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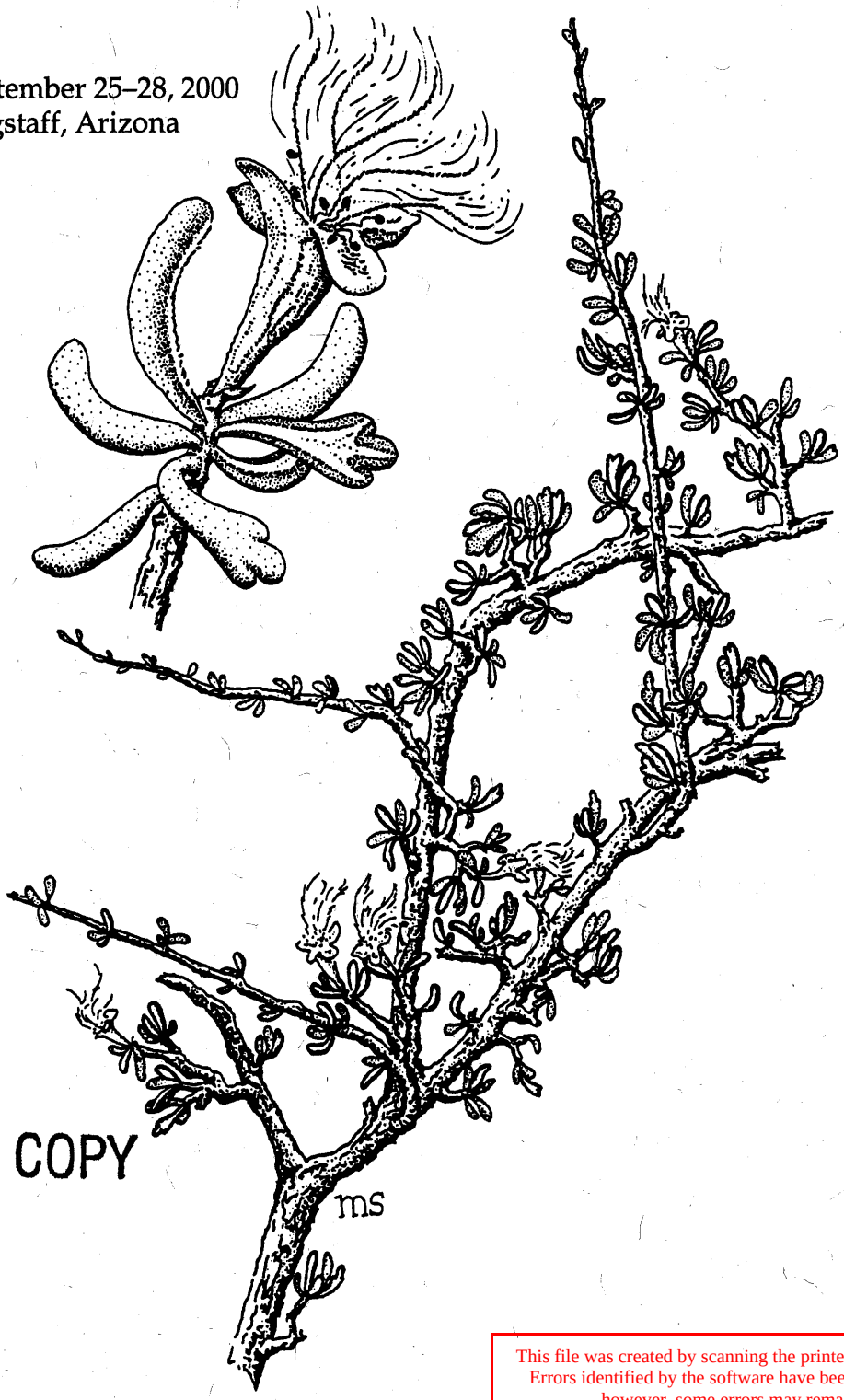
Proceedings
RMRS-P-23

September 2001

Southwestern Rare and Endangered Plants:

Proceedings of the Third Conference

September 25–28, 2000
Flagstaff, Arizona



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Maschinski, Joyce, and Holter, Louella, tech. eds. 2001. Southwestern rare and endangered plants: Proceedings of the Third Conference; 2000 September 25–28; Flagstaff, AZ. Proceedings RMRS-P-23. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 250 pp.

Abstract

These contributed papers review current research findings related to the demographic, monitoring, reintroduction, ecological and genetic studies done on southwestern rare plant species.

Key Words: plant conservation, genetics, demography, reproductive biology, monitoring, endangered species

Manuscripts were peer reviewed for statistical, editorial, and experimental content. Views expressed in each paper are those of the author and not necessarily those of the sponsoring organization or the USDA Forest Service.

Cover illustration of *Purshia subintegra* by Merion Sharp.

USDA Forest Service
Proceedings RMRS-P-23

Southwesten Rare and Endangered Plants: Proceedings of the Third Conference

September 25–28, 2000
Flagstaff, Arizona

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Foreword

The rising concern about preserving biodiversity has motivated conservationists throughout the world to seek opportunities to increase awareness about the plight of rare species. In the southwestern United States, nearly 1200 rare plant species are imperiled. Yet plants receive little attention from the public and few know about the threats that these unique species face. In an effort to promote understanding about rare plant biology and conservation strategies, the Third Southwestern Rare and Endangered Plant Conference convened more than 150 individuals working for state, federal, academic, and private agencies. Some of the 51 oral and poster presentations given at the conference are included herein. We wish to thank the authors for these fine contributions.

After the conference, the Southwest Rare Plant Task Force convened to develop an Action Plan for rare plants in our region. The Task Force identified key species of concern in Nevada, Utah, Colorado, New Mexico, and Arizona, and identified gaps in research, monitoring, reintroduction, threat management, and in situ and ex situ conservation. The top 10 regional concerns identified by the Task Force and conference attendees are given below.

1. There is currently not enough money or personnel devoted to plant conservation in the Southwest. There is a need for more botanists in federal and state agencies. Botanists need to make connections to sell the importance of plants and to encourage botanical input in decision-making. Botanists must be advocates for their profession, and find ways to engender respect for plant conservation, just as wildlife, commodities, range landowners, and houses are respected.

2. There is a need to give more attention to plants and rare plants within the context of other management programs.

- Conservation strategies for rare plant species and communities should be coordinated with efforts to reintroduce fire into the ecosystems of the Great Basin and Southwest forests and deserts. Fire restoration programs are underway (Section 7 consults, T&E, NEPA), yet the fire ecology of rare plants is largely unknown. Exotics and aggressive plants that out-compete rare and native plants should be controlled.
- Conservation strategies for rare plants should be coordinated with efforts to control invasive exotic species, along with developing best management practices and specific guidelines for individual species. Potential conflicts exist between weed management and preservation of native and rare plants; the impacts of noxious weeds on rare plant habitats are unknown. Guidelines for weed control and eradication are needed, and training in plant identification is needed.
- Pollination issues should be incorporated into land management activities and planning.

3. Public education programs are needed to promote advocacy for plant conservation and partnerships that support plant conservation. Landowners and the public should be educated about the value of native and rare plants. We must continue to share ideas, research, and stories of conservation successes and failures with each other. We must try to reach the public on conservation issues through education, increased law enforcement presence on public lands, and community involvement.

4. Revegetation and habitat restoration with native species following construction, wildfire, or other disturbance is critical. There is a need to develop native species revegetation guidelines, sources of species, mixes to use, native seed warehouses, and seed transfer protocol.

5. Plant conservation and botanical resources should be included in agency management plans, as well as general botanical issues. Ideas and specifics should be set forth about what to include in management plans, state endangered species laws, weed legislation, and so forth.

6. Highest priority sites and associated species should be identified for conservation; priorities should be set that focus energy on species under the greatest threats.

7. More research in plant conservation is needed, along with publications on rare plant research. More conservation internships and seminar programs are needed, especially to provide opportunities for communication between academia and the conservation community.

8. There is a need for increased communication across state lines so we can better assess the status of wide-ranging species throughout their ranges.

9. Leadership is needed to coordinate plant conservation efforts across all interested groups, such as the Plant Conservation Alliance, the Center for Plant Conservation, and regional task forces. The Arboretum at Flagstaff is willing to play a role in coordinating such efforts.

10. We must work together to control the spread of noxious weeds and to develop strategies for encouraging use of native plants in landscaping. We must educate and encourage commercial growers to switch to native plants such as grasses that can be harvested for seed or live plants for restoration of burned or other disturbed lands.

Efforts for plant conservation will continue. We look forward to future conferences, meetings, and proceedings.

Acknowledgments

For their generous support, we wish to thank the sponsors of this conference, proceedings, and Task Force: The Arboretum at Flagstaff, Northern Arizona University, the Bureau of Land Management – Colorado Plateau Coalition of Managers Group under the auspices of the Colorado Plateau Cooperative Ecosystem Studies Unit, New Mexico Ecological Services Field Office – U.S. Fish and Wildlife Service, USDA Forest Service Rocky Mountain Research Station, and the Utah Native Plant Society. Special thanks to those who helped make the conference possible: staff and volunteers of The Arboretum at Flagstaff – Joanne Baggs, Scott Baxter, Marilyn Brookshire, Jan Busco, Jackie Campbell, Sarah Cassatt, Mark Gullyes, Mary Dell Gunn, Ted Martinez, Marian McCollister, Nancy Morin, Nancy Nahstoll, Marie Pickle, Tomas Robison, Lael Tennyson, Steve Yoder; volunteers Elaine Ferris, Karen Hueston, Edward Smith; moderators Lori Armstrong, Robert Frye, Dan Godec, Kristin Huisinga, Juanita Ladyman, Charlie McDonald, Elizabeth Taylor; field trip leaders Joanne Baggs, Kristin Huisinga, Barbara Phillips, and Daniella Roth. Louella Holter, Ron Redsteer, and Dan Boone adeptly orchestrated the camera-ready copy of the proceedings. Lane Eskew of the Rocky Mountain Research Station provided technical assistance and encouragement for the publication.

We dedicate this work to Frances B. McAllister, who has devoted her life to education, conservation, and community, and has inspired many to follow.

About the Editors

Joyce Maschinski is Director of Research at The Arboretum at Flagstaff and adjunct professor in the Department of Biological Sciences, Northern Arizona University. She is actively involved in research on rare plant species in the Southwest and has presented work in the first two *Proceedings of Southwestern Rare and Endangered Plant Conferences, The American Naturalist, Biological Conservation,* and *Conservation Biology*. She organized the Third Southwestern Rare and Endangered Plant Conference and the Southwest Rare Plant Task Force.

Louella Holter has many years of experience as an editor at the Bilby Research Center, a multidisciplinary facility at Northern Arizona University.

National and International Conservation Efforts and Their Relevance to Plant Conservation in the Southwest

NANCY R. MORIN

The Arboretum at Flagstaff

Plant conservation in the United States benefits directly and indirectly from national and international conservation initiatives. The United Nations Convention on Biological Diversity, which began in December 1993, serves as a guiding force for conservation in the United States even though the U.S. is not a party to the convention. An international meeting in 1998 of leaders concerned with biological collections and the field of systematics addressed what was called the Taxonomic Impediment, consisting of gaps of knowledge in our taxonomic system, a shortage of trained taxonomists, and the negative impact these have had on our ability to manage and use our biological diversity. This meeting resulted in the Darwin Declaration (Anonymous 1998), which calls for initiatives to inventory and provide taxonomic information on the world's organisms and to support the scientific collections and expertise needed to do the work. The Gran Canaria Declaration (Anonymous 2000), stemming from an international meeting in April, 2000, of leaders in botanical conservation, issued a call for global plant conservation.

Within the United States, several networks provide both standards and a framework for plant conservation efforts. State and national agencies are responsible for enforcing laws relating to conservation, and various nongovernmental organizations are devoted to habitat protection through land acquisition or actively advocating for plant and animal conservation.

The Convention on Biological Diversity (CBD), fondly thought of as the mother of all conventions, has many components, all aimed at achieving three basic objectives:

- Conservation of the world's biological diversity
- Sustainable use of its components
- Fair and equitable sharing of benefits

The parts of the CBD most relevant to plant conservation in the Southwest are summarized here; the full text is available online at www.biodiv.org. This paper addresses issues within the Southwest or within the United States, but it is important to remember that Canada and Mexico are signatories to the CBD, and any cooperative work that crosses these borders will be legally constrained by the articles of the CBD.

Develop National Strategies

Article 6 of the CBD calls for the development of national strategies for the conservation and sustainable use of biological diversity and specifies steps to achieve this:

> Article 6: Convention on Biological Diversity
>
> Develop or adapt national strategies, plans, or programs for the conservation and sustainable use of biological diversity.
>
> Integrate, as far as possible and as appropriate, the conservation and sustainable use of biological diversity into relevant sectoral or cross-sectoral plans, programs, and policies.

The Plant Conservation Alliance was established in 1984 (as the Native Plant Conservation Initiative) to develop a comprehensive plan for plant conservation in the United States. Plant conservation receives only about 3 percent of total federal conservation funding, even though more than half of the federally listed taxa are plants, and almost 30 percent of U.S. native plant species are considered threatened (Walter and Gillett 1998). Furthermore, the general public tends to be much less aware of the plight of plants than they are of charismatic animals. The importance of plants in maintaining healthy ecosystems, and as essential links in the web of life that sustains animals and virtually all other organisms, is poorly understood and not appreciated. Consequently, the agenda set out by the Plant Conservation Alliance includes a significant public education component.

Botanic gardens and arboreta in the United States are participating in the development of a plant conservation action plan to implement the International Agenda for Botanic Gardens in Conservation (Wyse Jackson and Sutherland 2000). The Center for Plant Conservation, with its central office at the Missouri Botanical Garden in St. Louis, and its network of botanical gardens and arboreta elsewhere in the United States, provides a national framework for conservation of genetic material of threatened and endangered plants.

Native plant societies or their equivalents, field offices of the Nature Conservancy, Natural Heritage Programs, and formal or informal groups of plant or conservation experts in state agencies, nongovernmental organizations, and academic institutions meet annually or more often to evaluate the status of individual species of concern and to develop plans for their protection. In the past several years regional rare plant task forces have begun meeting to assess status, set priorities, and develop conservation plans. The Southwest Rare Plant Task Force had its inaugural meeting in conjunction with the Third Southwest Rare Plant Conference held in Flagstaff, Arizona.

Although these activities are all encouraging, there is still a need for a nationally adopted comprehensive plan for plant conservation.

The first directive in Article 6 of the CBD also speaks to the sustainable use of biological diversity, perhaps one of the most divisive and difficult issues in the United States today. Attention in the conservation community is focused largely on the restoration of natural processes following resource use that proved unsustainable and on preventing further degradation.

Survey and Monitor

Article 7 of the CBD addresses our current state of knowledge about biological diversity, as well as the need to monitor the components, to discover what is likely to adversely affect biological diversity, and to manage the information.

> Article 7: Convention on Biological Diversity
>
> Identify components of biological diversity important for its conservation and sustainable use.
>
> Monitor the components, paying particular attention to those requiring urgent conservation measures and those which offer the greatest potential for sustainable use.
>
> Identify processes and activities likely to have significant adverse impacts on the conservation and sustainable use of biological diversity.
>
> Maintain and organize data derived from identification and monitoring.

The U.S. Bureau of Land Management, National Park Service, and Fish and Wildlife Service have responsibility for surveying and monitoring terrestrial biological diversity. The National Biological Survey, part of the National Partnership for a Biological Survey (Committee on the Formation of the National Biological Survey 1993) brought together the scientific expertise of these various agencies to develop coordinated programs. The National Biological Survey was moved into the U.S. Geological Survey as its Biological Resources Division, which has provided national leadership to many governmental and nongovernmental partners to address regional conservation needs and to develop a mechanism for sharing information through the National Biological Information Infrastructure.

Efforts such as the Gap Analysis (Scott et al. 1993), which maps keystone species and habitats on a regional level, and environmental monitoring and assessment by the Environmental Protection Agency, provide broad baseline data for identifying large-scale trends. The Nature Conservancy has published a survey of the rare plant communities of the United States (Grossman et al. 1994).

Our knowledge of plant taxa and their distribution in the United States varies considerably. All 50 states have natural resource agencies and natural heritage data centers, and 20 percent also have biological surveys. Excellent floras have been published for the Northeast, Great Plains, and Intermountain regions. Flora of North America is a multi-institutional project that brings together information on all of the plant taxa growing outside of cultivation in the United States and Canada. Many new taxa are still being discovered. For instance, between 1975 and 1995 about 1,000 plant taxa new to science were described from the contiguous 48 states (Hartman and Nelson 1998). Of these, 217 were from California, 183 from Utah, 63 from Nevada, 57 from Arizona, and 41 from New Mexico. Yet many areas of the country are still very poorly known floristically. For instance, despite 20 years of relatively intensive collecting, the Klamath Mountains of southwestern Oregon can still be considered underexplored (Morin 1995). In contrast, the number of herbarium specimens from the Intermountain Region has more than doubled since 1975, and systematic exploration of the Rocky Mountains is underway by botanists at the University of Wyoming. Arizona may be one of the floristically richest areas in the United States but is one of the most poorly known. In need of further collecting are the Arizona Strip region, Navajo Reservation, Glen Canyon, Grand Canyon, the Mogollon Rim, and the eastern Mojave. For bryophytes, the states of Nevada, Arizona, New Mexico, and part of Texas are in most need of work (Whittemore and Allen 1995).

Population level information on rare plants is monitored by responsible state and federal agencies, the Nature Conservancy, Center for Plant Conservation gardens and arboreta, and botanists studying specific taxa.

Table 1. Floristic statistics (Stein et al. 2000).

	Total species	Conservation concern	Endemic
North America north of Mexico	20,000	23%	–
Arizona	3510	604	164
California	6400	1735	1517
Nevada	2844	479	90
New Mexico	3290	409	81
Utah	2960	515	169

The basic requirements for survey and monitoring are expert knowledge and collections that both underpin and document that knowledge (Heywood 1995). Although the lack of botanical experts and collections is much more serious in biologically rich developing countries, we also face many challenges in the United States. The need for basic taxonomic facilities, collections, specialists, and mechanisms for managing and sharing information is being addressed by several initiatives. An agenda for action is set out most broadly in the Darwin Declaration:

> Darwin Declaration:
>
> Countries should invest in the development of appropriate infrastructure for their national collections.
>
> Encourage partnerships between institutions in developed and developing countries to promote scientific collaboration and infrastructure rationalization. Should include training initiatives. Should develop national priorities in taxonomic training, infrastructure, and new technology.
>
> Adopt internationally agreed levels of collection housing.
>
> Provide training programs at different educational levels.
>
> Use information systems to maximize effect in taxonomic institutions.

The Global Taxonomy Initiative (www.biodiv.org) provides some specific recommendations. It has been adopted by the Conference of Parties (representatives of the countries signatory to the Convention on Biological Diversity) and provides a vehicle by which countries can develop their expert capacity as well as a vehicle for funding. The Global Taxonomy Initiative calls for development of a national taxonomic needs assessment and creation of employment opportunities for taxonomists. It includes building capacity for bioprospecting, habitat conservation, sustainable use of biological diversity, and adequate, long-term housing of collections and records. Countries are to designate national reference centers to make information housed in collections available to countries of origin.

We need to conduct a national assessment of taxonomic capacity. For instance, it is well known that many groups of invertebrates have no specialist, and there are many major plant groups for which there is no specialist. A recent survey of herbaria in the southeastern United States (Funk and Morin 2000) showed that although most of the larger herbaria were active and secure, many smaller regional herbaria were at risk. Surprisingly, even the fate of one of the largest of the herbaria was in doubt. Similar surveys should be done for each region in the United States.

Processes Affecting Biodiversity and Sustainable Use

The greatest threat to biological diversity in the United States, as in the rest of the world, is population growth. The U.S. population is increasing by 2.8 million each year. Eighty percent of the population lives in metropolitan areas, making a great impact on natural areas adjacent to them. Agriculture affects grasslands in particular, grazing impacts grasslands and arid regions, and forests are harvested for timber.

