude as the effects of \underline{G} in each year and population (Table 9). Thus, delaying seed germination to subsequent years (i.e., increasing $1-\underline{G}$) had the potential to increase population growth rates, especially in xeric populations and in dry years. The importance of the germination strategy for population growth across years, as measured by the sum of the absolute values of $\epsilon' \underline{G}$ in the four seasons, was greater the more xeric

the population (7.7, 6.3, 5.7, 3.2 for Sentinel, Gila Bend, Organ Pipe and Florence, respectively).

DISCUSSION

In a four-year period, four natural populations of the desert annual Plantago insularis exhibited large temporal fluctuations in population size, population growth rate and reproductive success. This variation was positively correlated with, and greater than, among-year variability in winter precipitation. The population closest to the center of the species' range and in the most xeric environment had the largest population size. This population also had the greatest variability in population size, growth rate, reproductive success and precipitation as measured by coefficients of variation. Yearly population growth rates as low as $\lambda=0.03$ were observed and are among the lowest reported in the literature (Werner and Caswell 1977; Bullock et al. 1994; Silvertown et al. 1996; Pfister 1998). Nonetheless, geometric mean growth rates over the four-year period were fairly close to one (0.9-2.0), suggesting that all four populations are persistent. As predicted by models of life history evolution in variable environments, each population had a fraction of seeds that did not germinate. These non-germinated seeds decreased λ in wet years and increased λ in dry years, thus reducing temporal variation in population dynamics and lowering the risk of local extinction.

Temporal variability in life history parameters

Overall population sizes, as measured by the fall seed density, fluctuated primarily in response to temporal variation in the rates of seedling survivorship and fecundity. Mean fecundity per reproductive plant showed the greatest temporal variation, as measured by the coefficient of variation (c.v.) and by the orders of magnitude spanned by the range. Temporal variation in survivorship to reproductive maturity was less and was correlated with variation in fecundity (Tables 3,4). Reproductive success (LB), calculated as the mean of per quadrat survival times fecundity of survivors, was more variable than its component. In contrast, variation in seed survivorship in the soil was half the variation in reproductive success. Seed survival was correlated neither to survivorship, reproduction nor seasonal precipitation.

Desert annual populations are expected to experience large temporal variability in reproductive success that can select for variance-reducing life history strategies (Cohen 1966, 1967; Venable and Lawlor 1980). When temporal variability is unpredictable and has a coefficient of variation above one, only life history strategies with multiple reproductive events, each of which is relatively small in magnitude, as seen in iteroparous perennials and seed bank annuals, are predicted to have positive long term growth rates (Orzack 1997). Strong selection for life histories that reduce variance is predicted when variability in reproductive success is greater than $c.v.=1.5$ (Tuljapurkar 1990). The coefficients of variation in LB observed in four populations of P. insularis were 1.28, 1.59, 1.64 and 1.79. Thus, at least three of four populations are likely to be

subject to strong selection pressures for variance reduction, as is expected in the variable environments in which desert annuals are found. The coefficients of variation in reproductive success for *P. insularis* reported here are among the most variable observed in the literature (Pfister 1998).

Empirical tests of life history evolution in variable environments generally assume that temporal variability in abiotic factors is correlated with temporal variability in reproductive success (Stearns 1992; Philippi 1993, Davidowitz 1998). There are few published data, even for a single population, to support this assumption. Here, I show that for a desert winter annual relative variability in seasonal precipitation among years was correlated with relative variability in reproductive success (Tables 1,3). There was complete correspondence between population ranks based on the c.v. of LB and the c.v. of precipitation during the four-year study (with Sentinel > Florence > Organ Pipe > Gila Bend). Furthermore, within populations, 68% of variation in mean reproductive success was explained by seasonal precipitation (Table 7). LB was greater than one in two seasons with greater than average winter rainfall, and less than one in two seasons with less than average rainfall. A similar response in LB for relatively wet versus dry years was observed at all four populations even though the absolute amount of precipitation during the four-year period decreased by half from the most mesic to the most xeric population (Tables 1,7 ; Figs.5,6).

These results support the use of seasonal precipitation to identify years of potential population growth and decline over a period of decades within desert annual

populations. Long-term data on variability of an environmental factor together with reaction norms of the study species to the environment can be used to predict historical selection regimes (Philippi 1993; Appendix B). For desert annuals, as for the plants in a temperate hayfield (Silvertown et al. 1994), measures of precipitation variability relative to the mean, and not absolute measures of variability, were most predictive of plant responses (Table 1; Figs. 3,5). Therefore, characterization of differences in temporal variability among populations should take into account the fact that reaction norms may differ systematically among populations. Experimentally investigating factors other than total seasonal precipitation that affect LB would add to our understanding of the proximate and ultimate causes of temporal variability in desert annuals. In particular, the distribution of precipitation and germination within the season (Wagner and Spira 1994; Sans and Masalles 1997; Pake and Venable 1996; Clauss unpubl. data), competitive interactions with other annuals and perennials (Davidson et al. 1984; Rees et al. 1996; Holzapfel 1997; Clauss, unpubl. data), herbivory and seed predation (Davidson et al. 1985; Reader 1985; Clauss, unpubl. data) may affect survival and reproduction.

Population growth in wet and dry years

The positive relationship between precipitation and reproductive success, and the relatively small temporal variation in the fate of seeds in the soil, resulted in very different population dynamics among years. Eqn. 1 decomposes population growth into a component due to non-germinated individuals and a component due to germinated

individuals (Appendix 1). The benefit of germinating can be quantified by the elasticity of \underline{G} and $1-\underline{G}$, which describe the population dynamical consequences of the two pathways, $\underline{G}*\underline{L}*\underline{B}*\underline{S}$ and $(1-\underline{G})*\underline{R}*\underline{S}$. Values of $\epsilon'\underline{G}$ were large and positive in the wet years, whereas $\epsilon'(1-\underline{G})$ was large and negative (Table 9). This indicates that increasing the germination fraction in wet years would have a large effect on current population growth. In the first dry year, $\epsilon'(1-\underline{G})$ was positive for all populations because non-germinated seeds in the seed bank contributed more to population growth than the germinated seeds. Because the populations were declining ($\lambda < 1$), increasing the dormant seed pathway would slow the rate of decline. In the second dry year, the most xeric population again had a positive elasticity for delaying germination. The remaining populations would have experienced a small decrease in population growth if delayed germination were increased. Thus, non-germinated seeds often (but not always) increased population growth in dry years. This resulted in an alternation in the population dynamical consequences of the two pathways (\underline{G} and $1-\underline{G}$) between wet and dry years. In a two year study of the annual plant Collinsia annua, Kalisz and McPeck (1992) also demonstrated greater elasticities for seed stages in a year of population decline and smaller elasticities for seed stages in a year in which lambda was large. As expected, the magnitude of temporal fluctuations observed for P. insularis in a desert environment were greater than those for C. annua, an eastern deciduous forest herb. The buffering effect of the persistent seed bank of P. insularis reduced temporal variance in population dynamics and reduced the risk of extinction.

Elasticities describe the effect of a small change in a life history parameter on the population growth rate. The population growth rate associated with a genotype or "strategy" is equivalent to fitness of individual genotypes. Therefore elasticities can be used to predict selection gradients on life histories traits for small deviations away from the population mean (sensu Fisher 1930; Caswell 1989). Elasticities, which are proportional sensitivities, were used to indicate the selective environment because proportional effects on lambda are representative of fitness consequences in temporally fluctuating environments (Freckleton and Watkinson 1998). Furthermore, elasticities are comparable among life history stages because they are calculated in units of proportional change, and allow an integrated view of selection on the seed versus seedling pathways of the life cycle (van Tienderen 1995). Partial derivatives based on population level dynamics only reflect phenotypic selection, sometimes called the opportunity for selection, and not the response to selection because these measures do not indicate whether uncorrelated heritable variation exists within the population for the traits of interest (van Tienderen 1995). Given these caveats, I used the population level data to assess whether there is phenotypic selection for delayed seed germination as is predicted in variable environments by life history theory (Cohen 1966).

The optimal germination fraction for a population with a smaller probability of a favorable year (when L_B is greater than one) is lower than the optimal fraction for a population with a larger probability of a favorable year (Cohen 1966; Venable and Lawlor 1980). The mean germination fractions for more xeric populations of P. insularis

(with a lower probability of a favorable year; Appendix B) were lower than for more mesic populations; but, populations exhibited extensive temporal variation in \underline{G} (Appendix 1). The fluctuations in elasticities for germination fraction observed between years suggest phenotypic selection for intermediate germination fractions in *P. insularis* (Table 9). The strength of selection on the germination strategy, as indicated by the sum of the absolute values of $e'G$ during the four year period, was two times greater at the more xeric populations. An example of the crucial role of delayed germination and the seed bank at Sentinel (>12 seeds/m² in all years) was illustrated when there was no germination and no seed production in the dry 1996-97 season. The population would have gone locally extinct had there not been a persistent, multi-year seedbank. Although micro-habitat variation in population dynamics is common in some deserts systems (Venable and Pake 1999; Kadmon 1993), no individuals of *P. insularis* germinated or reproduced within a 100m radius of the quadrats at Sentinel in this dry year, including habitats under shrubs, trees, sticks and in washes (M. Clauss, pers. obs.).

It is also of interest to know how changes in reproductive success and seed survival affect population in different years and populations. The elasticity for LB in wet years was large and positive in all populations. A proportional increase in LB had the potential to cause an almost equal proportional increase in λ (Table 9). In contrast, increasing the persistence of individuals in the seed bank over the winter had only a small positive impact on λ . The situation was reversed during dry years, when non-germinated seeds in the soil had a large potential to increase population growth. In dry

years, elasticities for \underline{LB} varied among populations. More mesic populations had some large positive elasticities for \underline{LB} . At Sentinel, however, the $\epsilon_{\underline{LB}}=0.00, 0.01$ indicating that increasing \underline{LB} would have had little or no effect on lambda. This is because there were very few individuals in the seedling pathway ($\underline{G}=0.01, 0.00$) and, therefore, no population dynamical consequences to proportional changes in \underline{LB} . If it is generally true that in dry years there is little or no germination in xeric populations, then post-germination traits may rarely be expressed during these years and specialization for traits conferring high reproductive success in wet years may be possible (Templeton and Levin 1978; Brown and Venable 1986; Evans and Cabin 1995). In contrast, post-germination traits may more frequently be expressed in dry years in mesic populations and thereby experience selection in all year types. The difference between mesic and xeric populations in the relationship between reproductive success and water availability may be the result of specialization in the xeric populations to relatively wet years (Fig. 6). In a comparison of two populations, Åberg (1992) reported that a population of the seaweed Ascophyllum nodosum experiencing a greater frequency of unfavorable extreme ice years had higher fertility in favorable normal ice years than a population in an environment that was, on average, less extreme.

The large variation in elasticities among years seen in the life history parameters for this annual plant cautions against the use of particular elasticity values as properties of populations or species (Silvertown et al. 1993). Elasticities have been at the forefront of demographically oriented conservation strategies for the recovery of declining

populations (Crouse et al. 1987; Oostermeijer et al. 1996; Ratsirarson et al. 1996; Silvertown et al. 1996) and biocontrol of weeds (Shea and Kelly 1998). Although caution is suggested by simulations demonstrating large confidence limits associated with elasticities (Alvarez-Buylla and Slatkin 1994; Wisdom and Mills 1997), here I presented empirical support for the existence of large environmentally determined variation in elasticities within populations. Previous studies spanning several years (Bierzychudek 1982; Kalisz and McPeck 1992; Horvitz and Schemske 1995; Damman and Cain 1998; Valverde and Silvertown 1998) and several populations (van Groenendael and Slim 1988; Horvitz and Schemske 1995; Menges and Dolan 1998; Valverde and Silvertown 1998) report fluctuations in elasticities and λ that are smaller in magnitude than the variation observed in this desert plant. If rare plant populations are subject to similarly large temporal fluctuations, it will be difficult to predict the elasticities of different life history parameters and thereby the selective environment of the near future when designing protection and recovery plans. In conducting a study over multiple years and populations, I have demonstrated that, although not evident in all years, the seed bank is critical to the long-term persistence of annuals in desert environments. Furthermore, the potential contribution to population dynamics of seeds that delayed germination was greater in more xeric populations and in drier years.

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Table 1. Precipitation (mm) between September and April in the historical record and during the four-year study period at four weather stations in southern Arizona. Mean, variance, coefficient of variation (c.v.), minimum and maximum precipitation are given for weather stations within 20km of each population. Historical record for Sentinel is not available, values are for Dateland AZ. n=number of years with complete winter season precipitation record prior to 1991 (NOAA). The percentiles of the historical distributions that encompass the minimum and maximum rainfall amounts observed during the four years are given for each location.

	Historical precipitation record						4 year study period (1994-1998)					
	n	mean*	variance	c.v.	min.	max.	mean	variance	c.v.	min.	max.	percentiles
Sentinel	23	71.8 ^a	2498	0.70	4.3	183.1	65.7	5938	1.17	2.5	167.6	1-95
Gila Bend	100	104.3 ^b	3519	0.57	8.6	344.7	93.3	2042	0.48	49.0	136.7	25-70
Organ Pipe	46	147.3 ^c	5218	0.49	30.0	368.0	160.3	9809	0.62	59.2	245.4	10-85
Florence	58	182.3 ^d	5938	0.42	72.6	422.1	167.2	12013	0.66	68.0	295.9	1-90

* F=24.06; df=3,223; P<0.001; means with different letters are significantly different (P<0.05) in Student-Newman-Keuls a posteriori multiple comparison.

Table 2. Population growth (λ) and the four year geometric mean of lambda (GM (λ)) in four populations of *Plantago insularis* in southern Arizona. λ was calculated as N_{t+1}/N_t where N is the fall seed population density.

Population	1994-95	1995-96	1996-97	1997-98	GM (λ)
Sentinel	0.63	0.28	0.48	44.34	1.39
Gila Bend	10.49	0.11	1.12	12.58	2.01
Organ Pipe	2.56	0.05	0.57	22.46	1.13
Florence	1.67	0.03	1.08	12.18	0.90

Table 3. Among-year variation in life history parameters in four populations of *Plantago insularis* calculated as the coefficient of variation (c.v.) of population means. Reproductive success (**LB**) was calculated as the mean of per quadrat survival (**L**) times fecundity (**B**). For seed survival only, $n=3$ years and the c.v. of **LB** in the same three years was 1.73, 1.65, 1.64 and 1.28 for Sentinel, Gila Bend, Organ Pipe and Florence, respectively.

	Sentinel		Gila Bend		Organ Pipe		Florence	
	range	c.v.	range	c.v.	range	c.v.	range	c.v.
Fecundity (B)	0.0-228.2	1.73	3.8-89.9	1.16	3.9-113.5	1.40	4.2-59.9	1.39
Survival (L)	0.00-0.73	1.14	0.03-0.83	0.87	0.00-0.90	0.99	0.07-0.76	0.81
LB	0.0-190.5	1.79	0.2-68.5	1.28	0.1-104.8	1.59	0.5-44.0	1.64
seed survival (S)	0.17-0.45	0.46	0.33-0.98	0.68	0.21-0.38	0.32	0.09-0.73	0.82
germination (G)	<0.00-0.97	1.60	0.06-0.89	0.77	0.53-0.81	0.20	0.54-0.84	0.19

Table 4 . Pearson correlation coefficient for variation in life history parameters and seasonal precipitation in four populations of *Plantago insularis* in four years. $n=16$, except for correlations with \underline{S} where $n=12$.

	<u>L</u>	<u>B</u>	<u>S</u>	<u>G</u>
Survival (<u>L</u>)	-			
Fecundity (<u>B</u>)	0.604**	-		
Seed survival (<u>S</u>)	-0.163	0.422	-	
Germination (<u>G</u>)	0.380	-0.281	-0.214	-
Precipitation	0.795***	0.471 ^a	-0.241	0.528 ^a

^a $P < 0.10$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

Table 5. Random effects analysis of variance for survival (**L**), fecundity (**B**) and reproductive success (**LB**) in four populations of *Plantago insularis* in four years. Significances determined by randomization (n=1000). Variance components (%V.C) calculated for arcsin sqrt transformed **L** and log-transformed **B** and **LB**

Source	Survival to reproduction (L)				Fecundity (B)			Reproductive success (LB)		
	df	Z	P	% V.C.	Z	P	% V.C.	Z	P	% V.C.
Year	3	1.22	< 0.001	82.5	1.08	< 0.001	67.8	1.08	< 0.001	80.8
Population	3	0.00	> 0.950	1.6	0.11	0.850	4.4	0.13	> 0.800	4.9
Year* Pop	8	1.53	< 0.050	0.0	1.72	< 0.001	1.4	1.67	< 0.001	0.0
Error	427	14.6		15.9	14.6		26.3	14.6		14.3

* sum of variance components deviates from 100% due to rounding errors

Table 6. A) Mean and standard error of survival to reproduction (**L**) among quadrats in four populations of *Plantago insularis* in four years. Means comparison across years demonstrated that 1997-98 > 1994-95 > 1996-97 > 1995-96 (Student-Newman-Keuls (SNK) *a posteriori* multiple comparison at P<0.05). B) Mean and standard error of fecundity (**B**). Means comparison across years demonstrated that 1997-98 > 1994-95 > 1995-96 = 1996-97 (data were log-transformed prior to analysis with SNK test). Although forty and twenty quadrats were surveyed at all populations in 1994-97 and 1997-98, respectively, quadrats were not included in the analysis when no individuals germinated or survived to reproduction. The best estimate of **L** and **B** at Sentinel in 1996-97 is 0.00.

