Energy Research and Development Division
FINAL PROJECT REPORT

MEASURING AND EVALUATING RARE PLANT DEMOGRAPHY IN THE CALIFORNIA DESERTS

Implications for Solar Energy Development

Prepared for: California Energy Commission
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JUNE 2016
CEC-500-2016-045

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ACKNOWLEDGEMENTS

This project was funded under California Energy Commission Contract #500-10-047. We thank Energy Commission staff Misa Milliron, Janna Franks, Joe O'Hagan, and David Stoms for providing administrative support and guidance from the inception of the project to its completion.

Project management on behalf of BMP Ecosciences, including budgeting, invoicing, record keeping and field logistics, was expertly performed by Alison Stanton – her diligence and experience are much appreciated.

We express our gratitude to experts James André, Tasha LaDoux, Naomi Fraga, Shannon Still, Kelly Amsberry, Amber Swanson, Bruce Baldwin, and Danny Reinke, who provided valuable information on plant distributions in the field, helped us to select our focal species, and locate our study sites. Christina Lund, Larry LaPré, and Chris Otahal of the Bureau of Land Management (BLM) helped provide access to BLM properties and provided information on rare plants on BLM land. We are thankful to for the help of Michael Vamstad and others who facilitated our research permit and our study at Joshua Tree National Park.

From the California Native Plant Society we thank Greg Suba for helpful and knowledgeable discussions on energy policy and plant conservation, and Aaron Sims and Amber Swanson for sharing rare plant data and providing feedback on candidate modeling species. We thank Duncan Bell of Rancho Santa Ana Botanical Garden for sharing survey data and enthusiasm for locating novel occurrences of rare species.

We deeply thank Drew Maraglia for leading the field crew for all four seasons with enthusiasm. We thank our field survey team, including Karen Tanner, Alison Stanton, Jon Clark, Carli Morgan, Tony Cockerell, Eli Kitchel, Tasya Herskovits, Kat Moon, Angelica Sauceda, Lisbeth Louderback, Richard Hiett, Matthew Pavlik, Elizabeth Axton, Dave Bloch, Fred Smith, Ethan Peck, Annie Jonasson, Brandon Tonokawa, Sailor Banks, and Kevin Moore-O'Leary for their efforts in the field detailed demography across the entire California desert region. We thank Patrick McIntyre for his work in locating and establishing study sites and overseeing field staff. We also thank Christopher Knight for assistance with data base management and Lauren Connell for geographic information systems support, map generation, editorial support, and report formatting. We thank Milo Bird and Julian Moore-O'Leary for accompanying us on field trips at an early age and Mark Bird and Rowan Boswell for support in the field.

We thank Janet Terry and Frances Stanley of the Millennium Seed Bank, Royal Botanic Gardens Kew (London) who provided access to, and training on, the Faxitron Specimen Radiographic System for x-raying seeds. And we thank Stephanie Herbert for her work steadfast work on seed germination of all focal species, and for her creativity and enthusiasm in her study of seedling morphology.

We thank David Stoms, Kevin Rice, Greg Suba, and Sarah Swope for their careful review and helpful comments on the draft report.

Kara Moore and Bruce Pavlik designed the research and conceptual approach and reviewed and revised all chapters.

The research in Chapter 2 was designed by Karen Tanner, Kara Moore, and Bruce Pavlik. Tanner led the field research, conducted the analyses, and wrote the chapter.

The research in Chapter 3 was designed by Kara Moore, Drew Maraglia, Alison Stanton, and Bruce Pavlik. Stanton conducted the analyses and wrote the chapter.

The research in Chapter 4 was designed by Kara Moore, Bruce Pavlik, and Drew Maraglia. Moore conducted the analyses and wrote the chapter.

The research in Chapter 5 was designed by Kara Moore, James André, Drew Maraglia, and Bruce Pavlik. André provided a 10-year dataset that enabled the study, as well as substantial expertise on the study species. Moore, Maraglia, and Pavlik led the recent field study. Moore conducted the analyses and wrote the chapter. Patrick McIntyre provided Bayesian analyses.

The research in Chapter 6 was designed by Kara Moore, Drew Maraglia, Alison Stanton, and Bruce Pavlik. Pavlik conducted the analyses and wrote the chapter.

The research in Appendix C was designed by Stephanie Herbert and Kara Moore. Herbert implemented the experiment, conducted the analyses, and wrote the chapter.

PREFACE

The California Energy Commission Energy Research and Development Division supports public interest energy research and development that will help improve the quality of life in California by bringing environmentally safe, affordable, and reliable energy services and products to the marketplace.

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Measuring and Evaluating Rare Plant Demography in the California Deserts is the final report for the Population Viability and Restoration Potential for Rare Plants Near Solar Installations project (grant number PIR-10-047) conducted by BMP Ecosciences. The information from this project contributes to Energy Research and Development Division's Environmentally Preferred Advanced Generation Program.

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ABSTRACT

The coming decade will bring radical physical and biological changes to the California deserts as utility-scale solar energy development advances throughout the region. In the direct path of those changes are at least 372 special-status desert plant taxa (species, subspecies, or varieties), rare plants with state or federal protected status, which are largely unknown in terms of basic biology and potential for conservation. State and federal permitting processes under the California Environmental Quality Act and National Environmental Policy Act require that significant impacts to special-status plants are minimized and mitigated. This project provided vital information on a suite of rare plant species that are potentially impacted by renewable energy development in the Mojave and Sonoran Deserts of California. From 2011-2014, researchers conducted rigorous demographic studies at 53 populations of six rare and one common plant species that are either directly impacted or likely to be impacted by solar energy development. Field, laboratory, and modeling methods were applied to fill important information gaps in the ecology and conservation of rare plants. The gaps are major impediments to deploying large-scale renewable energy developments while conserving these important public biological resources. Population viability models used the information collected by these studies to predict the likelihood of local extinction or persistence, reveal sensitivities to environmental change, and understand the factors that affect population trends. From these efforts, there were 19 recommendations to improve conservation and mitigation actions for rare plants in relation to utility-scale solar energy development in the California deserts. These recommendations should be adopted by energy developers, agencies, and their biological consultants to generate environmental impact assessments/reports, reduce project impacts during construction and operation, and design and implement mitigation actions.

Keywords: Rare plant, desert plant, demography, population viability analysis, renewable energy, solar energy, herbivory, plant conservation, rare plant mitigation, restoration ecology, *Asclepias nyctaginifolia*, *Eriophyllum mohavense*, *Eriophyllum wallacei*, *Grusonia parishii*, *Mimulus mohavensis*, *Penstemon albomarginatus*, *Penstemon thurberi*, *Castela emoryi*

Please use the following citation for this report:

Moore, Kara A. and Bruce M. Pavlik. (BMP Ecosciences). 2015. ***Measuring and Evaluating Rare Plant Demography in the California Deserts: Implications for Solar Energy Development.*** California Energy Commission. Publication number: CEC-500-2016-045.

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EXECUTIVE SUMMARY

Introduction

Numerous existing and proposed utility-scale solar energy developments in the Mojave and Sonoran deserts of California have the potential to cause significant, long-lasting impacts on rare (i.e., special-status) plants. Fortunately, management and mitigation actions exist that could minimize these impacts, including (1) permanent protection of target populations outside of renewable energy sites, (2) onsite avoidance of critical habitat features and established populations, (3) relocating plants within energy project sites to offsite unoccupied habitat, (4) removing plants to botanical gardens or other shelters, and (5) preserving seeds in permanent facilities for future planting. To assess potential impacts and to implement one or more of these actions successfully, land managers require answers to many questions about plant demography, such as: How many individual plants of a given species are in the California deserts? How fast do they grow and produce new seeds? How frequently are new individuals established, and how quickly do new individuals die under natural conditions? What are the effects of disturbance from human and non-human activities? Unfortunately, there are many unknowns for rare plants, especially those residing in remote and extreme environments, such as found in the California deserts. For this reason, biologists often cannot provide the necessary information to answer pertinent management questions without conducting focused and long-term studies.

Designing and implementing effective management and mitigation actions for conserving rare desert plants impacted by human disturbance is a challenge that begins with detailed studies under field conditions. Simple surveys in which the presence or absence of species are recorded and mapped are not sufficient to predict the long-term outcome of development/management on the trajectory of rare species populations. Rigorous studies lasting several years are required to observe how plants respond to different climate conditions and to impacts from human activities, such as the construction and operation of energy facilities. Useful field studies can be extended through modeling experiments, such as population viability analyses, that simulate future plant population trends given the data collected in the field. Models can be used to explore the effects of ecosystem change over time and to predict the outcomes of alternative scenarios, such as changes in land management practices or climatic regimes. This study combined field studies, laboratory investigations, and modeling experiments to provide information for improving the management of special-status plants in the California deserts and to suggest ways to mitigate the impacts of renewable energy development.

Project Purpose

This project provides demographic information on populations of rare desert plants and the conditions that affect their persistence in relation to utility-scale solar energy development in the Mojave and Sonoran Deserts of California. From 2011-2014, researchers conducted rigorous field studies for 53 populations of six rare and one common plant species that are either directly impacted or likely to be impacted by the construction and operation of desert renewable energy facilities. The authors used this new information as appropriate for each species' life history and their biological activities during the four-year field data-collection period in various analyses to

assess population performance. The field-generated demographic information was statistically analyzed and projected into the future when possible. The analyses explored links between population characteristics and: 1) differences in longevity (annual species that live aboveground for less than a year vs. perennial species that live more than one year), 2) the ability to spread as a creeping, perennial clone, rather than producing new plants from seeds, 3) differences between closely related species, one rare and one common, 4) variations in landscape and climate, 5) the effects of predicted changes in climate, 6) the impacts of desert herbivores (animals that eat plants), and 7) the value of current mitigation practices. The research contained in this report is a significant first step to improving the understanding of rare desert plants and reducing the impacts of future energy development on these important public resources.

Project Process and Results

As in any study of natural processes, the quality of the outcomes is highly dependent on the quantity and quality of the information that forms the basis of the analysis. The demographic data fed into population models should include all stages of plant life history (reproduction, seeds, germination, and the establishment of seedlings or clonal sprouts). This data must be collected during a minimum of four to five years to capture a complete range of environmental conditions experienced by the population, especially climate. For three of the desert species studied it was not possible to collect data on all life-history stages, especially because two of the four years (2012 and 2013) were exceptionally dry. Aboveground demographic activity within these populations was virtually absent. Consequently researchers evaluated the limited data available on the appearance of seedlings, population density, plant growth, and fruit and seed output.

Four desert species were more "cooperative" and provided data on all life-history stages for at least two study years. The researchers could apply population models for these species to assess potential management actions for reducing impacts and improving population viability. The models were built on ecological, life history, and demographic data, extending over a longer time frame (often 50 or 100 years) to explore how survival or extinction could be influenced by disturbance (such as energy facilities development) or environmental variation (such as rainfall patterns). These techniques estimated extinction risks under different climatic conditions and produced forecasts affected by existing mitigation actions, including those at the Ivanpah Solar Electric Generating System. For each of seven desert species, a set of management recommendations was developed. These recommendations should be the basis for improving field surveys, delineating populations and essential habitat features, selecting populations to preserve, choosing between mitigation alternatives, and designing new mitigation actions for a broader suite of desert plant species potentially affected by renewable energy development in the California deserts and elsewhere.

The generalized conclusions and recommendations from these field, laboratory, and modeling efforts on six rare and one common desert plant species are summarized and organized by how they apply to field survey methods, responses to disturbance, responses to other threats, and mitigation.

Field Survey Methods for Rare Plant Populations

1. **Field surveys for rare annual species must be conducted in favorable, less than favorable, and unfavorable climatic conditions to determine the full extent of species' occurrences, distributions, and abundances.** The essential relationships between population performance and very subtle landscape features and environmental triggers will most certainly remain undetected without a full range of various survey years. Management actions, without this information may not be adequate to conserve these plants. Furthermore, the full distributions of many annual species are poorly known and existing databases (e.g., California Natural Diversity Database) may only account for a fraction of occurrences. New efforts to conduct extensive surveys are required to document current distribution, population sizes, habitat characteristics, eminent threats, and potential for protection in a connected reserve system.

2. **Only long-term demographic studies will provide necessary insights into how plant characteristics (growth form, seed output, seed dispersal) and ecological factors (disturbance, habitat fragmentation, climate change, and species interactions) influence population persistence.** Desert perennial plants may temporarily survive the demographic effects of disturbance by adapting to the desert climate, such as where adult plants and seeds can become dormant (inactive).

3. **Successful demographic monitoring for rare desert annual plants must begin when seeds first germinate and be sustained for at least six weeks of nearly continuous measurements to capture all significant demographic events.** Timing is critical and is made difficult because annual plants grow and develop very rapidly.

4. **Surveying seedbanks, where seeds survive in the soil for many years, is as important as surveying for active, aboveground plants for all annual species and many seed-dependent perennials.** Populations can appear to move in response to yearly and local climatic variations because seedbanks are potentially present throughout a large area and germination occurs only where conditions are favorable. Surveying seedbanks is necessary to identify which areas require protection to allow long-term perseverance under climatic uncertainty.

5. **Monitoring programs for perennial clonal species (species that spread from rootstocks and creeping rhizomes more frequently than from seeds) should adopt the clump-cluster methodology used in this report.** This would allow long-term and comparable data for evaluating management and mitigation efforts.

Demographic Responses to Impacts from Development

1. **Populations of an herbaceous perennial occurring within developed habitat areas produced fewer seeds in each fruit and fewer fruits than nearby undisturbed populations under similar climatic conditions.** Reduced seed production limits the chance to recruit new individuals. Possible causes for reduced seed production include shade, reduced soil moisture, and increased herbivory (animals eating plants). The authors suggest that attention must be paid to how the siting, design, construction, and operation of facilities will affect water availability, shading, and species interactions for rare perennials.

2. **Inactivity (dormancy) of seeds and adult plants during unfavorable conditions allows herbaceous perennials to endure short-term environmental stress, including the direct impacts of development.** Dormancy allows species to survive disturbance or lack of resources for one to several seasons. Monitoring and analysis during at least 10-15 years will be necessary to document the long-term responses of these populations to disturbance and changes in desert climate. Caution must be taken not to assume that short-term tolerance (3-10 years) of altered conditions indicates long-term tolerance (>30-100 years). Thus, typically deployed monitoring durations in mitigation measures are inadequate to document long-term responses for many plants.

3. **Changes to the food web within areas affected by solar energy development can reduce the ability of plant populations to persist.** It may be necessary to manage herbivore populations within project areas so that their impacts are not unnecessarily magnified.

    a) Herbivores caused greater impacts within areas developed for solar energy than nearby populations under similar climatic conditions. The effects of herbivores on fruit output, for example, were frequently increased within the established solar array field and mitigation (transplant) areas. Reduced output of fruit and seeds directly limits establishing new individuals.

    b) Granivores (animals that eat seeds) may be a concern for the survival of populations that have strong reliance on the seedbank. Predators that keep granivore populations in check tend to be excluded from solar energy installations because of human presence, fencing, and constructed facilities. This could lead to lower seed survival and declining plant populations.

Demographic Responses to Other Threats

1. **An herbaceous perennial near the edge of its geographic range and at the limits of the ecological conditions that it tolerates has a high risk of extinction within the**

next 20 years. Such tenuous populations warrant an increase in conservation priority, particularly because of their unique value to genetic diversity. Methods for conservation may include improved habitat management, collecting seeds for long-term storage in special repositories, propagation studies, and assisted migration methods.

2. **In the future, dry years are likely to have stronger negative effects on the ability of herbaceous perennial populations to grow and persist than the positive effects of wet years.** In addition to depending on rainfall, rare desert species are commonly associated with low-relief washes for habitat. Care must be taken to preserve as much integrity of these washes as possible within and adjacent to energy developments. An increasing probability of more drought years will require special attention to maximizing rainfall storage in the available soil. For example, upslope obstructions to natural runoff patterns could be avoided or removed and activities that cause soil erosion curtailed.

3. **It is unlikely that the detailed demography of a rare species can be predicted from the demography of a closely related common species for meaningful conservation, restoration, or site management.** Despite many similarities, two species can exhibit very different responses to variations in landscape and climate. Rare species may have unique characteristics that will require individualized approaches to their conservation.

4. **Some rare species may have limitations imposed on population growth because of their specialized pollinators.** Determining how to mitigate the impacts of energy development on a rare desert plant should include understanding what the pollinators are, where they reside, and what effect they have on plant reproduction, especially plants that require pollen from another individual of the same species.

5. **Long-term seed dormancy is likely a critical adaptation that allows a dwindling population to recover when more favorable conditions finally re-occur.** Conservation of seed banks is absolutely essential for conserving both common and rare seed-producing desert plants. Once the extent and size of a rare species seed bank is known (see #4 above), special care (e.g., avoiding seed banks, preserving soil and small-scale landscape features) is essential on- and off-site.

Mitigating the Impacts of Development on Rare Plant Populations

1. **Avoiding rare plants is the best possible mitigation strategy when siting, constructing, or operating renewable energy facilities.**

a) For herbaceous perennials, preserving larger plants has the strongest effect on a population's survival by enhancing long-term seed output.

b) For annuals, preserving diverse landscape features is critical because subtle relationships between soil, topography, and hydrology can affect population persistence. Attempting to transport a sensitive, specialized species out of harm's way and to off-site, unoccupied habitat by redistributing the seedbank-containing "topsoil" is an unproven mitigation action in arid environments. Where disturbance to the population cannot be completely eliminated, sustaining topographic complexity within energy installations is recommended by employing sensitive array designs and construction methods.

c) If a proposed site for energy development harbors rare species with very specific habitat requirements (such as depending on small-scale landscape features), there would be a very low probability that mitigation (on-site and off-site) or restoration would be successful. This study found that a rare annual was highly sensitive to small-scale landscape variation as yearly rainfall patterns varied. It was also documented that transplanting a rare perennial into adjacent habitat had low success.

2. **The "halos" (openings between the mirrors established to avoid rare plants during solar field construction/operation) within the Ivanpah Solar Energy Generation System are an effective mitigation action when combined with the preserving intact, off-site populations.** Survival of individuals within the solar field halos provides substantial ecological benefit compared to other field designs that remove rare plant populations by grading away the natural soil surface and its vegetation cover. In contrast, transplanting as a mitigation action appears to be less effective for long-term conservation because of lower fruit output, higher dormancy, and increased herbivory.

3. **For clonal perennials, reproduction by seeds is suspected to be a rare event in the wild, even though seed output may be high.** Given that the seeds of these species may be available (especially when flowers are protected from herbivory) and contain valuable genetic variation, this study recommends using seeds to propagate perennial species for mitigation.

4. **Mammals and insects that eat plants (herbivores) may be the single greatest non-human threat to the vitality of natural populations of rare perennials in the California deserts.** Jackrabbits and caterpillars are responsible for damage on two rare perennials. Small cages proved very effective in reducing herbivory and enhancing growth and sexual reproduction, even during a drought year. If intense mammalian herbivory is

shown to impact rare perennial species within a solar array field, then an herbivore control program might be necessary to maintain vitality of both created and conserved natural populations.

5. **The scarcity of genetic data for California desert rare plants is a significant impediment to conservation.** Populations contain essential genetic variation for occupying more types of habitat, enduring stress, responding to environmental change, and ultimately evolving. A concerted effort must soon be made to survey rare plant populations for genetic variation so that genes can be conserved either by plants in the field or by seeds in special repositories.

Project Benefits

Population sustainability information for rare desert plants is necessary for managing these important public resources and improving the tools used for siting, designing, permitting, operating and mitigating the impacts of renewable energy projects. This research has contributed to meeting state and federal environmental quality standards while promoting the timely permitting of energy facilities in the California deserts. In the long-term it will help protect fragile desert species and ecosystems while achieving California's ambitious Renewable Portfolio Standard goal by 2020. This project also facilitates developing stable, secure, and reliable sources of clean energy in an environmentally responsible manner.

CHAPTER 1: Introduction

1.1 Background and Problem Statement

The coming decade will bring radical physical and biological changes to the California deserts. Utility scale solar energy development will help meet California's ambitious Renewable Portfolio Standard goal, under which electricity retailers are mandated to provide 33% of their load from renewable energy by 2020. Facilities designed to generate electrical power from solar and wind energy are now moving rapidly from the proposal and planning stages to construction and operation. The Bureau of Land Management (BLM) currently has almost 50 applications for solar energy projects located within the Desert Renewable Energy Conservation Plan (DRECP) area. The DRECP is a joint effort of four state and federal agencies (http://www.drecp.org). This draft plan is undergoing public review as this report was being written and cites lack of knowledge of population trends for covered species as an impediment to conservation efforts.

The state and federal permitting process under California Environmental Quality Act (CEQA) and National Environmental Protection Act (NEPA) requires that significant impacts to special-status plants, those protected by their federal or state listing status, are minimized. Potential mitigation measures include (1) permanent protection of offsite target population; (2) onsite avoidance of critical habitat features, seed banks and established populations; (3) translocation of existing plants to an offsite location; (4) salvage of the plants to botanical institutions or the general public; or (5) mitigation banking of seed. Successful implementation of these measures and the restoration of impacted populations require managers and policy makers to utilize population size thresholds for different kinds of special-status plants that have a low probability of extinction under desert conditions.

To advance state and federal conservation goals, targeted research of special-status species in the vicinity of proposed solar installations is necessary to determine the size and viability of current populations, assess their habitat requirements, and provide information on the feasibility of establishment of novel mitigation sites within suitable habitat. Successful management, restoration, and mitigation of natural populations of rare species require clear targets for population size that will ensure persistence into the future.

Desert ecosystems in southwestern North America face multiple direct and indirect effects of disturbance by utility-scale renewable energy development including population reduction, fragmentation, and altered herbivore and pollinator densities (Hernandez et al. 2014, Hernandez 2015). Each of these stressors can have detrimental effects on plant demographic responses and the outlook for population persistence Management of populations of rare plant species amid this advancing regional development requires understanding of the ecological requirements of rare species and

their demographic drivers to design appropriate programs for species avoidance, mitigation, and restoration. This study was designed to help fill these knowledge gaps in the DRECP plan area by providing recommendations for rare plant species management based on rigorous demographic field study.

Desert plants have adaptations that buffer extended drought conditions such as succulence, deep roots, adult and seed dormancy, and seed longevity, among others (Smith et al. 1997). These mechanisms have evolved to buffer the incredible environmental variability of deserts. These adaptations can allow populations to persist through extended periods of unsuitable conditions with little measureable effect on population demographic rates. Where subpar conditions persist, decline occurs over relatively long time-scales congruent with prolonged mortality and lack of recruitment. Long-term studies are necessary in order to witness the demise of some populations and/or species. Similarly, species adapted to endure challenging climatic periods may be resilient, at least initially, to anthropogenic stressors that reduce resource availability or lower reproductive rates. Adaptations to the desert offer resilience, but also introduce challenges for field study of demography such as extended longevity and cryptic dormant seeds and adult plant stages (Moore and André 2014, Pavlik 1998).

1.2 Selection of Target Species

Target species were carefully chosen to meet several different criteria, including potential for inclusion in the sister study on geographic distribution modeling (Moore and McIntyre, in press; Table 1.1), relevance to conservation decision-making, and feasibility of demographic field study. Researchers leading this study initially queried the California Natural Diversity Database (CNDDB) for species with at least fifteen occurrence records and were listed by the state of California, the federal Endangered Species Act, or the California Native Plant Society (CNPS) or considered imperiled by the NatureServe heritage network. The objective was to provide information about a wide geographic extent and taxonomic spectrum in order to increase the applicability of findings to other locations and species throughout the desert region. The researchers included a range of life histories, with perennial succulents, woody shrubs, and herbaceous annuals. They also selected species based on their affinity for site conditions that are most likely to be impacted by utility scale solar energy development. For example, the researchers selected species that occur at low to moderate elevations (0-3500'), in non-forested sites, and with a significant proportion of occurrences outside of already designated conservation areas. In addition, some species were included that are known to occur within areas suitable for energy installations (*Asclepias nyctaginafolia* and *Grusonia parishii*), and/or species that have been previously identified in the permitting process for renewable energy projects (*Penstemon albomarginatus*). Additional detailed information on the species selection process is available in Moore and McIntyre (In press).

The unique life history of each rare plant species necessitates the development of distinctive field and analytical methods for demographic study. There is no one-model-

fits-all application for observational and experimental study of rare plants or prediction of rare plant species population dynamics. This diversity required the application of two analytical approaches: integrated and non-integrated population viability analyses (PVA).

Table 1.1: Plant Species Covered by This Report

Scientific name	Species code	Common name	Habit	Federal	CRPR
Asclepias nyctaginifolia	ASCNYC	Mojave milkweed	Herbaceous perennial		2.1
Eriophyllum mohavense	ERIMOH	Barstow woolly sunflower	Annual	BLM Sensitive	1B.2
Eriophyllum wallacei	ERIWAL	Wallace's wooly daisy	Annual		
Grusonia parishii	GRUPAR	Parish's club-cholla	Cactus		2.2
Mentzelia tridentata	MENTRI	Creamy blazing star	Annual		1B.3
Mimulus mohavensis	MIMMOH	Mojave monkeyflower	Annual	BLM Sensitive	1B.2
Penstemon albomarginatus	PENALB	White-margined beardtongue	Herbaceous perennial		1B.1

California Rare Plant Ranks (CRPR) are rarity designations given by the California Native Plant Society. 1B= Plants rare, threatened, or endangered in California and elsewhere; 2 = Plants rare, threatened, or endangered in California, but more common elsewhere; .1 = very threatened; .2 = moderately threatened; .3 = not very threatened.

1.3 Analytical Approaches

1.3.1 Population Viability Analyses

PVAs have become commonly used tools for plant conservation and management of populations (Menges 2000a, Schwartz and Brigham 2003). PVAs are commonly conducted by assembling multiple seasons of detailed life history table data into Leslie matrices (discrete stage- or age-structured models), and then projecting population growth through time (Caswell 2001). PVAs or population projection models (PPMs) can be useful at comparing the effects of different management strategies on population growth (Menges 2000b, Reed et al. 2002) and an extension of PPMs, life table response experiments (LTREs) can be used to quantify the effects of different strategies on population growth rates and to assess how impacts on specific vital rates influence changes in the population growth rate (Caswell 2001, 2010, Endels and Jacquemyn 2007).

However, conducting PVAs for plants presents a number of challenges due to their unique life histories. In particular, long-lived stages and cryptic life stages are challenging to study and often require estimation through indirect means (Schwartz and

Brigham 2003). Accurate parameterization for management also requires clear understanding of threats and potential impacts, but these data are commonly unavailable. For example, it is unknown how perennial desert plants will be influenced by changes in pollinator movement around and within solar installations, or how annual dormant desert plant seeds will be influenced by solar panel shade.

1.3.2 Integrated and Non-integrated Population Viability Analyses

To inform the management of solar energy development with respect to rare plants in the California desert region, detailed population-level studies were conducted on six rare plant species and a common congener of one of the rare species. Each of these studies necessitated species-specific methods in both field observations and experimentation and analyses. Two methods were deployed. First, where it was possible to collect high-quality data on the entire life history of a given species over a number of seasons, the researchers assembled the available data into fully integrated PVAs. They did these analyses for the annuals *Eriophyllum mohavense* (rare) and its congener *E. wallacei* (common) and the perennials *Penstemon albomarginatus* (and *Asclepias nyctaginifolia* (Table 1.1). For the latter two species, studies within Ivanpah Solar Electric Generating System (ISEGS) allowed the authors to directly compare the demographic consequences of management and mitigation within this solar installation to undisturbed populations offsite. Second, where integrated PVAs could not be fully assembled, the authors proceeded with analysis as appropriate to each species to assess population vitality and threats to persistence. This includes a non-integrated population viability analysis for *Grusonia parishii* across ecological reserves and sites impacted by solar energy. The following chapters detail these studies and conclude with their resulting management recommendations for rare plant species in desert landscapes impacted by utility-scale solar and other forms of large-scale anthropogenic disturbances. Succinct conclusions from this body of work are presented in the Executive Summary.

1.3.3 Geographic Information Systems

Spatial data was analyze and represented using ESRI Geographic Information Systems (GIS) software and data. Spatial data utilized in the analyses of this report include layers referenced Renewable Energy Project Applications in California (Renew 2015), California BLM State Office GIS Department. Accessed February 2015. http://www.blm.gov/ca/gis/; Areas of Critical Environmental Concern (ACEC 2014), California BLM State Office GIS Department. Accessed February 2015. http://www.blm.gov/ca/gis/; California Natural Diversity Database Biogeographic Data Branch (CNDDB 2014). Department of Fish and Game. Accessed spring 2011. https://www.dfg.ca.gov/biogeodata/cnddb/cnddb_info.asp; National Lands Conservation System (NLCS 2015). California BLM State Office GIS Department. Accessed February 2015 http://www.blm.gov/ca/gis/; and Mojave National Preserve Tract and Boundary Data (Mojave 2015). National Park Service, Department of the Interior Data Catalog. Accessed February 2015. https://catalog.data.gov/dataset/mojave-national-preserve-tract-and-boundary-data.

Chapter 2: Comparative Demography of *Eriophyllum mohavense* and *E. wallacei* in Relation to Variations in Landscape and Climate

2.1 Introduction

A central theme in plant ecology concerns the impact of spatial and temporal variation on population distribution and dynamics (DeWoody, Feng, and Swihart 2005; Hanski 1998). Populations respond to spatial heterogeneity by occupying suitable habitat patches in a landscape, subject to dispersal limitations. In a desert those patches could be obvious, large-scale ("first-order") habitat features, such as washes, offering an extensive ribbon of moist soil conditions that could ameliorate the effects of limited rainfall on plant growth. They could also be subtle, small-scale ("second-order") habitat features, such as bowl-shaped depressions in a pavement that provide highly localized hydrological benefits to a species, thus allowing activity during years with minimal rainfall. Temporal variation resulting from weather patterns, human activities, or other sources can further restrict habitat patch occupancy to particular seasons or years. Migratory and short-lived species may be especially affected by the temporal component of variation – annual plants are an excellent example (Pavlik 2008). A particular desert winter annual may tend to occupy open, south-facing slopes, but presence in such large-scale habitat patches is ultimately controlled by rainfall and temperature, components of variation that change unpredictably through time. Spatial and temporal conditions together, operating on multiple scales, determine where and when a given species occupies and persists in suitable habitat. Defining the nature of these conditions, including their spatial and temporal scales, is essential to understanding the effects of disturbance (e.g., solar energy development) on populations of annual plants.

An emerging field of research explores how variations in landscape features and climate interact to influence population performance and long-term persistence (Scheffers, Edwards, Diesmos, Williams, and Evans 2014; Stephens, Tye, and Quintana-Ascencio 2014). Such approaches can be applied to predicting the impacts of renewable energy development on plant populations during multiple project phases. Construction activities alter the ground surface, potentially changing topography, vegetation cover, drainage patterns and soil characteristics on large and small scales. The installations themselves (e.g., panels, towers, conduits) could impose novel shade and moisture gradients across the ground surface, and plant performance may then vary due to small-scale variations in resource abundance. Species with annual life history strategies may be most affected by construction and operation of energy facilities because once germination occurs they must have enough resources to survive and reproduce and thus replenish themselves in the seed bank (Tevis 1958). Consequently, annuals are among the most sensitive to landscape alterations and climatic variability (Morris et al. 2008).

The present study measured and evaluated how populations of rare and common annual plants utilize landscape variations to persist when there is great uncertainty in the temporal patterns of rainfall (i.e. high levels of environmental stochasticity). Large and small landforms will be affected by construction and operation of industrial solar facilities in California's Mojave Desert, a region supporting 450 special-status plant species (Moore and André 2014), as well as a booming renewable energy industry. Two closely related annual plant species, therefore, were chosen as the foci for a comparative four-year demographic study; Barstow woolly sunflower (*Eriophyllum mohavense*, "ERIMOH") and Wallace's woolly daisy (*E. wallacei*, "ERIWAL"). ERIMOH is a rare species previously affected by solar energy development that may face additional development threats in the future. It is a California endemic, with all known occurrences clustered around Kramer Junction in the central Mojave Desert. The species is proposed for regulatory coverage under the DRECP. ERIWAL is in the same genus (a "congener") and thus shares much of its genome with ERIMOH. It is widespread throughout the Mojave occurring in the same vicinity as ERIMOH but rarely occupying the same exact location. A comparison of ERIMOH and ERIWAL will show whether intrinsic (i.e., genetically based) biological characteristics are leading to rarity in one species and ubiquity in another. Those characteristics could be morphological, physiological, or developmental, the result of relatively few genetic differences in the case of congeners. If such characteristics were not detected demographically, researchers would then suspect that ERIMOH's highly restricted distribution might be attributed to a recent evolutionary origin or possibly a range contraction in the past caused by external factors (e.g. extinction of pollinators or dispersal agents).

In this comparison, both species are small in size (generally <1 cm in diameter) and have similar morphology and developmental patterns. Therefore, similar demographic responses would be attributed to similar physiological responses to landscape and climate, perhaps allowing rare and common species to persist in a generalized habitat underneath installations within energy project sites (if avoided during construction activities). Different demographic responses would mean that the rare ERIMOH responds uniquely to its environment according to genetic distinctions and requires special habitat features that may be difficult to maintain or mitigate for on project sites.

To compare the demography of ERIMOH and ERIWAL in relation to landscape features and yearly climatic variation, observational studies were conducted over a four-year period (2011-2014). Data on survivorship and fecundity were collected in each year, allowing construction of matrix models comparing population performance and addressing the following questions:

a) Do closely related, rare and common annual species respond similarly to desert conditions, especially with respect to variations in landscape features and climate?

b) What are the expected population growth rates of closely related, rare and common annual species given different climatic scenarios projected into the future?

c) What are the environmental conditions (landscape features and climatic factors) that enable populations of rare and common species to grow and persist?

d) What are the life history traits that enable populations of rare and common species to grow and persist?

e) What are the management recommendations, derived from answers to the previous questions, regarding *in situ* conservation of rare desert annuals such as ERIMOH during construction and operation of renewable energy facilities?

2.2 Methods

2.2.1 Study Species

Eriophyllum mohavense (I.M. Johnst, Asteraceae), Barstow woolly sunflower (ERIMOH) is an endemic annual forb with limited distribution in California's Mojave Desert region (Baldwin et al. 2012). ERIMOH is a designated Bureau of Land Management (BLM) Sensitive Species with a global element rank of G2 (imperiled) (NatureServe 2010) and State element rank of S2 (imperiled) (CDFW 2014). The California Native Plant Society (CNPS) ranks it as a CRPR 1B.2 species (endangered in California and elsewhere, with 20 to 80% of occurrences threatened) (CNPS 2014). All known occurrences of the species are clustered around Kramer Junction, California, near the intersection of Kern, Los Angeles, and San Bernardino Counties (elevation 500-800 m). ERIMOH is 1-2.5 cm tall, forming dense tufts of white-woolly herbage and discoid heads bearing yellow tubular flowers (Baldwin et al. 2012). During the four-year study period, annual precipitation had a strong effect on ERIMOH density throughout the study area, with average density ranging from several hundred plants/m^2 in the wettest year to zero plants/m^2 in the driest year (Tanner, Moore, and Pavlik 2014).

Eriophyllum wallacei (A. Gray, Asteraceae), Wallace's woolly daisy (ERIWAL) is a widespread annual forb in California's arid regions with populations extant in Utah, Arizona, and Baja California (in California elevation 30-2400m) (Baldwin et al. 2012). ERIWAL is 1-15 cm tall with heads producing yellow ray and disc flowers (Baldwin et al. 2012). ERIWAL also exhibited a strong response to annual precipitation over the study period, with average density ranging from <1 plant/m^2 in the driest year to several hundred plants/m^2 in the wettest year (Tanner et al. 2014).

ERIMOH and ERIWAL are both winter annuals, germinating in response to fall or winter rains, growing during the winter and early spring, and completing their life cycles by flowering and setting fruit (achenes, but herein referred to as "seeds") during the late spring (usually April to May). Spring rains may prolong reproduction, but senescence and death occur rapidly as temperatures rise and soil moisture is depleted.

Seed banks appear to be important for both species, but average and maximum duration of dormancy in native soil are unknown.

2.2.2 Landscape Features and Climates of Study Sites

2.2.2.1 Barstow Woolly Sunflower Sites

All populations of ERIMOH lie within the Kramer Hills quadrangle, San Bernardino County, California (Figure 2.1). They are scattered across suitable habitat along BLM Route FP 7140 west of the intersection with Harper Lake Road. The Kramer Junction area was developed for solar energy production in the late 1980's and the Kramer Hills population of ERIMOH lies between SEGS (Solar Energy Generating Facility) III-VII at Kramer Junction and SEGS VIII-IX Harper Dry Lake to the east, with power line right-of-ways and BLM off-highway vehicle (OHV) routes crossing the habitat. Researchers observed direct impacts of OHV traffic at study sites on at least four separate occasions, with tire tracks disturbing rare plant habitat and destroying several established plots. The climate station nearest all three ERIMOH sites is at Edwards Air Force Base, California (KEDW, ~45-km southwest of sites), which receives a mean annual rainfall of 141 mm and has mean temperatures in the range of ~15º C to ~25º C during the growing season.

The first order landscape features of ERIMOH developed from a series of terraces, probably uplifted during and since the Pleistocene and initially the result of depositional processes (Beeler 1992). The soils are slightly alkaline (pH=7.6), with high levels of calcium, sodium and carbonate, and range from sandy loams, to sandy clay loams, or loamy sands. There is often a crust-like surface composed of a thin layer of fine quartzite pebbles. There may also be an underlying, impermeable layer of cemented carbonate that effectively excludes perennial plant species (Beeler 1992). These areas often appear as distinctive "islands" surrounded by alluvial materials from gently sloping bajadas (Figure 2.2). Site 1 consists of a flat, open and sparsely vegetated pan area ~15 m north of BLM FP 7140 at 691 m elevation. Site 2 is at 712 m elevation, ~42 m north of BLM FP 7140, and exhibits substantial variation in large-scale topography, with broad knolls separated by drainage creases. ERIMOH Site 3 is at 696 m elevation, in an open, primarily flat and sparsely vegetated pan area ~ 112 m south of BLM FP 7140.

The second order landscape features associated with all ERIMOH sites probably originated from slow erosion processes over long periods of time. Where the ground surface is sloping, there may be a series of very shallow, almost imperceptible drainage channels called "rills", containing rill habitat. Rills may typically be a couple meters or less in width and only a few centimeters in depth. A rill may lead to an equally shallow depression called a "divot", providing divot habitat, which can also be found where there is essentially no slope whatsoever (Figure 2.2). Unlike the first order landscape features, rills and divots cannot be seen on aerial photos or topographic maps. Surrounding rill and divot habitats is termed "broad" habitat – the intervening, often extensive, first order terrace surfaces described above.

Under favorable weather conditions, ERIMOH emerges in abundance with other annual species across broad, pan-like areas or on gentle slopes where no perennial vegetation is present. *Larrea tridentata* and *Ambrosia dumosa* are prominent in the vegetation surrounding these habitat islands. Inventories of ERIMOH populations on Edwards Air Force Base (Mitchell, D., Surdzial, C., Surdzial, A., Pamiljans 1995) found *Lepidium flavum* and *Chorizanthe spinosa* to be common associates of ERIMOH on the terrace soils, and a high incidence of co-occurrence with these species were also observed.

2.2.2 2 Wallace's Woolly Daisy Sites

ERIWAL study populations are located in the Newberry Mountains above Daggett, California. All lie within the Minneola quadrangle, San Bernardino County, California (Figure 2.1). Sites are located southeast of Barstow, off Camp Rock Road, a well-maintained dirt road running NE to SW. BLM off-highway vehicle routes cross this area, and the researchers have observed direct impacts of OHV traffic on four of six study sites. The nearest climate station to ERIWAL sites is at Barstow-Daggett Airport (KDAG, ~9-km northeast of sites) where the mean annual rainfall is 99.5 mm, and mean temperatures range from ~15º C to ~30º C during the growing season.

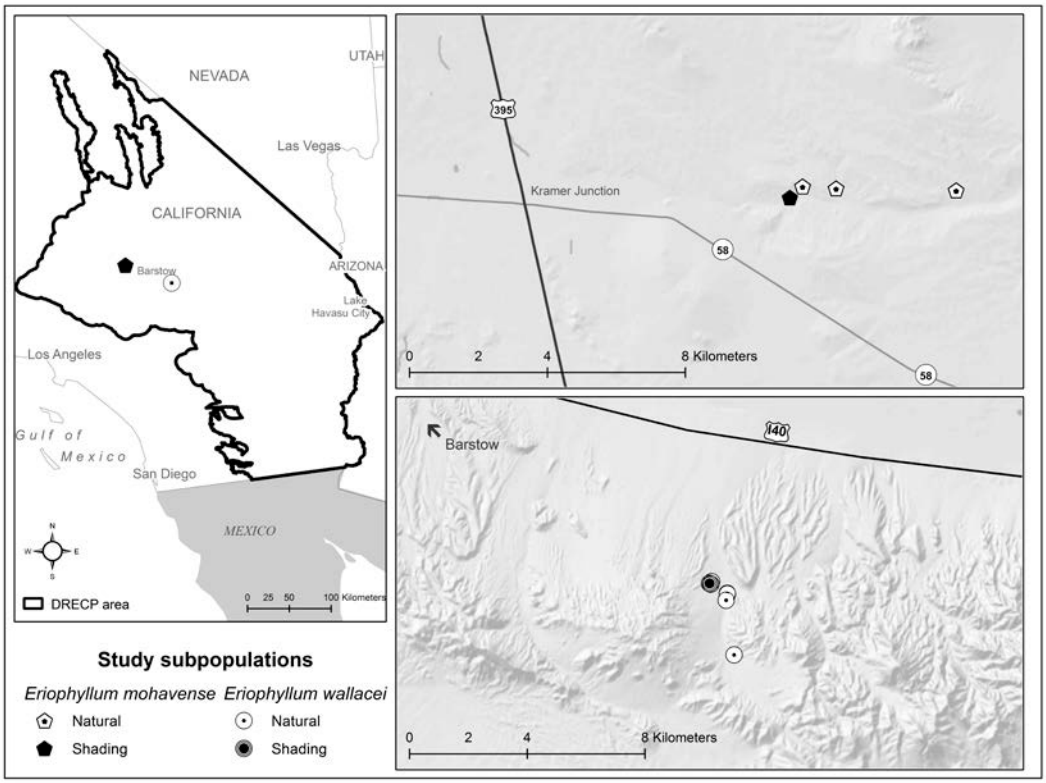
The first order landscape features of ERIWAL consist of rocky or gravelly, gently sloping bajadas that emanate from canyons at the base of steep bedrock outcrops or mountainsides. Coarse alluvium can appear cemented together with finer silts and clays, forming a homogenous surface over large areas. This uniform bajada surface is called "broad" habitat for the species. Sites 1 and 4 are dominated by a large northeast-facing bajada bordered by volcanic outcroppings, situated ~40 m west of BLM Route #6635 at an elevation of 939 m. ERIWAL Site 3 is also on a broad, alluvial surface but is situated upslope at an elevation of 1,026 m, ~50 m east of Camp Rock Road, and is well separated from all other sites. At some sites the bajada is dissected by washes, sometimes 50 m wide and up to 1 m deep. Soils are poorly developed and consist of everything from boulders to fine sand. A wash may actually be a series of adjacent channels that can carry vast amounts of water during flash flood events, expanding laterally to capture the toe of adjacent bajadas. ERIWAL Sites 2, 5 and 6 are found within or along the western edge of a large, very rocky wash at 920 m elevation, located ~126 m east of Camp Rock Road. These sites may experience flowing water during heavy rain events.

The second order landscape features of ERIWAL sites are essentially absent. The ground surface of bajadas tends to be of uniform microtopography and texture, with few, if any, divot and rill features that were observed. To varying degrees, small rocks and gravel cover and probably armor the surface of all three bajada sites with broad habitat (1, 3, and 4). The surface of the ground at wash sites 2, 5 and 6 is much more heterogeneous, but the predominately coarse materials drain rapidly after a flood event and do not collect moisture as do the rills and divots at ERIMOH sites.

Perennial shrub cover on the bajadas is high (*Larrea tridentata*, *Ambrosia dumosa*, *Yucca schidigera*), accompanied by a rich annual community within shrub canopies and in intershrub spaces. In the washes there are scattered mesquite (*Prosopis julifora*), with

short-lived perennials (*Hymenoclea salsola, Cucurbita palmata*) and patches of annuals in wet years.

Figure 2.1: Map of ERIMOH and ERIWAL Study Sites.



Locations of three observational and one experimental study site for Barstow woolly sunflower (Eriophyllum mohavense), and six observational and one experimental study site for Wallace's woolly daisy (*E. wallacei*).

Figure 2.2: Google Earth Satellite Imagery of ERIMOH Site 2

Google Earth satellite imagery (2012) of ERIMOH Site 2, where broad, largely unvegetated knolls of terrace soil are separated by large drainage creases and surrounded by alluvial materials (with perennial shrubs). Green pins show origin and endpoints for randomized transects within the broad habitat, and white squares mark the approximate locations of transects sampling rill habitat (not visible at this scale).

2.2.2.3 Climatic Analysis

Climatological data for KDAG (Barstow-Daggett Airport, California) were obtained from NOAA and data for KEDW (Edwards AFB, California) from the Armstrong Flight Research Center (https://weather.dfrc.nasa.gov/wxclimatology.htm) and Weather Underground websites (http://www.wunderground.com/). A September to August "activity year" was used to better align annual climate patterns with the phenologies of the study species. Each activity year included the months September-December from the previous calendar year because rainfall during these months can stimulate germination of winter annuals (Beatley 1974). The researchers calculated monthly precipitation and daytime temperature averages for the 2010-2011 activity year through the 2013-2014-activity year. Trace amounts of rainfall were treated as zeroes. They also calculated monthly precipitation and temperature means for a fifty-year period (1964-2014), except for temperature at KEDW. Temperature records for this station were provided in the form of monthly averages spanning the full period of record, 1942-2014.

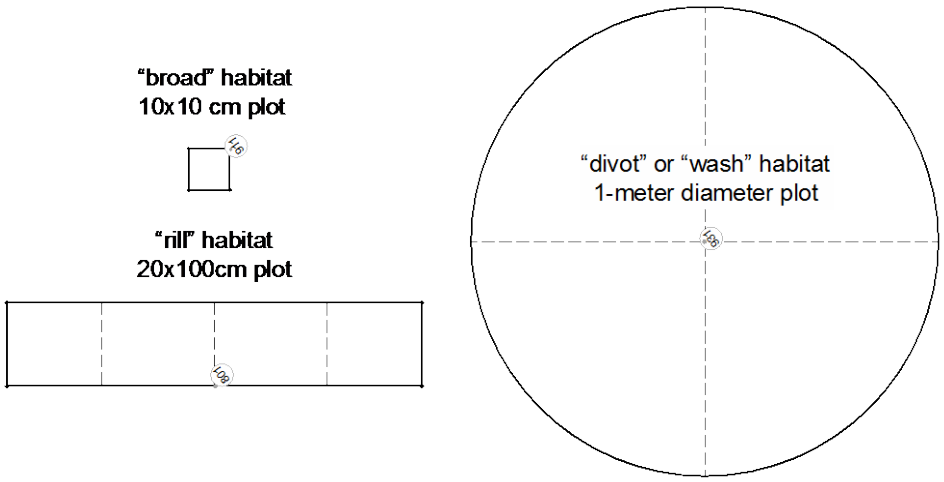
2.2.3 Population Responses to Landscape and Climate

2.2.3.1 Plot Establishment

Annual weather patterns, combined with landscape features, create varying local distributions and densities of the two focal species. Consequently, sampling strategies to mark enough individuals for assessing demographic responses were amended. Researchers began with establishing the same randomly located plots at all sites in 2011, but added new plots in subsequent years to capture the unique responses of both species to landscape and climatic variation across the four-year period (Tables 2.1 and 2.2).

For demographic studies three different plot types: 10 x 10 cm plots, 20 x 100 cm plots, and 1 m diameter plots were employed (Figure 2.3). The 10 x 10 cm plots were established for both species in 2011 and were randomly positioned in "broad habitat" (terrace or bajada surface for ERIMOH or ERIWAL, respectively) where individuals of these species were generally present. Subsequently, the authors (non-randomly) added 20 x 100 cm plots within rills and 1 m diameter plots within divots at all three ERIMOH sites. They also (non-randomly) added 1 m diameter plots to broad (bajada) and wash habitats at all ERIWAL sites, the exact locations determined by the presence of at least two individuals.

Figure 2.3: Diagram of Demographic Plot Types for Sampling Landscape Features



Dashed lines indicate divisions used for subsampling within plots.

Table 2.1: Plots Established and Surveyed - Barstow Woolly Sunflower

Site	Year Est.	# Broad Habitat Plots	# Divot Habitat Plots	# Rill Habitat Plots	Plot Area (cm2)
ERIMOH 1	2011	49	-	-	100
ERIMOH 2	2011	48	-	-	100
ERIMOH 3	2011	52	-	-	100
ERIMOH 1	2013	-	17	-	7854
ERIMOH 2	2013	-	-	25	2000
ERIMOH 3	2013	-	9	-	7854

All plots were surveyed every year subsequent to establishment.

Table 2.2: Plots Established And Surveyed - Wallace's Woolly Daisy

Site	Year Est.	# Broad Habitat Plots	# Wash Habitat Plots	Plot Area (cm2)
ERIWAL 1	2011	47	-	100
ERIWAL 2	2011	40	-	100
ERIWAL 3	2011	40	-	100
ERIWAL 4	2012	-	24	7854
ERIWAL 5	2012	-	16	7854
ERIWAL 6	2012	-	11	7854

All plots were surveyed every year subsequent to establishment.

2.2.3.1.1 Broad Habitat Plots and Sampling

Three demography study sites (1, 2, 3) were set up for both ERIMOH and ERIWAL during 2011 (a high rainfall year) using 10 x 10 cm plots. These were sampled in all four years with a stratified random approach comprised of four transects, with plots established at randomized locations perpendicular to the transects.

2.2.3.1.2 Rill, Divot, and Wash Habitat Plots and Sampling

During 2012 rainfall totals were very low, and no ERIMOH individuals emerged at any site or habitat. ERIWAL did emerge but at very low density compared to 2011. Consequently, new 1 m diameter plots in ERIWAL wash habitat were established in 2012, and 1 m diameter plots in ERIMOH divot habitat in 2013. The researchers also established 20 x 100 plots in ERIMOH rill habitat in 2013. All plots were surveyed in all subsequent years.

2.2.3.2 Sampling Population Density

Population densities were used to measure general responses to landscape and climate variations. Densities were estimated as the maximum number of plants counted within each plot during periodic surveys between late-January to mid-March. In years where the average number of plants in 1 m diameter plots exceeded 50 plants per plot, researchers subsampled two randomly selected quadrants within the plot. If subsampling was employed in multiple years, surveys were always carried out in the same pair of quadrants within each plot.

Both species exhibited patchy distributions across landscape features, and plant densities in 100 cm^2 plots that were scaled-up to 1 m^2 led to very high, perhaps unrealistic estimates. Consequently, calculated densities were downsized to the 100-cm^2 scale. The MASS package version 7.3-33 (Venables and Ripley 2002) and R 3.1.1 (R Core Development Team, 2014) were used to examine the response of population density across years. The most appropriate model was selected from negative binomial, Gaussian and Poisson options based on Akaike information criteria (AIC) values, with the lowest value indicating best fit. Calculated densities were rounded to integer values to conform to model expectations. The effects of year, site, and their interaction were included in the models and effects considered to be statistically significant when $P < 0.05$ for all analyses.

2.2.3.3 Determining Life History Stages and Transitions

Early in the growing season of each activity year, a random subset of emergent and/or juvenile plants within each plot was marked to determine the probability of each life history stage transition. Life history stages were defined as follows: E (emergent), J (juvenile), B (budding), F (flowering) and Fr (fruiting) (Figure 2.4). The total number of whorls of true leaves (i.e. excluding cotyledons) was the most reliable indicator of emergent ($\leqq$ 2 whorls) and juvenile (> 2 whorls) stages. On subsequent surveys plant status (alive/dead), stage class, and maximum diameter (mm) were recorded.

The most advanced phenological stage observed in the field was used to assign the individual's final fate as either pre-reproductive (E, J) or reproductive (B, F, Fr). Plants not progressing past the emergent or juvenile stage classes by late season surveys (~late March to early April) were assumed to have died in a pre-reproductive stage. Fates for marked plants that could not be located (due to herbivory or other causes) were assigned based on the last observation made. From 2011-2014, 989 ERIMOH and 1,396 ERIWAL individuals were marked and their fates recorded.

Figure 2.4: The Life Stages of ERIMOH (top) and ERIWAL (bottom)

Barstow Woolly Sunflower Stage Classes

Photo Credit: Karen Tanner 2012.

Wallace's Woolly Daisy Stage Classes

First row, emergent and juvenile individuals. Second row: budding, flowering, and fruiting individuals. Note U.S. coinage for scale.

Photo Credit: Karen Tanner 2012.

2.2.3.4 Estimates of Survivorship to Reproduction

The probability of survivorship to reproduction was calculated as the proportion of plants marked at first appearance in winter that reached the reproductive stage class (= total marked reproductive plants/total marked plants).

2.2.3.5 Estimates of Seed Output

During late season surveys, a random subset of marked, mature Fr individuals of each species were collected to measure seed output (# achenes per individual) The dense "wool" on ERIMOH made it difficult to obtain accurate capitula (floral head) counts, so mean seed output per plant was calculated instead of mean seed per capitulum. The researchers did not collect ERIMOH for seed counts in 2014 because only 25 marked plants attained reproductive maturity among all sites and plots.

2.2.3.5.1 Barstow woolly sunflower

Negative binomial general linear models were used to test for differences in seed output by site and habitat type in 2011 and 2013, the only years fruiting adults could be collected. Data from ERIMOH Site 1 - Broad Habitat and ERIMOH Site 3 – Divot Habitat in 2013 were excluded from analyses due to small sample sizes (n=3 and n=13, respectively). An ANOVA on seed counts in the remaining data set revealed significant effects of year and site/habitat combinations on seed output, motivating separate estimates of seed output for each year/site/habitat type combination to use in population growth models. (A repeated measures method could not be used to assess year effects because adequate replication would be lacking in dry years.) There were no field measurements possible for ERIMOH seed output in 2014, a very dry year, so the observed 2013 mean seed output rates were arbitrarily reduced by 50% for substitution into the population growth model.

2.2.3.5.2 Wallace's woolly daisy

Mean seed output per plant was calculated for ERIWAL for each season. A negative binomial general linear model was used to test for differences in seed output by year/site combination. ANOVAs revealed significant differences between some year and site combinations, motivating separate estimates of mean seed output for each year/site combination to use in population growth models.

2.2.3.6 Estimates of Seed Viability

X-ray assessment of seed collected at the end of the 2013 field season was used to estimate seed viability (= 1 – non-viability, see Appendix A). Fruiting plants were collected from demographic plots and stored under ambient lab conditions for ~1 year prior to shipment to Royal Botanic Gardens, Kew for X-ray. Estimates of viability obtained were used directly as 1-year old seed viability rates in the model (see Appendix B, Table B1). Seed viability was allowed to have the same value in year 2, such that viability of 2-year old seed is (1-year old seed viability) squared. Seed that is three years or more old was assigned a survival rate of 0.01, a conservative value allowing for the accumulation of a long-lived dormant seed bank with low probability of emergence. The

authors acknowledge that seeds in the seed bank could persist for many years, but data from the field are lacking.

2.2.3.7 Estimates of Seedling Emergence

Seeds were collected in spring of 2011 and used for an experiment to measure seedling emergence rates in the field. Three seeds were affixed to the midpoint of a wooden toothpick with a minimal amount of water-soluble glue. The amount of seed available for each species varied, so the number of toothpicks prepared differed (ERIMOH with 884 toothpicks bearing 2,652 total seeds and ERIWAL with 364 toothpicks bearing 1,092 total seeds). These toothpicks were sown in 10 plots each at ERIMOH and ERIWAL sites during the summer of 2011 and checked for seedling emergence on each visit in subsequent years.

2.2.4 Modeling Population Growth Rates

2.2.4.1 Projection Matrices

The measured responses of ERIMOH and ERIMAL were used to assess population dynamics by building projection matrix models. The models provide deterministic and stochastic estimates of the population growth rate (λ, lambda) (Caswell 2001). Values of λ <1 indicate population decline, those with λ =1 indicate stability, and those with λ >1 indicate population growth. λ can also be interpreted as an indicator of average population fitness under the set of environmental conditions represented by values in the matrix (Caswell 2001). Projection matrices were generated and analyzed using functions from the Popbio package (Stubben and Milligan 2007) in R version 3.1.1 (R Core Development Team, 2014).

As a prerequisite step, ANOVAs were performed on estimates of seed output of marked plants from demographic plots. These revealed significant differences between year, site and/or landscape feature combinations at ERIMOH and ERIWAL sites (see Appendix B Tables B2 and B3). Consequently, individual projection matrices were generated for each year-site-landscape combination, resulting in a set of 18 site-, habitat- and year-specific transition matrices for ERIMOH (Table B4), and 21 site- and year-specific transition matrices for ERIWAL (Table B5).