Many of our major habitats have been severely impacted. Freshwater wetlands in the United States occupied 200 million acres (81 million hectares) in presettlement times. Only 95 million acres (38 million hectares) remain and some states have lost 90 percent of their wetlands. It is thought that 240,000 to 360,000 acres are impacted each year (Raven et al. 1993).

Grasslands once covered 40 percent of the U.S. landmass. Originally these grasslands were dominated by perennial grasses; now they are mostly annuals. Only 1 percent of virgin grassland remains. For instance, in the California Floristic Province, needlegrass originally covered 5 million hectares and is now reduced to 400 hectares, whereas annual grasses once covered only 400 hectares and now cover 3.5 million hectares (Bryant 1998).

Only 10 percent of old-growth temperate rain forests survive, and that is in scattered patches. More than half of the forest land in the United States is privately owned. The U.S. Forest Service governs 300,000 square miles of forest, of which 136,000 square miles are classified for commercial logging.

Deserts occupy 5 percent of the North American landmass. In 1981, 350,000 square miles in the

United States were undergoing severe or very severe desertification. Changes in succession due to fire suppression, grazing, and other disturbances are leading to tree and shrub dominance in deserts. Erosion is severe in some areas.

Organization of data

The number of initiatives to compile information on the world's organisms is large. Although they may seem to overlap, in fact each one serves a specific purpose (Table 2).

Many museums and herbaria are computerizing data from their collections to make those data more generally available and usable. These databases, many available as Internet resources (and prefixed by http://), are compiled mostly on a state or regional basis. Examples include the SMASCH database of the University of California at Berkeley and Jepson Herbaria (ucjeps.herb.berkeley.edu), the Vascular Plant Catalog of the Intermountain Region of the Western United States (www.nybg.org/bsci/hcol/intf), the Atlas of the Vascular Plants of Utah (www.nr.usu.edu), the Atlas of the Vascular Plants of Wyoming, the Flora of Texas Consortium (csdl.tamu.edu/flora; www.esb.utexas.edu), the Atlas of the Flora of New England (www.herbaria.harvard.edu), the Atlas of Tennessee Vascular Plants (www.bio.utk.edu/botany/ herbarium), the Pennsylvania Flora Database (www.upenn.edu/paflora/ dbsearch.html), the South Carolina Plant Atlas (cricket.biol.sc.edu/herb), and the Atlas of Florida Vascular Plants (www.plantatlas.usf.edu).

Table 2. Hierarchy of taxonomic initiatives.

Clearing House Mechanism	As specified by the CBD, every country must designate a national center through which information on its own biological diversity, and information it holds on the biodiversity of other countries, must be made available.
Global Biodiversity Information Facility	A mechanism for coordinating and making interoperable diversity databases; ultimately a digital library of biodiversity knowledge (Edwards et al. 2000).
Species 2000	A database of basic taxonomic information about all organisms worldwide. Species 2000 acquires data for major taxonomic groups, e.g. birds (Bisby 2000).
International Organization for Plant Information	IOPI is compiling taxonomic and distributional data on plants of the world. Their World Checklist brings together data from various floras, which are then checked by taxonomic specialists (Morin 1998). It provides the plant component of Species 2000. The Species Plantarum Project of IOPI provides expanded treatments of plant families.
Flora of North America	An example of a continental flora that provides basic taxonomic information for IOPI and Species 2000. It contains new scientific work as well as information from other floristic works (Morin et al. 1989).
Intermountain Flora	An example of a regional flora based on field work, examination of specimens, and evaluation of the literature. Local floras and checklists.

Databases that synthesize information from many different sources for the entire country include the Plants Database (plants.usda.gov), the Association for Biodiversity Information (www.natureserve.org), and the American Bryophyte Catalog (www.nybg.org/bsci/hcol/bryo/). An example of a special-topic database is the Southwest Exotic Mapping Program (www.usgs.nau.edu/swemp).

Protecting Plants in Place

Almost 60 percent of the land in the United States is privately owned. About 30%, or 655 million acres, is under federal management, distributed as follows: BLM 265 million acres, USFS 191 million acres, NPS 83 million acres, FWS 91 million acres, and DOD 25 million acres. Three percent is owned by Native American tribes, and the remainder is state or municipal (M. Olwell, personal communication, February 2000). Federal agencies are legally mandated to manage much of their land for multiple uses, and even lands not subjected to extractive economic use may be severely impacted by those simply wishing to enjoy them; nearly 60 million people visit the 50 U.S. National Parks each year. The Nature Conservancy owns and provides stewardship for more than 12 million acres. In the past decade various agencies and the Nature Conservancy have begun to manage land on a very large scale in recognition of the impact that adjacent land use has on preserved areas and the necessity of maintaining the integrity of natural processes, such as water drainages and catchments. Within states, decisions about which areas need to be protected are often made as a collaborative effort among federal, state, and non-governmental biologists and resource managers. Educating the public, and especially private landowners, is a key element to in situ conservation.

Article 8: In Situ Conservation

Establish a system of protected areas.

Develop guidelines for their selection, establishment, and management.

Promote the protection of ecosystems, natural habitats, and the maintenance of viable populations of species in natural surroundings.

Establish buffer areas.

Rehabilitate and restore degraded ecosystems and promote the recovery of threatened species through the development and implementation of plans or other management strategies.

Control risks associated with use of living organisms.

Prevent the introduction of, control, or eradicate the alien species which threaten ecosystems, habitats, or species.

Respect, preserve and maintain knowledge, innovations, and practices of indigenous and local communities.

Perhaps the greatest challenge to in situ conservation, after direct use for development, is the extent to which land management practices have altered natural processes. Fire suppression and grazing practices have resulted in unhealthy forests in many areas of the United States, but most conspicuously in the West. Grasslands have been irreversibly altered; wetlands completed converted. Catastrophic fires now occur on an enormous scale, and we have little knowledge of how to seed or replant millions of acres in a way that facilitates normal succession of native plants rather than extreme erosion or invasion by nonnative plants.

Invasive plants pose the second greatest threat to endangered plants after habitat destruction; nonnative species threaten two-thirds of all endangered native species. Some 8–47 percent of the total flora of most states is composed of introduced invasive plants (Randall and Marinelli 1996). Invasive weeds cost the U.S. economy more than $20 billion each year, according to a 1994 figure (Westbrooks 1998). According to Pimentel et al. (2000), yellow star thistle (*Centaurea solstitialis*) now dominates more than 4 million hectares of northern California grassland. European cheatgrass (*Bromus tectorum*) now forms monocultures on 5 million hectares in Idaho and Utah, where it has fundamentally altered cyclical fire patterns. A U.S. Department of the Interior survey reported that noxious weeds are invading western wildlands at a rate conservatively estimated to be nearly 5,000 acres per day (Environmental News Network, Inc. Web site, 6 October 1998). On BLM land alone, approximately 35 million acres are infested with invasive species.

To halt intentional introduction of nonnatives, a 1994 Executive Memo and a 1999 Executive Order (EO 13112) by President Clinton directs that native plants be used in plantings and seeding on federal lands whenever feasible. "Feasibility" is a serious issue, however. A workshop called in February 2000 by W. Brown, Science Advisor to Secretary of the Interior Babbitt, tried to identify and address the barriers to using native plants. The greatest problem is lack of appropriate material in large enough quantities. In 1999, 2.5 million acres of BLM land burned in the Great Basin alone. To reduce erosion due to rain after the fire, it is necessary to seed the burned area quickly, and there is not enough time to propagate and bulk up seeds from appropriate genetic material. Most nurseries cannot afford to maintain large stores of seeds with no assurance of a buyer. Because it is very labor intensive to gather seeds of native plants, the seeds are much more expensive, even in small quantities, and this is another factor in what is considered feasible. The workshop recommended that internal federal purchasing procedures be changed to make it economically possible for nurseries to gather, grow, and store the seeds that will be needed. Large areas with mostly native plant communities, such as reserves, military installations, and botanical gardens, could serve as sources of native seeds.

Botanical gardens and arboreta can help to educate the public about weeds and the problems they cause, as well as helping prevent introduction of new invasives through the horticultural trade. Regional nonnative plant pest councils play an important role in identifying local problems and developing management plans, including public education and public weed eradication activities. President Clinton created an Interagency Invasive Species Council and a Federal Interagency Weed Committee, and Secretary Babbitt established an Invasive Weed Awareness Coalition.

In the West, Native SeedSearch may be one of the best-known organizations devoted to preservation of indigenous knowledge and heritage seed material. Local botanists and herbalists work individually with Native American elders to learn and preserve their knowledge of plants, plant remedies, and foods. There are other organizations

that research, acquire, and maintain heritage cultivars, but we are probably on the brink of losing a tremendous amount of knowledge held by people born in the early part of the 1900s for whom native plants and home-grown foods were an essential part of life. Many of these people transferred knowledge and experiences that they had gained in their birth countries to the plants they found in the United States. Their knowledge is likely to die with them.

Protecting Plants Outside Their Habitats

Direct conservation of genetic material of plants of conservation concern is the goal of the Center for Plant Conservation (CPC). Established in 1984, CPC is a network of 29 botanical gardens and arboreta that have agreed to maintain genetically viable material of threatened or endangered plant species. In June 2000, the U.S. Fish and Wildlife Service designated CPC as an official partner and clearinghouse in plant conservation. Currently, the network holds material of 570 critically imperiled taxa out of 735 threatened or endangered species listed by USFWS.

Article 9: Ex Situ Conservation

Adopt measures for ex situ conservation of components of biological diversity, preferably in the country of origin.

Establish and maintain facilitites for ex situ conservation of and research on organisms, preferably in the country of origin.

Adopt measures for the recovery and rehabilitation of threatened species and for their reintroduction into their natural habitats under appropriate conditions.

Regulate and manage collection of biological resources.

Cooperate in providing financial and other support for ex situ conservation.

In addition to selecting, acquiring, and maintaining genetic material for permanent protection, the Center for Plant Conservation has provided leadership in developing standards and protocols for seed storage, handling of recalcitrant seeds, tissue culture of difficult plants, and documentation (e.g., Falk and Holsinger 1991). CPC and its member gardens now are extending their work to full recovery plans, in which ex situ conservation plays an essential role (Falk et al. 1996). The Gran Canaria meeting also recommended integrating ex situ and in situ conservation strategies:

Gran Canaria Declaration

- Set agreed levels and standards in plant diversity conservation and services worldwide to be achieved within a defined time frame.
- Give special attention to the conservation of the world's most important centers of plant diversity, including the ecosystems and the species they contain.
- Support the maintenance of genetically diverse and accessible samples of the world's plant species in botanical collections throughout the world.
- Pay special attention to the conservation of plant species of direct economic importance to human societies.
- Control invasive alien plants and animals, which pose one of the greatest threats to natural habitats.
- Develop and implement best practices in plant conservation which will ensure the fullest community and institutional participation at all levels.

Much of the tension in our communities these days comes from differences of opinion and perception about the value of preserving native biological diversity and natural processes versus economic or social benefits of actions that destroy biological diversity and upset natural processes. Housing developments, grazing, logging, dams, and recreation, are all traditional uses of natural resources. The livelihood of individuals, families, or entire communities may depend on these uses. At the same time, some citizens consider their desire for conservation of species, for pristine habitats, and for a return to natural processes to be as legitimate as any economic need.

Article 10: Sustainable Use of Components of Biological Diversity

Promote incentives for the conservation and sustainable use of components of biological diversity.

Ensure adequate incorporation of market and nonmarket values of biodiversity into plans, policies, and programs, including national accounting systems and investment strategies.

Develop training and capacity building programs and promote private sector initiatives.

Incorporate biodiversity considerations into impact assessments.

Research supports the concept that biological diversity, as individual components or as communities or habitats, provides essential services to people and the environment, including cleaning water and removing pollutants from the air (Pimentel et al. 2000). The Nature Conservancy's ecoregion programs address conservation issues on a large scale and engage the interest and par-

ticipation of human communities in addressing sustainable use of the area. The Gran Canaria workshop summarized the issues as they relate to plants specifically.

Gran Canaria Declaration

- Identify and assess the socio-economic value and the cultural value both of particular species of plants and of plant diversity itself.
- Identify and assess the existing and potential products and services provided by plant diversity.
- Ensure that benefits derived from the use of plants are fairly and equitably shared.
- Identify the underlying causes of plant diversity loss and assess the potential risks and constraints on conservation, particularly in countries that are rich in plant diversity.

Build Capacity

The CBD and the Gran Canaria Declaration both emphasize the need for research on the biology of organisms, on their ecology, and on their relevance to social, cultural, and economic factors. A full inventory of the plant diversity of the world and information systems to manage the data is urgently needed. As discussed above, much floristic work is needed in the United States as well.

Article 12: Convention on Biological Diversity

Establish and maintain programs for scientific and technical education and training for the education, conservation, and sustainable use of biological diversity.

Promote and encourage research which contributes to the conservation and sustainable use of biological diversity.

Promote and cooperate in the use of scientific advances in biological diversity research in developing methods for conservation and sustainable use of biological resources.

The establishment of programs in conservation biology in a number of universities is encouraging; the loss of traditional expertise and training in descriptive botany is discouraging. There are 628 herbaria in the United States and 110 in Canada. As mentioned above, a recent survey of herbaria in the southeastern United States showed a pattern of smaller, regional herbaria being abandoned or absorbed by larger herbaria (Funk and Morin 2000).

Gran Canaria Declaration

- Undertake international programs of research on plant biology and interactions with social, cultural, and economic factors that impact biodiversity.
- Document the plant diversity of the world, including up-to-date information on its distribution in the wild, its conservation status and trends, and its use and preservation in protected areas and ex situ collections.
- Develop an integrated, distributed, interactive information system to manage and make accessible information on plant diversity.
- Monitor the status and trends in global plant diversity and its conservation and produce regular reports.

Educate!

It seems fitting to close this paper with statements from the Convention on Biological Diversity and the Gran Canaria Declaration. If we are to achieve conservation goals, we must engage the interests and emotions of people whose decisions will, in the end, decide the fate of plant and animal species. We must do this for every age group, economic group, and ethnic group. We must reach taxpayers and legislators, individuals, groups, communities, and countries. Plants are essential to our lives and to the lives of generations yet to come, and it is only by understanding this that we can save them and ourselves.

Article 13: Convention on Biological Diversity

Promote and encourage understanding of the importance of, and the measures required for, the conservation of biological diversity, as well as its propagation through media, and the inclusion of these topics in educational programs.

Gran Canaria Declaration

- Articulate and consistently emphasize the benefits of conserving plant diversity, to raise awareness of the importance of plants and the threats they face, thereby encouraging active participation in their conservation.
- Inform citizens and policy makers in every country about conservation priorities and policy options for plant species and their ecosystems.
- Use relevant botanical institutions as shop windows for plant conservation by demonstrating the interdependence of human beings and plants within all ecosystems.
- Incorporate the importance of plants and plant conservation into formal and informal education. Cooperate, as appropriate, with other States and international organizations in developing educational and public awareness programs with respect to conservation and sustainable use of biological diversity.

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A Case for Conserving Imperiled Plants by Ecological Area

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Abstract: Imperiled plants are sometimes protected as endangered or threatened species at state and national levels. However, politically based geographic units fall short for conservation purposes. For example, only 19 percent of plant species considered imperiled in the San Juan region of Colorado and New Mexico appeared on recent state or federal endangered species lists. Conservation of imperiled plants by ecological area is proposed. This would help (a) safeguard plant populations of evolutionary significance; (b) maintain the integrity of biotic communities; (c) draw attention to imperiled regional endemics, which often fail to make government endangered species lists; and (d) preserve wild plant populations locally for conservation education and for medicinal, aesthetic, scientific, and other cultural reasons. A focus on ecological areas would broaden modern conservation practice, making it better able to protect and restore the natural world.

Plant species in danger of disappearing from significant geographic areas of the United States often receive little or no attention in conservation planning. For example, a recent tally of imperiled plants of the San Juan Mountains and adjacent areas of Colorado and New Mexico revealed that only 10 of 54 (19%) of these species appeared on federal or state endangered species lists (Povilitis 2000; Table 1). Of 28 imperiled plant species in the San Juan region occurring in New Mexico, less than half were on the rare plant list of the New Mexico Rare Plant Technical Council (2000). The council, which encourages conservation by landowners and others, does not list plants that are rare in New Mexico if substantial populations occur elsewhere.

In cases where a species is imperiled throughout its geographic range, protection for each existing population can be justified to help prevent extinction of the species as a whole. This is true for federally listed San Juan region plants like Mancos milkvetch *Astragalus humillimus* and Mesa Verde cactus *Sclerocactus mesae-verde*. It is also true for vulnerable local endemic species such as skiff milkvetch *Astragalus microcymbus* and Pagosa gilia *Ipomopsis polyantha*, which for one reason or another are not currently listed.

What about protecting species that are jeopardized over portions—but not all—of their ranges? This paper proposes recognizing and conserving imperiled plants by ecological area. An ecological area can be defined as a sizable land area that differs broadly from other areas in its biological, edaphic, and geographical features or patterns. For illustrative purposes, the San Juan Mountains and surrounding highlands, valleys, and basins are considered an ecological area. Ecological area boundaries can be determined by examining the distribution of organisms and coinciding physical landscape features (such as soils, topography, and climate).

Some observers may argue that it is unnecessary to protect a species in every ecological area in order to maintain it, and that attempting to do so would spread conservation resources too thin. Why not focus on state or nationally endangered species and on conserving them in places where environmental conditions are most optimal? Notwithstanding its practical appeal, this approach neglects important evolutionary, ecological, and cultural aspects of plant and animal populations; it implies "preservation" of species as diminished evolutionary units, truncated ecologically, and divorced from a larger relevance to humans. I find three compelling reasons to conserve species by ecological area:

1. Adaptation and organic evolution – Species that are geographically widespread over varied environments tend to have large, diverse gene pools (Hamrick and Godt 1989, Soltis et al. 1997). Consequently, they are best able to environmentally adapt and generate new taxa (Fisher 1956, Fréville et al. 1998). Significant genetic differences are commonly recorded between populations of wide-ranging plant species across ecological areas. Examples from North America include wake-robin *Trillium ovatum* (Fukuda 1989) and Skinner's purple false foxglove *Agalinis skinneriana* (Kercher and Sytsma 2000).

There are 21 imperiled plants of the San Juan region with broad geographic distributions and another 20 species with more restricted yet still

Table 1. Geographic and legal status of imperiled plant species of the San Juan ecological area (based on Povilitis 2000). (P) indicates species whose San Juan populations are peripheral or disjunct from their main geographic ranges. (L) indicates species that appear on federal or state endangered species lists.