Population	1994-95			1995-96			1996-97			1997-98		
	n	mean	s.e.	n	mean	s.e.	n	mean	s.e.	n	mean	s.e.
A) Survival (L):												
Sentinel	40	0.728	0.018	8	0.007	0.007	0	-	-	20	0.728	0.042
Gila Bend	37	0.828	0.016	40	0.026	0.005	33	0.217	0.046	20	0.806	0.027
Organ Pipe	39	0.754	0.033	40	0.004	0.002	39	0.131	0.033	18	0.901	0.044
Florence	40	0.685	0.037	40	0.069	0.015	13	0.191	0.054	15	0.761	0.081
B) Fecundity (B):												
Sentinel	40	21.99	2.46	1	4.00	-	0	-	-	20	228.20	46.48
Gila Bend	37	38.61	3.25	24	5.84	0.57	18	3.82	0.46	20	89.84	16.06
Organ Pipe	38	25.26	2.02	6	3.92	0.88	20	5.22	0.74	18	113.50	23.75
Florence	40	8.52	0.57	25	6.60	1.00	9	4.15	0.69	13	64.49	16.23

Table 7. Test of heterogeneity of slopes for the relationship between seasonal precipitation and reproductive success (LB) among four populations of Plantago insularis. Seasonal precipitation and the population mean LB were log-transformed prior to analysis. The interaction term designating the slope was non-significant and was removed from the analysis. Model $R^2=0.87$ of which precipitation within populations explains 0.68 of total sums of squares.

Source	df	MS	F	P
Population	3	6.5	8.0	0.004
Precipitation	1	59.6	72.8	<0.001
Error	11	0.8		

Table 8. Nested analysis of variance and variance components (%V.C.) for log-transformed fecundity of individuals surviving to reproduction in four populations of *Plantago insularis* in two wet years.

Source	1994-95					1997-98				
	df	MS	F	P	%V.C.*	df	MS	F	P	%V.C.*
Population	3	139.0	19.4	<0.001	13.7	3	19.6	6.7	0.002	6.4
Site(Pop)	16	8.0	2.8	0.001	1.5	16	4.0	1.6	0.095	3.9
Quad (Site)	135	3.1	2.9	<0.00	16.1	52	2.9	2.3	<0.001	7.7
Individual(Quad)	3947	1.1			78.7	1048	1.2			82.0

* sum of variance components deviates from 100% due to rounding errors

Table 9 Elasticities of life history parameters in four populations of *Plantago insularis* in wet and dry years. The proportional effect on population growth (λ) of proportional changes in reproductive success (\underline{LB}), winter seed survivorship (\underline{R}), germination (\underline{G}) and delay in germination ($1-\underline{G}$) in two wet years (1994-95 and 1997-98) and two dry years (1995-96 and 1996-97). See methods for details on the calculation of $\epsilon' \underline{G}$ and $\epsilon'(1-\underline{G})$. Elasticity of summer seed survival =1 for all years and populations.

Population	year type	$\epsilon \underline{LB}$		$\epsilon \underline{R}$		$\epsilon' \underline{G}$		$\epsilon'(1-\underline{G})$	
		year1	year2	year1	year2	year1	year2	year1	year2
Sentinel	wet	0.88	1.00	0.12	<0.00	4.73	1.03	-4.73	-1.03
	dry	<0.01	0.00	1.00	1.00	-0.95	-1.00	0.95	1.00
Gila Bend	wet	1.00	0.98	<0.01	0.02	1.10	3.25	-1.10	-3.25
	dry	0.38	0.10	0.62	0.90	-1.25	0.66	1.25	-0.66
Organ Pipe	wet	0.98	1.00	0.02	<0.01	1.80	1.23	-1.80	-1.23
	dry	0.05	0.85	0.95	0.15	-2.30	0.34	2.30	-0.34
Florence	wet	0.98	0.99	0.02	0.01	1.07	1.56	-1.07	-1.56
	dry	0.51	0.78	0.49	0.22	-0.11	0.42	0.11	-0.42

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Figure 1. Life cycle of a winter annual plant showing pathways for germinated (G) and non-germinated individuals (1-G), with survivorship of non-germinated seeds in the winter (R), survivorship of the seeds in the summer (S), survivorship of germinated seedlings to reproduction (L) and fecundity of surviving seedlings (B). * indicates the stage of the life cycle at which fall seed density was estimated.

Figure 2. Description of sampling design for a four year field study of four populations of Plantago insularis, from most mesic to most xeric; Florence (FL), Organ Pipe (OP), Gila Bend (GB) and Sentinel (SE). Sites and quadrats are nested within each population.

Figure 3. Winter season precipitation (September and April) between 1994 and 1998, expressed as percent deviation from the historical precipitation mean in each of four populations of Plantago insularis in southern Arizona. ●=Sentinel, ▼=Gila Bend, ■=Organ Pipe and ◆= Florence.

Figure 4. Population size estimated as the density of seeds in the fall prior to germination at four populations of Plantago insularis in five years (●=Sentinel, ▼=Gila Bend, ■=Organ Pipe and ◆= Florence). The mean population size in seeds/m² and coefficient of variation in size were 6634 (1.34), 1985 (1.16), 1046 (0.98) and 1778 (0.99) in the four populations, respectively.

Figure 5. Reproductive success (LB) between 1994 and 1998 in each of four populations of Plantago insularis. Bars represent standard errors and means with different letters are significantly different ($P < 0.05$) with Student-Newman-Kuels a posteriori multiple comparison. ●=Sentinel, ▼=Gila Bend, ■=Organ Pipe and ◆= Florence.

Figure 6. The relationship between winter season precipitation (September to April) and LB in four populations of Plantago insularis in four years. Regression lines are drawn for descriptive purposes. ●=Sentinel, ▼=Gila Bend, ■=Organ Pipe and ◆= Florence.