Time-invariant, linear models of the form $n_{(t+1)} = A\ n_{(t)}$ were initially built. The term $n_{(t+1)}$ is a vector of individuals broken down by stage class one time step in the future, and $n_{(t)}$ is the vector of stage-classified individuals at time t. The term A is a 3 x 3 matrix of fecundity and transition probabilities as shown in Table 2.3. The matrix A is multiplied by a starting vector (initial population) of seed in each stage class. A starting vector of 100 individuals was used in each seed stage class (S1, S2, S3) and projected population growth 100 time steps (100 years) into the future.

Table 2.3: General Form of the Projection Matrices with an Age-Structured Seed Bank

		Seed age at time t		
Seed age at time t + 1		**S1**	**S2**	**S3**
	S1	α_{11}	α_{12}	α_{13}
	S2	α_{21}	0	0
	S3	0	α_{32}	α_{33}

S1 is a new seed, S2 is 2-year old, and S3 is 3-year old seed.

A projection interval from September to September, in which no aboveground individuals survive from one time step to the next, was employed. This is consistent with the focal species ~January – May aboveground life cycle, age-structured seed bank and annual habit. The focus of the model is thus on seed survival and fecundity rates. In this model S1, S2, and S3 represent seed aged 1, 2, and 3+ years old. The top row of the matrix represents estimated seed output per seed, and non-zero rates in the second and third rows represent seed survival rates in the seed bank. Zeroes are shown for rates that are zero by definition; e.g., a 1-year old seed can survive to become a 2-year old seed at the next time step, but a 2-year old seed cannot remain a 2-year old seed into the next time step. The matrix above shows how seeds at stage j in time t progress to stage i at time t+1, one time step into the future. Newly produced seeds have a chance of being viable and surviving to the next time step, when they have a probability of emerging (or remaining in the seed bank). If emerging, individuals have a probability of surviving to the reproductive stage and producing some number of seeds.

2.2.4.2 Defining Transition Rates

Transition rates were calculated from demographic parameters as follows:

α_{11}, α_{12}, α_{13} = seed viability * probability emergence * survival to reproduction * est. seed output

α_{21} = seed viability * proportion not emerging * survival of 1 year old seed in seed bank

α_{32} = seed viability * proportion not emerging * survival of 2 year old seed in seed bank

α_{33} = constrained to 0.01

2.2.4.3 Seedling Emergence Rates

Seedling emergence rates used in the model are informed by the seedling emergence experiment described in 2.2.3.7. For ERIMOH, the experimental emergence rate was zero in 2012 and 2013 and extremely low in 2014 (Tables B6 and B7), though sparse, natural seedling emergence was observed in 2013. Of necessity the 2014 rate was re-used for 2011 and 2013. A similar strategy was followed with ERIWAL, which had an experimental emergence rate of zero in 2012, though plants naturally emerged in modest numbers outside experimental plots. Low emergence rates were observed in 2013 and

slightly higher ones in 2014. The lower 2013 rate was re-used for 2012, since conditions during that year seemed to be more stringent for emergence in the broad habitat and thus more similar to 2013 than 2014. The higher 2014 rate was re-used for the favorable year 2011. By necessity, a constant emergence rate was assumed regardless of seed age for both species.

2.2.4.4 Survivorship and Seed Output

Our study was initiated during 2011, so the start date was not early enough in the growing season to track the proportion of young plants that transitioned to reproductive adulthood (stage B, F or Fr) in that year. For this proportion in 2011 the best rate observed across all sites and years was used (because 2011 was a "good" year). Seed output was assigned based on calculation of mean seed output per plant in each year, site, and habitat type combination. A constant seed output rate was assumed regardless of seed age.

2.2.4.5 Stochastic Modeling

Yearly matrices were combined in a stochastic model to compare estimates of the stochastic growth rate of each species under three different demographic scenarios (observed, improved and optimistic, see below). In a stochastic projection, at each time step one matrix is randomly chosen from the established set and used to generate a new population vector serving as the starting point for the next time step. Thus an element of stochasticity is incorporated into population growth estimates, simulating variation in environmental conditions through time (Caswell 2001). The resultant value of λ provides an estimate of stochastic population growth – the rate of growth that would occur according to the random draw among matrices representing varying environmental conditions (Caswell 2001). By modifying the weight of each matrix, the probability that a given matrix will be selected via random draw will change through time. In desert systems, only ~10% of years may be "favorable" so random selection of the matrices could be constrained to limit selection of the 2011 matrices (yielding the highest deterministic population growth for both species) to 10% of random draws. It was then possible to explore how growth responded to increasing the frequency of favorable years in the projection. A starting vector of 100 individuals was used in each stage class and population growth was projected for 100 time steps, given the observed range of demographic variation.

Weather patterns during 2012-2014 were fairly dry so the analyses were repeated using "improved" and "optimistic" transition rates to get a sense of how population growth might respond to improved rainfall events (e.g., more rain, earlier in the activity year). An optimistic scenario should be considered the "best possible case" and extremely infrequent, whereas an improved scenario is "better than existing" but occasional. A literature review uncovered germination rates for the congener *Eriophyllum lanosum*. An average seedling germination rate of 2.02% (range 0.03 - 3.83) for *E. lanosum* had been experimentally determined under "realistic" temperature and moisture conditions in the Sonoran Desert (Adondakis and Venable 2004). The authors substituted 3.83%, the high

end of the range identified for germination in *E. lanosum*, for the observed values of seedling emergence in a set of "improved" matrices. An "optimistic" set of matrices were then created using 3.83% as the emergence rate, coupled with a doubling of the highest seed output rate observed in the present field study. This matrix was applied across all sites and years.

2.2.4.6 Life Table Response Experiments

If population growth rates are affected by landscape features and climate, it is then possible to tease apart the relative contributions of these factors to variations in λ using Life Table Response Experiments (LTREs, Caswell 2001, Angert 2006). It is also possible to determine how sensitive variations in λ are to variations in life history traits that are represented by values in the transition matrices. LTREs assess the effect of individual matrices on λ by relating the contribution of matrix transition rates to variation in λ. The effect of an individual matrix on mean λ is obtained by summing transition elements for that matrix – the result is the sum of a_{ij} (transition element) contributions to variation in mean λ. When a transition element has a small effect on variation in mean λ, λ may not be sensitive to change in that particular element, or λ may be sensitive to the element but that element lacks substantial variation between matrices.

For each species LTREs were used to evaluate demographic differences between sites and years (Caswell 2001). In this approach, the contribution of transition rates for each individual matrix was compared to variation in mean λ obtained from a reference matrix. A reference matrix was generated by taking the mean of observed transition rates for all 18 year / site/ habitat type combinations for ERIMOH (Table B8), and for all 21 year/site/habitat type combinations for ERIWAL (Table B9). The authors chose to take the mean of the set of matrices rather than building a pooled reference matrix from the raw data because they lacked certain aboveground data (in 2012 across all ERIMOH sites, and in 2013 and 2014 for certain site / habitat type combinations). LTRE's were also used to decompose contributions of matrix values (e.g., seed output, seed survivorship) in each habitat type to variations in mean λ.

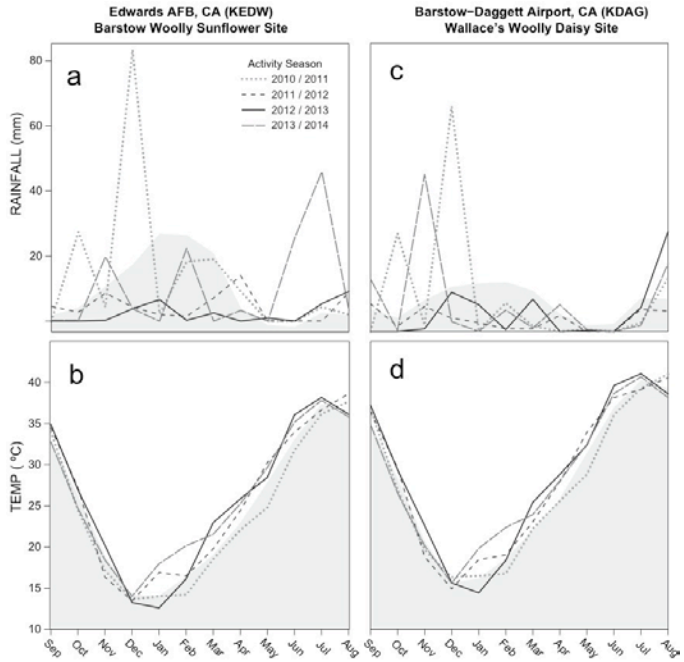
Elasticity, a proportional measure of sensitivity that accounts for differences in scale of survival and fecundity rates (survival is constrained to a value between 0 and 1, while fecundity can be > 1) was also analyzed. Elasticity identifies which small changes in individual rates would result in the largest changes to λ.

2.3 Results

2.3.1 Yearly Variation in Climate

Rainfall was highly variable between years with dramatic differences in late fall / early winter rainfall received during 2010-2011 compared to 2011-2012 and 2013-2014 (Figure 2.5). Precipitation records from Edwards AFB (KEDW) and Barstow-Daggett Airport (KDAG) stations showed unusually high rainfall in October and December of 2010. Rainfall at both stations was much lower than average from December through March of 2011-2012 and 2012-2013.

Figure 2.5: Rainfall and Temperature Patterns 2011-2014



(a) Rainfall and (b) temperature at Edwards AFB (KEDW). (c) Rainfall and (d) temperature at Barstow-Daggett Airport (KDAG), summarized for 2011-2014 activity years. Patterns of mean precipitation and temperature for the fifty-year period 1964-2014 are shown in gray.

2.3.2 Population Responses to Landscape and Climate

The patchy distributions of the two focal species coupled with landscape and climatic variability inherent to desert systems, produced the expected high variance in population responses.

2.3.2.1 Population Densities

2.3.2.1.1 Barstow Woolly Sunflower

The population density of ERIMOH varied widely from 2011-2014, in apparent response to timing and quantity of rainfall (Figure 2.6) as well as the influence of landscape features (comprising broad, rill and divot habitats). The data set was broken down by year, site, and habitat type.

Figure 2.6: Barstow Woolly Sunflower Habitat in 2011 and 2012

Photos taken during peak flowering (~March) at ERIMOH Site 1 in 2011 and 2012. Note the flowers in broad habitat and concentration around the divot habitat in 2011 (with complete absence from broad and divot habitats in 2012).

Photo Credit: (left) Alison Stanton 2011; (right) Karen Tanner 2012.

There were significant effects of year and site on population density of ERIMOH within the broad habitat that generally tracked trends in precipitation (Year: deviance = 15.814, d.f. =1, P<0.0001, Site: deviance 14.948, d.f. =2, P<0.0006, interaction NS). Density in the broad habitat was highest in 2011 and zero in 2012, with very few occupied plots in 2013 (Figure 2.7). Density values for broad habitat in the 2012 and 2013 years were not included in statistical analyses (in 2012 no plants emerged, and in 2013 sample size was too low to test for differences).

Differences in density of ERIMOH were observed within the divot habitat when comparing 2013 and 2014 (Figure 2.7), but significance tests were not conducted because these plots were established non-randomly. The highest densities of ERIMOH in the rill habitat occurred in 2014 (Figure 2.7), but again significance testing was not done because these plots were established non-randomly.

2.3.2.1.2 Wallace's Woolly Daisy

Population densities of ERIWAL varied widely during 2011-2014, but plants were produced from the seed bank every year.

There was a significant effect of year on ERIWAL population density in broad habitat (Year: deviance = 44.191, d.f. =2, P<0.0001, Site and interaction NS). Density in the broad habitat was highest during 2014 (Figure 2.7) and did not differ significantly between

sites within each year (Site 4 plots were established non-randomly and were not included in tests of significance). During 2012 only a single randomly located plot (out of 149 total) was occupied by ERIWAL.

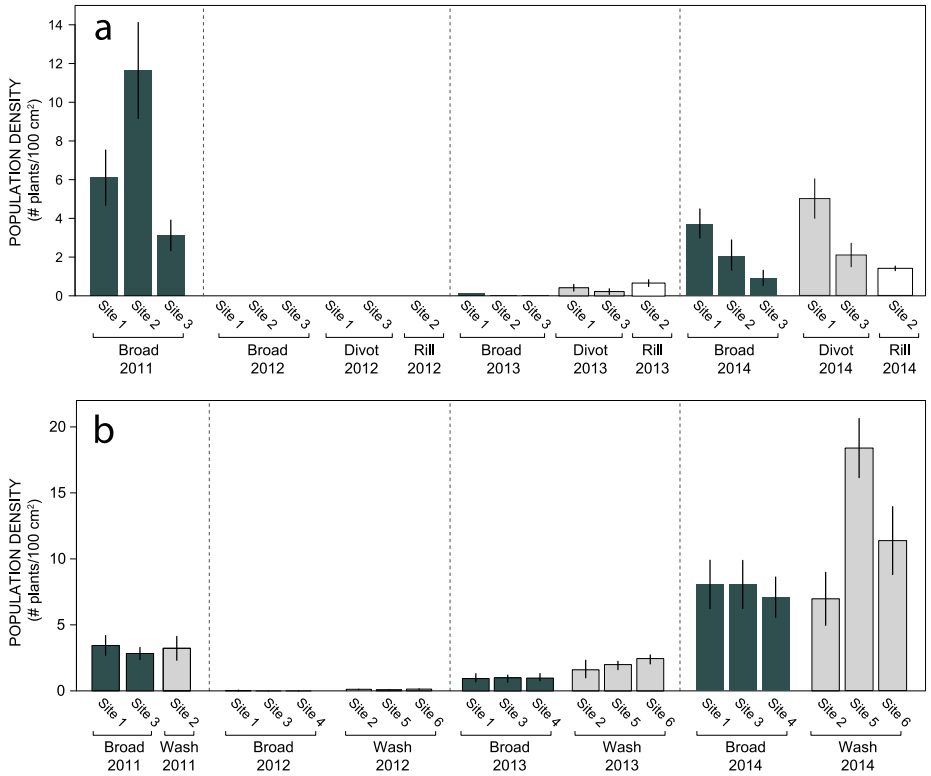
There were substantial differences across ERIWAL population density in the wash habitat across years, and between some sites (Figure 2.7). The wash plots were occupied during 2012, but when scaling densities to 10 x 10 cm^2 the values became very low. Density in the wash habitat was highest in 2014.

2.3.2.2 Survivorship to Reproduction

2.3.2.2.1 Barstow Woolly Sunflower

Survivorship to reproduction of marked ERIMOH plants fluctuated widely during the 2012-2014 study period in apparent response to rainfall and the influence of landscape features (comprising broad, rill and divot habitats) (Figure 2.8). During 2012 no plants emerged at any of the ERIMOH sites. During 2013 the broad habitat supported few plants and none survived to adulthood. By contrast, greater numbers emerged during the same year in divot and rill habitats and ~50% survived to adulthood. During 2014, conditions appeared to be less favorable across all habitats, and fewer than 20% of marked plants survived to reproductive stages. Survivorship was again lower in the broad habitat compared to the divot and rill habitats.

Figure 2.7: Density of Barstow Woolly Sunflower and Wallace's Woolly Daisy by Habitat, Year, and Site



(a) Responses of ERIMOH population density. During 2012 density was zero in all plots. During 2013 only four broad habitat plots had non-zero counts. Bars are ± 1 standard error. (b) Responses of ERIWAL population density. Note the different y-axis scales. Bars are ± 1 standard error.

2.3.2.2.1 Wallace's Woolly Daisy

With few exceptions, survivorship of ERIWAL was much higher (generally 60-80%) than observed for ERIMOH (10-50% at best) (Figure 2.8). But during the exceedingly dry 2012 no ERIWAL seedlings emerged in broad habitat plots at Site 3, and survivorship to reproduction in the broad habitat plots at Site 1 was the result of single individual. Nevertheless, many seedlings emerged and survived in broad habitat plots at Site 4. No plants were observed in wash habitat plots at Site 2 during 2012, but they were present at low density outside of established plots. More favorable conditions returned during 2014, with survivorship to reproduction ranging between 60 and 90%, except at Site 1.

2.3.2.3 Seed Output

2.3.2.3.1 Barstow Woolly Sunflower

A negative binomial general linear model was the best fit for the aggregated seed output from the broad habitat, revealing a significant effect of year only (Year: deviance = 15.288, d.f. =1, P<0.0001, Site NS; Figure 2.9). Broad habitat was excluded in 2013 from

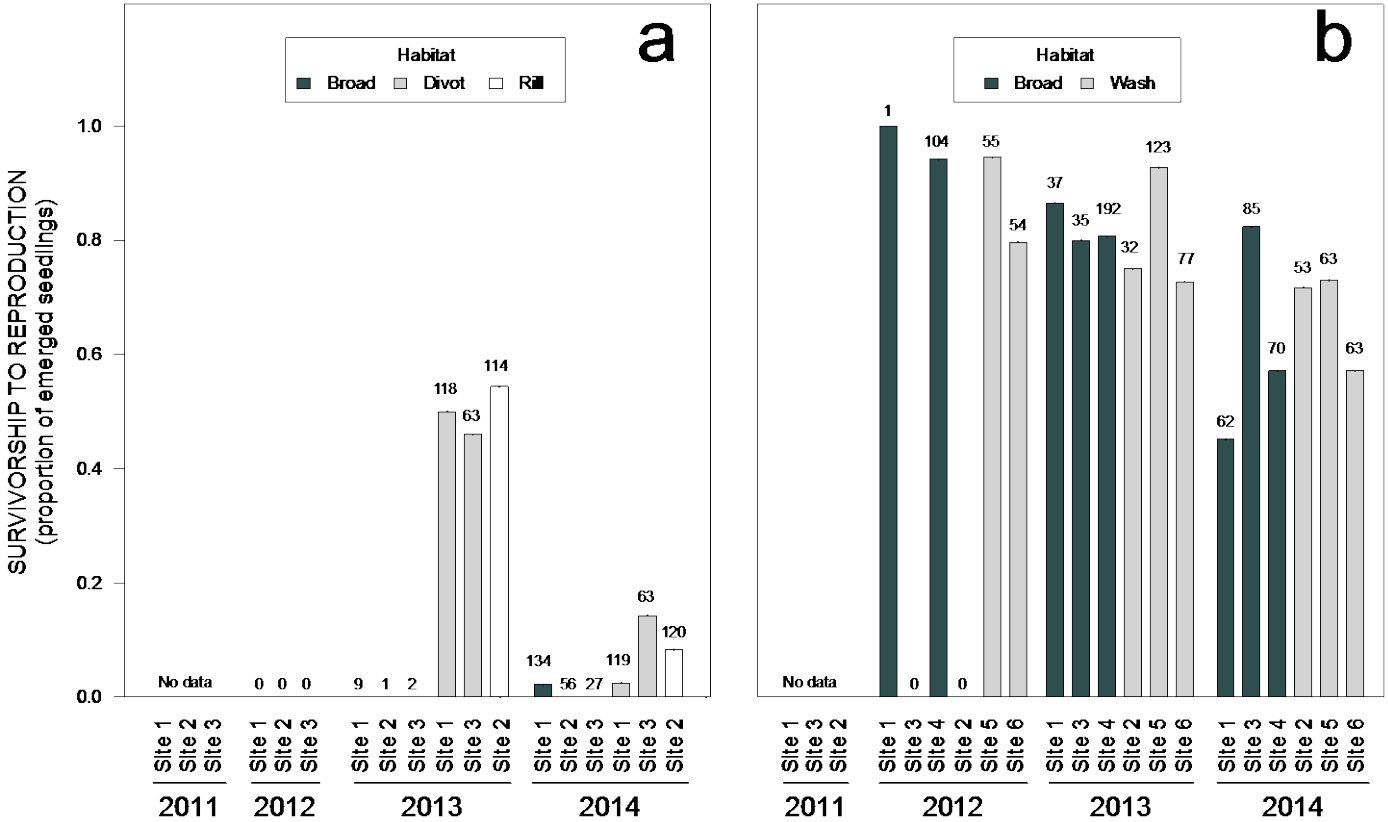
statistical testing due to low sample size (n=3). In 2011 weighted average seed output across all sites was 18.43 seeds per plant. Seed output during 2013 was much lower than observed in 2011, with mean output of ~1 seed per plant. Mean seed output in 2013 divot habitat was 0.35 seeds per plant, and output in rill habitat was 1.68 seeds per plant. It is unclear whether populations were pollen-limited (the breeding system is unknown as well), and differences in seed output within years cannot definitely be ascribed to a moisture limitation. Nevertheless, patterns of seed output within habitat types in 2013 may suggest relaxation of these constraints in divot and rill habitats.

2.3.2.3.2 Wallace's Woolly Daisy

A negative binomial general linear model was the best fit for the aggregated seed output from the broad habitat, revealing significant effects of year, site, and their interaction (Year: deviance = 12.807, d.f. =3, P<0.006, Site: deviance = 7.599 d.f. =2, P=0.022382, Year*Site: deviance = 12.040, d.f. =3, P<0.008). In 2011, mean seed output per plant was 12.75 seeds in the broad habitat and 5.75 seeds in the wash habitat (Figure 2.9). In 2012 no plants emerged in broad habitat plots at Site 2 or 3, and only a single plant emerged at Site 1. A seed count was not obtained from this individual, and so the overall 2012 seed output in broad habitat was treated as zero. Mean output per plant in 2012 was 45.25 seeds in the broad habitat and 59.27 seeds in the wash habitat. During 2013, mean output per plant was 10.86 seeds in broad habitat and 14.71seeds in wash habitat. Mean output per plant in 2014 was 11.87 seeds in broad habitat, and 5.89 seeds in wash habitat.

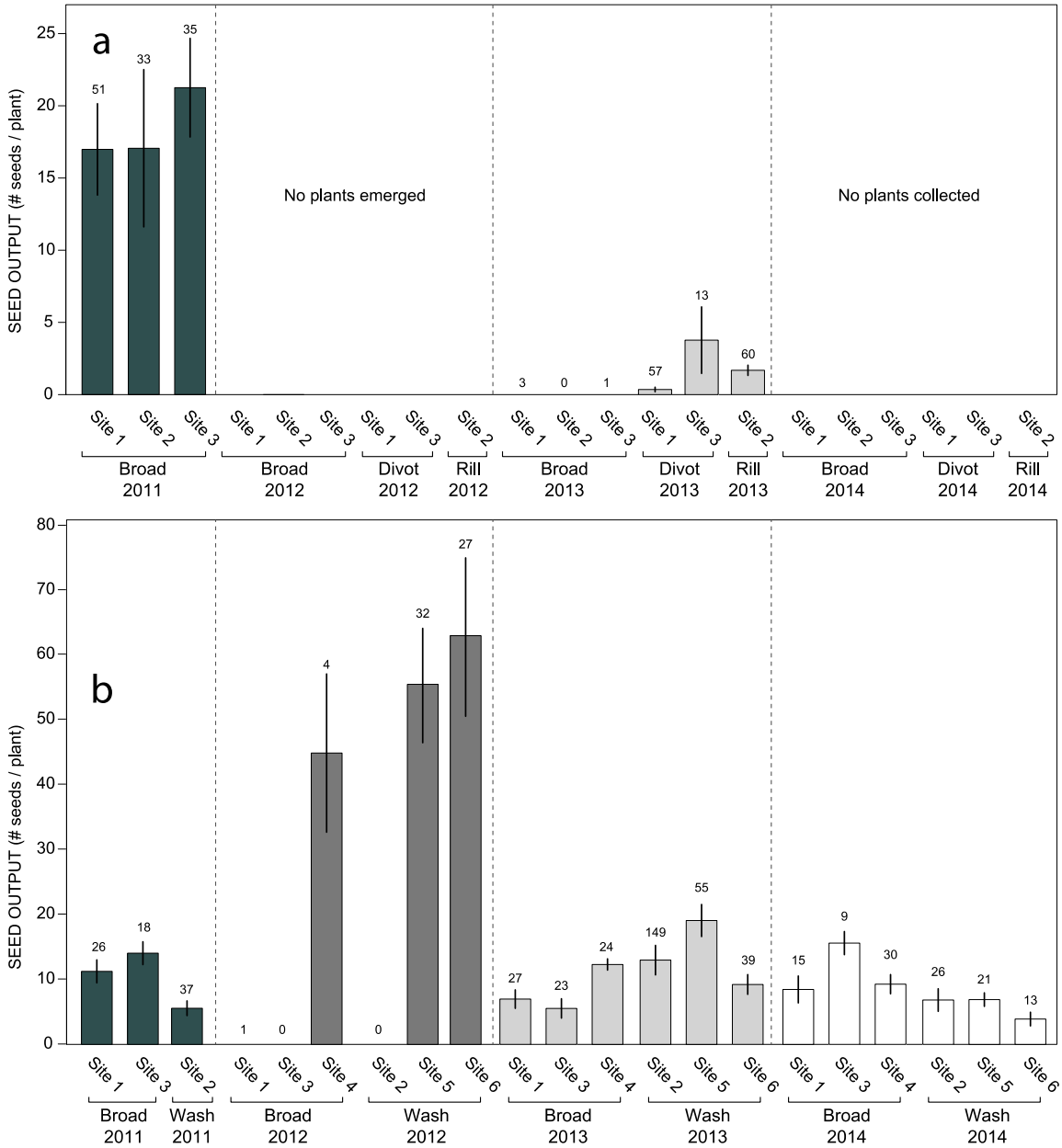
Patterns of seed output across sites varied by year within each habitat type (Figure 2.9), and the sites producing the most seed were not consistent from year to year.

Figure 2.8: Survivorship to Reproduction of Barstow Woolly Sunflower and Wallace's Woolly Daisy by Habitat, Year and Site



(a) Proportion of ERIMOH seedlings and (b) ERIWAL seedlings surviving to reproduction. Numbers above bars indicate marked plants monitored at each site. Zeroes indicate sites where no plants were present inside established plots. The study was initiated well after emergence in 2011, so there were no comparable estimates of survivorship from that year.

Figure 2.9: Barstow Woolly Sunflower and Wallace's Woolly Daisy Seed Output by Year, Site and Habitat Type



(a) Responses of ERIMOH seed output. Numbers above bars indicate number of plants collected for seed counts at each site. No plants emerged in 2012, and no plants emerged at Site 2 in 2013. Three plants emerged at Site 3 during 2013 but produced no seeds. No fruiting plants were collected during 2014 due to very low reproductive success. (b) Responses of ERIWAL seed output. A single plant emerged at Site 1 in 2012, but no seed count was obtained for this individual and assume a value of zero. No plants emerged at Site 2 or 3 during 2012. Bars are ± 1 standard error and numbers indicate sample size for seed output.

2.3.2.4 Seedling Emergence

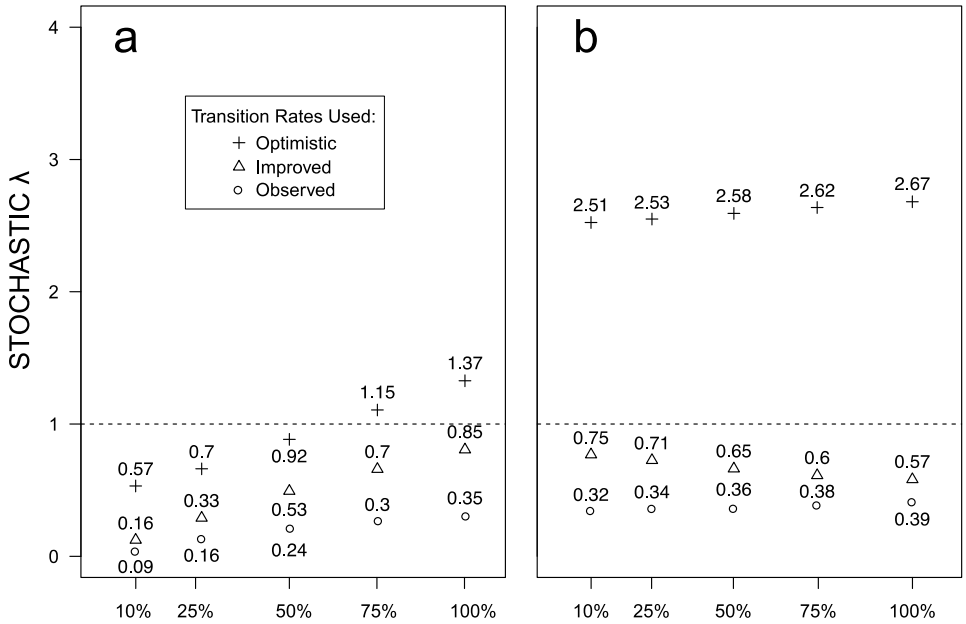
At all ERIMOH sites no seedlings emerged in 2012 or 2013, and less than one percent of seeds germinated and emerged as seedlings in 2014 (Table B6). At the ERIWAL sites no seedlings emerged in 2012, less than one percent emerged in 2013, and~1.8 percent emerged in 2014 (Table B7).

2.3.3 Modeling Population Growth

2.3.2.1 Barstow Woolly Sunflower

Only the optimistic matrices predicted increasing population growth ($\lambda > 1$), and only when the percentage of favorable years was greater than 50% (Figure 2.10). With selection of the favorable 2011 matrix occurring 50% of the time, population growth approached but did not attain stability (λ=.92). The 10% favorable years scenario most closely represents current climate conditions in the Mojave Desert, and it never predicted population growth regardless of which matrix was used.

Figure 2.10: Stochastic Growth Rates of Barstow Woolly Sunflower and Wallace's Woolly Daisy over a Century with Varying Proportions of Favorable (high, early rainfall) Years



a) Response of ERIMOH population growth (λ) to varying proportions of favorable years in a century. (b) Response of ERIWAL population growth (λ) to varying proportions of favorable years. The 10% column represents a realistic frequency of favorable years in CA deserts, and the 25% column an unweighted scenario (years 2011-2014 had an equal chance of being drawn at each time step in the projection). See Figures B1 and B2 for λ generated by deterministic matrices (the matrices used to generate this stochastic projection).

2.3.3.2 Wallace's Woolly Daisy

Projected population growth for ERIWAL was consistently higher than for ERIMOH, but no estimates from the observed matrix set predicted population increase (λ>1) (Figure 2.10). In the

25% scenario (equivalent to an unweighted projection, where all 4 years have an equal chance of selection at each random draw), population increases were only produced with the optimistic matrix.

2.3.4 Life Table Response Experiments

2.3.4.1 Barstow Woolly Sunflower

Conditions during 2011 had a positive effect on mean λ (Figure 2.11). Those in all other years had negative effects, with the magnitude order 2012 > 2014 > 2013. The direction and magnitude of these effects aligns with expectations (given the lack of aboveground activity in 2012) and the much lower survival rate of marked plants observed in 2014 compared to 2013. Patterns of response to interaction effects were similar to those observed for year effects.

Sensitivity analyses of the set of four by-year matrices show that population growth rate was most sensitive to variation in the modeled fecundity of 3-year old seeds (Table B10). For all year, site, and habitat matrices the most elastic rate was $\alpha 21$, survival of new seed to 2-year old seed, suggesting small increases in seed survival would have a disproportionate positive effect on λ.

2.3.4.2 Wallace's Woolly Daisy

Conditions during 2011 and 2014 had positive effects on mean λ while those in 2012 and 2013 had a negative effect (Figure 2.11). Responses to interaction effects were similar to those observed for year effects. Negative contributions from Site 2 during 2011 were likely a consequence of lower seed viability (Table B1) or seed output rates, as models for each site used the same rates for emergence and survival to reproduction. Site 5, the only site making a positive contribution to λ during 2013, had higher seed output rates as well as higher survival to reproduction than any other site in that year. During the 2014 year, Site 3 was the only broad habitat site exhibiting a positive effect on λ – again, this site had the highest survivorship to reproduction and seed output rates within the broad habitat. Low seed output at Site 6 in 2014 was probably responsible for the small positive impact of this site/year combination on λ.

Sensitivity analyses of the set of four by-year matrices show that the greatest sensitivity resided in the fecundity of 2-year old seed in 2011 and 3-year seed in all other years. For all year, site, and habitat matrices the most elastic rate was $\alpha 21$, survival of new seeds to 2-year old seeds, suggesting small increases in seed survival have a disproportionate positive effect on λ (Table B11).

2.4 Discussion and Management Recommendations for Renewable Energy

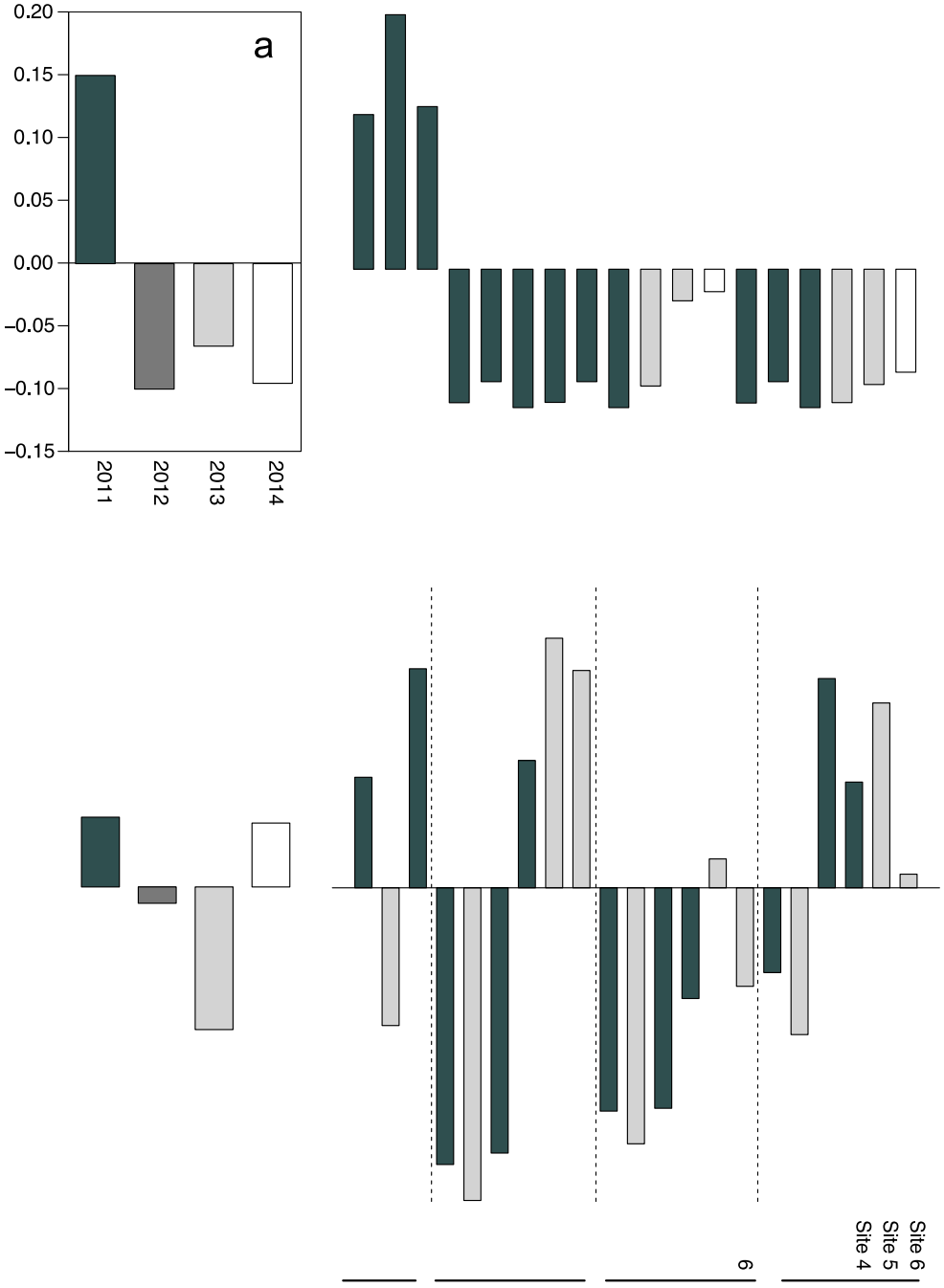
Our study compared the demography of two desert annuals, Barstow woolly sunflower (*Eriophyllum mohavense*, "ERIMOH"), a rare species, and Wallace's woolly daisy (*E. wallacei*, "ERIWAL"), a common congener. ERIMOH has very restricted distribution in California and is likely to be affected by solar energy development, whereas ERIWAL is widespread and unlikely to be seriously impacted. Survivorship and fecundity data were collected over a four-year period (2001-2014), allowing construction of matrix models comparing population performance

in relation to landscape features and climatic variation. This allows four major questions to be addressed.

2.4.1 Do closely related, rare and common annual species respond similarly to desert conditions, especially with respect to variations in landscape features and climate?

Despite similar morphology and developmental patterns, and a high degree of taxonomic relatedness, the two species exhibited very different demographic responses to variations in landscape and climate. ERIMOH is restricted to unusual terrace soils of unknown origin that form distinct islands surrounded by vast areas of unsuitable desert habitat (Figure 2.2). The terrace soils have low cover by perennial species (perhaps due to subsurface calcareous concretions, Beeler 1992) and have surface erosion that results in fine-scale, second-order landscape features termed rills and divots (Figure 2.6). ERIMOH occupies, and appears to rely heavily upon, rills and divots both to emerge (from the seed bank) and succeed (i.e., survive to reproduce) during years with marginal conditions (e.g., low or late winter precipitation, such as 2013 and 2014, Figure 2.7, 2.8 and 2.9). Rill and divot habitats, therefore, act as refuges for the rare ERIMOH, allowing completion of the life cycle in many more (less than favorable) years than would otherwise be possible. In contrast, the common ERIWAL is found on the alluvial soils typical of first-order landscape features (bajadas and washes) that are spatially extensive throughout the California deserts. There is no restriction to, or apparent use of, second-order landscape features and the species emerges and succeeds in almost every year (although with great variation in abundance and distribution).

Figure 2.11: Contributions of Year, Habitat Type, and Site to Variation in Population Growth (λ) of Barstow Woolly Sunflower and Wallace's Woolly Daisy



(a) ERIMOH life table response experiments by year, 2011-2014. (b) ERIMOH LTRE by site/habitat interaction effects. (c) ERIWAL LTRE by year effects, 2011-2014. (d) ERIWAL LTRE by site/habitat interaction effects. Contributions to lambda were estimated based on differences between site and year specific matrices and a mean matrix generated by averaging the 18 ERIMOH matrices or 21 ERIWAL matrices represent each species-specific year/site/habitat type combination.

The responses of these two species to climate variation are also distinct. ERIMOH appears to have a specialist "trigger" response that initiates the transition from seed to plant only when precipitation exceeds a critical minimum during the fall or early winter, conforming to the general model for winter annuals presented by Beatley (1974). Rainfall during fall of 2010 was much greater than usual, and the 83 mm received at nearby Edwards Air Force Base during December 2010 was the fourth highest month on record. Once triggered, this species was able to emerge and succeed in broad habitat on terrace soils in great numbers, as it did at all three sites during spring 2011 (Figures 2.7 and 2.9). Presumably, the seed bank is always present in broad habitat soils but remains quiescent in years without the trigger (e.g. 2012, 2013, 2014). Most germination and survivorship to reproduction in such years is confined to rill and divot habitats where small amounts of soil moisture collect, which produces low numbers of plants over a very small area. In contrast, ERIWAL has a generalized, almost proportional, response to rainfall that was more consistent across years. The fall 2010 rains did not trigger mass germination and reproduction events in either broad or wash habitats. The ERIWAL response in this year was quite moderate compared to ERIMOH. But unlike ERIMOH, ERIWAL was able to emerge and succeed, even during the extremely dry 2011-2012 activity year. ERIWAL density was low but individuals survived to output very large numbers of seeds in both habitats (Figure 2.9). Despite low densities in 2013, survivorship and seed output were significant. Late rains in February 2014 produced high densities of ERIWAL plants that reproduced well, but solicited only weak responses from ERIMOH and mostly in rill and divot habitats.

2.4.2 What are the expected population growth rates of closely related, rare and common annual species given different climatic scenarios projected into the future?

Regardless of which matrices (optimistic, improved, observed) were used to stochastically model population growth, the resultant values of λ for the rare ERIMOH were always less than those of ERIWAL (Figure 2.10). Only the optimistic matrix produced positive λ's for ERIMOH, and this outcome only occurred when the favorable climate scenario (such as conditions in 2010-2011) occurred more than 50% of the years in a century. From these results it seems unlikely that ERIMOH populations could sustain themselves under current or expected conditions. Values of λ that indicated stable or increasing growth of ERIWAL populations were achieved with all proportions of favorable years using the optimistic matrix (see below and Figure 2.10b). The exceedingly high value of λ achieved under current conditions (the 10% climate scenario) suggests that "boom" years (represented by the optimistic 2011 matrix) could compensate for lower growth rates in less favorable years, thus leading to long-term persistence of this common species.

Our models of population growth contain several sources of error that influenced the estimated values of λ, especially when the observed matrix was applied. First, the only year that appeared optimal for ERIMOH performance was 2010-2011. The study began in late winter 2011, possibly several months after emergence. Thus researchers were unable to measure emergence rate and survivorship to reproduction for that year and had to simply apply the best available rates for both species (those observed in other years). This could mean that lower rates were applied than what really occurred during 2010-2011, leading to lower values of λ. Secondly, the survivorship of 3+ year-old seeds in the seed bank was constrained to 0.01 out of practicality. It

is likely that seeds maintain viability for much longer periods than that, which would increase values of λ across the board. For example, if survivorship of 3+ year-old seeds is increased from 0.01 to 0.05, estimates of yearly lambda increase from 3 to 34% for ERIMOH and 2 to 5% for ERIWAL when inserted into the deterministic growth model using the observed matrices. Finally, the α_{11}, α_{12}, and α_{13} transition rates, which represent seed fecundity (i.e., the ability of a seed to produce more seeds), may have been overestimated because seed decay was not expressed as an exponential function (e.g., α_{12} would include (prob. viability) squared, α_{13} would include (prob. viability) cubed. The decision to simply use the (prob. viability) term was based on the absence of data on how emergence, survival and seed output would vary as a function of seed age. Seed survival and fecundity terms should also include a separate term for the proportion of germinated seeds that actually emerge as seedlings, estimated by germination of seeds in dormancy packets. In both of these cases values of λ would be overestimated. Nevertheless, these sources of error would affect both species in a similar manner, thus maintaining the integrity of this comparative study.

2.4.3 What are the environmental conditions (landscape features and climatic factors) that enable populations of rare and common species to grow and persist?

As would be expected for desert annuals, the amount and pattern of rainfall during the activity year contributed significantly to the performance of both species across the landscape. ERIMOH could only occupy broad habitat to any great extent during the 2010-2011 activity year (Figure 2.7), when the effect on λ was positive at all three sites (Figure 2.11a and b). Years such as 2013 and 2014 could allow emergence in broad habitat (Figure 2.7), but survivorship to reproduction (Figure 2.8) and seed output (Figure 2.9) were so low that the overall contribution to λ was always negative (Figure 2.11b). Rill and divot habitats could lessen the negative effects in these years, but population growth would nevertheless be inhibited. This means that seed banks in refuge habitats do not completely make up for the losses in unfavorable years (but still allow some compensatory seed bank replenishment compared to those in the broad habitat). Thus, the extirpation of the ERIMOH seed bank is delayed by the presence of rill and divot habitats, increasing the probability of encountering another favorable year when λ becomes positive and seed bank replenishment finally takes place (perhaps accentuated by dispersal of seeds from broad habitat into rills and divots). This appears to be a tenuous life history "strategy", especially if climate change or altered surface runoff (due to development impacts) decrease the occurrence of years that produce the trigger response (i.e., below 10% of years in a century).

The situation with ERIWAL was very different. In three of the four years (2011, 2012, 2014), this common species could occupy broad habitat with positive contributions to λ found in at least one site (Figure 2.11d). The same is true for the wash habitat, although the years with positive contributions to λ were different (2012, 2013, 2014). Taken together, these habitats contributed positively to λ in all four study years, even when two years (2012 and 2013) had a negative effect on λ (Figure 2.11c). Therefore, two of the four years had positive effects on λ across all sites and habitats, indicating a more consistent ability to maintain population growth. Being able to occupy widespread, "general" habitats such as bajadas and washes nearly guarantees population growth in most years, even those with very low rainfall. It is unlikely that climate change or development would have immediate negative effects on a species such as ERIWAL.

2.4.4 What are the life history traits that enable populations of rare and common species to grow and persist?

The ability of a population of annuals to grow and persist under desert conditions has little to do with the tolerance limits of established plants and everything to do with the fates of seeds in the seed bank. Sensitivity analyses performed on matrices of both ERIMOH and ERIWAL suggest that small increases in seed survival in the seed bank have disproportionate, positive effects on λ (Tables B10 and B11). The converse would also be true – decreased seed survival due to predation (e.g. by ants, birds, rodents), dispersal into poor habitat or anything that decreased viability through time, would lead more rapidly to extirpation than impacts on other life history stages. This is one of the only demographic similarities between these two species, driven by the bet-hedging strategy common to all annuals – investments in the underground life of the seed bank outweigh (in selective value) investments in the aboveground traits commonly observed after emergence.

2.4.5 What are the management recommendations, derived from answers to the previous questions, regarding in situ conservation of rare desert annuals such as ERIMOH during construction and operation of renewable energy facilities?

1. **Field surveys for the occurrence, distribution and abundance of rare annual species such as ERIMOH must occur in multiple years in hopeful anticipation of making observations during favorable, less than favorable and unfavorable years.** Without a full range of survey years, the essential relationships between population performance and very subtle landscape features and environmental triggers will most certainly remain undetected so that management actions may not be adequate to conserving these kinds of plants. When this comparative study was begun there was no idea that rill and divot habitats existed, let alone were demographically significant with respect to ERIMOH populations. It will thus be necessary to train people conducting surveys for annuals to anticipate, observe, and record such relationships as hypotheses for additional, detailed studies.

2. **Surveying the seedbanks of annuals, where seeds survive in the soil for many years, is as important as surveying for active, aboveground plants.** Modeling confirms that persistence of rare species such as ERIMOH is achieved by the abundance and longevity of seeds in multiple microhabitats. Consequently, once an aboveground population is located it can only be used to roughly approximate the fine-scale distribution of a population. That distribution can move (or appear to move) in response to yearly and spatial climatic variations because seedbanks are potentially present throughout a large area and germination occurs only where conditions are favorable. Surveying seedbanks is necessary to identify which areas need protection. The researchers acknowledge that methods for surveying seedbanks are laborious but argue that avoidance based solely

upon aboveground plants will have unintended impacts on persistence of the target species.

3. **The islands of terrace soils that restrict the distribution of ERIMOH are an essential component of habitat, providing unique, small-scale erosional rills and divots, which allow some level of population performance under less than favorable climatic conditions.** It is also likely that these soils have unique chemical and physical properties that exclude perennial plants and somehow facilitate ERIMOH persistence (perhaps through reduced competition and/or allowance of erosional processes). Therefore, field surveys for development must identify and map these islands, even if currently unoccupied by the species. These studies have not investigated the potential for metapopulation dynamics of ERIMOH with respect to occupied and unoccupied islands of terrace soils.

4. **Avoidance is the best possible mitigation strategy when subtle relationships between an annual species and its habitat are suspected.** It seems highly unlikely that the requirements of another annual species that are as subtle as those found herein could be understood, much less mitigated for, or replicated. Transporting a sensitive, specialized species out of harm's way and on to off-site, unoccupied habitat by redistributing the seedbank-containing "topsoil" is unproven in arid environments. Where avoidance cannot be done completely, preservation of topographic complexity within installations with sensitive designs (such as the impact minimization "halos" around individual rare plants at ISEGS) and construction methods should be employed.

5. **Despite similar morphology and developmental patterns, and a high degree of taxonomic relatedness, the two species of *Eriophyllum* studied herein exhibited very different demographic responses to variations in landscape and climate.** Therefore, there is very little one could predict about the behavior of the rare species from the behavior of a closely related common species for purposes of meaningful conservation, restoration or site management. This reinforces the hypothesis that rare species are idiosyncratic (Fiedler 1986, 1987), with unique characteristics that will require individualized approaches to their conservation.

6. **If a proposed site for solar development had populations of ERIMOH, and/or islands of terrace soils, there would be a very low probability that mitigation (on-site and off-site) or restoration would be successful.** This is because any level of disturbance to second order landscape features, such as rills and divots, would alter runoff patterns and hydrological conditions essential to performance of this species in mediocre climate years. Even footprints are enough to disturb these subtle features and care was taken during this fieldwork to minimize such impacts.

7. **Decreased seed survival due to granivory (especially by rodents) in altered trophic systems may be a concern for the persistence for species such as ERIMOH that have strong reliance on the seedbank.** Predator-prey relationships that keep granivore populations in check may not operate as effectively within installations because of human presence, fencing and constructed facilities. Populations of rare annuals such as ERIMOH that are avoided during construction and operation of an installation may be subject to increased seed mortality, leading more rapidly to extirpation. Conversely, increased dispersal of seeds because of granivore activity (e.g., "lost" caches) may be beneficial, but there are no studies in relation to developments on the scale of a solar installation.

CHAPTER 3:
Field surveys for two rare annual plants: *Mimulus mohavensis* and *Mentzelia tridentata*

3.1 Introduction

Current efforts to understand the potential impacts of energy development on rare desert plants began with the selection of eight species with different life history characteristics. Along with woody shrubs, stem succulent cacti, and herbaceous perennials, three rare and one common annual species (*Mentzelia tridentata, Mimulus mohavensis, Eriophyllum mohavense,* and *E. wallacei*) were included. Multiple annuals were chosen because it was not known at the onset which of these ephemeral species would yield sufficient demographic data for population viability modeling during the four-year study period. This study was only able to obtain survivorship and fecundity data on the two *Eriophyllum* species (see Chapter 2). Nevertheless, considerable effort was expended gathering data on *Mentzelia tridentata* ("MENTRI") and *Mimulus mohavensis* ("MIMMOH") at multiple sites in the two years that plants emerged (2011 and 2014). MIMMOH is proposed for regulatory coverage under the Desert Renewable Energy Conservation Plan (DRECP), a joint effort of four state and federal agencies. Plants of both species are small in size, suggesting they may be able to persist underneath installations within energy project sites if avoided during construction activities. Although it was not possible to conduct population viability modeling and determine extinction threshold probabilities, the report herein summarizes the available data on these two annual species, laying a foundation for further conservation studies that may be required in the future.

3.2 Methods

3.2.1 Study Species

3.2.1.1 Mimulus mohavensis

Mimulus mohavensis (Lemmon), Mojave monkeyflower, is a member of the lopseed family (Phrymaceae), but formerly included the figwort family (Scrophulariaceae (Beardsley and Olmstead 2002). It is a distinctive member of the genus that was previously placed in its own section (Beardsley et al. 2004). MIMMOH is a small annual plant that grows from 2 to 10 centimeters high with purplish-red stems and leaves that are covered with minute glandular hairs (Figure 3.1). The unique corollas are distinguished from other species by five spreading maroon lobes that fade into white margins with a tube throat that appears as a black hole (Baldwin et al. 2012). Another common name is Black hole monkeyflower.

MIMMOH is designated by the Bureau of Land Management (BLM) as a BLM Sensitive Species and was formerly on the ESA candidate list, but was removed in 1996 because it was more widespread and abundant that previously thought (Fed Reg 1996). The global element rank is G2 (NatureServe 2010) and the State element rank is S2.2 (CDFW 2014). The California Native Plant society ranks MIMMOH as a CRPR 1B.2 species (rare, threatened, or endangered in CA and elsewhere, 20 to 80% of occurrences threatened).

Figure 3.2: The Mojave Monkeyflower, *Mimulus mohavensis*

Photo credit: Bruce Pavlik (2012)

The species is found in Joshua tree woodland and creosote bush scrub communities within an elevation range of 600 to 1,200 meters (Baldwin et al. 2012). MIMMOH primarily occurs on granitic soils on the gravelly banks of desert washes and along rocky slopes above washes, but may also be found in sandy openings between creosote bushes (McKay 2006). Common species is these communities include creosote bush (*Larrea tridentata)*, desert senna *(Senna armata),* cheese bush *(Hymenoclea salsola),* rattany *(Krameria* sp.), cholla *(Opuntia* sp.), burro bush *(Ambrosia dumosa),* indigo bush *(Dalea* sp.), cat-claw acacia (*Acacia greggii),* Bigelow's monkeyflower *(Mimulus bigelovii),* desert bells *(Phacelia campanularia)*, and desert trumpet *(Eriogonum inflatum).*

3.2.1.1 Mentzelia tridentata

Mentzelia tridentata (Davidson), creamy blazing star, is a rare annual forb in the Loasa family (Loasaceae). MENTRI is 10-25 cm tall with several, spreading to erect, pubescent herbaceous stems arising from a single root (Baldwin 2012; Figure 3.2). Each individual produces one to many light yellow to cream colored flowers, which produce a single capsule with multiple seeds. Flower and fruit production are variable, and heavily dependent on water availability during late winter and early spring.

MENTRI is endemic to California with most populations in San Bernardino County. The global element rank is G2 (NatureServe 2010), but it has no State element rank. The California Native Plant society ranks MENTRI as a CRPR 1B.3 species (rare, threatened, or endangered in CA and elsewhere; < 20% of occurrences threatened).

Figure 3.2: The Creamy Blazing Star, *Mentzelia tridentata*

The red object is a seasonal marker for these individuals and is about 2 cm across.
Photo credit: Alison Stanton (2011).

MENTRI is found in creosote bush scrub communities within an elevation range of 600 to 1,200 meters (Baldwin et al. 2012). MENTRI primarily occurs on the gravelly banks of desert washes and also on steep metamorphic rocky slopes above washes. Common species is these scrub communities include creosote bush (*Larrea tridentata)*, cheese bush *(Hymenoclea salsola),* burro bush *(Ambrosia dumosa)* with a diversity of herbaceous vegetation occurring in the bottoms of the washes.

3.2.2 Study Sites

3.2.2.1 Mimulus mohavensis

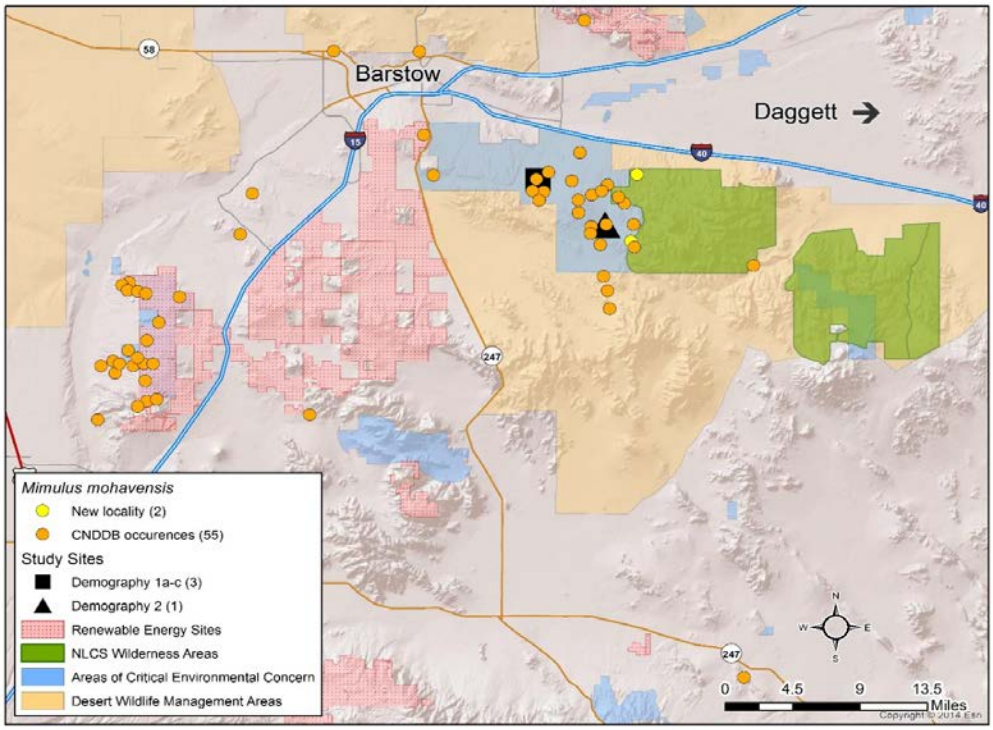
There are a total of 57 California Natural Diversity Database (CNDDB) occurrences recorded for MIMMOH (Figure 3.3). Of these, five occurrences were historical records dating from 1906 to 1952, and another four were from the 1980's. All nine are considered possibly extirpated (CNDDB 2014). An extensive survey effort in 1992 added 21 records from northeast of Adelanto extending to Helendale, and another survey in 2010 added 14 records from south of Daggett and Barstow to Ord Mountain. A total of 47 records have been recorded in the CNDDB since 1990 and are presumed extant. Of these, approximately 89% (42 occurrences) are on BLM lands, and the ownership of the other five occurrences is private or unknown. A majority of occurrences on BLM lands are contained within two separate Areas of Critical Environmental Concern (ACEC). However, wind energy development is not precluded in ACECs in California (BLM Instruction Memorandum #2009-043 -Wind Energy Development Policy). Five or fewer occurrences are protected in the Natural Landscape Conservation System (NLCS) wilderness area.

A concentration of occurrences in the Newberry Mountains near Daggett was selected as the focal point for establishing a study site. Occurrences farther west were excluded to reduce travel time and future studies should establish plots in those populations. Beginning in February 2011, known occurrences were visited in the vicinity of Camp Rock Road, approximately 10 miles east of Barstow, CA. Plants were apparently active only during the spring seasons of 2011 and 2014, because none were found when thorough searches were conducted in 2012 and 2013.