Wide Distribution

(P) Venus'-hair fern *Adiantum capillus-veneris;* (P) American spikenard *Aralia racemosa;* (P) Alpine aster *Aster alpinus* variety *vierhapperi;* (P) Bodin milkvetch *Astragalus bodinii;* Green sedge *Carex viridula;* (L) Little beeplant *Cleome muticaulis;* (L) Yellow lady's-slipper *Cypripedium parviflorum* variety *pubescens;* (P) Mountain bladder fern *Cystopteris montana;* Gaint helleborine *Epipactis gigantea;* (P) Low fleabane *Erigeron humilis;* (P) Altai cottongrass *Eriophorum altaicum* variety *neogaeum;* (P) Dwarf rattlesnake-plantain *Goodyera repens;* (P) Spiny-spored quillwort *Isoetes echinospora;* (P) Gay-feather *Liatris ligulistylis;* (P) (L) Wood lily *Lilium philadelphicum;* Canyon bog-orchid *Platanthera sparsiflora* variety *ensifolia;* Marsh cinquefoil *Potentilla palustris;* Parish's alkali grass *Puccinellia parishii;* Hoary willow *Salix candida;* Blue-eyed grass *Sisyrinchium demissum;* (P) Wild hyacinth *Triteleia grandiflora.*

Restricted Distribution

Galisteo sand verbena *Abronia bigelovii;* (P) Sessile-flowered false carrot *Aletes sessiliflorus;* Brandegee milkvetch *Astragalus brandegei;* Cronquist milkvetch *Astragalus cronquistii;* (L) Mancos milkvetch *Astragalus humillimus;* Chaco milkvetch *Astragalus micromeris;* Naturita milkvetch *Astragalus naturitensis;* Kachina daisy *Erigeron kachinensis;* Comb Wash buckwheat *Eriogonum clavellatum;* (L) Clay-loving wild buckwheat *Eriogonum pelinophilum;* New Mexico butterfly plant *Gaura neomexicana neomexicana;* Colorado desert-parsley *Lomatium concinnum;* Eastwood monkey-flower *Mimulus eastwoodiae;* Little penstemon *Penstemon breviculus;* Abajo penstemon *Penstemon lentus;* Adobe beardtongue *Penstemon retrorsus;* Splendid scorpionweed *Phacelia splendens;* (P) Giant cinquefoil *Potentilla ambigens;* (L) Mesa Verde cactus *Sclerocactus mesae-verde;* and Pale blue-eyed grass *Sisyrinchium pallidum.*

Regional Endemic

Gunnison milkvetch *Astragalus anisus;* (L) Cliff-palace milkvetch *Astragalus deterior;* Skiff milkvetch *Astragalus microcymbus;* Taos milkvetch *Astragalus puniceus* variety *gertrudis;* Ripley milkvetch *Astragalus ripleyi;* Schmoll milkvetch *Astragalus schmolliae;* Sleeping Ute milkvetch *Astragalus tortipes;* San Juan saltplant *Atriplex pachypoda;* (L) Aztec gilia *Gilia formosa;* San Juan Gilia *Gilia sedifolia;* Mesa Verde stickweed *Hackelia gracilenta;* Pagosa gilia *Ipomopsis polyantha;* Pagosa bladderpod *Lesquerella pruinosa;* (L) Knowlton cactus *Pediocactus knowltonii;* Pagosa phlox *Phlox caryophylla;* (L) Brack's cactus *Sclerocactus cloveriae brackii.*

sizable ranges (see Table 1). San Juan region populations of these plants could be important evolutionary units, though their genetic uniqueness has not been tested. Testing for allozyme or DNA variation would of course be useful in assessing their distinctiveness. However, given current technical limitations, such work would be time consuming, expensive, and possibly inconclusive (Schaal et al. 1991). Moreover, genetic information may be of limited value to long-term conservation planning because the degree of existing differentiation is not necessarily predictive of future change. Based on Hunter et al. (1988) and Lammi et al. (1991), populations occupying distinct ecosystems and subjected to varied regimes of natural selection deserve protection, regardless of their current degree of genetic or morphological differentiation.

Some observers may question the value of conserving geographically peripheral populations, arguing that they occupy marginal habitat where conservation efforts are unlikely to succeed. In the San Juan Mountains region, 22 of 54 (41%) regionally imperiled plants occur as peripheral or disjunct populations (see Table 1). Nevertheless, these populations may be, or may become, the most differentiated, being subject to physical and biotic challenges of marginal environmental conditions (Hazlett and Sawyer 1998). As Lesica and Allendorf (1995) have argued, peripheral populations are an important potential source of local adaptation and future speciation events.

2. *Ecosystem integrity* – Conservation of locally occurring populations is needed to maintain the biological integrity of natural (Callicot et al. 1999) or quasi-natural communities, where composition, diversity, and functional organization remains comparable to what occurred naturally (Angermeier and Karr 1994). Maintaining viable populations of all native species in situ is a primary goal of ecosystem manangement (Grumbine 1995, Temple 1997). As species disappear due to human causes, the ecosystems of which they were part become degraded and artificialized, often irreversibly so.

In terms of ecosystem management, Aldo Leopold's (1946) observation that keeping "every cog and wheel is the first precaution of intelligent tinkering" certainly has merit. However, apart from the obvious loss of a natural element, it is often difficult to determine what the disappearance of a species may mean for a given ecosystem as a whole. Nevertheless, each species affects the biotic community to a greater or lesser degree, be

it through competition, predation, herbivory, parasitism, mutualism, modification of the abiotic environment, or some other mechanism (Roughgarden and Diamond 1994). Seldom can biologists say what is ecologically consequential, except perhaps after the fact.

Although many imperiled plants of the San Juan Mountains region appear insignificant in terms of the region's overall flora, they may have important roles in shaping local biotic communities. For example, Adobe beardtongue *Penstemon retrorsus*, Colorado desert-parsley *Lomatium concinnum*, and Pagosa gilia *Ipomopsis polyantha* grow on clay soils derived from Mancos shale, a substrate that limits plant community development and presents special adaptive challenges to plant and animal life.

Whatever the precise function of a species in an ecosystem, its extirpation by humans serves notice that other species and the ecological processes upon which they depend may be at risk. An imperiled species typically means an imperiled habitat. Indeed, threats identified for imperiled plant species of the San Juan region, such as livestock overgrazing or poorly planned land and water development (Povilitis 2000) adversely impact a host of other plants and animals, many of which could eventually be lost.

3. *Cultural value* – Since the dawn of *Homo sapiens*, people have relied on wild plants for food, medicine, clothing, shelter, tools, weapons, insect repellants, dyes, use in rituals, aesthetic appeal, and other purposes. For example, American spikenard *Aralia racemosa*, an imperiled plant of the San Juans, has been used in soups, teas, and as medicinal preparations to treat respiratory ailments, skin conditions, backache, and menstrual and birthing problems (Moore 1989, Swerdlou 2000).

Intact local floras could provide new scientific, medical, and educational benefits as well as continued historical uses. For instance, populations of American spikenard and other species occurring along the margins of their geographic ranges may produce a greater concentration of bioactive chemicals, being exposed to tighter environmental constraints that restrict range (Hazlett and Sawyer 1998). New technologies may soon allow rapid assessment by plant aficionados of potentially important substances from local plant populations at various levels of development (bioactive substances may be present only at certain life history stages; recall, for instance, that opium is present only in unripe seedpods of *Papaver somniferum*).

Perhaps the greatest contemporary benefit of an intact local flora is the opportunity for people to gain first-hand knowledge of vulnerable plant species. For someone living in the San Juans, for example, the experience of seeing attractive or unusual rare species like Wood lily *Lilium philadelphicum* or Giant helleborine *Epipactis gigantea* may trigger heightened appreciation of the challenges that living things face in a human-dominated world. If lack of public awareness of the extinction problem is an impediment to conservation (Wilson 2000), the opportunity to learn about it in one's own "neighborhood" should have considerable merit.

Conservation ultimately succeeds or fails to the extent that people lessen their impacts on the biota and engage nature in a harmonious manner. Cultural shifts of this type have occurred in the past (Nabhan 1994), and they can occur in today's world (Western et al. 1994). There is no fundamental reason why we cannot develop a culture that sees humans as being part of nature, and protects and nurtures the local biota as a matter of everyday stewardship (Povilitis 2001).

Biologists can help enormously by identifying imperiled plant and animal populations by ecological area and by working to conserve them in collaboration with private landowners, environmental organizations, and public natural resource and planning agencies. They can also advocate that state and federal agencies adopt the ecological area approach in endangered species management. At the very least, doing so would help focus attention on currently unlisted imperiled endemics, including 12 plant species found only in the San Juan ecological area (see Table 1). At best, it would also substantially broaden the scope of modern conservation practice, making it more successful at protecting and restoring the natural world.

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The Role of Landscape Anomalies in Regional Plant Conservation

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Abstract: Landscape anomalies are regionally restricted habitats created by unusual geologic, edaphic, or hydrologic factors. Barrens, cliff faces, canyons, hanging gardens, and playas are all examples of landscape anomalies in the arid Southwest. Such sites often harbor an unusual and rich flora, including endemic, disjunct, or relictual plant species. Using examples from our studies on the chalk barrens and riparian canyons of southeast Colorado, we show how regional diversity can be enriched by the biota of habitats that are small in extent but biologically distinctive. Landscape anomalies are relatively easily surveyed and monitored, provide opportunities for comparative studies, and can serve as flagship habitats for capturing public interest. Because of their small size, however, they may be easily destroyed by development or overlooked in regional planning. Although coarse filter conservation approaches can be effective for the protection of regional ecosystems, a focus on small landscape anomalies as specific conservation targets may also be desirable to protect biota with low prominence but high biogeographic significance.

The geological term "anomaly" refers to a local feature distinguished by its unusual geophysical, geochemical, or geobotanical aspects (American Geological Institute 1976). The term "landscape anomaly" is used here in a similar sense: a regionally restricted habitat with unusual geologic, edaphic, microclimatic, or hydrologic factors. Examples of landscape anomalies in the arid Southwest include such habitats as shale barrens, riparian canyons, hanging gardens, and playas. In other regions, habitats such as coastal plain pond margins, dunes, prairie potholes, vernal pools, or cliff faces may fit the criteria for landscape anomalies.

Regional conservation efforts today often focus on different scales of protection. "Ecoregional" protection (Nature Conservancy 2000), sometimes called a "coarse filter" approach, typically addresses widescale communities or ecosystems and large tracts of land. A fine filter approach specifically protects rare species that might be missed in a larger ecological context. Somewhat in between the coarse and fine filters lies the keystone or focal species approach, which targets species whose individual ecology makes their protection an effective and inclusive umbrella for other species (Soulé and Kohm 1989, Lambeck 1997). All of these approaches have considerable merit in conservation but may be costly to implement.

We highlight landscape anomalies that provide another scale between ecosystem and species approaches and additional targets for regional conservation planning. Because of their relatively small physical size, landscape anomalies may be overlooked in planning for broad ecosystem conservation, or, because of their typically restricted biotas, they may not include species with a sufficiently high ecological profile to warrant recognition as critical habitat for keystone species. However, we suggest that these habitats can be valuable conservation targets on the basis of three important attributes: significance for regional biodiversity, research potential, and practical application for community-based conservation. We use two examples of southeastern Colorado landscape anomalies, chalk barrens and riparian canyons, to illustrate their importance in our regional biodiversity, their potential heuristic value as research sites, and their practicality for local conservation efforts.

Landscape Anomalies of Southeastern Colorado

The Pikes Peak region, which extends from about 30 miles south of Denver, Colorado to the Arkansas River Valley near the cities of Pueblo and Cañon City, is one of the country's fastest growing areas. Development pressures continue to climb here as the region sees a dramatic growth in population, housing development, urban infrastructure, and industry, with additional growth predicted for the coming decades.

For the past 5 years, we have been studying the botany of two landscape anomalies in this region: the chalk barrens of the Arkansas River Valley and the riparian canyons in the lower Front

Range foothills. They provide unusual edaphic conditions and microclimate in a regional landscape that transitions from dry plains grassland through pinyon pine woodlands to ponderosa pine forests in the upper foothills. Both of these study habitat types occupy limited areas, contain unusual and rich floras, and can succumb readily to the impacts of development or recreational use.

The Chalk Barrens

The Niobrara Formation contains the stratigraphic remains of a Cretaceous mid-continental interior seaway. It underlies much of eastern Colorado and Kansas (Scott and Cobban 1964) as a calcareous bedrock of shale, limestone, and chalk. The Middle and Upper Chalk layers of the Smoky Hills unit in the formation occur as a more geographically limited subset of the Niobrara, and form the Niobrara barrens. Here thinly bedded, fissile chalk layers erode easily and form moderate slopes with a surface covering of rock fragments over a shallow mineral soil (Scott 1969, Kelso et al. 1999). The chalk barrens occur only in areas with topographic relief, particularly where rivers or tilted uplift have provided erosion-prone slopes. Although they may reach several kilometers in length, Niobrara chalk barrens often cover as little as 10 m, with short vertical slopes 3–10 m from base to summit. These patches form small islands of exposed calcareous bedrock within a surrounding grassland or pinyon pine–juniper community. Although a few chalk barrens occur around the Comanche National Grasslands in southeastern Colorado, they appear mostly in a narrow belt along the Arkansas River between Pueblo and Cañon City. These barrens contain a number of plant species of concern (Colorado Natural Heritage Program 1999). Because of their small size and primary occurrence in a region with spreading development, they are viewed as highly vulnerable habitats. None of the barrens, however, has gained formal protection, though several occur on state or federal lands under the jurisdiction of Colorado State Parks, the Colorado Division of Wildlife, and the Department of the Army.

In previous studies we have examined numerous aspects of the barrens, including soil geochemistry, plant endemism, and autoecology of selected species of concern (Kelso et al. 1995a, 1995b, 1996, 1997, 1999). We found that the endemism here is not related to any unusual geochemistry of the soils; in fact, the barrens plant taxa also grow extremely well in "normal" transplant garden soils if sufficient water is supplied. The restricted nature of these species in the wild is probably due to their lack of ability to compete for water in sandy soils with other native species, especially grasses. However, on the barrens with a very shallow, fine soil on top of shallow, layered bedrock, they can occupy moisture-retentive bedrock cracks via extensive rhizomes and other belowground organs, and exploit a habitat that is inhospitable for more competitive species. This flora, though less than 100 species, contains an unusual association of plants, including rare, endemic, and disjunct species, as well as a high concentration of the Southwestern phytogeographic element at the northern periphery of its range. A comparison with the flora of Fort Carson, a U.S. Army base located just south of Colorado Springs, highlights the differences between the barrens flora and a typical regional shortgrass prairie flora (Table 1).

The data shown in Table 1 illustrate how the barrens flora is rich despite its small size: Rare endemics and geographically anomalous species show an unusually high profile here. In particular, the Southwestern phytogeographic element plays a prominent role. This element surfaces more frequently on the barrens than in the surrounding regional shortgrass prairie flora, approaching or perhaps exceeding its representation in the Mesa de Maya flora on the Colorado–New Mexico border, which predictably favors the warm climate, Southwestern species. For that region, Clark (1996) has shown that in a flora of approximately 570 vascular plant species, 17 percent have Southwestern phytogeographic affinities. Although most of the Southwestern species found on the barrens are not state or globally rare, they are nonetheless locally significant in our regional biodiversity profile. These northward or disjunct species are probably relictual elements from a previous climatic regime, such as in the early Holocene when the regional climate was periodically hotter, drier, or both than it is now (Dick-Peddie 1993, Thompson et al. 1993, Vierling 1998).

The Foothills Riparian Canyons

Unlike the foothills in the northern Front Range where continual moisture is available from mountain chains such as the Indian Peaks, the Pikes Peak massif and Rampart Range foothills are very dry. Not only are moisture-bearing weather systems less common here, but also water catchment areas on Pikes Peak now channel precipitation and snowmelt into reservoirs that were previously a system of natural lakes and streams. These larger reservoirs now curtail and direct the

Table 1. Comparative floras of Fort Carson and the chalk barrens of southeast Colorado. Fort Carson data from the Directorate of Environmental Compliance and Management, Fort Carson, CO (unpublished). Chalk barrens data from Kelso et al. (1999).

Attributes	Fort Carson	Barrens	
		Total Flora[a]	Core Flora[b]
Total flora	457	95	40
Number of high S-rated plant species[c]	8 (1.7%)	7 (7.4%)	5 (12.5%)
Southwestern element[d]	13.8%	15.6%	24.3%
Adventive element	18.6%	1%	< 1%

[a]Total flora found on 29 study sites in a 240 km transect across southeast Colorado.

[b]Core flora defined as species found in at least 25 percent of the study sites.

[c]High S-rated species are given the highest priority for conservation by the Colorado Natural Heritage Program. They carry an S1 or S2 rating under the ranking system used nationally by Heritage Programs (Colorado Natural Heritage Program 1999).

[d]Southwestern (or Chihuahuan) elements are species distributed primarily in Arizona, Colorado, New Mexico, Utah, and Mexico (Clark 1996).

water flow into just a few drainages in the region. In the approximately 100 km of foothills bordering Colorado Springs, there are several hundred topographic canyons, but few of these have permanent or semipermanent water. Prior to reservoir construction, these canyons, and perhaps others as well, were part of a hydrologic system fed by snowmelt and alpine lakes on Pikes Peak. Their perennial flows currently attract recreational use from the growing urban population here, and housing developments proliferate in the nearby foothills. None of these riparian canyons has explicit conservation protection thus far; ownership lies primarily with the City of Colorado Springs, the Pike National Forest, and private landowners.

The arid climate limits vegetation diversity in the foothills. The dominant species here are drought tolerant, many showing Southwestern phytogeographic affinities. A shrub community composed of *Quercus gambelii* Nuttall (Gambel oak), *Cercocarpus montanus* Rafinesque (mountain mahogany) and *Rhus aromatica* Aiton ssp. *trilobata* (Nutt.) Gray (skunkbrush) covers the lower elevations of Pikes Peak. In the middle elevations, montane forests of *Pinus ponderosa* Douglas (ponderosa pine) predominate, but on north-facing slopes the forests typically include *Abies concolor* (Gordon) Lindley (white fir) and *Pseudotsuga menziesii* (Mirbel) Franco (Douglas fir).

The riparian canyons, however, offer specialized habitats within the dominant foothills shrub or pine communities. We found that these landscape anomalies, like the chalk barrens, contain a rich flora that includes endemic, disjunct, and rare species as well as a regionally unusual phytogeographic profile (Hall 2000). This diversity arises from the cooler temperatures and more humid conditions found in the canyons than in adjacent areas of comparable elevation and topography.

Riparian canyons occur on a larger scale than the chalk barrens: They typically extend ca 10 km in length, and therefore can encompass a diversity of plant communities. Several of these, such as the *Alnus incana* (L.) Moench-*Cornus sericea* L. (thinleaf alder-red osier dogwood) and the *Corylus cornuta* Marshall (hazelnut) communities are recognized by the Colorado Natural Heritage Program (1999) as rare. Riparian canyons also provide critical wildlife habitat as corridors and nesting sites for bird species, including Mexican spotted owls, ovenbirds, and peregrine falcons, which are also

Table 2. Biological diversity in riparian canyons of the Pikes Peak region. Primary study sites included Queen's Canyon, Bear Creek Canyon, North Cheyenne Canyon, and Little Fountain Creek Canyon in El Paso County, Colorado.

Total vascular flora: 262 spp.
High S-rated plant community types: 10
S-rated plant species: 8
S-rated nesting bird species: 3
Phytogeography
  Southwestern:10%
  Eastern-Boreal: 18%
  Adventive: 14%

Data from Hall (2000). High S-rated community types are those recognized by the Colorado Natural Heritage Program to have high conservation priority for the state of Colorado (Colorado Natural Heritage Program 1999).

considered as rare at the state or global level. Table 2 summarizes this biological diversity.

Along with a significant number of rare species occurring in these wet canyons, the presence of the disjunct cool-climate species (the Eastern-Boreal element) stands out. For comparison, this element provides a barely visible signal at 3.5 percent of the regional shortgrass prairie flora present at the base of the canyons (unpublished data from the Directorate of Environmental Compliance and Management, Fort Carson). As the Southwestern element may be relictual from a previous warm climate and now prevails on the chalk barrens, the Eastern and Boreal elements may be relictual from the late Pleistocene (Weber 1965, Kaul et al. 1988, Hogan 1993). Although these species were probably more regionally widespread 12,000–15,000 years ago, they can now persist only under the cool moist conditions found in isolated canyon habitats.

Biological Richness of Landscape Anomalies

Although very different with respect to their specific biology, both the chalk barrens and the riparian canyons share the general characteristics typical of landscape anomalies. They contain rare or sensitive species that are habitat specialists, a low adventive component, and a high disjunct component that creates a biogeographic profile strikingly different from the regional one and suggests a relictual aspect to the biota occurring there. These qualities are important attributes of overall biological richness, which too often carries the connotation of mere species richness defined purely on a numerical basis. Species numbers alone may not do justice to the significance of certain individual species or phytogeographic suite of species in the local landscape.