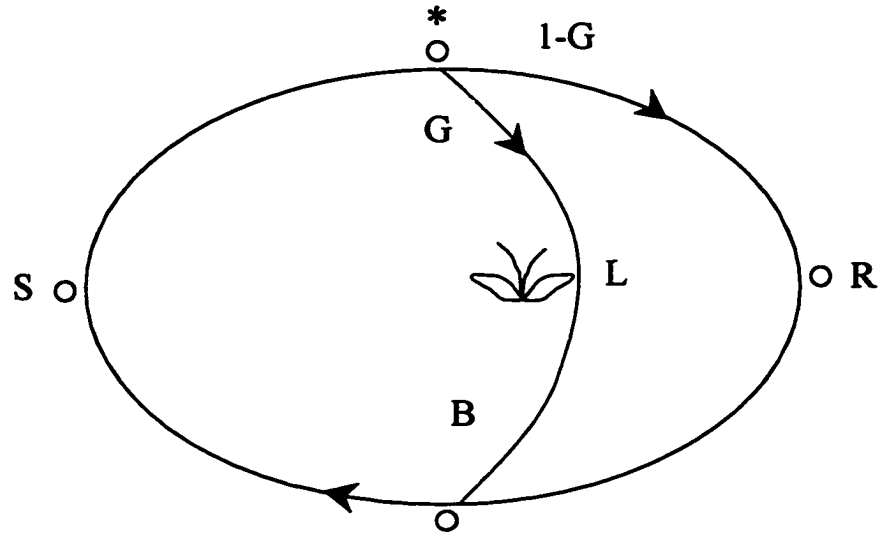


Fig. 1

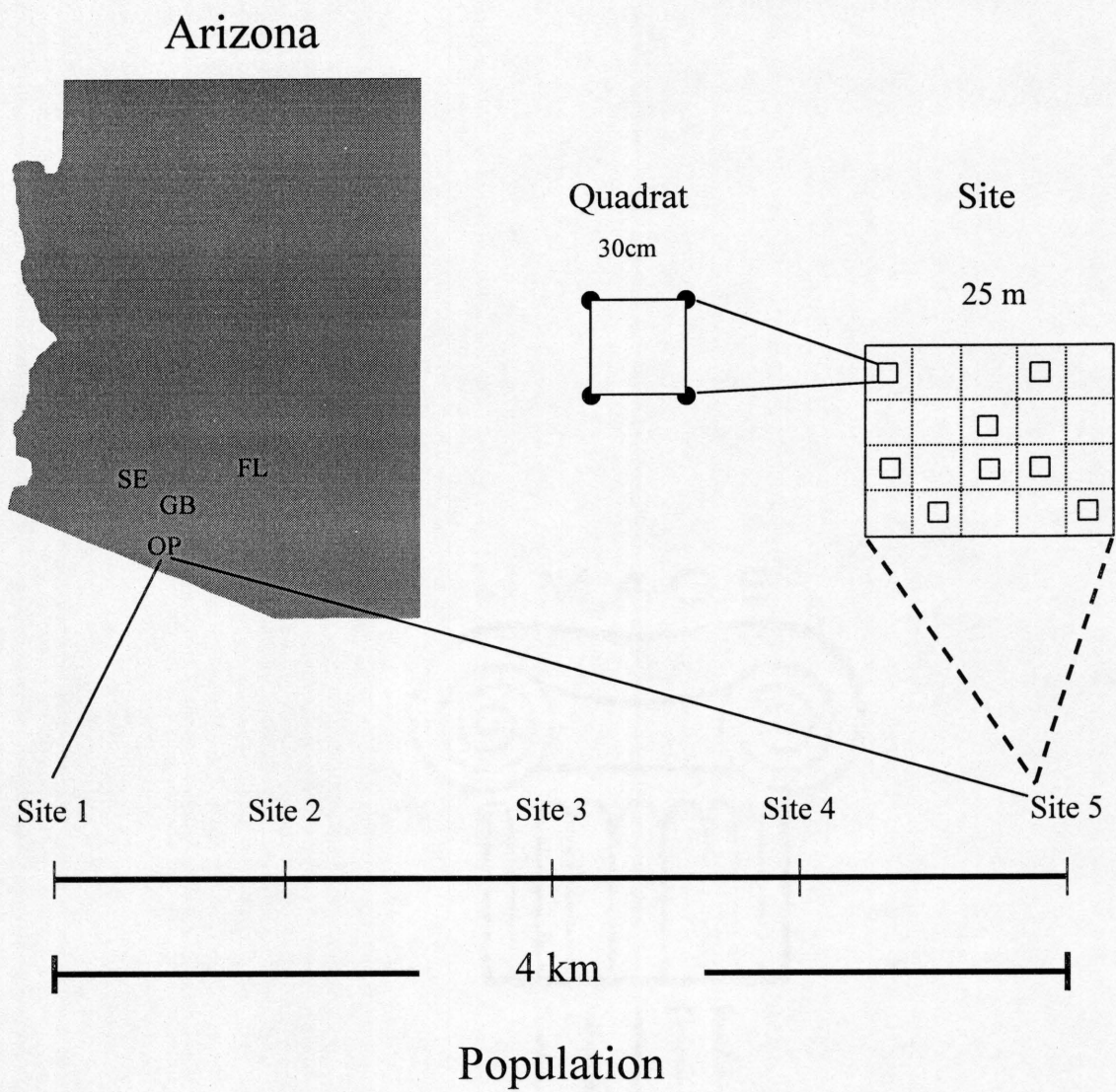


Fig. 2

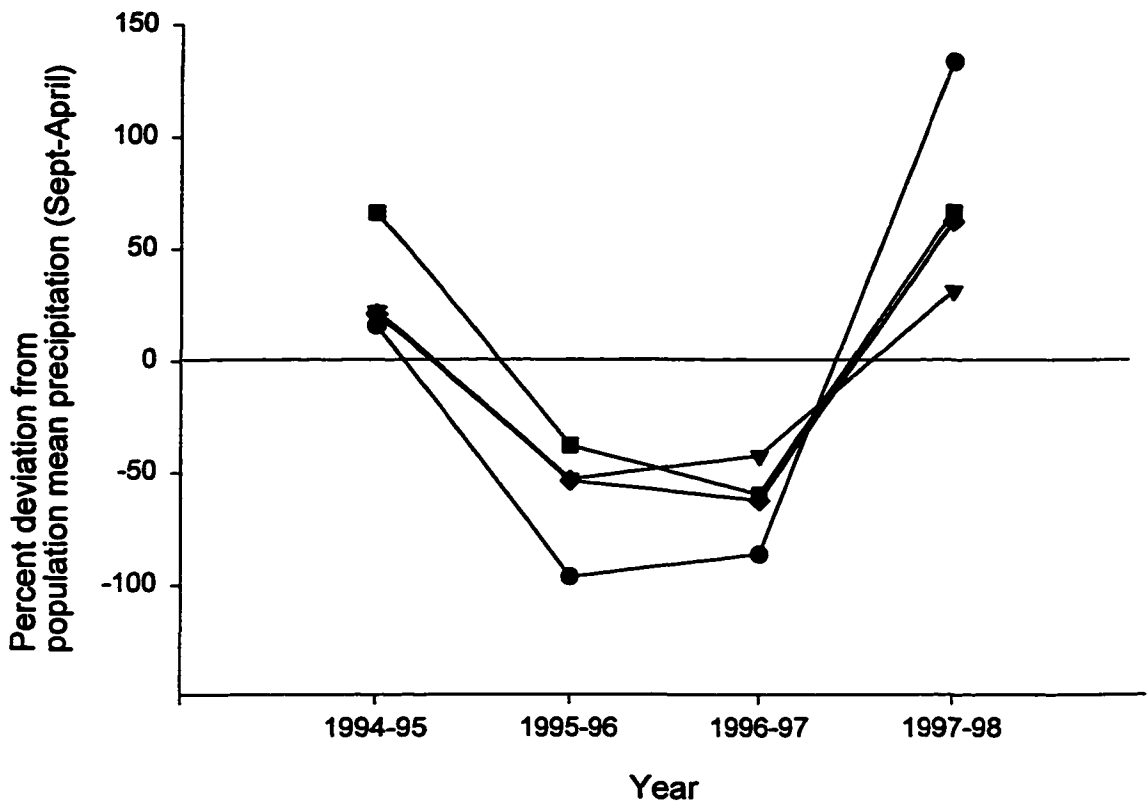


Fig. 3

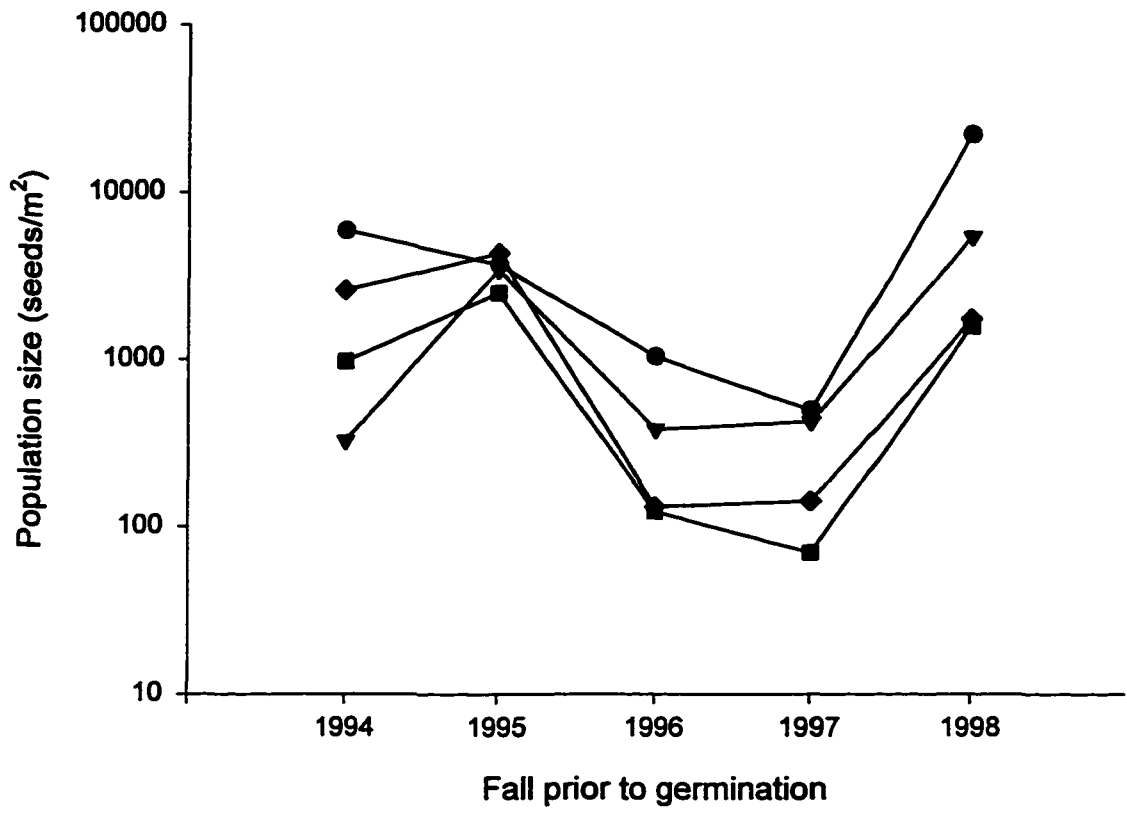


Fig. 4

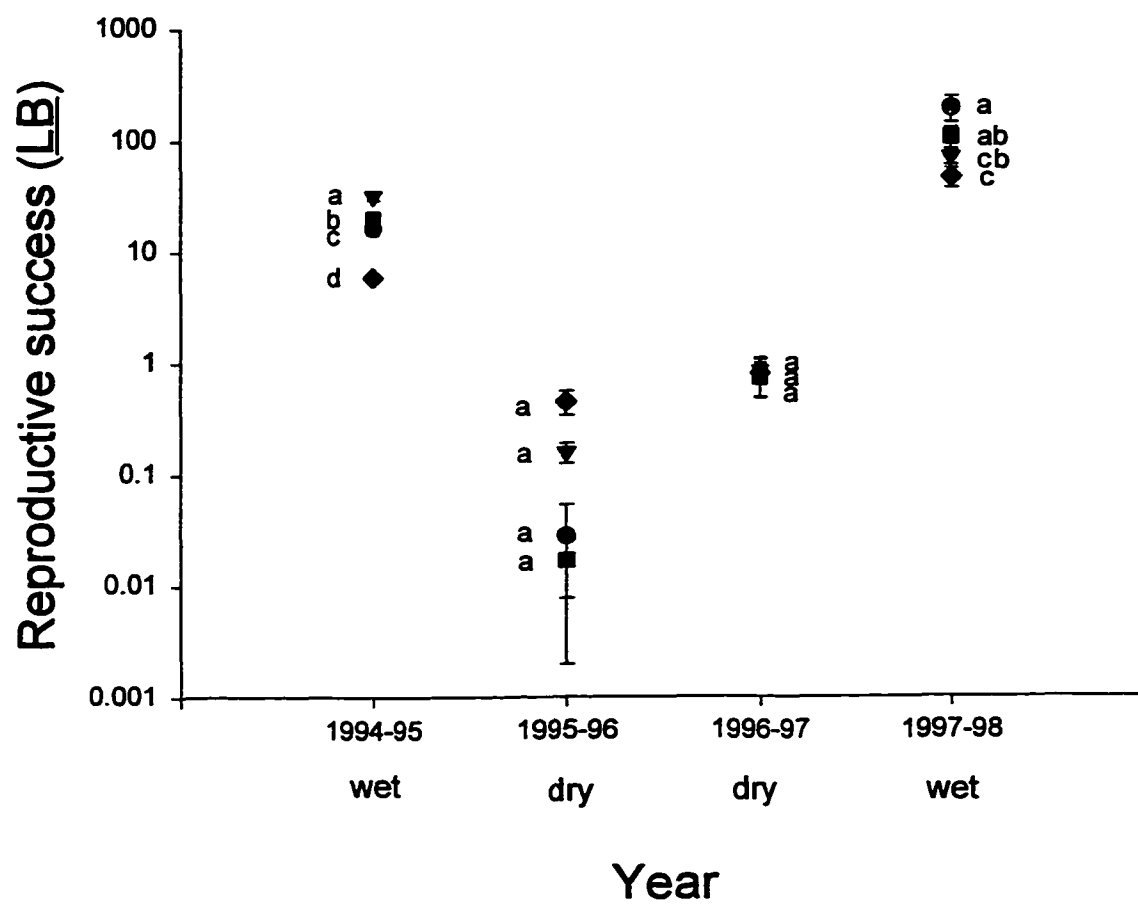


Fig. 5

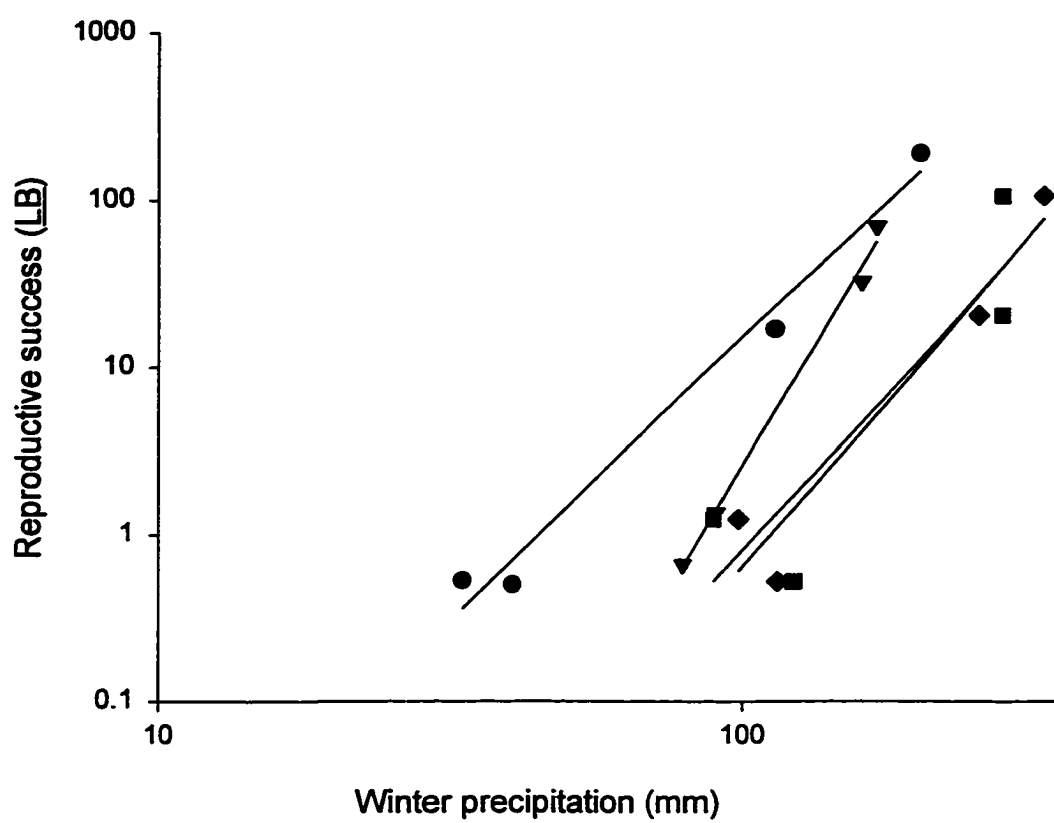


Fig. 6

Appendix 1. Calculation of lambda according to eqn. 1 in four populations of Plantago insularis in four years. Mean density of germinated seedlings (**E**) and density of seeds in the spring after germination (**D**) were used to calculate germination fraction (**G**) (Appendix B). Survival*reproduction of germinated seedlings (**LB**), seedlings/m² and seeds/m² were used to calculate summer seed survival where $S = (D_{t+1} + E_{t+1}) / (D_t + E_t * LB_t)$ and t=year (see methods). Column VI and VII are the seed and seedling population dynamics in eqn. 1, respectively; these sum to lambda. $R=0.5$ for all calculations.

Population	Year	I	II	I/(I+II)	IV	V	VI	VII	VI+VII
		seedlings/m ² (E)	seeds/m ² (D)	Germination Fraction (G)	Reproductive success (LB)	Seed Survival (S)	(1-G)*S*R	G*S*L*B	lambda (λ)
Sentinel	1994-95	1052	4787	0.18	16.37	0.17	0.07	0.49	0.56
	1995-96	13	3656	0.01	0.03	0.30	0.15	0.01	0.15
	1996-97	0	1037	0.00	0.00	0.45	0.23	0.00	0.23
	1997-98	486	13	0.97	190.50	*0.31	0.01	56.73	56.73
Gila Bend	1994-95	291	36	0.89	31.65	0.34	0.02	9.63	9.65
	1995-96	2254	1178	0.66	0.16	0.33	0.06	0.03	0.09
	1996-97	24	358	0.06	0.84	0.98	0.46	0.05	0.51
	1997-98	128	298	0.30	68.52	*0.55	0.19	11.39	11.58
Organ Pipe	1994-95	519	453	0.53	19.78	0.23	0.05	2.38	2.43
	1995-96	1495	997	0.60	0.02	0.22	0.04	<0.01	0.05
	1996-97	97	26	0.79	0.73	0.38	0.04	0.22	0.26
	1997-98	57	13	0.81	104.75	*0.27	0.03	23.25	23.27
Florence	1994-95	2163	417	0.84	5.94	0.35	0.03	1.74	1.77
	1995-96	2313	1994	0.54	0.45	0.09	0.02	0.02	0.04
	1996-97	91	40	0.69	0.79	0.73	0.11	0.40	0.51
	1997-98	90	52	0.63	43.99	*0.39	0.07	10.75	10.82

^a average of previous three years

APPENDIX B

**LIFE HISTORY STRATEGIES IN VARIABLE ENVIRONMENTS:
A STUDY OF BET-HEDGING AND DELAYED SEED GERMINATION IN
POPULATIONS OF THE DESERT ANNUAL PLANTAGO INSULARIS**

Running Head - Bet-hedging and delayed seed germination

Life history strategies in variable environments: a study of bet-hedging and delayed seed germination in populations of the desert annual Plantago insularis

Maria J. Clauss

Department of Ecology and Evolutionary Biology

University of Arizona, Tucson, AZ 85721 USA

Tel. 520-621-5956

FAX. 520-621-9190

clauss@u.arizona.edu

Key Words - annual plant, bet-hedging, environmental gradient, phenotypic plasticity, seed germination, variable environments

ABSTRACT

Temporal variability in survival and reproduction is predicted to affect the evolution of life history characters. Desert annual plants experience temporal variation in reproductive success that is largely caused by precipitation variability. I studied populations of the desert annual Plantago insularis along a precipitation gradient. Whereas evolutionary models of bet-hedging predict one optimal germination fraction for a population, empirical studies have demonstrated that environmental conditions during germination can cause a range of germination fractions to be expressed. Here, I report on three studies that measure germination fractions under various environmental conditions. In a field study, I found that populations in historically more xeric environments had lower mean germination fractions, as is predicted by bet-hedging models. In two experimental studies, I demonstrate that the field observation resulted from two underlying processes. Low precipitation caused low germination fractions (<0.07). When water was amply available, all populations could express high germination fractions (>0.80). A pattern of delayed germination consistent with among year bet-hedging predictions arose in the field because the frequencies of wet and dry germination seasons differed among populations located along the environmental gradient. Higher germination fractions and a longer germination season when water was amply available contributed to the mean response in more xeric environments.

INTRODUCTION

Temporal variability in survivorship and reproduction has major consequences for life history evolution and population dynamics (Cohen 1966; Levins 1968; Gillespie 1981; Stearns 1992; Rhodes et al. 1996). When temporal variability is large, and in some years all individuals can experience complete reproductive failure, selection will favor life history strategies that buffer against local extinction. Annual plants in highly variable environments such as deserts are particularly vulnerable to mortality during the vegetative phase (Beatley 1974; Venable and Pake 1998). The potential for delayed seed germination in desert annuals to reduce variance in individual fitness has been at the center of studies for life history evolution in variable environments. When seeds of a genotype germinate over a number of years, the probability is lower that seedlings in all years will die before reproducing. This type of delayed seed germination is termed a bet-hedging strategy when it reduces temporal variance in reproductive success for a genotype while also reducing the arithmetic mean fitness. Bet-hedging is adaptive when it increases geometric mean fitness in variable environments (Seeger and Brockmann 1987). Delayed seed germination as an adaptive bet-hedging strategy has been the subject of a large number of theoretical models (Cohen 1966, 1967; MacArthur 1972; Venable and Lawlor 1982; Bulmer 1984; Cohen and Levin 1985; Ellner 1985, 1986, 1987; Leon 1985; Brown and Venable 1986; Klinkhamer et al. 1987; Venable and Brown 1988; Venable 1989) and a much smaller number of rigorous empirical tests

(Philippi 1993b; Pake and Venable 1996).

Conditions under which fitness (\bar{W}) is maximized by bet-hedging via delayed seed germination in unpredictably variable environments were first formalized by Cohen (1966) using the equation,

$$\bar{W} = \prod_i [s(1-G) + Y_i G]^{P_i}, \quad (1)$$

where s is the survival rate to the following year of non-germinated seeds, G is the fraction of seeds germinating in any given year, Y_i is the average seed yield per germinated seed in type i years and P_i is the probability of a type i year. When s is held constant and there are only two year types, good years (g), where $Y_g \gg 0$, and poor years (p), where $Y_p=0$, the germination fraction that maximizes fitness is approximately equal to the probability a year will be good for survivorship and reproduction (P_g). Populations differing in the probability of a good year are predicted to differ in their optimal germination fractions (G^*).

Empirical tests of adaptive variation in germination fractions generally use seeds collected from maternal plants in natural populations that differ in climate. Because direct estimates of the probability of a good year for survival and reproduction (P_g) for multiple populations are rare, differences in climatic regimes among populations are assumed to reflect differences in the among-year probability distribution of survival and reproduction for germinated individuals. For example, precipitation and temperature have been used to characterize good and poor year types in multiple populations of a

desert annual (Philippi 1993b). Seed germination fractions are then determined in the greenhouse or growth chamber (e.g., Jain 1982; Philippi 1993b). Such studies record germination fractions in benign environments that are conducive to germination of non-dormant seeds and, under these conditions populations have been shown to differ significantly, yet without a consistent relationship to the climatic gradient under investigation (Jain 1982; Hacker 1984; Gutterman and Ednine 1988; Philippi 1993b; Kigel 1995). Several empirical studies have focussed on the role of additive genetic variation, dominance and epistatic effects as well as maternal effects in such population differences (Schmitt et al. 1992; Philippi 1993b; Platenkamp and Shaw 1993; Wulff et al. 1994; Wulff 1995).

Less emphasis has been placed on examining the role of environmental conditions during germination on the differences among populations. Environmental factors such as water, temperature and photoperiod have been found to affect germination responses in almost all species investigated (Gutterman 1993; Baskin and Baskin 1998). Furthermore, the phenotypic response to these factors can differ among species, populations and genotypes (Schmitt et al. 1992; Beckstead et al. 1996; Baskin and Baskin 1998). Therefore, germination fractions in the field may differ among years and populations, and from those observed in controlled conditions, simply as a result of variation in environmental conditions during germination. Such phenotypic variability would cause actual germination fractions to deviate from any fixed optimum predicted by bet-hedging models. The direct effect of the environment on germination fractions is

particularly evident in deserts where small rainfall events may not provide sufficient moisture for mass germination of non-dormant seeds (Beatley 1974; Freas and Kemp 1983). Along precipitation gradients in deserts, more xeric populations can be characterized as having frequent small and occasional large rainfall events (Sellers and Hill 1974). As a consequence, germination in more xeric environments may frequently be limited by water availability and differ greatly from the germination responses seen under benign experimental conditions. A study of systematic differences among populations in environmental conditions during the germination season, in addition to differences in P_g , may be necessary for understanding variation in germination fractions in nature along environmental gradients. Neither the among-year distribution environmental conditions during the germination season nor the effect of environmental conditions on germination has been considered in previous empirical studies of bet-hedging.

I conducted a multi-year study of germination in several populations of the desert winter annual, Plantago insularis. The goal was to estimate optimal germination fractions for populations of this species and to determine whether variation in observed germination fractions matched bet-hedging predictions. Populations were chosen along a precipitation gradient. Optimal germination fractions for each population were estimated a) from the proportion of good years in the historical precipitation record (P_g) and b) from observed among-year variation in survivorship and reproduction (\bar{Y}). Germination fractions were then measured in three environmental settings. In situ seed germination in

four populations of P. insularis was observed in four years, including one El Niño season. In a common garden experiment with five populations, I tested the effects of water quantity and timing within the season on germination fractions. Finally, I assessed differentiation across the range of the species by sampling the soil seed bank from twelve populations in southwestern Arizona and southern California and measuring germination fractions in the growth chamber.

SPECIES, POPULATIONS AND PRECIPITATION

Plantago insularis Eastw. [incl var. fastigiata (E. Morris) Jepson] (section Leucopsyllium, Plantaginaceae) (desert Indian wheat) is a scapose winter annual endemic to the Sonoran and Mohave Deserts of southwestern United States and northwestern Mexico. The species occurs on low elevation desert bajadas and flood plains (0-1000m) in association with other annuals such as Amsinckia intermedia, Chorizanthe rigida, Erodium texanum, Lepidium lasiocarpum, Pectocarya recurvata, and Schismus barbatus, as well as perennial vegetation (Ambrosia dumosa, Atriplex canescens, Carnegiea gigantea, Larrea tridentata, and Opuntia spp.). P. insularis is one of the most abundant winter annual species, and is a preferred native forage species of desert herbivores (Reichman 1975; Krausman et al. 1989; Seegmiller et al. 1990). Seeds germinate between September and March in response to winter rainfall events and cool temperatures. December and January tend to be the wettest and coolest months (Sellers and Hill 1974). Rainfall in the several months following germination is critical for

survival of plants to reproductive maturity. Plants set seed and senesce before the early summer dry period. *P. insularis* has a persistent soil seed bank that is formed when seeds remain ungerminated in the soil after the end of the germination season (Pake and Venable 1996).

The twelve study populations of *P. insularis* are located in the Arizona Upland and Lower Colorado Valley subdivisions of the Sonoran Desert, and in the Mohave Desert. Each population is within 20km of a weather station for which climatic data are available from National Oceanic and Atmospheric Administration (NOAA). There was significant variation in historical precipitation among the twelve locations, and the mean winter season rainfall (September to March) varied from a low of 53mm (Brawley CA) to 171mm at the most mesic site (Florence AZ) (Table 1). Populations with lower mean precipitation had significantly higher coefficients of variation for winter precipitation (Table 1). The slope of linear regression of the log standard deviation and log mean winter precipitation ($b=0.552$) was significantly less than 1 ($F=67.91$; $df=1,10$; $P<0.001$), indicating that drier populations had proportionately greater standard deviations. Although all populations are found in dry desert environments, I refer to populations as relatively more mesic and more xeric throughout the paper.