During April 2011, two study sites were established in the vicinity of Camp Rock Road. Sites were described using the California Native Plant Society-California Department of Fish and Wildlife (CNPS CDFW) combined vegetation rapid assessment and relevé field survey form. Total vegetation cover at the sites was generally less than 15%. Prevalent species in the shrub layer included *Larrea tridentata, Ambrosia dumosa, Ephedra nevadensis,* and *Hymenoclea salsola.* Herbaceous cover included *Amsinckia tessellata, Vulpia octoflora, Salvia columbariae, Eriophyllum wallacei,* and *Eriogonum* sp.

Site 1 was comprised of three clusters (1a, 1b, 1c) of MIMMOH individuals located within a short distance of each other. These occurred at an elevation of 850 m, within an undulating, sandy wash. Plots were installed on southwest facing slopes of varying steepness (1-5˚). The geology is volcanic and sedimentary in nature and surrounding soils consist of loamy sands that are coarse in texture. The main form of disturbance in the area was light erosion from storm runoff.

Figure 3.3: Location of Demographic Study Sites for the Mojave Monkeyflower Within the Species' Known Distribution.



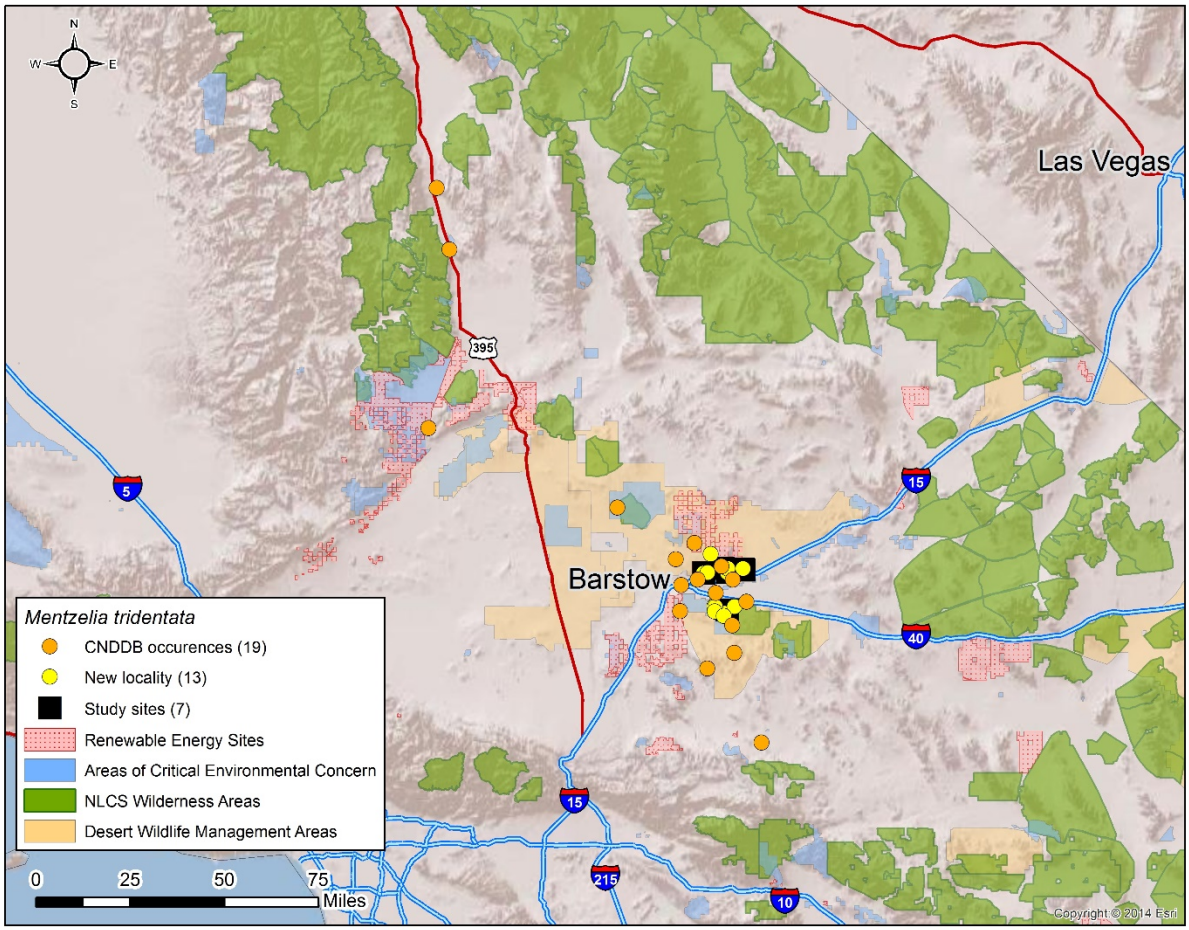
Occurrences are in protected areas and in potential renewable energy projects (Mojave Water Agency, *Renewable Energy Projects May 2014*).

Site 2 was at an elevation of 1040 m in a concave, sandy wash area. The plot was installed on a southwest-facing slope of roughly 15˚. The geology is sedimentary, and surrounding soils are sand with a moderately coarse texture. The main forms of disturbance in the area are moderate erosion from storm runoff and nearby OHV roads.

3.2.2.2 Mentzelia tridentata

There are only 32 known CNDDB occurrences of MENTRI (CGFG 2014) (Figure 3.4). The majority of populations occur in the lowest slopes of the Calico and Newberry Mountains, in San Bernardino County in the central Mojave Desert. The northernmost occurrence in Kern County is unverified and based on a 1930 herbarium specimen. At least 12 other occurrences are also based on old herbarium specimens from before 1970. However, surveys during 2011 and 2014 documented MENTRI at 12 new localities and suggest that within its narrow range, the species may be more common than previously documented (Moore and McIntyre, in press).

Figure 3.4: Location of Demographic Study Sites for the Creamy Blazing Star within the Species' Known Distribution.



Occurrences are in protected areas and in potential renewable energy projects (Mojave Water Agency, *Renewable Energy Projects May 2014*).

While the status of many MENTRI occurrences is unknown, some occurrences on BLM lands are contained within ACECs that may be subject to conversion to wind energy (BLM Instruction Memorandum #2009-043 - Wind Energy Development Policy). Fewer than four occurrences are protected in NLCS wilderness.

During April 2011, six study sites were established near the town of Yermo, about 13 miles east of Barstow. Sites were described using the CNPS CDFW combined vegetation rapid assessment and relevé field survey form. Total vegetation cover at the sites was generally less than 10%. Prevalent species in the shrub layer included *Larrea tridentata, Ambrosia dumosa,* and *Hymenoclea salsola.* Herbaceous cover included *Amsinckia tessellata, Vulpia octoflora, Chaenactis carphoclina, Cryptantha sp.* and *Eriogonum* sp.

Demographic Sites 1, 2 and 3 were located on the eastern slope of the Calico Mountains, near the entrance of Sunrise Canyon, at an elevation of 650 m. Demographic Site 4 occurs on the southeast face of a volcanic hill, northwest of Lead Mountain (elevation 675 m). Demographic Sites 5 and 6 occur on the south slope of the Calico Mountains, at the entrance of Mule Canyon (Site 5) and Odessa Canyon (Site 6) at elevation 670 m. Demographic Site 7 was found in February, 2014 and was installed on the steep west facing slope of the wash that parallels Camp Rock Road (elevation 866 m).

Plots were installed primarily on south facing banks along deep washes in dry, well-drained soils that are typically composed of fine erosional sediment overlaid by cobble sized rock (Figure 3.5). Soils are metamorphic, have poorly developed organic layer, and are composed primarily of alluvial outwash. The main form of disturbance in the area was light erosion from storm runoff.

Figure 3.5: Demography Site 1 for the Creamy Blazing Star, *Mentzelia tridentata*

Photo credit: Alison Stanton (2012)

3.2.3 Field demography

3.2.3.1 Mimulus mohavensis

The first year of sampling occurred during spring 2011. A minimum of 30 marked individuals per site was required, so plot locations were selected according to population density. But at Site 2, the MIMMOH population consisted of only 28 individuals so all were marked for study. A larger population at Site 1 required a selection process. Individuals were selected by their proximity to a predetermined, random point. From this point, one grid plot of 1250 x 250 cm, 900 x 500 cm, or 700 X 250 cm was established for each of the clusters (a-c), respectively. Random points within the grid were selected using an iterative process. MIMMOH individuals

situated nearest these random points were marked until 30 individuals had been selected. The total number of MIMMOH individuals within 50 x 100 cm quadrats was counted to obtain a density estimate for each cluster. Quadrats were placed every 100 cm on the longest transect so the density estimate sample size ranged from 7-12 quadrats.

Early in the season (April 15- 26, 2011), plant height (cm) and the number of reproductive structures (buds, flowers, fruits) were recorded. Fruits were collected later in the season (May 3-16, 2011). Two to three fruits were collected per individual if possible, depending upon plant size and vigor. Because of the small size of the plants and indistinctness of the reproductive structures, a fruit was identified as a flower possessing an intact, senescing corolla. Fruits were dissected in the laboratory to obtain seed counts. A total of four MIMMOH seed dormancy packets were constructed that had a grid of six cells with four seeds per cell for a total of 24 seeds per packet. Packets were buried in May 2011 and exhumed the following May.

Sites were searched again in April of 2012 and 2013, but no plants were observed. In April 2014, 14 plants were found and marked at Site 1c.

3.2.3.2 Mentzelia tridentata

The first year of sampling occurred during spring 2011. A minimum of 30 individuals per site was required. Sites 1, 2 and 3 were installed on March 30, 2011 and Sites 4 and 5 installed on April 14. Site 6 was installed on April 28-29 during the full count of reproductive structures for the other five sites. Final fruit counts were completed on May 6. At all sites, MENTRI individual plants were marked with small red markers (Figure 3.2) and the total number of reproductive buds, open flowers, or fruits was tallied for each and plant height measured (cm). From 40 to 70 fruits were collected from each site and dissected in the lab to obtain seed counts per fruit.

At sites where MENTRI densities were high, baseline transect grids were installed at the base of the slope. To select 50 to 60 individuals, grid points on the baseline were selected using a random number generator and the nearest plant was marked. The process was repeated if necessary. At Sites 2 and 6 all MENTRI plants present were marked. At Sites 3 and 5, MENTRI plants were on very steep (>45° and > 50m high) slopes where it was not possible to access plants on the higher portions of the slope without causing a scree avalanche that would damage plants below. Therefore, 25 plants each were marked in two discreet and accessible clusters.

Sites were searched again in April of 2012 and no plants observed. In 2013, four MENTRI plants were found at Site 6, but this was insufficient for demographic study. During February 2014, a total of 76 MENTRI were marked at four sites. Most plants were already reproductively active at the time of initial monitoring. Between five and 15 MENTRI were marked on February 22 at sites 1, 2 and 3. Only two plants were found at Site 4 and one at Site 5, and these were not checked again. On February 26, 40 MENTRI were discovered and marked at Site 7 and all were reproductive. Plant height and two width measurements of the rosette were recorded. Fruit counts were conducted on March 13.

3.3 Results

3.3.1 Field demography

3.3.3.1 Mimulus mohavensis

In the four years of this study, MIMMOH plants only emerged in sufficient numbers during April 2011. Density at Site 1c appeared to be two times higher than Sites 1a-b (Table 3.1), but the standard deviation among plots was very high and it was not significantly different (Tukey Kramer HSD α=0.05). For sites 1a-c, the highest observed density in the 0.5-m^2 quadrats was 28 plants, the lowest was 0 and mean density was 10.6 plants/m^2. Only 28 plants were present at Site 2 so no density estimate was possible. Sites were also searched in 2012 and 2013, but no MIMMOH were observed. During 2014, 14 MIMMOH were found and marked at Site 1. Measured MIMMOH plant height ranged from 0.4 to 4.2 cm and average plant height was very similar at all four sites and across years.

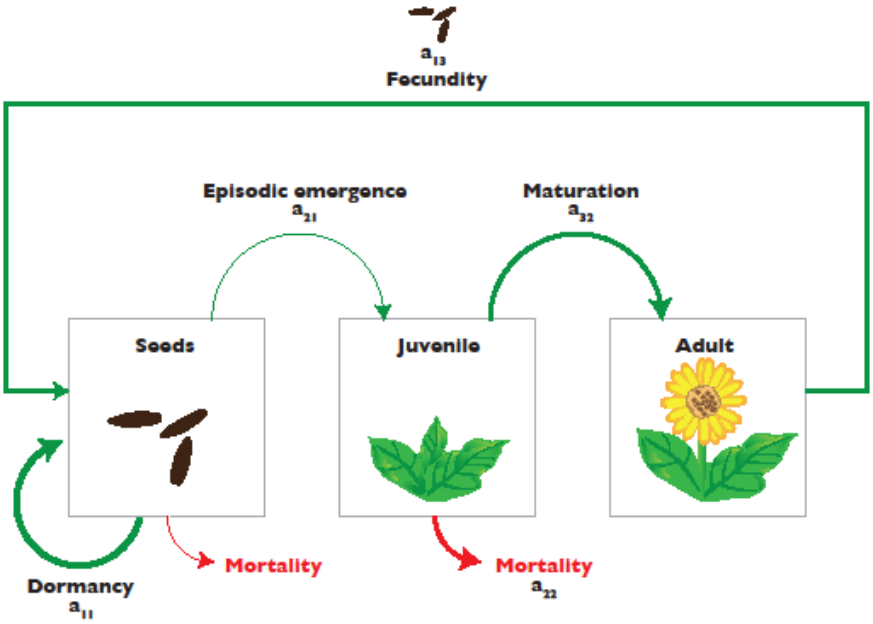
Table 3.1: MIMMOH Density Estimates and Plant Height at Four Study Sites from 2011 to 2014

Year	Site	macroplot size (m^2)	# marked plants	# density quadrats	mean density (plants/m^2)	*s.d.*	mean plant height (cm)	*s.d.*
2011	1a	30	30	12	6.3	7.6	2.2	1.1
	1b	45	30	9	8.9	13.1	2.3	1.1
	1c	17.5	30	7	20	16.7	2.2	0.7
	2	na	28	na	na		2.5	0.9
2012	all		0		0			
2013	all		0		0			
2014	1c	na	14		na		2.2	0.6

Na = data not available

During the surveys of spring 2011 and 2014, all marked plants were already adults, with reproductive structures present in the form of buds or flowers. This meant that demographic events leading to this stage were not measured. Therefore, researchers were unable to obtain estimates of the transition rates between seed, juvenile and adult life stages (Figure 3.6). Without following the fates of seeds and seedlings, dormancy (a_{11}), mortality (a_{22}) and fecundity (a_{13}) could not be measured.

Figure 3.6: Matrix Diagram of Life Stages of an Annual Plant



The presence of an intact senesced corolla was used as an indicator of mature fruit and formed the basis for the percentage of plants with "apparent reproduction" (Table 3.2). Smaller plants may have had inconspicuous fruits, but these were not collected (and therefore the fecundity estimates are limited). Furthermore, corollas were not always accompanied by fruits, so a better indicator would be desirable. Seed counts were ultimately obtained from 11 or fewer MENTRI plants per site. The number of seeds per fruit varied from 2 to 160, with a high proportion that were immature, suggesting that the collection may have occurred too early in the season. The high variation in the mean number of seeds per fruit among the sites likely reflects small samples sizes rather than biological factors. These data highlight the difficulties associated with measuring vital rates of diminutive annual plants. All corollas from a much greater range of plant sizes would have to be collected to properly assess a population reproduction rate, but such a high intensity of collection goes against ethical conservation practice and could result in significant impacts.

After one year of burial, MIMMOH seed dormancy (transition (a_{11}) in Figure 6) in the four packets ranged from 75-96% with a mean rate of 87.5% (±10.2 *s.d.*).

Table 3.2: Seed Counts of MIMMOH at Four Sites in 2011 and One Site in 2014

Year	Site	Apparent reproduction (%)	corollas examined (n)	Corollas with fruit (%)	plants with seed (n)	mean # seeds/ fruit	*s.d.* seeds/ fruit
2011	1a	63	22	40.9	4	34.0	26.8
	1b	50	26	57.7	10	40.7	25.3
	1c	63	18	22.2	3	15.8	11.1
	2	100	33	69.7	10	48.6	36.6
2014	1c	100	18	61.1	11	39.2	33.9

Apparent reproduction was indicated by an intact senesced corolla, but many did not contain any mature fruit or seed.

3.2.3.2 Mentzelia tridentata

Density estimates were difficult to obtain for MENTRI because of steep slopes with unconsolidated rock, which elevated the risk of damaging plants. However, MENTRI density estimates were obtained from five of the six sites in 2011 and at five sites in 2014 (Table 3.3). There were no clear factors to explain differences in density estimates among the sites in 2011, and some of it may be due to problems with the timing of sampling during the growing season. Very few MENTRI emerged in 2014, with sufficient sample size occurring only at two established sites and one new site. 2014 density estimates were very low. Site 7 was located in the same geographical area as the MIMMOH study sites.

Table 3.3: MENTRI Density Estimates at Seven Study Sites from 2011 to 2014.

	2011			# plants		2014		
Site	sampled area (m^2)	# plants (n)	density (#plants/ m^2)	2012	2013	sampled area (m^2)	# plants (n)	density (#plants/ m^2)
1	63	160	2.5	0	0	100	5	0.05
2	75	50	0.7	0	0	600	32	0.05
3	na		na	0	0	400	92	0.2
4	78	122	1.6	0	0	25	2	0.1
5	240	134	0.6	0	0		1	
6	75	50	0.7	0	4			
7	na			na	na	500	275	0.6

Na = data not available. Site 7 is located in a different geographical area.

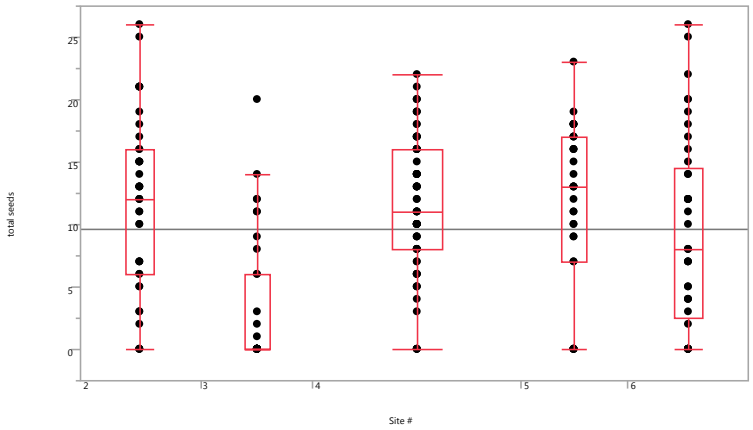
During 2011 the measured differences in plant height and the number of fruits output per plant among the sites were likely a function of sample timing (Table 3.4). Sites 1, 2 and 3 were marked on March 30, Sites 4 and 5 were marked 2 weeks later, and Site 6 was not marked until the very end of April. With the rapid growth and development typical of most desert annuals, two weeks would likely be sufficient to make a significant difference in reproductive output between sites. Likewise, the majority (or all) MENTRI individuals that were marked later in the season were already reproductively active (with buds, flowers, and/or fruits present), and these were highly likely to survive, mature, produce fruit and, therefore, have more successful reproduction than plants marked earlier in the season.

Table 3.4: Reproductive Output of MENTRI at Six Sites in 2011

Site	# plants marked (n)	mean plant height (cm)	*s.d.* plant height	# plants marked with early repro	# plants that fruited (at any time)	reproductive success (%)	mean fruit output (#/plant)	*s.d.* fruit output
1	51	3.7	2.0	19	18	35	0.7	1.3
2	53	4.3	2.5	42	42	79	2.5	3.8
3	55	6.5	4.4	51	49	89	1.2	2.0
4	50	12.0	6.1	49	48	96	11.6	15.3
5	50	12.0	7.4	49	47	94	10.1	12.5
6	48	13.3	10.3	48	48	100	10.9	10.1

The number of total seeds (mature and green) per fruit was much lower at Site 3 than at other sites (Figure 3.7). Even though MENTRI individuals were small at that site, reproductive success (the proportion that fruited) was high so it's not clear why there were so few seeds.

Figure 3.7: Seed Output (# Total Seeds/Fruit) in MENTRI at Five Sites in 2011



The number of seeds/fruit was significantly lower at Site 3 (ANOVA F= 12.987 p<0.0001).

Sample sizes were very small in 2014 at Sites 1, 2 and 3, but plant heights and the pattern of reproductive success were surprisingly similar to what was observed in 2011 (Table 3.5).

Table 3.5: Reproductive Output of MENTRI at Four Sites in 2014

Site	# plants marked (n)	mean plant height (cm)	*s.d.* plant height	# marked plants with early repro	# plants that fruited (at any time)	reproductive success (%)	mean fruit output (#/plant)	*s.d.* fruit output
1	5	3.1	1.1	2	2	40	0.6	0.9
2	14	3.6	1.2	10	10	71	1.0	1.1
3	16	5.7	2.0	15	16	100	3.3	1.9
7	41	5.1	1.9	36	26	63	4.2	6.8

Fruit output in 2014 was too low to allow collection, so it was not possible to determine if the low seed output per fruit observed at Site 3 in 2011 was repeated. As in 2011, MENTRI at Sites 1a-c that had reproductive structures early in the season were highly likely to survive to make fruit. This did not appear to be the case at Site 7, where buds or flowers on 10 plants apparently failed to mature to fruit. The variation in fruit output was high; several large plants at that site produced more than 15 fruits each but many small plants produced none.

3.4 Discussion

The short reproductive season, rapid growth, and diminutive stature of many desert annuals makes it difficult to study their demography. Surveys could not be timed to include the juvenile

stage of MIMMOH and unable to assess population reproduction because mature fruits were not equally conspicuous on the full array of plant sizes. Intact, but senesced corollas had been collected in hopes of obtaining mature fruit, but over half of the attached ovaries were empty. This could be consequence of a pollen/pollinator limitation, but information on the breeding system is lacking. Over the next three years the fruit collection methodology could not be refined because only 14 MIMMOH plants emerged at a single location. Therefore, a successful sampling protocol would need to begin at the moment of emergence from the seed bank and would require six weeks of nearly continuous monitoring in order to capture all stage transitions and significant demographic events.

There was somewhat greater success with MENTRI because the fruits are easy to see on mature plants. However, it was still difficult to anticipate the juvenile stage of this species and so reproductive effort was measured in relation to marked adult plants, rather than the earlier stages essential to developing a full demographic model. A small sample of juveniles was fortuitously marked at one site, but again the timing issue presented difficulty with respect to reproduction; there was no way to know if the peak at Site 3 had been missed or whether there was an actual biological limitation (e.g. lack of a pollinator) that reduced fruit and seed output.

Limitations on population growth of desert annuals occur primarily from events affecting the seedbank, especially environmental conditions that inhibit germination. This was observed for both MENTRI and MIMMOH during 2012 and 2013, when essentially no plants emerged. Desert annuals complete their life cycles during brief wet periods when they channel all resources to seed production before they die (Pavlik 2008). The seeds can remain dormant in the soil for long periods of time spanning years, decades or perhaps even centuries while they wait for favorable conditions to germinate. The authors were able to confirm that MIMMOH seeds buried for one year retained high viability in a dormant state but otherwise gained no information on the status of the soil seedbank of either species. As noted in Chapter 2 for the two annual species of *Eriophyllum*, the ability of a seed in the seed bank to germinate, survive to reproduction, and ultimately produce more seeds is the key to population persistence.

In years when there is sufficient rainfall to stimulate germination, limitations on population growth may subsequently occur in the juvenile stage as the result of desiccation (from soil drought), pathogens, or herbivory. With MIMMOH especially, these sources of mortality would likely result in the same outcome; marked plants disappearing from study plots as they are blown away or being completely consumed with no apparent cause. If a juvenile escapes desiccation or herbivory, reproductive success may be limited by pollinator availability. This could not be rigorously assessed in MIMMOH, but pollinator limitation seems unlikely. MIMMOH has very showy flowers that probably attract a wide array of generalist pollinators in the Hymenoptera (bees, wasps, ants, and sawflies) and Lepidoptera (butterflies and moths) (Beardsley and Olmstead 2002).

In contrast, there may be pronounced pollinator limitation in MENTRI. It has long been recognized that *Mentzelia* species are associated with specialist pollinators (Darlington 1934). A complex of four allopatric *Mentzelia* species, including MENTRI, *M. hirsutissima, M. involucrata,* and *M.tricuspis*, have exerted stigmas that preclude pollination except by certain bees that must

orient in a particular way to access nectar (Snelling and Stage 1994). The ghost plant (*Mohavea confertifolia*, in the plantain family) should also be included in this group as a floral mimic (Little 1980). The pollinator guild includes certain bees (Hymenoptrera, Halictidae, Rophitinae) with two species each of *Xeralictus* and *Hesperapsis,* and one of *Megandrena (*Snelling and Stage 1994). The distribution of the pollinator guild is complex and may be limited to one or two species per site whose females have distinct color markings (Snelling and Stage 1994). While field crews did not specifically look for other *Mentzelia* species during their fieldwork or conduct any pollinator observations, ghost plants were observed in proximity to several of the study sites. Recent study has suggested that ghost plant flowers have markings in the center of the corolla that resemble female Xeralictus bees in order to attract male bees that would otherwise ignore the flowers because they do not produce nectar (http://entmuseum.ucr.edu/bug_spotlight/posted%20Images-pages/33.htm). Future studies on MENTRI should investigate pollinator limitation as a potentially important factor determining reproductive success and population growth.

Threats to the persistence of MIMMOH and MENTRI populations are many and include urban development, mining, non-native plants, recreation (especially off-highway vehicles) and energy projects in the DRECP plan area (e.g., utility-scale solar and wind, powerline and pipeline installation). Transfer of federal land to private entities is also a concern. Further plans for large-scale changes in land use in the Mojave Desert may impact these populations and their habitats.

The level of protection for known occurrences of MIMMOH is variable or absent. Fewer than five occurrences are protected in NLCS wilderness (Figure 3.3). During 2005, the West Mojave Plan designated 4,318 acres of BLM managed lands in two separate ACECs for MIMMOH that include the majority of the known populations (BLM 2006). The western 50% or more of the species range occurs mostly within the southern Brisbane Valley Unit of the ACEC that is almost completely contained within the footprint of a proposed wind energy project (Silver Mountain Wind Energy Project, LLC CACA 053214). In California, BLM allows for a 0 to 12% development cap on terrestrial disturbance within ACECs (2005 BLM WEMO Plan, Chapter 2, Section 2.2.1.3). Wind energy is an allowable disturbance, but the cap may apply only to where wind projects install pads, roads, trenching, gen-tie lines, and substations, and not the entire project site area. The level of habitat fragmentation and the conditions that encourage invasive plants resulting from a wind energy project being sited inside an ACEC are unknown. Many of the eastern occurrences of MIMMOH are within the Daggett Ridge Unit of the ACEC. There are no large-scale energy projects currently planned for that area, but a proposed transmission line project could impact occurrences around Daggett and possibly the Newberry Mountains.

Many MIMMOH occurrences need to be verified by field surveys to better assess threats to the species. This study did not survey the large cluster of occurrences in the Brisbane Valley, but the Daggett Ridge area was extensively surveyed but MIMMOH were only found at the two study sites and at two new localities. The survey years (2011-2014) were characterized by moderate to severe drought, this suggest that these four populations could either be more resilient than surrounding occurrences or in slightly more favorable locations. It may be critical to preserve these occurrences as they best respond to a warmer, dryer climate.

Compared with MIMMOH, MENTRI has an even narrower distribution that would make it vulnerable to impacts from renewable energy and other disturbances. The steep, erodible habitat that MENTRI prefers, however, reduces the likelihood of development taking place in the same locations. Many occurrences were within the footprint of a proposed wind energy project (Bellevue Renewable Power - Calico Wind CACA 053321), but the application for that project was withdrawn in December 2014. The large number of new localities found during the present study suggests that MENTRI may be more abundant within its range than previously thought. The northernmost occurrences outside of San Bernardino County need to be verified to determine if these disjunct populations would warrant special protection.

Researchers were unable to conduct population viability modeling and determine extinction threshold probabilities for MIMMOH or MENTRI, but the basic data gathered here highlights information gaps and some of the inherent problems with monitoring rare annual species and lays a foundation for further conservation studies.

3.5 Management recommendations for renewable energy

a) **Successful demographic monitoring for rare desert annuals such as MIMMOH and MENTRI needs to be begin when seeds first germinate from the seed bank and would require at least six weeks of nearly continuous measurements in order to document emergence, capture all stage transitions and significant demographic events and estimate fecundity.** Timing the sampling is critical and is made difficult by rapid growth, rapid development, and diminutive stature of many of these species.

b) **Surveying the seedbanks of annuals is as important as surveying for active, aboveground plants**. Once an aboveground population is located, it can only be used to roughly approximate the fine-scale distribution of a population. That distribution can shift (or appear to shift) in response to temporal and spatial climatic variations that cause differential responses in the seedbank. Surveying seedbanks is necessary, therefore, to identify which areas need protection to allow long-term persistence under great climatic uncertainty. The authors acknowledge that methods for surveying seedbanks are laborious but argue that avoidance based solely upon aboveground plants will have unintended impacts on persistence of the target species.

c) **Some rare annual species may have limitations imposed on population growth because of their specialized pollinators.** Therefore, determining how to mitigate the impacts of energy development on a rare desert annual should include an understanding of what the pollinators are, where they reside, and what effect they have on reproductive output, especially plants that require pollen from another individual of the same species (outbreeders).

d) **Extensive field surveys for occurrences of rare annuals such as MIMMOH and MENTRI are required to document current distribution, population sizes, habitat characteristics, eminent threats, and potential for protection in a connected reserve system.**

CHAPTER 4:
Comparative demography of *Asclepias nyctaginifolia* across impacted and unimpacted populations

4.1 Introduction

Management of populations of rare perennial species necessitates detailed understanding of their life histories, reproductive biology, interactions with other species, and the genetic and ecological traits that make them vulnerable to extinction (Soule' 1986, Menges 2000a and 2000b, Ohara et al. 2006). Information on each of these topics is required for species recovery where species are greatly imperiled. Key among the needed information is how stochastic environmental processes affect long-term population growth via their effect on individual or correlated vital rates at different life history stages (Pavlik 1994).

Desert plants have adaptations that buffer extended drought conditions such as succulence, deep roots, adult and seed dormancy, and seed longevity, among others (Smith et al. 1997). These mechanisms have evolved to buffer the incredible environmental variability of deserts. These adaptations can allow populations to persist through extended periods of unsuitable conditions with little measurable effect on population demographic rates. Where subpar conditions persist, decline occurs over relatively long time scales congruent with prolonged mortality and lack of recruitment. Long-term studies are necessary in order to witness the demise of some populations and/or species. Similarly, species adapted to endure challenging climatic periods may be resilient, at least initially, to anthropogenic stressors that reduce resource availability or lower reproductive rates.

Desert ecosystems in southwestern North America face multiple direct and indirect effects of disturbance by utility-scale renewable energy development including population reduction, fragmentation, and altered herbivore and pollinator densities. Each of these stressors can have detrimental effects on plant demographic responses and the outlook for population persistence. Demographic buffering by desert perennials may allow populations to have fairly constant population growth rates for some time, despite impacts or changing climate. For example, survival of adult plants may be high despite stressors and low fecundity, or bet hedging may gradually reduce fitness if it exposes seeds or emergent adults to risks (Salguero-Gómez et al. 2012).

Population projection models (PPMs) can be useful at comparing the effects of different management strategies on population growth (Menges 2000a and 2000b, Reed et al. 2002). Furthermore, life table response experiments (LTRE) can be used to quantify the effects of different strategies on variation in population growth rates observed and to assess how impacts on specific vital rates influence changes in the population growth rate (Caswell 2001, 2010, Endels and Jacquemyn 2007).

Asclepias nyctaginifolia, Mojave milkweed (hereafter ASCNYC), is a special-status iteropareous (characterized by multiple reproductive cycles over the course of its lifetime) perennial that is

directly impacted by solar energy development in the north central Mojave Desert. ASCNYC occurs at low elevations in low relief washes throughout the eastern Mojave Desert. Although it is more common in Arizona and Nevada, ASCNYC has a very limited range in California (Figure 4.1) and its populations are generally small and widely spaced. A significant portion of the California range of ASCNYC has recently been impacted by extensive utility-scale solar energy development in Ivanpah Valley and the surrounding area at the state line of California and Nevada (Figure 4.2). The first energy generating system installed in the prime range of this rare species is Ivanpah Solar Electric Generating System (ISEGS), which was designed and constructed by BrightSource and is now operated by NRG Energy. ISEGS is one of the few energy installations globally in which a significant portion of the landscape under the mirrors was not leveled or graded. This has provided a unique opportunity for the persistence of ASCNYC and other rare plant species in the industrialized landscape.

For seven seasons over a four-year period, the research team conducted detailed field observational studies on the demography of ASCNYC in California. They used field-collected data to compare the demographic performance of ASCNYC across three unimpacted populations and two mitigation treatments on the population directly impacted by ISEGS. They used experiments at two unimpacted populations and observational studies throughout to quantify site-specific differences in herbivory. Analysis of population projection matrices was used to compare the seasonal estimates of the population growth rate (λ) across sites and treatments and applied LTREs to assess the effects of season, site, and treatment on population growth.

Specifically, the authors asked:

1) Are there demographic differences between populations adjacent to and within ISEGS in comparison to natural, undisturbed populations?
2) How does herbivory vary across the disturbance gradient?
3) Do adult plant seasonal dormancy rates vary across the disturbance gradient?
4) Are the strategies deployed at ISEGS an effective means of mitigation?

The overarching objective of this part of the study was to provide information for the adaptive management of ASCNYC in California and to inform conservation strategies for other affected rare desert perennials that occur in locations developed for utility-scale solar energy.

4.2 Methods

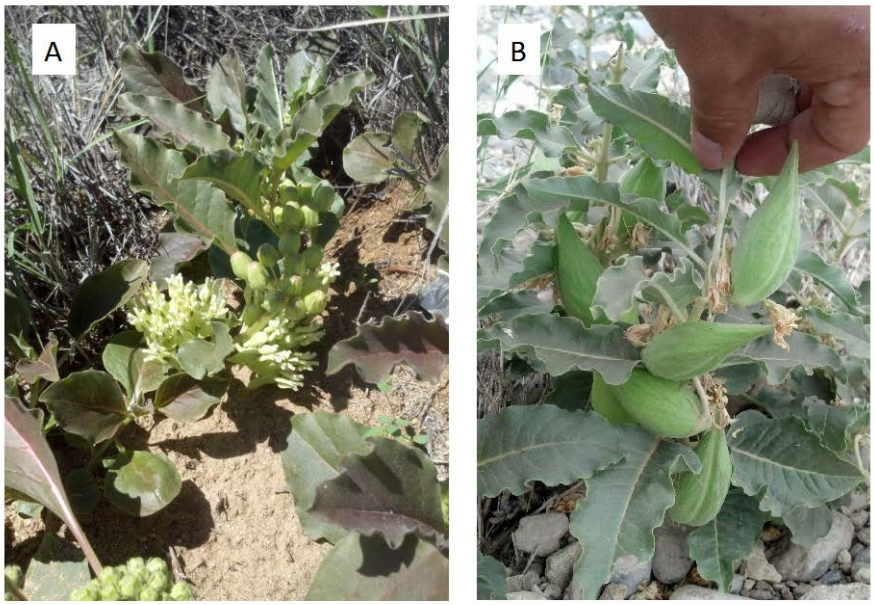
4.2.1 Study species

Asclepias nyctaginifolia (A. Grey, Apocynaceae), formerly included in the milkweed family (Asclepiadeceae; Baldwin et al. 2012) is a rare perennial herb with populations in California, Arizona, Nevada, and New Mexico. The California Native Plant Society ranks ASCNYC as a CRPR 2.1 species (rare, threatened, or endangered in CA; common elsewhere). ASCNYC in California is directly impacted by utility scale solar power facilities in the Ivanpah Valley. The densest assemblages of California Natural Diversity Database (CNDDB) Occurrences are found

on, and adjacent to, the Ivanpah Solar Electric Generating System footprint (CDFG, 2014). Further plans for large-scale changes in land use in the Mojave Desert will additionally impact this species and its habitat.

ASCNYC is 12-60 cm tall with one to several, decumbent to ascending, herbaceous stems arising from a rhizome (Figure 4.1). Rhizome dimensions are largely varied, and can reach up to 2 meters in length. The sparingly branched stems produce one to many inflorescences, a dense umbel-like cyme, with up to 18 flowers. In the vast majority of seasons, ASCNYC has a low rate of successful fruit production. Of the potentially thousands of flowers produced by an individual, a small fraction of those will produce a follicle containing 40 to 150 seeds. ASCNYC is an "ephemeral" iteroparous perennial, emerging for the winter-spring growing season, and then dying back to the ground during the hot Mojave summer. When monsoon rains provide sufficient moisture, leafy stems may re-emerge in late summer, providing opportunity for an early fall reproductive cycle. These are referred to as the "spring" and "fall" growing seasons. For much of the year, however, plants are not visible above ground, except for the remains of past year's inflorescences. Seed dormancy is low (Appendices A and C).

Figure 4.1: Photos of ASCNYC in Flower and Fruit



Reproductive ASCNYC individuals with A) abundant flowers on a ramet within a genet (see description below) and B) developing fruits on a single ramet with hand for scale.

Photo Credit: Bruce Pavlik (2012).

4.2.2 Species interactions

ASCNYC has strong negative and positive interactions with both vertebrate and non-vertebrate species. Herbivores have temporally variable, but generally strong negative effects on many ASCNYC individuals. Jackrabbits and small rodents snip leaves and entire stems. In some

seasons and populations, the effect of mammalian herbivory may effectively prevent all sexual reproduction. In addition to stem pruning, jackrabbits dig out the base of the stems, putatively in search of additional moisture (Moore and Pavlik, personal observation). Evidence for this activity includes both plant damage and ample jackrabbit and rodent scat around affected plants. Post-dispersal, seeds show signs of rodent predation on occasion (<1% of seeds).

Interactions were also observed between a diverse invertebrate community and ASCNYC. In both spring and fall seasons, monarch butterflies and other Lepidoptera, including sphinx moths, oviposit on milkweed leaves. Caterpillars feed heavily on the species, particularly in the fall season when caterpillars and their frass are evident on the majority of plants. Damage ranges from scattered scalloping of leaves to skeletonization of entire plants. Plants can also be heavily infested with aphids; the majority of aphid activity appears to be after fruit production.

Like other milkweed species, pollination of ASCNYC requires specialized insect activity in order to transfer the pollinia (pollen sac) from one flower to another. Insects visiting the flowers must insert their mouthparts or feet into five slits generated by the anthers in order to trigger mechanical attachment of the pair of pollinia in the flower to the pollinator or to deposit pollinia from another flower.

4.2.3 Study sites

California populations of ASCNYC are restricted to suitable microhabitats throughout the eastern Mojave Desert (CDFG 2014). Population sizes range from a handful of plants to approximately 100 per acre, and tend to be composed of multiple sub-populations confined to narrow drainages in low-lying depositional sites, such as stream channels, alluvial fans, and at the base of mountain ranges and monolithic formations. ASCNYC occurs on well-drained soils that are typically sandy, gravelly, and rocky. Soils are calcareous, have poorly developed organic layers, and are composed primarily of alluvial granite and limestone. These alluvial soils support a broad diversity of low scrub vegetation that varies greatly with elevation and aspect.

4.2.3.1 "Unimpacted" study populations

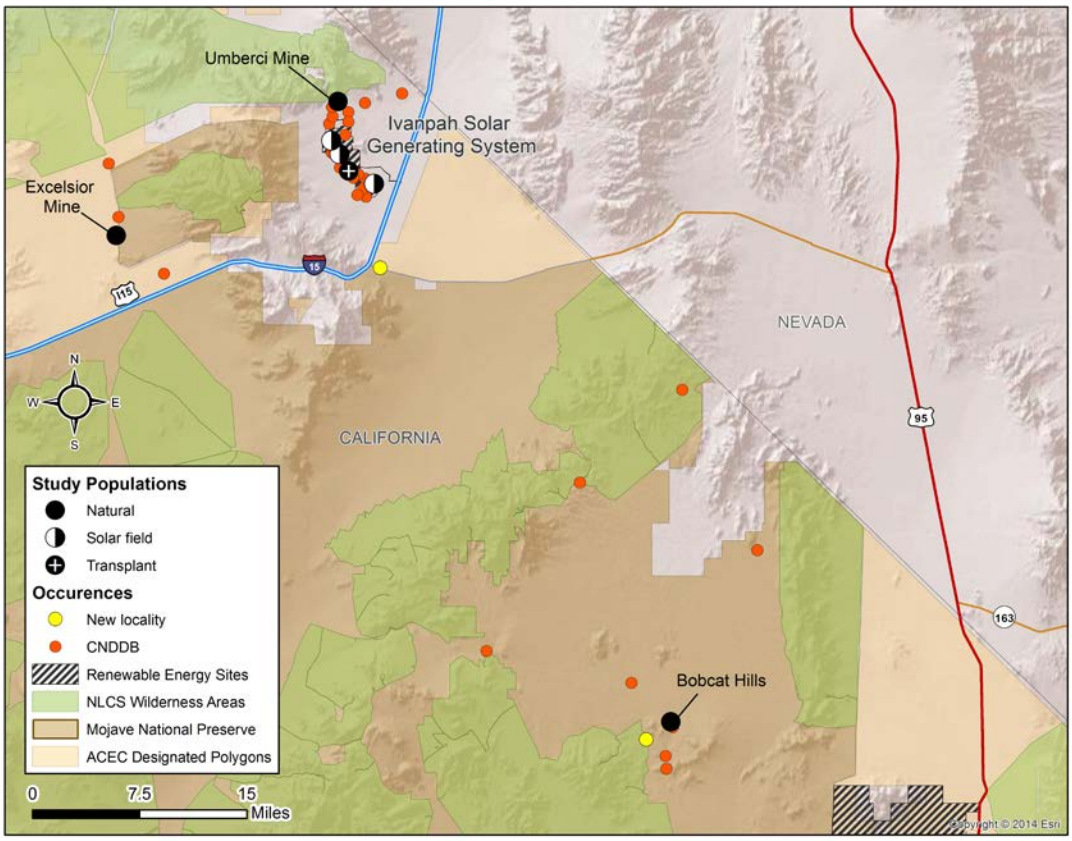
In May of 2011, researchers selected three study locations not directly impacted by solar energy development across the California range of the species (Figure 4.2). Note that although these populations are referred to as "unimpacted," the site at closest proximity to ISEGS (Umberci) may experience unquantified indirect impacts. Because of their distance, these were assumed to be genetically distinct populations; a subsequent study to assess genetic distance is currently underway. Study population selection criteria included a population density of >20 individuals, distribution of study sites across the range of the species in California, inclusion of the observed habitat characteristics, and site accessibility. The selected populations each contained 32 to 52 adult plants in 2011 (Figure 4.2). Each is considered a separate demographic unit due to geographic isolation and discontinuous suitable habitat from surrounding populations.

The Excelsior population occurs on the western bajada of Clark Mountain in Shadow Valley near the historic Excelsior Mine site (elevation 1053 m). The population occupies a 500 m-section of a seasonally active wash that runs southeast to northwest. This site supports dense Joshua

tree woodland, including a diverse cacti assemblage dominated by *Opuntia acanthocarpa, Opuntia erinacea*, and *Grusonia parishii.* Total vegetation cover in the area is around 7%, with 5% being shrub cover and 2% being herbaceous cover. Prevalent species in the shrub layer are *Ambrosia dumosa (1-5%), Larrea tridentata (<1%), Hymenoclea salsola (<1%), Yucca brevifolia (>=1%),* and *Yucca schidigera (<1%).* Herbaceous cover consists of *Vulpia octoflora (1-5%).*

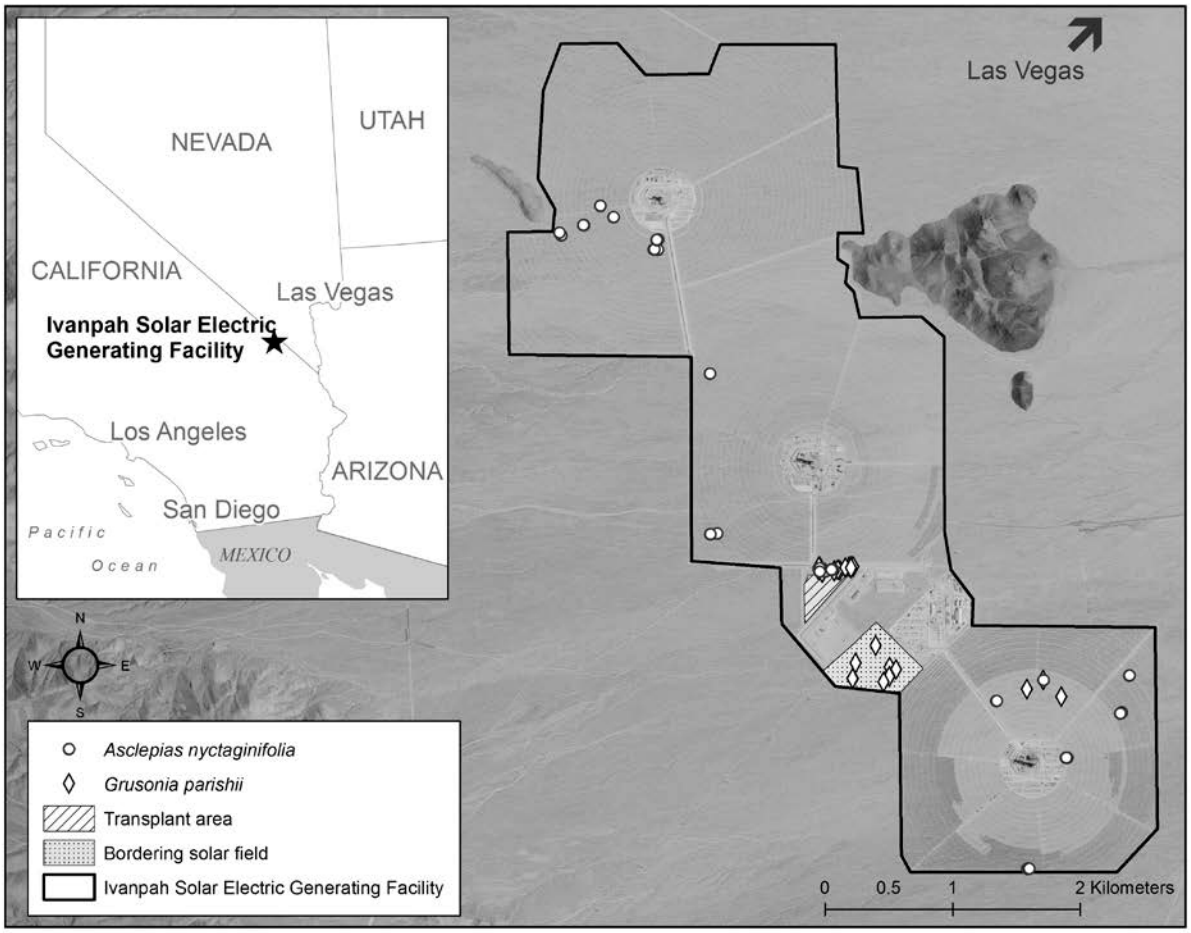
The Umberci population is located in a seasonally active wash on the northern slope of Ivanpah Valley near the historic Umberci Mine site (elevation 981m). Occurring at the lowest elevation of the study populations, this location supports a diverse creosote scrub community, dominated by *Amsonia tomentosa* and *Ambrosia dumosa* and includes riparian species like *Acacia greggii.* Total vegetation cover in the area is around 5%, with 3% being shrub cover and 2% being herbaceous cover. Prevalent species in the shrub layer are *Ambrosia dumosa* (<1%), *Larrea tridentata* (<1%), *Ephedra nevadensis* (<1%), *Hymenoclea salsola* (<1%), *Opuntia ramosissima* (<1%), and *Yucca schidigera* (<1%). The herbaceous layer is comprised by the dominant *Hilaria rigida*, in addition to *Bromus madritensis* (1-5%) and *Pectis papposa* (1-5%).

Figure 4.2: Map of ASCNYC Study Populations



"Natural" populations are not directly impacted by solar energy development. See Figure 4.3 for detail of the population at ISEGS. Renewable energy and conservation lands are shown only for California.

Figure 4.3: Map of ASCNYC Study Populations at Ivanpah Solar Electric Generating System



Individuals within the solar field are located within halos, openings between the mirrors established during construction as rare plant mitigation. Additional transplants from the solar field are located in a transplant area adjacent to the solar field.

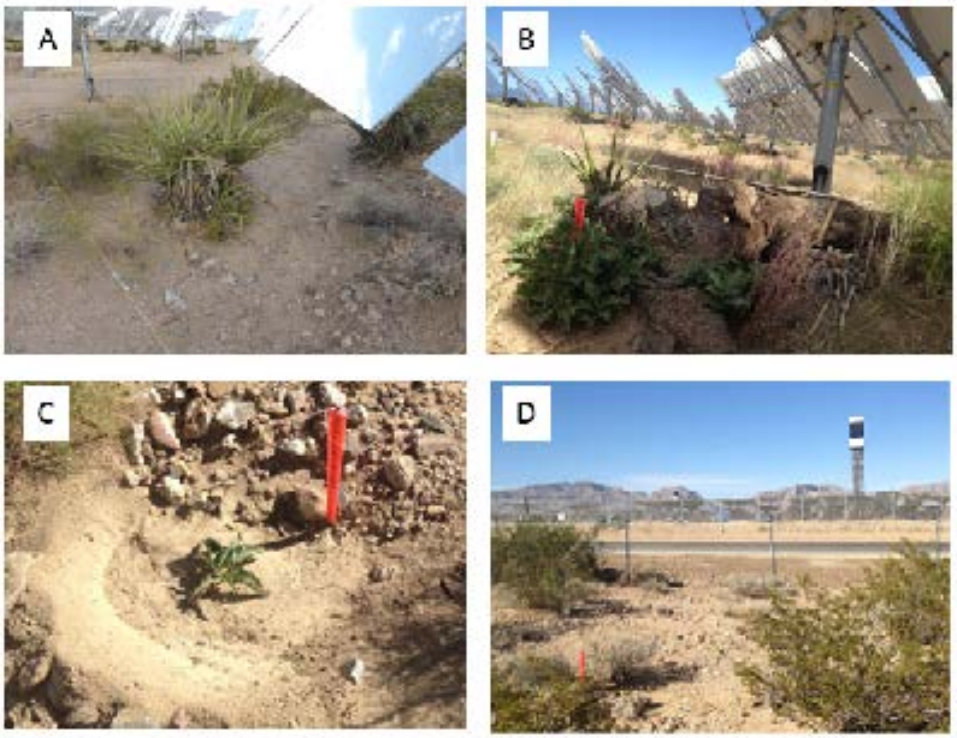
The Bobcat population occurs on the southeast slope of Bobcat Hills in Mojave National Preserve (elevation 1145 m). This high elevation site supports Joshua tree woodland and a creosote scrub community. The herbaceous layer is dominated by *Hilaria rigida.* Fall annuals include *Pectis papposa*. Total vegetation cover in the area is around 40%, with 20% being shrub cover and 20% being herbaceous cover. Prevalent species in the shrub layer are *Larrea tridentata* and *Yucca brevifolia*.

In each of these sites, as is typical for its populations, ASCNYC occurs at a rate of less than one percent. Herbaceous plants of all species were generally <20 cm in height.

4.2.3.2 "Impacted" study population

A fourth study population is located in the north-central Ivanpah Valley (920 m; Figures 4.2 and 4.3). This relatively low-elevation and low relief site is dominated by creosote scrub dominated by *Ambrosia dumosa.* Total vegetation cover in the area is around 15%, with >10% being shrub cover and 1-2% being herbaceous cover. Prevalent species in the shrub layer are *Ambrosia dumosa* (<1%), *Larrea tridentata* (<1%), *Hymenoclea salsola* (<1%), *Opuntia ramosissima* (<1%), and *Yucca schidigera* (<1%). The herbaceous layer is comprised by the dominant *Hilaria rigida*, in addition to *Bromus madritensis* (1-5%) and *Pectis papposa* (1-5%).

Figure 4.4: ASCNYC Individuals at Ivanpah Solar Electric Generating System



ASCNYC individuals in A and B, solar field "halos." Plants are marked with orange or yellow plastic stakes. Halos are delineated with surveying twine. In C and D, individuals transplanted from the solar field to an adjacent transplant area.

Photo Credit: Kara Moore (2013 and 2014).

In 2011, construction of Ivanpah Solar Electric Generating System (ISEGS) was initiated on a 4000-acre leased tract of public land including this population. All ASCNYC individuals within the solar field were mapped prior to construction (Figure 4.3). Where it was possible to shift pylons such that they would avoid direct damage to ASCNYC individuals, small gaps between the mirrors, termed "halos" by the California Energy Commission, were established and plants were allowed to persist within the solar field. These locations were termed solar field mitigation areas or halos and the focal plants within them solar field individuals. The average size of a solar field mitigation area is 0.043 acre and 1.4 acres of these mitigation areas were established

for ASCNYC, nearly half of the 3.093 acres of the mitigation areas within the solar field that were established for three rare plant species across the 3500-acre construction area.

Where plants would be directly impacted by heliostat pylons, roads, or other major disturbances, they were transplanted to an otherwise low disturbance area adjacent to the construction-staging center and the edge of the installation termed the transplant area (Figures 4.3 and 4.4). Painstaking transplant methods were followed to maintain belowground plant architecture including fine roots. Rhizomes were excavated from 4-6 feet in soil depth and their connectivity was carefully maintained. Despite the care taken, some fragmentation of rhizomes occurred.

Study was initiated in spring of 2012 of the ASCNYC population within ISEGS where researchers subsequently tracked over 95% of the persisting plants (52): 29 transplant and 33 solar field individuals.

4.2.3.3 Regime change within Ivanpah Solar Electric Generating System

Landscape conversion at ISEGS has yielded clear changes in the interactions between ASCNYC and its herbivore and pollinator communities. Grazing by cattle and burros is common in the surrounding BLM lands, including the Excelsior and Umberci mine populations, and in Mojave National Preserve where the Bobcat population is located. The perimeter fence surrounding ISEGS excludes desert tortoises and larger mammals, such as cattle, burros and coyotes, but is porous to small wildlife including blacktailed jackrabbits, kangaroo rats, pack rats, badgers, bobcats, and kit fox, all of which are active in the solar field (CH2MHill, personal communication). Population increases in the kangaroo and pack rat populations were observed by biological consultants at ISEGS in 2014 (CH2MHill, personal communication). Avian, bat and butterfly activity at ISEGS is reduced by mortality due to in-flight impacts with towers and mirrors and singeing of flight feathers in the solar flux (Harvey and Associates 2014, Kagan et al. 2014). Effects of regime change within ISEGS on invertebrates have not, to the authors' knowledge, been quantified; however, researchers have noted evidence of butterfly and caterpillar mortality within the installation seasonally, especially during periods of intense monarch activity (seasonally some springs and falls).

Indeed, it has been suggested that the solar field may act as a trap, attracting insects and their avian predators (Kagan et al. 2014). Avian mortality estimates on-site in 2013 include 49 species including several species that predate on butterfly larvae (Kagan et al. 2014). In addition, the ecological regime change within the solar field includes periodic mowing of vegetation and occasional washing of the heliostats with minimal amounts of water.

4.2.4 Field censuses

4.2.4.1 Field demography

At each unimpacted population, field crews established a 500-m transect through the population center, generally following the dominant drainage that the focal plants occupied. Plants occurred in an approximately 20-m wide band through the dominant drainage; all known individuals within each population were included. At ISEGS, all ASCNYC plants within

the transplant area and all known plants within the solar field were included. In each site, individuals were marked with a robust wooden stake with a numbered tree tag and GPS coordinates were recorded to facilitate relocation. Table 4.1 gives maximum sample sizes of each study site from spring 2011 to fall 2014.

Individuals were comprised of one to many stems representing a single rhizomatous root system (genet, Figure 4.1). Stems were assumed to be of the same genet if they were < 0.5 m from nearest adjacent stem and were not separated by any obvious natural barriers such as boulders, deep drainage features, or significant shrubs. This was confirmed by exhumation of the area between of a subset of distantly located ramets.

Seasonal censuses were conducted in the spring and fall of each year to capture seasonal survival, growth, and fecundity and to mark all new recruits. Vegetative growth was recorded at the peak of each season by measuring the cross-section diameter of each rhizome and the cross section diameter of each stem within a rhizome. Height of the tallest stem and number of stem were also recorded for each genet.

Fecundity was assessed throughout the season by counting inflorescences, flowers per inflorescence and fruits as they developed. Inflorescences commonly failed either before or after flowers fully developed, thus the number of "aborted inflorescences" per plant was also tallied. In 2013, a small subset of fruits, <5 % in the population, were collected to assess seed/fruit, seed viability and perform experiments on seed demography (see Appendices A and C). Researchers were not permitted to collect fruit or seeds in 2011 or 2012 within ISEGS. In the fall of 2013, consultants for NRG Energy conducted seed counts with the project team for a sample of fruits that they collected from solar field and transplant individuals. In 2014, the researchers were not permitted to survey the ISEGS sites until after fruit dehiscence and as such were unable to attain additional data on seeds per fruit.

Table 4.1: Spatiotemporal Variation in Activity of ASCNYC.