Finally, although the biological community is the obvious focal point for botanists to assess, the abiotic core of these communities should also be considered. Because landscape anomalies are defined geologically through their bedrock, hydrology, or topography, protection of their biotic communities needs to incorporate consideration of the structure and process critical to habitat maintenance. This may be particularly important if the supporting system is not directly *sub situ*, a situation common in complex hydrologic regimes that maintain habitat anomalies like vernal pools, playas, or pond margins.

Research Potential of Landscape Anomalies

As discrete landscape units, regional anomalies like chalk barrens and canyons provide opportunities for comparative, temporal, and autecological studies of their signature organisms. Because these floras (or more broadly, the total resident biotas) are typically small, they can be surveyed completely or almost completely on a yearly basis, providing the breadth of biodiversity information that is rarely available for large-scale landscape units. Complete floras can be useful for comparative studies across a geographic transect or for monitoring change through time. They also facilitate comparisons of species richness and analysis of the ecological or human factors that promote or diminish richness.

The value of continuing studies of ecosystems and ecosystem change has been recognized by the National Science Foundation with its Long-Term Ecological Reserves (LTER) network located in major terrestrial biomes. Long-term studies of small ecological units will also be critical for understanding local and regional changes, especially at the population level. As corridors or islands in increasingly fragmented regional terrain, landscape anomalies provide venues for this scale of monitoring, and their rich biotas suggest multiple research topics relevant for conservation biology. Multiyear analyses of population size, dormancy, pollination systems, herbivory, seed set, granivory, and other biological processes are critical for understanding rare plant biology (Schemske et al. 1994, Pavlik 1997). In the Southwest, where erratic weather cycles have brought both moisture excess and severe drought in recent years, it will be especially important to monitor dormancy and reproductive responses in sensitive species, especially in ecologically constrained populations.

Our continuing studies on the chalk barrens and the riparian canyons have provided a number of ecological insights about communities and species in these landscape anomalies. We have found, for example, that inter-annual drought and moisture regimes profoundly influence the appearance and reproductive output of certain rare plant species on the chalk barrens and thus can skew assessments of apparent population health in surveys conducted on a single-year basis. Chalk barrens species are not pollinator limited, nor do they require pristine conditions to thrive (Kelso et al. 1995a, 1995b, 1996, Heckmann 1997). We have

found that moderate disturbance may enhance the abundance of certain endemic species on the barrens, a result that enabled us to make management recommendations to accommodate current grazing, recreation, and military use practices for sites under state and federal ownership. Despite their small size and island nature, chalk barren communities appear to be composed of species that are well adapted to climatic vicissitudes by having opportunistic reproductive systems that tolerate or perhaps require some degree of disturbance, and that appear to function well with relative isolation and fragmentation. In these respects, they may be typical of anomaly communities that have evolved as constrained systems, and thus perhaps instructive for us to understand what life history attributes are adaptive for success under conditions of isolation, small size, and disturbance.

Practical Considerations

The financial and political costs of both ecosystem and species level conservation can be enormous, particularly if large tracts of land must be purchased at development-inflated prices, or if economic activities need to be curtailed to protect critical habitat of focal or keystone species. In contrast, landscape anomalies may be small enough that outright purchase by communities or conservation trusts may be feasible, or they may be taken out of high-impact use without major economic consequences. A third avenue of conservation may be the most viable of all: using private landowners and conservation easements to protect small habitats with biological interest.

Conservation easements held by local land trusts are a rapidly growing phenomenon in the United States. Private landowners seeking preservation of family land coupled with tax relief are providing increasingly substantial protection for open space and native habitat across the country, particularly in Colorado where development is explosively changing the landscape. Preserving land through easements that restrict development while maintaining private ownership is an attractive option for landowners because easements can reduce taxes substantially; easements are also an attractive option for nonprofit conservation organizations because they can maintain open space and habitat at a low cost. Well-funded land trusts may actively seek land parcels on which to purchase development rights. Attributes of landscape anomalies such as high biological values encompassing overall diversity, presence of rare species, or intact habitats can be useful criteria for identifying conservation targets.

Unlike large ecosystems that may loom as too distant and complex for personal connection or a sense of stewardship responsibilities, landscape anomalies may be a perfect size for communities and private landowners to recognize and appreciate, or to identify as a special feature of their personal sense of place. In working with private landowners of riparian canyons, we found a biological interest and sense of connection to them, as well as appreciation for what we could tell them about the unusual biota found there. Such sensitivity to land attributes and appreciation for landscape features enhances the likelihood of responsible private stewardship; this can be extremely effective in land conservation without the costs inherent in public ownership of land. Rare plants need not necessarily be seen by landowners as a threat to their autonomy; if viewed as an asset, an archive of biological history, or a statement of land quality, unusual species can encourage landowners to be valuable allies in protection, monitoring, and providing access for ongoing scientific studies.

Although small landscape parcels may be problematic with respect to maintaining the long-term population viability of some species (e.g., Franklin 1980, Barrett and Kohn 1991, Primack 1998), small size also confers some positive attributes for conservation, such as the feasibility of relatively complete biodiversity surveys and the ease of monitoring change, as noted earlier, as well as the relative ease of controlling the incursion of undesirable species. Both the canyon habitats and the chalk barrens we surveyed contained a remarkably low component of nonnative plants, even in sites that had considerable human use. A similar situation has been found on other barrens in the eastern United States (Braunschweig et al. 1999), and may reflect a general tendency for ecologically or edaphically extreme sites to be at least somewhat protected against noxious weed invasions. Sites with a predominantly or exclusively native biota are highly desirable conservation targets, and a small size makes control or eradication of noxious weeds a much more manageable task than it is in large-scale conservation units.

Summary and Conclusions

Landscape anomalies are valuable targets for conservation efforts for a number of reasons. They typically contain a rich and regionally unusual biota that enhances local biodiversity with endem-

ic, rare, or disjunct species. Their small size offers the opportunity for relatively complete biodiversity assessments and for geographic or temporal comparisons. Their phytogeographic profile is often very different than the regional one, especially if they provide microclimatic conditions that allow relictual species to persist. In that context, landscape anomalies can act as biological archives. As islands or corridors with a constrained biota of small populations, landscape anomalies offer multiple research opportunities for monitoring population and species responses to climatic patterns, and autecological studies of rare species. If isolation has been in effect for a long time, these biotas can demonstrate life history strategies or adaptations that enable populations to successfully persist under conditions of ecological constraint, perhaps of increasing interest for our understanding or management of other fragmented communities.

In addition to being biologically valuable targets, landscape anomalies are also practical targets for conservation by local communities or private landowners. Small size makes them affordable for outright purchase or appropriate to include under the umbrella of conservation easements on larger pieces of land. Although many negative aspects of rapid growth affect communities like those of the Pikes Peak region, one positive result of growth may be heightened awareness of the need for open space conservation and increased resources to do so. As sensitivity to land issues rises, funding opportunities for land preservation may concomitantly rise as well through venues such as local sales taxes or state lottery funds. Communities may begin actively searching for locally significant conservation targets. In this context, landscape anomalies, with their concrete, often charismatic and biologically distinctive profiles, may provide significant reference points for connection to the local landscape.

Perhaps the most important message left for us in our contemporary landscape quilt of communities and ecosystems is the remaining importance of small places. Our small dune, wetland, canyon, and crevice niches contain some of our richest habitats with diverse biological stories. If, in the face of perhaps unstoppable change, we intend to keep our biological archives, then even small landscape patches may be important. Although large reserves play an undeniably valuable role in the preservation of ecosystems and wide-ranging species, smaller reserves forming an archipelago of mesas, sand dunes, canyons, or playa basins may also provide critical leverage and space for species, if only as a temporary resting point in time or place. Conservation is composed of theory, knowledge and appreciation, effort, and expense. Success lies as much, or more, in the hands of the average citizen as in those of the politicians or biologists. Landscape anomalies offer rich opportunities as conservation targets that are locally or personally meaningful for communities and landowners and often biologically significant in a regional context.

Acknowledgments

Funds for the studies described here were provided by the Colorado Natural Areas Program and the Howard Hughes Medical Institute Undergraduate Research Program. We would also like to thank the personnel at the Natural Areas Program, the Heritage Program, Colorado State Parks, Fort Carson, and Pinyon Canyon Maneuver Site for their assistance in various aspects of these studies. Additional assistance was provided by the City of Colorado Springs, the Palmer Foundation, the Douglas County Land Conservancy, and many private landowners in El Paso, Douglas, Pueblo, Teller, and Fremont Counties, Colorado. Special thanks to Janet Coles and Kathy Carsey of the Colorado Natural Areas Program for their comments on a draft of this manuscript, and to Caron Rifici of the Division of Environmental Compliance for information about the Fort Carson flora.

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Introducing Two Federally Listed Carbonate-Endemic Plants onto a Disturbed Site in the San Bernardino Mountains, California

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Abstract: *Erigeron parishii* and *Eriogonum ovalifolium* var. *vineum* are federally listed local-endemic plants occurring almost exclusively on carbonate soils in the northeastern San Bernardino Mountains. In 1991 and 1992, both species were planted onto a barren cut slope above a limestone quarry haul road. The plants were irrigated through the first summer and fall after planting. No soil amendments were provided other than the nursery potting mix surrounding their roots at planting. No effort was made to restore other components of natural habitat (e.g., soil conditions or plant associates). Each plant was tagged. Growth and survival were monitored for 2–3 years after planting, and again 6–7 years after planting. Of the initial plantings, 77 percent of *E. ovalifolium* var. *vineum* and 66 percent of *E. parishii* survived to the 1998 monitoring period. We estimated average half-lives of established *Eriogonum ovalifolium* var. *vineum* and *Erigeron parishii* as 20 years and 28 years, respectively. Both species have grown, flowered, and reproduced so that hundreds of progeny of both species now occur at the site. Most progeny of the two taxa were within a few meters of parent plants, and none were found beyond about 30 m from the study site. Progeny of both taxa became established on granitic material adjacent to the study site. *E. parishii* seems to have greater seedling production but lower establishment rates than *E. ovalifolium* var. *vineum*.

Eriogonum ovalifolium Nutt. var. *vineum* (Small) Jepson (Cushenbury buckwheat) and *Erigeron parishii* Gray (Parish's daisy) are narrow-endemic taxa of carbonate substrates in the northern San Bernardino Mountains, listed as endangered and threatened, respectively (U.S. Fish and Wildlife Service 1994).

Both are long-lived perennials with deep woody taproots (Sanders 1998a, 1998b, Neel 2000). *Eriogonum ovalifolium* var. *vineum* is a cushion-forming plant, only a few inches tall, but older plants on stable sites sometimes become quite wide. It generally occurs in rocky sites, in either talus or crevices in bedrock outcrops, but also on deeper colluvial soils. Its elevational range is about 4800–6500 ft. It is uncommon in washes or human-disturbed sites, but occasionally will colonize abandoned roads or quarry benches. Its pollinator is unknown, but observations of insect visitors suggest a generalist rather than specialist pollinator (Sanders 1998a, S. Morita personal communication).

Erigeron parishii is an erect plant with herbaceous stems rising to about 30 cm from a much-branched woody caudex at and just above the ground's surface. It occurs at about 3700–6200 ft elevation, most often in washes and canyon bottoms, but sometimes also on alluvial benches or steep rocky mountainsides.

Typical of the Asteraceae, *Erigeron parishii* produces plumed achenes adapted for wind dispersal. *Eriogonum ovalifolium* Nutt. var. *vineum* may also be wind dispersed; its achenes remain with the tepals as they dry, perhaps forming a "plane winged seed" (Burrows 1986). Neither taxon appears to have a seed dormancy mechanism (Mistretta 1994).

Both plants are generally considered carbonate-endemic, and the overwhelming majority of all known occurrences are on soils derived from limestone, dolomite, or other material high in calcium carbonate. There are scattered occurrences of these and other carbonate-endemic taxa on other parent materials. For example, *Erigeron parishii* occurs on quartz monzonite at the eastern end of its range (Neel 2000). Both taxa were successfully grown in soil mixes containing little or no carbonate material during propagation work at the Rancho Santa Ana Botanic Garden (Mistretta 1994).

Omya, Inc. (formerly Pluess-Staufer of California) contracted with the Rancho Santa Ana Botanic Garden (RSABG) to experiment with propagation of both taxa near its limestone quarry at White Knob, in the northern San Bernardino Mountains. One goal of the project was to establish populations of both plants on a barren cut slope above the

quarry haul road. The planting site is a north-facing slope at about 5200 ft. elevation, on partially consolidated carbonate alluvial and colluvial subsoil, exposed by grading for the haul road. The site is at the northern margin of the San Bernardino Mountains, just above the toeslopes and bajadas where the mountain range grades into the Mojave Desert. The site itself is nearly unvegetated; surrounding vegetation is dominated by *Pinus monophylla, Juniperus osteosperma, Cercocarpus ledifolius, Arctostaphylos glauca,* and *Coleogyne ramosissima* (Neel 2000). A natural population of Eriogonum ovalifolium var. vineum occurs about 200 m upslope from the planting site.

Methods

Propagules (seeds and cuttings) were salvaged from the quarry site prior to initial grading. Nursery stock was propagated from seeds or cuttings at RSABG during the year preceding each year's planting. They were planted at the site as 4-inch container stock in May of 1991, and as 2-inch stock in May of 1992 (Table 1). They were planted without soil amendments other than the nursery planting mix included in their root balls. Each plant was marked with a numbered metal tag for follow-up monitoring. Irrigation was supplied through the summer and fall following initial planting, and some limited weeding was done, but no other supplemental care was given the plants. The 1991 cohort was watered thoroughly at the initial planting and through the following dry season by manually supplying enough water to fill the small soil berm around each plant, twice weekly, from the planting date until November 1991. The 1992 cohort was irrigated with a drip system. Each plant was supplied with a 1 gal per hr emitter. They were irrigated for 2 hours 2 days after planting, for 1 hour daily for the following week, and for 1 hour 2–3 times weekly through October 1992.

The planting sites were monitored monthly by Rancho Santa Ana Botanic Garden staff through November of 1993, providing survival and seedling establishment data over two and three growing seasons for the 1992 and 1991 cohorts, respectively. (The term "cohort" is used throughout this report to describe a group of individual plants of either species, planted at the site in the same year.) Tables 1 and 2 summarize monitoring data through November of 1993 (Mistretta 1993, 1994). Scott White revisited the site in August of 1998 to monitor survival of the original plantings and establishment of progeny.

Plants were censused by systematically walking over the entire planting site along parallel belt transects marked in the field to ensure a thorough census and to avoid double-counting plants. Every individual *Eriogonum ovalifolium* var. *vineum* and *Erigeron parishii* seen during the census was noted, along with its metal tag number (if present), length (longest cross-sectional distance), and flowering condition.

Results

Both species had high survivorship and reproduction through the monitoring period, and appear to have become established as self-sustaining populations at the site (Table 3).

In total, 454 *Eriogonum ovalifolium* var. *vineum* were censused: 128 of the original plantings and 326 of their presumed progeny. Survival from planting to 1998 was 77 percent, with most mortality occurring in the first year following planting (Figure 1; note that two plants were mistakenly recorded as dead in 1992, but they survived and were recorded as living in 1993). The average size

Table 1. Survival and reproduction of 1991 and 1992 plantings after 1 year (Mistretta 1993, 1994).

Species	Cohort	No. planted	Survival	Progeny
Eriogonum ovalifolium var. *vineum*	1991	70	54 (77%)	0
	1992	97	89 (92%)	See Table 2
Erigeron parishii	1991	81	55 (68%)	266
	1992	74	61 (82%)	See Table 2

Table 2. Survival and reproduction of 1991 cohort after 2 years (Mistretta 1994).

Species	Survival	Avg. length	Progeny
Eriogonum ovalifolium var. *vineum*	56 (80%)	6 in	3
Erigeron parishii	52 (64%)	8 in	±180

Table 3. Summary of 1998 monitoring results.

Species	Cohort	Survival of initial plantings[1]	Progeny number	Total number	Average length	Reproductive
Eriogonum ovalifolium var. *vineum*	1991	43/70 (61%)			7.8 in	35 (81%)
	1992	77/97 (79%)			6.1 in	74 (96%)
	Sum 91+92	128/167 (77%)			6.8 in	116 (90%)
	Progeny		325		3.2 in	141 (43%)
	Total			453	4.2 in	257 (57%)
Erigeron parishii	1991	44/81 (54%)			8.4 in.	44 (100%)
	1992	55/74 (74%)			4.3 in.	55 (100%)
	Sum 91+92	101/155 (65%)			6.9 in.	101 (100%)
	Progeny		452		2.9 in.	423 (94%)
	Total			553	3.6 in.	425 (95%)

1. Summed survival reported here is greater than the sum of 1991 and 1992 due to inclusion of plants whose tags were illegible.

of surviving plants of the 1991 cohort increased from 6 inches in 1993 to 7.8 inches in 1998; the 1992 cohort averaged about 6.1 inches (1993 sizes not available). Of the surviving plants, 90 percent produced flowers in 1998. The 326 *E. ovalifolium* var. *vineum* not tagged are presumed to be progeny resulting from reproduction among the original plantings and probably also second-generation reproduction. The ratio of original plantings to progeny was about 1:2.

The total count for *Erigeron parishii* was 553, consisting of 102 of the original plantings and 451 presumed progeny (Figure 2). Since the 1993 monitoring, mortality in the *Erigeron parishii* cohorts was about 10 percent, and overall survival of the two cohorts to 1998 was 66 percent. The average size of surviving plants in the 1991 cohort increased from 8 inches in 1993 to 8.4 inches in 1998; the 1992 cohort average was about 4.3 inches in length. All surviving plants were reproductive. The 451 *E. parishii* presumed to be progeny included second and later generations of the original plantings. The ratio of original plantings to progeny was about 1:3.

In some cases, metal tags were found but their corresponding plants were missing or dead. These plants were considered dead for this analysis. In other cases, tags were not found, and those plants are also considered dead, but note that in some cases tags may have been lost or concealed by plants. Actual survival was probably slightly higher than reported here.

Survivorship among 1992 cohorts of both species was markedly improved over the 1991 cohorts. This effect may be due to different planting or irrigation methods, or it may be due to external effects such as rainfall (the 1991-92 July-June rainfall year was slightly below average, whereas the 1992-93 year was well above average). Since 1993, survival of 1991 and 1992 cohorts was comparable; that is, plants that survived beyond their first year have had similar survival rates in the ensuing years.

Discussion

Survival and reproduction patterns on the Omya site provide some insights into *Eriogonum ovalifolium* var. *vineum* and *Erigeron parishii* seed dispersal, pollination, and other biotic interactions, as well as demography and life history strategies. This small study cannot provide precise or detailed descriptions of these ecological parameters, but these inferences should be useful hypotheses for further ecological research.