Southwestern North America receives more than average winter precipitation (September-March) during El Niño Southern Oscillations (ENSO) (Ropelewski and Halpert 1986). I identified ENSO years from sea-surface temperatures (Japan Meteorological Agency), and calculated total winter precipitation in all ENSO and non-

ENSO years from 1949-1990 for the 12 study populations. ENSO years had higher mean winter precipitation than non-ENSO years for all 12 populations ($P < 0.05$ for 9 of 12 populations). A linear regression of the log-transformed population mean precipitation in ENSO years versus in non-ENSO years estimated a slope of 0.73. This value was significantly less than 1 ($F = 6.87$; $df = 1, 10$; $P = 0.026$), indicating that drier populations received proportionately more precipitation during ENSO years. ENSO also affected the timing of precipitation during the winter. In non-ENSO years, the month during which the most rain fell was December or January in 11 of 12 populations. In contrast, significantly fewer populations (3 of 12) had maximal rainfall in December or January in ENSO years ($\chi^2 = 8.4$; $df = 1$; $P < 0.005$). During ENSO years, most populations had maximal rainfall in either October or March when average day length was longer and temperatures were higher (Sellers and Hill 1974). Both Florence and Organ Pipe, the two most mesic populations, had maximal rain in December in ENSO as well as non-ENSO years.

I. ESTIMATION OF OPTIMAL GERMINATION FRACTIONS

I estimated the optimal germination fractions for populations of *P. insularis* using two sources of information. The first approach made use of the historical precipitation records for each of the 12 populations as well as biological information on germination and growth of desert winter annuals. Germination takes place in the Sonoran and Mohave Deserts following winter rainfall events of more than 15-25 mm (Juhren et al.

1956; Tevis 1958a,b; Beatley 1974) and can be predicted from precipitation records (Noble and Crisp 1979/80). Years in which germination is followed by rains in the subsequent several months generally have high survivorship and reproduction of germinated individuals and are termed good years (Beatley 1974; Loria and Noy-Meir 1979/80; Venable and Pake 1998). Using known seasonal precipitation requirements for germination, growth and reproduction in desert annual plants, I predicted years with positive population growth from the historical precipitation record as follows. For each location and in each winter season with a complete precipitation record, I assessed whether any one month between September and March had greater than the 17mm rainfall that I considered necessary for germination. Then, for each germination month with >17mm rain I determined whether monthly precipitation was greater than 24mm or 30mm, respectively, in the following one or two months. The season was designated as being good (\underline{Y}_g) if at least one sequence of three months met the criteria. The proportion of good winter seasons (\underline{P}_g) was estimated as the proportion of seasons with sufficient rain for germination that also had conditions favorable for survival and reproduction (referred to as 17/24/30). I then used two other threshold values (17/20/20, 5/20/20) and also recalculated \underline{P}_g with the total number of years as the denominator (17/24/30 of total).

The proportion of germination years that were good years (17/24/30) varied widely, from 0.11 at Sentinel to 0.78 at Florence (Table 1). Although the proportion of good years was affected by the exact threshold values used, the rank orders, and

therefore the positions of the populations along the precipitation gradient, were highly correlated for alternative calculations ($r_{\text{spearman}} > 0.75$; $P < 0.005$). The four measures of proportion of good years (17/24/30, 17/20/20, 5/20/20, 17/24/30 of total) were also positively correlated with the mean winter precipitation ($r_s > 0.88$; $P < 0.001$) and negatively correlated with the coefficient of variation ($r_s < -0.59$; $P < 0.04$). This method of estimating the probability of a good year (\underline{P}_g) combines biological information for the study species with data on temporal variability over decades that is not generally available from demographic studies.

I then estimated the optimal germination fraction (\underline{G}^*) by maximizing \underline{W} in eq. 1 with respect to \underline{G} using the 17/24/30 threshold for the calculation of \underline{P}_g . When $\underline{s}=1$, $\underline{Y}_p=0$ and $\underline{Y}_g=100$, \underline{G}^* was less than one and approximately equal to \underline{P}_g for all populations (Table 1). Optimal germination fractions varied among populations from 0.10 to 0.78. Increasing \underline{Y}_g from 5 to 500 caused \underline{G}^* to approach \underline{P}_g from below. When seed survival was increased from 0.1 to 1, \underline{G}^* decreased slightly from \underline{P}_g , as seen in Table 1 for the more xeric populations. Because \underline{G}^* was always less than one, delayed seed germination was predicted to be a bet-hedging adaptation in all twelve populations of *P. insularis*.

A second method of calculating optimal germination fractions was based on four years of field observations of survival and reproduction of *P. insularis* at four of the twelve study populations (Appendix A). Geometric mean growth rates of hypothetical genotypes at each population were calculated using eq. 1 for a range of \underline{G} from 0.1 to 1, assuming 100% seed survival and observed values of \underline{Y} in four years. For Sentinel, Gila

Bend and Organ Pipe, hypothetical germination fractions of 0.5, 0.8 and 0.6 maximized growth rates, respectively. Only at Florence, the most mesic population, did a hypothetical genotype with no delayed germination ($G^*=1$) have greatest fitness in this four year period. Florence also had the greatest optimal germination fraction as calculated from the historical precipitation data ($G^*=0.78$). Thus, direct measures of reproductive success in P. insularis confirm for three of four populations that bet-hedging via delayed seed germination can be an adaptive strategy.

II. MEASUREMENT OF GERMINATION FRACTIONS

Study 1: In situ germination at four populations

Methods

Germination under natural conditions was studied in four populations of P. insularis in southern Arizona between September 1994 and March 1998 (Table 1). Five groups of eight quadrats each were deployed at 1km intervals, for a total of forty permanent plots per population. The eight quadrats were positioned using stratified random sampling in a 25m X 20m area, with 5mx5m grid squares and the provision that the minimum distance between two quadrats was 2m. To obtain adequate numbers of plants, quadrat size varied from 225 to 2500cm², depending inversely on the density of plants each year. All individuals of P. insularis germinating within quadrats were mapped on acetate sheets using a clear plexiglass table during 10, 8, 9, and 13 censuses, in 1994-95, 1995-96, 1996-97 and 1997-98, respectively. By surveying the populations

following all rainfall events between September and March, I determined the timing and amount of precipitation that resulted in seedling emergence. Seeds germinate within 12 days of a rainfall event (M. Clauss pers. obs) and new seedlings recorded during a census were referred to as a germination cohort.

I estimated in situ germination fractions (G) for each population in each season. Germination fractions were calculated by dividing the density/m² of seedlings (from the germination monitoring) by an estimate of the density/m² of seeds in the soil seed bank prior to germination, determined as follows. In three out of four years I estimated the seed bank by sampling 22.06cm² by 2cm deep soil cores in early March, following the last germination cohort and prior to the dispersal of new seeds. Shallow soil cores provide an appropriate estimate of the seed bank because most (>89%) viable seeds lie within the top 2cm of the soil surface in desert sites (Reichman 1984; Pake and Venable 1996) and because P. insularis seeds buried under greater than 1cm of sand do not germinate (Clauss unpubl. data). In March 1995, one core was collected adjacent to each of five randomly chosen permanent plots at each of the five sites per population (for a total of 25 samples per population). In March 1996, a core was taken adjacent to six plots at each of the five sites from each population (30 samples per population). In March 1998, one soil core was collected adjacent to each of seven permanent plots at each of five sites (35 samples per population). For these three years, the density of seeds in the soil prior to germination for each population was estimated by the average seedling density for that season plus the density of viable non-germinated seeds in the

soil core taken at the end of the germination season (March). This method assumes no seed mortality during the germination season. The seed bank in the Fall of 1996 was directly estimated from 16, 480cm² by 2cm deep soil samples taken from each population in November 1996 prior to germination for the common garden experiment (see Study 2: Methods). In all years, the soil from each sample was sieved, all P. insularis seeds were removed and viable seeds were counted. All seeds were cut or poked through the seed coat to determine viability. Seeds with fleshy endosperm were regarded as viable. I found this technique for testing seed viability superior to tetrazolium chloride because some deeply dormant viable seeds show minimal staining with tetrazolium and because embryos and endosperm in the field usually undergo easily recognizable changes upon death (e.g., desiccation, decay).

Results

The average in situ germination fractions in more xeric environments were lower than in more mesic environments (Fig.1; $r_{\text{pearson}}=0.935$; $P=0.065$). Germination fractions ($G=L/(D+L)$) differed greatly among populations and among years (Fig. 1) because both seed (D) and seedling densities (L) varied significantly (Table 2). The two populations in more xeric environments, (Sentinel (SE) and Gila Bend (GB)) had greater ranges of germination fractions among years than the populations in more mesic environments (Fig. 1). Whereas all populations had high G (>0.80) in at least one season, SE and GB had both the highest (0.97 and 0.89, respectively) and the lowest (<0.07) germination

fractions. The lowest germination fractions for the more mesic populations were 0.53 and 0.54 for OP and FL, respectively.

The historically more xeric populations (Table 1) received approximately half as much rainfall as the mesic populations during the four year study period (Table 2). Because winter storm systems are regional in the Sonoran Desert, most populations experienced most rainfall events. However, the more xeric populations generally received less rainfall per event (Fig. 2). Germination occurred between September and March and in three of four years all populations had multiple germination cohorts (Fig. 2). If I assume similar seed germination responses to water availability for all populations, I would expect fewer germination cohorts at more xeric sites. However, in most years, germination occurred as or more often at SE and GB in comparison to Organ Pipe (OP) and Florence (FL) (Table 3). The relatively high number of germination cohorts at more xeric populations occurred because the seeds responded to small rainfall events at SE and GB (Table 3). Furthermore, even with less precipitation, germination at SE occurred over the widest range of dates, spanning 5 to 6 months in three of four years (Fig. 2). Shorter germination seasons at more mesic populations were not the result of a paucity of rainfall early and late in the season. For example, substantial rains (>25mm) occurred in September 1994 and February 1995 at OP, but did not result in germination (Fig. 2a). Nor was there evidence that the germination seasons were truncated due to depletion of the seed bank (Table 2).

Study 2: Common garden germination trial with five populations

Methods

In order to compare germination responses for seeds originating from historically mesic and xeric environments under similar conditions, I conducted an outdoor common garden experiment in Tucson, AZ. Seeds from soil seed banks of five populations were tested for germination in four trials during the 1996-97 winter. The population from Yuma (YU) was added to the four populations in Study 1 because this location is more xeric and extended the climatic gradient under investigation (Table 1). Soil containing *P. insularis* seeds was collected from each population in November 1996 prior to any in situ germination. I allowed seeds to experience ripening, over-summering, and early fall conditions in situ because environmental conditions during this time can have significant effects on germination responses of desert winter annuals, including *P. insularis* (Adondakis in prep.). In each population, 16 soil samples, 480cm² by 2cm in depth were taken in a stratified random manner (one random sample in each 10m block along four 40m transects). Transects were separated by 1km. Except for Yuma, these transects were associated with the permanent quadrats at sites 1-4 in the four populations described in Study 1. The 16 samples from each population containing seeds and soil were combined, well mixed, and divided into 4 equal parts. The soil was stored outside of the University of Arizona greenhouses and was protected by a roof from rain and direct sunlight. For each germination trial in December 1996, January, February and March 1997, one fourth of the soil from each population was used as a seed source. A 500cm³ sample of the soil

seed bank was placed on top of 7500cm³ of commercial topsoil in each of fifty 26x53x6cm trays. The sample constituted a layer ca. 5mm deep in each tray. Five populations and two watering treatments were arranged in a randomized complete block design with five blocks and no replication within blocks. The trays in the high watering treatment (HW) received 100ml in both morning and evening, daily for 30 days. Trays in the low watering treatment (LW) received 100ml daily, only in the morning. Five additional trays with only topsoil were used as controls for seed contamination and received the high water treatment. The amount of water applied in the high water treatment was chosen to simulate high soil humidity after large winter rains. This treatment kept the soil surface damp at all times in the December trial. Soil surfaces underwent periods of drying during the day in both treatments for all subsequent germination trials. Germination trays were protected from natural rains with clear plastic sheets that were removed immediately following rainfall. All trays were covered with 40% shade cloth to reduce evaporation.

Newly germinated seedlings were individually marked and counted every 5 days. Trials lasted 30 days because after this period emergence had ceased. Seedling survivorship was recorded at the end of the 30 day trial. The soil from each tray was then sieved and all remaining seeds of P. insularis were removed, tested for viability, and counted. The number of viable seeds remaining in the soil (D) and the number of germinating seedlings (L) in each tray were used to calculate germination fraction: $G=L/(D+L)$. All P. insularis seeds and seedlings originated from the field collected seed

banks because no individuals were found in the control trays. Germination fractions were analyzed with a generalized linear model assuming a binomial response variable, a logit link function and adjusting chi-squares to account for over-dispersion (PROC GENMOD, SAS Institute). Germination fraction means and standard errors given in the tables and figures were back-transformed after calculation on logit transformed data ($\log((a+0.5)/(b+0.5))$), where a =number of germinated seeds and b =number of non-germinated seeds; Sokal and Rohlf (1995)).

Results

Mean germination fractions differed significantly among populations in the common garden experiment (YU: 0.44, SE: 0.27, FL: 0.26, GB: 0.19, OP: 0.17; Table 4 - Population main effect). These population differences are interpreted below in the context of the significant differences among populations in response to trial date and watering treatment (Table 4; Pop*Trial and Pop*Water interactions).

Trials conducted later in the winter season had lower average germination fractions (Dec. 0.45; Jan. 0.19; Feb. 0.25; Mar. 0.16; Table 4 - Trial main effect). Aside from the low \bar{G} in January (Table 5), average differences among trials coincided with seasonal changes in environmental conditions over the four trials (Table 6). However, populations differed significantly in their response to the germination trials (Fig. 3; Table 4 - Pop*Trial interaction). Whereas there was a decline in \bar{G} in later trials for the more mesic populations (FL, OP GB), \bar{G} values were high throughout the season for SE,

and even tended to increase in March for YU (Fig. 3). Thus, lower average \bar{G} values for the more mesic populations were due to declining germination in the January, February and March trials (Fig. 3). This pattern was consistent with my in situ observations that seeds from SE germinated more with late (and early) rains when they occurred than did seeds in more mesic populations (Fig. 2).

The germination fractions for all populations declined when water was limiting (HW 0.38; LW 0.16; Table 4 - Water main effect), although the plastic response to water availability varied among populations (Fig. 4; Table 4 - Water*Pop interaction). The driest two sites, YU and SE, had the highest germination fractions in the high water treatment. Reducing water availability in the LW treatment resulted in the largest absolute decline in \bar{G} for these two xeric populations (Fig. 4). Yuma, however, still had the greatest \bar{G} in the LW treatment (Fig.4). Throughout the experiment, the germination fractions for YU and SE were often equal to, or higher than, comparable treatments for the mesic populations (Table 5, Fig. 4). This is in contrast to the average in situ measurements of \bar{G} that were lowest for SE and higher for GB, FL and OP (Fig.1).

The two-way interaction between water and trial was also significant (Table 4). Germination fractions were consistently greater in the HW than in the LW treatment and \bar{G} in HW decreased linearly with later trial dates in the high water treatment. A seasonal decline was also observed in the LW, except for the January trial where \bar{G} was unexpectedly low (Table 5). During the January trial there was less natural rainfall, and therefore the seeds experienced fewer days with cloud cover and high humidity (Table

6).

Population, watering and trial date treatments all had strong effects on the survivorship of seedlings. In December, all germinated seedlings survived to day 30 of the trial (Fig. 5). Seedlings in the HW treatment had higher survivorship than LW individuals in January. In February and March no seedlings survived to day 30, with the exception of the YU high water treatment in which survival to day 30 was 0.89 and 0.49, respectively (Fig. 5).

Study 3: Germination fractions from twelve populations tested in a growth chamber

Methods

I tested for population differentiation at the regional level by collecting soil seed banks of twelve populations throughout the range of *P. insularis* and determining seed germination in two growth chamber trials. In October 1995, prior to any in situ germination, I collected six soil cores in a stratified random fashion (one sample from each 10m block) along a 60 meter transect from each of twelve populations in southern Arizona and California (Table 1). Each core sampled an area of 98.2cm² by 2cm in depth. *P. insularis* seeds were removed from the sample and rinsed with a 2% solution of bleach to reduce superficial fungal and bacterial contaminants. For each trial, ten seeds per sample were weighed and placed on 0.4cm³ of water saturated silica sand in a 100X15mm petri dish. The 72 dishes were placed into a growth chamber and positions

were re-randomized daily. Growth chamber environmental conditions were set to average temperatures and photoperiod across the environmental gradient and were adjusted as the seasons progressed during the germination trials. In the first, early season trial, the growth chamber was set to 26°C/10°C day and night temperatures and 11:30hrs of daylight in October. In November, the conditions were adjusted to 23°C/7°C with 10:15hrs of daylight and in December to 18°C/3°C with 10hrs daylight. Water was supplemented as required to maintain saturation of the sand. Germination was scored daily until there was no germination for 5 consecutive days. Seeds not used in the first germination trial were stored outside the University of Arizona greenhouses in Tucson AZ, where they experienced natural fluctuations in light, temperature and humidity but were protected from direct precipitation. A second, mid-season trial was conducted in January through March 1996 with the growth chamber set to 18°C/3°C with 10hrs daylight in January, 23°C/7°C and 10:30hrs in February and 26°C/10°C with 11:45hrs daylight in March. Population differences in germination fraction were analyzed with a generalized linear model assuming a binomial response variable and using a logit link function (PROC GENMOD, SAS Institute). Variation in seed mass among populations was analyzed using analysis of variance.