Season	Site	Active aboveground	Dormant rhizome
Spring 2012	Bobcat	16	13
	Excelsior	15	9
	Umberci	2	54
	Solar field	6	27
	Transplants	6	23
Fall 2012	Bobcat	29	0
	Excelsior	19	5
	Umberci	52	4
	Solar field	31	2
	Transplants	22	7
Spring 2013	Bobcat	29	0
	Excelsior	20	4
	Umberci	53	3
	Solar field	28	5
	Transplants	21	8
Fall 2013	Bobcat	28	1
	Excelsior	22	2
	Umberci	50	6
	Solar field	31	2
	Transplants	21	8
Spring 2014	Bobcat	19	11
	Excelsior	3	21
	Umberci	12	44
	Solar field	11	22
	Transplants	2	27

The number of adult plants for each site and season that were either active aboveground or persistent as dormant rhizomes.

At each site, seedling recruits were carefully scouted for on each survey throughout the entire established population boundary. Seedlings were scouted for within the solar field mitigation areas and the transplant nursery at ISEGS and for an additional 20 m along the adjacent washes. Seedlings were marked and the distance and azimuth to the nearest adult was recorded. All seedling and adult plants observed on any survey were searched for on all subsequent surveys. Multiple surveys were conducted at each population in the spring (April-June) and fall (August-October) of each year from 2011 through the spring of 2013. In fall of 2014 a reduced survey was completed at all study sites except Excelsior. Activity or dormancy of each genet and its fruit production were tallied. New seedlings were counted and marked. Size data were collected for only a subset of individuals.

4.2.4.2 Quantification of herbivory

For each plant, vegetative and fruit damage and activity of invertebrate and vertebrate herbivores was quantified. Damage to each was assigned a scalar value 1 to 5 that represented 20% incremental reductions in overall canopy volume. Damage occurred throughout the aboveground plant on leaves, stems, and fruits, although leaves were most severely affected. On fruits, herbivory was scored on a per-fruit basis as either pre- or post-dispersal damage.

In fall of 2014, the researchers assessed activity of caterpillars by counting frass within 2.5 x 2.5 cm squares on a 30 x 30 cm grid centered on the target genet (Henderson 2003). For very large plants, they expanded this to a 60 x 60 cm grid with the same resolution. Counts were taken after the majority of caterpillar activity, growth, and fruit production in mid-November. At this time, the activity of jackrabbits was also quantified by scat counts within a 50 x 50 cm frame centered on the target genet.

4.2.5 Field seeding experiment

Field seed germination rates were assessed through a seeding experiment at each of the three undisturbed populations. In each population, seven seeding plots were randomly located in fall of 2012. Randomly selected seeding plots were rejected if they met predetermined criteria including presence of woody shrubs, rocks larger than 20 cm in diameter, or if they fell in obviously harsh or turbulent segments of the drainage. Germination plots were 0.5 x 1 m and were oriented with the long edge perpendicular to the drainage. The top 2 cm of soil was scraped away, then 50 seeds were scattered throughout the plot and the removed soil was replaced on top a 0.75 x 1.25 m section of hardware cloth was secured over the plot with rebar in each corner to gently secure the soil and seeds in the plot location. Plots were surveyed for seedlings in all subsequent seasons through fall of 2014.

4.2.6 Field seed dormancy experiment

Researchers conducted a seed dormancy experiment at Bobcat and Umberci, in which packets of seed were buried in fall of 2012 and exhumed them in 2013 to assay rates of germination, mortality, and persistence in the seed bank. For each replicate, 20 or 40 seeds collected in fall of 2012 from within each focal population were sewn into a packet of polyorganza synthetic fabric; five packets were buried at each site adjacent to the seeding plots. Seed number per packet was determined by seed availability. Seed packets were exhumed the following spring after germination and emergence and persistent seeds and empty seed coats were tallied. X-ray analysis was used to estimate annual rates of seed mortality for both untreated and buried and exhumed seed produced in the fall 2013 season (Appendix A). In addition, seed germination rates were estimated based on a lab germination experiment (Appendix C).

4.2.7 Analyses of variation in individual performance and herbivory

Researchers used generalized linear models to evaluate differences in seasonal growth, fruit production, and herbivory across the three undisturbed populations and the two disturbance treatments within the ISEGS population. They first asked if these metrics differed across all study sites and seasons. For growth and herbivory, they then looked for within season differences across study sites. Seasons or sites with no non-zero data were dropped. Because fruit production was very low and the authors were interested in its long-term demographic

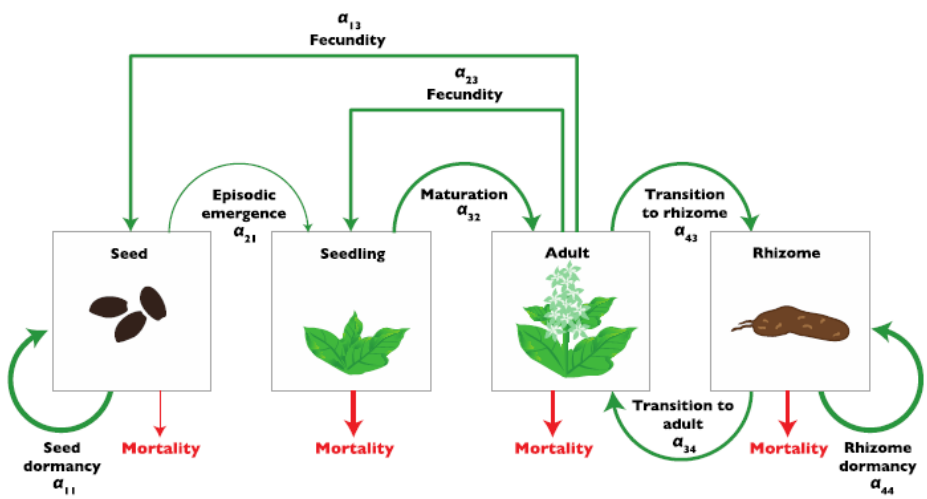
effect, they summed fruit production per individual and assessed variation in cumulative fruit production across the five sites for all seasons combined. They compared performance of plants and their herbivory scores between undisturbed populations with and without mammalian herbivore exclusion (Excelsior and Bobcat) and between these sites and the disturbance treatments at ISEGS. Finally, counts of caterpillar frass and jackrabbit scat were compared across sites in fall 2014.

The researchers used either Gaussian or negative binomial GLMs, as appropriate for each response, and applied Tukey's HSD to conduct post-hoc comparisons when necessary. Consistent with the study questions, all post-hoc comparisons were limited to within season. They conducted these analyses using the MASS, multcomp, and lsmeans libraries in R (R Core Team 2014).

4.2.8 Stage classification

A stage-based population projection model with four stages (seed, seedling, aboveground adult, and dormant rhizome) was used and a seasonal projection interval to evaluate observed data (Figure 4.5). Individuals were classified into four stages present at each post-breeding census. Seeds represent those produced by the end of the season at hand, reduced by non-viability.

Figure 4.5: Stage Diagram of ASCNYC



Stage diagram of the seasonal life cycle of ASCNYC. Emergence of seeds and dormant rhizomes occurs in the spring and/or fall in apparent response to precipitation. Boxes represent four life stages. Mortality, dormancy (a_{11}, a_{43}, and a_{44}), growth (a_{32}), or re-emergence (a_{34}) are the possible transitions between seasonal intervals. Fecundity (a_{31}) of adult plants results in contribution to the seed bank for the next season.

The authors calculated a single estimate of annual seed dormancy, a_{11}, as viable seed less the mean seed germination rate, where seed viability was estimated as the mean viability rate from x-ray analysis at all sites in both years (Appendix A) and seed germination was estimated as the mean germination rate for one and two year old seeds (Appendix C). Because dormancy and

germination data was from a subset of fruiting plants in two of seven seasons at the majority of sites, these rates were averaged and applied across all seasons and sites. As seeds age, they likely have reduced rates of viability, non-mortality, and germination. However, because of the difficulty in attaining age-structured estimates of seed dormancy, a single rate is commonly used (Kalisz and McPeek 1992, Griffith and Forseth 2014).

Fecundity, a_{13}, the rate of individual seed production, was calculated as the product of site- and season-specific individual fruit counts and a random, site-specific sample of seed per fruit. Note that when conditions are favorable seeds can germinate and yield seedlings directly within the same season (a_{23}). Fruits for seed counts were collected in all possible sites and seasons, but since fruit collections prior to dehiscence were limited, counts from all seasons were pooled.

The authors estimated seedling survival and maturation, a_{32}, as the rate at which seedlings recruit to the adult size class. New seedlings were present at the study sites in only two of the seven study seasons: fall 2013 and fall 2014. Seedling maturation varied considerably across populations (Umberci 46.67%, Bobcat 5.26% and solar field 15.38%); the mean seedling maturation rate across sites in these seasons was 22.43%. There were no seedlings in any year in the transplant area at ISEGS. Because seedling maturation rate is likely highly variable across years and highly dependent on local rainfall, they conservatively assigned the mean rate 22.43% to all populations for the Fall 2013-Spring 2014 projection period.

The transition rates between aboveground adult plants and dormant rhizomes a_{33}, a_{43}, and a_{34}, were calculated based on the proportions observed for each site, season, and treatment (Table 4.2). Seasonal mean transition rates were used in cases where there were 5 or fewer individuals in a stage class for a given site.

Table 4.2: Spatiotemporal Variation in Aboveground and Dormant Rhizomes of ASCNYC

	Spring 2011	Spring 2012	Fall 2012	Spring 2013	Fall 2013	Spring 2014
% of all plants dormant	47.1	73.3	10.5	11.6	11.0	11.6
% dormant to aboveground	18.5	88.1	22.2	45.0	15.8	45.0
% dormant stasis	79.0	7.9	33.3	15.0	(84.2)	(55.0)
% mortality	2.5	4.0	44.4	35.0	---	---

Percent of the population (N=172) in the dormant stage and making seasonal transitions to aboveground, dormant stasis, or death. Mortality of rhizomes was assumed when a plant remained belowground for four or more consecutive seasons; 30% of these cases were field-verified. Parentheses indicate where dormant stasis is assumed but mortality cannot be estimated.

For a_{44}, the rate of plant stasis and survival below ground as a rhizome across seasons, the rate of rhizome mortality was first calculated and then multiplied against the observed proportion of dormant plants for each site, season, and treatment. Where no dormant plants were directly observed for a site and season, the authors valued rates of transition to emergent adult and dormant stasis as identical to the rates of emergent adult to emergent adult and emergent adult to dormant rhizome transitions for the same site and season. Mortality could occur in any season, but seasonal dormancy is very common. In addition, rhizomes of other *Asclepias* species

have been shown to be sensitive to disturbance, so the researchers limited disruption at the study populations. Rhizomes were considered to be dead when they had not re-emerged for four or more consecutive seasons. In fall of 2014 a subset of these rhizomes was exhumed (30%) and morality of this sample was confirmed. Researchers estimated the mortality of rhizomes in dormant stasis as the average of the thus observed rates of mortality for dormant rhizomes in spring and fall 2012 and spring 2013 seasons, i.e., those in which they had the ability to confidently track dormancy for four consecutive seasons (Table 4.2).

4.2.9 Matrix analyses

The general form of transition matrix models project population size as:

$$n_{(t+1)} = A\, n_{(t)}$$

where n is a vector of population sizes representing the stages in the model and A is a matrix of probabilities that define the transitions between stage classes and the fecundities of each of those classes between times *t* and *t*+1 (Caswell 2001, Table 4.3).

Table 4.3: Seasonal Projection Matrix for ASCNYC

Stage	Seed	Seedling	Aboveground adult	Dormant rhizome
Seed	a_{11}	0	a_{13}	0
Seedling	a_{12}	0	a_{23}	0
Aboveground adult	0	a_{23}	a_{33}	a_{34}
Dormant rhizome	0	0	a_{34}	a_{44}

ASCNYC is a perennial plant with seed and rhizome banks.

Projection matrices were generated for each season and site, and for control and herbivore exclusion plants within seasons and sites where these treatments were deployed. Each transition probability and fecundity value denotes the rate at which individuals in stage *j* at time *t* progress to stage *i* at time *t*+1. The top row of the projection matrix indicates fecundity of each stage, in this case the rate of persistence of dormant seeds a_{11} and the rate of seed production a_{13}.

For each projection matrix, the authors calculated several population parameters including the asymptotic population growth rate (λ), matrix element sensitivities (S_{ij}) and matrix element elasticities (E_{ij}, Caswell 2001). Values of $\lambda > 1$ represent increasing population size whereas values $\lambda < 1$ represent population in decline. The sensitivity of a matrix element is the change in λ resulting from a small change in the focal element, calculated as

$$\mathrm{Sij} = v_i\, w_j \,/\, (\mathbf{w},\mathbf{v})$$

Where v_i is the reproductive value of the ith stage and w_j is the stable stage distribution of the jth stage and (**w,v**) is the scalar product of the vectors of the stable stage distribution and the fecundities (Caswell 2001). Sensitivities often vary greatly between different matrix elements and as such are not easily comparable. In contrast, matrix element elasticities are the proportional change in λ given a change in a focal matrix element

$$E_{ij} = S_{ij}(a_{ij}/\lambda)$$

and are comparable between different elements in the same matrix or across different matrices from the same population model. The sum of the elasticities in each column of a matrix gives the proportional influence of that stage to change in λ (Kalisz and McPeek 1992, Caswell 2001).

Life table response experiments (LTREs) compare the sensitivities of matrices derived under different conditions by decomposing the variability in λ generated by differences in the matrix elements into the contributions from each matrix element (Horvitz et al. 1997, Caswell 2001, Angert 2006). This decomposed variance can be calculated for the effect on λ caused by the difference between two treatments (Caswell 2001). The project team used fixed-design LTRE analyses in which sensitivities were evaluated midway between treatment and reference matrices to compare the effects of seasons, sites, and their interaction on λ and to contrast the effects of herbivore exclusion and controls on λ at the Bobcat and Umberci unimpacted sites. Researchers chose to use a pooled reference matrix in order to weight observed transitions by their frequency in the entire dataset (Horvitz and Schemske 1995).

LTREs yield a matrix of the contributions of each stage transition to the quantified variation in λ between the treatments (Caswell 2001, Angert 2006). In cases where the contribution of a specific matrix element to λ does not vary among treatments, the focal matrix element either does not vary in response to treatments or has little effect on λ. Where the contribution of a matrix element has high sensitivity but is not affected by the treatment, it will have low or no contribution to variation in λ. Large contributions to variation in λ are generated where matrix elements have sensitivity coupled with variation between treatments (Caswell 2001, Angert 2006).

For each site, season, and treatment, ~1000 bootstrapped projection matrices were generated. The authors used these matrices to evaluate the uncertainty in population projections and the resultant parameters by calculating 95% confidence intervals (CI) around estimates of $\boldsymbol{\lambda}$ and LTRE contributions (Caswell 2001, Angert 2006). For each site and season, individuals with their stage, fruit production, and fate in the subsequent season were randomly selected with replacement to generate a bootstrapped dataset of equal size to the sampled population. Transition probabilities between aboveground adults and dormant rhizomes and number of fruits per individual were calculated from each bootstrapped dataset. A randomly selected site-specific sample of seeds per fruit was drawn for each individual in each bootstrap and multiplied by fruit production to yield individual fecundity estimates. Estimates of seed dormancy, seedling recruitment, and dormant rhizome mortality were calculated as above for each resultant projection matrix.

The authors used nonparametric randomization tests to assess hypotheses on differences in λ across sites for each seasonal transition interval (Caswell 2001). Datasets for each season comprised of permuted individuals were compared to the observed site-specific datasets. To generate a null model for seasonal comparisons of λ, they permuted individuals with their stage and fate randomly among sites within each seasonal transition intervals, keeping sample sizes for each seasonal transition interval fixed (Caswell 2001, Freville et al. 2004, Angert 2006). All rates were otherwise calculated as described for the seasons and site-specific bootstrapped projection matrices. A two-tailed *t*-test was then used to evaluate the significance of the observed standard deviation of λ for each site within season against the randomized standard deviation of λ for that season.

Finally, researchers compared versions of the projections for each season and site with different rate estimations to examine the influence of variation in the rates of annual seed dormancy, survival and maturation of seedlings, and dormant rhizome mortality on lambda. They systematically varied estimates of each of these rates by +/- 50% while holding all other rates constant and recorded the resultant change in λ.

4.3 Results

4.3.1 Spatiotemporal variation in performance

There was strong seasonal and site variation in the production of aboveground vegetation and fruits (Table 4.4, Figure 4.6). Plants were generally more robust in fall than in spring seasons, although there was considerable within-season variation in growth. Plants in the transplant site at ISEGS were generally smaller than the majority of plants at undisturbed sites, whereas plants in the solar field were generally comparable in size (Table 4.4, Figure 4.6). There was a high degree of variation in individual plant growth within each site and season.

Fruit production occurred predominantly in the two fall seasons, when fruits were produced at all study sites (Table 4.4, Figure 4.7). Only three fruits were produced in spring 2013: two at Bobcat and one at Umberci. No fruits were produced in spring of 2012 or 2014. In fall of 2012, both Umberci and Bobcat had significantly greater fruit production than the transplant site. In fall of 2013, all sites except Bobcat had higher fruit production than the solar field and transplants. Variance in fruit production within sites was large, with a few plants producing the vast majority of fruits.

Adult seasonal dormancy, the average proportion of seasons that each individual remained dormant below ground for a season or more, ranged widely across sites and seasons from 0 to 100%, such that in some seasons all plants, or the majority of plants were dormant whereas in others the majority of plants had active growth above ground (Appendix D, Table D1). Across all seasons dormancy was significantly higher in the transplant area than in all other sites (Figure 4.8). Dormancy was least common at Bobcat (Figure 4.8).

Because of the inability to exhume dormant adult plants non-destructively, the estimate of seasonal dormancy likely includes some deceased individuals. Recall that individuals were considered to be deceased when they were observed to be below ground for three seasons or

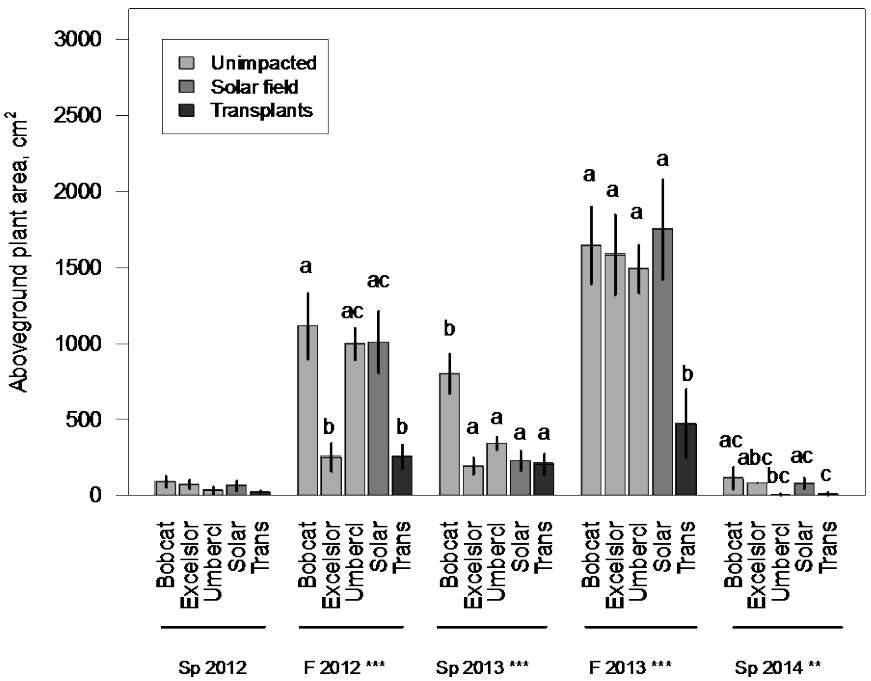
more. It is possible that high rates of dormancy in the transplant area in 2014 indicate higher mortality at this site that may be confirmed in subsequent seasons (Table D1).

Table 4.4: Variation in Performance of and Herbivory on ASCNYC Across Study Sites and Season

Response:	d.f.	Deviance	Residual d.f.	Residual deviance	*P*
A. Vegetative growth					
Site	4	64.07	618	1161.37	<0.0001
Season	5	368.74	613	792.63	<0.0001
Site:Season	18	69.4	595	723.23	<0.0001
B. Fruits/individual					
Site	4	46.854	299	298.64	<0.0001
Season	1	1.96	298	296.69	0.1615
Site:Season	4	23.42	294	273.27	<0.0001
C. Herbivory score					
Site	4	33.485	478	771.32	<0.0001
Season	4	207.782	474	563.54	<0.0001
Site:Season	16	97.714	458	465.83	<0.0001

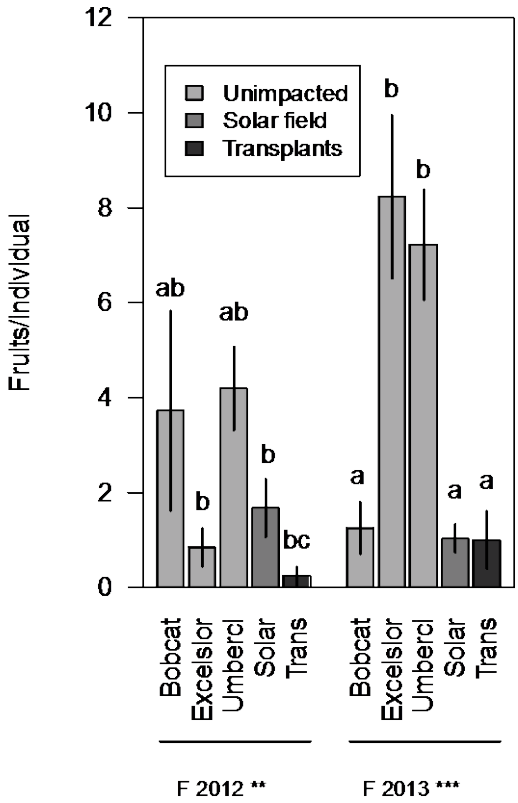
Results of separate negative binomial general linear analyses on A) Vegetative growth measured as seasonal total stem area (cm^2), B) fruits per plant, and C) herbivory score (range: 0-5). Seasons from spring 2012 – spring 2014 were included in the models for vegetative growth and herbivory. Only fall 2012 and fall 2013 were included in the model for fruit production due to lack of significant fruit production in all other seasons.

Figure 4.6: Temporal Variation in Seasonal Aboveground Plant Area of ASCNYC Across Unimpacted and Impacted Sites



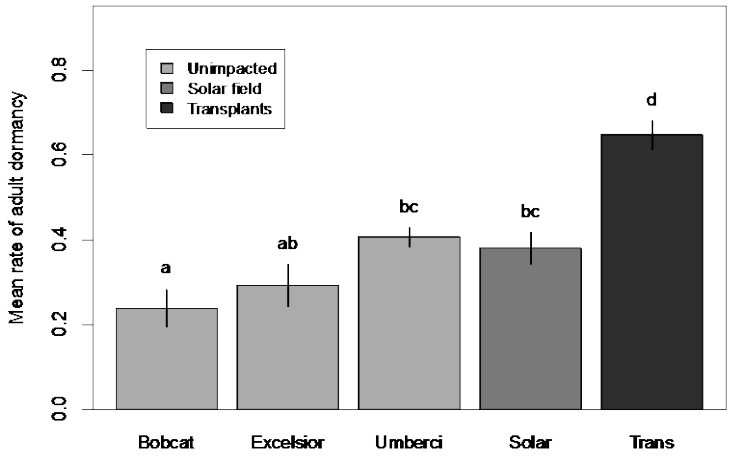
Spatiotemporal variation in aboveground total stem area, a metric of seasonal growth, over five study sites and five seasons. Solar field and Transplant sites are directly impacted by ISEGS; "Unimpacted" do not experience direct impacts. Data presented are means ± SE. Sp and F refer to spring and fall seasons, respectively. Asterisks indicate significant variation among sites within a season based on individual negative binomial linear analyses (***P*<0.001, ****P*<0.0001). Different letters within season represent significant differences in *post hoc* contrasts of sites within season to the level *P*<0.001. For example, in spring of 2013 plant area at Bobcat (b) was significantly greater than plant area at any other site (all a).

Figure 4.7: Spatial Variation in Fruit Production of ASCNYC across Three Unimpacted Populations and Two Impacted Sites at ISEGS



Spatiotemporal variation in fruits per individual for each site in the seasons of successful sexual reproduction: fall 2012 and 2013. Solar field and Transplant sites are directly impacted by ISEG; "Unimpacted" are located >5 miles from ISEGS. Data presented are means ± SE. Asterisks indicate significant variation among sites within a season based on individual negative binomial linear analyses (**P<0.001, ***P<0.0001). Different letters within season represent significant differences in post hoc contrasts of sites within season to the level P<0.002.

Figure 4.8: Spatial Variation in Seasonal Dormancy of Adult ASCNYC Individuals across Three Unimpacted Populations and Two Impacted Sites at ISEGS.



Adult seasonal dormancy rate is the proportion of adult plants that remain below ground in a given season. Error bars indicate standard errors around the mean of seasonal dormancy rates for each study site. Different letters denote differences between sites significant to the *P*<0.03 level or less.

4.3.2 Recruitment

In fall of 2012 emergence of new seedlings were observed in all of the focal populations, including within the solar field at ISEGS. There were no significant differences in seedling density between populations and sites.

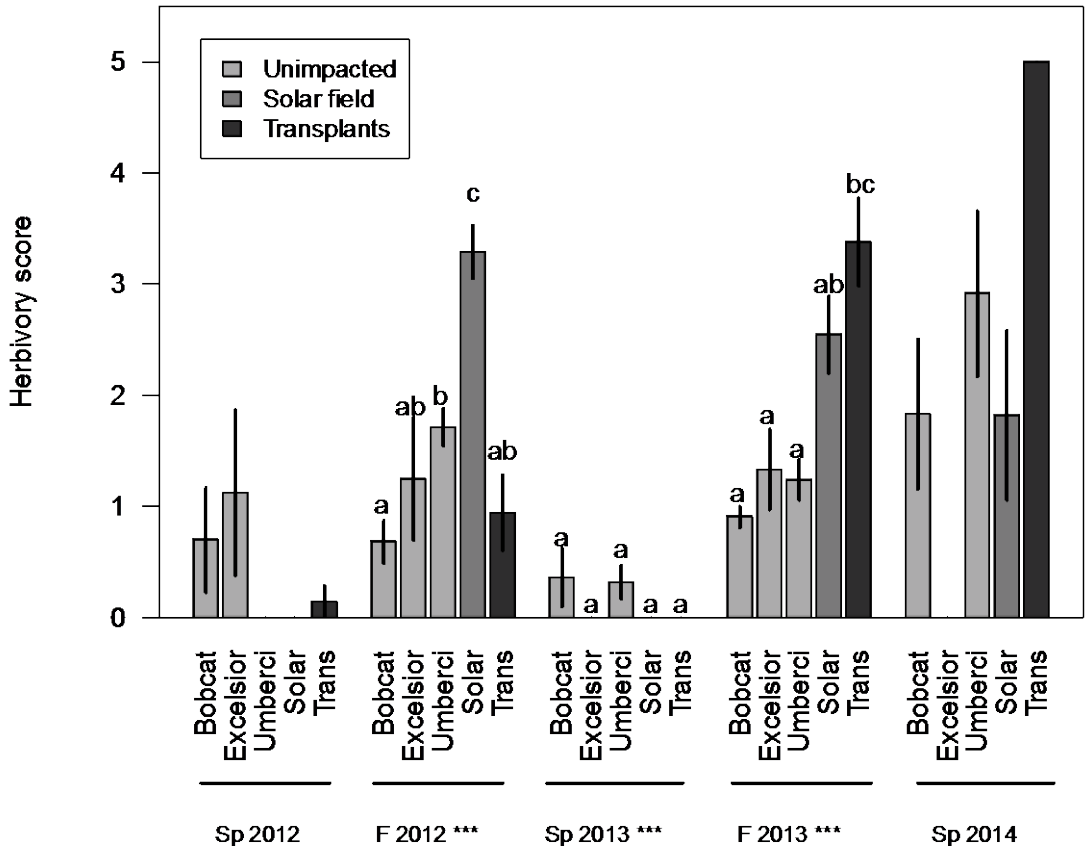
4.3.3 Spatiotemporal variation in herbivory

Herbivory rates differed significantly between season and across sites (Table 4.4C, Figure 4.9). Variation in the proportion of plants active aboveground in each season interacted with the intensity of herbivore pressure. For example, out of 59 aboveground plants in all populations (34%) in the spring of 2013, only a single plant at Excelsior had evidence of herbivory. In contrast, in spring of 2014 there were very low rates of plant emergence (34 of 172 individuals across all 5 sites, 20%) and relatively high herbivory damage across all sites (Figure 4.9). At the transplant site in ISEGS only two plants were active and each of these scored the maximum value for herbivory, five, indicating that the entire plant was damaged or removed. At Excelsior there were only three plants active above ground in spring of 2012, none of which had signs of herbivory. In the transplant site only two plants were active above ground and both had over 80% herbivore damage. In the fall of 2012 and 2013, herbivory damage was generally greater in the solar field and the transplant site in comparison to undisturbed populations (Figure 4.9).

There was an overall negative effect of herbivory on fruit production across all sites, even when controlling for the strong effects of site and season on fitness (Table 4.5). Despite these

differences in herbivory, the authors found no differences in jackrabbit scat in fall of 2014 across all surveyed sites (negative binomial GLM deviance=4.58, *d.f.*=56, *P*=0.3323).

Figure 4.9: Spatiotemporal Variation in Herbivory on ASCNYC Across Three Unimpacted Populations and Two Impacted Sites at ISEGS.



Spatiotemporal variation in herbivory score (range: 0-5) across sites within five seasons. Solar field and Transplant sites are directly impacted by ISEGS; "unimpacted" sites do not experience direct impacts. Data presented are means ± SE. Asterisks indicate significant variation among sites within a season based on individual negative binomial linear analyses (***P*<0.001, ****P*<0.0001). Different letters within season represent significant differences in post hoc contrasts of sites within season to the level *P*<0.001.

Table 4.5: Effects of Herbivory Score on Fruits per ASCNYC Individual at Two Undisturbed Sites Over Seven Seasons: Fall 2012-Fall 2014.

	Df	Deviance	Resid. Df	Residual deviance	*P*
Herivory score	1	6.87	630	716.74	**0.0087**
Site	4	70.8	626	645.94	**<0.0001**
Season	5	334.26	621	311.68	**<0.0001**
Herbivory score * Site	4	10.38	617	301.3	**0.0345**
Herbivory score * Season	5	8.83	612	292.47	0.1159

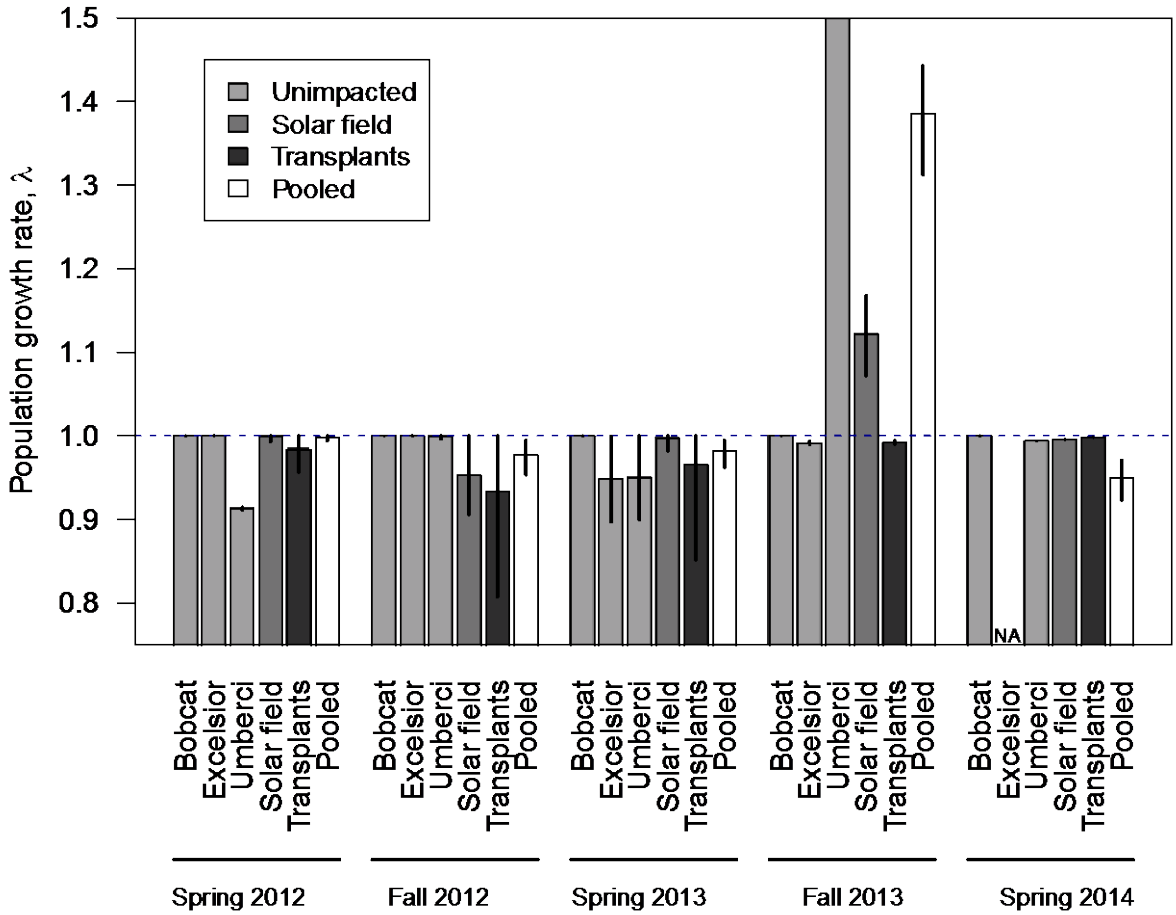
Differences were evaluated by negative binomial generalized linear regression. The non-significant three-way interaction between herbivory score, site, and season was dropped from the final model.

4.3.4 Spatiotemporal variation in asymptotic population growth rate

For each site and season, mean values of the asymptotic growth rate, λ, generally fluctuated at values near or slightly below one (Figure 4.10). This suggests two interpretations: that the focal ASCNYC populations were in a period of slight to moderate decline over the study period, which is reasonable considering the drought conditions, and/or that the model incorporates considerable demographic resilience, namely in the capacity for rhizomes to remain dormant for multiple seasons.

Values of λ ranged from 0.91 at Umberci in spring of 2012 to 3.38 at the same site in fall of 2013 (Figure 4.10). The pooled λ was significantly higher in fall of 2013, driven by the population boom at Umberci ($P<0.0001$ after Bonferoni correction for multiple seasons tested). There were no significant difference between values of λ between sites in any season other than fall of 2013, where λ at Umberci was significantly greater than all other sites (all sites $P<0.001$; Figure 4.10). This local boost was likely due to the prevalence of very localized monsoon rains, which stimulated high fecundity and seedling growth and recruitment to the aboveground adult class over this season. λ in the solar field was also significantly higher than in all sites other than Umberci in the same season due to this same precipitation event. In contrast, the transplant area received this precipitation, yet showed no such demographic response. Life table response experiments comparing the effect of season, site and their interaction on variation in λ reiterated these differences (Appendix D, Figure D1). There were strong effects of site-to-site variation on λ in fall 2013 and at Umberci (Figure D1).

Figure 4.10: Spatiotemporal Variation the Asymptotic Population Growth Rate (λ) of ASCNYC across Three Unimpacted Populations and Two Impacted Sites at ISEGS from Fall 2012 to Fall 2014.



Error bars represent bias-corrected 95% CI for each site and seasonal transition interval. Labels give the first of the seasons in the transition interval. Open bars represent permuted pooled population matrices. In fall of 2013, the pooled λ was significantly greater than in any other season and Umberci had a significantly higher value of λ than any other site, $P<0.001$. In fall of 2013, λ=3.38 at Umberci (CI: 2.48, 5.47).

4.3.5 Effects of herbivore exclusion

Herbivore exclusion at the Bobcat and Excelsior sites reduced herbivory scores and protected individuals from biomass reduction by herbivores (Table 4.6). However, cages did not exclude all insects, including some herbivores; caterpillars and grass were observed to be present within cages at both sites and in each season.

Table 4.6: Effects of Herbivore Exclusion on ASCNYC (Herbivory score and Aboveground Biomass at Two Undisturbed Sites during Seven Seasons Fall 2012-Fall 2014.

Response	Effects	Df	Deviance	Resid. Df	Residual deviance	*P*
A) Herbivory score						
	Exclusion Treatment	2	24.0635	257	179.17	**<0.0001**
	Site	1	0.0069	256	179.16	0.9336
	Interaction	1	0.0168	255	179.14	0.8969
B) Aboveground biomass						
	Exclusion Treatment	2	20.8394	244	311.58	**<0.0001**
	Site	1	4.9311	243	306.64	**<0.0001**
	Interaction	1	0.1039	242	306.54	0.74718

Differences were evaluated by negative binomial generalized linear regression. The non-significant three-way interaction between herbivory score, site, and season was dropped from each final model.

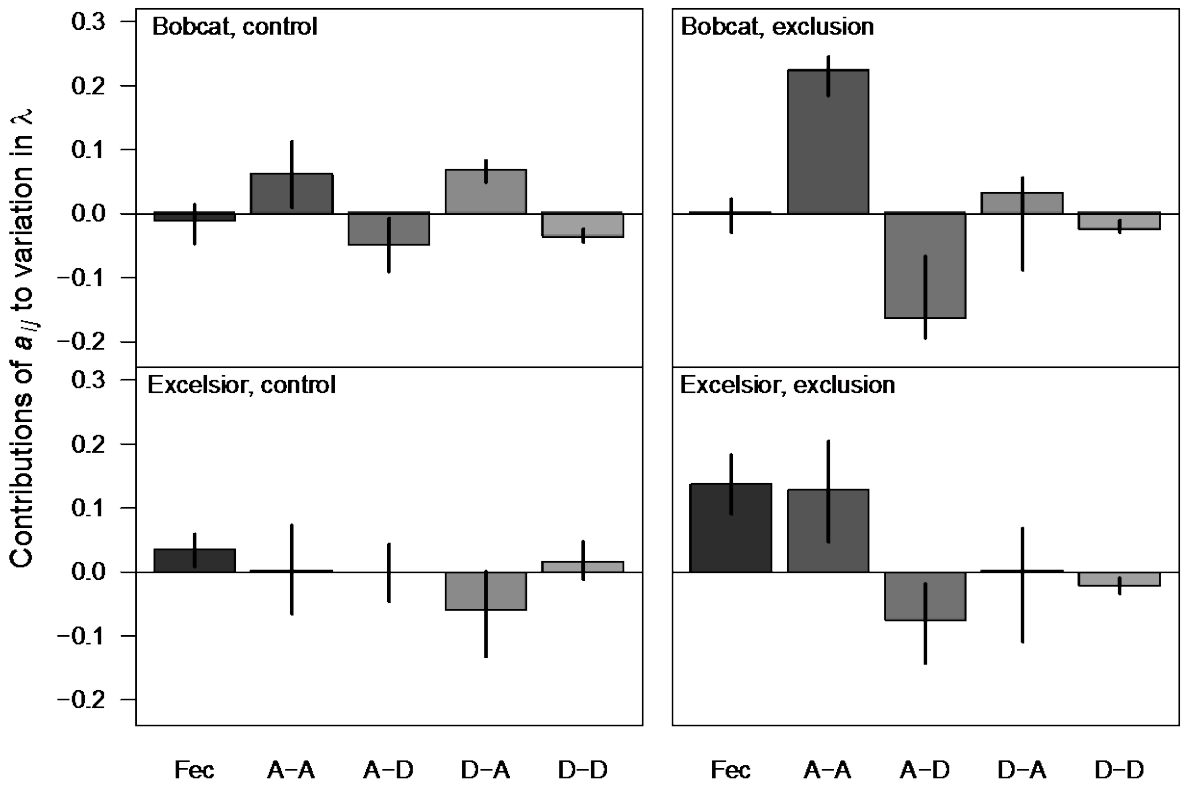
Herbivore exclusion cages had no effect on the population growth rate at either exclusion site or in any season (Table 4.7). However, LTRE revealed significant effects of herbivore exclusion cages on specific vital rates (Figure 4.11). The positive contribution of the adult-to-adult (A-A) transition and negative contribution of the adult-to-dormant rhizome transition were increased in herbivore exclusion. At Bobcat, the difference in A-A transition rates was significant as determined by non-overlapping confidence intervals. These findings suggest that herbivore exclusion reduces the demographic cost of adult emergence. Similarly, there was a significant increase in the contribution of fecundity to variation in λ at Excelsior under herbivore exclusion (Figure 4.11).

Table 4.7: Effects of Herbivore Exclusion on the Population Growth Rate, λ, of ASCNYC at Two Undisturbed Populations During Six Seasonal Projection Intervals Fall 2012-Fall 2014.

Site	Treatment	λ	CI, lower	CI, upper
Bobcat	No exclusion	0.95	0.77	1.00
	Exclusion	0.95	0.88	1.00
Excelsior	No exclusion	1.01	1.01	1.02
	Exclusion	1.02	0.97	1.02

Values of λ presented are the mean bootstrapped matrices with bias-corrected upper and lower confidence intervals. There were no significant differences between seasons or sites.

Figure 4.11: Contribution of Vital Rates to Variation in Population Growth Rates at Two Undisturbed Sites With and Without Herbivore Exclusion Fall 2012-Fall 2014.



Contribution of fecundity (Fec), adult stasis rate (A-A), adult-to-dormant rhizome transition rate (A-D), dormant rhizome-to-adult transition rate (D-A) and dormant rhizome stasis rate (D-D) to variation in λ at two undisturbed sites for control and herbivore exclusion plants.

4.4 Discussion

4.4.1 Overview

ASCNYC showed considerable demographic resilience over the four-year and seven-season study period. Despite comparatively dry conditions over the study period, estimates of the asymptotic population growth rate hovered within 5% of the replacement rate. Indeed, a significant population bonanza occurred at a single site, Umberci, in fall of 2013 following a localized strong monsoon event. The relatively stable population growth rate and successful recruitment demonstrate the species' ability to persist through dry conditions and capitalize on resource pulses.

The study found similar resilience to disturbance by utility-scale energy development at ISEGS. Individuals occurring within the solar field at ISEGS had similar aboveground growth and population growth rates for subpopulations in the solar field and transplant area were similar to those in undisturbed populations. Individuals in the solar field also responded to the local

monsoon precipitation event that stimulated the adjacent Umberci population, yielding a boost in the population growth rate. In contrast, transplant individuals showed no response to this resource pulse, highlighting their general failure to thrive.

Clear signs of impacts were found that are likely to reduce population growth at ISEGS over time. Fruit production was significantly reduced at ISEGS, and herbivory was increased. In addition, the rate of adult plant dormancy was increased in the solar field. Based on the analysis of dormant/deceased rhizomes during fall of 2014, the authors suspect that higher dormancy rates observed in the transplant area and solar field include many plants that will be concretely deemed deceased in the coming seasons.

Because of its strong effects on aboveground vegetation and fruit production, the negative effects of increased herbivory within the solar field may limit long-term persistence of this population. The findings of increased caterpillar herbivory within the solar field warrant additional study to determine if the solar field acts as an attractant to Monarch butterflies and other Lepodoptera. Despite these concerns, the study found clear evidence that the lower impact design of the solar installation, whereby native vegetation is left in place within the solar field, allows for recruitment and persistence of ASCNYC comparable to rates of recruitment in undisturbed locations. Direct assessment of the effects of the solar installation on the trophic system including the focal species, its herbivores and their predators is essential in order to inform the demography of this species and adaptive management.

4.4.2 Findings and Management Recommendations for Renewable Energy

4.4.2.1 Are there demographic differences between populations adjacent to and within ISEGS in comparison to natural, undisturbed populations?

Despite similar seasonal projections of the asymptotic growth rate, researchers found that the subpopulations in the solar field and transplant area had lower fruit production in comparison to undisturbed sites. Dormancy rates for adult plants were significantly elevated in the transplant area, suggesting higher mortality.

4.4.2.2 How does herbivory vary across the disturbance gradient?

The study found that herbivory was frequently increased in the solar field and transplant area at ISEGS. Given the negative effects of herbivory on fruit production, this is an important demographic effect that may have long-term repercussions for population persistence. Further research is needed to quantify the contributions of mammalian and invertebrate herbivores across sites. If mammalian herbivory is inflated within solar facilities, herbivore control measures or plant protection measures, such as caging, may be warranted. Where invertebrate herbivory includes sensitive species such the Monarch butterfly, herbivore control measures must clearly be implemented with great care. Furthermore, additional research is called for to determine how whole-trophic systems are altered by solar facilities. Data supporting a potentially important trophic system change at ISEGS that may influence several rare species include high bird mortality and high caterpillar abundance, which are suggestive of predator release.

4.4.2.3 Do dormancy rates vary across the disturbance gradient?

The two dormancy strategies deployed by ASCNYC, seed and adult plant dormancy, buffer the demographic effects of ecological stresses including drought and direct impacts of development. In the short term (our 4-year study), ASCNYC has shown considerable demographic resilience. However, long-term monitoring and analysis, over the course of 10-15 or more years, will be necessary to determine the long-term response of this species and other desert perennials to changes in desert climate and impacts of development including fragmentation and changes to local resources such as pollinator movement, eolian (windborne sediment) deposition, water, and shading.

4.4.2.4 Are the avoidance strategies deployed at ISEGS within the solar field effective means of mitigation?

The results of this study indicated that the avoidance measures within the solar field, termed halos, are an effective mitigation measure when paired with preservation of intact populations off site, at least in the short term. Persistence of individuals within the solar field halos and provides substantial ecological benefit over standard designs that eliminate rare plant populations and habitat entirely. In comparison, higher dormancy of transplant individuals and herbivory in the transplant area suggests that transplants are likely to be less effective in long-term conservation of this population.

Despite some negative effects of the solar field on individuals (reduced seeds/fruit, higher dormancy rates), survival and recruitment throughout halos in the three units of ISEGS in one of the study seasons indicates clear benefit over conventional utility-scale solar design in which entire developments are graded.

CHAPTER 5: Demography of *Penstemon albomarginatus* in California under varying climate regimes

5.1 Introduction

New regimes of temperature, precipitation, and extreme weather events are predicted for the "climate change century." Rare species are expected to be most impacted because of genetic and ecological constraints on population size, distribution, and response to perturbations (Morris and Doak 2002). For rare desert plants living on the geographic edge of their climatic tolerance, global change may severely reduce compensatory responses to a diminishing, unreliable resource base, thus increasing the probability and rate of population decline and ultimate extinction of such populations.

Population projection models can provide information on the trajectory of populations and the rates and stages that are most sensitive to environmental change and/or management. However, biological information on all vital rates is necessary in order to generate sound models. The uncertainties in vital rates that are impossible or challenging to measure can undermine confidence in model predictions and their applications.

The plants of arid-land ecosystems may be particularly sensitive to rapid effects of climate change because of the dramatic extent to which water shapes their biology and ecology (Noy-Meir 1973, 1974, Diffenbaugh 2008, Giorgi and Pal 2008). In addition, the desert southwest of North America is predicted to have a highly responsive climate (Kerr 2008, Diffenbaugh et al. 2009), with increased storm intensity, increased frequency and severity of drought and increased variation in water availability (IPCC 2007, Seager et al. 2007). Global climate change is anticipated to amplify the inter-annual climate cycles, including El Niño, or the Southern Oscillation (Chesson et al. 2004), which is responsible for significant variations in precipitation in the desert southwest. Extreme events with uncertain frequency will alter population dynamics and interactions among species, resulting in ecosystem-wide changes of considerable magnitude (Breshears et al. 2005, McKechnie and Wolf 2010). But desert plants also have traits that facilitate their persistence in extreme and uncertain environments, such as succulence, deep rooting, and C4 photosynthesis (Pavlik 2008). Many species also possess forms of bet hedging, by which temporal environmental variation is buffered by a perennial, stress-tolerant life form, exceptional seed dormancy, or physiological diapause (e.g. Venable 2007). These traits allow for a trade-off between the mean and variance of demographic performance and can provide greater long-term success by allowing the organism to capitalize on periodically favorable conditions.

Seed banking is a classic example of bet hedging that is common among desert plants. Multi-generational accumulations of seeds within the soil safeguard plant populations against environmental variation and genetic depletion by spreading the probability of miscued germination across many years (e.g., Cohen 1966, Doak et al. 2002, Ellner 1985, Venable 2007). Seedlings are recruited from the seed bank to the population *en masse* after 'trigger events',

storms that deliver an inch or more of precipitation in a short amount of time (Went 1949, Tevis 1958, Defalco and Esque 2014). However, such cryptic and ephemeral life stages pose a challenge for population modeling because they are difficult to monitor *in situ* and thus to quantify (Doak et al. 2002). Given that the seed to seedling transition in plants is analogous to birth in animals, it is essential to model the sensitivity of population growth rate to recruitment and to determine the effects of increasing climatic uncertainty on the predicted trajectory of the population through time. Improved monitoring and modeling techniques, as illustrated in this chapter, are critical to generating sound projections of population persistence and species extinction in rare desert plants as environmental change progresses.

Population viability analysis (PVA) is a primary tool for developing species-level conservation strategies because they provide predictions of population responses under alternative environmental and management conditions (Menges 2000a, Caswell 2001, Beissinger 2002, Morris and Doak 2002). Based on annual estimates of fitness components (survivorship, recruitment, and transitions between life history and/or size classes, PVAs estimate both deterministic and stochastic growth rates and explore the sensitivities of these measures to manipulations of fitness components (e.g., Tuljapurkar et al. 2009, Beissinger and Westphal 1998). Although PVAs have great potential for evaluating components that promote the increase or decline of populations, the vast majority of studies on plants are limited to 2-3 years of field survey data and few studies link growth rates to temporal environmental variation (Crone et al. 2011).

Herein the authors apply a projection modeling approach to estimate population growth rates of the rare desert perennial, *Penstemon albomarginatus* (hereafter PENALB), and the sensitivity of those rates to changes in fitness components, variations in climate, and impacts of herbivory. A 12-year study was conducted on the sole California population of PENALB at the western limit of its range in the Mojave Desert. Estimates of the asymptotic population growth rate (lambda, λ) were derived using deterministic and stochastic methods for ten seasonal transition intervals. The sensitivity of lambda, λ, to changes in fitness components was analyzed, especially the recruitment of seedlings from seed. Researchers then evaluated the effects of three alternative climatic scenarios to estimate quasi-extinction probabilities under different drought frequency regimes. Life-table response experiments were applied to assess the sensitivity of lambda to those regimes and to determine the relative impacts of herbivores by simulated exclusion. Specifically, the following questions were addressed:

1) What is the likelihood of persistence of the California population of PENALB?
2) Which life cycle (stage) vital rates most affect persistence?
3) To what extent does herbivory affect the trajectory of population decline?
4) How are fitness components (survivorship, recruitment) and lambda affected by changing climate (drought) regimes?
5) How do seasonal climatic attributes affect lambda and quasi-extinction probability?

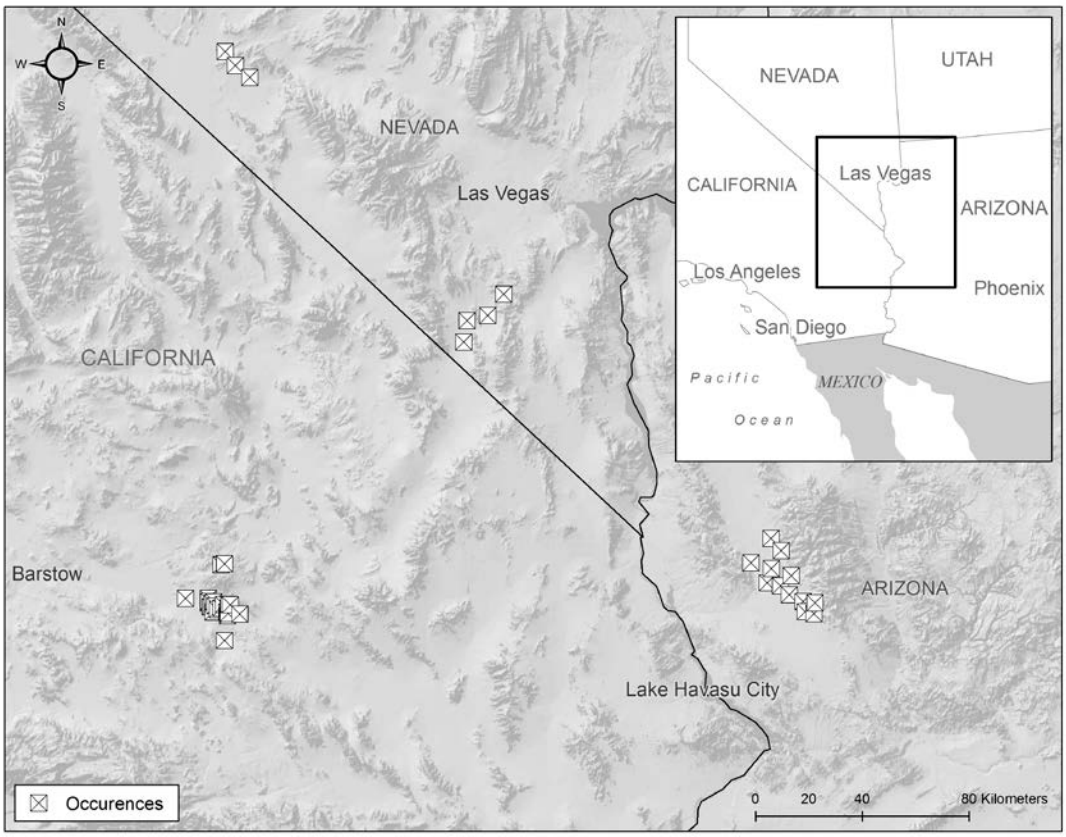
The overall goal is to use these analyses to develop a framework for mitigation of solar energy impacts on PENALB and explore the implications of these findings for other plants in the region that are similarly positioned at the edges of their climatic niches.

5.2 Methods

5.2.1 Study Species, Population Attributes and Habitat Characteristics

Penstemon albomarginatus (M.E. Jones, Plantaginaceae), white-margined beardtongue, is a rare perennial hemicryptophyte with disjunct populations in California, Arizona, and Nevada (Figure 5.1). The California Native Plant Society ranks PENALB as a CRPR 1B.1 species (endangered in California and elsewhere; very threatened), but due to the existence of three larger populations in Nevada and Arizona, it has yet to be protected by federal or state endangered species laws. Plans for large-scale changes in land use in the desert southwest, including the proposed construction of utility scale solar energy facilities near both the California and Nevada populations, may impact these populations and their habitats directly and/or indirectly in the near future.

Figure 5.1: Map of the Complete Distribution of PENALB



PENALB grows up to 35 cm tall with several to many herbaceous stems arising from a buried root crown (Figure 5.2). For much of the year, plants are not visible above ground, except for the remains of past year's inflorescences. As an iteroparous perennial, stems emerge for the winter-spring growing season, dying back to the ground during the hot Mojave summer. When infrequent monsoon rains provide sufficient moisture, leafy stems can re-emerge in late summer, though the authors have not observed them to be reproductively successful. Inflorescences produced in spring bear pink-lavender flowers with an ovary containing 50-52 ovules. Self-compatibility is unknown for this species, though common for other members of the same genus. Seed set is low in natural populations, limited to 15-35 seeds per fruit (Scogin 1989, Baldwin et al. 2012). The analysis of seeds collected in 2011 and evaluated via x-ray found that over 95% of seeds contain viable embryos (Appendix A). No special dispersal mechanism is apparent. Seedling emergence is episodic and is rarely observed during dry years (author observations, Scogin 1989).

Figure 5.2: PENALB in Flower

Photos of PENALB: A) An individual plant within the California population. Coin tag shown for scale is 1.5 inches in diameter. B) Detail of flowers and while leaf margins for which it is named.
Photo credit: Kara Moore (2011).

PENALB occurs in four populations in the Easter Mojave and Sonoran Deserts of California, Nevada, and Arizona (Figure 5.1). The sole California population of PENALB consists of small, scattered subpopulations limited to an approximately 4-mile long complex of sand sheets and shallow washes near Pisgah Crater and Lavic Lake, San Bernardino County, USA (N34.7851°, W116.39940°; Figure 5.3). Throughout this area, the subpopulations have ranged from a single individual to up to several hundred plants over the last 20 years (CDFG 2012). Several of these are found within an Area of Critical Environmental Concern (ACEC) designated by the Bureau of Land Management (Figure 5.3). The study utilized data obtained from nine subpopulations first monitored in 1994 and another seven, apparently new subpopulations added in 2011

(Figure 5.3). During the 12-year observation period the largest subpopulation size was 29 plants. The minimum subpopulation size was arbitrarily set at six plants in an area of 100 m^2. Overall, the average subpopulation size was 7.47 plants (σ^2=32.77).

Multiple surveys suggest that the collective size of these subpopulations fluctuates greatly over short periods of time. Scogin (1989) reported that the Pisgah occurrence consisted of "more than 450" individuals. Only four years later, Sheldon reported 4420 (Smith 2001). In 1997, a census led by André counted 2200 in individuals greater than 3-cm in diameter (unpublished data). The 2011 survey located approximately 200 adult plants, as did another independent survey (Stephen Zitzer, unpublished data). In addition, researchers located a previously unknown subpopulation 16 km north of Pisgah that consisted of eight adults. They attempted to find all other known historic occurrences in California observed since 1950, but none outside of a 20-km area in the vicinity of Pisgah Crater were located (Figures 5.1 and 5.2). Populations may be extirpated or historic collections may have been mapped to incorrect locations. Some could persist in areas of private or military property that were inaccessible during these surveys.