Progeny of both taxa became established a few meters beyond the bounds of the original planting areas, especially downslope. No progeny were seen more than about 30 meters from the original plantings. *Erigeron parishii* is surely wind dispersed and *Eriogonum ovalifolium* var. *vineum* may also be. Presumably, seeds of both taxa, especially *E. parishii,* dispersed well beyond the bounds of the study site. Observed seedling establishment suggests that most "seed rain" falls within about 2 m of parent plants for both species. This is consistent with patterns reviewed by Willson (1992), who thought that wind-dispersed seeds tend to have greater maximum dispersal distances than

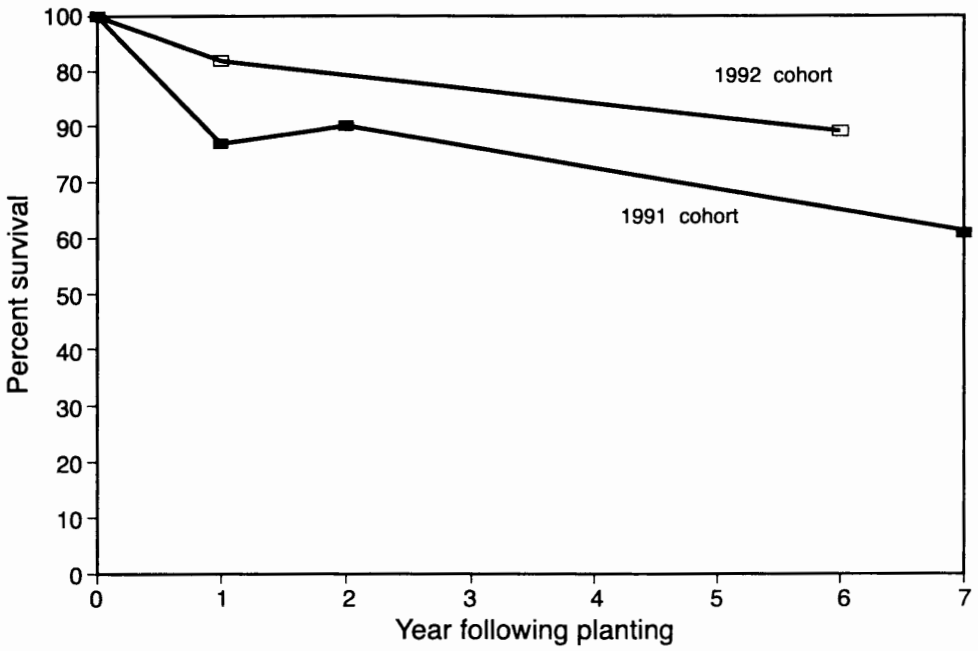


Figure 1. Survivorship of *Eriogonum ovaliflium* var. *vineum* initial plantings (1991 and 1992 cohorts).

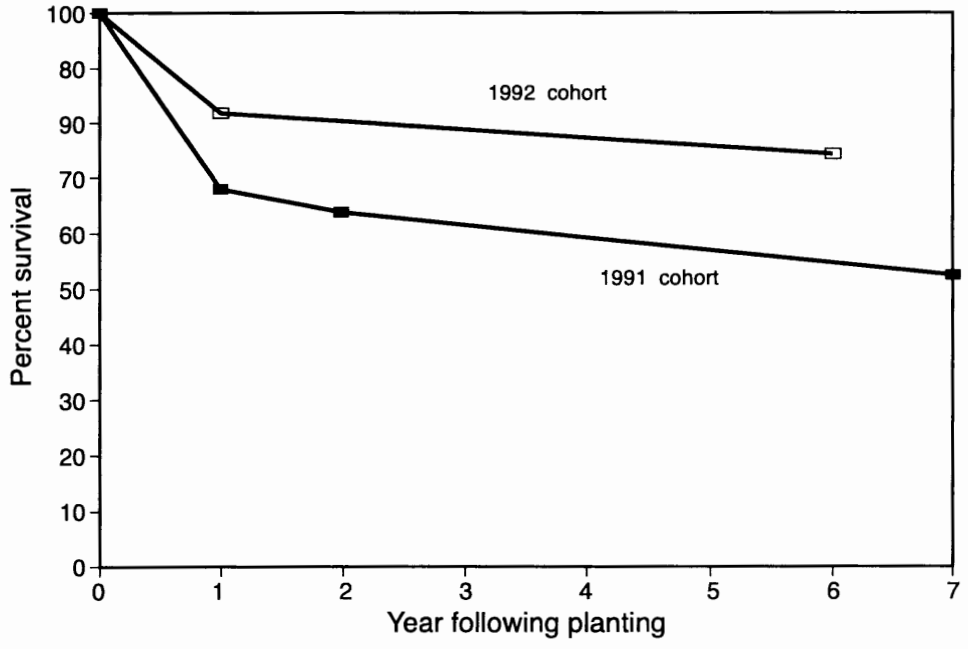


Figure 2. Survivorship of *Erigeron parishii* initial plantings (1991 and 1992 cohorts).

"ballistically" dispersed seed, but that peak distances were about the same for both mechanisms.

Progeny establishment beyond the original planted areas is particularly noteworthy at the northeastern corner of the original planting area, where there is a contact between carbonate-dominated alluvial and colluvial substrate (where the plantings were made) and the underlying granitic bedrock. Seventy-two *Eriogonum ovalifolium* var. *vineum* progeny and five *Erigeron parishii* progeny had become established in the weathered granitic bedrock. The higher establishment rate of *E. ovalifolium* var. *vineum* on non-carbonate material is likely due to the short dispersal distance rather than a greater tolerance for non-carbonate substrate. This granitic material is directly downslope from *E. ovalifolium* var. *vineum* plantings, and more distant from *E. parishii* plantings.

Both taxa set seed and produced progeny on the study site and in experimental planting boxes at RSABG. Breeding systems and pollinators are unknown for both plants, but successful reproduction in these settings indicates that neither plant is dependent upon a specialized pollinator. Successful seedling establishment in these habitats further suggests that neither plant is dependent upon specialized soil microorganisms.

We estimated seed production for the 1991 *Eriogonum ovalifolium* var. *vineum* cohort in 1993 at roughly 10,000 by multiplying mean seed number per inflorescence (6.2, N = 45) by the total number of infloresences (1612) on plants of the 1991 cohort. We estimated seed viability at 96 percent (Mistretta 1993). Only three *E. ovalifolium* var. *vineum* seedlings were found on the site in 1993. Presuming similar seed production in 1992, we calculate the survivorship rate from seed to established seedling for *E. ovalifolium* var. *vineum* at 0.0003 (3×10^{-4}). *E. parishii* seed viability was about 50 percent (Mistretta 1993). We did not calculate seed production or survivorship rates for *Erigeron parishii*, but it produces many more seeds per inflorescence, over a larger part of the growing season, and on many more inflorescences per plant. Its seed production is probably at least 2–3 orders of magnitude greater than for *E. ovalifolium* var. *vineum*.

Seedling production and recruitment for the two taxa was markedly different during the first years of the study, but was similar by 1998 (Figures 3 and 4). *Eriogonum ovalifolium* var. *vineum* produced no seedlings the first year and only three the second year, but had produced 325 progeny by 1998. Because we have no data for 1994–1997, we have no explanation for this pattern. We suggest that *E. ovalifolium* var. *vineum* may have infrequent years of very high recruitment, whereas most years have little or no recruitment due to climate variation (cf. *Larrea tridentata*; Barbour 1969). A second hypothesis is that seed set may generally be low, but very high in infrequent years, following a "mast fruiting" pattern (cf. *Coleogyne ramosissima*; Pendleton et al. 1995). Or, third, the large increase in seedling establishment over the later years of the study may simply have resulted from a large increase in seed production by the parent plants as they became better established, grew, and increased their inflorescence numbers.

Erigeron parishii produced 266 seedlings in the first year of the study (1992, Figure 4). By the second year (1993), only about 180 progeny were present, including any surviving seedlings from 1992 and any new seedlings produced during 1993. Of the 180 progeny, 35 were in flower. We infer that these 35 plants were seedlings germinated in 1992 that survived the intervening year and became reproductive in 1993. We presume that many, and perhaps all, of the remaining 1992 progeny died before spring 1993. If the 35 flowering progeny represent the entire recruitment cohort from 1992, then the survivorship rate was 13 percent of the previous year's seedlings, and the additional 145 progeny present in 1993 represented that year's reproduction. Alternately, if more than 35 1992 seedlings survived to 1993 but did not flower, then survivorship of the 1992 progeny would have been greater, but new reproduction during 1993 would have been less.

Table 3 and Figure 4 indicate surprisingly little increase in *Erigeron parishii* progeny by 1998. We believe that this is largely an artifact of census methods rather than a real decline in reproductive rates. Monitoring was done monthly through the growing seasons in 1992 and 1993, and all seedlings present during spring and early summer were censused. But in 1998, monitoring was done during August, near the end of the annual boom/bust cycle. Of the progeny counted in 1998, 94 percent were in flower, indicating that they were established plants from previous years. We believe that the 1998 data represent well-established plants, whereas the 1992 and 1993 data represent, in large part, seedlings that never became established. *Erigeron parishii* seems to have high annual seedling production and mortality, with only a moderate annual increase in established plants, as illustrated by Silvertown (1982, Figure 3.5b).

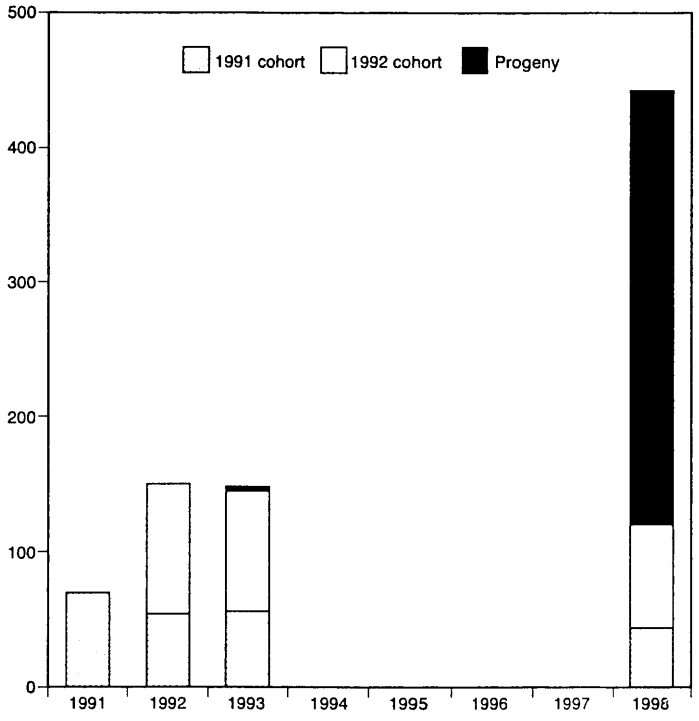


Figure 3. Total number of *Eriogonum ovaliflium* var. *vineum,* by year and cohort.

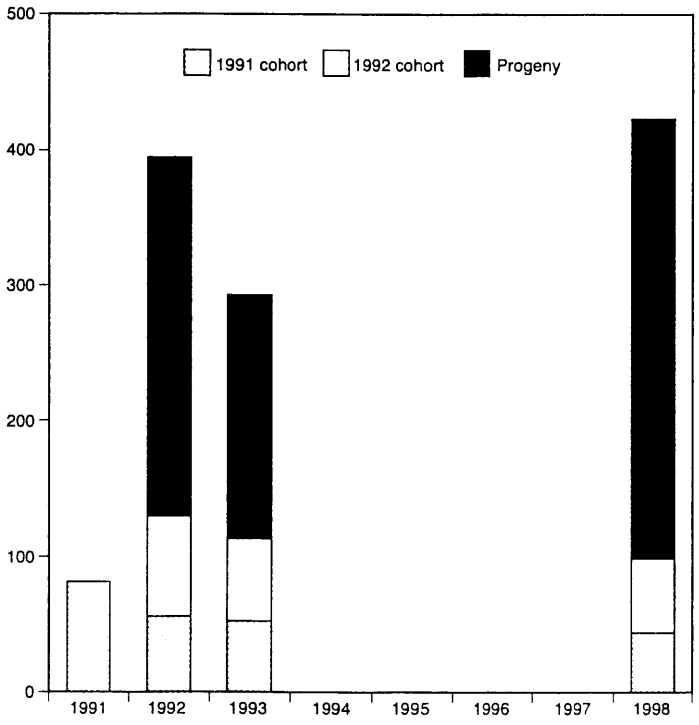


Figure 4. Total number of *Erigeron parishii,* by year and cohort.

The increase in number of *Erigeron parishii* progeny from 1993 to 1998 is considerable, but not nearly so striking as the increased establishment of *Eriogonum ovalifolium* var. *vineum* (Figure 3). Note also that only 43 percent of the *E. ovalifolium* var. *vineum* progeny produced flowers in 1998, compared with 95 percent of *E. parishii* progeny. These survival and reproductive patterns suggest that *E. ovalifolium* var. *vineum* is slower growing and slower to reach reproductive condition than *E. parishii*. The contrasting progeny numbers suggest greater seedling production but lower establishment rates for *E. parishii* than for *E. ovalifolium* var. *vineum*. We infer that *E. ovalifolium* var. *vineum's* survivorship curve resembles the Deevy type II form (Silvertown 1982), whereas *E. parishii's* survivorship curve resembles the Deevy type III form.

After plants became established, mortality was low for both taxa. Using Silvertown's (1982) formula, we calculated the average half-lives for an individual *Eriogonum ovalifolium* var. *vineum* and *Erigeron parishii* surviving beyond the first year after planting as about 20 years and 28 years, respectively. Both plants appear to be long-lived.

Acknowledgments

We thank John Dolan, Mike Wall, Linda Aberbom, Bart O'Brien, and Tom Hayduk for assistance with horticulture and monitoring; Howard Brown and Omya for logistical assistance and irrigation; Claudia Steiding for data entry; and Tasha La-Doux and Andrew C. Sanders for reviewing earlier drafts. Special thanks to Kitty Blassey for assistance throughout the first years of the project. O.M. dedicates this work to Mike Hammit who knew, grew, and loved the plants.

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The White-Margined Penstemon (*Penstemon albomarginatus* Jones), a Rare Mohave Desert Species, and the Hualapai Mountains Land Exchange in Mohave County, Arizona

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Abstract: The white-margined penstemon (*Penstemon albomarginatus* Jones) is a rare Mohave Desert species with an unusual tripartite distribution with disjunct localities in Arizona, California, and Nevada. The Arizona population is the largest single population occurring with a range of 15 miles by 5 miles in Dutch Flat near Yucca, Arizona in Mohave County. The land ownership pattern in Dutch Flat was a checkerboard of public and private land, a legacy of railroad lands. Although the Bureau of Land Management (BLM) designated the white-margined penstemon Area of Critical Environmental Concern (ACEC) in 1993 for conservation of this Arizona BLM sensitive species, the checkerboard pattern of public and private lands within the ACEC made its conservation management difficult. Rural development was increasing impacts to the Dutch Flat area as the private land was being sold off in 40 acre parcels. The Hualapai Mountains Land Exchange between the Santa Fe Pacific Railroad and the BLM provided a tool for consolidating a portion of the ACEC into a solid block of public land, thereby increasing its manageability for the conservation and survivability of the white-margined penstemon.

A real estate artifact of the westward U.S. expansion in the nineteenth century is the large areas of checkerboard land ownership patterns between public and private land. To encourage pioneer settlement, the federal government gave railroad companies every other section (the odd-numbered sections) along railroad routes they constructed. Because of the resultant checkerboard land ownership pattern, there are no large areas of contiguous ownership; consequently, these areas are both hard to manage for natural resource values on public land (either federal or state) and hard to develop for private land owners. Throughout the West, the Bureau of Land Management (BLM) has entered into various land exchanges with private land owners to consolidate federal land ownership to facilitate natural land resource management and protection of special habitats and species (Los Angeles Times 2000). In Mohave County, Arizona, one such checkerboard example is the Dutch Flat and Hualapai Mountains area east of Interstate 40 and approximately 20 miles south of Kingman (Figure 1). Here, the private land was originally owned by the Atchison, Topeka, and Santa Fe Railroad (Figure 2).

In 1997 the BLM and the Santa Fe Pacific Railroad, through its representative, Ironhorse Investors (the proponent), began the Hualapai Mountains Land Exchange (Figure 3) involving approximately 70,000 acres of selected lands (public lands selected by the proponent) and 70,000 acres of offered lands (private lands offered to the BLM by the proponent). The area covered by the Hualapai Mountains Land Exchange contained occupied habitat of a rare Mohave Desert plant (BLM 1995), *Penstemon albomarginatus* Jones, the white-margined penstemon (Figure 4), a member of the Figwort family (Scrophulariaceae). An analysis of the impacts of the Hualapai Mountains Land Exchange on the white-margined penstemon and its habitat was conducted to determine whether the effects of the exchange to the plant would be positive or negative (BLM 1998).

Penstemon albomarginatus was described by Marcus Jones (1908), who said it was "a most conspicuous and remarkable plant." It is indeed a distinctive species that has never been confused with any other species of *Penstemon*. A member of subgenus *Penstemon*, which is characterized by glabrous anthers that dehisce the full length and are usually widely spreading, *Penstemon albomarginatus* is a low growing plant 15–35 cm tall with several herbaceous stems arising from a buried root crown. It has a glabrous inflorescence of medium-sized, lavender-pink, campanulate flowers, 13–17 mm long, with a glabrous staminode and yellow hairs in the throat. The most distinguishing morphological character of the white-margined penstemon is the scarious white margins of the leaves, which are lanceolate to oblanceolate,

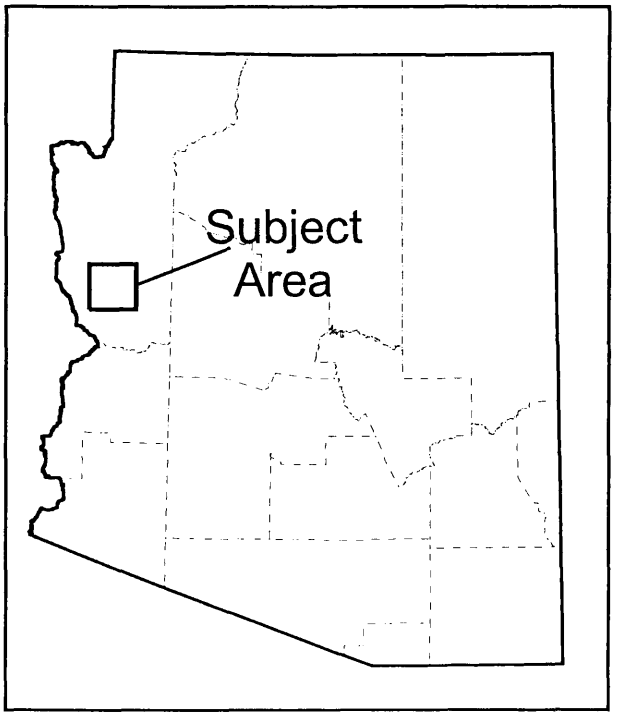


Figure 1. Subject area location within Arizona.

usually entire, and shiny glabrous with a bluish green color.

In his type description, Jones (1908) cited specimens from Good Springs Station, Nevada, in 1905, and Yucca, Arizona, where he had first collected it more than 20 years earlier on May 19, 1884 (in the area of the Hualapai Mountains Land Exchange). Ironically, his 1884 trip to the Yucca area was probably made possible by the completion that year of the Santa Fe Railroad to Needles, California (Lenz 1986). Jones (cited in Lenz 1986) wrote that "The whole spring flora was collected at Yucca and the desert was a perfect garden in all directions, never was as good for 20 years afterwards." The white-margined penstemon is one of the few *Penstemon* species that grows exclusively at low elevations in the Mohave Desert (Kearney and Peebles 1960, Munz 1974); others are *Penstemon bicolor* (T. S. Brand.) Clokey & Keck ssp. *roseus* Clokey and Keck and *Penstemon subulatus* A. Nels. As an adaptation to the arid conditions of Mohave Desert valleys, the white-margined penstemon is an "ephemeral" perennial whose stems die back to the ground after the spring growing season and during the hot, dry Mohave Desert summer and the cold Mohave Desert winter. Occasionally, the plant will green up in late summer if there is monsoon activity. For much of the year it is not visible above ground.

As a rare plant, *Penstemon albomarginata* has an unusual tripartite distribution pattern in the Mohave Desert (Scogin 1989). It occurs in three widely disjunct localities between three states—Arizona, Nevada, and California. The Arizona locality in Dutch Flat near Yucca is the single largest occurrence, extending in a band approximately 15 miles long and 5 miles wide along the western base of the Hualapai Mountains and Dutch Flat between Rock Creek on the northwest to Cow Creek on the southeast, although the entire area does not contain the appropriate soil habitat (Figure 5). Nevada has the widest scattered colonies (approximately 15 colonies) in two metapopulations over a hundred miles apart, one at Jean-Goodsprings 30 miles southwest of Las Vegas and one at Amargosa Valley 80 miles northwest of Las Vegas. California has the smallest occurrence, one 4 mile long population of scattered colonies 30 miles east of Barstow at Sleeping Beauty Mountain (MacKay 1999).