I analyzed the relationship between germination fractions and four measures of the proportion of good years as well as the mean winter precipitation and the coefficient of variation of winter precipitation for the twelve populations. The proportions of good years were estimated as detailed in Estimation of Optimal Germination Fractions. I

tested for linear trends among populations in \bar{G} and seed mass using linear contrasts within the generalized linear models described above. The linear contrasts were constructed by weighting the populations by their position along the environmental gradient. Separate analyses were conducted for each of the six environmental measures.

Results

Germination fractions differed significantly among populations and among trial dates (Table 7a - main effects). On average, \bar{G} values were higher in January than in October (Fig. 6), however populations differed significantly in their response to trial date (Table 7a - Pop*Trial interaction).

A significant proportion of the variation among populations in germination fraction was explained by the position of populations along the environmental gradient in five of six linear contrasts (Table 7b). Populations with a lower proportion of good years had higher germination fractions (Table 7b I-iv; Fig. 6). The relationship between germination fraction and precipitation regime was significantly negative when the environment was measured by 1) any of several combinations of threshold values for evaluating frequency of good years among germination years (Table 7b i-iii), 2) using the total number of years as the denominator for the proportion of good years (Table 7b iv), or 3) the mean precipitation (Table 7b v). The germination fraction did not vary significantly with the coefficient of variation of precipitation (Table 7b vi). Thus, there was no evidence of the predicted positive relationship between germination fractions in

favorable growth chamber conditions and the characteristics of the environment from which populations originated. Xeric populations expressed a large range of \underline{G} under growth chamber conditions, but in all cases \underline{G} was equal to, or exceeded, the \underline{G} for the more mesic populations (Fig. 6).

Seed mass varied significantly among populations, but not among trial dates (Population $\underline{F}=28.8$; $\underline{df}=11,127$; $\underline{P}<0.001$; Trial $\underline{F}=1.25$; $\underline{df}=1,127$; $\underline{P}=0.266$). Linear contrasts testing for differentiation of seed mass along the environmental gradient indicated a positive relationship (Fig. 7) that was significant in four out of six comparisons (data not shown).

DISCUSSION

I. Delayed seed germination and adaptive bet-hedging

The seeds of *Plantago insularis* exhibited delayed seed germination under all conditions: population mean germination fractions were always less than one. Non-germinated seeds of *P. insularis* were viable and were able to germinate under similar conditions at a later date. In order to function as a bet-hedging mechanism, delayed germination must result in a reduction of both the arithmetic mean and variance in fitness relative to 100% germination (Cohen 1966; Seger and Brockmann 1987). Delays in seed germination will result in a decrease in the arithmetic mean and variance of fitness in any population for which a) mean of survival times reproduction ($\underline{lb}=\underline{Y}$ in eq. 1) is greater than mean survival of seeds delaying germination (\underline{s}) and, b) the population

growth rate (λ) varies more with 100% germination than with fractional germination. Four field populations of *P. insularis* (Sentinel, Gila Bend, Organ Pipe and Florence) meet these criteria because, in addition to expressing delayed seed germination ($G < 1$; Table 2), each population had greater average λ than s , and temporal variance in λ that increased as germination fraction approached one (Claus *in prep.*). Therefore, delayed germination in these populations can function as a bet-hedging mechanism.

Cohen (1966) predicted that bet-hedging via delayed germination is adaptive for annual plants if seasons occur during which all germinated individuals die before reproducing. If the characteristics of variability in survival and reproduction for *P. insularis* are captured by the measures of the proportions of good and poor years in the historical precipitation data, then delayed germination ($G < 1$) was adaptive in all twelve populations (Table 1). Optimal germination fractions (G^*) were less than one at all populations for all values for s and Y_g tested, and for each method of calculating the proportion of good years (P_g). In contrast to the large range of G^* among populations (0.10-0.78), varying s and Y_g , and the method of calculating P_g , resulted in only small changes in G^* . Thus, populations of *P. insularis* along the climatic gradient are predicted to differ systematically in their G^* . The model for the evolution of germination fractions discussed above assumes density independent population dynamics. In a density dependent model of the evolution of seed germination, Ellner (1985) incorporates differences in variance in reproductive success under high and low density. The subset of

assumptions in Ellner's model most applicable to this desert annual system are intermediate levels of seed survivorship, variance in total reproductive yield that is large, and the possibility of years with zero reproductive yield (Appendix A). Simulations with these conditions demonstrated that the density dependent model predicts optimal germination fractions that are less than one and that are qualitatively similar (although somewhat lower) to the predictions from the density independent model (Claus and Venable unpubl. results).

When the fitness consequences of delayed germination were evaluated directly using four years of field measurements of lb, geometric mean growth rates were maximized by $\underline{G} < 1$ in three of four populations. Only at Florence, the most mesic population located near the edge of the species' range, did a hypothetical genotype with no delayed germination have greatest fitness. Thus, bet-hedging via delayed seed germination appears to be an adaptive strategy for at least three of the four populations of P. insularis even during a particular short four-year period. Together, the direct observations of variability in survival and reproduction and the estimates of the proportion of good years from the historical precipitation record suggest strongly that there is selection for delayed germination as a bet-hedging strategy in this species.

II. Measurements of germination fraction in Plantago insularis

The amount of delayed germination, indicated by the magnitude of the germination fractions, varied systematically among populations. Consistent with the

optimal germination fractions predicted in the Cohen (1966) model for unpredictably variable environments, there was an increase in mean field \bar{G} for populations with higher proportions of good years (Fig. 1). However, the observed variation in germination fractions among years, although consistent with previous empirical studies of phenotypic variability in germination fractions, was not predicted by the bet-hedging model. This is the first study to measure *in situ* germination fractions for more than one population in multiple years. The mean *in situ* germination responses were composed of two unexpected elements. The more xeric populations, Sentinel and Gila Bend, exhibited the greatest range in \bar{G} among years, including some very high germination fractions. Also Sentinel, which received the least rainfall throughout the study, had the widest range of germination dates in three of the four years. In the following sections I address these two field results in the context of the experimental studies of germination in *P. insularis*.

Among - year variation in germination fractions

The range of among-year germination fractions was greater for Sentinel and Gila Bend than for the more mesic populations at Organ Pipe and Florence because both maximum and minimum \bar{G} were more extreme (Fig. 1). The highest *in situ* germination fractions were recorded at Gila Bend and Sentinel in 1994-95 and 1997-98, respectively, even though the more mesic populations received more precipitation (Table 2). Although caution must be exercised when interpreting field \bar{G} in only four years, the experimental data indicate that high germination fractions at xeric populations, such as $\bar{G}=0.97$ at

Sentinel in the wet 1997-98 ENSO year, are a repeatable phenotypic response to high water availability. When seeds were supplied with ample water in common garden and growth chamber experiments, germination fractions were as high or higher for xeric, in comparison to mesic, populations of *P. insularis* (Figs. 4,6; Tables 5,7). The high germination fractions I observed in populations from more xeric environments were opposite the \underline{G}^* predicted from the bet-hedging models for populations with a low probability of a good year (Table 1). Although data of *in situ* germination fractions for other desert annuals are not widely available (but see Venable and Pake 1998), there are multiple reports of unusually high population densities in years with high rainfall (Beatley 1974; Gutterman 1993; Polis et al. 1997), suggesting that the results reported here may represent a more general pattern of germination in extremely xeric environments.

Minimum germination fractions for Sentinel and Gila Bend (0 and 0.06, respectively) occurred in 1996-97 during which there was little precipitation (Table 2). In contrast, more than 50% of seeds germinated during all years at the more mesic locations (Fig. 1). Because seed banks collected from the field in November 1996 had higher germination with ample watering in the common garden experiment, I infer that the low germination of these same seed banks *in situ* at Sentinel and Gila Bend was due to water limitation. Together, the among-year variation in the field measurements of \underline{G} and experimental data demonstrate that the environment during germination greatly affected germination responses. Low germination fractions in the field were the result of

a plastic response to low precipitation. Furthermore, when water was amply available, germination fractions for seeds from more xeric populations tended to be higher than those from mesic environments. Increased germination in wet seasons that are also good years for reproductive success may indicate predictive germination (Cohen 1967; Venable and Lawlor 1980) in xeric populations, however, this remains to be tested.

Seasonal range in germination dates

A second previously undocumented aspect of in situ seed germination for P. insularis was the greater range of germination dates within the season for the most xeric population at Sentinel. Even though rainfall was least at Sentinel in each of the four years, seeds germinated as often as in the more mesic populations (Table 3) and at more extreme times within the season in three of four years at this location (Fig. 2). Seeds at Sentinel germinated in September in both of the years that had September precipitation (1994-95 and 1997-98). Even though Organ Pipe and Florence received greater than 15mm precipitation in September during four and two years respectively, these more mesic populations never had an early germination cohort (Fig. 2). Similarly, both Sentinel and Gila Bend had March germination cohorts in at least one year, whereas seeds never germinated in March at the more mesic Organ Pipe and Florence populations, even when there was substantial rainfall (Fig. 2). In a 15-year study of an even more mesic desert annual community near Tucson, AZ, germination dates for P. insularis have consistently been after October 1 and before the end February (Venable

and Pake 1998).

Differences in germination responses between more mesic and more xeric populations across trials in the common garden experiment (Fig.3) illustrated how variation in the length of the germination season among populations may be achieved. For the xeric Yuma and Sentinel populations \bar{G} was relatively constant throughout the trials (Fig. 3). In contrast, the more mesic populations experienced a decline in \bar{G} as the temperatures increased and days lengthened later in the spring (Table 4,6; Fig. 3). Sensitivity of seed germination to temperature and photoperiod is well documented and can vary among populations (Gutterman 1973).

Increased germination early and late in the season in the more xeric populations may be favored by the seasonal distribution of precipitation during El Niño Southern Oscillations (ENSO). ENSO seasons are disproportionately wet in xeric environments and the additional rain falls early and late in the season, at a time when there is less rain in non-ENSO years (see description of Species, Populations and Precipitation). ENSO years are likely to contribute disproportionately to population growth and to evolutionary change at xeric locations because the amount of seasonal precipitation is positively correlated with both survival and reproduction in annual plants (Beatley 1974; Templeton and Levin 1979; Loria and Noy-Meir 1979/80; Brown and Venable 1986; Venable and Pake 1998). If germination has a genetic basis in this species, genotypes with the ability to germinate early or late in the season will increase in frequency during ENSO years.

One consequence of a longer germination season is that populations from more xeric environments will have an increased number of potential germination opportunities within a year. A greater range of within-year germination dates, as seen in some years in Sentinel, has been proposed as an alternative to among-year bet-hedging (Leon 1985; Venable 1989). As opposed to spreading the risk among years, differences in success of early, middle and late germinating offspring may provide a hedge against complete reproductive failure. The germination responses in *P. insularis* suggest that species in xeric desert environments may have the potential to combine within and among-year strategies for bet-hedging.

Synthesis

The synthesis of field and experimental data for germination in *P. insularis* leads to a more complete but also more complex picture of delayed germination in a desert annual plant. If the among population pattern for *in situ* germination fractions reflects adaptation to variable environments through bet-hedging, then *P. insularis* did not attain this strategy through consistent differences in germination fractions as the most common interpretation of bet-hedging models suggests (i.e., Sentinel seeds should have lower G than Florence seeds under any conditions tested). Rather, the mean population response resulted from the interaction between the germinability of seeds and the among-year distribution of precipitation during the germination season in the field. Mesic populations generally receive more rainfall, have seeds that germinate at intermediate

rates and have a narrower germination season. In contrast, populations in more xeric environments receive less rainfall in most years and therefore, germination fractions, which are sensitive to amount of rainfall, will be lower. However, given the same amount of rain, seeds from xeric populations are equally, or even more, likely to germinate. Furthermore, seeds from the xeric populations germinate over a wider range of environmental conditions and dates. Together, germination characteristics and rainfall distributions during the germination season at different positions along the environmental gradient produce a pattern of mean germination fractions among populations that is consistent with bet-hedging predictions. Optimality models, such as Cohen's (1966), are useful for determining conditions under which delayed germination, or some other form of risk reduction, should be adaptive. Patterns such a decrease in mean germination fractions for more xeric field populations of *P. insularis* and increases in the size of persistent seed banks in desert communities (Leck et al. 1989) provide evidence of the important role that seeds play in the life histories and population dynamics of desert annuals. However, the manner in which annual plants attain reduction in temporal variance in reproductive success will remain obscured until we move away from the broad framework and look at the details of seed germination in variable environments.

Germination fractions across environments - Previous empirical evidence

In the past thirty years, a number of empirical studies have compared germination

responses among populations differing in historical precipitation regimes. Generally, seeds are collected from maternal plants in a number of “wet” and “dry” populations, and germination is monitored under common conditions resembling a good year for germination in the field (providing a measure of first-year germination (Philippi 1993a)).

The results of these studies have not provided consistent support for Cohen's (1966) model. In a study of seven grassland annuals, Jain (1982) observed higher seed dormancy (lower G) in the laboratory for populations with higher probabilities of precipitation. Comparing twelve populations of Digitaria milaniana from a combination of wet and dry, African tropical and equatorial habitats, Hacker (1984) found that after one generation in a common garden, populations from habitats with higher rainfall had higher average growth chamber germination fractions than populations from drier habitats. However, there was a great deal of variation in G among equatorial and tropical habitats of similar rainfall as well as among seeds harvested in different seasons. Using a similar experimental design, Hacker and Ratcliff (1989) demonstrated that equatorial populations of Cenchrus ciliaris experiencing high rainfall also had higher G . In contrast, in tropical habitats it was populations of Cenchrus ciliaris with intermediate rainfall that had maximal G . Gutterman and Ednine (1988) found that for two species of Helianthemum, populations from drier and hotter locations had higher G . Seeds originating from a xeric population of Anthoxanthum odoratum had higher G in a growth chamber than seeds from a mesic population after a reciprocal transplant experiment (Platenkamp 1991). In the most exhaustive comparison to date, Philippi

(1993b) demonstrated a significant positive correlation between G in a growth chamber and rainfall among eleven populations of Lepidium lasiocarpum in the Southwestern U.S.A. However, on the basis of further experiments with this species, Philippi (1993b) concluded that this correlation was most likely driven by variation in maternal plant size among populations in the years of seed production. Kigel (1995) observed the opposite pattern with drier populations of Stipa capensis in Israel exhibiting higher G in a growth chamber than those from wetter habitats. In a comparison among populations from wet, dry and intermediate habitats for 29 Mediterranean leguminous species, Ehrman and Cocks (1996) found significantly more hard-seededness (lower G) at drier sites for only five species. The remaining 24 species exhibit no ecotypic differentiation among sites that differ up to 88% in seasonal precipitation. The results of the my study suggest that it is difficult to draw conclusions concerning evolution in response to variable environments from such data, as the key factor is the interaction between germinability and the distribution of the climatic conditions encountered in the field during germination.

Alternatives to delayed seed germination

Recent evolutionary models have demonstrated that selection in variable environments can affect traits other than germination fraction (King and Roughgarden 1982; Ritland 1983; Venable and Brown 1986; Evans and Cabin 1995). High temporal variance in survival and reproduction can select for increased seed size or seed dispersal

into dissimilar patches (Venable and Brown 1988). In *P. insularis* seed mass varied significantly among the twelve populations but more xeric populations had slightly lower, not greater, seed mass (Fig. 7). Neither seed morphology related to dispersal, nor habitat patchiness, varied systematically across the precipitation gradient (M. Claus pers. obs). Post-germination traits can also reduce variance in \ln (Ritland 1983; Brown and Venable 1986). High seedling survival, as seen for Yuma in March (Fig.6), may increase the probability of survival to reproduction for germinated seedlings, thereby reducing variance in reproductive success among years. Phenological observations at the four field populations over four seasons indicated that, controlling for germination time, plants at more xeric locations have a younger age at maturity and set seeds earlier in the season (Claus in prep.). Earlier age at maturity in unpredictable environments can also reduce variance in reproduction (King and Roughgarden 1982). It remains to be determined whether the plants in more xeric environments possess morphological or physiological adaptations to drought that function synergistically with, or as an alternative to, delayed germination to reduce temporal variance in \ln (Brown and Venable 1986; Venable and Brown 1986; Evans and Cabin 1995).

CONCLUSIONS

This investigation of bet-hedging in *P. insularis* differs from previous studies because I considered the interaction between germination characteristics and environmental conditions during germination in several populations. The historical

precipitation record predicted delayed seed germination as a form of adaptive bet-hedging for all populations under study. A more complex picture arose from the empirical data for germination fractions in this winter annual plant. Mean in situ germination fractions increased with increasing probability of a good year (P_G). In common environment experiments germination fractions were high for all populations and either remained constant or decreased with increasing P_G . A synthesis of these seemingly divergent results suggests that the pattern of delayed germination among populations may reflect a bet-hedging adaptation, but not as a result of constant and optimal germination fractions. Rather, the mean germination response was attained through an interaction between the distribution of germination environments in mesic and xeric populations, and plasticity in the germination response. Populations in mesic environments generally received more rainfall, had seeds with intermediate germination fractions and had a narrow germination season. In contrast, populations in more xeric environments received less rainfall, had higher germination fractions when water was available and had a longer germination season. This study illustrates the need to consider the ecological expression of characteristics in studies of life history evolution in variable environments.