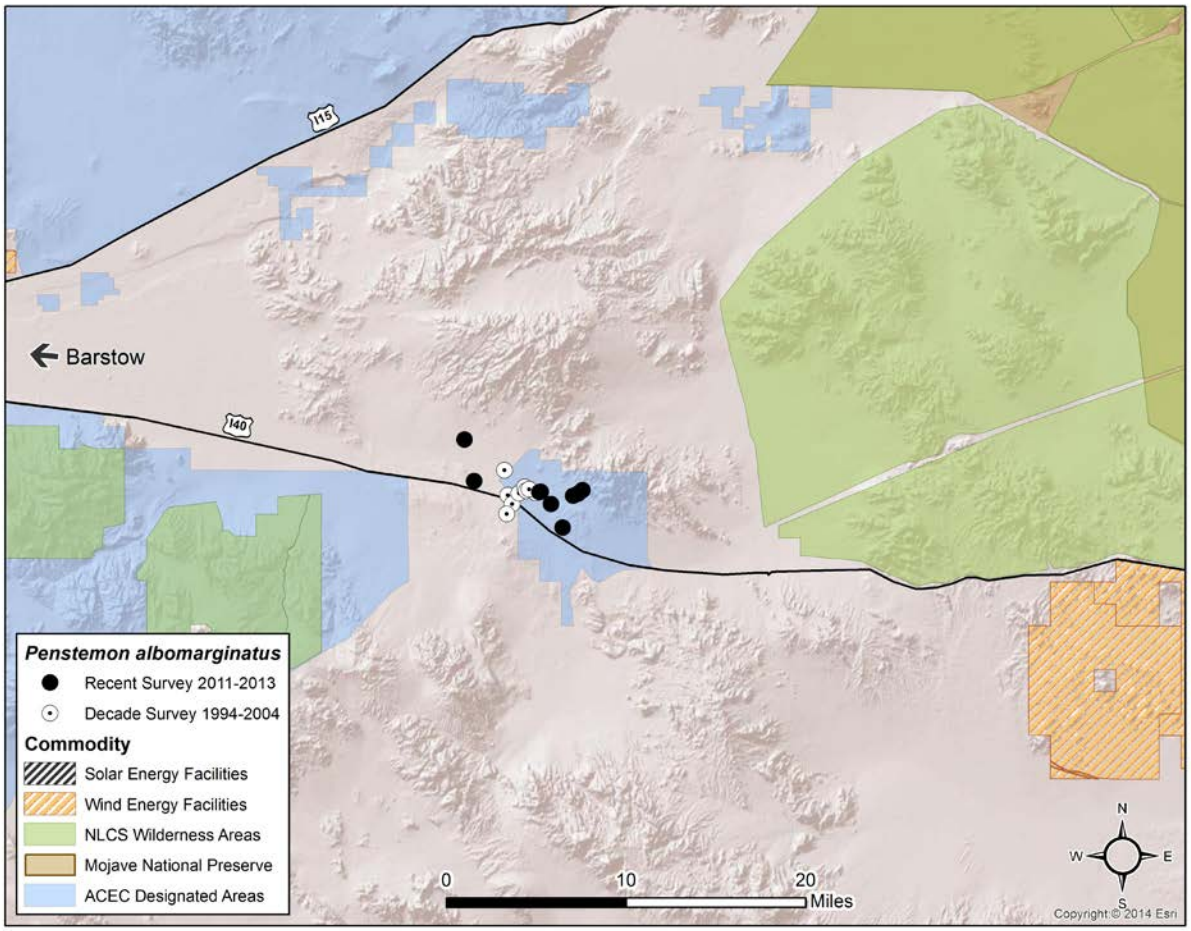
The habitat of the Pisgah occurrence consists of deep but semi-stabilized deposits of windblown sand that originated from the escarpment to the west (Etyemezian et al. 2010). Some sands are captured in shallow washes carved into the site; others are gathered into an undulating sheet with 10 to 30 cm of total relief. Chemically, the sands are slightly alkaline (average pH = 7.6), and typically nutrient poor (Scogin 1989). The vegetation is low dune scrub vegetation dominated by *Tiquilia plicata*, *Abronia villosa,* and *Hilaria rigida*. A regional matrix of *Larrea tridentata* and *Ambrosia dumosa* surrounds and interdigitates with the sand sheet. This habitat is bisected by CA Highway 40, a major railway, electric power transmission lines, and service roads that facilitate disturbance from off-highway vehicles.

5.2.2 Modeling Population Growth Rates

5.2.2.1 Monitoring the demography of subpopulations

Demographic data from the Pisgah PENALB subpopulations were collected during two sampling periods: one lasting ten years (1994-2003, "decade sampling") and one lasting two years (2011-2012, "recent sampling"; Table E1, Figure 5.3). Decade sampling data were collected and contributed by James André (University of California, Granite Mountains Desert Reserve). During the decade sampling, cohorts in nine subpopulations were sampled: two beginning in 1994 with seven more added a year later. All individuals greater than 3 cm diameter were permanently tagged, and in each subsequent year, plant survival, canopy size and reproductive data were recorded during peak flowering, early to mid April. Size was measured as the average of the widest canopy diameter and its perpendicular chord. Seedlings (plants 3 cm or less) were noted as present but were not quantified; sampling was conducted in late March or early April, after some seedling mortality was likely to have occurred. In the decade sampling period, all tags were surveyed each year, even where a plant had not emerged in the previous year; individuals that died or failed to emerge were not "replaced" in the population sample.

Figure 5.3: Demographic Subpopulations Surveyed in the Decade and Recent Sampling of PENALB in California



Recent survey points indicate subpopulations surveyed by André, recent survey points indicate the field study implemented for this report.

The recent sampling was initiated in 2011 at nine Pisgah subpopulations: two that persisted from the decade sampling and seven that were recently added to the study and are of unknown age. All were comprehensively tagged and subsequently monitored. Considerable effort was made to relocate the previously delineated subpopulations (from the decade sampling), but all except a single subpopulation (represented by two adult plants both ~ 20 cm in diameter) had been extirpated due to unknown causes. At peak flowering, plant size was recorded as above. The number of inflorescences was tallied on each individual and three inflorescences per plant marked to determine the numbers of buds, flowers, and fruits output by each. Several (usually three) individual mature fruits were collected from each plant prior to dehiscence and the number of mature seeds per fruit counted.

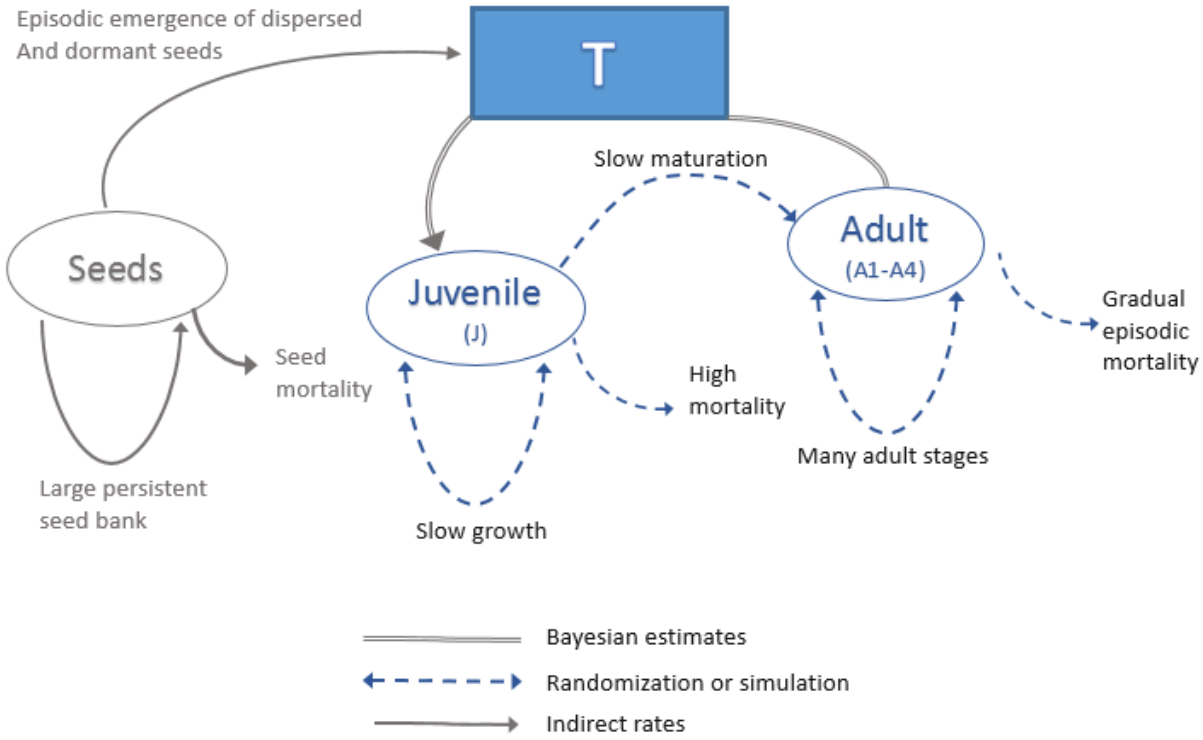
During recent sampling, the impacts of herbivory were recorded on individual plants. Damage to each was assigned a scalar value 1 to 5 that represented 20% incremental reductions in

overall canopy volume. At each subpopulation, a random subset of seedlings (if present) and adults were selected for herbivore exclusion. These were caged prior to inflorescence growth using 1-cm wire mesh screen, closed at the top and weighted at the bottom, effective against lagomorphs and rodents. In April of 2011, 97 seedlings were caged, 26% of all observed, and 39 marked adult plants (35%). Prior to caging in 2011 there were no observations of herbivory recorded, but just two weeks after cage installation, stem herbivory (clipping) was apparent on non-caged control plants. Cage integrity was maintained as necessary throughout the study. Non-caged plants were used as controls. The authors used generalized linear models to compare adult plant survivorship between subpopulations and seasons, and to assess the effects of herbivore exclusion. Multiple comparisons were made using Tukey's HSD.

5.2.2.2 Estimation of stage structure

Projection matrices were constructed based on the field demographic data for life history stages and individual size classes prior to seed dispersal (Caswell 2001). Matrices included the juvenile size class (J) and four adult size classes (A1-A4; Figure 5.4) for each season during the two sampling periods (1994-2003 and 2011-2012). By necessity, the juvenile class included seedlings (true recruits, < one year old) and very small plants (re-emerged, > one year old) because these could rarely be distinguished in the field. Survivorship within adult size classes was estimated from re-emergence of marked plants between years. Because re-emergence after a year of non-emergence was not observed over either study period, non-emerged plants were assumed to have died. In this model the matrix elements in row 1 for each column incorporate both the estimated population seed output (fecundity) and J class survivorship.

Figure 5.4: **Diagram of the Herbaceous Perennial Life History of PENALB**



Parameters in the population viability analysis (PVA). A persistent seed bank and re-emergence of adult plants buffers environmental variation, but are challenging to survey directly. Emergence of seedlings and mortality occur in response to episodic favorable and stressful conditions in a subset of seasons. The transition from seed to juvenile, T, is estimated via a Bayesian model based on observed seed output and juvenile survivorship. Juvenile and adult survivorship are randomized and/or simulated. Observations of seed mortality, dormancy, and episodic emergence are used indirectly to bound values of T used in permutations of the PVA.

Plants from all subpopulations were assigned to five stage classes based on average diameter (largest diameter and its perpendicular chord), recorded at peak flowering in each sampling year. These classes were J= 0-10 cm, A1 = 11-20 cm, A2 = 21-30 cm, A3 = 31-40 cm, A4 = 41+ cm. The juvenile class (J) included both new emergent and re-emergent (> 1 year old) plants < 11 cm in diameter; these small plants were all non-reproductive. The smallest individual to produce seed in any year was 11 cm (class A1). Plant size class was assigned annually, independent of previous determinations because above ground size of herbaceous perennials commonly fluctuates from year-to-year and is not strictly related to age (Roach et al. 2009).

5.2.2.3 Seed to juvenile transition

Seed output data were collected in the field during 2011 and 2012 for all marked individuals within each adult size class. Yet, these seasons differed in both seed and fruit output per individual and rates of inflorescence and fruit failure were high (see Appendix E). To incorporate uncertainty in the estimates of seed, fruit, and inflorescence output, the researchers used Bayesian estimation of their mean values (see Appendix E – Bayesian framework).

Number of seeds per fruit and numbers of fruit per inflorescence were estimated without regard to size class. For inflorescence number per plant, where there was sufficient data across size classes, the model provided mean inflorescence number in each size class. The authors saved 10,000 draws from the estimate of the posterior negative binomial distribution of the estimates of seed, fruit, and inflorescence output by size class. For plant p in year y, seed output (number per individual plant) was estimated as the product of seeds per fruit, fruit per inflorescence, and inflorescences per plant for diameter class c, drawn randomly from these posterior distributions:

$$\text{Seeds}_{py} = \text{NB}(\text{seeds/fruit}_p) * \text{NB}(\text{fruits/infl}_y) * \text{NB}(\text{inflorescences})_c$$

A negative binomial posterior distribution of seed to J transition rates (T) was generated based on the observed values for the population-level relationship between seed output and J class recruits. NB indicated variables with negative binomial distributions.

$$T = \text{NB}(\Sigma\, J_{py}/\Sigma\, \text{seeds}_{py})$$

By estimating T based on these comprehensive metrics, researchers inherently incorporate seed dormancy, seed mortality, and seed bank origin into the pool of recruits (Figure 5.4).

Census for J (juvenile) plants was conducted in four years (1994, 1995, 2011, and 2012) resulting in three matrices of observed data from measured J class densities and transition probabilities. For years without J surveys, these densities and probabilities were estimated using a randomization procedure. The procedure added an annual simulated 100 J class individuals, drawn from the pool of all J observed in any census year. These individuals were added to the J class in each year 1996-2003 to account for the fact that a number of emergents were likely overlooked in some years without explicit seedling and J surveys. To be directly comparable, the four census years with observed J census data were also randomized, such that each size class was built with the same number of randomly drawn plants as recorded in the field data set (Morris and Doak 2005). Because classes were drawn with replacement from the year under construction, a typical class could include some individuals more than once others not at all. The authors used this method to construct 10,000 bootstrapped projection matrices for each year (Morris and Doak 2005).

5.2.2.4 Growth rate estimation

A bootstrap resampling procedure was used to construct annual projection matrices and subsequently estimate deterministic and stochastic values of lambda (λ), matrix sensitivities and elasticities, and the corresponding bias-adjusted confidence intervals (Caswell 2001, Morris and Doak 2005). For each year, the authors took the mean of the resultant set of n=10,000 bootstrapped matrices generated at the mean transition rate from seed to J class individual, T:

$$H_y|T = \frac{\sum_{b=1}^{b=n} A_{yb}|\bar{x}T}{n}$$

which were calculated based on the mean seed to J transition rate, $\bar{x}T$. They used $Hy|T$ to calculate three versions of the asymptotic growth rate: 1) λ_a, the mean matrix arithmetic growth

rate for the 10-year period, 2) λ_s, the stochastic population growth rate estimated by simulation, and 3) λ_T, the stochastic population growth rate by Tuljapukar's approximation.

To calculate the deterministic growth rate, λ_a, they first averaged the 10 $H_y \mid T$, then projected this grand mean matrix via the formula $n_{(t+1)}=A * n_{(t)}$ for 100 time steps. The dominant eigenvalue of this projection matrix is the asymptotic population growth rate, λ_a, based on average survivorship and fecundity (seed output) over time, and describes average population performance (Caswell 2001). It commonly differs from the long-term stochastic growth rate, λ_s, in highly variable environments (Tuljapurkar et al. 2003; Boyce et al. 2006). Here the authors focus on these metrics as comparative measures of demographic success under different climatic and herbivory scenarios.

They calculated λ_s, by randomly selecting successive matrices from $H_y \mid T$ and averaging the successive growth rates for 50,000 time steps (Stubben and Milligan 2007, Morris and Doak 2005). They calculated matrices of reproductive values and stage distributions as part of the stochastic demographic analysis following Caswell (2001). The difference between λ_a and λ_s can be used to estimate the influence of temporal variation in survivorship and fecundity on population growth rates (Buckley et al. 2010). Finally, they calculated λ_T, Tuljapurkar's approximation, which takes into account how stochastic variation in the matrix elements affects the long-term stochastic growth rate, for 50,000 time steps (Caswell 2001). It can be more accurate in cases where there is co-variation between matrix elements within the same year but may not be as accurate when there is a high level of temporal variation (Morris and Doak 2005, Stubben et al. 2012). Estimates of the population growth rate were log-transformed ($\log \lambda_{a,\, s,\, T}$, = $k_{a,\, s,\, T}$) when comparing between expressions of λ. Population growth rate $\lambda>1$ ($k > 0$) denotes an increasing population size, whereas $\lambda<1$ ($k< 0$) denotes decreasing population size.

5.2.2.5 Sensitivity and elasticity analysis

The authors conducted a sensitivity analysis of the effect of variation in estimated T (seed to J transition rate) on λ_s (stochastic population growth rate). Twelve replicates of the population dynamic model were run in which a single value of T was used to generate the bootstrapped projection matrices. They first included the 20% quartiles of the $\bar{x}T$ (mean seed to J transition) distribution, including the smallest and largest probabilities, as well as $\bar{x}T$. In addition, they included replicates of the even multiples of mean $\bar{x}T$ up to max$T$. In all subsequent analyses, they used $H_y \mid T$ (annual mean projection matrices) which were from the bootstrap analysis generated based on $\bar{x}T$.

In addition, the authors calculated eigenvalue sensitivities and elasticities of λ_s of $H_y \mid T$ (Caswell 2001). These values can identify targets and tools for conservation management and mitigation because they highlight transitions that have the strongest effects on population growth rate (Heppell et al. 2000). Because they sum to one, they can be interpreted as the relative contribution of each fitness component to λ_s. The researchers also summed the elasticities calculated for each T into groups representing seed output and recruitment (eF), positive growth (eG), and survival and stasis (eL) and compared the relationship between the elasticity of these groups and λ_s (Silvertown and Franco 1993, De Kroon et al. 2000).

5.2.3 Responses of Fitness Components to Alternative Climate Regimes

5.2.3.1 Effects of seasonal variations

Climatological data were obtained from the National Oceanic and Atmospheric Administration's station at the Barstow-Daggett airport (http://madis.noaa.gov/) for the period of the study, October 1993 to August 2012. These included monthly-accumulated precipitation and mean, maximum, and minimum monthly temperatures. PRISM weather data were also extracted for the HADGEM A1B future (2080-2099) climate model for comparison with weather recorded at Barstow-Daggett over the observation period (PRISM 2010).

5.2.3.2 Effects of dry and wet season frequency on quasi-extinction risk

The frequencies of dry and wet precipitation cycles (equivalent to years) can affect fitness components, population growth rates and persistence. The authors used stochastic simulation to compare the effects of three dry and wet regimes on the persistence of PENALB populations. Quasi-extinction probabilities were estimated as the frequency of fitness component values from a severe dry year (2001-2002) and from a high precipitation year (1997-1998) varied in the demographic dataset. During the dry year, precipitation from October to April was a mere 3.4 mm, 34% of mean precipitation for the same monthly interval during 1991 to 2011. During the wet winter, precipitation from October to April was 117.6 mm, 158% of mean precipitation for the same monthly interval during 1991 to 2011. Based on the annual matrices $H_y \mid T$, projected population responses were compared to 1) current climate regime (using all seasonal matrices, $H_y \mid T$, for the two sample periods, 1994-2003, 2011-2012), 2) a regime having a 30% increase in the frequency of dry growing seasons (Kelly and Goulden 2008) and 3) a regime having a 30% increase in wet growing seasons. Each stochastic simulation was run for 50 seasons with 1000 replications.

5.2.3.3 Effects of geographic variation

To assess variations in climate regimes between the California population and populations in adjacent states, researchers determined the locations of PENALB in Nevada and Arizona by georeferencing occurrences catalogued on by the Global Biodiversity Information Facility (GBIF, http://www.gbif.org/) in ArcMap (10.1, ESRI 2015). They located a total of 14 occurrences outside of California, constituting 3 large populations documented to have more than 100 individuals of the species (Etyemezian et al. 2010). PRISM climate data for these locations were then used to compare 30-year normal and seasonal precipitation regimes during the 1990 to 2012 period. The authors used ANOVA to assess differences and Levene's tests to explore patterns in variance in precipitation between locations and seasons.

5.2.3.4 Life-table response experiments

They used two separate fixed-design life table response experiments (LTRE) to model λ as a linear function of 1) seasonal climate transition interval, y, and 2) herbivore exclusion during 2011, h via the models:

1. $\lambda_y = \lambda_{..} + \alpha_y$ and
2. $\lambda_h = \lambda_{..} + \alpha_h$

where α_y is the effect of the yth climate season and α_h is the effect of the herbivore exclusion treatment relative to the projected growth rate of the reference matrix $\lambda_{..}$ (Horvitz and Schemske 1995, Caswell 2001, Angert 2006). Main effects were compared to assess the differences between individual matrix entries and the sensitivity of that entry against a mean or pooled matrix representing the general response of the population (Horvitz and Schemske 1995, Caswell 2001, Angert 2006). A pooled reference matrix was used, which weighted transitions by their frequency over the entire set of observations (Angert 2006).

The authors followed the same bootstrap, simulation, and resampling procedures as described above to generate separate transition matrices for; 1) drought seasons that had less than 25% of average precipitation (2001-2002, 2011-2012), favorable seasons that had greater than 25% more than the average precipitation (1994-1995, 1997-1998), and all other years and 2) caged and non-caged plants (in 2011 only). In each LTRE the pooled matrix was generated from all non-caged plants. They ran 200 bootstrap replicates, generating novel transition matrices for the treatments and the pool and estimated of the mean sensitivity of each treatment (Caswell 2001). From these replicates the authors calculated the mean and bias-adjusted 95% confidence intervals. Differences in mean sensitivity were considered significant when confidence intervals were non-overlapping (Efron 1987, Caswell 2001).

All analyses and simulations were performed by writing custom scripts, many of which utilized functions from the popbio library (Stubben et al. 2012) in R (R Development Core Team 2007).

5.3 Results

5.3.1 Population Attributes

5.3.1.1 Fluctuations in population size

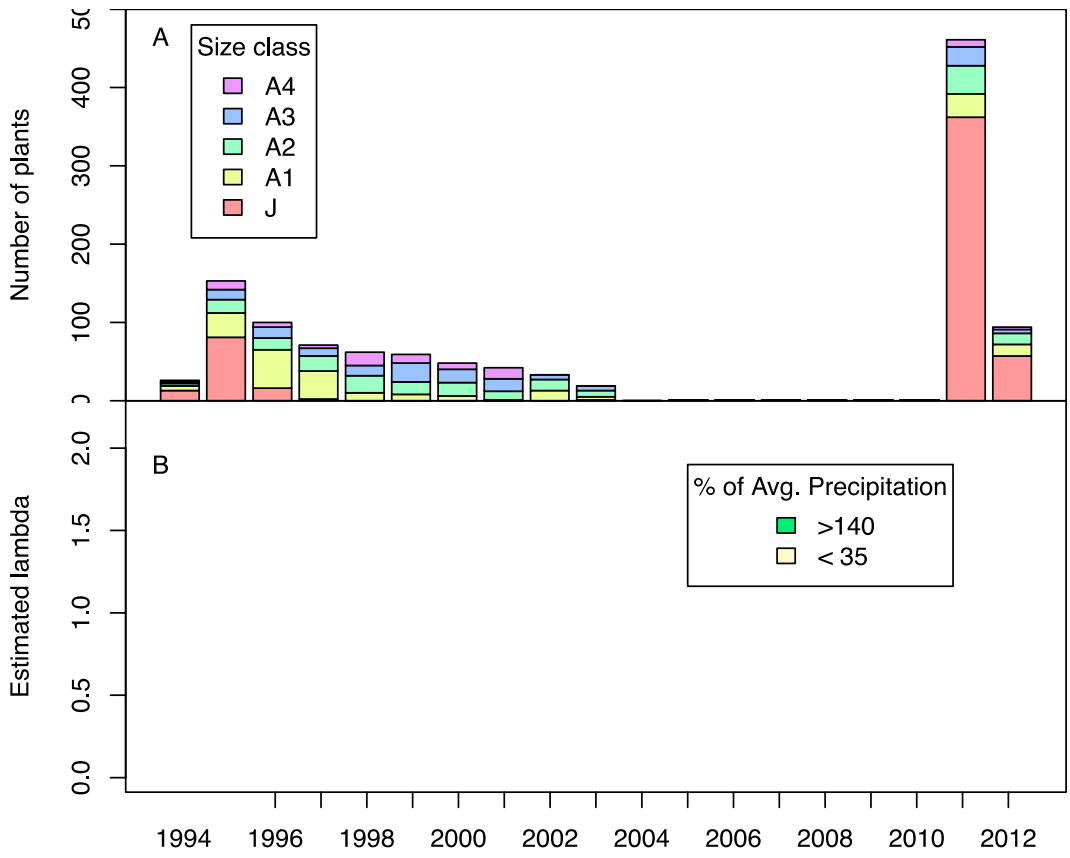
Population size of PENALB at Pisgah both at large and within the subpopulations fluctuated considerably over both the decade and recent sampling periods (Figure 5.5, Table 5.1). The study found considerable decline from the 1993 local peak population size of 4420 individuals to a count of only 67 adult individuals in 2012, none of which yielded fruit. Indeed, researchers tallied the 2011 population size to be 461 individuals, a count that included 362 new seedlings. However, only 37 of these seedlings survived to the 2012 season, which was largely due to experimental protection that the project team provided them from herbivores (see results below).

Table 5.1: Population Size and Mean Size and Inflorescence Number of Individuals During the Study Period.

	Year	# S-pops	# Active Plants	Diameter (cm)		# Inflorescences/plant	
	Decade sampling	n	n	$\bar{x}$	*CV*	$\bar{x}$	*CV*
	1994	1	26	0.87	13.3	2.97	35.3
	1995	9	153	0.88	13.3	2.37	47.8
	1996	9	100	1.00	12.7	1.75	10.7
	1997	9	71	0.86	13.0	1.99	21.1
	1998	9	62	0.54	15.1	1.29	66.0
	1999	9	59	0.40	12.4	1.23	62.4
	2000	9	48	0.58	14.4	1.48	32.9
	2001	9	42	0.48	15.1	1.09	71.9
	2002	9	33	0.63	11.4	1.53	6.6
	2003	9	19	0.97	14.2	2.42	31.9
	Recent sampling						
	2011	9	461	1.52	11.4	1.94	22.3
	2012	9	94	3.00	7.2	1.96	4.7

Number of subpopulations (S-pops) and active PENALB plants present at study populations in the decade and recent sampling periods and their diameter and inflorescence counts. Diameter is the mean of the largest cross section. For the decade sampling, number of inflorescences was estimated as the median of the inflorescence classes deployed by André. In the recent sampling number of inflorescences given reflects actual counts for each individual.

Figure 5.5: Population Stage Structure and Deterministic Growth Rate



Population A) size class distribution and size B) deterministic asymptotic growth rate, λ_a, over both sampling periods; note that there was no plant data collection 2004-2010. In A, bars show the number of plants in each size class across all subpopulations surveyed. Two subpopulations were surveyed in 1994, nine were surveyed in each subsequent year. In B, box plots show 10,000 annual bootstrap estimates of λ_a for each year. Box limits are the 25th and 75th quantiles of λ_a. Whiskers extend to the minimum and maximum values, excluding outliers, which are marked by circles. Boxes shaded yellow represent "dry" years in which precipitation was less than 35% of mean precipitation whereas those in green represent "wet" years in which precipitation was greater than 140% of the mean. Year labels are the second year of the transition interval.

5.3.1.2 Survivorship and mortality

Over the 12-years of sampling, there were no significant differences in survivorship between subpopulations. Survival rates were driven by local factors that have similar effects on the individual subpopulations, such as weather and herbivory. The inability of researchers to relocate 99% of the decade sampling plants most likely indicates that very few are long-lived. In fact, the study could only document two individuals that equaled or exceeded 10 years old (André and Moore, personal observation). On average, decade sampling individuals were surveyed for a mean of 5.2 years prior to mortality. Though this is a poor surrogate for longevity, it does indicate that plants are unlikely to persist for longer periods of time.

The relationship between diameter and survival varied significantly among years (z= -3.944, P<0.0001), with larger plants having higher rates of survival. Mortality of seedlings and additional mortality of adult plants following the 2011 season was significantly higher than mortality in all previous observed seasons except in 2002, the driest year (all significant to the P<0.05 level in Tukey's HSD).

During the sampling decade (1994-2003), the presence of seedlings were noted but were not added to the monitored demographic cohort (André, unpublished data). Only 17 (15.2% of the cohort) of the 112 J class individuals marked on initial surveys in 1994 or 1995 persisted for more than one season. A single, non-reproductive juvenile persisted for a third season (0.8% of the cohort).

Rigorous monitoring for seedlings took place during the recent sampling, as seedlings with evident cotyledons were observed in four subpopulations, including 319 seedlings in one subpopulation (most likely the progeny of a single large plant nearby). Of the 352 seedlings marked during spring 2011, 157 (44.6%) were alive in May and 57 (16.2%) survived to re-emerge in spring 2012. The authors suspect that survival of these seedlings was a result of localized summer precipitation not registered by weather stations off-site. No new seedlings were observed during the dry 2012 season despite extensive searches throughout the study area.

5.3.1.3 Fecundity

Surveys in the decade sampling were conducted at peak flowering and recorded abundant showy inflorescences at all subpopulations. However, during 2011 and 2012, many of the abundantly flowering plants later failed to produce seeds due to severe herbivory, apparent desiccation (indicated by leaf wilt), and/or a possible lack of effective pollinators. All 106 adult plants marked in 2011 flowered, but only 69 (65.1%) succeeded in producing mature fruits. Researchers observed a high incidence of inflorescence failure, such that an average of only 1.8 fruits was output per inflorescence (typically bearing 20-40 flowers). Only four individuals out of the entire population produced mature fruits during 2012. Fruits collected in 2011 bore on average of 8.1 mature seeds (*s.d.* 7.7). The prevalence of aborted fruits and flowers on herbarium specimens (Table E2), high variation in fruit output per inflorescence, and variation in the seeds output per fruit all indicate considerable reproductive limitation warranting additional study.

5.3.2 Population Growth Rates

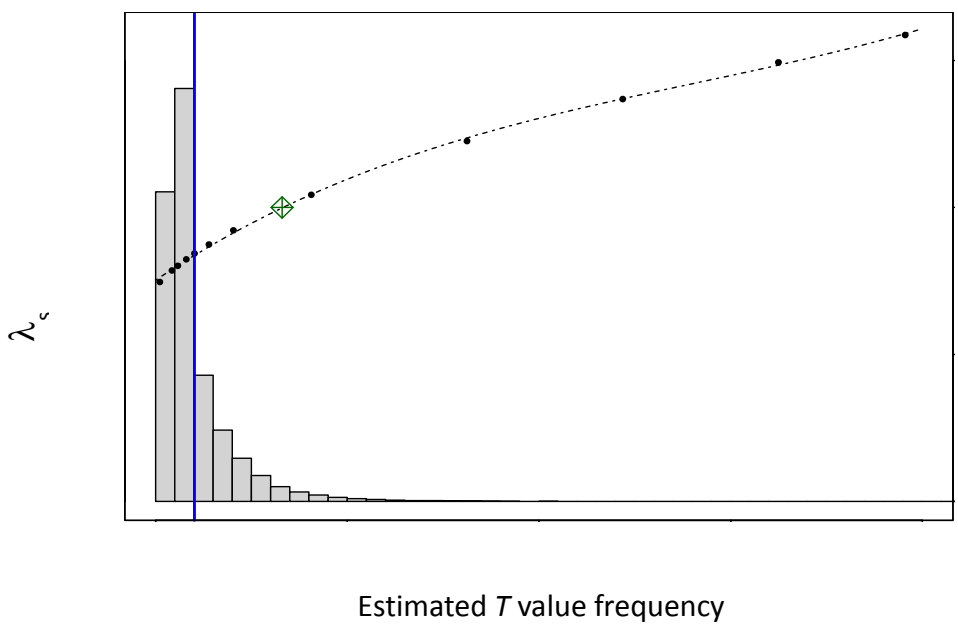
5.3.2.1 Population Growth Rate Estimates

Estimates of long-term population growth rate (λ_a) show that the California population of PENALB illustrate population decline over the study period (Figure 5.5B). Mean annual estimates of λ_a ranged from a high of 1.399 in 1995 to a low of 0.158 in 2012 (Figure 5.4B). Projected long-term λ_a was 0.926 (k_a= -0.10). Values from stochastic modeling were significantly lower; λ_s was 0.778 and had a very narrow confidence interval (k_s= -0.251, CI = -254, +0.248). By all estimates this population is experiencing a decline and stochastic projections imply a considerable rate of deterioration towards potential extirpation.

5.3.2.2 Sensitivity and Elasticity Analyses

Sensitivity analysis of the seed to J class transition rate, *T*, indicated that a large increase is needed for an increase in this parameter alone to yield a positive growth rate (Figure 5.6). Estimates from the posterior distribution of *T* ranged widely from 0.002 to 0.0421 ($\bar{x}$= 0.0020, σ^2 <0.0001; Figure 5.7). A cubic polynomial function was the best fit for the relationship between *T* and λ_s (R^2_{adj} = 0.9784, $F_{3,8}$=167.1, P<0.0001). This function predicted a positive population growth to occur at values of seed to J class transition greater than 0.0066, over three times the observed mean value of *T* during the surveys, $\bar{x}T$ (Figure 5.6).

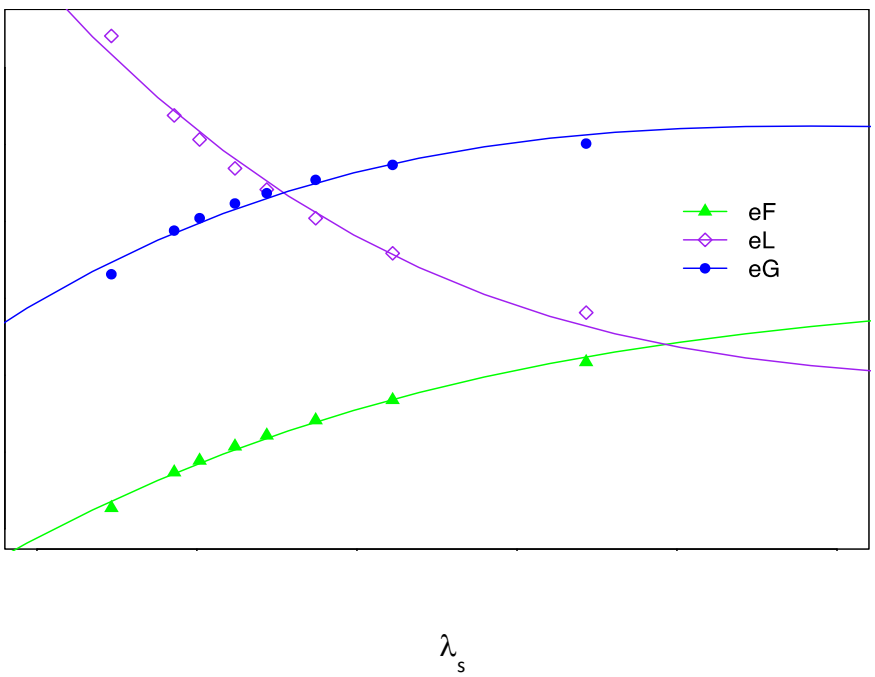
Figure 5.6: Effect of the Seed to J Class Transition Rate on Population Growth Rate



Sensitivity analysis determining the effect of the seed to J class transition, *T*, on stochastic population growth rate, λs. Histogram shows the frequency distribution of estimated values of *T*. Values of *T* used in iterations of the population dynamic model are plotted in black. The predicted value of *T* at which λ_s becomes 1 is 0.0066 (green diamond), over three times $\bar{x}T$ (blue vertical line).

Elasticity analysis revealed that plant growth (i.e., procession to larger size classes) and survival had the strongest effects on the long-term stochastic population growth rate (λ_s) and have similar magnitudes of effect on λ_s (Figure 5.6). Elasticity of the seed to J class transition, eF, by comparison, had only about half the effect on λ_s (Figure 5.6). Functions for the elasticity of fecundity (eF), survival (eL), and growth (eG) were best -estimated as cubic polynomials (each $P<0.001$). All three functions plateau shortly after λ_s surpasses a value of 1.0. The elasticity of growth transitions, represented by eG, has the greatest ongoing ability to increase λs.

Figure 5.7: Elasticity of the Long-Term Stochastic Growth Rate λ_s to Fecundity (eF), Survival (eL), and Growth (eG)



Elasticity of the long-term stochastic growth rate λs to fecundity (eF), survival (eL), and growth (eG). Points show values for λs for each of the estimates of $\bar{x}$T iterated for the population dynamic model. Cubic polynomial functions for each curve are detailed in Table E3.

5.3.3 Response of Fitness Components to Alternative Climate Regimes

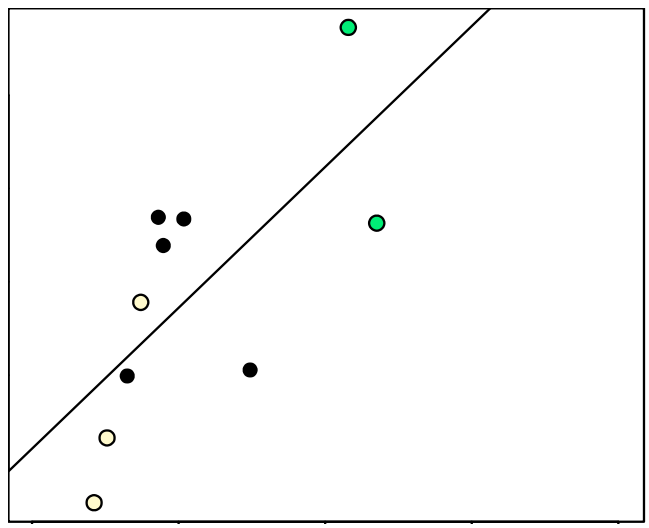
5.3.3.1 Effects of yearly variation

There was strong variation in precipitation across years ($\bar{x}$=49.38 mm, σ^2=1437.003). During the decade sampling there were two years (2002 and 2007, 20% of survey seasons) in which precipitation was below 35% of the average for the 20-year observational period. These were considered to be "dry" years for additional climate modeling. There were two additional dry years for which there was not enough demographic survey data: 2005 and 2006. Notably, André discontinued survey of the population in 2005 after he assumed that it was very likely to be locally extirpated. During the 2011 growing season (Oct-Apr) precipitation was slightly above

the long-term mean, whereas during 2012 it was 19.8% of the mean. There was a positive linear relationship between growing season precipitation and J class survivorship ($F_{1,1}$=550.2, P=0.0271, R^2_{adj}=0.9964), even with this low sample size (n=4). There was no significant relationship between growing season precipitation and survivorship of any adult classes.

Population growth rate was significantly driven by precipitation within sample years. Mean annual bootstrap estimates of the population growth rate (λ_a) had a significant positive relationship to growing season (Oct-Apr) precipitation within each year (linear fit: $F_{1,8}$=2.744, P=0.0253, R^2_{adj}=0.4204, Figure 5.8).

Figure 5.8: Deterministic Population Growth Rate and Precipitation



Seasonal deterministic population growth rate of PENALB versus cumulative wet season precipitation. Annual growth rate values are means of seasonal bootstrapped estimates λ_a. Yellow open symbols represent dry seasons in which precipitation was 20% below the mean precipitation rate; green open symbols represent wet seasons in which precipitation was 20% or more above the mean precipitation rate.

5.3.3.2 Effects of alternative precipitation regime on population growth

The forecast of precipitation regimes by the HADGEM A1B future climate model produced higher values of growing season precipitation, and these had a positive effect on population growth metrics. Using 52 mm of precipitation, the amount forecast as the decade mean for October to April 2080-2099, the authors estimated λ_a to be 1.04. However, they expect that

stochasticity in both λ_a and precipitation have significant, correlated effects on long-term stochastic growth rate, λ_s.

Using predicted values for the linear relationship between λ_s and seasonal precipitation, the study found that the PENALB population was most responsive to the frequency of drought years. Increased drought frequency had a strong negative effect on λ_s (Table 5.2). Furthermore, the population was more responsive to the frequency of droughts than to the long-term mean of precipitation. A long-term reduction in mean Oct-Apr precipitation without an increase in drought frequency yielded an increase in λs over the observed seasonal range (Table 5.2). Under all regimes, λ_s indicated population decline.

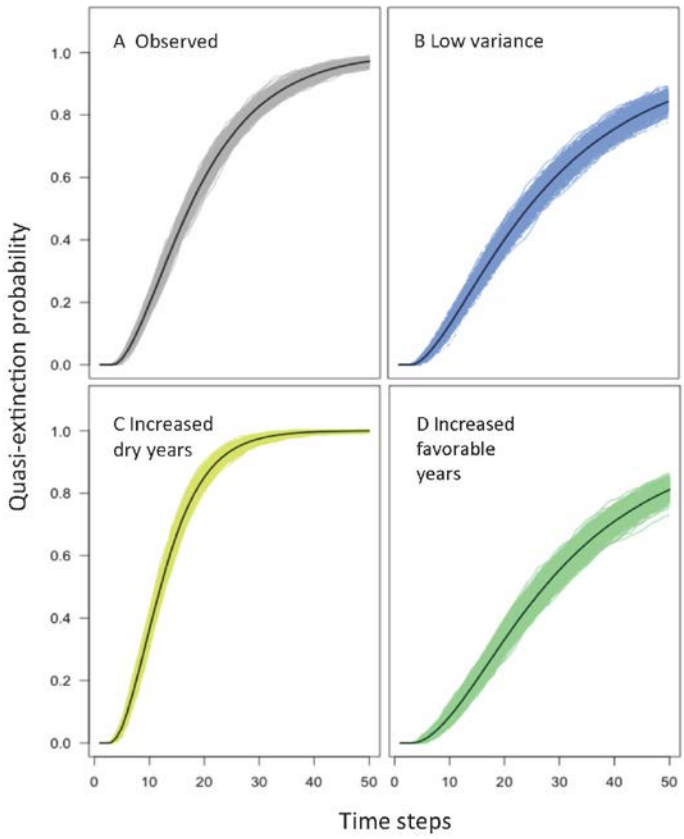
5.3.3.3 Effects of alternative precipitation on quasi-extinction probability

The probability of quasi-extinction (population size at or below 10 individuals) within the next two decades was high under any of the precipitation regimes that were simulated, including the current data (Figure 5.9). Under current conditions, quasi-extinction was 80% likely within 27 years. Under the higher drought frequency regime, the time to quasi-extinction probability of 80% was reduced to 19 years. Even under favorable growing conditions, those with precipitation more than 25% higher than currently observed, the quasi-extinction probability is 80% within 43 years.

Table 5.2: Long-Term Stochastic Growth Rate, λ_s for Current and Alternative Precipitation Regimes

	Growing season precipitation (mm)			Bias-corrected confidence intervals	
Climate regime	$\bar{x}$	***s.d.***	λ_s	**Left**	**Right**
Current regime (actual ppt and frequencies)	54.12	32.94	0.778	0.775	0.781
Increase in frequency of favorable years (ppt >135% of average)	63.36	36.95	0.805	0.802	0.808
Increase in frequency of drought years (ppt <35% of average)	47.12	31.48	0.732	0.729	0.734
Drought ppt (<35% of average) with actual frequencies of favorable and drought years	47.24	29.64	0.834	0.831	0.837

Figure 5.9: Stochastic Simulations of Quasi-Extinction Probability for PENALB for Four Climatic Scenarios



Stochastic simulations of quasi-extinction probability over 50 years given four climatic regimes: A) 10 current years, B) the probability of wet years increased by 30%, C) the probability of dry years increased by 30%, and D) a scenario in which mean precipitation is equivalent to that in the drought scenario, C, but variation in precipitation is similar to the observed variation in scenario A. Each panel shows 1000 stochastic simulations; the mean of these simulations is plotted in black. Quasi-extinction is equal to 1.0 when population dips below 10 individuals.

5.3.3.4 Effects of climatic variation on population growth rate

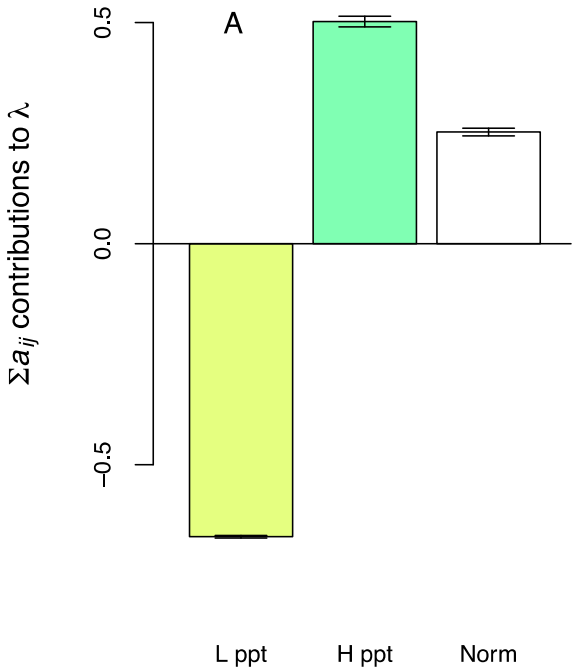
Comparison of the effects of normal, dry, and wet years on variation in the population growth rate showed that favorable growing seasons had significant positive effects on λ in comparison to seasons with precipitation closer to mean levels (Figure 5.10 A). Dry seasons had a strong negative effect on the population growth rate. Dry and wet seasons both had a magnitude of effect on λ at least twice that of "normal" seasons, although they represented only 20% each of the recorded temporal demographic variation.

5.3.4 Demographic Effects of Herbivory

Protection from herbivores during the 2011-2012 season greatly increased the survivorship and reproductive success of plants in 2012. Survivorship of seedlings excluded from herbivores by cages was 21.1% compared to 6.0% without exclusion. Caging also increased the probability of successful fruit set: 56.7% of uncaged plants output mature fruits vs. 78.4% of caged plants. On average, plants that were not caged experienced greater than 62% loss of canopy, whereas those that were caged for some or all of the season experienced approximately 23% loss. Caged plants had more reproductive structures per inflorescence, 1.5 (*s.d.* = 5.53) versus 0.3 (*s.d.* = 0.25) combined total buds, flowers, and fruits ($F_{1,96} = 4.617$, $P = 0.0342$). Plants without protection produced no fruits in 2011 (n=63 plants). Fruit output from caged plants was still extremely low at only 0.4 fruits per inflorescence (*s.d.* = 2.4, n = 35).

The life table response experiment also illustrated the positive effects of herbivore exclusion on population growth rate. Amid the overall negative contribution of 2011-2012, herbivore protection improved λ_a significantly (Figure 5.10 B).

Figure 5.10: Effects of Precipitation Variation and Herbivore Exclusion on Population Growth Rate



Two life-table response experiments (LTREs): A) Effects of dry, wet, and normal seasonal precipitation on λ_a, and B) effects of cage (herbivore exclusion) and no cage on λ_a in 2011-2012. Effects were obtained by summing the contribution of each transition matrix element a_{ji} to variation in λ_a. Error bars indicate bias-adjusted 95% confidence intervals.

5.4 Discussion

5.4.1 Will PENALB persist in California?

This extensive field and modeling study suggests that there is a high risk of extirpation of the rare perennial PENALB in California in the near future. Under the current range of climatic variation and using 12 years of demographic data from 1994-2004 and 2011-2012, the study found a significant likelihood that the population will dip below 10 individuals, representing quasi-extinction of this population.

This prediction is made considerably bleaker by climate forecasts that project increased frequency of drought years (Nobel and Gitay 1996, Abatzoglou and Kolden 2011). When the authors simulated an increase in dry years of 30%, they found that risk of quasi-extinction increased to 80% within less than 20 years (Figure 5.8). If precipitation increases slightly in the next 50 years, as some climate models suggest and drought frequency does not increase, persistence of PENALB may be much more likely. The analysis illustrated a strong relationship between precipitation and the observed dramatic fluctuations in the abundance and vital rates of this species population in California. Similarly, analysis of the effects of sensitivity using LTRE's highlighted the negative effects drought years had on lambda. Clearly, water availability is a key mitigating factor that limits survival and growth of desert plants, and thus population growth or decline.

Small and/or very localized precipitation events have strong demographic effects on desert plants (Sala and Lauenroth 1982). The majority (60-90%) of precipitation in the Pisgah area falls during winter months and only sparse precipitation falls in summer as localized monsoons (Hastings and Turner 1965; Hereford et al. 2006). For this study, the closest weather station at a similar elevation was greater than 30 miles west of the site and unlikely to record summer monsoon precipitation relevant to the PENALB population at Pisgah. Given the regionally dry conditions during the summer of 2011, the authors suspect that persistence of a few seedlings from the 2011-2012 activity year was the result of late summer precipitation in 2011 not recorded by the Barstow-Daggett weather station.

5.4.2 Which vital rates most affect persistence?

In the demographic surveys the study found low frequency of recruitment and potentially severe restrictions on seed output, including pre-dispersal loss of inflorescences to herbivory. Similarly, Scogin (1989) noted that seed set was one third of the natural maximum. For other *Penstemon* species, pollinator limitation and Allee effects, and lack of pollinators can limit seed set even though plants are self-compatible (Zorn-Arnold and Howe 2007). These factors may contribute to the low seed output observed for PENALB in 2011 and 2012 and warrant further study.

Through sensitivity and elasticity analysis, the study found that seed output and recruitment from seed had very low influence on the long-term population growth rate. This is particularly interesting, since estimation of both events (from new and seed bank origin seeds) is by far the most challenging aspect of demographic modeling for this and many other seed banking

perennials. Sensitivity analyses of the seed to J class transition rate, *T*, showed that relatively strong increases in seed output would be necessary for positive long-term population growth rate. Similarly, the population was even less responsive to addition of simulated J plants: addition of 10, 100, or even 1000 J class plants to years without J census data had no substantial influence on the long-term stochastic growth rate.

Elasticity analysis showed that the survival and growth of plants have the largest effect on increasing population growth. In fact, survivorship is often found to have high importance for perennial plants, in many cases higher than fecundity (Crone 2001, Crone et al. 2011). These findings suggest that management actions that preserve intact large plants, such as avoidance of impacts and protection from herbivory, will have the strongest demographic effect on the population.

5.4.3 Herbivory influences decline

The project found that herbivores had dramatic negative effects on plants that could be easily mitigated by protecting individual plants with cages. Comparison of plants with herbivore exclusion cages versus unprotected plants showed a significant effect of protection on the population growth rate, even during a dry year.

PENALB is just one of the many rare plant species in the desert southwest that are limited by interactions with herbivores (e.g., Pavlik et al. 2011), as well as positive interactions with dispersers and pollinators (Boggs and Inouye 2012). In arid lands, species interactions may be even more sensitive to rapid fluctuations in climate than they are in other terrestrial systems (McCluney et al. 2012). Under drought conditions, mutualistic interactions such as seed dispersal, can shift to negative interactions such as strong herbivory that limits reproduction (McCluney et al. 2012, Scogings and Mopipi 2008, Ernest et al. 2000). When water is unavailable, interactions can become strongly negative as herbivores consume foliage to maintain their water balance (McCluney and Sabo 2009). However, at the extreme, when water availability is severely low, interactions may be neutral if herbivore abundance substantially declines (McCluney et al. 2012). Changes in species interactions will likely become very diverse and perhaps novel, under new climatic regions. For example, temperature changes in the deserts have also already affected the distribution of soil biocrust microbes that benefit plants by mitigating dust storms and promoting nutrient cycling (Garcia-Pichel et al. 2013).

5.4.4 The California population is at the dry climatic edge of the PENALB distribution

The California population of PENALB differs ecologically and demographically from populations in Nevada and Arizona. It occurs at lower elevation than the Nevada populations and on significantly sandier substrate, growing with sand-restricted species such as *Oenothera deltoides*, *Abronia villosa*, *Gilia latifolia*, and *Nama depressa*. In comparison, the Arizona and two Nevada population centers are in sandy gravel and often associated with bajada species, such as *Ambrosia dumosa*, *Accamptopappus shockleyi*, *Yucca brevifolia*, *Larrea tridentata*, *Grayia spinosa*, and *Atriplex confertifolia*. Populations in Nevada and Arizona are longer-lived, as denoted by their size class distributions, and individuals commonly re-emerge after a single season, or more, of dormancy (André, personal observation). Relatively rapid, local extinctions of subpopulations

commonly observed in the California population are not observed elsewhere. California plants that are not active during one year generally will not re-emerge in another. However, occasional re-emergence of plants greater than 30 cm was observed by André after dry years in 2002 and 2006.

Significantly, the California population of PENALB receives less precipitation than those in adjacent states, particularly during summer months. Comparison of PRISM climate data shows that over the past 30 years, the California population has received, on average, a third less precipitation than populations elsewhere. It is possible that the lack of summer monsoon rain at Pisgah is a source of increased mortality of individuals, including seedlings, in comparison to the more eastern populations. Improved data on localized summer precipitation would be necessary to test this hypothesis.

5.4.5 Predicted response to more variable precipitation

Increasing temperatures have been observed across many high elevation sites in central and southern California and there is building evidence of the rapid response of plants to global change. For example, Kelly and Goulden (2008) found higher precipitation variability (in addition to warmer minimum temperatures, warmer mean temperatures, and increased precipitation) from 1977-2006 than in the preceding three decades in the Santa Rosa Mountains on the eastern edge of the Mojave and Sonoran Deserts in North America. Over the 30-year period they observed rapid response of dominant plants to climate change in the form of a 65-m upward movement in elevation (Kelly and Goulden 2008). They noted a significant drought from 1999-2002 that had dramatic effects on the mortality of common plant species. If climate does becomes more variable, it is likely to affect many rare plants strongly via their sensitive demographic response to the environment (Seager et al. 2007, Science, Keer 2008). Furthermore, the effects of climate change on population size are likely to be greatest at the boundaries of species' ranges (Blinova 2002), suggesting that populations at range boundaries or disjunct from main range might be at higher extinction risk due to climate change.

Over the past 30 years, weather stations nearest the California population of PENALB (including at Granite Mountain Desert Research Center) have shown high precipitation variability, increases in winter maximum temperature, but cooler summer maximum temperature (Unpublished data, André). Overall, there has been only a very slight increase in mean annual temperature. The regional variation observed is consistent with predictions of various warming models. It is possible that, given no change in precipitation, warmer winters, and cooler summers may in fact improve the demographic performance of some desert perennials such as PENALB.

It is however, it more likely that the instability of the California population of PENALB is representative of the demographic sensitivity of a species near the geographic edge of its environmental tolerance. In California, PENALB is at the low end of its range in terms of both elevation and precipitation. Species are more vulnerable to stochastic events, including those driven by climate variation, when they are at such edges (Gaston 2009). If and when rapid directional warming occurs PENALB will be at much greater risk of local extinction than populations near the geographic range center. Extinction risk due to climate change, loss of

critical habitat and/or connectivity is further elevated for rare plants such as PENALB that are relatively sensitive to drought or stress. Other herbaceous perennials that occur at their geographic range limit in the Central Mojave and might share similar risk include *Astragalus lentiginosus* spp. *borreganus*, *A. mohavensis hemigyrus*, *A. jaegerianus*, *Cymopterus deserticola*, *Androstephium breviflorum*, *Mentzelia puberula*, *M. polita*, *Sidalcea neomexicana*, *Wislizenia refracta*, and *Pediomelum castoreum*. However, populations at climatic range boundaries are also vanguards driving evolutionary change via adaptation to changing conditions. Conservation of populations at range boundaries, and thus their adaptive traits, is critical to preservation of genetic diversity.

5.4.6 Population genetics

A study of PENALB genetics from 12 populations across California, Nevada, and Arizona found that the four largest populations, including the one in California, were genetically distinct (Wolfe, unpublished data, Wolfe et al. 2006). The overall genetic diversity of the species is thus dependent on the size and persistence of each of these populations. Heterozygosity was lower than expected, which suggests that there is some degree of inbreeding within most populations (Wolfe, unpublished data). There also appears to be minimal genetic exchange between the four main populations. However, it's likely that demographic constraints and their relationship to environmental stochasticity implicit in the California population are more important than genetic limitations.

5.4.7 Can PENALB beat the odds?

Despite the significant threats to PENALB, including development of its critical habitat, climate change, and herbivore pressure, there are reasons to believe that it might just beat the odds and persist into the foreseeable future. It is possible that persistence of dormant seeds throughout the putatively suitable habitat in the Pisgah area and beyond will be sufficient for recolonization if and when favorable climatic conditions do occur. This possibility is evident in the described history of subpopulation sizes at Pisgah, which were documented by Scogin prior to 1989 to number at 450 individuals, then only 4 years later by Sheldon to number at 4450. Had the recruitment event in 2011 been wider than a single area around a maternal plant (with nearly 300 seedlings in 100 m^2) and coupled with a mild, or even wet summer and fall, it could have turned into a population boom. After all, desert perennials such as PENALB are well adapted to harsh conditions and periodic drought by bet hedging over periods of 10-15 years or longer. Seed dormancy, long-term persistence of rare large old plants, and/or rare high seed output during a few years might create a buffer that researchers have yet to witness. Furthermore, intense herbivory and high inflorescence failure rates observed during 2011 and 2012 may be correlated with climatic conditions that are alleviated in rare favorable years with high fecundity and survivorship. If this population is able to persist through the current drought episode by means of its large adult plants and/or its small seeds in the seed bank, a widespread population at Pisgah may again be seen.