At all three widely separated localities, the white-margined penstemon grows on a similar habitat—sandy soils—but these sandy soils are of different origins. In California and Nevada the plants occupy stabilized sandy soils derived from colluvial sand deposits (personal observation), whereas in Arizona the plants occupy sandy loam uplands on alluvial fan terraces, and a smaller number of plants also occupy sandy wash bottoms. There is also a difference in associated vegetation of the white-margined penstemon between Arizona and the other two states. In Arizona the white-margined penstemon occurs with Joshua tree (*Yucca brevifolia* Engelm.) and mixed shrub association (Brown 1982), primarily creosotebush (*Larrea tridentata* (DC) Coville) and white bursage (*Ambrosia dumosa* (Gray) Payne) with big galleta grass (*Pleuraphis rigida* Thurb.), whereas in Nevada and California it occurs with simply the creosotebush and white bursage association (Brown 1982), and Joshua trees are not present (personal observation). In degraded habitats rayless goldenhead (*Acamptopappus sphaerocephalus* (Gray) Gray) and burro bush (*Hymenoclea salsola* T & G) increase as associated species. There is seemingly much potential sandy soil habitat for the white-margined penstemon between the existing sites that does not contain the plant. The reasons for its disjunct distribution pattern, whether biological or physical, are unknown but this pattern probably indicates that the *Penstemon albomarginatus* is a relict species.

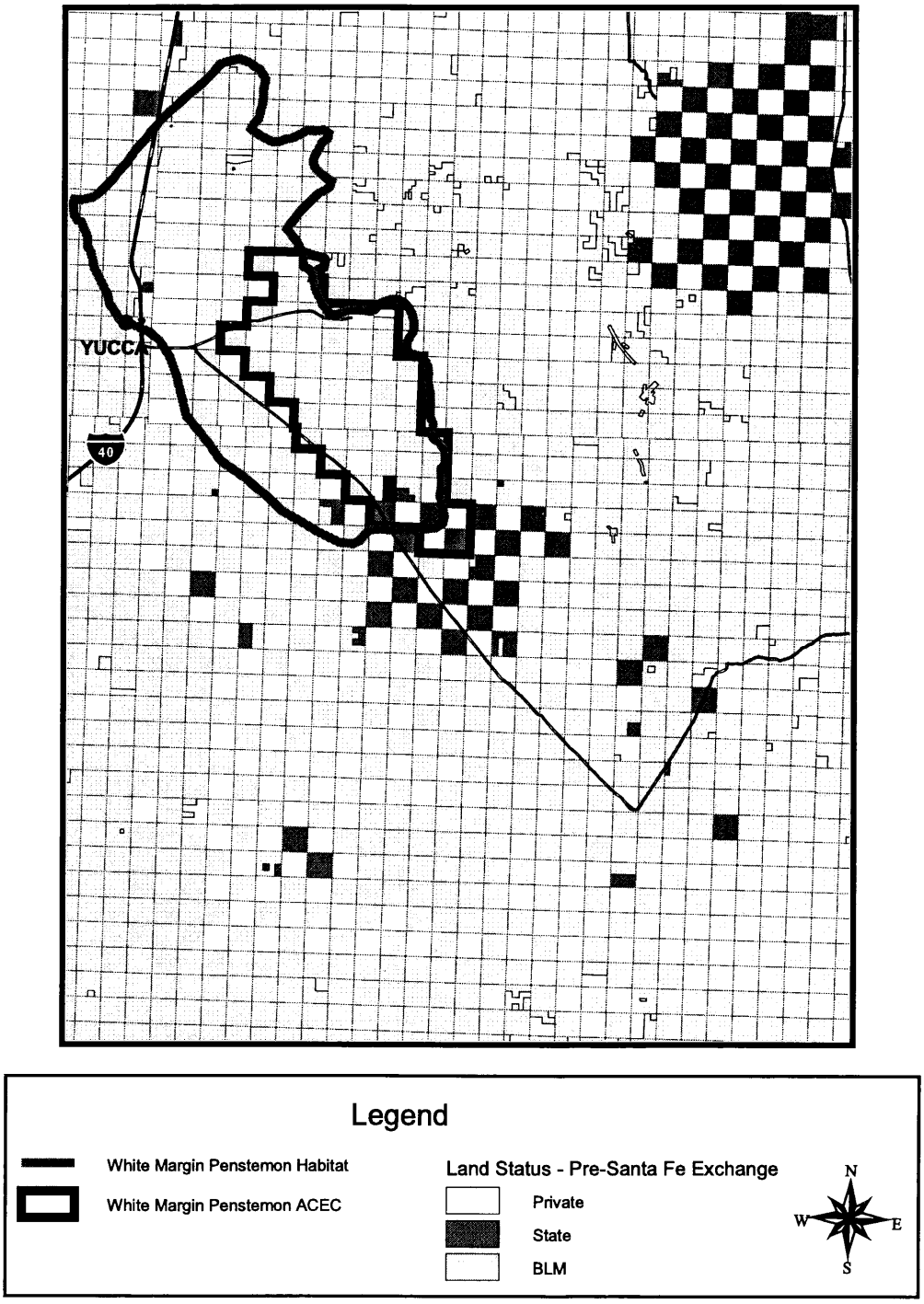


Figure 2. Checkerboard land status pattern in Hualapai Mountains–Dutch Flat area.

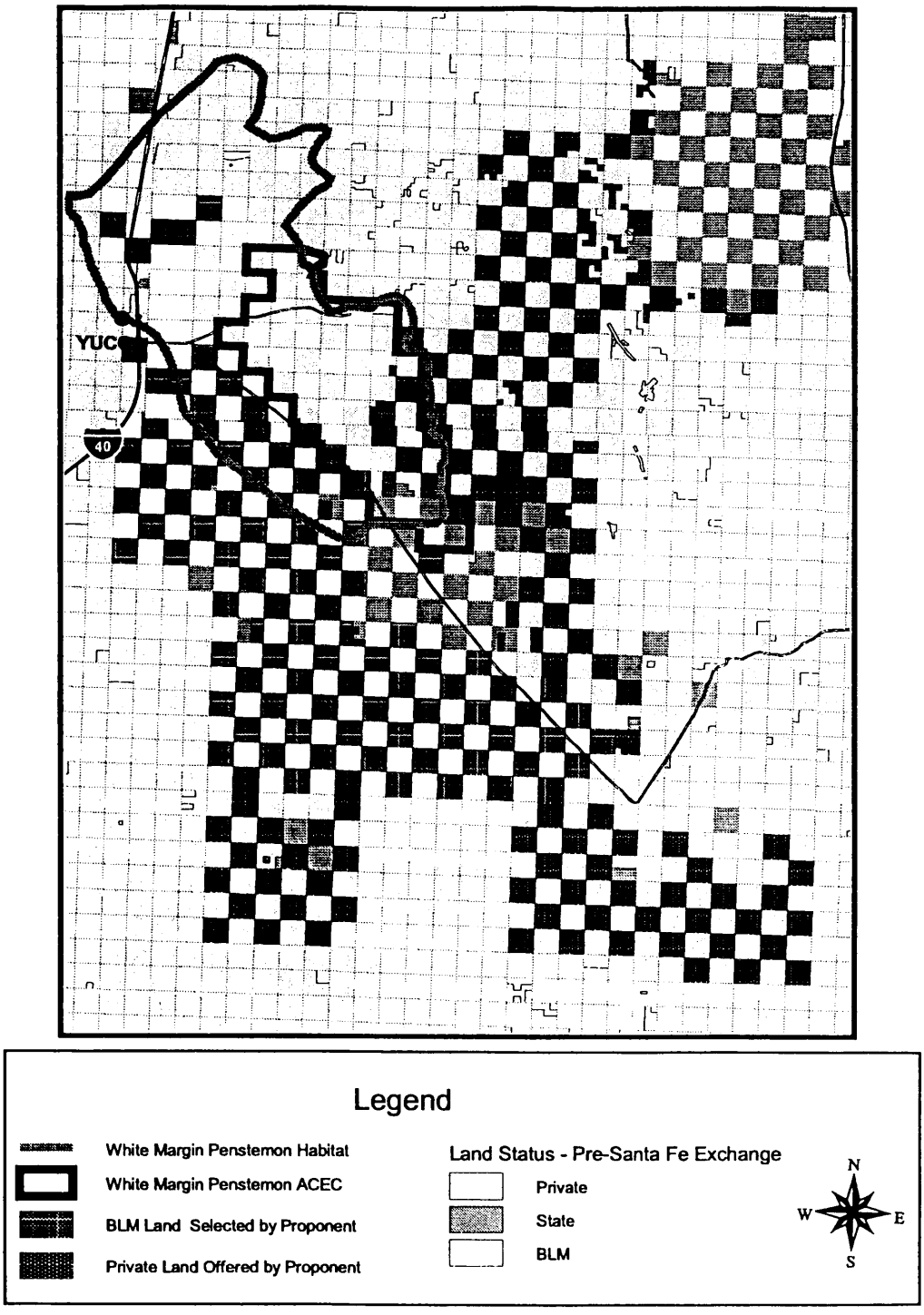


Figure 3. Selected and offered lands of the Hualapai Mountains Land Exchange.



Figure 4. *Penstemon albomarginatus* Jones.

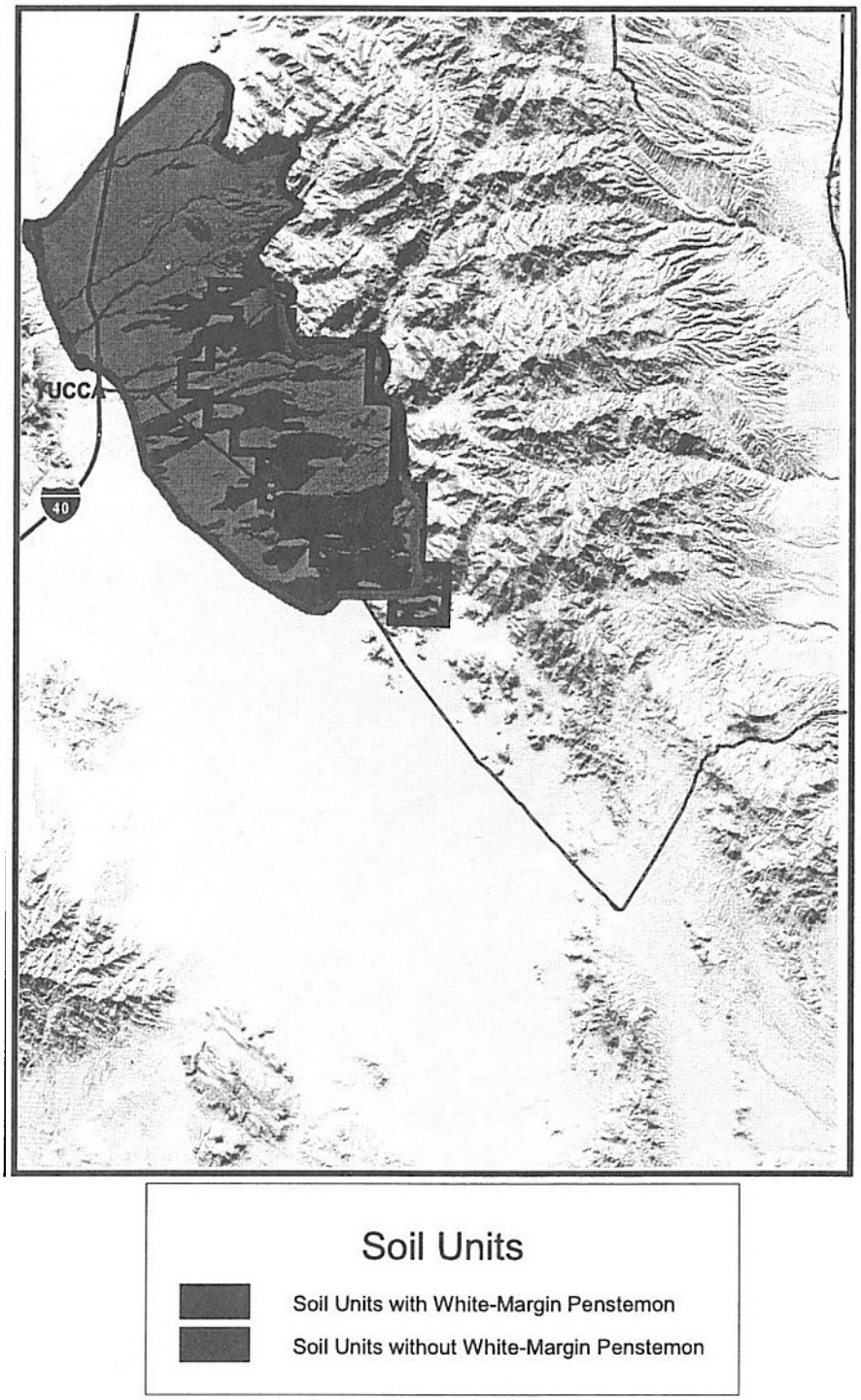


Figure 5. Soil units with white-margined penstemon present.

Penstemon albomarginatus is a BLM sensitive species; it was a Category 2 candidate species under the old U.S. Fish and Wildlife Service ranking. The Kingman Resource Area Resource Management Plan (BLM 1995) designated Dutch Flat as the white-margined penstemon ACEC to protect the best-quality habitat of the species. However, the ACEC contained a checkerboard land ownership pattern of roughly equal amounts of public land, 17,489 acres, and private land, 16,038 acres, making management of the white-margined penstemon difficult. The management prescriptions for the ACEC in the Kingman Resource Area Resource Management Plan (BLM 1995) called for acquistion of the private land within the ACEC.

Methods

The parameters of the effects (and their analysis) of the Hualapai Mountains Land Exchange on the white-margined penstemon were largely set by the mutually agreed upon locations of the "selected" and "offered" lands proposed in the exchange. Selected lands are the federal public lands that a private entity, in this case Ironhorse Investors (the proponent), wants to acquire, and offered lands are the private lands that the proponent is offering to the BLM in exchange for the selected public lands. The approximate boundary of the white-margined penstemon in the Dutch Flat–Yucca area had been mapped previously by the BLM. Sections adjacent to the previously mapped white-margined boundary were inventoried to further confirm the accuracy of that boundary. A qualitative method of inventory was chosen over a quantitative method because of the large amount of acreage involved. In this way every selected and offered section of the Hualapai Mountains Land Exchange within this area was visually inspected on the ground by BLM personnel trained in identification of the white-margined penstemon, except for the sections eliminated with the stratification system described below.

The sections were ranked qualitatively into high, medium, or low quality habitat based on the occurrence of the white-margined penstemon as abundant, infrequent, or rare respectively (Oosting 1956). Soil differences exist within the overall habitat boundary and not all of this area is suitable soil habitat. Abundance of white-margined penstemon within a given section was a function of the amount of appropriate soil type present. The soils of the exchange area had been previously mapped into soil mapping units as part of the Mohave County soil survey (Natural Resources Conservation Service 1996). Based on field observations, the Kingman Field Office BLM soil scientist, Paul Hobbs, and the author defined which soils were habitat, soil mapping units 50, 54, 54B, and 150B, and which soils were not habitat, soil mapping units 52, 73, and 76. These soil mapping units are also given ecological site names in the NRCS report, which are used here. The primary ecological site supporting the white-margined penstemon is the sandy loam upland in the 6–12 precipitation zone; fewer plants grow on clay loam uplands (the surface texture of this unit is still a sandy loam) and along sandy (wash) bottoms. These sandy loam upland units are interspersed with coarse sandy loam (limy) and limy uplands ecological sites that do not support the white-margined penstemon. These ecological sites were sorted into two groups, habitat and non-habitat. This stratification of habitat and non-habitat by ecological sites reduced the amount of on-the-ground inventory that needed to be done. Selected and offered sections containing only non-habitat ecological sites were not inventoried. Also, sections on the west side of the exchange containing sandy loam uplands, but in the 3–6 precipitation zone, were not inventoried after initial surveys showed them to be too dry for white-margin penstemon habitat.

After the on-the-ground inventory was completed, the habitat acreage totals for the selected and offered land were modified by two factors, habitat quality and manageability. First, the habitat acreage totals were multiplied by numerical habitat importance values of 1.0 for high-quality habitat, 0.75 for medium-quality habitat, and 0.25 for low-quality habitat. The low-quality habitat was given a much lower rating because the plants on this habitat were very widely scattered. Second, these modified acreage totals were further multiplied by a land ownership pattern ranking factor. Using as a manageability criteria the concept that blocked-up units of public and private ownership were more or less favorable respectively for the long-term survivability of the white-margined penstemon, the different ownership patterns were given correspondingly reduced manageability ratings of 1.0 for blocked public land ownership pattern (no reduction) and 0.2 for blocked private ownership pattern after the land exchange (the preferred alternative); intermediate reduced ratings used for the existing situation (no action alternative) were 0.6 for checkerboard public ownership pattern and 0.4 for checkerboard private ownership pattern. Multiplying the modified habi-

tat value acreage figures by the reduced manageability ratings gave the final habitat unit figures that could be used to compare the effects of the land exchange on the white-margined penstemon to the existing land ownership pattern situation. The totals were also compared separately between habitat quality units and within the ACEC.

Results

The analysis of the total habitat units for the land exchange and the existing situation produced mixed results (Table 1). The actual acreage total of the selected lands (public lands becoming private land) is much higher than that of the offered lands (private lands becoming public lands), 3,575 acres compared to 1,040 acres, but after the acreage figures are multiplied by the habitat value ratings and management value ratings, there were only 14 percent more habitat units with the existing checkerboard ownership pattern, 1,683 habitat units, than with the blocked ownership pattern after the land exchange, 1,449 habitat units. In comparing actual differences between habitat quality ratings, the offered lands contained 980 acres of high-quality habitat and 60 acres of medium-quality habitat, and the selected lands contained 480 acres of high-quality habitat, 1,735 acres of medium-quality habitat, and 1,360 acres of low-quality habitat. Because the amount of high-quality habitat gained in the offered lands is nearly twice as much as that lost to the selected lands, 980 acres compared to 480 acres, the public land habitat gained in quality of acreage versus quantity of acreage.

Within the ACEC approximately 4,000 acres of offered private land (all or portions of eight sections) became public land after the land exchange and approximately 1,800 acres of selected public land (all of three sections on the western edge of the ACEC) became private land (exact acreages depend on cadastral surveys). The entire ACEC contains all or portions of 57 sections, but not all of the acquired public lands contained habitat for the white-margined penstemon and not all of the selected public lands that became private lands after the land exchange contained habitat either. There were 980 acres of high-quality habitat and 60 acres of medium-quality habitat in the acquired public land (all of the offered lands with white-margin penstemon habitat were within the ACEC), and there were 815 acres of medium-quality habitat and 320 acres of low-quality habitat in the selected public lands that became private. Thus, the ACEC gained greatly in the overall amount of public acreage within the ACEC as well as the amount of high-quality habitat in public ownership (T16-1/2 N, R16 W, S19, 29, and 33), although slightly more acreage of white-margined penstemon habitat within the ACEC became private land. Nearly 20 percent of the sections within the ACEC were affected by the land exchange. Sixteen sections of public land in the southeastern part of the ACEC are now contiguous by at least two sides with another section of public land, forming a large core area of manageable public land. Before the land exchange, only one section of public land within the ACEC was contiguous on two sides with more than one other public section, and in four instances, two public sections shared one mutual side.

Discussion

The proponent owned the checkerboard private lands in the southern half of the ACEC and their plans were to develop this land by selling it in 40 acre tracts. Individual land owners could then further subdivide their land into smaller tracts for sale. Therefore, the Dutch Flat area and the habitat of the white-margined penstemon would be subject to rural development whether

Table 1. White-margined penstemon habitat units for the proposed action (preferred) alternative and the no-action alternative based on habitat value and management value ratings.