ACKNOWLEDGMENTS

I thank C. Van Hemert, K. Moriuchi and J. McGilton for laboratory assistance and T. Philippi for an insightful discussion on El Niño. G. Fox, L. McDade, N. Moran, R. Robichaux and B. Walsh provided constructive comments on an earlier version. This research was supported by a National Science and Engineering Research Council of Canada Post-graduate Scholarship, a National Science Foundation Doctoral Dissertation Improvement Grant and funding from the Research Training Group in the Analysis of Biological Diversification at the University of Arizona to MJC.

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Table 1. Description of precipitation (mm) between September and March (mean, variance and coefficient of variation), probability of a good year (P_g) and optimal germination fraction (Q^*) at twelve locations in Southern Arizona and California. n =number of winters with complete precipitation record. Locations are listed in order of decreasing mean winter precipitation.

Location	Latitude- Longitude	n	Mean ^a	Variance	C.V.	P_g ^b	Q^* ^c
Florence AZ (FL)	111°20' 33°08'	58	171 a	5296	43	0.78	0.78
Organpipe Cactus							
Nat'l Mon. AZ (OP)	112°46' 32°05'	46	142 b	5197	51	0.63	0.63
Gila Bend AZ (GB)	112°48' 32°36'	100	99 c	3052	56	0.56	0.56
Barstow CA (BA)	116°59' 34°52'	38	81 cd	1843	53	0.48	0.47
Needles CA (NE)	114°45' 34°55'	91	80 cd	2495	62	0.42	0.41
Blythe CA (BL)	114°45' 33°40'	76	71 c	1962	63	0.21	0.20
Wellton AZ (WE)	114°10' 32°40'	47	70 c	2424	70	0.26	0.25
Sentinel AZ ^d (SE)	113°15' 32°57'	23	69 c	2315	70	0.11	0.10
Indio CA (IN)	116°05' 33°45'	89	69 c	2458	72	0.23	0.22
Eagle Mt. CA (EM)	115°05' 33°50'	56	63 c	2072	73	0.25	0.24
Yuma AZ (YU)	114°32' 32°24'	120	59 c	1617	69	0.14	0.13
Brawley CA (BR)	115°26' 32°58'	80	53 c	1530	73	0.18	0.17

^a $F=30.0$ $df=11,812$; $P < 0.001$; means with different letters are significantly different ($P<0.05$) in Student-Newman-Keuls a posteriori multiple comparison

^b Proportion of germination years that are good (17/24/30): defined as years with at least 17mm precipitation in any one month between September and March that were followed by ≥ 24 mm in following month OR ≥ 30 mm in second month.

^c Optimal G calculated from eq.1 with $P_g=17/24/30$; $s=1.0$; $Y_g=100$; $Y_p=0$

^d Long-term data not available, estimated from Dateland, AZ.

Table 2. Total winter rainfall (September - March), density of seedlings (L) and non-germinated (D) of *Plantago insularis* in four winter annual season at four populations in southern Arizona. Letters indicate significant differences among populations in Student-Newman Keuls means comparison for each year separately. Germination fractions are calculated as $G=L/(D+L)$.

Year	Population	¹ Seedlings/m ²	² Seeds/m ² not germinated	Germination Fraction	Total winter rainfall (mm)
1994-95	Sentinel	1052 ^b	4787 ^a	0.18	82.8
	Gila Bend	291 ^c	36 ^b	0.89	127.0
	Organ Pipe	519 ^c	453 ^b	0.53	243.8
	Florence	2163 ^a	417 ^b	0.84	220.0
1995-96	Sentinel	13 ^c	3656 ^a	0.003	2.5
	Gila Bend	2254 ^a	1178 ^b	0.66	49.0
	Organ Pipe	1495 ^b	997 ^b	0.60	91.4
	Florence	2313 ^a	1994 ^b	0.54	84.3
1996-97	Sentinel	0 ^a	1037 ^a	0.00	9.6
	Gila Bend	24 ^a	358 ^b	0.06	59.2
	Organ Pipe	97 ^a	26 ^c	0.79	57.9
	Florence	91 ^a	40 ^c	0.69	67.5
1997-98	Sentinel	486 ^a	13 ^b	0.97	167.6
	Gila Bend	128 ^b	298 ^a	0.30	136.6
	Organ Pipe	57 ^b	13 ^b	0.81	245.4
	Florence	90 ^b	52 ^b	0.63	295.2

¹ Population $F=57.3$ $df=3/544$; $P<0.0001$, Year $F=56.6$; $df=3/544$; $P<0.0001$;
Populations*Year $F=28.1$; $df=9/544$; $P<0.0001$.

² Population $F=14.3$ $df=3/424$; $P<0.0001$, Year $F=11.7$; $df=3/424$; $P<0.0001$;
Populations*Year $F=5.7$; $df=9/424$; $P<0.0001$.

Table 3. Mean and minimum precipitation (mm) that resulted in germination cohorts at four populations of *Plantago insularis* in four years. Precipitation from the same storm falling within 48 hours was summed and recorded as one event. n = the number of germination cohorts. There was no germination at Sentinel in 1996-97. Because rainfall is from nearby weather stations, the minimum precipitation resulting in germination is approximate.

	1994-95			1995-96			1996-97			1997-98			All years		
	n	mean	min	n	mean	min.	n	mean	min.	n	mean	min.	Total no. cohorts	Grand mean	Mean min.
Sentinel	6	10.8	3.0	2	1.3	1.3	0	-	-	5	25.0	14.5	13	12.4	6.3
Gila Bend	4	22.2	8.1	2	13.8	5.6	1	24.4	24.4	3	17.4	12.9	10	18.9	12.7
Organ Pipe	4	37.8	14.7	2	21.3	17.3	1	20.4	20.4	4	35.5	7.6	11	28.7	15.0
Florence	3	21.8	17.2	2	32.8	15.2	3	10.7	6.8	6	53.1	12.7	14	29.6	13.0

Table 4. Generalized linear model analyzing germination fraction (number of germinated seeds/total number of seeds) for *Plantago insularis* in the common garden experiment. Block effect and 3-way interaction term were not significant and were removed from the model.

Source	df	F*	P
Population	4	51.8	0.0001
Water	1	47.3	0.0001
Trial	3	48.1	0.0001
Water*Pop	4	13.5	0.0001
Pop*Trial	12	45.9	0.0001
Water*Trial	3	14.7	0.0001

* χ^2 divided by Pearson χ^2/\underline{df} (3.18) to correct for over-dispersion in the data. F-test denominator $\underline{df}=170$.

Table 5. Mean and standard error of germination fraction for *Plantago insularis* for each treatment in the common garden experiment. Means and standard errors calculated on logit transformed data and then back-transformed.

Trial	Water	Yuma		Sentinel		Gila Bend		Organ Pipe		Florence	
		mean	s.e. bounds	mean	s.e. bounds	mean	s.e. bounds	mean	s.e. bounds	mean	s.e. bounds
Dec.	High	0.487	0.429-0.546	0.658	0.596-0.714	0.603	0.539-0.663	0.614	0.355-0.822	0.431	0.299-0.574
	Low	0.410	0.322-0.503	0.269	0.180-0.382	0.392	0.335-0.452	0.220	0.120-0.368	0.446	0.362-0.534
Jan.	High	0.696	0.672-0.720	0.496	0.445-0.547	0.179	0.105-0.289	0.280	0.211-0.362	0.330	0.269-0.380
	Low	0.115	0.070-0.181	0.021	0.009-0.047	0.056	0.033-0.093	0.102	0.075-0.137	0.184	0.110-0.290
Feb.	High	0.626	0.518-0.723	0.546	0.507-0.584	0.275	0.232-0.323	0.163	0.105-0.245	0.356	0.226-0.510
	Low	0.345	0.295-0.400	0.148	0.096-0.222	0.163	0.107-0.241	0.058	0.050-0.067	0.228	0.160-0.315
Mar.	High	0.772	0.720-0.816	0.539	0.423-0.650	0.132	0.089-0.192	0.102	0.078-0.134	0.124	0.097-0.157
	Low	0.501	0.410-0.592	0.093	0.051-0.163	0.058	0.043-0.078	0.093	0.076-0.113	0.148	0.112-0.193

Table 6. Environmental conditions during common garden experiment in Tucson, AZ, December 1996 through April 1997.

	December	January	February	March
	Dec. 12	Jan. 15	Feb. 21	Mar. 25
	<u>- Jan. 10</u>	<u>- Feb. 13</u>	<u>- Mar. 22</u>	<u>- Apr. 23</u>
Avg. Temperature (°C)	10.9	12.4	16.0	18.3
Max. Temperature (°C)	25.0	25.0	33.3	32.8
Min Temperature (°C)	-3.3	-3.3	0	4.4
Total Precipitation (mm)*	18	2	16	13
Avg. Daylength (hrs)	10:05	10:37	11:37	12:42

* Germination trays were covered during rainfall but seeds were exposed to the associated changes in relative humidity and air temperature.

Table 7. A) Analysis of germination fractions for 12 populations of *Plantago insularis* at two trial dates. A generalized linear model was used assuming a binomial response variable and applying a logit link function. B) Linear contrast testing whether among population variation was significantly explained by the environment. The environment was measured by three threshold criteria for the proportion of germination seasons that are good for growth and reproduction i) 17mm/24mm/30mm, ii) 17mm/20mm/20mm and iii) 5mm/20mm/20mm; and one threshold criterion for the proportion of all years iv) 17mm/24mm/30mm of total (see Estimation of optimal germination fractions). The environment was also described by v) the mean average winter precipitation and vi) the coefficient of variation of winter precipitation.

A) Source	df	F*	P
Population	11	83.5	< 0.0001
Trial	1	56.7	< 0.0001
Pop*Trial	11	72.9	< 0.0001

B) linear contrasts:	df	F*	P
i) 17/24/30	1	6.2	< 0.05
ii) 17/20/20	1	12.6	< 0.002
iii) 5/20/20	1	10.5	< 0.005
iv) 17/24/30 of total	1	12.1	< 0.002
v) Mean precipitation	1	24.4	< 0.001
vi) Coefficient of variation	1	1.2	< 0.50

* X² divided by Pearson χ^2/df (1.58) to correct for over-dispersion in the data.

F-test denominator df=120

LIST OF FIGURES

Figure 1. Mean in situ germination fractions for populations of Plantago insularis with different proportions of good years (P_g). Two letter population abbreviations are positioned at population means; SE=Sentinel, GB =Gila Bend, OP=Organ Pipe, FL=Florence. Bars represent the range of germination fractions observed among four years. The dotted line indicates the optimal germination fractions predicted for different values of P_g (Table 1).

Figure 2. Daily precipitation amount (mm) and germination for Plantago insularis at four populations in southern Arizona in a) 1994-95, b) 1995-96, c) 1996-97 and d) 1997-98. Percentage of the year total seedlings germinating for each population is indicated above the rainfall event that resulted in emergence. Total density of emerging seedlings is given under each population name.

Figure 3. Mean seed germination fractions on a logit scale for five populations of Plantago insularis in a common garden experiment at four times in the season. ▲ Yuma; ● Sentinel; ▼ Gila Bend; ■ Organ Pipe; ◆ Florence.

Figure 4. Mean seed germination fractions on a logit scale for five populations of Plantago insularis in a common garden experiment at two watering treatments. ▲ Yuma; ● Sentinel; ▼ Gila Bend; ■ Organ Pipe; ◆ Florence.

Figure 5. Proportion of seedlings surviving 30 days in each of four germination trials for five populations of Plantago insularis in a common garden experiment with two watering treatments. Filled symbols = high water and open symbols = low water. Symbol shapes correspond to populations as in Figures 4 and 5.

Figure 6. Seed germination fractions on a logit scale for twelve populations of Plantago insularis in two growth chamber trials at ambient conditions in a) October and b) January plotted against the frequency of years with at least 17mm precipitation in any one month between September and March and with 24 mm in following month or 30 mm in second month (17/24/30). The slope of the relationship between \underline{G} and proportion of good years did not differ significantly among trials ($\underline{F}=0.025$; $\underline{df}=1,140$; $\underline{P}<0.5$). Population abbreviations as in Table 1.

Figure 7. Mean mass and standard error of 12 groups of 10 seeds from twelve populations of Plantago insularis plotted against the proportion of good years (17/24/30). Linear contrast: $\underline{F}=18.78$; $\underline{df}=1,116$; $\underline{P}<0.001$.