5.5 Management Recommendations for Renewable Energy

a) **Rare perennials that are impacted by solar energy might require additional mitigation and conservation strategies to support their populations through dry and/or variable climatic periods.** The study found that dry years and climate variability had strong negative effects on the population growth rate of this rare perennial. Population simulations under alternative climatic regimes showed a stronger negative effect of increase in dry years on the population growth rate than the effect of increased occurrence of wet years over the same time period. In addition, it found that increased variability in precipitation stronger negative effect on the population growth rate than a similar reduction in mean precipitation.

b) **Avoidance is the best possible mitigation strategy.** Preservation of large plants has the strongest demographic effect on the population by enhancing long-term fecundity. Renewable energy facility designs that allow for the avoidance of intact populations or at minimum allow for persistence of populations, including large plants, within lower-impact areas within installations will be most successful at reducing impacts to rare perennials.

c) **Providing herbivore protection may be a simple and cost-effective management action to conserve this and other rare desert species in cases where renewable energy causes direct impacts or increases in herbivore pressure.** The study found that protection from mammalian herbivores significantly improves demographic success. Installation of exclusion cages significantly improved the population growth rate for protected individuals, even during a drought year.

d) **Persistence of dormant seed and existence of a dormant seed bank may be the key to withstanding demographic lows, such as the decline currently observed in the California population.** Although seed dormancy and output had relatively low values of elasticity in the models, long-term seed dormancy is likely a critical adaptation that might allow for rescue of a dwindling population when more favorable conditions do occur. X-ray analysis of PENALB seeds collected in 2011 and 2012 found high rates of seed viability (81.8-97.8%; Appendix A). Methods for surveying, including repeated field surveys, that acknowledge the significance and cryptic nature of seed banks will be essential for conservation of rare plants amid renewable energy developments.

CHAPTER 6:
Non-integrated Population Vitality Analysis of *Grusonia parshii* across its Range in California

6.1 Introduction

Population viability analyses (PVAs) have been used on a wide range of organisms to assess the probable trajectories of populations and to determine the relative sensitivity of those trajectories to factors that affect vital rates (Caswell 2001, Morris and Doak 2002, Menges 2008, Knight 2012). Field data on population characteristics and vital rates, especially population size, age/stage structure, survivorship and fecundity are integrated by matrix-based models (usually Monte Carlo simulations) that calculate values of λ (lambda, the dominant eigenvector of the Leslie matrix). λ indicates the potential for population decline, stability, or growth ($1.0 < \lambda > 1.0$, respectively) in the face of environmental or demographic stochasticity. Manipulations of vital rates (e.g., changing the mean values of fecundity parameters or increasing the variance around any rate) produce a sensitivity analysis that identifies critical factors that conservationists can manage to (hopefully) improve the actual trajectory of the population in situ. Thus, PVAs only move beyond their academic value when producing management recommendations that are subsequently applied.

The challenge of using PVA comes from life history features of the target organism that do not readily conform to short study periods or discrete categories found in structured matrices. Species that are long-lived, clonal, cryptic, highly fecund or rarely establish either require modeling "contortions" to accommodate (Menges 1991, Linares 2007, Spencer and Janzen 2010) or negate integration into a matrix-based model, such as used in PVA. Many rare plants, such as the uncommon cactus, *Grusonia parshii*, and the rare shrub, *Castela emoryi*, are long-lived (with cryptic deaths), apparently clonal in their growth forms, and seldom established from seeds. Without fine-grained genetic studies there is simply no way to tell the difference between genetically distinct individuals (genets) and genetically identical branch (stem) units arising from clonal growth (ramets). These plant species do not, therefore, lend themselves to an integrated PVA using field data from a three-year study.

"Non-integrated" analyses can be substituted for PVA when it is difficult to determine what an "individual" is in a population due to clonal growth or a creeping growth form and when birth and death are difficult to quantify (Pavlik 1994, Menges and Gordon 1996, Guerrant and Pavlik 1998). These alternative analyses of measurable population characteristics and vital rates can determine sensitivity of a target species and developing management actions based on available, though limited, data (Pavlik 1994, Menges and Gordon 1996, Guerrant and Pavlik 1998). The non-integrated PVA approach requires independent assessments of demographic variables, preferably from multiple populations of the same species, for comparative purposes. Relative population viability (perhaps better referred to as population "vitality") is then inferred from comparing population characteristics (size, stage/age structure), vital rates (clonal growth rate, survivorship, fruit/seed output) and responses to perturbation (human

disturbance, herbivory) in a "performance rubric" that summarizes the data and facilitates development of management recommendations.

To perform a non-integrated population analysis of *Grusonia parshii*, permanent study plots were established in seven natural populations across the range of the species in California. Extensive surveys, trial measurements, and discussions were applied to overcome the problems of defining individual plants, characterization of populations and assessment of vital rates in this long-lived, clonal and cryptic cactus. The team 1) developed practical and repeatable definitions and measurement protocols for "clumps" and "clusters" (approximating the distinction between genets and ramets), 2) recorded data on new shoot output (clonal growth), floral bud output (potential fecundity), mature fruit and seed output (realized fecundity), and seed non-viability (effective fecundity) between 2011 and 2014, and 3) measured the effects of vertebrate herbivory on new shoot output and fruit and seed output with a caging experiment. In addition, some of these protocols were applied to plants found within the footprint of the Ivanpah solar fields and to experimental populations that originated from stem fragments transplanted into mitigation gardens (by other researchers).

6.2 Methods

6.2.1 Study Species

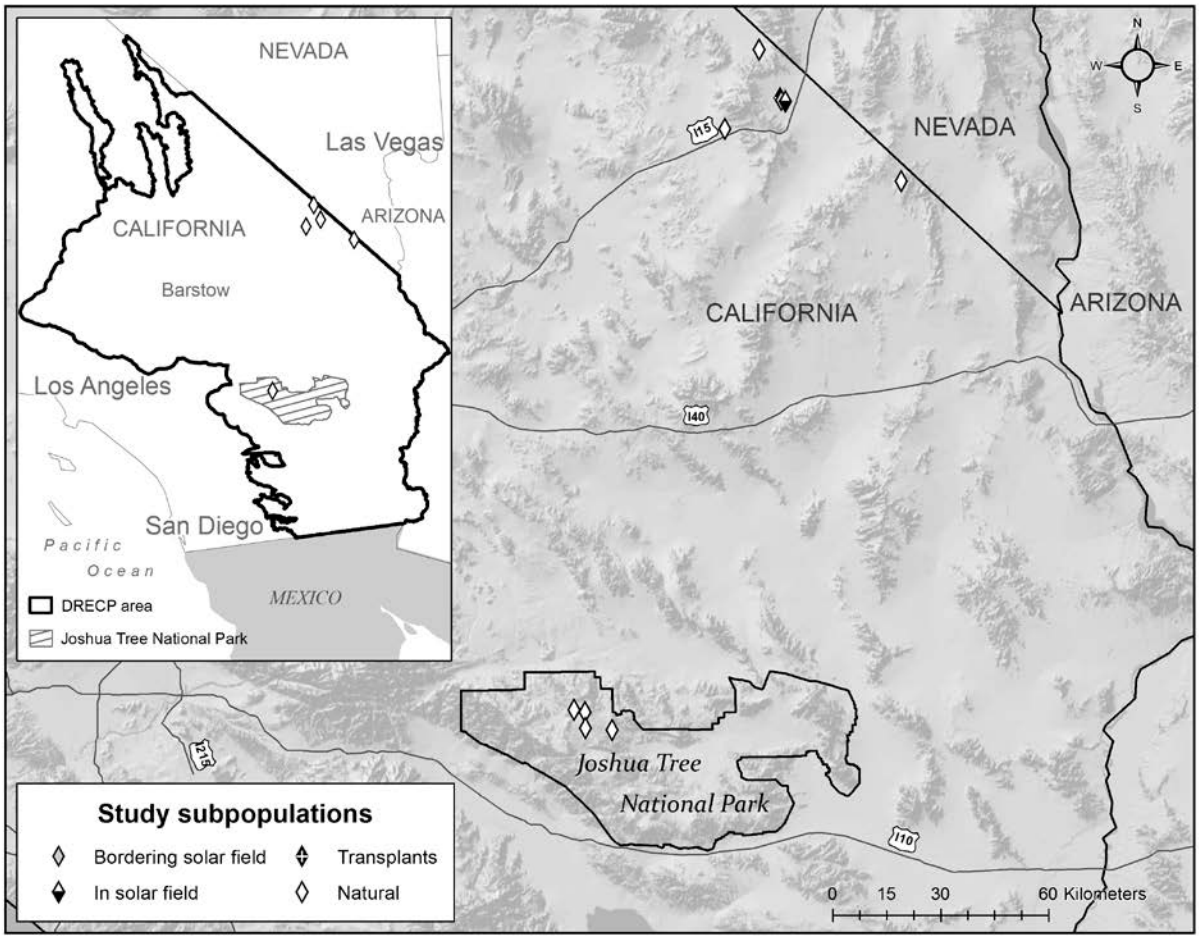
Grusonia parshii (Orcutt) Pinkava, or Parish's club-cholla, is an uncommon, stem succulent cactus (Cactaceae) that is native to California, Nevada, and Arizona. The California Native Plant Society ranks this taxon "GRUPAR" as a List 2.2 species (rare, threatened, or endangered in California; common elsewhere; moderately threatened). GRUPAR occurrences in California are found in two, widely disjunct sub-regions of the Mojave Desert; one in the northeastern Mojave roughly centered around the Ivanpah Valley and one more than 170 km to the southwest in Joshua Tree National Park (Figure 6.2). Some of the northeastern Mojave occurrences are close to or within the boundaries of the Ivanpah Solar Electric Generating System footprint, while those to the south are largely held in reserve with minimal impacts from human activity.

GRUPAR is a perennial cactus with a prostrate, creeping growth habit. The densely spinose stems appear grey and dead in dry months but regain color and stem volume in response to seasonal precipitation. Vegetative reproduction is likely, but its success and frequency are unknown.

GRUPAR individuals grow slowly as dense perennial mats, or "clumps", often more than two meters in diameter. Clumps are composed of "clusters", or smaller usually circular groupings of stems, each 10 to 20 cm long, joined by an interconnected root crown (Figure 6.1). From the apex of each stem, a solitary inflorescence can originate, producing a single flower having a yellow to red perianth (petals and sepals) and green filaments on the stamens. Each flower can produce a single, mature fruit containing an average of 56 seeds (n = 80, range of 0 to 203). Fruit maturity is indicated by a yellowing and swollen floral tube, ovary, and receptacle with succulent or fleshy tissues. The fruit may persist on the stem for multiple years if left undisturbed.

Figure 6.1: A "Clump" of GRUPAR is Composed of Many "Clusters"

Figure 6.2: Locations of GRUPAR Populations in California.



6.2.2 Study Populations and Habitat Characteristics

California populations (for study purposes the same as "occurrences" in the California Natural Diversity Database) of GRUPAR are found in two disjunct sub-regions of the Mojave Desert. Populations in the northeastern Mojave ("NEM" populations) are broadly centered around Ivanpah Valley, adjoining those in western Nevada. The only other known large California populations all occur near and in Joshua Tree National Park ("JTNP" populations), and in the southwestern corner of Mojave National Preserve (Moore and McIntyre In review). The 170+ km disjunction includes multiple mountain ranges, broad valleys and dry lake beds, all to the east of the Mojave River drainage (a major biogeographic boundary).

Population densities and sizes are highly variable. The northeastern Mojave populations NEM1, NEM2 and NEM3) have densities that range from 57 to 225 clumps per hectare (Table 6.1). The total population sizes, however, were difficult to ascertain for NEM1 and NEM2 because individual clumps (genets) were sparse and scattered, with lone stems often occurring between the denser clumps. It was roughly estimated that 80 to 90 clumps formed the population in each of these two occurrences. The Joshua Tree National Park populations (JTNP1, JTNP2, JTNP3,

JTNP4) have a wider range of density (3 to 228 clumps per hectare) but are probably composed of a similar number of clumps overall (20 to 88 per population) when compared to the northeastern populations.

GRUPAR occurs in dry, well-drained soils that are typically sandy, gravelly, and rocky. These are derived from alluvial granite and limestone materials (hence calcareous) and have poorly differentiated profiles with little organic matter. The soils support a variety of low scrub vegetation types that vary greatly with elevation, aspect, and Mojave Desert sub-region. Indicator species associated with GRUPAR are difficult to ascertain, based on the ecological heterogeneity of vegetation types associated with the project's demographic study sites.

Table 6.1: Population Characteristics of *Grusonia Parishii* (GRUPAR) at Northeastern Mojave (NEM) and Joshua Tree National Park (JTNP) sites, 2011 to 2014.

site	statistic (2012)	Total Pop Size (# clumps)	Pop Survey Area (ha)	Pop Density (# clumps/ha)	Clump Size (m2)	n	Max Clump Size (m2)	Min Clump Size (m2)	2011-2014 Survivorship
NEM1	mean				1.097	40			
	s.d.				0.616				
	CV				0.561				
	individual	80-90*	0.120	225.0			3.000	0.230	0.80
NEM2	mean				0.870	28			
	s.d.				0.744				
	CV				0.856				
	individual	80-90*	0.300	56.7			3.000	0.175	1.00
NEM3	mean				0.273	16			
	s.d.				0.171				
	CV				0.626				
	individual	16	0.069	218.0			0.563	0.050	1.00
						84			
JTNP1	mean				1.687	37			
	s.d.				3.037				
	CV				1.800				
	individual	88	0.825	106.7			18.250	0.075	1.00
JTNP2	mean				0.972	38			
	s.d.				0.694				
	CV				0.714				
	individual	57	0.250	228.0			2.625	0.063	1.00

Table 6.1 (cont)

site	statistic (2012)	Total Pop Size (# clumps)	Pop Survey Area (ha)	Pop Density (# clumps/ha)	Clump Size (m2)	n	Max Clump Size (m2)	Min Clump Size (m2)	2011-2014 Survivorship
JTNP3	mean				0.526	20			
	s.d.				0.455				
	CV				0.866				
	individual	20	1.425	14.0			1.875	0.038	1.00
JTNP4	mean				1.584	26			
	s.d.				1.735				
	CV				1.095				
	individual	26	8.216	3.2			3.625	0.038	1.00
						121			
CLA1	mean				0.501	9			
	s.d.				2.586				
	CV				5.159				
	individual						8.100	0.163	1.00
ISE1	mean				0.678	4			
	s.d.				0.720				
	CV				1.062				
	individual						1.575	0.0125	1.00
ISE2	mean								
	s.d.								
	individual								
						13			

*Population sizes for NEM 1 and 2 estimated.

Our study obtained data from three populations in the northeastern Mojave (NEM1, NEM2 and NEM3), totaling 89 marked clumps (although only 81 would survive the entire 2011 to 2014 study period). Each population is considered a separate demographic unit due to geographic isolation and discontinuous suitable habitat between them. Data from four populations in Joshua Tree National Park (JTNP1, JTNP2, JTNP3, JTNP4) were also obtained, totaling 121 marked clumps. Two of these (JTNP1 and JTNP2) are probably sup-populations because they occur in portions of a single, extensive Queens Valley population, while the other two are well separated and occur in peripheral, outlying areas. Some data were opportunistically (and, therefore, inconsistently) obtained from the transplant garden (CLA1) and within the Ivanpah Solar Electric facility (ISE1 and ISE2).

6.2.2.1 Northeastern Mojave (NEM) Populations

NEM1 occurs on the northeast bajada of the Clark Mountain Range in Mesquite Valley (UTMW 633008, UTMN 3948429, elevation 842 m). Occurring at the lowest elevation of the demographic sites, this location supports a creosote scrub community and a diverse cactus assemblage. The topography is undulating to flat and soils are gravely to rocky. Bioturbation (soil disturbance by organisms) and burrows occur frequently within GRUPAR clumps. A deeply scoured wash and a BLM road border the site.

NEM2 occurs on the western bajada of Clark Mountain in Shadow Valley (UTMW 623557, UTMN 3926506, and elevation 1253 m). This site supports a dense Joshua Tree woodland, including a diverse cacti assemblage. The topography is undulating to flat with several interweaving runnels feeding into deep washes throughout the site. The soils are gravely to rocky. Burro tracks and scat have been noted. Bioturbation and burrows occur rarely within GRUPAR clumps. Transmission lines and a powerline road cut through the population.

NEM3 occurs on the eastern bajada of the New York Mountains, directly east of the Castle Peaks (UTMW 672663, UTMN 3911970, and elevation 1349 m). This site supports a dense Joshua Tree woodland and creosote scrub community. The surface slopes towards the southwest into a large wash and soils are gravely to sandy. Bioturbation and burrows occur seldom within GRUPAR clumps. A BLM road and large wash cuts through the population.

6.2.2.2 Joshua Tree National Park (JTNP) Populations

JTNP1 occurs in Queens Valley (UTMW 581642, UTMW 3765175, and elevation 1344 m). This site supports a Joshua Tree woodland and dense low scrub community. The topography is predominately flat and soils are gravely to sandy. Bioturbation and burrows occur frequently within GRUPAR clumps. The site is bordered to the north by a road and to the west by a large wash.

JTNP2 occurs along the eastern edge of Queens Valley (UTMW 584740, UTMN 3764543, and elevation 1346 m). This site supports Joshua Tree woodland and dense low scrub community. The topography is predominately flat and soils are sandy to gravely. The site is bordered on the west by a dirt road and to the south by a trailhead.

JTNP3 occurs of off Geology Tour Rd, between Ryan Mountain and the Hexie Mountains (UTMW 584909, UTMN 3760164, and elevation 1335 m). This site supports a Joshua Tree

woodland and dense low scrub community. Site topography is predominately flat. The soils are mostly sandy with some gravel. The site is bordered on the east by a dirt road.

JTNP4 occurs in the Pinto Basin, in the western bajada of the Pinto Mountains (UTMW 592662, UTMN 3759590, and elevation 1344 m). This site supports a Joshua Tree woodland and dense low scrub community. The topography is predominately flat with small knolls. The soils are mostly sandy to gravely. The site is bordered on the east by a paved road.

Plants in CLA1 were transplanted to this area in 2011 from their home sites within the solar field. CLA1 is a relatively open, upland low scrub community on fine textured to sandy soils. The topography is dominantly flat. The site is boarded to the east by a paved road and the solar field.

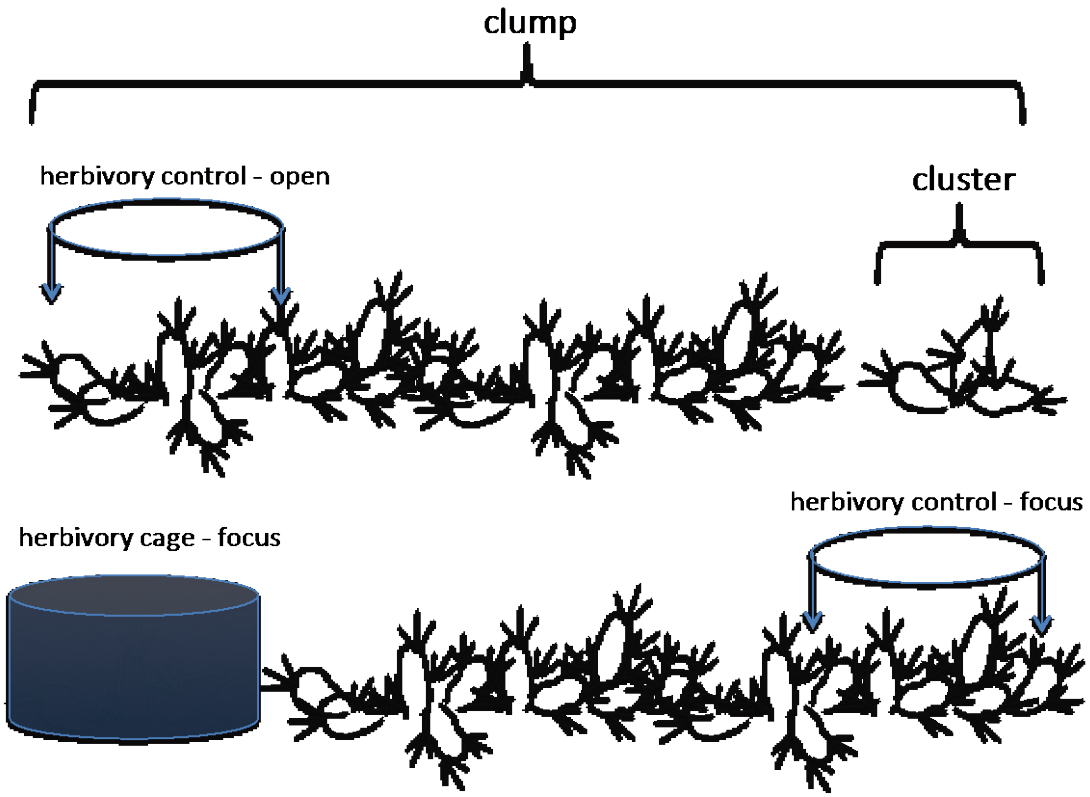
Three plants that remained in ISE1 were located and surveyed as site access permitted. These individuals were located directly under heliostat mirrors and sustained substantial disturbance during construction, including fragmentation. ISE1 has a dense low scrub community. Topography is predominantly flat with frequent low-relief washes. Soils are soft sandy to gravely. The landscape is occupied by heliostats and access roads that permit occasional mowing of vegetation and washing of the mirrors.

6.2.3 Population Characterization

The slow-growing, long-lived nature of this species prevented true demographic analysis (e.g., the birth, death, and reproductive output of individual plants) over the short study period (2011 to 2014). However, the detailed location information and permanent marking with numbered, metal tags deployed for this study might permit viability analysis if populations were carefully re-surveyed over five- and ten-year intervals using the methods detailed here. Details of site and plant selection, including randomized sampling and transect methods are available by contacting the authors.

In order to accommodate the clonal, creeping growth form of GRUPAR, which made delineation of true individuals (genets) impossible, useful and potentially universal terminology and methods for sampling this type of plant species were defined (Figure 6.3).

Figure 6.3: Clumps and Clusters of GRUPAR



Also illustrated is an "open" (uncaged) clump (top) and a "focus" clump that has a cage. The controls are uncaged, marked portions used for measuring herbivore impacts (see 6.2.5).

The basic demographic unit of GRUPAR populations was defined as the "clump," roughly (and hopefully) equivalent to an individual plant with its own unique genotype (but it may or may not represent a genet). A clump, like any other perennial plant, is composed of repeating branch units (a stem internode with a vegetative bud in the axil of an attached leaf), each of which is genetically identical and called a ramet. With specific reference to GRUPAR, the creeping growth form of the clump is due to production of branches along the ground surface and away from the point of establishment of the genet (from seed). Due to repeated and dense outgrowth of buds over (possibly long periods of) time, the clump appears to be composed of aggregations of branches here termed "clusters." Therefore:

Cluster - a collection of living branch units (stems, ramets) that are, or once were, interconnected and that probably share the genotype. Clusters bear new vegetative buds (forming new stems) and reproductive buds (floral buds) that can eventually produce seeds and fruit. Bare ground, dead stems or litter can separate clusters from one another as they grow and root away from the point of establishment (which may no longer be apparent). The cluster is the sampling unit for observation of stem dynamics (the "birth" of new stems, stem death) and fecundity (floral bud and fruit output).

Clump – a collection of clusters less than 2 m apart (an arbitrary but necessary distinction), with similar phenology and presumably the same point of establishment and genotype. The clump is the population-level sampling unit, roughly and imperfectly representing individual plants.

Single stems of this species were not selected as working units in this study because any one stem has a low probability of producing a new branch or a floral bud in any given year. Study of aggregations of stems (i.e., clusters) greatly increased the probability of observing these vital phenomena over the relatively short study period. So although it was not possible or desirable to use single stems to understand the growth and fecundity of GRUPAR, it was possible to mark and measure clusters for that purpose.

6.2.4 Growth and Fecundity Measurements

6.2.4.1 Monitoring Clumps

In order to repeatedly monitor GRUPAR clumps, it was necessary to delineate their boundaries so as to define, in a replicable way, the size of each demographic unit. This allowed all measures of growth and fecundity to be normalized per unit area of that clump (e.g., new stems/m^2, floral buds/m^2, fruits/m^2) and, therefore, compared within and between populations. After trial measurements were conducted in 2011, it was concluded that measuring the rate of clonal expansion (areal growth) using changes in clump size between adjacent years was insufficiently precise. Therefore, cluster-level measurements were employed to infer clonal expansion (see below). Over longer periods of time, say between 5 and 10 years, it may be possible to monitor changes in clump size and the "migration" of ramet units across the habitat.

> *Clump Size (m^2/clump)* – Calculated by measuring two diameters (D1 and D2) that were superimposed across a clump. Spine lengths were included in this measurement. D1 was the longest diameter of apparently live (see below) or dead but attached stem material. D2 was the second longest diameter, perpendicular to D1, again including apparently live and/or dead (but attached) material. This sometimes meant that satellite clusters were not accounted for in the D2 measurement because they were not a part of the longest extent of living and/or attached dead material. However, satellite clusters were included in the number of clusters per clump. The origin and endpoint of these diameters are indicated in the field by a sod staple or tile nail and they serve as point of reference for subsequent surveys. The tags will be useful for resurveying clump size, cover, growth and reproduction.
>
> *Clump Vigor (% dead cover)* - A point-intercept method was employed to estimate the fraction of a clump that was covered by dead stem material. At the NEM sites the linear cover (projected onto a measuring tape along D1) was recorded at 1 cm intervals. At JTNP sites it was a recorded in the same way, except that if D1 exceeded 5 m (i.e. if clumps were very large), 15 cm interval were used. For clump diameters between 1 and 5 m, 10 cm intervals were used, and for clump diameters less than 1 m, 1 cm intervals were used. The linear cover was considered "alive" if spine and stem material could not be separated from the plant when flicked by a finger or gently tugged and appeared to have intact tissues (live epidermis color in this species can be green, red, orange, yellow,

brown or black). Linear cover was considered "dead" if a spines or stems could be separated from the clump in this way, or otherwise seemed to be decaying.

Clump Composition (# clusters/clump) – Clusters were counted for each delineated and measured clump. These were distinguished from one another when two or more decaying stems or a patch of bare ground created a distinct separation.

During field visits clump phenological state was also recorded (simply vegetative vs. reproductive), total number of new stems and flowers per clump, evidence of herbivory on stems, flowers and fruits, and any forms disturbance. These data have been archived in databases and are available to future researchers, though not summarized herein.

6.2.4.2 Monitoring Clusters

When monitoring clusters within GRUPAR clumps, a random sampling method was used. A non-magnetic arrow was spun against a circular 360-degree compass grid to identify which area of the clump would be sampled for a cluster. If the arrow was spun and came to rest at 90°, the eastern-most side of the clump was examined for any cluster that could be easily delineated by multiple observers from an adjacent cluster in that area. If the cluster within that area could not be delineated, then the next apparent cluster occurring clockwise beyond 90° (e.g. 91°-360°) was delineated and selected. As mentioned above, cluster growth was used as a surrogate measurement of clonal expansion (growth) because measurements of cluster size were much more precise than measurements of clump size and because counts of new stems on clusters (rather than in whole clumps) were much more repeatable between observers. The following measurements were made within each cluster:

Cluster Size (m^2) - Calculated by measuring two diameters (D1 and D2) that were superimposed across a cluster. Spine lengths were included in this measurement. D1 was the longest diameter of apparently live or dead but attached stem material. D2 was the second longest diameter, perpendicular to D1, again including apparently live and/or dead (but attached) material. There were no permanent markers to indicate where these readings were taken. However, a mason string delineated the boundaries of a surveyed cluster and is useful for re-surveying cluster size, growth and reproduction.

Cluster Growth (# new stems/cluster, # new stems/m^2 cluster) - To quantify the rate of new stems produced (and eventually the potential rate of ramet output and clonal expansion), it was necessary to distinguish vegetative from reproductive buds that form within clusters. Early in the spring, however, they are impossible to tell apart so they can be referred to collectively as "budding structures." These appear as minute fleshy red shoots arising out of a white, soft callous anywhere on a joint (apex, midsection, and/or base). In May or June these develop into distinct "stem buds/new stem segments" (which lack calyx and corolla whorls at their apices) and "floral buds" that have those whorls and develop into flowers. During June sampling of clusters researchers could make separate tallies of "new stems" and "floral buds" per cluster, which could then be normalized per unit area by dividing by cluster size, thus giving new stem density.

Cluster Composition (# stems/cluster) - Within the cluster area, the apices of live stems were tallied, usually as observed from above. Live stems, even those with some necrotic tissue, can resist the tugging or pulling on spines. A stem was considered dead when its spines separated easily. This was challenging because some stems are nestled within larger stems and are difficult to see and access for this test.

Stem Volume (cm^3) - The volume of stem units (typically referred to as "joints" for cacti) was observed to differ between study populations. To calculate an average joint volume, a subsample of 10-joint cross-sectional areas and lengths were measured at each population. Spine lengths were not included in these measurements. Joint diameter was recorded at the thickest cross section by placing two metal skewers parallel against the sides of the joint and measuring the distance between them. For length, a metal skewer was placed alongside the joint until it reached the point of attachment to the adjacent joint. Then another metal skewer was placed perpendicular to the joint apex, and the intersection of the two skewers was used as the endpoint.

Cluster fecundity (# floral buds/cluster, # floral buds/m^2 cluster, # fruits/cluster, # fruits/m^2 cluster) – Once floral buds could be distinguished from vegetative (stem) buds in June, the authors could estimate cluster fecundity. This could then be normalized per unit area by dividing by cluster size, thus giving floral bud density. By returning roughly a month later (July), it was possible to count the number of flowers that had developed into fruit. Only persistent, succulent or fleshy fruits were counted because dried, brittle, or shriveled fruits did not contain seeds. However, it was observed that fruits were highly affected by herbivory, so the results of fruit counts are presented in relation to caged and uncaged portions of clumps (see below).

During field visits the researchers also recorded cluster phenological state (simply vegetative vs. reproductive), evidence of herbivory on stems, flowers and fruits, and any forms disturbance.

6.2.4. Monitoring Seed Output and Non-Viability

Observation of persistent fruits on clumps began in early spring 2011. Initial collections were made at NEM3 and other surveyed populations at this time. After researchers established study plots in 2012, however, they made random collections of red, fleshy and attached fruits in November of that year at all locations except NEM1 because so few could be found. These were returned to the lab where they were dissected so that seeds could be counted.

Estimates of seed non-viability were obtained using the x-ray laboratory of the Millennium Seed Bank at the Royal Botanic Gardens Kew (London). GRUPAR seed lots from 2011 (79 seeds) and 2012 (358 seeds) were composed from five to 20 individual clumps from multiple sites (NEM2, NEM3, and JTNP1), being careful not to bias in favor of the larger, heavier and (presumably) higher viability seeds. These were arranged in plastic petri dishes and imaged using a Faxitron Specimen Radiographic System. Magnification was adjusted for differences in seed size of the species and each image was digitally stored for later analysis.

Non-viability was inferred by the absence of fully formed embryos and the relative transparency of cotyledon and embryo tissue to the x-ray. Guidance on interpreting embryo

morphology at the level of family and genus was obtained from the comprehensive survey by Martin (1946). Damage by predators or other factors was also noted and incorporated into the estimates. Comparisons between viable and non-viable seeds or fruit, as revealed by x-ray, were subsequently made with dissection under a light microscope to ensure correct interpretation of embryo morphology and condition.

6.2.5 Quantifying the Effects of Herbivory on Growth and Fecundity

To quantify the effects of vertebrate herbivores (principally rodents and lagomorphs, but perhaps also lizards and feral burros), the project team built exclusion cages around randomly selected GRUPAR clusters or sometimes around entire (small) clumps (also randomly selected), within six populations (NEM1, NEM2, NEM3, JTNP1, JTNP2 and JTNP3). Collectively, clumps with cages are called "focus" clumps because they were the focus of this set of measurements. A total of 58 cages were installed (29 at NEM, 29 at JTNP), but only four would be disturbed (probably by burros) by November 2012 and 16 by November 2013.

The cages were built from fine-mesh hardware cloth and ranged from 60 to 76 cm in diameter, with a closed top and anchored at the bottom with irrigation staples. Near-transparency ensured that little or no shade was cast, large-bodied insects could enter, and the probability of vandalism was low. All were installed in April 2012 and used for two years of monitoring new stem, floral bud and fruit output, normalized for the actual area of a "focus" clump (Figure 6.3) that was covered by the cage (thus allowing normalization). To compare these parameters of caged clumps to uncaged, two forms of control were used; 1) tallies of new stems, floral buds and mature fruits on whole, uncaged clumps ("open clumps"), and 2) tallies of new stems, floral buds and mature fruits on uncaged portions of focus clumps (i.e., on a different portion of the same clump that has a cage). There were 160 open clumps and 36 uncaged focus clumps in 2012, and 155 and 37 in 2013 (the same ones in both years).

6.3 Results and Discussion

6.3.1 Population Characterization

The seven natural populations of *Grusonia parishii* (GRUPAR) studied occurred in widely separated regions of the Mojave Desert. They were all small by plant conservation standards, appearing to contain less than 100 clumps (roughly individuals) each and as few as 16 clumps (Table 6.1). Population densities ranged from a high of 228 clumps/ha (JTNP2) to a low of 3.2 clumps/ha (JTNP4), but there was no geographic pattern (i.e., large and small, high and low density populations can occur in either portion of the California range of the species). Each clump, however, can be composed of hundreds to thousands of stem units (joints) and each of those has the potential of rooting and establishing itself (as a ramet that vegetatively propagates the genet). An absence of data on genetic structure prevents knowing how resilient these clonal populations might be in the face of intense disturbance or climate change. A lack of genetic variation (due to small population size, dominance of ramet establishment over genet (seed) establishment and/or lack of pollen exchange among individuals or populations) within populations could be one important factor leading to extirpation and range contraction.

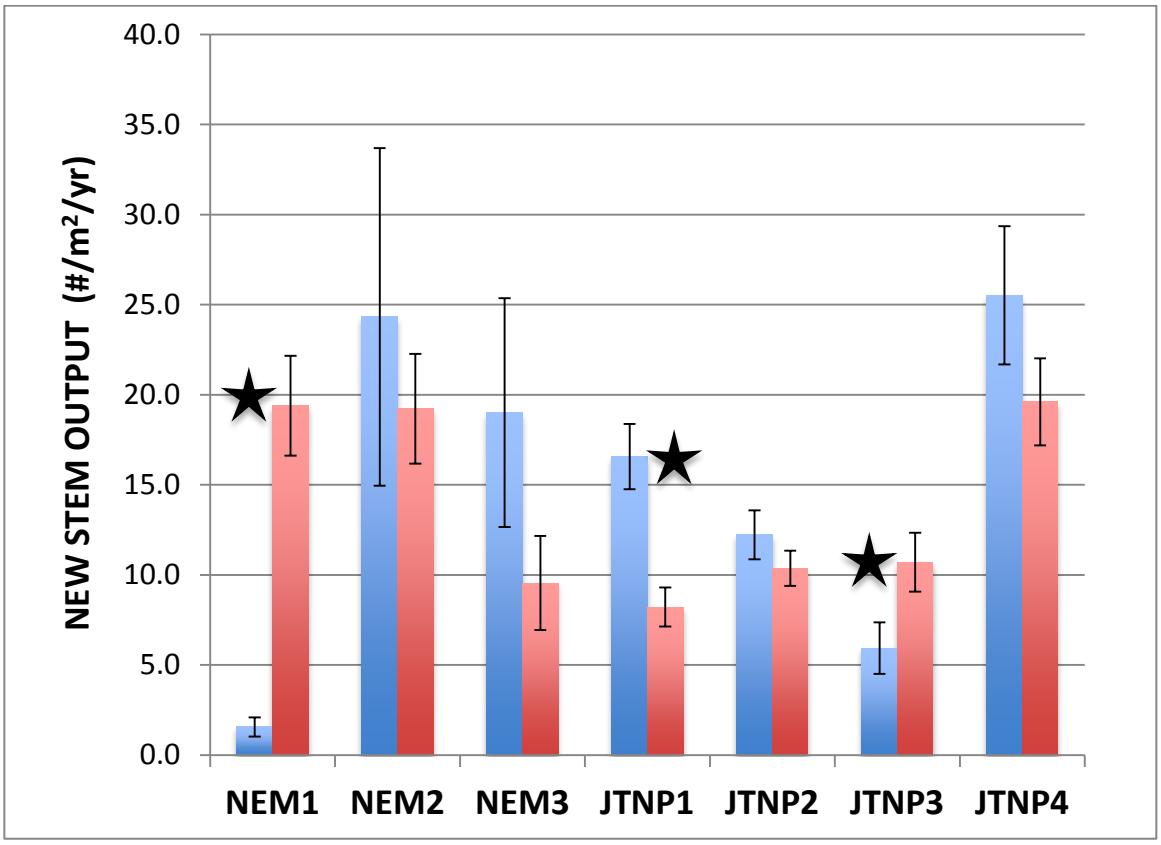
Clump sizes varied greatly among populations and appeared to have a geographic pattern. Size means, standard deviations and coefficients of variation were highest in the JTNP populations, indicating they have a more heterogeneous size/age structure (i.e., with both larger and smaller clumps in the frequency distribution). If clonal (cluster) growth rates are similar between NEM and JTNP populations, or especially if growth rates are greater in the NEM than JTNP, then larger clumps in JTNP would be older than those in NEM and smaller clumps younger. This indicates greater population age and higher reproduction (sexual and asexual combined), respectively, in JTNP.

During the 2011 to 2014 period of observation, eight whole GRUPAR clumps were destroyed and presumably killed during a monsoonal flash flood during fall 2013. A large wash eroded its banks and swept away the marked clumps from NEM1. This is the only mortality observed, resulting in a survivorship of 0.80 (compared to 1.00 in all other populations at the same time). One observation resulting in a single, short-term measurement of survivorship is simply insufficient for PVA, but it does illustrate one of the desert's unpredictable disturbance factors that could result in the death of an entire, long-lived clone (Or, it could result in dispersal and population growth if separated ramets subsequently become established "downstream").

6.3.2 Growth and Fecundity Measurements

Clonal growth as measured within clusters varied between 2012 and 2013 at most study sites (Figure 6.4). In two cases (NEM1, JTNP1) the difference was significant but for the most part new stem output was the same in both years. In five of the seven populations a relatively high rate of growth was achieved in at least one of two years, but in the other two (JTNP2 and JTNP3) rates were low in both years.

Figure 6.4: Clonal Growth of GRUPAR as Measured by New Stem Output of Clusters



Clonal growth of GRUPAR as measured by new stem output of clusters (mean + 1 SE) at seven study populations in the Mojave Desert. 2012 = blue, 2013 = red. Star indicates significant difference ($P<0.05$) between years at a site (two-sample t-test assuming unequal variances, one-tailed). See Tables 6.2 and 6.3 for a complete data summary.

When these growth rates were linked to cluster size and populations within regions combined (NEM vs. JTNP), it was apparent that 1) more clusters had higher growth rates in 2012 than 2013 in both regions, 2) smaller clusters produced more new stems in a year than larger ones, and 3) JTNP populations had larger clusters overall (Figures 6.5 a, b, c and d). But these regressions were not significant, because a large number of clusters in all populations and years produced no new stems.

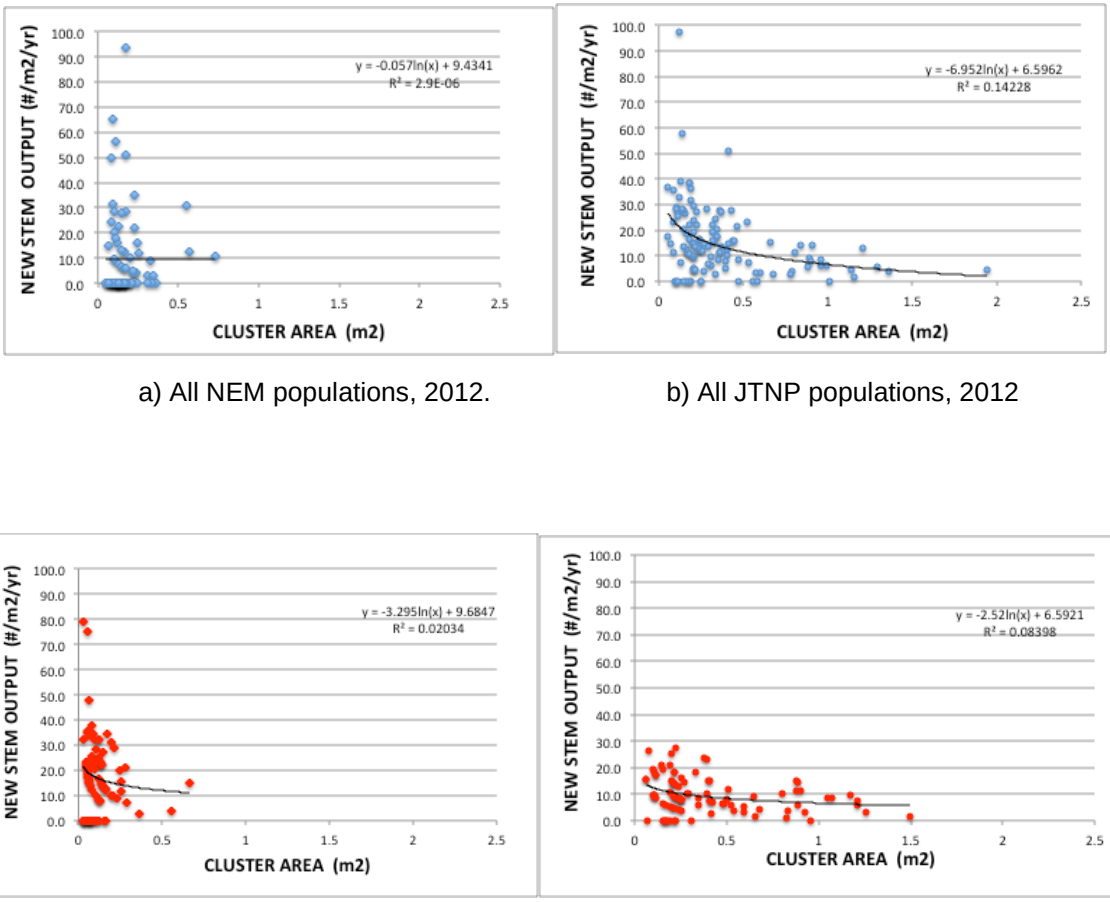
Table 6.2: Summary of GRUPAR Cluster Growth Characteristics, 2012

site	statistic	cluster size (m^2)	total # stems /cluster	% dead	# new stems per cluster	# new stems /m^2/yr	# floral buds per cluster	# floral buds /m^2/yr	n
NEM1	mean	0.1830	11.6	7.4	0.45	1.57			40
	s.d.	0.1154	6.2	13.3	1.34	3.35			
NEM2	mean	0.1592	18.9	10.4	3.0	24.32			29
	s.d.	0.0937	7.7	13.7	4.5	50.45			
NEM3	mean	0.1653	17.9	20.9	3.7	19.01			16
	s.d.	0.1275	10.8	17.7	5.4	25.39			
JTNP1	mean	0.4211	18.4	4.8	5.8	16.56	6.59	1388.02	37
	s.d.	0.3024	18.4	8.7	4.5	11.00	7.66	1046.90	
JTNP2	mean	0.5120	36.1	4.1	4.3	12.23	8.29	1823.11	38
	s.d.	0.4169	27.8	6.5	2.5	8.40	7.50	1637.57	
JTNP3	mean	0.2589	16.0	0.0	1.4	5.94	3.30	873.93	21
	s.d.	0.1991	11.6	0.0	2.0	6.57	5.29	1155.68	
JTNP4	mean	0.2252	21.2	11.2	4.7	25.53	1.42	468.13	26
	s.d.	0.1500	11.9	15.5	3.2	19.56	2.74	680.84	
CLA1	mean	0.4555	27.9	0.0	1.0	1.98	6.89	1694.69	9
	s.d.	0.2970	16.8	0.0	1.7	2.85	10.91	2992.87	
ISE1	mean								
	s.d.								
ISE2	mean	0.4765	31.4	0.0	3.2	6.43	0.15	29.12	30
	s.d.	0.2787	15.5	0.0	3.6	5.59	0.36	81.69	
									246

Table 6.3: Summary of GRUPAR Cluster Growth Characteristics, 2013

site	statistic	cluster size (m^2)	total # stems /cluster	% dead	# new stems per cluster	# new stems /m^2/yr	# floral buds per cluster	# floral buds /m^2/yr	n
NEM1	mean	0.1370	16.3	23.6	2.4	19.39	0.71	339.63	34
	s.d.	0.1269	7.6	16.0	2.1	16.15	1.95	751.70	
NEM2	mean	0.1119	20.6	23.9	2.0	19.22	0.50	601.13	28
	s.d.	0.0743	9.1	16.0	1.6	16.09	0.84	1262.97	
NEM3	mean	0.1236	15.25	10.3	0.9	9.55	0.88	1261.67	16
	s.d.	0.1297	8.3	10.5	1.0	10.44	1.02	1908.90	
JTNP1	mean	0.3749	32.4	15.7	2.6	8.22	0.62	182.50	37
	s.d.	0.2821	19.4	11.8	2.6	6.61	0.98	313.76	
JTNP2	mean	0.4975	41.8	11.3	4.3	10.37	2.89	556.51	38
	s.d.	0.3871	29.5	8.7	3.3	6.03	3.68	693.66	
JTNP3	mean	0.2786	20.5	5.7	2.8	10.71			21
	s.d.	0.2248	15.7	4.8	2.6	7.50			
JTNP4	mean	0.2812	29.0	18.5	5.5	19.61			25
	s.d.	0.1607	16.9	11.2	3.9	12.07			
CLA1	mean	0.3009	29.3	11.4	4.4	19.22	1.88	469.77	8
	s.d.	0.1892	9.5	7.1	1.7	13.08	4.16	791.63	
ISE1	mean	0.1871	20.0	29.4	2.7	20.83	0	0.0	3
	s.d.	0.1054	8.2	21.5	0.6	18.60	0	0.0	
									217

Figure 6.5: Clonal Growth of GRUPAR Measured by New Stem Output of Clusters



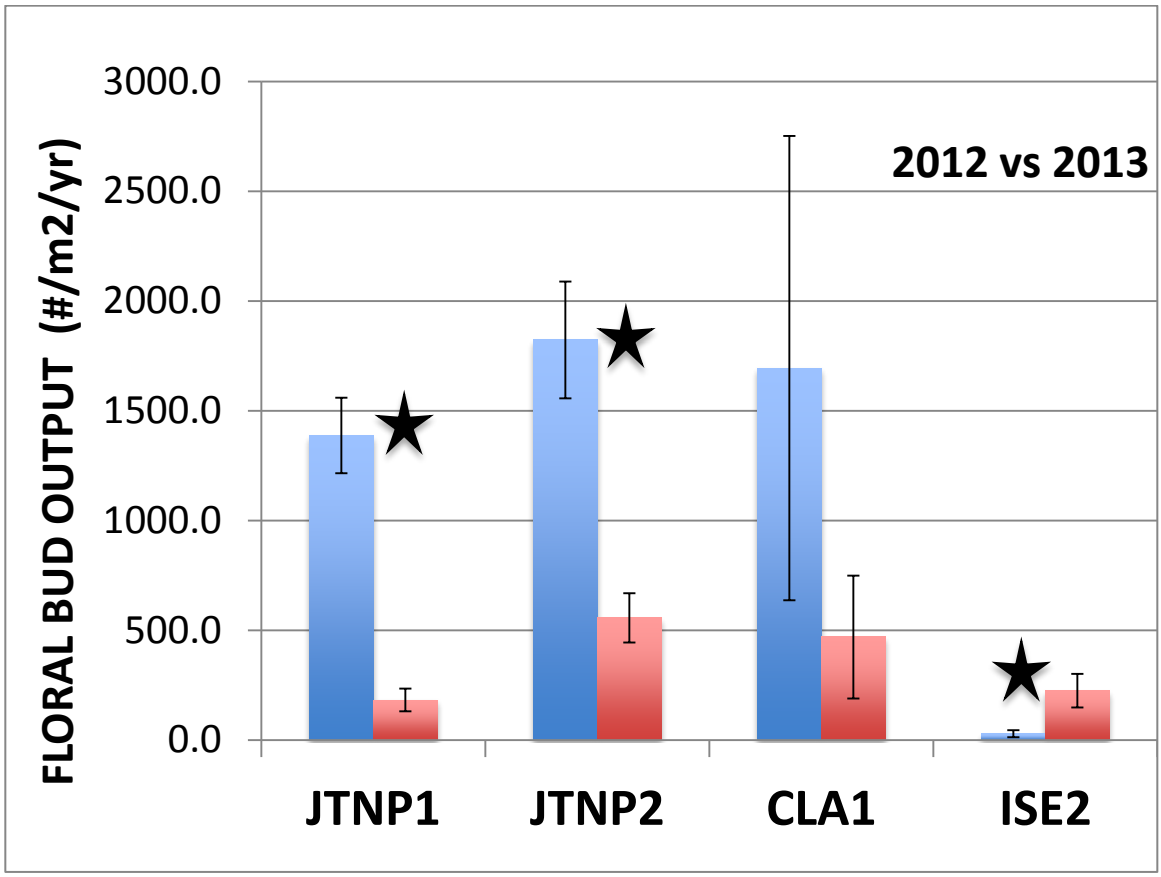
a) All NEM populations, 2012. b) All JTNP populations, 2012

c) All NEM populations, 2013 d) All JTNP populations, 2013

Clonal growth of GRUPAR measured by new stem output of clusters (mean + 1 SE) as a function of cluster area. Seven study populations in the Mojave Desert were combined into two regions. 2012 = blue, 2013 = red. R^2 values indicate the relationships explain only small amounts of variation in stem production.

The rates of floral bud output varied between sites and years, sometimes significantly (Figure 6.6). Natural populations in Joshua Tree National Park had high output in 2012, as did the CLA1 transplant site. Natural populations also had their best floral year in 2012, coinciding with higher stem output rates. Attempts to find evidence of allocation trade-offs between floral output and stem output (i.e., lowered stem output as the result of floral output) were not successful in any population or year (data not shown).

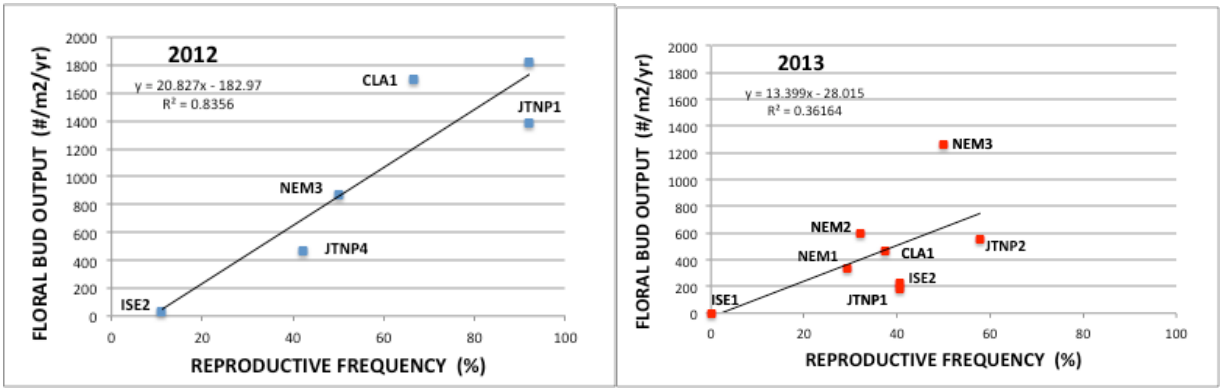
Figure 6.6: Fecundity of GRUPAR as Measured by Floral Bud Output of Clusters



Fecundity of GRUPAR as measured by floral bud output of clusters (mean + 1 SE) at four study populations in the Mojave Desert. Star indicates significant difference (P<0.05) between years at a site (two-sample t-test assuming unequal variances, one-tailed). 2012 = blue, 2013 = red. See Tables 6.2 and 6.3 for a complete data summary.

There was a strong correlation between the frequency of individuals in a population that produced floral buds (i.e., the proportion of clumps that bore at least one reproductive bud) and the mean floral bud output for that population (Figures 6.7 and 6.8). In general, the frequency of floral bud output tended to be low in ISE populations and higher in natural populations, although this was not consistent between years. Both frequency and output were highest in 2012. These data suggest that favorable conditions for reproductive growth that affect the populations as a whole also manifest themselves in clump performance. This would indicate there is not much microsite variation among clumps at a given location because of a uniform response to reproductive stimuli or resource availability. This could be some aspect of soil water availability and/or precipitation.

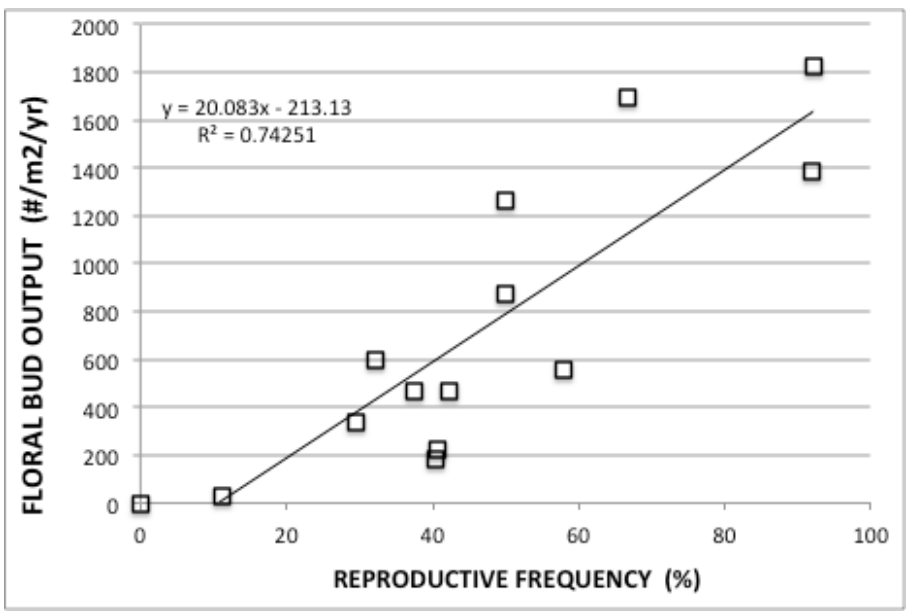
Figure 6.7: Relationship Between Frequency of Reproduction Among Clumps in a Population and the Mean Floral Bud Output (per cluster) of Those Populations in Two Study Years



a) 2012 b) 2013

R^2 values indicate that the variation in floral bud activity is well explained by reproductive frequency ($P<0.05$).

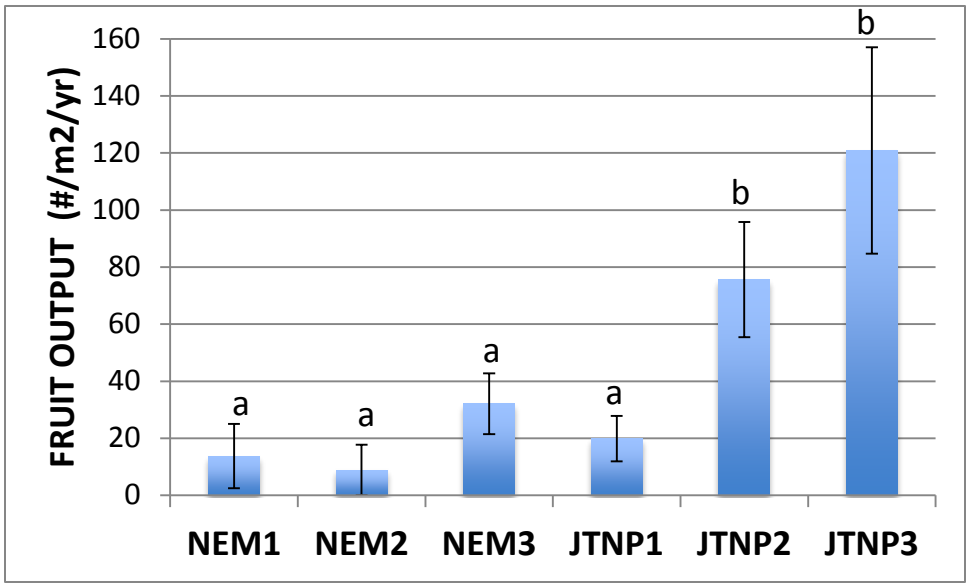
Figure 6.8: Relationship Between Frequency of Reproduction Among Clumps in a Population and the Mean Floral Bud Output (per cluster) of Those Populations, Sites and Years Combined



The relationships are significant ($P<0.05$).

There appeared to be a weak geographic pattern with respect to fruit output in 2012 as measured only within cages (Figure 6.9). (Using only caged counts was necessary because of intense herbivory outside the cages (see below). The data for 2013 are not shown because 2012 fruits were not removed from inside or outside of the cages between years.) NEM1 and NEM2 populations had much less than 25% of the fruit output of JTNP 2 and JTNP3 populations, whereas NEM3 and JTNP1 were intermediate.