Habitat value	High (1.00)	Medium (0.75)	Low (0.25)	Management value	Total
Public acres (blocked)	980	60	0	1.00	424
Private acres (blocked)	480	1735	1360	0.20	1025
Total habitat units					1449
Public acres (checkerboard)	480	1735	1360	0.60	1273
Private acres (checkerboard)	980	60	0	0.40	410
Total habitat units					1683

the Hualapai Mountains Land Exchange took place or not. With the large increase in population of the Sun Belt, impacts to the white-margined penstemon and its habitat would happen anyway. Without the land exchange, the inevitable impacts of the rural development would be dispersed over a wider area of the plant's habitat; with the land exchange a large core area of high-quality habitat would be consolidated as public land within the southeastern part of the ACEC (Figure 6). Based on landscape ecology, this area is the largest continuous piece of high-quality habitat. It contains a broad fan terrace below a broad mountain face. Farther north the fan terrace below the mountains is dissected by three large washes, Bar I-L, Happy Jack, and Mackenzie Washes, coming out of the Hualapai Mountains, that have eroded the fan terrace and left only smaller strips of uneroded fan terrace for white-margined penstemon habitat. The BLM thought that the survivability of the white-margined penstemon would be improved by the increased manageability of the solid block of public land habitat for conservation of the species by easing the implementation of proactive measures such as fencing and off-road vehicle restrictions. With the existing checkerboard land ownership pattern, BLM management would be primarily reactive to actions derived from the interspersed private land.

The environmental tradeoff from the land exchange is the conversion of the western edge of the white-margin penstemon habitat in Dutch Flat to private land. Basically, the Alamo Road which runs down the center of Dutch Flat has become the dividing line between the consolidated public land to the east and the consolidated private land to the west. However, the elevation in Dutch Flat descends from the east to the west down the fan terrace from the Hualapai Mountains, and the western edge of the white-margined habitat that became private land contains the lower elevation, lower precipitation, lower quality habitat. Even though a much larger amount of habitat acreage became private (3,575 acres) than public (1,040 acres), most of this newly private acreage is the lower quality habitat. With the conversion factors applied, the comparative habitat unit values are similar between the preferred alternative (1,025 federal, 424 private, and 1,449 total) and the no-action alternative (1,273 federal, 410 private, and 1,683 total; Table 1). In addition, even with the inevitable rural development taking place in Dutch Flat, much of the private land will still remain in a natural condition. This situation already exists at the north edge of Dutch Flat near Cactus Mountain, where the author has observed white-margined penstemon plants growing on private land in between the widely scattered dwellings and associated paraphernalia.

The generosity of the proponent allowed the BLM to acquire an additional 320 acres of high-quality habitat as a donation. Although this half section was not part of the offered lands, previous BLM surveys for the white-margined penstemon had found it to be high-quality habitat. The author approached the proponent about the possibility of a land donation and they were agreeable to the idea. Because of its location, this half section, T16-1/2 N, R16 W, S31 E1/2, was very important in the conservation of the white-margined penstemon. It borders the core area of high-quality habitat within the ACEC, is contiguous on two sides with other public land sections, and extends the core area further westward (Figure 6).

Another benefit of this analysis of the effects of the Hualapai Mountains Land Exchange on the white-margined penstemon is with its use as a baseline for the analysis of cumulative effects from future land exchanges. The BLM is currently processing the Cane Springs Land Exchange involving primarily another area of checkerboard lands east of the Hualapai Mountains. However, one of the selected sections is in Dutch Flat, T17 N, R17 W, Section 4 at the north end of Dutch Flat near Cactus Mountain (Figure 6). There are no offered sections of white-margined penstemon habitat in the Cane Springs Land Exchange. Using the same habitat quality and management criteria, this section was found to have 480 acres of low-quality habitat, which corresponds to 120 habitat quality units. Applying the ranking factors for manageability criteria, this section would have 72 habitat units under the existing situation of checkerboard federal ownership and 24 habitat units under the proposed land exchange action of blocked private, a difference of 48 more habitat units under the existing situation. The cumulative effect combined with the Hualapai Mountains Land Exchange will then be 1,473 habitat units with both exchanges and 1,755 habitat units under the existing situations, for an additional 2 percent loss in habitat units (but low-quality habitat) for the white-margined penstemon with the Cane Springs Land Exchange.

In summary, the white-margined penstemon would fare better if Dutch Flat was still the "perfect garden" that Marcus Jones saw in 1884. With the inevitable rural development presently

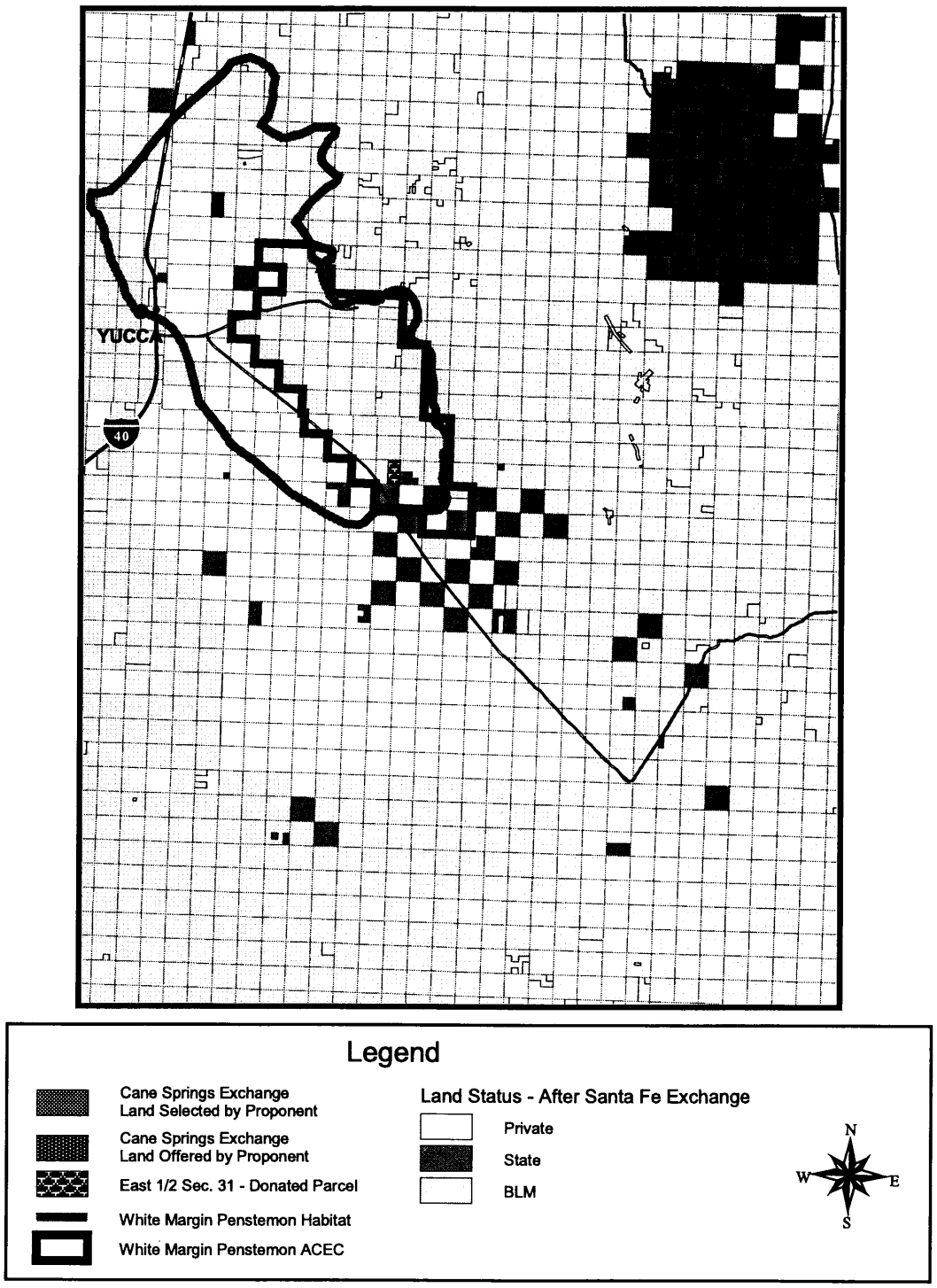


Figure 6. Blocked land ownership pattern after the Hualapai Mountains Land Exchange.

occurring, the land use situation in the Dutch Flat area was already causing impacts to the white-margined penstemon. The Hualapai Mountains Land Exchange provided the BLM with its best tool for implementing one of the white-margined penstemon ACEC management prescriptions of acquiring the private land within the ACEC for proactive management. Even though a large amount of low-quality white-margined penstemon habitat was lost in the exchange, the BLM was able to consolidate a core area of high-quality habitat to support the future survivability of the species. White-margined penstemon will also be able to continue to exist amongst the rural development scenario on the private land habitat.

Acknowledgments

Paul Hobbs from the BLM Kingman assisted in the field work with the white-margined penstemon inventory and soil mapping. Pam MacKay from Victor Valley Community College, Victorville, CA, showed the author the California locations of the plant; Buddy Smith from Western Ecological Services, Inc., Millville, UT, and Gayle Marrs-Smith from the BLM Las Vegas Field Office showed the author the plant in Nevada and provided slides of Nevada habitat and plants. The Hualapai Mountains Land Exchange Team, Bob Posey from the Arizona Game and Fish Department and Bob Hall and Becky Peck from the BLM Kingman provided helpful comments on the data analysis. Chris Horyza, Judith McDonald, and Bill Harrison from the BLM Phoenix prepared the figures and tables in both print and slide format with ArcView, Adobe Illustrator, and Power Point programs.

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Determining Habitat Potential and Surveying for Nine Rare Plant Species in South-Central Utah

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Abstract: In south-central Utah, lands within and adjacent to Capitol Reef National Park contain populations of nine rare plant species. In an effort to enhance the combined knowledge about these species, the Bureau of Land Management, the USDA Forest Service, and the National Park Service signed an Interagency Agreement and hired an interagency biologist and field crew to conduct field surveys for each of these species. Eight of these species are federally listed and one is a candidate for listing. Survey efforts, beginning in 2000 and continuing through 2002, will satisfy the inventory requirements of the recovery plans and conservation agreement for the nine species. The geology of this area has created conditions that have allowed unique plant species to evolve. The nine target species tend to be restricted to specific geologic formations. Prior to the field season, habitat modeling using geologic formations, elevation, slope, aspect, and plant community associates will be done to predict potential habitat for each species. This information is overlain with known populations, and areas are selected for field surveys. This inventory information will be used to develop monitoring and habitat management protocols. Monitoring will also be an interagency effort with locations throughout the range and in places appropriate to answer the specific questions for each species.

In 2000, Capitol Reef National Park (CARE) received funding for a 3-year (through 2002) rare plant species inventory through the National Park Service (NPS). This funding enables CARE staff and an interagency biologist to collect critical data on several of the rarest plants occurring in and around the park.

The Bureau of Land Management (BLM), USDA Forest Service, Dixie National Forest (DNF), Fishlake National Forest (FNF), and CARE share management responsibilities for many of the same threatened, endangered and sensitive plant species (TE & S). To enable each of them to better manage their shared TE & S species, these agencies decided to create an interagency botany position and hire an employee to survey and monitor for these species throughout their ranges, regardless of agency boundaries. A BLM employee was hired for this position and was stationed at CARE to act as project leader. Through the interagency agreement, the agencies are able to pool funding in order to extend surveys onto federal lands adjacent to CARE. This has expanded the scope of the NPS project to include FNF, DNF, and BLM land around CARE.

Eight federally listed species and one candidate for federal listing were selected as the primary focus for this study: *Cycladenia humilis var. jonesii* (Jones cycladenia), *Erigeron maguirei* (Maguire's daisy), *Pediocactus despainii* (San Rafael cactus), *Pediocactus winkleri* (Winklers cactus), *Sclerocactus wrightiae* (Wright's fishhook cactus), *Spiranthes diluvialis* (Ute ladies-tresses), *Townsendia aprica* (Last Chance townsendia), *Schoencrambe barnebyi* (Barneby's reed-mustard), and *Gilia caespitosa* (Rabbit Valley gilia). An additional 18 sensitive species occur within the study area and are recorded when found during surveys. The Utah State Natural Heritage Division ranks these 18 species as global 1 or 2/state 1 or 2. This ranking is defined as both critically endangered throughout its range, with five or fewer occurrences known; and endangered throughout its range, imperiled globally or statewide because of rarity with only 6–20 known occurrences.

CARE is located in south-central Utah, in the Colorado Plateau region, 72 km (45 mi) west of Hanksville on U.S. Highway 24. It was established to protect the longest exposed monocline in North America and is approximately 97,000 ha (241,903 acres) in size. This wrinkle in the earth's crust runs about 160 km (100 mi) north to south and is named the Waterpocket Fold. Unique geological conditions in combination with the arid climate within the fold have created microhabitats that support more than 40 rare and endemic plant species. BLM and Forest Service lands border CARE, so these agencies also contain unique geology and the corresponding endemic plant species.

The park is primarily a backcountry park that receives about three-quarters of a million visitors each year. Many of these visitors hike the trails and backcountry, and many of these areas have rare plant populations within or adjacent to them. Therefore, information on the whereabouts of rare plants in these high-use areas and whether they are being affected by visitation is essential for park management. Three of the listed plant species occur in the northern portion of the park and on adjacent BLM lands, and are in active cattle grazing allotments. For these three species it is also essential for park and BLM management to know the whereabouts of these species and whether cattle grazing may affect them.

Species Backgrounds

Cycladenia humilis var. *jonesii* Welsh & Atwood (Apocynaceae) was listed as a federally threatened species by the U.S. Fish and Wildlife Service (FWS) on May 5, 1986. It is a herbaceous perennial 11–36 cm tall. The oval leaves are thick and fleshy, and are covered with a whitish waxy coating. Flowers are rose pink in color and have two forms depending on the population site; they may be large and broadly opening or smaller and narrowly opening. Flowering occurs from early May to early June. In flower this species cannot be confused with any other species; however, when only leaves are present, it is easily mistaken for *Asclepias cryptoceras* or *Astragalus asclepiadoides* (Heil 1987).

Erigeron maguirei Cronq. (Asteraceae) was listed by the FWS as endangered in 1985. This status was later revised to threatened on June 19, 1996. Maguire's daisy is a herbaceous perennial with sprawling to slightly erect stems. Basal leaves are 2–5 cm long and 3–8 mm wide and oblanceolate to spatulate with a rounded tip. Flowers are white with 12–20 rays. Flowering occurs from early June through late July.

Gilia caespitosa Gray (Polemoniaceae) is currently a candidate for federal listing under the FWS Endangered Species Act (ESA). The BLM, USDA Forest Service, FWS, and NPS wrote a conservation agreement and strategy for Rabbit Valley gilia (USDA Forest Service et al. 1996) that addresses protection measures designed to achieve long-term conservation of the species so that listing under the ESA would not be warranted. Rabbit Valley gilia is a long-lived perennial that grows in a cushion-like mound. Leaves and stems are covered with glandular hairs that become covered with grains of sand. Flowering stems are 3–8.5 cm tall. The bright red flowers are usually solitary but there may be a few per cyme. Flowering occurs from May to July.

Pediocactus winkleri Heil and *Pediocactus despainii* Welsh & Goodrich (Cactaceae) are two very similar endemic cacti that occur only in Wayne and Emery counties in Utah. *Pediocactus despainii* Welsh & Goodrich was listed by the FWS as an endangered species on September 16, 1987 and *Pediocactus winkleri* Heil was listed as threatened on August 19, 1998. Both species are small, usually solitary cacti ranging from 3.8–6.8 cm tall and 2.7–9.5 cm wide. Tubercles lack central spines; radial spines are 1.5–4 mm long for *P. despainii* and 1.7–6 mm long for *P. winkleri*. Areoles are persistently white woolly, and elliptic for *P. winkleri* and wool is yellowish and typically caducous on *P. despainii*. Flowers are peach to yellowish pink. Slightly longer radial spines and caducous aerole wool on *P. despainii* are the only distinguishing characters between these two species. They bloom between March and May.

These two closely related species of *Pediocactus* share the unusual habit of shrinking into the ground after blooming every year and remaining underground until the following spring. When temperatures rise in mid February or early March, and given adequate rainfall, the cacti emerge from just below the surface to flower. At this time they may reach about 2.5 cm in height. After flowering and before the summer heat (mid May to June), the cacti set seed and shrink back under the surface of the ground for another year. Field observations have noted that the plants shrink into the ground, forming a small depression that then fills in with windblown debris, making the cacti invisible until they emerge the following spring.

Schoencrambe barnebyi Welsh & Atwood was listed as endangered by the FWS on January 14, 1992. Barneby's reed-mustard is a herbaceous perennial. Flower racemes have 2–28 flowers. Sepals are green to violet, with papery margins. Flowers are white to lavender with conspicuous purplish veins. Siliques are ascending to spreading. Flowering occurs from late April to mid June.

Sclerocactus wrightiae L. Benson was listed as endangered by the FWS on October 11, 1979. Wright's fishhook cactus is an obovoid to short-cyclindric shaped cacti. It typically grows as a single plant, but if damaged it will form clumps of stems. Tubercles are well developed with the aeroles circular to elliptic. Juveniles have glabrous spines and 1–4 central spines; the lower one is hooked and usually 1–2 cm long. Adults have only one central hooked spine. There are 8–11 radial

spines spreading out from the aerole. Flowers are yellowish to white or pinkish. Short spine length, early flowering time, and small flower size help distinguish this species. The critical differentiating feature between *S. wrightiae* and *S. whipplei* (a closely related common species) is the number of leaf scales on the fruits. *S. wrightiae* has zero to two scales, and *S. whipplei* has five or more. Flowering occurs between March and May.

Spiranthes diluvialis Sheviak (*Spiranthes romanzoffiana* var. *diluvialis* (Sheviak) Welsh) was listed as threatened by the FWS on January 17, 1992. Ute ladies-tresses is an erect, slender plant ranging from 0.8 to 6 cm tall. Cauline leaves are 2–6 in number and greatly reduced above. Floral bracts are ovate to lance-attenuate and flowers are creamy white. Flowering occurs from June to September, depending on elevation. Ute ladies-tresses is similar to *S. romanzoffiana* var. *romanzoffiana*, but it differs in having short flowers that are broad at the base and strongly ascending.

Townsendia aprica Welsh & Reveal was listed as threatened by the FWS on August 21, 1985. Last Chance townsendia is a pulvinate-caespitose acaulescent perennial herb. Leaves are spatulate to oblanceolate, and strigose. Flower heads are sessile, usually submerged in the leaves. There are 13–21 yellow rays, 4–7 mm long, that are purplish dorsally. Flowering occurs in April and May.

Methods

The primary purposes of this project are to conduct intensive surveys for the target species on potential habitat within and adjacent to CARE; and to determine the potential for impact by visitor, recreational, or livestock use if possible.

Prior to beginning field surveys available information and location data on the nine target species was compiled. The study began during the 2000 field season when the interagency biologist mapped as many known locations of the target species as possible using a global positioning system (GPS). All known location data were then entered into the geographic information system (GIS) and overlaid with geologic formations, slope, aspect, and elevation to create a profile of potential habitat by species. In addition to accurately depicting known and potential habitats, this refined the range of the target species and helped resource managers plan how many people would be needed to accomplish the tasks. A field guide booklet containing detailed information and photographs or line drawings for the nine target species and 18 sensitive species was written to assist the staff in learning each of the species.

After completing this initial work, field crews conducted surveys in potential habitat for the target species. By surveying from April through July when the majority of plants were in full bloom, crews ensured proper plant identification and increased survey accuracy. Surveys began in the early spring at lower elevations and as the season progressed the crew moved to higher elevations, thus ensuring proper search times for each species. Each area was surveyed both by walking wandering transects through all accessible areas and by using binoculars to search cliffs. The crews hiked established trails and other off-trail routes in CARE during the appropriate blooming time for each species. If a trail or route passed through potential habitat for two or more species and those species bloomed at different times, then those trails and routes were hiked multiple times to ensure that surveys were as thorough as possible for each species. For future reference, crews noted on maps all areas surveyed. Areas selected outside CARE for inventories this year were surveyed when the target species were expected to be in full bloom.