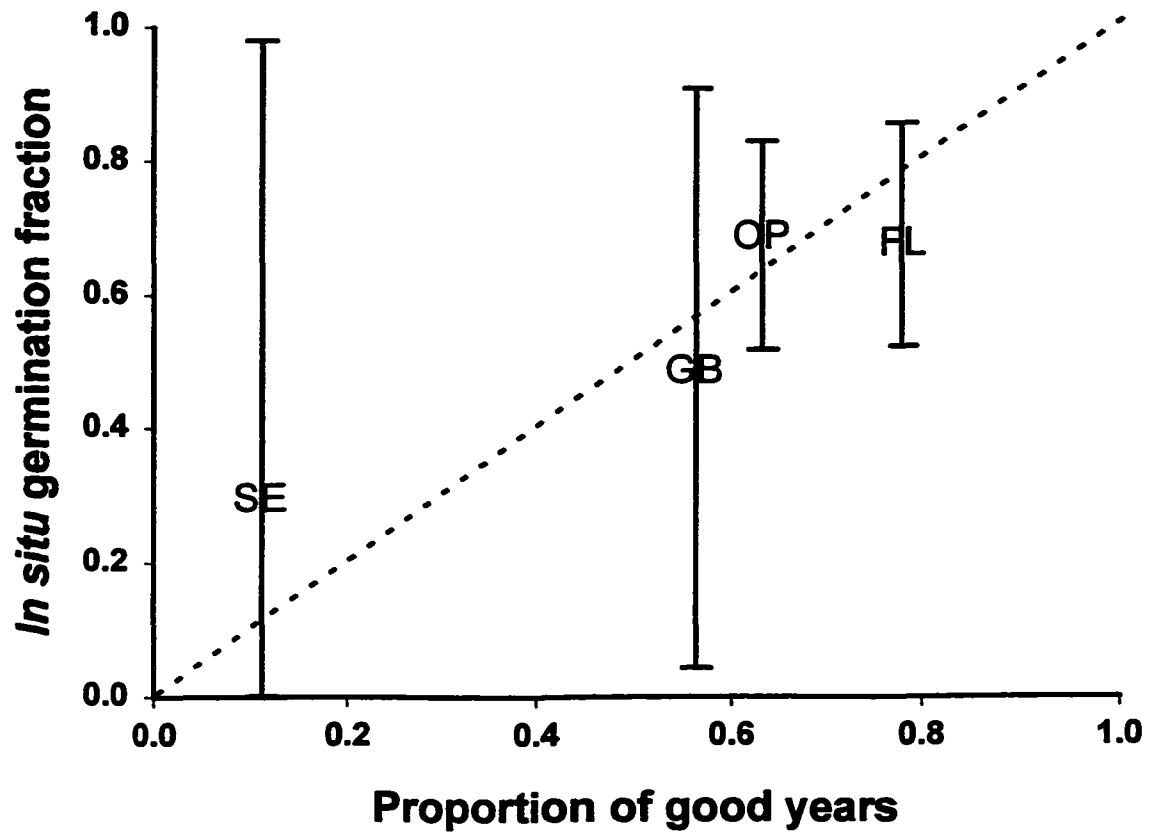


Fig. 1

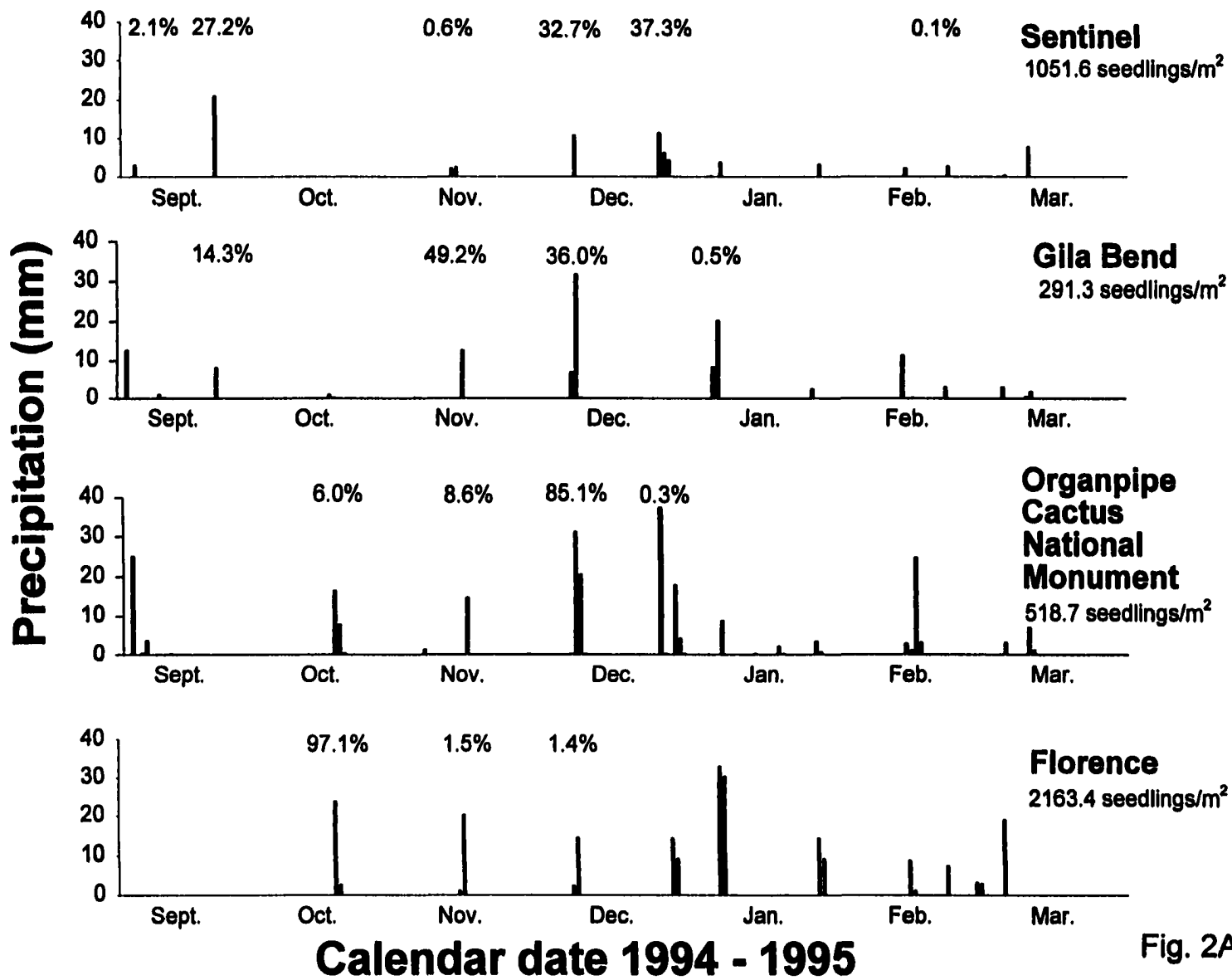


Fig. 2A

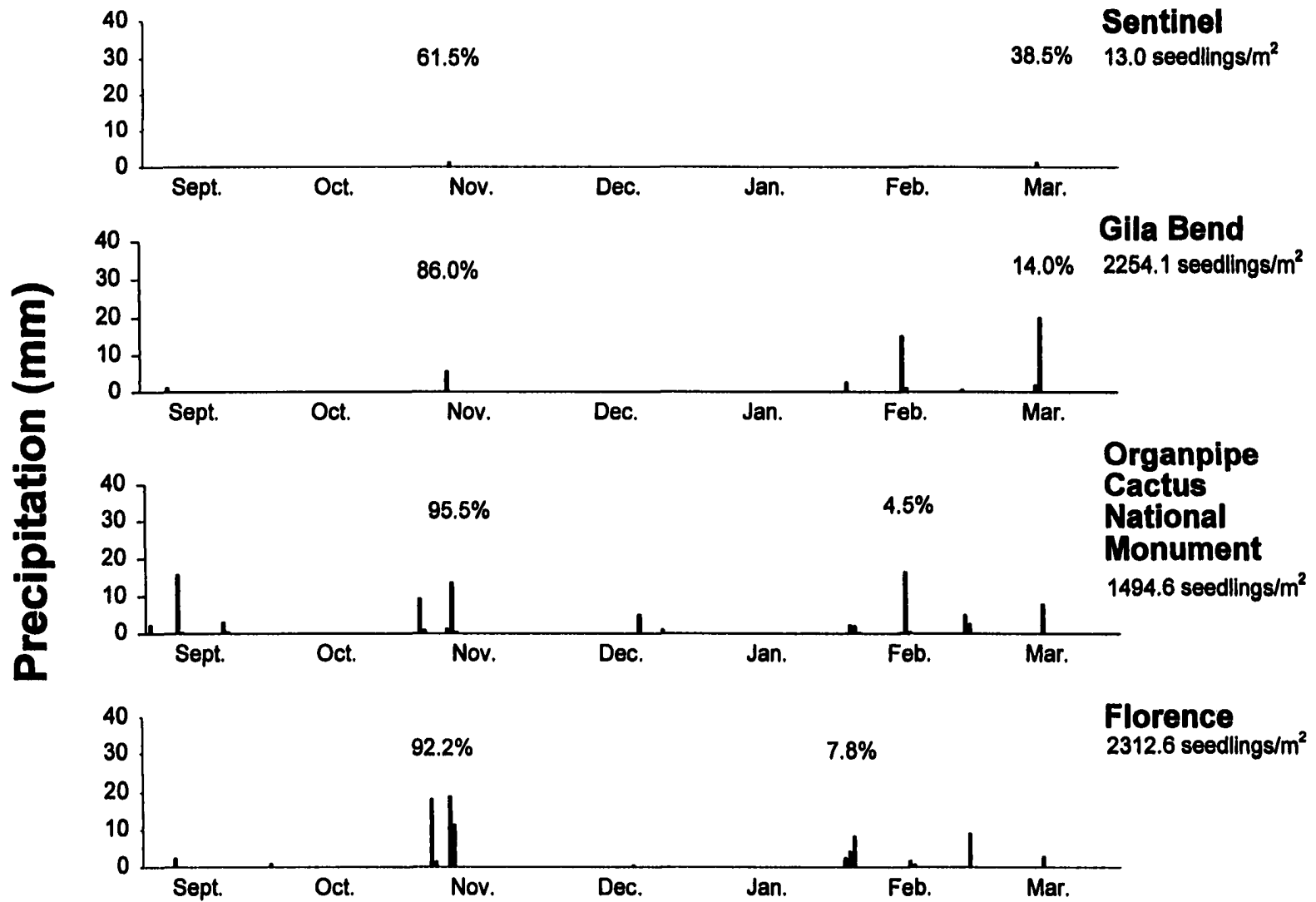


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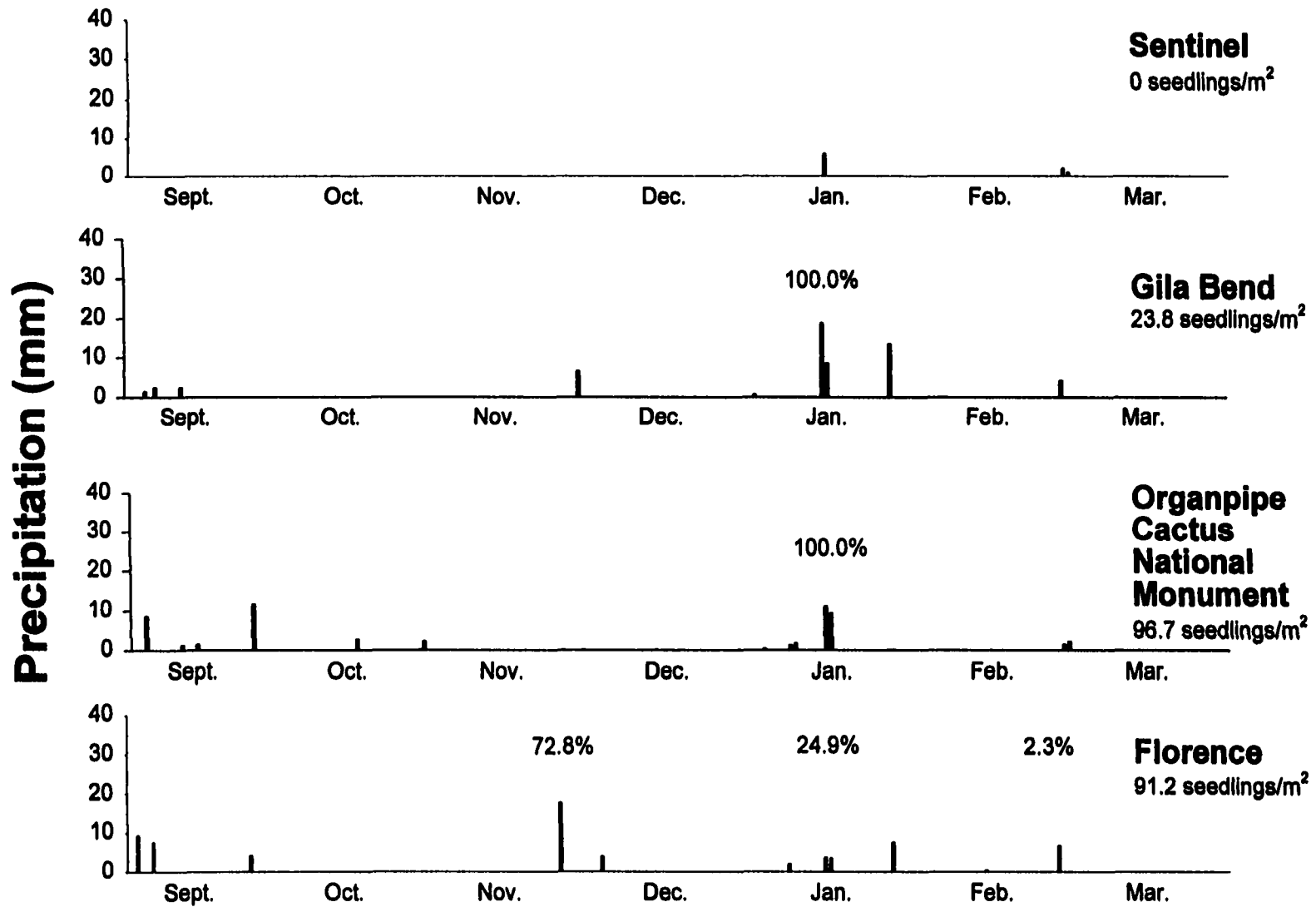