Figure 6.9: Fruit Output (mean ± 1 SE) of Six GRUPAR Populations, 2012



Columns marked by different letters are significantly different (P<0.05, pairwise two-sample t-test assuming unequal variances, one-tailed).

GRUPAR seeds are nearly spherical except for the "bump" of the radicle (Figure 6.10). The embryo axis is curved along the outside edge. Cotyledons are folded and attached along the side. The seed coat is spherical and regular. On average there were 56 apparently filled seeds per fruit (sites and years combined, n = 80, range of 0 to 203), but with considerable variation between populations (Figure 6.11). No fully formed, uneaten fruits could be found at NEM1 in any study year despite the fact that floral bud output was moderate in 2013 (Figure 6.5b). Means were much higher for other populations, but not significantly different from each other. The low number at JTNP1 could be due to small sample size (n = 3), but this does not explain the equally low number at JTNP4 (n=20).

Figure 6.10: X-rays of GRUPAR Seeds, Showing Representatives of Non-viable and Presumably Viable Individuals

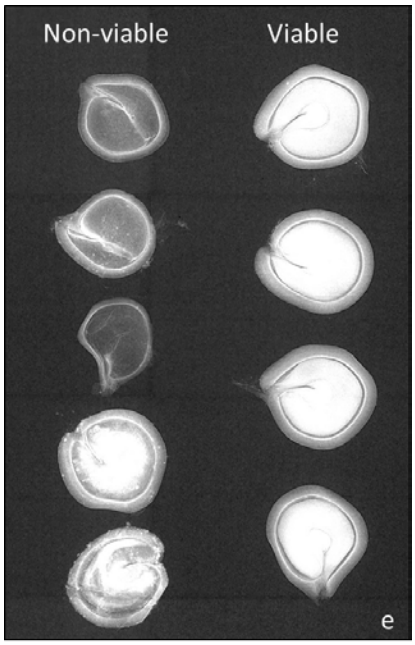
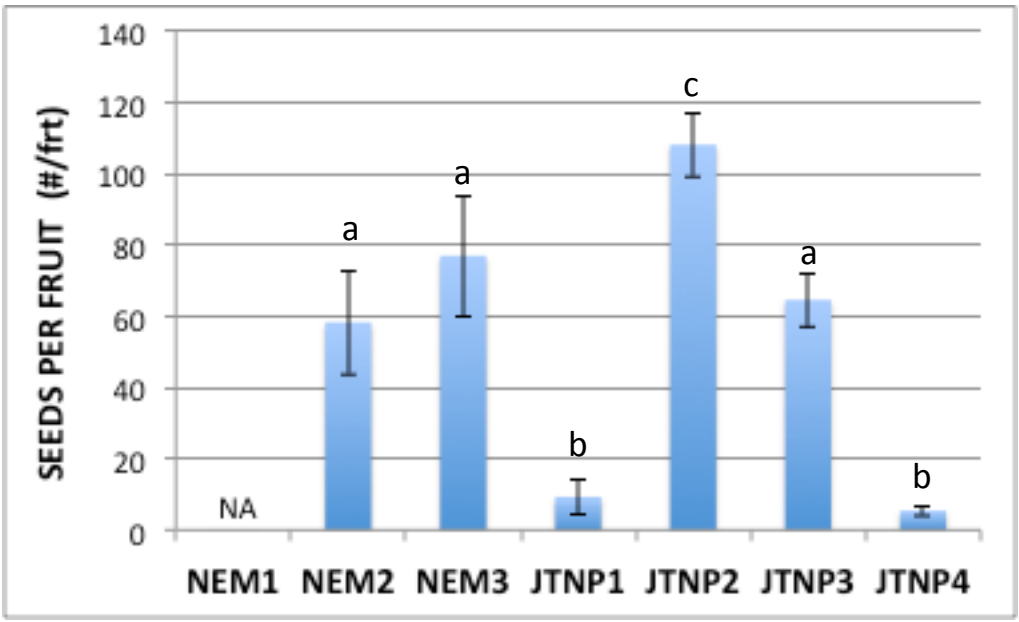


Figure 6.11: Number of Filled Seeds per Mature Fruit From Six Populations of GRUPAR, 2012.



Columns marked by different letters are significantly different (*P*<0.05, pairwise two-sample t-test assuming unequal variances, one-tailed). No fruits were available from NEM1.

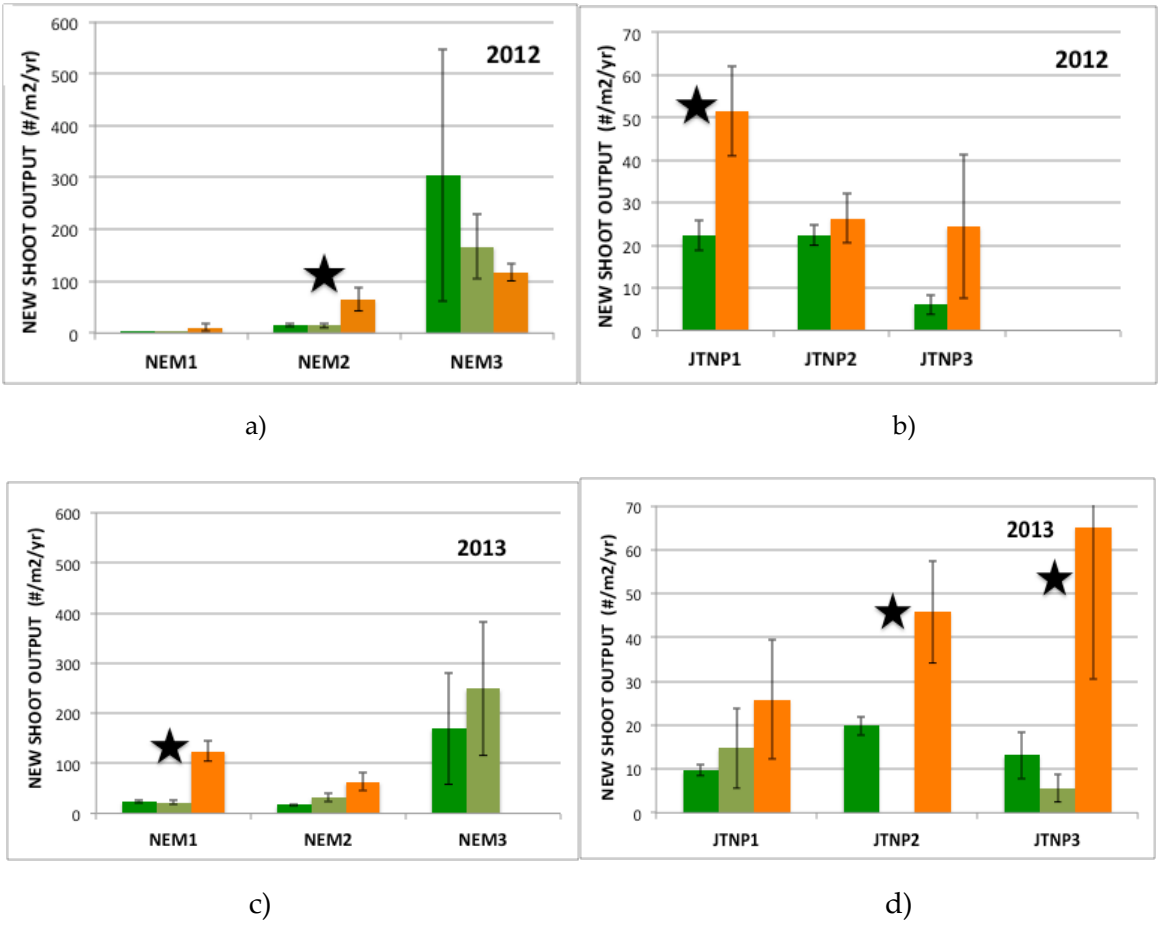
The size, color and degree of external fungal infection did not indicate embryo quality within the seeds, and therefore, non-viability. But X-rays readily revealed completely empty or partial embryos regardless of these external characteristics. GRUPAR seeds had low means for non-viability in both of the 2011 (17.1%) and 2012 (23.3%) crops. Across all sites and years, the highest % non-viability was 34.7% at NEM3 from a sample of 100 seeds and 6 clumps. Variability was moderate overall (CoVar ranged from 0.167 to 1.157) when compared to other rare Mojave taxa.

6.3.3 Quantifying the Effects of Herbivory on Growth and Fecundity

Efforts to obtain uniform data on new stem, floral bud, seed, and fruit output were hampered by the activities of herbivores within all GRUPAR populations (Tables 6.4, 6.5 and 6.6). Judging by scat it appeared that jackrabbits were the most widespread and abundant herbivores, with particular fondness for floral buds and fruits. Small rodents that burrow beneath clumps, as well as burros, might also contribute but evidence is lacking.

New shoot output was significantly greater within cages at NEM2 and JTNP1 in 2012 (Figure 6.12 a and b) and at NEM1, JTNP2 and JTNP3 in 2013 (Figure 6.12 c and d) when compared to either open clumps (without any cages) or the uncaged portions of focus clumps (that had cages on another part of the clump).

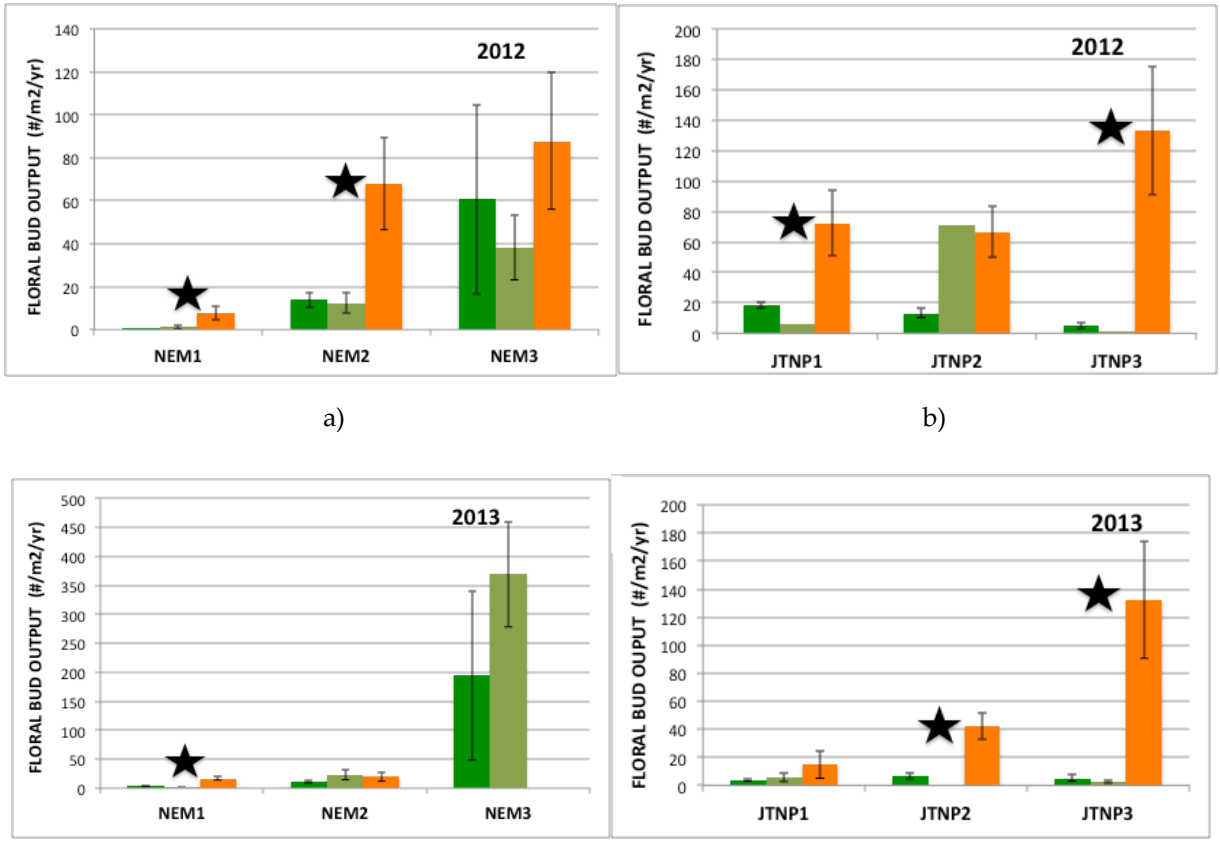
Figure 6.12: Effect of Caging on New Shoot Output of GRUPAR at Seven Study Populations in the Mojave Desert.



Effect of caging (orange bar, right column for each site) on new shoot output of GRUPAR at seven study populations in the Mojave Desert. Star indicates significant difference (P<0.05) between caged clusters and uncaged clusters (either open (dark green, left) or focus (light green, center) controls) (two-sample t-test assuming unequal variances, one-tailed). .See Table 6.4 for a complete data summary.

Even more widespread among sites and often more intense (i.e., with greater effect compared to controls) was the effect of caging on floral bud output (Figure 6.13). Caging significantly increased floral bud output by exclusion on each of six populations in at least one year. The greatest and most consistent increase was at JTNP3, where the caged output was approximately 133 floral buds/m^2/yr compared to the uncaged output (controls combined) of approximately 5 floral buds/m^2/yr, a 26-fold improvement.

Figure 6.13: Effect of Caging on Floral Bud Output of GRUPAR at Six Study Populations in the Mojave Desert.



Effect of caging (orange bar, right column for each population) on floral bud output of GRUPAR at six study populations in the Mojave Desert. Star indicates significant difference ($P<0.05$) between caged clusters and uncaged clusters (either open (dark green, left) or focus (light green, center) controls) (two-sample t-test assuming unequal variances, one-tailed). See Table 6.5 for a data summary.

Table 6.4: Effect of Caging on New Shoot Density (#/m^2) at Multiple Sites

		2012					2013				
		No Cage			Cage		No Cage			Cage	
site	statistic	Open	Focus	n/n*	Focus	n	Open	Focus	n/n*	Focus	n
NEM1	mean	0.082	1.254	30/10	10.667	10	23.366	21.352	27/9	124.286	10
	s.d.	0.372	2.295		25.762		14.915	12.577		63.045	
NEM2	mean	14.414	14.34	19/9	65.18	8	16.83	31.68	19/5	62.68	9
	s.d.	14.300	12.79		63.80		10.31	19.16		54.00	
NEM3	mean	304.64	166.78	6/10	117.15	7	169.08	248.58	6/10		
	s.d.	595.60	195.84		44.01		272.03	419.99			
JTNP1	mean	22.30		27/	51.51	10	9.66	14.72	27/4	25.81	6
	s.d.	18.23			33.25		6.15	18.24		33.13	
JTNP2	mean	22.43		27/	26.33	10	19.79		24/	45.75	8
	s.d.	12.65			18.14		10.75			32.81	
JTNP3	mean	6.04	1.96	12/7	24.44	9	13.10	5.60	12/9	65.19	9
	s.d.	7.86	2.97		50.77		18.71	9.42		104.44	
JTNP4	mean	1.19		26/			3.38		26/		
	s.d.	2.94					4.51				
CLA1	mean	9.92		9/			115.09		8/		
	s.d.	9.26					34.41				
ISE1	mean	3.57		4/			44.09		3/		
	s.d.	4.85					16.01				

* n/n is sample size for open/focus clusters with no cage, n is sample size for cage focus only.

Table 6.5: Effect of Caging on Floral Bud Density (#/m^2) at Multiple Sites

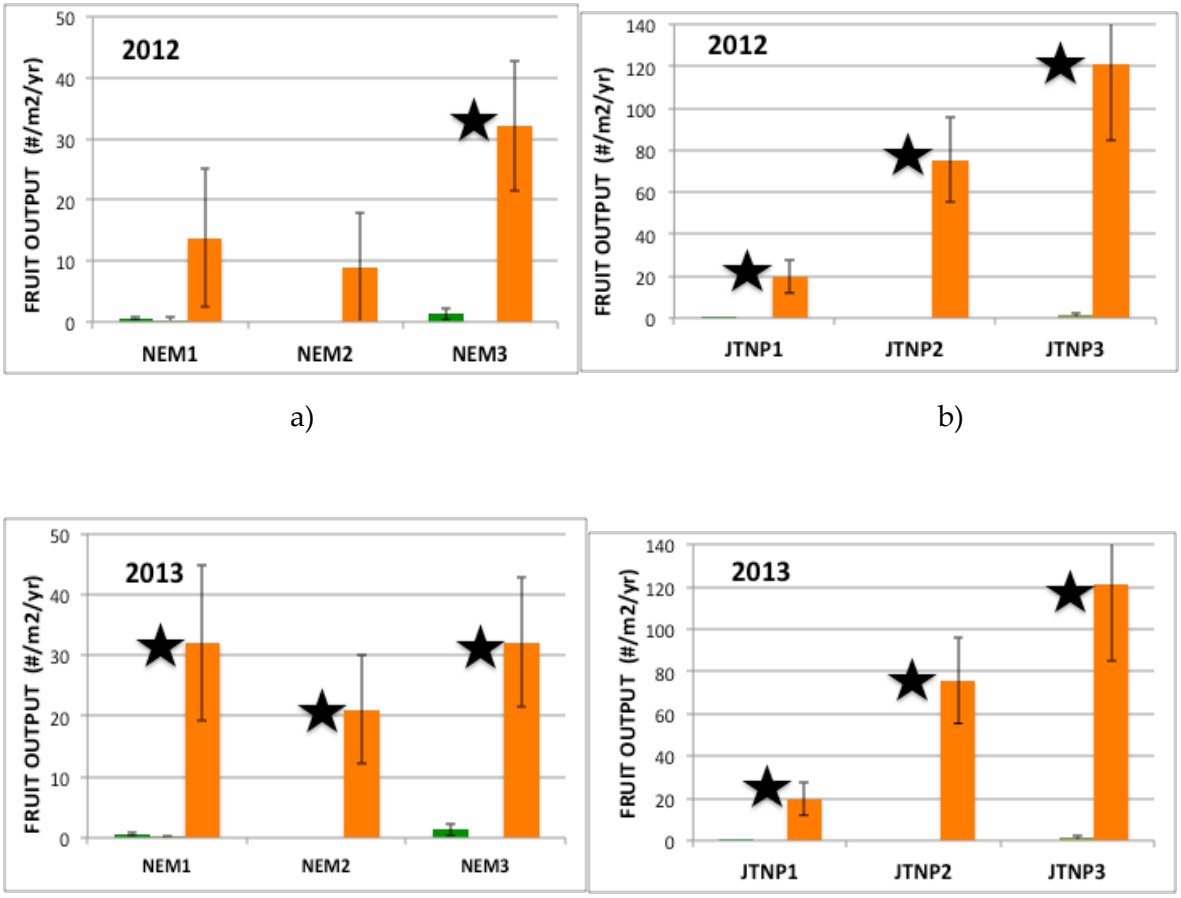
		No Cage			Cage		No Cage			Cage	
site	**statistic**	**Open**	**Focus**	**n/n***	**Focus**	**n**	**Open**	**Focus**	**n/n**	**Focus**	**n**
NEM1	mean	0.11	1.08	30/10	7.81	10	3.49	1.35	27/9	16.91	10
	s.d.	0.34	2.33		10.71		5.13	1.75		8.64	
NEM2	mean	13.77	12.3	19/7	68.04	9	10.83	22.99	19/6	20.0	8
	s.d.	14.65	12.5		64.40		9.30	20.34		22.3	
NEM3	mean	60.63	38.34	6/10	87.83	8	194.21	369.14	6/8		
	s.d.	107.98	47.85		89.80		356.76	257.05			
JTNP1	mean	18.11	6.11	27/1	72.34	10	3.63	5.53	27/5	14.60	6
	s.d.	10.28			67.30		3.74	6.44		23.41	
JTNP2	mean	13.21	70.77	28/1	66.66	10	6.48	0.00	26/1	42.23	7
	s.d.	15.35			52.59		11.86			25.64	
JTNP3	mean	4.88	0.15	12/7	133.19	9	5.08	2.62	11/7	132.07	8
	s.d.	7.17	0.40		127.11		7.09	3.28		117.27	
JTNP4	mean	7.70		26			6.93		26		
	s.d.	27.70					16.33				
CLA1	mean										
	s.d.										
ISE1	mean										
	s.d.										
				148/36		**56**			**142/36**		**39**

* n/n is sample size for open/focus clusters with no cage, n is sample size for cage focus only.

The effects of caging on fruit output, therefore, were also significant in all populations and in both years (Figure 6.14). The data for 2013 are somewhat problematic because 2012 fruits were not removed from inside or outside of the cages between years. The 2013 fruit counts could, therefore, include persistent mature fruits from 2012. Nevertheless, there were essentially no

mature fruits found on control plants at NEM1, NEM2, JTNP1 and JTNP2 populations in either study year, while those found at NEM2 and JTNP3 were less than 2% of those found in cages.

Figure 6.14: Effect of Caging on Mature Fruit Output of GRUPAR at Six Study Populations in the Mojave Desert



Effect of caging (orange bar, right column for each population) on mature fruit output of GRUPAR at six study populations in the Mojave Desert. Star indicates significant difference (P<0.05) between caged clusters and uncaged clusters (either open (dark green, left) or focus (light green, center) controls) (two-sample t-test assuming unequal variances, one-tailed). See Table 6.6 for a complete data summary.

Table 6.6: Effect of Caging on Fruit Output (#/m^2/yr) at Multiple Sites

		2012					2013				
		No Cage			Cage		No Cage			Cage	
site	statistic	Open	Focus	n/n*	Focus	n	Open	Focus	n/n	Focus	n
NEM1	mean	0.47	0.17	29/10	13.76	10	0.48	0.17	29/10	32.05	10
	s.d.	1.61	0.57		35.66		1.63	0.54		40.53	
NEM2	mean	0.00	0	19/6	8.89	9	0.00	0	19/6	21.06	9
	s.d.	0.00	0		26.67		0.00	0		26.56	
NEM3	mean	1.34	0	6/10	32.08	8	1.34	0	6/10	32.08	8
	s.d.	2.47	0		30.13		2.47	0		30.13	
JTNP1	mean	0.50	0	27/5	19.90	10	0.50	0	27/5	19.90	10
	s.d.	1.09	0		25.21		1.09	0		25.21	
JTNP2	mean	0.00	0	28/3	75.59	10	0.00	0	28/3	75.59	10
	s.d.	0.00	0		63.85		0.00	0		63.85	
JTNP3	mean	0.00	1.15	12/9	120.91	9	0.00	1.15	12/9	120.91	9
	s.d.	0.00	3.44		108.44		0.00	3.44		108.44	
JTNP4	mean										
	s.d.										

Effect of caging on fruit output (#/m^2/yr) at multiple sites. Open means clumps without cages, focus means clumps with cages. * n/n is sample size for open/focus clusters with no cage.

Despite the unpredictable occurrence and intensity of herbivore impact, the magnitude of its effects on multiple GRUPAR populations measured in just two study years suggests this could be a major factor in determining whether sexual reproduction is possible. A similar conclusion was reached by Pavlik et al. (2011) in a study of the effects of lagomorph herbivory on eight rare and endemic plant taxa at Ash Meadows National Wildlife Refuge, near Death Valley National Park.

6.4 Performance Rubric and Management Recommendations for Renewable Energy

Using 20 measured indicators of demographic performance and six measured indicators of herbivory impact, a performance rubric was constructed for the seven GRUPAR populations in California (see Appendix F for methods detail). With respect to demographic performance, the population on the edge of Queen's Valley (JTNP2) was ranked first, followed by JTNP1 and JTNP3 (Table 6.7). NEM1, NEM2 and JTNP3 (tie) and NEM3 were ranked lowest. This would strongly suggest a geographic divide, with southern populations out-performing those in the northwest that are nearest to the Ivanpah Solar Electric Generation Field (more demographic data from populations within the field (e.g., ISE1, ISE2) would provide a test). Although not all 20 indicators contributed to every population ranking, there was a minimum of 14 included. The method could be improved in the future by ensuring complete datasets for all indicators.

The ranking of six natural populations with respect to herbivory impacts alone (JTNP4 did not have cages) was somewhat different than the ranking for demographic performance. NEM3 was ranked first, having experienced the least amount of impact, followed by NEW2 and JTNP2. This would suggest that two of the worst performing populations from the standpoint of demography have been experiencing the least impact from herbivores, perhaps because they provide a lower quality resource to herbivores.

When the demographic and herbivory indicators are combined, then JTNP2, JTNP1 and NEW3 are the highest-ranking populations. Again there is slightly higher evidence for better performance in the south but the relatively low level of herbivory at NEW3 was beneficial.

The management recommendations of this non-integrated analysis follow from the rubric and the summary data Tables 6.1-6.6.

a) **Joshua Tree National Park constitutes an important and apparently vital reserve for the species in California**. Even though large GRUPAR populations are found in the northeast Mojave, overall better demographic performance was found in the park. The two highest performing populations (even with herbivore impact) were located in Queen's Valley (JTNP2 and JTNP1), within the boundaries and, therefore, the management regime, of Joshua Tree National Park. JTNP4 is small but high performing, albeit with herbivore impacts that lower its overall rank. Consequently, a high level of protection and the highest potential for best practices conservation management are already afforded to the southwest end of GRUPAR distribution.

b) **Vegetative growth in the form of stem output is most likely the mechanism that increases clump size, cluster size and the potential for sexual reproduction through floral bud output.** Environmental conditions that enhance these measurable features of GRUPAR populations are, therefore, likely to enhance persistence and resilience in natural and created populations. Monitoring programs should adopt this methodology so that long-term and comparable data can be used to evaluate conservation and restoration efforts.

c) **Despite the high potential for fruit output and the relatively low-levels of seed non-viability, sexual reproduction is probably a rare event *in situ*.** No seedlings were observed in the field during three years of observation, even with ample monsoon rains that fell during two summers (2012 and 2013). Although the breeding system and pollinators remain unknown, it does not seem that these are constraining factors. Given the availability and quality of seeds (when flowers are protected from herbivory), the authors thus recommend using seeds to propagate GRUPAR individuals for purposes of restoration. An *ex-situ* program, following guidelines of the Center for Plant Conservation (Maschinski and Haskins 2012) could be used to manage genetic diversity in created populations, broaden age structure in senescent natural populations, as well as form a conservation reserve. But the complete lack of genetic information is a major impediment to conserving this rare plant species, as it is for most others in the California deserts.

d) **The single greatest constraint on the vitality of natural GRUPAR populations in California appears to be intense and frequent herbivory, particularly on fruits.** Herbivory significantly reduces the output of new stems, floral buds and mature fruits, all of which constitute essential elements of population vitality. The principle culprits have yet to be identified with certainty, but the strong suspicion is that jackrabbits are responsible as they are in other parts of the California deserts (see Pavlik et al. 2011 for a broader discussion of lagomorph impacts). Small exclusion cages proved very effective in reducing herbivory and enhancing vegetation growth and sexual reproduction. Ironically, a large "cage", such as a chain link fence surrounding thousands of acres would likely increase impacts because herbivore populations would be confined within and unable to forage in other parts of the landscape. Therefore, the authors recommend that caging studies like ours be replicated within solar fields to test this prediction. If intense herbivory impacts rare species such as GRUPAR within those fields, then an herbivore control program might be necessary to maintain vitality of created and conserved populations.

Table 6.7: Performance Rubric for GRUPAR Populations Using 2012 and 2013 Demographic Data

pop	total pop size (#)	pop density (#/ha)	clump size (m^2)	clump size CoVar	2012 stems /cluster	2012 % dead	2012 new stems /m^2/ yr	2012 new stems CoVar	2012 floral buds /m^2/yr	2012 floral buds CoVar	2013 stems /cluster
NEM1	1	1	3	4	4	1	4	4			4
NEM2	1	4	3	4	3	1	1	4			4
NEM3	4	1	4	4	3	4	2	3			4
JTNP1	1	3	1	1	3	1	2	1	2	1	2
JTNP2	2	1	3	4	1	1	3	1	1	1	1
JTNP3	4	4	4	3	4		4	3	3	4	4
JTNP4	3	4	1	3	3	3	1	1	4	4	2
Quartile upper limit	80+	228.0	1.69	1.80	36.10	4.1	25.53	0.66	1823.11	0.75	41.80
to -25%	60	171.8	1.40	1.49	29.98	8.3	19.54	1.03	1484.37	0.93	35.16
-50%	40	115.6	1.11	1.18	23.85	12.5	13.55	1.40	1145.62	1.10	28.53
-75%	20	59.4	0.82	0.87	17.73	16.7	7.56	1.77	806.88	1.28	21.89
<75%						20.9		2.14		1.454	
						negative		negative		negative	

Table 6.7 (cont)

pop	2013 % dead	2013 new stems /m^2/ yr	2012 new stems CoVar	2013 floral buds /m^2/yr	2013 floral buds CoVar	2012 fruits /m^2/yr	2012 fruit CoVar	2012 seeds /fruit	2012 seeds /frt CoVar	Scores sum	n	demographic performance score	demographic performance rank
NEM1	4	1	3	4	4	4	4			50	15	3.3	6
NEM2	4	1	3	3	4	4	4	2	1	51	16	3.2	5
NEM3	2	4	4	1	2	4	1	2	1	50	16	3.1	4
JTNP1	3	4	1	4	3	4	1	4	3	45	18	2.5	2
JTNP2	2	4	1	3	1	2	1	1	1	35	18	1.9	1
JTNP3	1	4	1			1	1	2	1	48	15	3.2	5
JTNP4	3	1	1					4	4	42	14	3.0	3
Quartile upper limit	5.70	19.61	0.58	1261.67	1.25	120.91	0.84	108.2	0.448				
to -25%	10.25	16.76	0.71	1031.16	1.49	92.91	1.38	82.50	0.632				
-50%	14.80	13.92	0.84	800.65	1.73	64.90	1.92	56.80	0.816				
-75%	19.35	11.07	0.96	570.14	1.97	36.90	2.46	31.10	1.001				
<75%	23.90		1.09		2.213		3.00		1.185				
	negative		negative		negative		negative		negativ e				

Table 6.7 (cont)

pop	2012 shoot herb	2013 shoot herb	2012 floral bud herb	2013 floral bud herb	2012 frt herb	2013 frt herb	sum	n	herbivory impact score	herbivory impact rank	combined performance score	combined performance rank
NEM1	4	4	4	4	4	4	24	6	4.0	5	3.5	6
NEM2	4	3	4	1	4	4	20	6	3.3	2	3.2	4
NEM3	1		1		4	4	10	4	2.5	1	3.0	3
JTNP1	4	3	4	3	4	4	22	6	3.7	4	2.8	2
JTNP2	4	4	2	4	4	4	22	6	3.7	3	2.4	1
JTNP3	4	4	4	4	4	4	24	6	4.0	5	3.4	5
JTNP4												

GLOSSARY

Term	Definition
AFB	Air Force Base
AIC	Akaike information criteria
ASCNYC	*Asclepias nyctaginifolia*
BLM	Bureau of Land Management
CDFW	California Department of Fish and Wildlife
CEQA	California Environmental Quality Act
CI	Confidence interval
CNDDB	California Natural Diversity Database
CNPS	The California Native Plant Society
CNPS	California Native Plant Society
DRECP	Desert Renewable Energy Conservation Plan
ERIMOH	*Eriophyllum mohavense*
ERIWAL	*Eriophyllum wallacei*
ETP	extinction threshold population
GRUPAR	*Grusonia parshii*
ISEGS	Ivanpah Solar Electric Generating System
JTNP	Joshua Tree National Park
LTREs	Life Table Response Experiments
MENTRI	*Mentzelia tridentata*
MIMMOH	*Mimulus mohavensis*
MVP	Minimum viable population
NEM	northeastern Mojave
NEPA	National Environmental Policy Act
NLCS	Natural Landscape Conservation System
OHV	off-highway vehicle
PENALB	*Penstemon albomarginatus*
PPM	Population projection models
PRISM	Parameter Elevation Regression on Independent Slopes Model
SEGS	Solar Energy Generating Facility

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APPENDIX A:
Assessing Seed and Fruit Non-Viability of Rare California Desert Plants with X-Rays

A.1 Introduction

Assessing the viability of seeds and fruits of wild plant species has commonly used germination, tetrazolium and morphometric techniques. More recently, the availability of low power x-ray machines, normally employed for medical or histological purposes, has enabled application to plant materials. Use of the technique for commercial and industrial purposes (i.e. malting) came first (MacKay 1972), followed by assessments of forest and wildland seeds (Belcher 1973, Sahlen et al. 1995, Goodman et al. 2005) and then seed conservation (Gosling 2003, Tuckett et al. 2010). There is virtually no preparation required (other than arranging the sample inside a petri dish) and digital images are produced within two minutes after pilot scans establish the proper focal length (Millennium Seed Bank, Royal Botanic Gardens Kew 2011). Small, poorly formed or damaged embryos are relatively easy to spot, so rather than expressing the quality of a seed lot in terms of viability, it is more appropriate to express it as apparent non-viability.

Researchers collected seeds or fruits from eight taxa used in the demographic studies of rare plants of the central Mojave Desert. When possible, lots were collected from multiple population sites in more than one crop year.

A.2 Methods

A.2.1 Collection and Use

Seed and fruit lots for 2011, 2013 and/or 2014 crops from multiple study sites were collected and stored in paper envelopes under ambient laboratory conditions at UC Davis. Subsamples of pre-burial seeds from the lots were set-aside and stored in paper envelopes to obtain estimates of maximum non-viability using x-ray. In all seeds of eight of the study species were x-rayed: *Asclepias nyctaginifolia* (ASCNYC), *Castela emoryi* (CASEMO), *Eriophyllum mohavense* (ERIMOH), *E. wallacei* (ERIWAL), *Grusonia parishii* (GRUPAR), *Mimulus mohavensis* (MIMOH), *Penstemon albomarginatus* (PENALB), and *P. thurberi* (PENTHUR).

The same seed lots were also used to prepare seed bags and returned to the field for seed bank studies. Seed bags of five species (ASCNYC, CASEMO, ERIMOH, ERIWAL and PENALB) were composed of 50 seeds or fruits (herein referred to as "seeds") each and subsequently buried within demographic study plots.

A.2.2 X-Ray

Estimates of pre-burial non-viability were obtained using the x-ray laboratory of the Millennium Seed Bank at the Royal Botanic Gardens Kew (London) beginning in May 2013 and ending in September 2014. Seed lots were composed from at least three individual plants from multiple sites (usually three, often more) for each species, being careful not to bias in favor of the larger, heavier and (presumably) higher viability seeds. These were arranged in plastic petri dishes and imaged using a Faxitron Specimen Radiographic System. Magnification was adjusted for differences in seed and fruit size of the species and each image was digitally stored for later analysis.

Non-viability was inferred by the absence of fully formed embryos and the relative transparency of cotyledon and embryo tissue to the x-ray. Guidance on interpreting embryo morphology at the level of family and genus was obtained from the comprehensive survey by Martin (1946). Damage by predators or other factors was also noted and incorporated into the estimates. Comparisons between viable and non-viable seeds or fruit, as revealed by x-ray, were subsequently made with dissection under a light microscope to ensure correct interpretation of embryo morphology and condition. Imaging and dissection of some species was more difficult due to the small size of their seeds (e.g. ERIMOH, ERIWAL, MIMOH) and in the case of MIMOH, it was not possible to make viability estimates with a high degree of confidence.

A. 2.3. Seed Bank Non-Viability

In-situ burial usually lasted for one year, from fall 2012 to fall 2013. Seed bags were exhumed and sent to Kew for x-ray. Assessment of non-viability applied the same criteria as for pre-burial lots.

A.3 Results and Discussion

A.3.1 Visual Comparisons of Pre-Burial Seeds

We were able to obtain useful images of seeds from seven of the eight species (Figure 1). Only one useful image of a MIMOH embryo was produced despite numerous attempts, otherwise we could at least apply the x-ray technique to populations of embryos from the other seven with varying degrees of confidence.

A.3.1.2 Asclepias nyctaginifolia

Without pappus the winged seeds are ovate with a central radicle that protrudes from one side. The embryo is two ovoid and flattened cotyledons attached to a short, centered embryo axis on the proximal side. A thin, triangular layer of tissue connects them on both sides of the axis and is sometimes missing (then counted as a partial, non-viable embryo). Seed coat is distinctly vascularized in a radiating pattern from the embryo and extending into the wing (Figure 1a).

Size and color differences among seeds seem to indicate quality, with smaller and more reddish (rather than dusky brown) lacking embryos or having incompletely formed cotyledons. When the embryo does not form the x-ray image is very distinctive. In a few seeds there were "bite marks", which could simply be developmental irregularities or the result of insect predation.

A.3.1.2 Castela emoryi

The fruits are often firmly attached to the pedicel and are generally lanceolate with a blunt distal apex. Pericarp is thick and there does not appear to be a distinct seed coat underneath. The embryo appears curved along the outside edge and quite elongated. The cotyledons are thick and may only attach at the very apex of the embryo axis (Figure 1b).

Size differences in fruit (visible with the naked eye) may indicate quality but color was not linked to quality (i.e. red, tan and green can all have full embryos). Continuous variation in size and transparency makes determination of viability difficult in the pre-burial condition.

A.3.1.3 Eriophyllum mohavense

Achenes were deltoid-elongate, with a short crown of pappus and a dense vestiture of strigose pubescence. Internal features were indistinct despite attempts to enlarge and clarify the images (Figure 1c).

Nevertheless, non-viability was relatively easy to quantify as unfilled achenes were elongated to full size but very transparent. These tended to be tan, rather than black, in color when examined under a dissecting microscope. Presumably viable achenes had x-ray-opaque embryos, especially near the pappus end, while developing viable embryos had x-ray-opaque vascular strands in their centers.

A.3.1.4 E. wallacei

Achenes were lanceolate, with a short but distinct crown of pappus. Internal features were indistinct despite attempts to enlarge and clarify the images.

Non-viability was more difficult to quantify than in *E. mohavense* due to continuous variation in embryo transparency (Figure 1d). The embryos were not as x-ray dense as in *E. mohavense* and so confidence in ascertaining non-viability was considerably lower.

A.3.1.5 Grusonia parishii

The seeds are nearly spherical except for the "bump" of the radicle. The embryo axis is curved along the outside edge. Cotyledons are folded and attached along the side. The seed coat is spherical and regular (Figure 1e).

Size, color and degree of external fungal infection do not indicate quality. X-rays readily revealed completely empty or partial embryos regardless of these external characteristics.

A.3.1.6 Mimulus mohavensis

The very small, nearly spherical seeds were the most difficult of all study taxa to x-ray. The only clear, enlarged image obtained may not represent a viable seed because the embryo does not fill the seed coat and appears irregularly transparent (Figure 1f). Lower magnification did not allow assessment of non-viability with any degree of confidence.

A.3.1.7 Penstemon albomarginatus

Seeds and embryos are curved like a cocktail shrimp and "lumpy" due to protrusions of cell clusters (magnification was very high). The seed coat appears ghostly and irregular in shape. In some a distinct vascular trace can be seen permeating the embryo tissue near to the small, inner radius (Figure 1g).

The size and shape of seeds (visible to the naked eye) do not indicate quality. X-rays reveal completely empty or partial embryos regardless of regardless of these external characteristics.

A.3.1.8 P. thurberi

Seeds and embryos are less curved than those of P. albomarginatus but still "lumpy" (same as for *P. albomarginatus*). The seed coat is nearly invisible, unlike in *P. albomarginatus*. In most seeds a distinct vascular trace can be seen permeating the embryo tissue near to the small, inner radius (Figure 1h).

The size and shape of seeds (visible to the naked eye) do not indicate quality. X-rays do not show distinct differences, although most have bright white vascular trace, and these were interpreted as representing complete embryos (even if irregular in shape). Small embryos without trace were considered non-viable.

A.3.2 Evaluation of Pre-burial Non-Viability

The embryos of seed lots from seven species stored under laboratory conditions were visually evaluated using x-ray (Table 1).

Seeds of *Asclepias nyctaginifolia* had low means for non-viability in both of the 2012 (13.1%) and 2013 (3%) crops. Across all sites and years, the highest % non-viability was 26.1% at site 3 from a sample of 119 seeds and 6 individual plants. Excluding that, the range was 0.0 to 8.8% but with a potential for high variability among individuals (CoVar ranged from 0.000 to 1.223).

Non-viability of *Castela emoryi* embryos was 19.7% in the 2012 crop. Site differences were weak, with no clear geographic pattern. The lowest value was 7.7% from the Castela Reserve, but otherwise it ranged between 20 and 30%. Variability among individuals at a site ranged between 0.2 and 0.8 CoVar.

Achene samples of *Eriophyllum mohavense* had low means for non-viability in 2013 (10.1 to 14.5%), which increased in the 2014 (33.6%) crop. Some of this increase was due to a single site (EM2), but overall there was high variability among sites and individuals (CoVar always exceeding 0.82). This could be due to continuous maturation within heads so that samples always contained a high proportion of undeveloped achenes that

were not viable. Alternatively, lack of pollination or inherent genetic limitations could be operating to increase non-viability.

In contrast, achenes of *Eriophyllum wallacei* had low means for non-viability in 2013 (8.4 to 9.4%), with relatively low variability with samples (CoVar between 0.175 and 0.391). Given that this species also has continuous maturation within heads, it suggests fewer limitations on achene viability when compared to its rare congener.

Seeds of *Grusonia parishii* had low means for non-viability in both of the 2011 (17.1%) and 2012 (23.3%) crops. Across all sites and years, the highest % non-viability was 34.7% at site 3 from a sample of 100 seeds and 6 individual plants. Variability was moderate overall (CoVar ranged from 0.167 to 1.157).

Seeds of *Penstemon albomarginatus* had low means for non-viability (2.2 to 18.2%) in 2011 and 2012, respectively, from a single site. Variability within samples, however, was very high (CoVar between 1.400 and 1.692).

Seeds of *P. thurberi* had low to moderate means for non-viability, which were highly variable in 2011 and much less so in 2012.

A.3.3 Post-burial Non-Viability

After one year of burial, non-viability increased significantly in embryos of *A. nyctaginifolia,* from 11 to 62% (Table 2, Figure 3). Changes in the transparency of the cotyledons were obvious and radicles had become difficult to discern.

In contrast, there was no significant difference in post-burial non-viability of *Castela emoryi* embryos (Table 2, Figure 4). Some slight increase in the transparency of buried seeds was observed, but the mean and maximum non-viability were within the same range as pre-burial (Table 1).

Mean non-viability values for the two *Eriophyllum* species also did not change much (Table 2, Figure 5), although maximum non-viability estimates for a single individual could approach 100%. This could have been the result of early harvest prior to burial, rather than the effects of burial itself.

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A.5 Figures and Tables

Figure A1. Representative images of pre-burial, viable seeds or fruits of a) Asclepias nyctaginifolia , b) Castela emoryi, c) Eriophyllum mohavense, d) E. wallacei, e) Grusonia parishii, f) Mimulus mohavensis, g) Penstemon albomarginatus, h) P. thurberi.

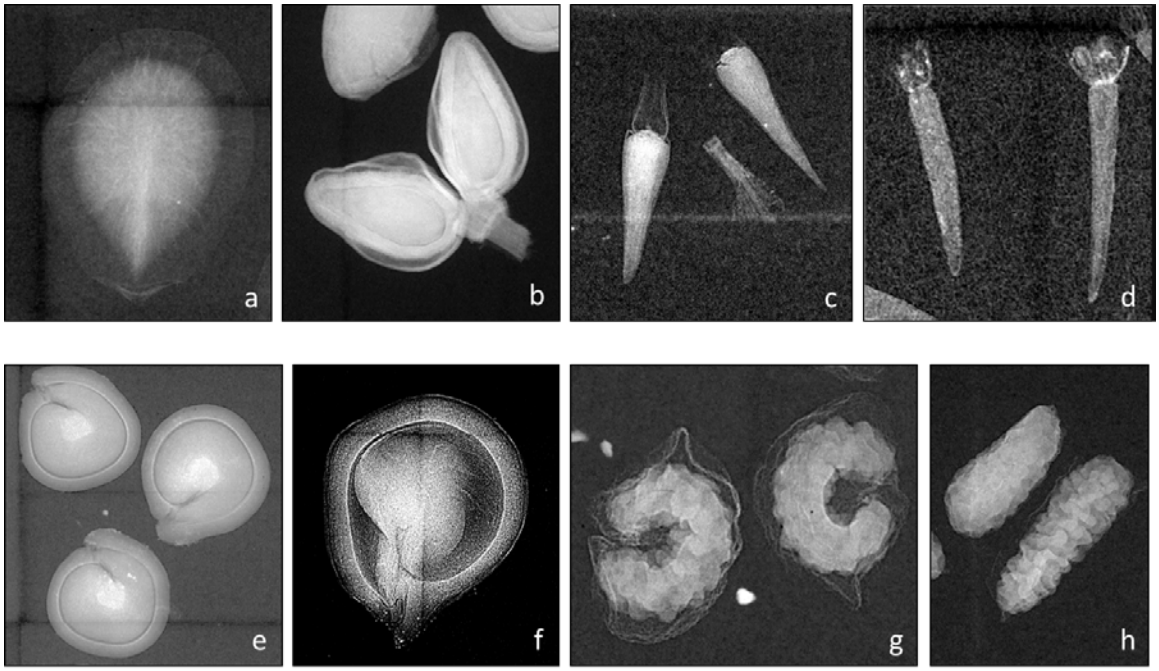


Figure A2. Representative images of non-viable and viable seeds of a) *Asclepias nyctaginifolia* and b) *Castela emoryi*.

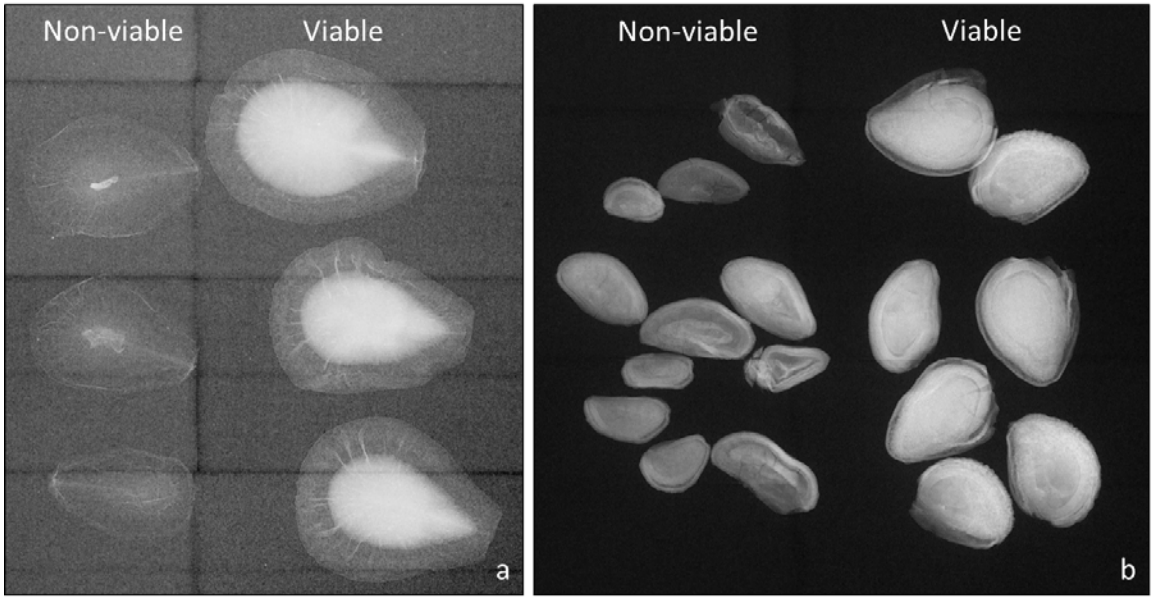


Figure A2 (cont.). Representative images of non-viable and viable seeds of c) *Eriophyllum mohavense* and d) *E. wallacei.*

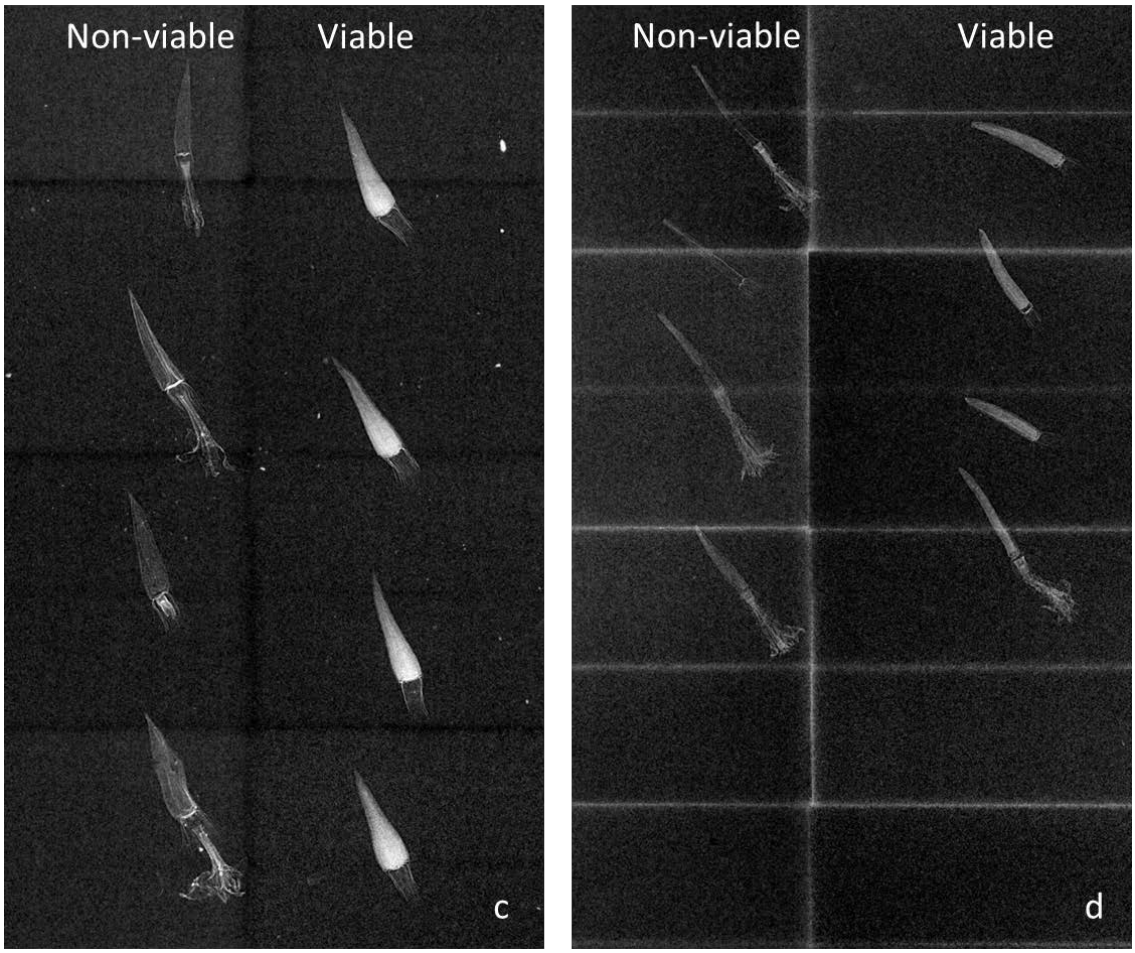


Figure A2 (cont.). Representative images of non-viable and viable seeds of e) *Grusonia parishii.*

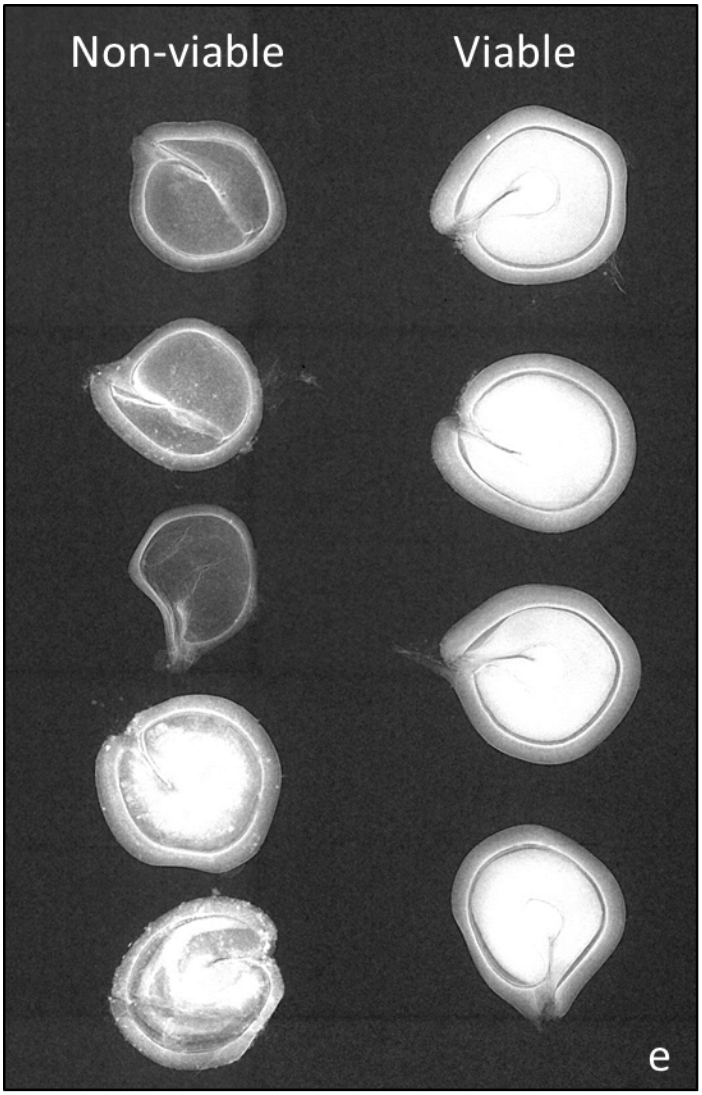


Figure A2 (cont.). Representative images of non-viable and viable seeds of f) *Penstemon albomarginatus* and g) *P. thurberi.*

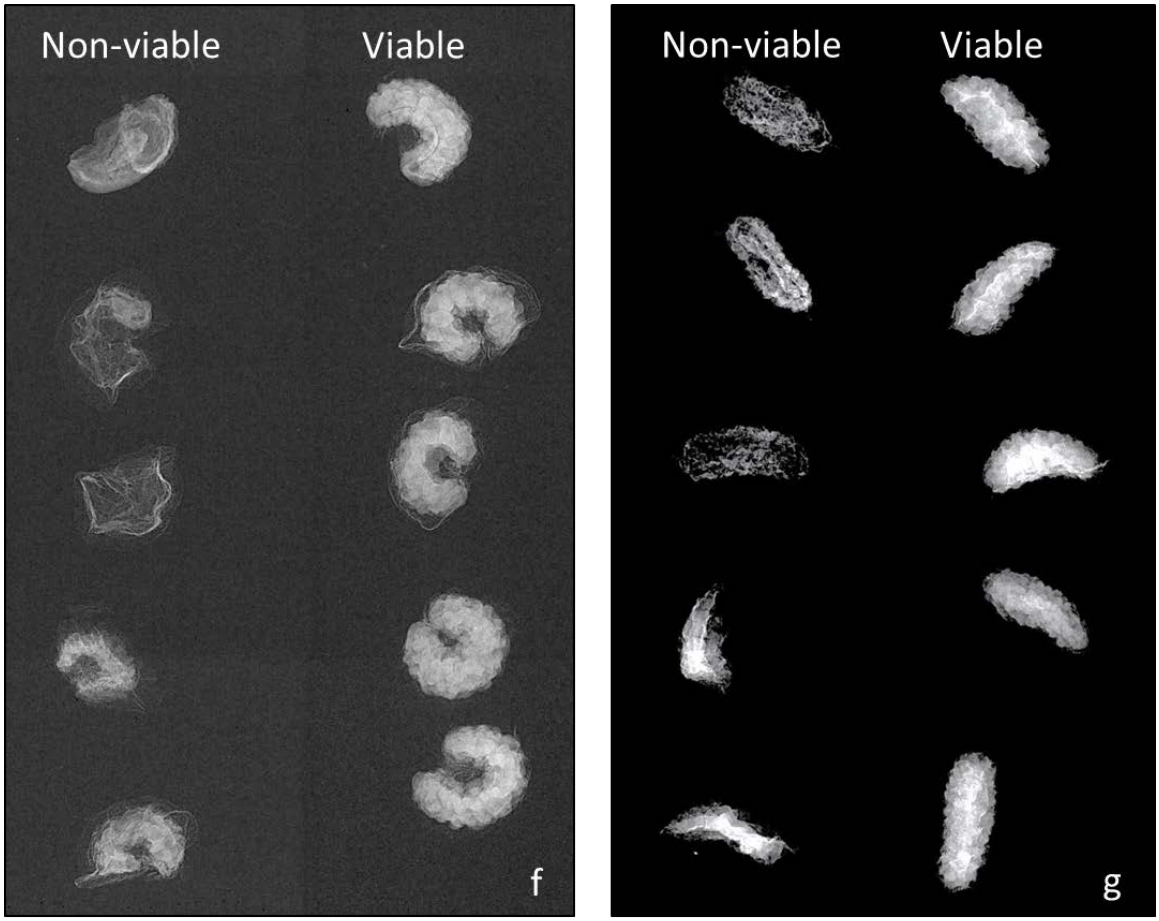


Figure A3. Comparison of pre-burial (left, 2012 crop) and one year buried (right) seeds of *Asclepias nyctaginifolia* from site 1. Bright spots are mineral particles. Note the very high frequency of empty seed coats ("ghosts") in the buried sample.

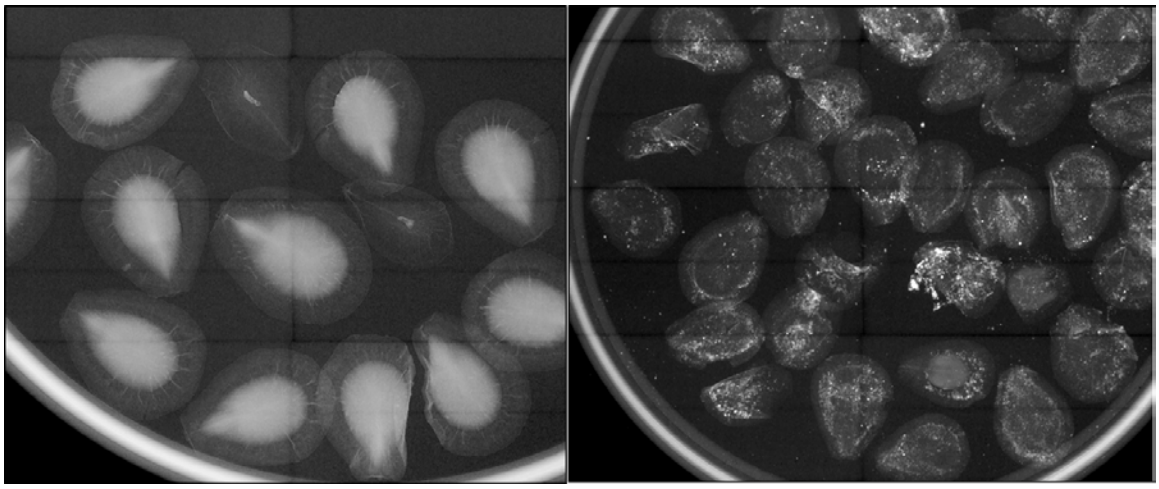


Figure A4. Comparison of pre-burial (left, 2012 crop) and one year buried (right) seeds (fruits) of *Castela emoryi* from site 1. Bright spots are mineral particles. Note the slight increase in transparency of buried seeds.

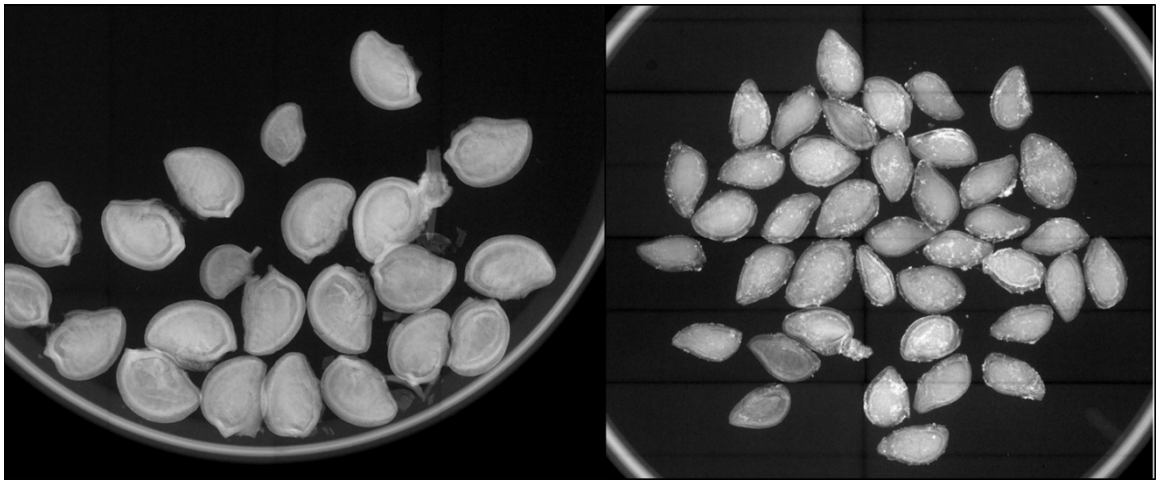


Figure A5. Comparison of pre-burial (left, 2012 crop) and one year buried (right) seeds (achenes) of *Eriophyllum mohavense* from site 1. Bright spots are mineral particles. There seems to be similar frequency of filled and unfilled achene walls.

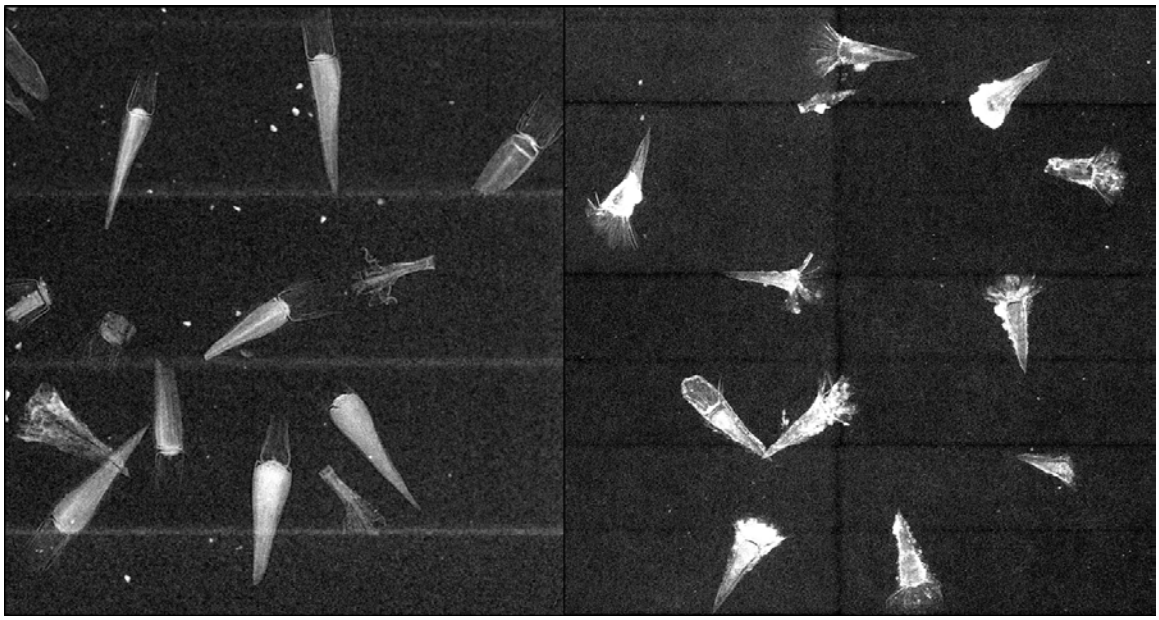


Table A1: Non-viability (non-via) of seeds/achenes of study species, as determined by x-ray inspection

taxon	yr	#sites/ sample	#plants/ Sample	sample # seeds	sample mean % non-via	SD	CoVar	site mean % non-via	SD	CoVar
ASCNYC	2012	3	16	356	13.1	13.9	1.06			
		1 (1)	5	88				8.8	10.4	1.174
		1 (2)	5	149				4.5	5.4	1.223
		1(3)	6	119				26.1	13.4	0.514
	2012	3	14	510	67.4	22.2	0.329			
	post-burial	1 (1)	5	212				61.4	21.8	0.355
		1 (2)	5	159				85.0	13.7	0.161
		1(3)	6	139				40.7	15.3	0.376
	2013	4	14	475	3.0	5.4	1.800			
		1 (1)	5	150				0.0	0.0	0.000
		1 (2)	4	150				4.5	1.0	0.222
		1(3)	1	25				(0.0)	nv	nv
		1(solarfield)	4	150				6.0	9.5	1.583
CASEMO	2012	6	16	736	19.7	11.9	0.604			
		1(2)	3	136				25.6	20.4	0.797
		1(3)	3	75				17.6	10.0	0.568
		1(6)	3	103				20.9	4.0	0.191
		1(7)	3	155				29.2	8.8	0.301
		1(Castela Reserve)	3	187				7.7	3.4	0.442
		1(Rice Valley)	1	80				(11.5)	nv	nv
CASEMO	2012	3	20	583	10.0	9.2	0.920			
	post-burial	1(5)		70				3.3	4.7	1.424
		1(8)		200				9.0	4.5	0.500
		1(Rice Valley)		313				11.0	10.0	0.909

taxon	yr	#sites/ sample	#plants/ Sample	sample # seeds	sample mean % non-via	SD	CoVar	site mean % non-via	SD	CoVar
ERIMOH	2011	1	5	53	37.5	26.2	0.699			
	post-burial									
	2013	3	9	52	10.1	13.2	1.307			
	2013	2	20	30	14.5	12.2	0.840			
	2014	2	12	224	33.6	30.8	0.917			
		1 (EM2)	9	130				39.8	32.7	0.822
		1 (EM3)	3	94				15.0	15.9	1.058
ERIWAL	2011	2	14	151	27.2	28.6	1.051			
	post-burial	1	6	13				36.1	42.7	1.183
		1	8	138				20.5	9.8	0.478
	2013	3	9	186	53.8	9.4	0.175			
		6	49	135	21.5	8.4	0.391			
GRUPAR	2011	2	5	79	25.5	17.1	0.671			
		1(3)	3	54				18.8	8.7	0.463
		1(4)	2	25				38.7	19.4	0.501
	2012	3	20	358	31.6	23.3	0.737			
		1(2)	8	185				19.4	10.6	0.546
		1(3)	6	100				30.0	34.7	1.157
		1(4)	6	73				49.6	8.3	0.167
PENALB	2011	1	13	327	13.0	18.2	1.400			
	2012	1	3	64	1.3	2.2	1.692			
PENTHU	2011	1	5	126	25.5	36.1	1.416			
	2012	1	3	105	32.0	12.3	0.384			

Table A2: Viability (expressed as % non-viable) of post-burial seed lots. Maximum values are means of a single site or for a single individual plant from any site.

species	crop year	buried	exhumed	# bags	# seeds	% non- viable	Max % non-viable by site	Max % non-viable by individual
Asclepias nyctaginifolia	2012	2012	2013	13	510	62.3 ± 22.2	85.0	100.0
Castela emoryi	2012	2012	2013	15	583	7.8 ± 4.0	11.0	35.1
Eriophyllum mohavense	2011	2012	2013	5	53	37.5 ± 26.2	NA	83.3
E. wallacei	2011	2012	2013	14	151	28.3 ± 11.0	36.1	100.0

APPENDIX B:
Details of Results for ERIMOH and ERIWAL

Table B1: Barstow Woolly Sunflower and Wallace's Woolly Daisy Seed Viability (Determined by X-Ray)

Species	Seed Year	Site	# Seeds (N)	% Viable	Mean % Viability Across Sites
ERIMOH	2013	1	14	0.786	0.841
ERIMOH	2013	2	36	0.944	
ERIMOH	2013	3	32	0.750	
ERIWAL	2013	1	93	0.602	0.601
ERIWAL	2013	2	78	0.462	
ERIWAL	2013	3	17	0.647	
ERIWAL	2013	4	27	0.778	
ERIWAL	2013	5	18	0.889	
ERIWAL	2013	6	18	0.889	

Viability estimates for 1-year old seed

Table B2: Barstow Woolly Sunflower Seed Output Differences (ANOVA)

Effect	Df	Deviance	Resid. Df	Resid. Dev	Pr(>Chi)
NULL	NA	NA	121	151.88	NA
Year	1	15.2888	120	136.59	**9.226e-05**
Site	1	0.7713	119	135.82	0.3798

Table B3: Wallace's Woolly Daisy Seed Output Differences (ANOVA)

Effect	Df	Deviance	Resid. Df	Resid. Dev	Pr(>Chi)
NULL	NA	NA	337	439.80	NA
Year	3	12.807	334	427.00	**0.005072**
Site	2	7.599	332	419.40	**0.022382**

Table B4: Barstow Woolly Sunflower Transition Matrix Rates by Year, Site And Habitat Type (Using Observed Data)

Year	Site	Plot Type	Habitat type	α11	α12	α13	α21	α22	α23	α31	α32	α33
2011	1	10x10 cm	Broad	0.037	0.037	3.79E-02	0.78	0	0	0	0.61	0.01
2011	2	10x10 cm	Broad	0.045	0.045	4.49E-02	0.94	0	0	0	0.89	0.01
2011	3	10x10 cm	Broad	0.044	0.044	4.45E-02	0.75	0	0	0	0.56	0.01
2012	1	10x10 cm	Broad	0	0	0	0.79	0	0	0	0.62	0.01
2012	2	10x10 cm	Broad	0	0	0	0.94	0	0	0	0.89	0.01
2012	3	10x10 cm	Broad	0	0	0	0.75	0	0	0	0.56	0.01
2013	1	10x10 cm	Broad	0	0	0	0.80	0	0	0	0.61	0.01
2013	1	1-meter diameter	Divot	7.07E-04	7.07E-04	7.07E-04	0.78	0	0	0	0.61	0.01
2013	2	10x10 cm	Broad	0	0	0	0.94	0	0	0	0.89	0.01
2013	2	20x100 cm	Rill	0.004	0.004	4.15E-03	0.94	0	0	0	0.89	0.01
2013	3	10x10 cm	Broad	0	0	0	0.75	0	0	0	0.56	0.01
2013	3	1-meter diameter	Divot	0.007	0.007	6.67E-03	0.75	0	0	0	0.56	0.01
2014	1	10x10 cm	Broad	0	0	0	0.78	0	0	0	0.61	0.01
2014	1	1-meter diameter	Divot	1.78E-05	1.78E-05	1.78E-05	0.78	0	0	0	0.61	0.01
2014	2	10x10 cm	Broad	0	0	0	0.94	0	0	0	0.89	0.01
2014	2	20x100 cm	Rill	3.33E-04	3.33E-04	3.33E-04	0.94	0	0	0	0.89	0.01
2014	3	10x10 cm	Broad	0	0	0	0.75	0	0	0	0.56	0.01
2014	3	1-meter diameter	Divot	0.001	0.001	1.04E-03	0.75	0	0	0	0.56	0.01

Transition rates for the 18 combinations of year, site and habitat type for ERIMOH.

Table B5. Wallace's Woolly Daisy Transition Matrix Rates by Year, Site And Habitat Type (Using Observed Data)

Year	Site	Plot Type	Habitat type	α11	α12	α13	α21	α22	α23	α31	α32	α33
2011	1	10x10 cm	Broad	0.118	0.118	0.118	0.591	0	0	0	0.356	0.010
2011	2	10x10 cm	Wash	0.045	0.045	0.045	0.454	0	0	0	0.210	0.010
2011	3	10x10 cm	Broad	0.159	0.159	0.159	0.635	0	0	0	0.411	0.010
2012	1	10x10 cm	Broad	0	0	0	0.602	0	0	0	0.362	0.010
2012	2	10x10 cm	Wash	0	0	0	0.462	0	0	0	0.213	0.010
2012	3	10x10 cm	Broad	0	0	0	0.647	0	0	0	0.419	0.010
2012	4	1-meter diameter	Broad	0.082	0.082	0.082	0.776	0	0	0	0.604	0.010
2012	5	1-meter diameter	Wash	0.103	0.103	0.103	0.887	0	0	0	0.788	0.010
2012	6	1-meter diameter	Wash	0.092	0.092	0.092	0.887	0	0	0	0.788	0.010
2013	1	10x10 cm	Broad	0.009	0.009	0.009	0.601	0	0	0	0.362	0.010
2013	2	10x10 cm	Wash	0.011	0.011	0.011	0.461	0	0	0	0.213	0.010
2013	3	10x10 cm	Broad	0.007	0.007	0.007	0.645	0	0	0	0.418	0.010
2013	4	1-meter diameter	Broad	0.019	0.019	0.019	0.776	0	0	0	0.604	0.010
2013	5	1-meter diameter	Wash	0.039	0.039	0.039	0.887	0	0	0	0.788	0.010
2013	6	1-meter diameter	Wash	0.015	0.015	0.015	0.887	0	0	0	0.788	0.010
2014	1	10x10 cm	Broad	0.043	0.043	0.043	0.591	0	0	0	0.356	0.010
2014	2	10x10 cm	Wash	0.042	0.042	0.042	0.454	0	0	0	0.210	0.010
2014	3	10x10 cm	Broad	0.154	0.154	0.154	0.635	0	0	0	0.411	0.010
2014	4	1-meter diameter	Broad	0.076	0.076	0.076	0.764	0	0	0	0.594	0.010
2014	5	1-meter diameter	Wash	0.083	0.083	0.083	0.873	0	0	0	0.776	0.010
2014	6	1-meter diameter	Wash	0.037	0.037	0.037	0.873	0	0	0	0.776	0.010

Transition rates for the 21 combinations of year, site and habitat type for ERIWAL.

Table B6: Barstow Woolly Sunflower Seedling Emergence

Year	Seeds (N)	Number Emerging	% Emerging	Standard Deviation	Standard Error
2012	1227	0	0	0	0
2013	975	0	0	0	0
2014	975	5	0.51%	0.041	0.002

Emergence rates each year in the seeding toothpick experiment. Some toothpicks bearing seeds were lost to disturbance, requiring a decrement in seed count.

Table B7: Wallace's Woolly Daisy Seedling Emergence

Year	Seeds (N)	Number Emerging	% Emerging	Standard Deviation	Standard Error
2012	477	0	0	0	0
2013	405	1	0.25%	0.032	0.003
2014	327	6	1.83%	0.076	0.007

Emergence rates each year in the seeding toothpick experiment. Some toothpicks bearing seeds were lost to disturbance, requiring a decrement in seed count.

Table B8: Barstow Woolly Sunflower Mean Transition Rates (Using Observed Data, 2011-2014)

α11	α12	α13	α21	α22	α23	α31	α32	α33
0.008	0.008	0.008	0.825	0	0	0	0.688	0.010

The mean matrix is constructed by averaging transition rates from 18 year/site/habitat type matrices.

Table B9: Wallace's Woolly Daisy Mean Transition Rates (Using Observed Data, 2011-2014)

α11	α12	α13	α21	α22	α23	α31	α32	α33
0.054	0.054	0.054	0.685	0	0	0	0.497	0.010

The mean matrix is constructed by averaging transition rates from 21 year/site/habitat type matrices.

Table B10: Barstow Woolly Sunflower Transition Rate Sensitivity / Elasticity

					Sensitivity			Elasticity			
Season	**λ**	**Site**	**Habitat Type**	**Stage**	**S1**	**S2**	**S3**	**S1**	**S2**	**S3**	**Reproductive Value**
2011	0.322	1	Broad	S1	0.40	1.00	**2.00**	0.05	0.12	0.24	1
				S2	0.14	0	0	**0.35**	0	0	0.36
				S3	0	0.12	0.24	0	0.24	0.01	0.12
2011	0.373	2	Broad	S1	0.40	0.94	**2.16**	0.05	0.11	0.25	1
				S2	0.15	0	0	**0.35**	0	0	0.37
				S3	0	0.11	0.25	0	0.25	0.01	0.12
2011	0.353	3	Broad	S1	0.41	0.94	**1.66**	0.06	0.13	0.23	1
				S2	0.16	0	0	**0.35**	0	0	0.38
				S3	0	0.13	0.23	0	0.23	0.01	0.14
2012	0.010	All	Broad	All	NA	NA	NA	NA	NA	NA	NA
2013	0.010	All	Broad	All	NA	NA	NA	NA	NA	NA	NA
2013	0.078	1	Divot	S1	0.33	3.41	**31.79**	0.003	0.03	0.30	1
				S2	0.03	0	0	**0.33**	0	0	0.10
				S3	0	0.04	0.34	0	0.30	0.04	0.01
2013	0.155	2	Rill	S1	0.35	2.00	**11.50**	0.01	0.05	0.29	1
				S2	0.06	0	0	**0.34**	0	0	0.17
				S3	0	0.05	0.31	0	0.29	0.02	0.03
2013	0.171	3	Divot	S1	0.36	1.71	**6.47**	0.02	0.07	0.27	1
				S2	0.07	0	0	**0.35**	0	0	0.20
				S3	0	0.08	0.29	0	0.27	0.02	0.05
2014	0.010	All	Broad	All	NA	NA	NA	NA	NA	NA	NA
2014	0.025	1	Divot	S1	0.27	8.73	**368.78**	0.00	0.01	0.27	1
				S2	0.01	0	0	**0.27**	0	0	0.03
				S3	0	0.01	0.45	0	0.27	0.18	0.00
2014	0.067	2	Rill	S1	0.32	4.28	**61.77**	0.002	0.02	0.30	1
				S2	0.02	0	0	**0.32**	0	0	0.08
				S3	0	0.02	0.35	0	0.30	0.05	0.01
2014	0.090	3	Divot	S1	0.34	3.03	**23.37**	0.00	0.04	0.29	1
				S2	0.04	0	0	**0.33**	0	0	0.11
				S3	0	0.04	0.33	0	0.29	0.04	0.01

For each matrix the rates with the highest sensitivity and elasticity are shown in bold.

Table B11: Wallace's Woolly Daisy Transition Rate Sensitivity / Elasticity

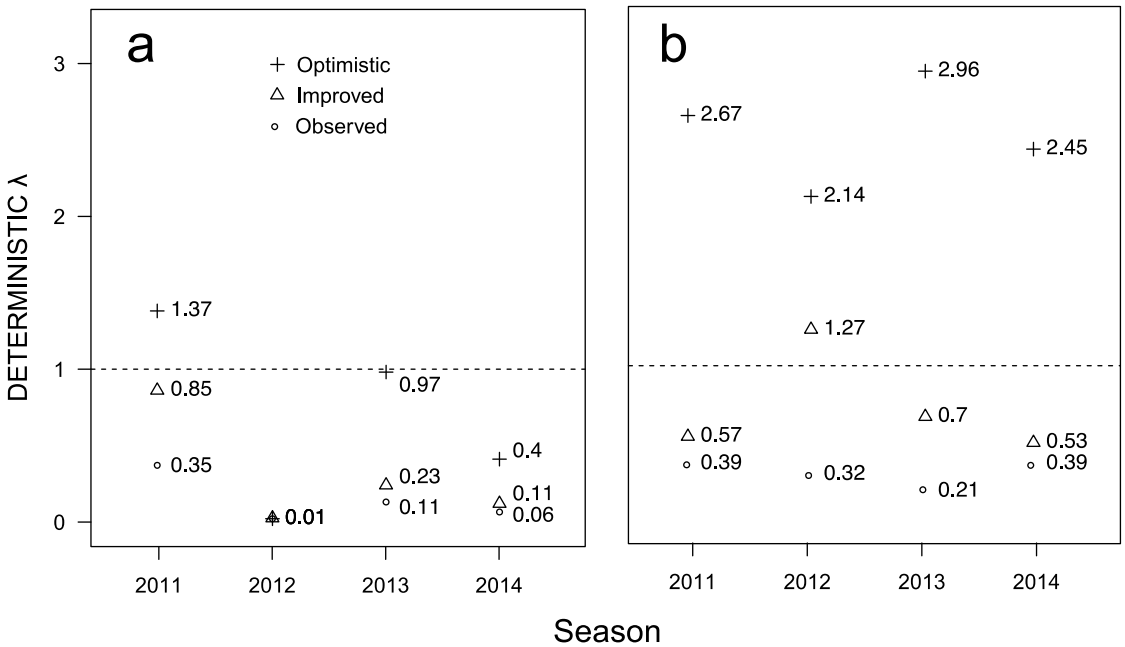
					Sensitivity			Elasticity			
Year	λ	Site	Habitat Type	Stage	S1	S2	S3	S1	S2	S3	Reproductive Value
2011	0.42	1	Broad	S1	0.48	**0.67**	0.58	0.14	0.19	0.16	1.00
				S2	0.25	0.00	0.00	**0.35**	0.00	0.00	0.52
				S3	0.00	0.19	0.17	0.00	0.16	0.00	0.29
2011	0.22	2	Wash	S1	0.45	**0.91**	0.89	0.09	0.18	0.18	1.00
				S2	0.18	0.00	0.00	**0.36**	0.00	0.00	0.40
				S3	0.00	0.19	0.19	0.00	0.18	0.01	0.21
2011	0.51	3	Broad	S1	0.50	**0.61**	0.50	0.15	0.19	0.15	1.00
				S2	0.28	0.00	0.00	**0.34**	0.00	0.00	0.56
				S3	0.00	0.19	0.16	0.00	0.15	0.00	0.31
2012	0.01	All	Broad	All	NA	NA	NA	NA	NA	NA	NA
2012	0.44	4	Broad	S1	0.43	0.78	**1.10**	0.08	0.15	0.21	1.00
				S2	0.20	0.00	0.00	**0.35**	0.00	0.00	0.46
				S3	0.00	0.15	0.21	0.00	0.21	0.00	0.19
2012	0.53	5	Wash	S1	0.43	0.72	**1.09**	0.08	0.14	0.21	1.00
				S2	0.21	0.00	0.00	**0.35**	0.00	0.00	0.48
				S3	0.00	0.14	0.21	0.00	0.21	0.00	0.20
2012	0.51	6	Wash	S1	0.43	0.75	**1.19**	0.08	0.14	0.22	1.00
				S2	0.20	0.00	0.00	**0.35**	0.00	0.00	0.47
				S3	0.00	0.14	0.22	0.00	0.22	0.00	0.18
2013	0.15	1	Broad	S1	0.37	1.54	**4.11**	0.02	0.10	0.26	1.00
				S2	0.09	0.00	0.00	**0.35**	0.00	0.00	0.23
				S3	0.00	0.10	0.27	0.00	0.26	0.02	0.07
2013	0.13	2	Wash	S1	0.39	1.43	**2.61**	0.03	0.13	0.23	1.00
				S2	0.10	0.00	0.00	**0.36**	0.00	0.00	0.25
				S3	0.00	0.14	0.25	0.00	0.23	0.02	0.10
2013	0.14	3	Broad	S1	0.37	1.67	**5.27**	0.02	0.08	0.26	1.00
				S2	0.08	0.00	0.00	**0.35**	0.00	0.00	0.21
				S3	0.00	0.09	0.28	0.00	0.26	0.02	0.05
2013	0.24	4	Broad	S1	0.38	1.23	**3.20**	0.03	0.10	0.25	1.00
				S2	0.11	0.00	0.00	**0.35**	0.00	0.00	0.29
				S3	0.00	0.10	0.27	0.00	0.25	0.01	0.08

Table B11 (cont)

					Sensitivity			Elasticity			
Year	**λ**	**Site**	**Habitat Type**	**Stage**	**S1**	**S2**	**S3**	**S1**	**S2**	**S3**	**Reproductive Value**
2013	0.36	5	Wash	S1	0.40	0.98	**2.23**	0.04	0.11	0.24	1.00
				S2	0.14	0.00	0.00	**0.35**	0.00	0.00	0.36
				S3	0.00	0.11	0.25	0.00	0.24	0.01	0.11
2013	0.25	6	Wash	S1	0.37	1.34	**4.45**	0.02	0.08	0.27	1.00
				S2	0.10	0.00	0.00	**0.35**	0.00	0.00	0.26
				S3	0.00	0.08	0.28	0.00	0.27	0.01	0.06
2014	0.27	1	Broad	S1	0.43	0.94	**1.30**	0.07	0.15	0.21	1.00
				S2	0.16	0.00	0.00	**0.36**	0.00	0.00	0.38
				S3	0.00	0.16	0.22	0.00	0.21	0.01	0.17
2014	0.22	2	Wash	S1	0.45	0.93	**0.94**	0.09	0.18	0.18	1.00
				S2	0.17	0.00	0.00	**0.36**	0.00	0.00	0.39
				S3	0.00	0.19	0.19	0.00	0.18	0.01	0.20
2014	0.51	3	Broad	S1	0.50	**0.62**	0.51	0.15	0.19	0.16	1.00
				S2	0.28	0.00	0.00	**0.35**	0.00	0.00	0.56
				S3	0.00	0.19	0.16	0.00	0.16	0.00	0.31
2014	0.42	4	Broad	S1	0.43	0.79	**1.15**	0.08	0.14	0.21	1.00
				S2	0.19	0.00	0.00	**0.35**	0.00	0.00	0.45
				S3	0.00	0.15	0.21	0.00	0.21	0.01	0.19
2014	0.48	5	Wash	S1	0.42	0.77	**1.27**	0.07	0.13	0.22	1.00
				S2	0.19	0.00	0.00	**0.35**	0.00	0.00	0.46
				S3	0.00	0.14	0.22	0.00	0.22	0.00	0.18
2014	0.34	6	Wash	S1	0.39	1.00	**2.31**	0.04	0.11	0.25	1.00
				S2	0.14	0.00	0.00	**0.35**	0.00	0.00	0.35
				S3	0.00	0.11	0.25	0.00	0.25	0.01	0.11

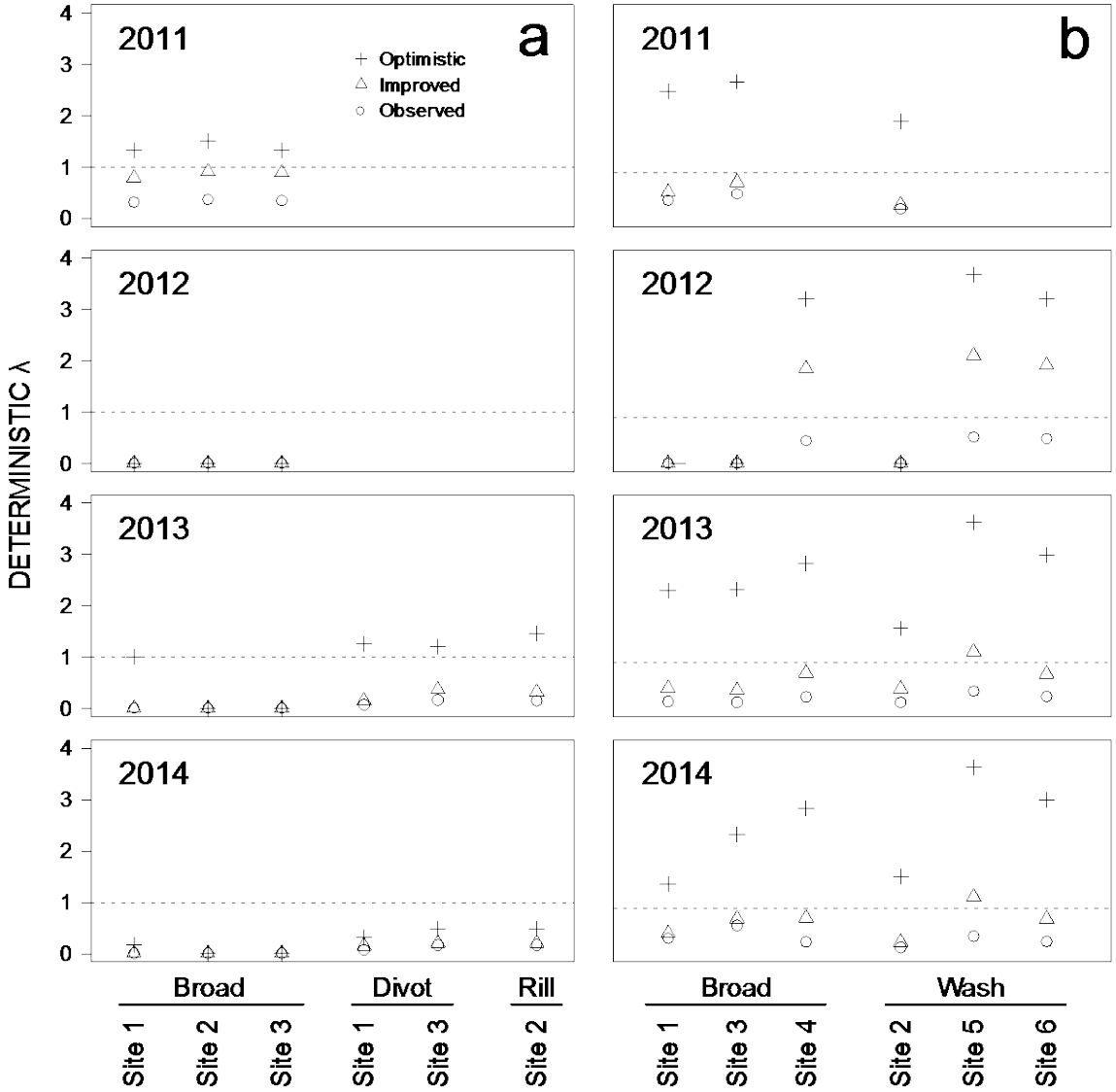
For each matrix the rates with the highest sensitivity and elasticity are shown in bold.

Figure B1: Yearly Deterministic Growth Rates of Barstow Woolly Sunflower and Wallace's Woolly Daisy Projected over a Century



Graphs depict (a) Response of ERIMOH and (b) ERIWAL deterministic population growth (λ) broken down by year.

Figure B2: Deterministic Growth Rates of Barstow Woolly Sunflower and Wallace's Woolly Daisy by Site and Habitat Type Projected over a Century



Graphs depict: (a) Response of ERIMOH and (b) ERIWAL deterministic population growth (λ) in each year, site, and habitat type combination.

APPENDIX C:
A Phenotypic Study of Early Growth of ASCNYC

C.1 Introduction

Asclepias nyctaginifolia (ASCNYC) is a rare desert perennial, commonly called Mojave milkweed, native to the American Southwest. This desert herb has a very limited range within California, which partially overlaps with the Ivanpah Solar Electric Generating System (ISEGS), the world's largest thermal power tower system (BrightSource 2013). This immense field of mirrors (3,500 acres) has strong impacts on the surrounding desert ecosystem by casting shade, lowering water content and temperature of the soil beneath the panels and increasing the occurrence of lightning strikes. These impacts change two key limiting resources for plants beneath the mirrors: water and sunlight. Additionally, it has been documented that the facility negatively impacts predator populations, such as migratory and resident bird species, which in turn could be responsible for increased herbivore activity and herbivory on ASCNYC observed within the solar field.

Considering the limited range and small population sizes of ASCNYC within California, it is important to understand germination and growth patterns for purposes of developing mitigation techniques. Ivanpah Solar Electric Generating System is unique in that the soil surface beneath the panels has not been graded. In addition, the design of the installation allowed for small mitigation sites ("halos") within the solar field by adjusting the placement of solar panels to create open areas around rare plant occurrences. This design is unusual as most solar facilities do not leave plant cover in place below the mirrors or panels during or after construction. This design could be combined with propagation from seed and outplanting to reduce overall impacts to rare plants such as ASCNYC. It may also be possible to conserve dormant seeds in the seed bank of these halos that propagate naturally. Seed dormancy is one of the adaptations that improve the persistence of ASCNYC populations in the variable climatic conditions of the Mojave Desert. Seeds remain dormant during dry seasons, waiting for cues such as summer monsoons and winter rains to trigger germination. Further, plant fitness (measured as survivorship and fecundity) depends on occasional climatic suitability; plants are more likely to persist and produce more seeds when not limited by soil water availability. Together, these two rain-dependent fitness components make the viability, germinability, and early growth characteristics of seedlings critical to the success of the population.

To further understand the persistence of ASCNYC populations in sites affected and unaffected by solar energy development we used a laboratory experiment to address several questions regarding germination and early life stages. We addressed the following questions:

1. Is there a difference in the germination and growth rate of seedlings between different populations across the California range of ASCNYC, including those in the Ivanpah solar field?
2. Are there changes in germination rate with seed age?

3. Lastly, is there a difference in germination rate between seeds that have been buried in an experimental seed bank in the field for a year and exhumed (Chapter 3), and those stored for the same amount of time under laboratory conditions at room temperature?

C.2 Methods

In August 2014 a germination and growth experiment was established for *Asclepias nyctaginifolia* (ASCNYC) seeds collected in 2012 and 2013 from three undisturbed populations in the Mojave Desert, as well as from mitigation halos in ISEGS. Additionally, some seeds collected during the fall of 2012 were bagged and buried in the field to examine *in situ* germination and seed dormancy. These seed bags were exhumed in the fall of 2013, one year later, and examined to determine if they still can an intact embryo. Only seeds with apparently intact embryos based on visual and manual inspection were used in the germination study. All seeds were stored at room temperature, about 30 ˚C after field collection.

The germination experiment consisted of 19 replicate blocks. Each contained 45 seeds from one of eight possible treatments. These treatments include seeds collected from four sites during two consecutive years: 3 natural field sites with seed collected in 2012 and 2013 and one solar field site with seeds collected in 2013. There were no seeds available for collection from Excelsior Mine in 2012. Additionally, only 22 seeds were available from the Bobcat Hills population in 2013, and therefore had a reduced seed number in the study. Seeds from each treatment were taken from five fruits per site, and assigned randomly to a block and cell position in the germination set up.

Seeds were sewn on 0.08 % Bactoagar in 15 well trays. The blocks containing cells of agarose were rotated daily to negate environmental variation. Germinating seeds were kept on the lab bench under white grow lights set on a 12-hour light/dark photoperiod. Growth lights were set up on a clean bench with dark materials draped over a PVC frame, to keep out sunlight that filters into the lab from nearby windows. Seeds were kept at 35˚C (+/-3˚) and at least 30% humidity. This required occasional misting with a spray bottle when ambient humidity was low. Germination was tallied and measurements on seedlings were taken between 7-9 am, daily for the first 60 days, then, plant measurements were decreased to every other day. These seedling measurements included leaf width, leaf length, stalk length, number of leaves, if the seed coat was intact, or had passively been shed.

Seven to nine days after seeds produced cotyledons, individuals outgrew their cells of agar and were transplanted into “cone-tainers” in a greenhouse facility, where they experienced 12-hour photoperiods of natural light. The longest root length of each plant was measured at transplant. Once transplanted, plants were established in potting soil containing soil, sphagnum, and perlite. Greenhouse plants were watered daily with reverse osmosis water. Fertilizer was added to the plants via irrigations once a week, after the plants had been in the greenhouse for approximately two months. Plants were measured daily for two weeks after transplant, before measurements were reduced to biweekly increments. After two months in the greenhouse, measurements were further limited to every other week, and eventually on a monthly basis. In

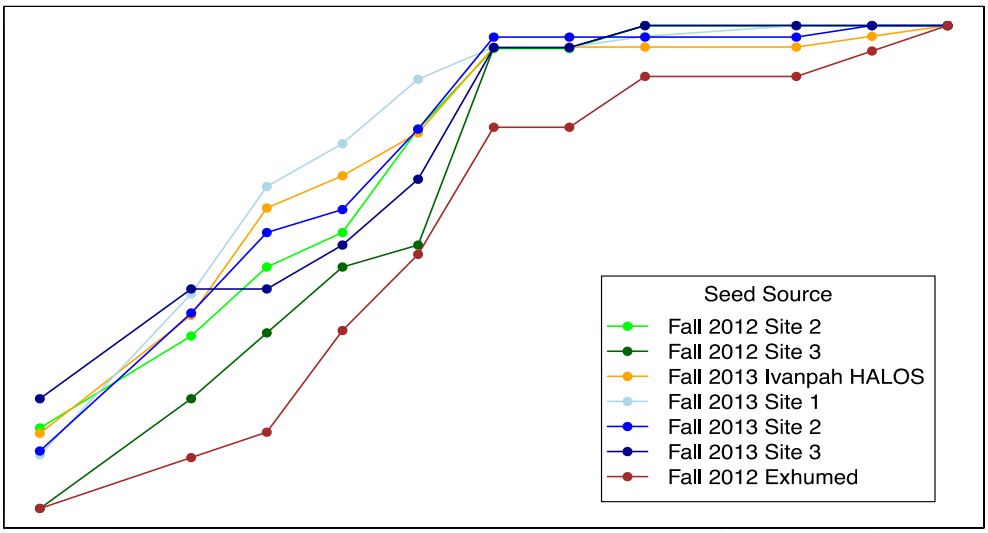
the greenhouse, internode growth, leaf number, diameter, axial buds presence, and number of leaves lost were recorded on each survey. As the plants grew larger, number of stems, branches, and the largest leaf were measured, to reduce measurement variation and to capture the most noticeable variation between plants. After the study concludes, plant biomass will be measured as a final comparison.

ANOVAs and linear regressions were used to assess the effects of population (collection site), collection year, and burial treatment on germination rate, timing, and seedling growth. Generalized linear models using negative binomial models were employed as appropriate to each response. *Post hoc* analysis using Tukey's T test was used when necessary to distinguish differences within a group. Analysis of lab and greenhouse data was performed in the statistical program R (R Core Team 2014).

C.3 Results

Overall germination of ASCNYC was between 80 and 100% in eight days (Figure C1). While population source and seed age were not significant sources of variation, burial in the field for one year resulted in significantly lower germination rates ($F_{2,127}$=5.008, P=0.0081). Almost all of the seeds planted germinated (98%) within 14 days after planting the seeds. Plants from seed collected in 2012 and 2013 at the same site showed the same germination rate and no variation in traits, therefore all subsequent comparisons were made only among sites.

Figure C1: Germination of ASCNYC seeds from natural populations (sites 1-3) and the solar field halos, as well as seeds buried and exhumed from the natural seed bank between 2012 and 2013



Seeds from the Bobcat Hills population (Site 3) produced the largest seedlings of all the natural and solar field sites. While this may be due to diffuse seed variation or small sample size, it is important to note that Site 3 is furthest away from the solar fields and other natural sites, adding to possible environmental variation as well. There were significant differences in height (P= 1.206e-08 ***) and number of leaves (P=0.003526) between seed collected from the solar field and undisturbed populations. Seed from mitigation sites within the solar field showed on average, increased number of axial buds than all undisturbed sites, though this was not a significant difference in negative binomial GLM and the data did not sufficiently conform to a standard distribution (Table C1, Fig. C2). Additional analyses via logistic regression showed a significant difference in the presence or absence of axial buds between the solar field site and the non-solar field sites (z=2.52, Residual Dev. 256 on 193 d.f., P=0.011). Plants from sites inside the solar facility had significantly more leaves than the undisturbed sites Umberci Mine and Bobcat Hills, and larger leaf area when compared to Exclesior Mine (Site 1, Fig C3) and Umberci Mine (Site 2). Lastly, seeds collected from solar sites produced plants with longer internode lengths compared to plants from Exclesior and Umberci. Bobcat hills showed a median internode stem length (Fig. C4).

Table C1: Significant differences between sites for each phenotypic trait

Trait	Degrees Freedom	Mean Square Value	F value	Pr (>F)
Internode Height	5	1780.64	9.3216	1.206e-08 ***
Number of Leaves	5	956	933.17	0.002264 **
Seedling Height	6	2821.09	6.1719	2.081e-06 ***
Leaf Area	6	51342	8.8628	1.608e-09 ***
Number of Axial buds	5	0.8685	1.9424	0.08488

Significance: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.'

Figure C2: Comparison of axial bud production in each site

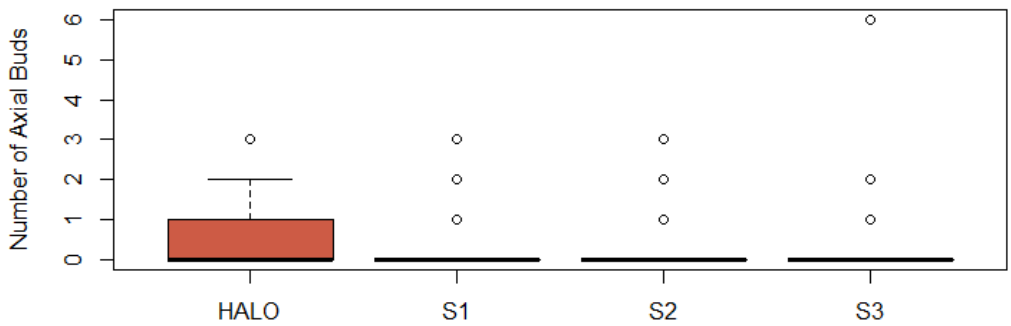


Figure C3: Comparison of number of leaves produced by plants from each site

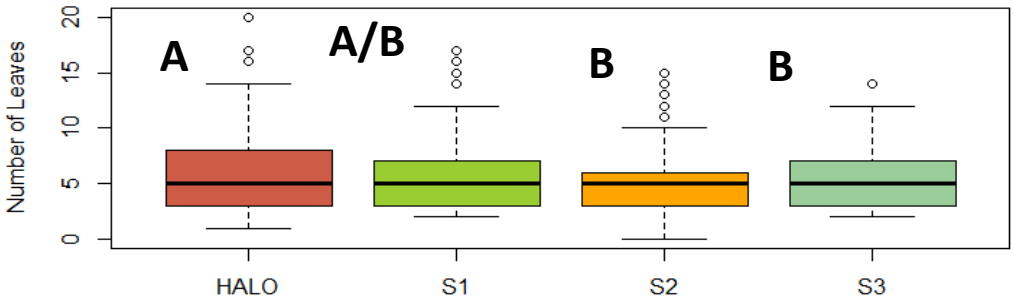
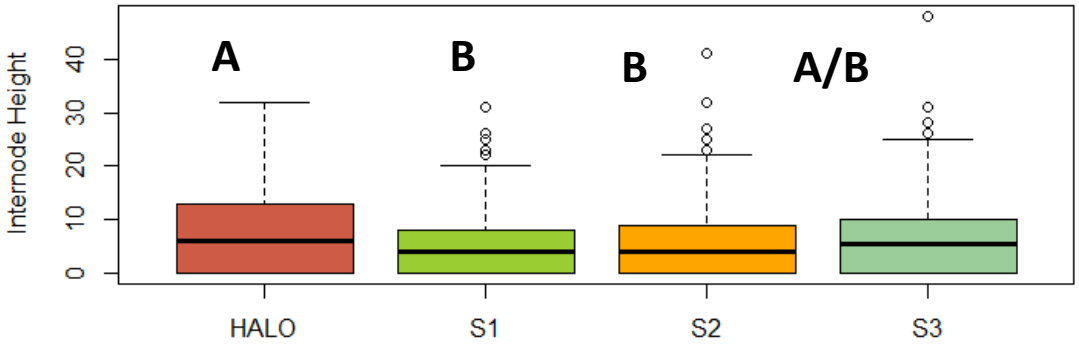


Figure C4: Lengths of second internode in each site



C.4: Discussion

Exhumed seeds of *Asclepias nyctaginafolia* exhibited slower germination and fewer successful germination events compared to seed stored at room temperature. This is to be expected because seeds in the seed bank experience considerable temperature variation, mechanical wear and exposure to microbes. This finding provides evidence that reduction in seed viability for this species may occur in the seed bank over relatively short periods of time.

Asclepias nyctaginafolia seeds have very high germination and seedling survival rates in the laboratory. Even after a year of burial in the field, seeds germinated readily, though at a slightly reduced rate (Figure C1). Seeds from the three undisturbed populations were indistinguishable in terms of germination rate, but differed slightly in seedling traits. By comparing seed collected at natural populations to those collected within the solar field at ISEGS, we found multiple phenotypic differences in seedling growth metrics that suggest the possibility for evolutionary changes to this population as a result of comprehensive ecological regime change and warrant further experimental study.

We have a speculative explanation for the observed differences in the early traits of seedlings from the solar field in comparison to those originating from plants undisturbed sites. First, it is possible that the population of plants that is now under the mirrors had pre-existing phenotypic seedling differences from other sites. Second, the observed differences in early seedling traits in the solar field could represent a transgenerational plastic response to the environmental change imposed. Two aspects of environmental change, shade and altered interactions with herbivores, might provoke such as response. A common garden experiment with seeds from all sites and shade treatments could be employed to fully assess these possibilities. A discussion of these possibilities and generation of hypotheses for future studies follows.

Studies on other milkweed species have found that phenotypic variation can be induced by shading. Shade can reduce plant performance and defense traits, since it reduces the ability of a plant to photosynthesize enough energy to muster an induced response to herbivory (Agrawal 2012). In *Asclepias syriaca*, greenhouse and field shading experiments explain why growing in shaded habitats will increase a plants susceptibility to herbivory (Agrawal et al. 2012). *A. syriaca* plants grown in full sun were able to produce a range of secondary defense chemicals, such as latex and cardenolides, as well as jasmonic acid, while plants grown in the shade were unable to induce a response to herbivory, and therefore were more susceptible to damage from monarch butterfly caterpillars (Agrawal et al. 2012). Moreover, plants grown in shaded conditions showed patterns of longer internode length as well as greater leaf area (Agrawal et al. 2012). These results are similar to the trends found in *A. nyctaginifolia* seedlings from maternal plants in the solar facility. We found that shade was associated with elevated internode and leaf growth. A follow-up study is recommended to investigate the effects of shade on *A. nyctaginifolia* seedlings and adult plants, including reproductive structures.

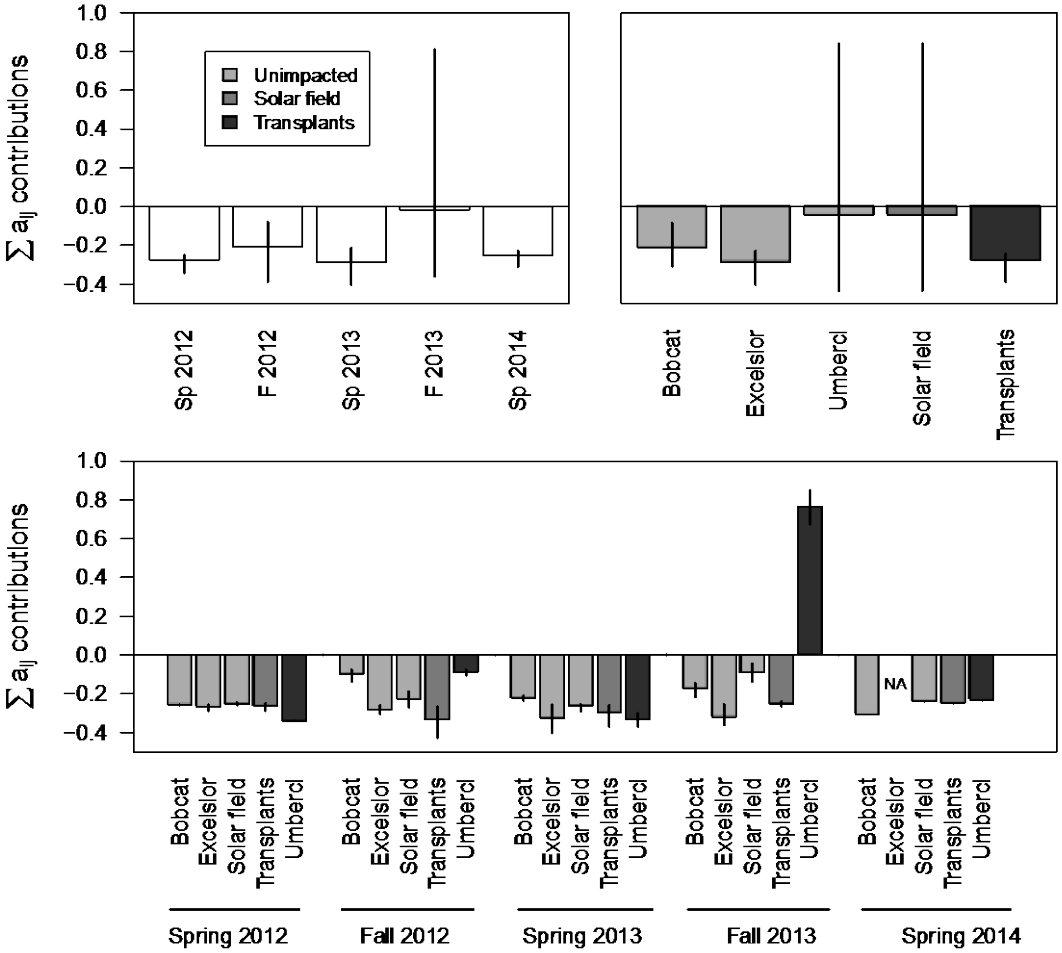
C.5 Literature Cited

Agrawal, Anurag, Kearney, Emily, Hastings, Amy, Ramsey, T. 2012. Attenuation of the jasmonate burst, plant defense traits, and resistance to specialist monarch caterpillars on shaded common milkweed (*Asclepias syriaca*). *Journal of Chemical Ecology*. 38: 893–901.

Brightsource. What Is Ivanpah? Ivanpah Project Facts. 2013. *Ivanpah Solar Electric Generating System*. Accessed December 15, 2014. http://www.brightsourceenergy.com/ivanpah-solar-project#.VTCSkiHBzGc

APPENDIX D:
Details of ASCNYC results

Figure D1: Contributions of season, site, and site-to-site variation to variation in population growth (λ) of ASCNYC



Contributions of (a) season, Spring 2012- Fall 2014, (b) study site, and (c) their interaction to variation in λ. Solar field indicates individuals in “halos” within the solar field at ISEGS. Transplants indicates individuals transplanted from the solar field to an on-site mitigation area. Exclesior was not sampled in spring of 2014.

Table D1: Percent of ASCNYC adult individuals dormant in each study season.

Season	Bobcat	Excelsior	Umberci	Solar	Trans
Spring 2011	0.03	0.38	0.30	---	---
Fall 2011	0.98	1.00	1.00	---	---
Spring 2012	0.45	0.17	0.96	0.82	0.79
Fall 2012	0.00	0.21	0.07	0.06	0.24
Spring 2013	0.00	0.88	0.05	0.15	0.28
Fall 2013	0.50	0.08	0.11	0.06	0.28
Spring 2014	0.37	0.00	0.79	0.67	0.93
Fall 2014	0.03	0.04	0.61	0.33	0.93

Solar and Trans sites were not accessible until spring of 2012.

APPENDIX E:
Available data for demographic analysis of PENALB

Table E: Demographic data from the Pisgah PENALB subpopulations

Seeds		**Data Years**
Juveniles (J)	Emergence	2011-2012
	Abundance	1994, 1995, 2011-2012
	Size	1994-2003, 2011-2012
	Survival	1994-2002, 2011-2012
Adults (A1-A5)	Abundance	1994, 1995, 2011-2012
	Survival	1995-2003, 2011-2012
	Size	1994-2003, 2011-2012
	Fecundity	1994-2003, 2011-2012

APPENDIX F:
Construction of the Population Performance Rubric for GRUPAR

Evaluation of the characteristics and vital rates of GRUPAR populations in California used a performance rubric to surmise relative vitality. The means and covariances measured between 2011 and 2013 (Tables 6.1 to 6.6) were categorized as either positive or negative indicators of vitality. Positive indicators were those thought to promote population growth, persistence and resilience in this species while negative indicators detracted. Specifically in reference to Table 6.7:

Positive indicators:

1) Total population size (number of clumps or genets found after survey of an entire element occurrence)
2) Population (clump) density (number of clumps or genets in a defined area of habitat within the element occurrence)
3) Clump size (area covered by an individual as circumscribed by field survey)
4) Clump size covariance (variability in clump size within a population, interpreted as age/stage/size structure variability and thus not dominated by a single age/stage/size class)
5) Stems per cluster (number of potential ramets in a circumscribed area of an individual, interpreted as the potential for producing new vegetative (clonal) and reproductive growth)
6) New stem output (number of new stems per m2 of a cluster per year, interpreted as the potential for producing new vegetation (clonal) and reproductive growth)
7) Floral bud output (number of new floral buds per m2 of a cluster per year, interpreted as the potential for producing fruits and seeds)
8) Fruit output (number of mature fruit per m2 of cluster per year, interpreted as the potential for producing seeds)
9) Seeds per fruit (number of mature seeds found in dissected fruits)

Negative indicators:

1) % dead (percentage of stems in a cluster that appear dead and/or decaying, interpreted as decreasing the potential for producing new vegetative and reproductive buds)
2) New stems covariance (variability in stem output of a cluster, interpreted as less potential for producing new vegetative and reproductive growth due to lack of live buds or resources)

3) New floral bud covariance (variability in floral output of a cluster, interpreted as less potential for producing fruits and seeds due to lack of live buds or resources)
4) Fruit covariance (variability in fruit output of a cluster, interpreted as less potential for producing seeds due to lack of live buds or resources)
5) Seeds per fruit covariance (variability in seeds per fruit due to lack of resources)
6) Shoot/floral bud/fruit herbivory (relative increase in outputs when caged clusters were compared to uncaged controls (open and focus combined) in the same population)

The range of a measured indicator obtained from all GRUPAR populations was then divided into performance quartiles and a high performance mean (a mean for a particular population falling in the upper 25% of the range) was assigned a score of "1." A low performance mean (falling in the lowest 25% of the range) was assigned a score of "4," and so on. The difference between positive and negative indicators was that the scores were reversed – positive indicators had scores that got progressively higher with higher means or variances (e.g. high values had a top score of 1), whereas negative indicators had scores that got progressively lower with higher means or variances (e.g. high values had a top score of 4). As an example, high means for stem output (those in the upper 25% of the range) got a performance score of 1 where as high means for % dead stems got a performance score of 4. Similarly, the largest differences between control and caged clusters in terms of stem or floral bud or fruit herbivory were assigned a performance score of 4 (indicating intense impact in those populations).

Performance scores could then be summed and averaged for the number of indicators used to evaluate a particular population. High performance then approaches a mean score value of 1 and relative vitality among populations is ascertained by its performance rank (1 being the highest relative vitality). When only population characteristics and vital rates are summarized, the mean score value measures "demographic performance," as does the ranking. When only herbivore impact scores are used, the mean score value measures "herbivory impact performance" and populations can be ranked accordingly. When all population and herbivory scores are included, then a "combined performance" score and rank are obtained.