Fig. 2C

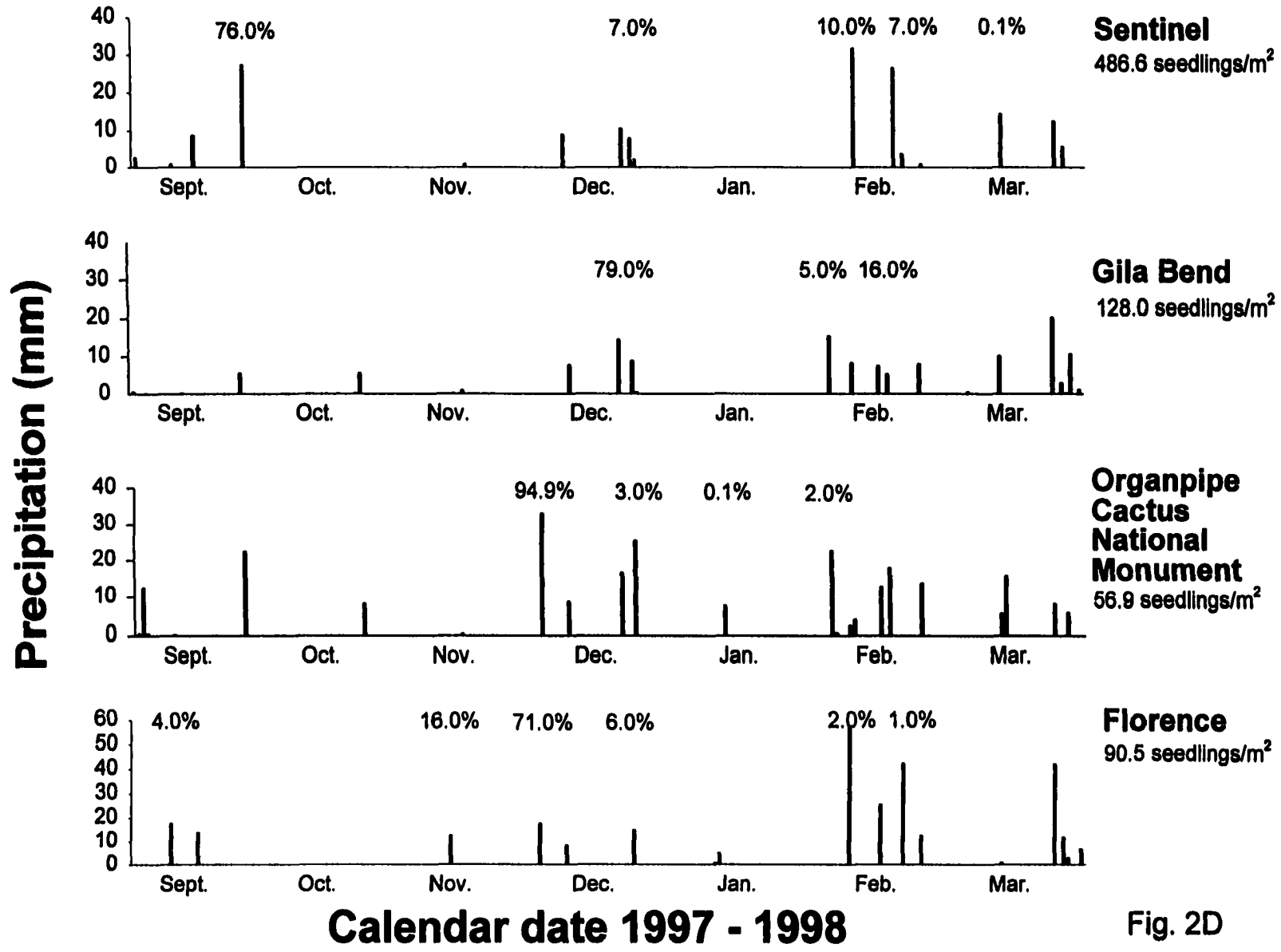


Fig. 2D

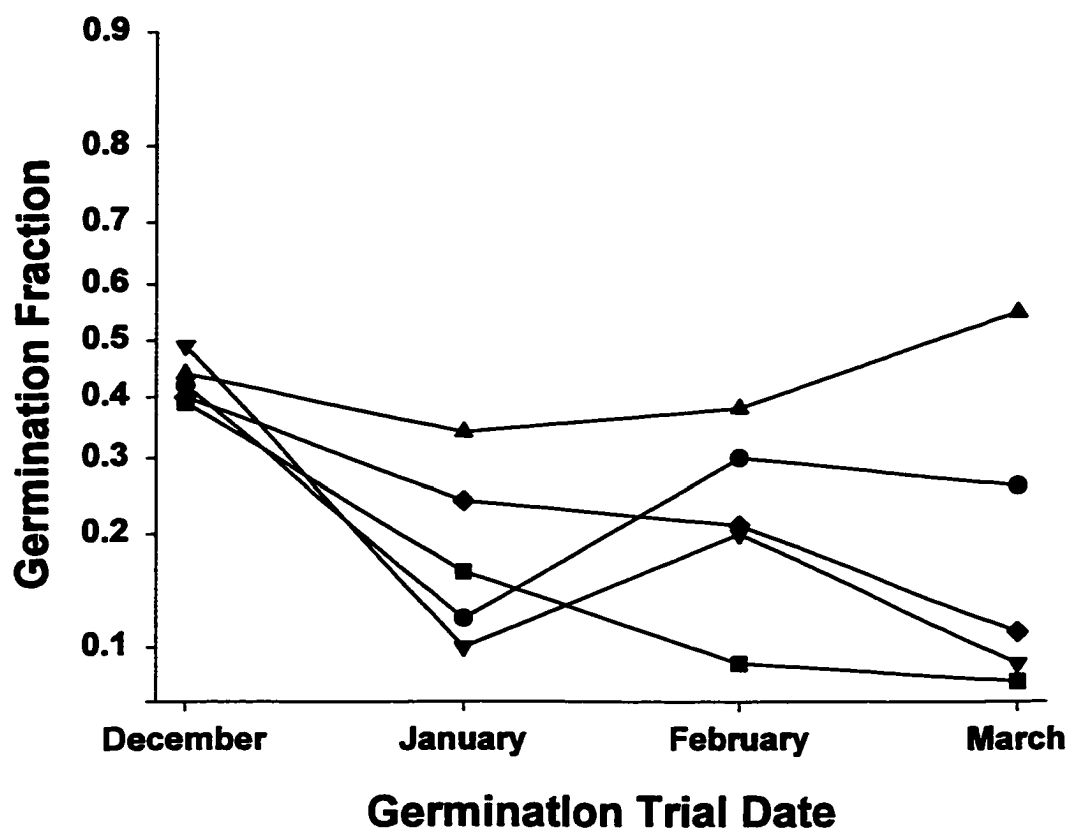


Fig. 3

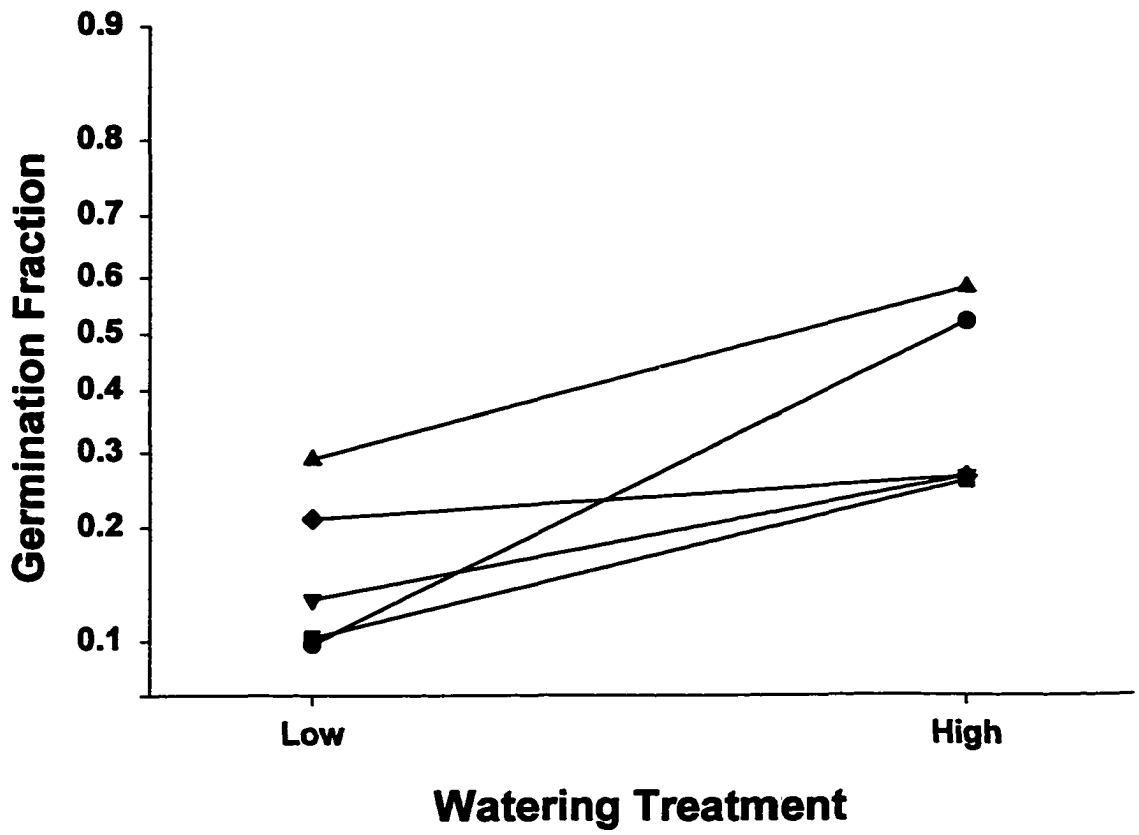


Fig. 4

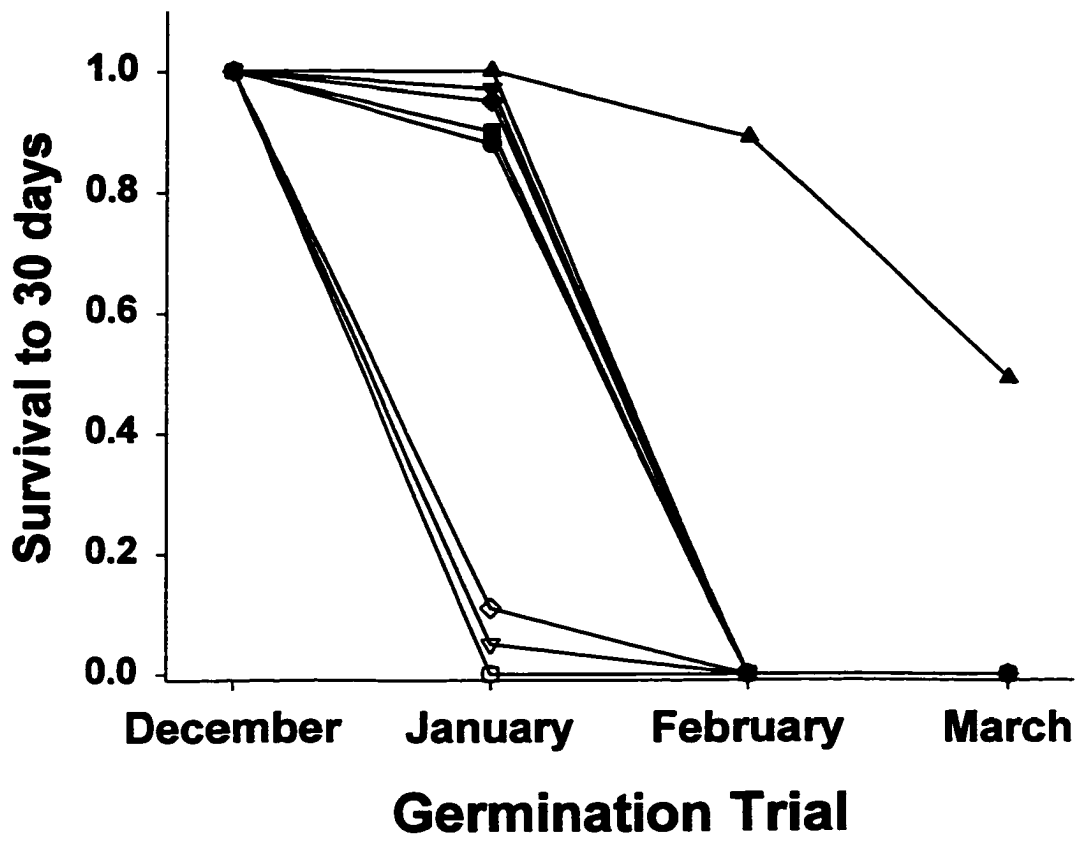
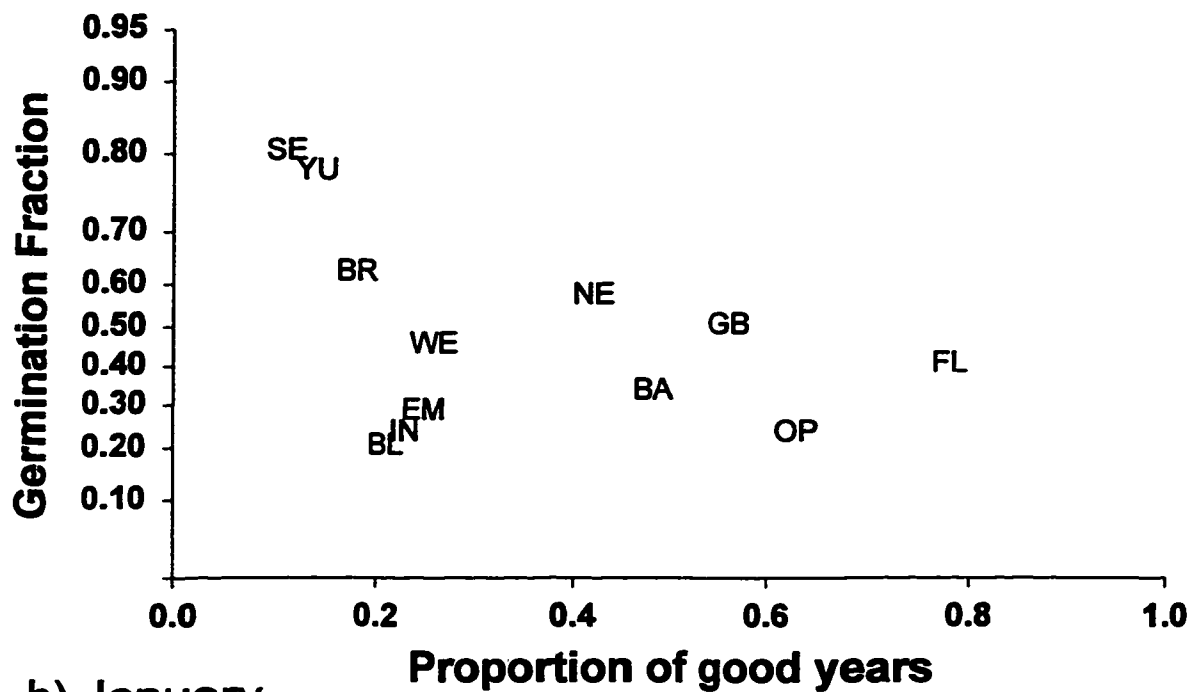


Fig. 5

a) October



b) January

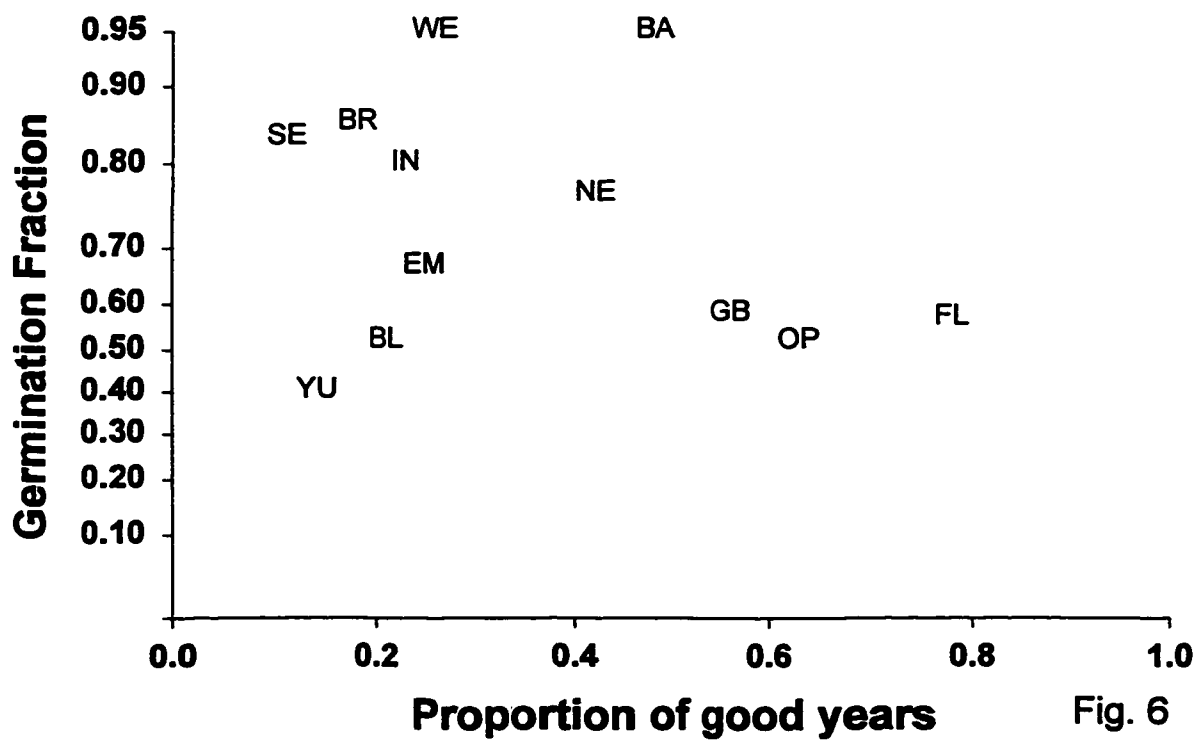


Fig. 6

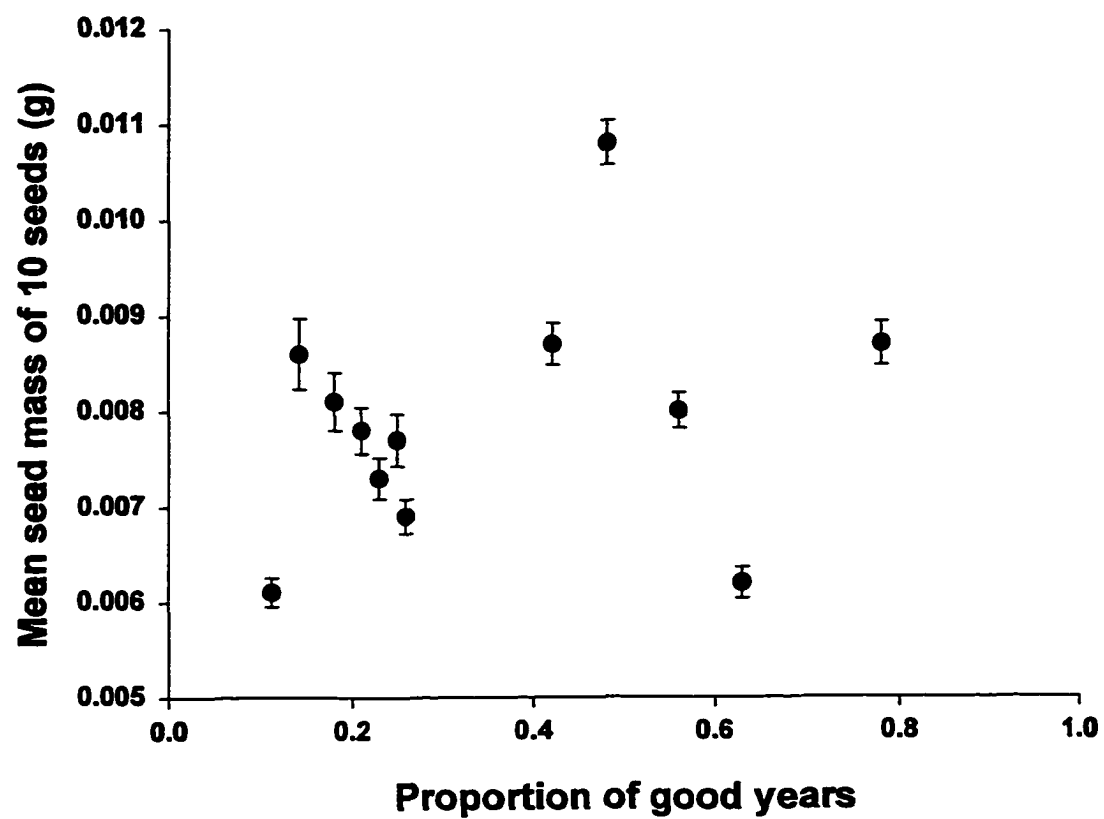
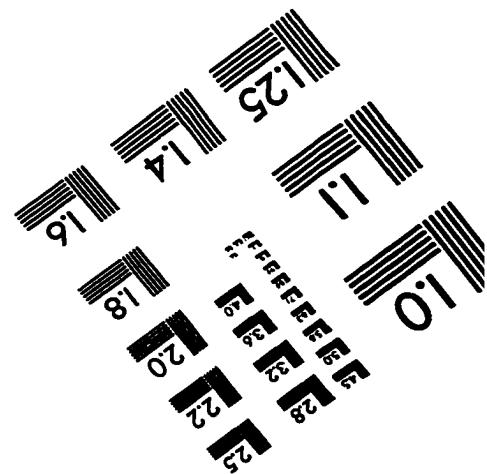
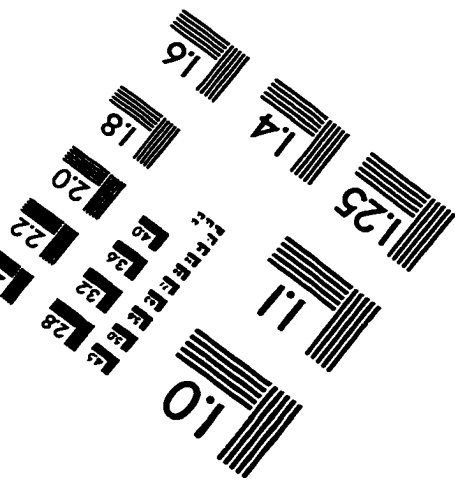
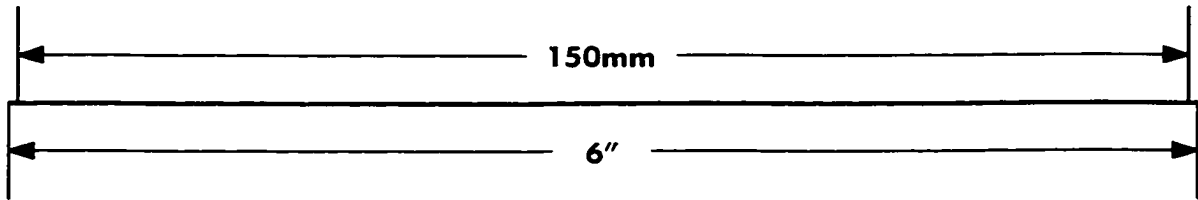
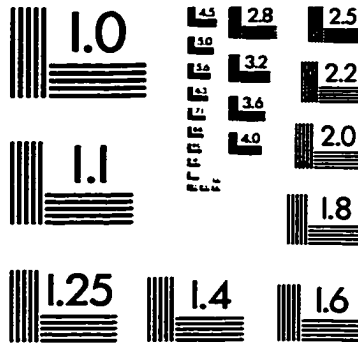
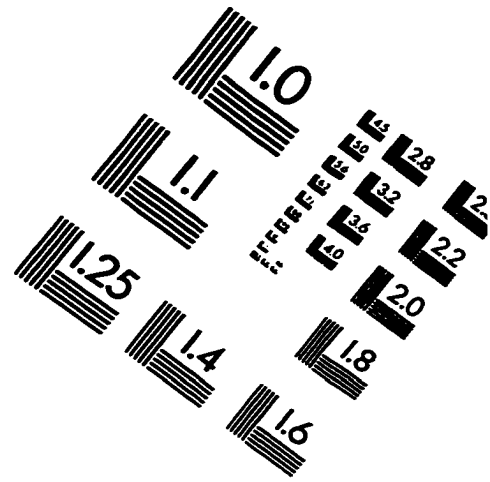
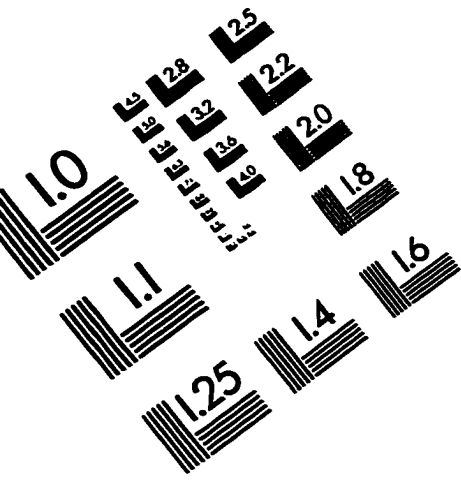


Fig. 7

IMAGE EVALUATION TEST TARGET (QA-3)



APPLIED IMAGE, Inc
1653 East Main Street
Rochester, NY 14609 USA
Phone: 716/482-0300
Fax: 716/288-5989

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