For each new occurrence of a species, crew members completed a modified version of the Utah Natural Heritage Division Site Visit Account Survey Form, took photographs, and mapped its location on 7.5' quadrangle maps. Wherever possible, a GPS was used to map the precise location of each new occurrence. All new localities will be entered into each agency's GIS along with a summary of data about the locality. This ensures long-term retrieval capabilities for future resource managers.

Results

Surveys were conducted by the interagency biologist employed by the BLM, a seasonal crew leader, and three seasonal crew members hired by CARE. If additional people were needed to survey specific areas, additional CARE Resources Division and Forest Service staff assisted. Surveys began on April 10 and continued through August 4, 2000. The field crew surveyed approximately 9,760 acres, and recorded 109 new site locations for 11 TE &S species. New locations for four of the primary targeted species were found and recorded. The remaining seven species recorded are sensitive species.

Calendar year 2000 was a very difficult year to survey for plants because it was extremely dry, following a dry year in 1999. Many of the plants

targeted for surveys either didn't bloom or if they did bloom it was for a short time period. To compensate for this, the crew moved to higher elevations sooner than originally planned and adjusted the list of species to look for the species that still came up and bloomed.

A preliminary review of the data showed that aspect and slope were not critical to selecting potential habitat areas to survey for most species. However, they are essential for selecting potential habitat for *Schoencrambe barnebyi*, which occurs only on steep, north-facing slopes in the Moenkopi Formation. Elevation or geologic formations were valuable in selecting survey areas for the target species. Tables 1 and 2 show the numbers of individuals (by species) by elevation and geology.

Erigeron maguirei most commonly occurs between 6,000 and 7,000 feet in elevation and only on Navajo Sandstone (see Table 2). *Gilia caespitosa* is another Navajo Sandstone endemic, with only one large population on Kayenta Sandstone. It is most numerous between 7,000 and 8,000 feet. The two species of *Pediocactus* were combined because they are so similar and occur in overlapping ranges. They occur primarily in the Morrison Formation between 5,500 and 6,500 feet. Elevation and geological data compiled on *Sclerocactus wrightiae* and *Townsendia aprica* show that they are more uniformly scattered over a wide range of formations, *Sclerocactus* below 7,500 feet and *Townsendia* all above 6,000 feet in elevation. As mentioned above, *Schoencrambe barnebyi* is restricted to the Moenkopi Formation, primarily between 5,500 and 6,500 feet. Geologic formation data were not useful for *Spiranthes diluvialis* because it is restricted to riparian or wetland areas, regardless of formation. It was not found this year at any of the survey locations, but it was a very dry year with low water tables and this orchid is known to remain dormant for years. Additional surveys for it will be conducted next year. No data were gathered on *Cycladenia humilis* var. *jonesii* because its habitat will be surveyed in the next 2 years.

The habitat modeling information was very useful in selecting potential habitat areas to survey. Approximately 90 percent of areas selected for surveys in 2000 using the above information on elevation range and geologic formation contained

Table 1. Approximate number of individuals for each species by elevation (in feet).

Elevation	Erigeron	Gilia	Pedio-Cactus	Sclero-Cactus	Schoencrambe	Townsendia
4000-4500	0	0	0	110	0	0
4500-5000	0	0	160	450	0	0
5000-5500	100	25	350	440	30	0
5500-6000	400	45	1560	40	1200	0
6000-6500	1580	180	1650	75	710	140
6500-7000	3400	55	110	0	150	340
7000-7500	50	5470	0	250	0	260
7500-8000	170	3150	0	0	0	75
8000-8500	250	0	0	0	0	300

Table 2. Approximate number of individuals for each species by geologic formation.

Elevation	Erigeron	Gilia	Pedio-Cactus	Sclero-Cactus	Schoencrambe	Townsendia
Moenkopi			250		2090	75
Kayenta		3000				
Navajo	6900	5250				
Carmel			35	40		1270
Entrada			200	30		200
Curtis				380		20
Summerville			60	90		80
Morrison			2340	195		850
Dakota			420	125		
Mancos				135		280
Alluvium				110		145

sites with one or more of the target species. Associate plant species lists will be analyzed in conjunction with elevation and geologic formations to determine if this three-way combination increases accuracy in predicting potential habitat.

Findings by Species

Cycladenia humilis var. *jonesii* is restricted to gypsiferous clay or saline soils in the Summerville, Cutler, and Chinle formations. It is known from only a few scattered populations in south-central Utah and one near Pipe Springs, Arizona. Areas where Jones cycladenia persists tend to be sparsely vegetated to barren slopes between 1,340 and 2,000 m (4,400–6,600 ft) in elevation. This is a strongly rhizomatous species, so counting the number of above-ground stems doesn't give an accurate picture of individuals. The FWS (1985a) has recognized this feature and states that there are approximately 3,000 known "above-ground plants." This probably far outnumbers the actual number of individual plants. No work was done on this species in 2000, but surveys are planned for Jones cycladenia in 2001 and 2002.

Erigeron maguirei is restricted to decaying talus slopes or in cracks and crevices in Navajo Sandstone within Emery and Wayne counties, Utah. Surveys were focused in this formation in pinyon-juniper, ponderosa pine, and desert scrub communities on CARE, DNF and on FNF land. Prior to these surveys it was known to occur between 1,615 and 2,160 m (5,400–7,100 ft) in elevation (Van Buren and Harper 2000). As a result of this project, the elevation range has been extended to 2,650 m (8,680 ft) onto the FNF. These are the first recorded locations of Maguire's daisy on there. The recovery plan (U.S. Fish and Wildlife Service 1995a) for Maguire's daisy estimates 5,000 individual plants known from 33 locations, representing seven separate populations. To date, the field crew has located 17 new sites on CARE and FNF land containing approximately 4,400 individual plants.

Gilia caespitosa occurs primarily on the Navajo Formation although one large population has been found in the Kayenta Formation. It grows in cracks and crevices in sandstone cliffs or on talus slopes below these cliffs in pinyon-juniper woodland or mountain mahogany scrub between 1,740 and 2,740 m (5,700–9,000 ft). Rabbit Valley gilia occurs only in Wayne County, Utah on FNF, DNF, BLM, and CARE land. Prior to this survey there were 34 known locations containing approximately 8,200 individual plants. The largest known site is on the FNF in the Kayenta Formation, containing about 3,000 individuals. Surveys this year located two new sites in CARE containing approximately 50 individuals.

Pediocactus winkleri and *Pediocactus despainii* occur in Wayne and Emery counties in south-central Utah. Approximately two-thirds of the known populations of both species are located on lands administered by the BLM, and the rest occur within CARE or on state lands. Both species occur in desert scrub or open pinyon-juniper woodland communities, between 1,370 and 2,088 m (4,500 ft–6,850 ft). The BLM and CARE conducted an intensive 2-year study on these two species in 1998 and 1999 (Clark 1998, 1999). This project will focus on specific sites not completed during the earlier study; however, no sites were recorded on these species this year.

Sclerocactus wrightiae is found in Emery and Wayne counties, Utah in desert scrub or open pinyon-juniper woodland communities, between 1,460 and 1,860 m (4,800–6,100 ft) in elevation. This species occurs on numerous geologic formations and has a much wider distribution than other target species. The recovery plan (U.S. Fish and Wildlife Service 1985b) for Wright's fishhook cactus states that there are 13 locations in Emery and Wayne counties in Utah, without an estimate of the total number of individuals. One new site of *Sclerocactus wrightiae* was found in CARE.

Spiranthes diluvialis is found in moist soils along streambeds, in bogs, and in open seep areas in cottonwood, tamarisk, willow, and pinyon-juniper communities where vegetation is fairly open. Its distribution is much wider than any of the other targeted species, as it occurs in Utah, Colorado, Wyoming, Montana, Washington, and Nebraska. Ute ladies-tresses has a wide elevation range, from 1,340 to 2,130 m (4,400–7,000 ft). Extensive surveys were conducted this year on BLM, DNF, and CARE land, but no plants were found.

Schoencrambe barnebyi is restricted to cool, north-facing, steep talus slopes in the Moenkopi Formation. It is associated with low desert scrub and pinyon-juniper communities between 1,705 and 1985 m (5,590–6,510 ft). The recovery plan for Barneby reed-mustard (U.S. Fish and Wildlife Service 1994) estimates 2,000 total plants known from two locations, one in CARE and one on BLM land in the San Rafael Swell. No surveys were done for this species in 2000; however, select BLM areas will be targeted for surveys in 2001 and 2002.

Townsendia aprica occurs on a wider range of geologic formations than most of the other targeted species. It is found on fine-textured shale

soils in pinyon-juniper woodland between 1,860 and 2,440 m (6,100–8,000 ft). Its range consists of a long narrow band stretching north-south through Wayne, Sevier, and Emery counties in Utah. There are a few scattered locations east of this main cluster. The FWS (1993) stated in the recovery plan that there were 15 populations containing about 6,000 plants. Most populations occur on BLM, CARE, and FNF land. Surveys this year resulted in the discovery of 11 new Last Chance townsendia sites containing a total of approximately 650 individuals. Eight of these new locations are in CARE, one is on BLM land, one is on Utah state land, and one is on DNF land. The site recorded on the DNF is the first known record of this species there.

Discussion

Work accomplished during this field season resulted in the discovery and documentation of several new localities for most of the target species. Some of the target species were recorded for the first time on CARE and DNF land, confirming that more work needs to be done before these species' ranges and niches are completely understood. Individual species reports summarizing findings this year will be submitted to each agency (if the species is located on that agency's land), the Utah Natural Heritage Division, and the FWS. Preliminary habitat data modeling was extremely useful in selecting survey areas for seven of the nine target species. As more data are added to these models, the habitat niches and ranges of each of these species can be further refined.

The creation of an interagency crew for this project has proven beneficial to all participating agencies. There are numerous TE & S plant species whose distributions overlap agency jurisdictions, so it is to the mutual scientific and economic benefit of the agencies to manage these TE & S plant species cooperatively on an ecosystem basis. Field work is conducted throughout the range of each target species regardless of agency boundaries so a more accurate picture of the species is gained. Agencies can pool scarce funding for TE & S plant species, so each agency gets more comprehensive information about each species, as well as increased services for each individual agency dollar spent.

Information gathered during this 3-year study enables the participating agencies to meet the legal requirements of the Endangered Species Act, comply with NPS, BLM, and USFS management policies, and address Government Performance and Results Act goals. Knowledge gained about these species and their specific habitat requirements will enable federal officials to ensure that these plants are protected and will assist in predicting which areas may contain additional occurrences. Results from this study will also help in determining which species should have monitoring plots to determine impacts.

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Results of a Conservation Agreement and Strategy for Rabbit Valley Gilia (*Gilia caespitosa*)

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Abstract: *Gilia caespitosa* Gray (Rabbit Valley gilia) is a rare species restricted to scattered occurrences from the northern Waterpocket Fold to Thousand Lakes Mountain and Rabbit Valley in Wayne County, Utah. This species is a very narrow endemic, known only from unstable and faulting soils of detrital Navajo Sandstone. Species occurrences are often found with limited numbers of plants and minimal potential for increasing. Information available regarding historic abundance, ecology, biology, and demographics is limited. These factors contribute to the need to develop a Conservation Agreement and Strategy to provide the initial direction for conservation. Initial objectives of the strategy were to survey for additional occurrences and identify and establish management guidelines that would ensure the overall long-term survival of the species. Through an interagency effort, most of the initial conservation measures have been achieved. Results from these efforts include greatly expanded numbers of known population occurrences, refined monitoring protocols, and increased public awareness efforts.

Rabbit Valley gilia (*Gilia caespitosa*) is a rare species that occurs in scattered locations within a very limited range in Wayne County, Utah. It is currently recognized as a candidate for listing by the USDI Fish and Wildlife Service (USDI 1997). Additionally, it is recognized as a sensitive species by the USDI Bureau of Land Management and Capitol Reef National Park, and the USDA Forest Service.

Prior to 1996, little information regarding life history, abundance, and general demographics of the species was known. In an effort to enhance species information and establish management protocols to ensure the survival of *Gilia caespitosa*, the Bureau of Land Management, Capitol Reef National Park, the National Forest Service, and the Fish and Wildlife Service developed a Conservation Agreement and Strategy in 1996 (USDA and USDI 1996). This strategy is a commitment by each of the cooperating agencies to address protection measures designed to achieve long-term conservation of the species and to ensure that management actions will not result in the need to list *Gilia caespitosa* as threatened or endangered. Management actions resulting from implementation of the *Gilia caespitosa* strategy will also benefit other sensitive species that occupy the same habitat sites as Rabbit Valley gilia.

Efforts taken as a result of the strategy have greatly expanded the knowledge base regarding *Gilia caespitosa*. The results of these efforts have led to better species management, further enhancing each agency's ability to protect Rabbit Valley gilia. Cooperation by each of the agencies has proven to be a vital factor in the ability to accomplish measures as outlined in the strategy.

Species Status Background

Gilia caespitosa has been documented in Federal Register Notices as rare since the 1975 Smithsonian Institution report to Congress. In 1976 it was listed as proposed endangered on the Fish and Wildlife Service mass listing proposal (USDA 1976); it was withdrawn in 1979. In the 1980 Notice of Review, the status of *Gilia caespitosa* was categorized as Category 1 Candidate (C1) (USDI 1980). The supplementary Notice of Review in 1983 listed *Gilia caespitosa* as a Category 2 Candidate (C2) (USDI 1983a, 1983b). Notice of Reviews from 1985 through 1993 listed *Gilia caespitosa* as a C1 species (USDI 1985, 1993). Changes in terminology in the 1996 Notice of Review resulted in categorizing *Gilia caespitosa* as a candidate, and it remains as such today.

On December 15, 1992, a settlement agreement was signed in the case Fund for Animals et al. v. Manuel Lujan et al. in which "by no later than September 30, 1996, defendants agree to propose for listing all species that were officially categorized as C1 as of September 1, 1992 or make a finding that the species no longer warrants listing published in the Federal Register" (Fund for Animals

1992). *Gilia caespitosa* is one of the species addressed in the lawsuit. Development of a conservation agreement and strategy satisfied the requirements with regard to the lawsuit settlement agreement.

Nomenclature and Description

Gilia caespitosa was first collected in 1875 by Lester F. Ward, in Rabbit Valley, near Teasdale, Utah. The specimen was identified and described the next year by Asa Gray (1876) as a member of the genus *Gilia*. The recognition of this species as a rare member of Polemoniaceae was brought to light in 1975 by James Reveal, who compiled a list of rare species for Utah for the Smithsonian Institute report to Congress in accordance with Section 12 requirements of the Endangered Species Act (Reveal 1976, USDI 1983a). Further discussion of the nomenclature of *Gilia caespitosa* is available in a status report for *Gilia caespitosa* prepared by J. Mark Porter and Kenneth D. Heil (1994). A name change has been proposed transferring this species, along with all other members of *Gilia* section *Giliandra*, to the genus *Aliciella* Brand. However, it is still recognized as *Gilia caespitosa* in "The Utah Flora" (Welsh et al. 1993) and in the conservation agreement and strategy, so this paper uses the name of *Gilia caespitosa*. The common name "Rabbit Valley gilia" comes from the original collection record.

Gilia caespitosa is a long-lived perennial. Flowering plants have 1 to 20 or more stems above the ground and a woody caudex below the soil surface. Plants are 3–11 cm tall with stems forming a tufted dome with a small cluster of leaves at the base. The leaves in the basal cluster are 0.4–2.5 cm long and 0.8–4.2 mm wide, and are always covered with sticky hairs (often sand adheres to the leaves, too). Above the cluster of leaves, along the stem, the leaves are much smaller. The stems have lateral branches starting about midway up the stem, but sometimes the lateral branches may start as low as within the basal leaf cluster. All of the stems have the same kind of sticky hairs as the leaves and end in a small cluster of 1 to 5 flowers. The flowers consist of five sepals as well as five petals, both fused and forming a narrow tube; the petals are 4.0–5.7 mm long. Flower color varies from scarlet to vermilion, crimson, or pink. The flowers have five anthers attached to the inside of the tube, but not all five are attached at the same level. The fruit is a capsule, 3.0–5.5 mm long with 5–11 seeds per locule (Porter and Heil 1994).

Distribution, Habitat, and Ecology

Gilia caespitosa is restricted to scattered occurrences from the northern Waterpocket Fold to Thousand Lakes Mountain and Rabbit Valley in Wayne County, Utah. Occurrences are often found with limited numbers of plants and limited potential for increasing. Plants are found on private, Utah State Trust, Bureau of Land Management, Forest Service, and National Park Service lands.

Gilia caespitosa occurs, almost exclusively, in Navajo Sandstone associated with cliffs, ledges, exposed outcrops, and drainages of eroded or detrital sandstone. Only one occurrence is known on the Kayenta Formation amongst broken cliff ledges and in rock crevices (Clark 1999). The habitat is associated with recurring, if not constant water and wind erosion. Erosion may be largely responsible for the presence of this type of habitat, as it is often marked by cracks in sandstone that are packed with eolian sand and detritus/eolian deposits (Porter and Heil 1994). Plants occur in full sun or in shaded canyons, on exposed sandstones, cliff walls, and less commonly sandy wash bottoms. Rabbit Valley gilia grows between 5200 and 8000 feet, primarily on slopes of 60–100 percent (USDA and USDI 1996).

Gilia caespitosa is found in association with open pinyon-juniper woodlands, which are often mixed with some elements of mountain brush, sagebrush steppe or ponderosa pine forest. The most frequently associated species include ponderosa pine (*Pinus ponderosa*), Utah juniper (*Juniperus osteosperma*), little leaf mountain mahogany (*Cercocarpus intricatus*), roundleaf buffaloberry (*Shepherdia rotundifolia*), and Indian ricegrass (*Stipa hymenoides*; Clark 1999).

Preliminary data suggest that this species is a self-incompatible, obligate, outcrossing species (Porter and Heil 1994). Little is known regarding the pollination or reproductive success of this species. Although various bee species have been observed frequenting its flowers, it is unknown whether any act as pollinators. Phenological patterns vary slightly from year to year due to variable weather patterns. Flowering generally begins in early to mid June and continues through July, and occasionally to mid-August. Fruiting closely tracks flowering and begins in late June.

Gilia caespitosa overwinters as a series of loose, basal leaves. Plants maintain the same taproot year after year (Porter and Heil 1994). After vernalization, the primary axes elongate and flowering begins. A few of the axial buds of the lower leaves

of the rosette develop into new basal rosettes of leaves, which again overwinter. This annual ramification might be interpreted as a type of vegetative reproduction. However, because the same taproot is maintained year after year and adventitious roots are not produced, in a strict sense this is not true clonal reproduction (Porter 1993). Flowering plants are at the smallest 2 cm x 2 cm, and are presumed several years old. Monitoring to date has documented that plants up to 3 years in age have not flowered and seem to be several years from the potential for flowering (C. Dawson, personal communication).

Conservation Agreement and Strategy

In 1995, an interagency technical team began development of a conservation agreement and strategy for *Gilia caespitosa*. All information known regarding Rabbit Valley gilia was analyzed for development of the strategy. One important component in the development of the strategy was the limited information available regarding *Gilia caespitosa*. No thorough inventories, detailed monitoring, or pollination, ecological, or habitat studies had been conducted. As this was the case, the obtainment of this information was an important first component of the strategy. The conservation agreement and strategy was signed by all parties in 1996 (USDA and USDI 1996).

The overall purpose of the strategy is "to attain the goal of long-term conservation of *Gilia caespitosa* throughout its range through proactive management of the species and the ecosystems upon which it depends" (USDA and USDI 1996). The strategy recognized that conservation of *Gilia caespitosa* would require removing threats and maintaining or expanding populations. The strategy recognized that efforts taken for *Gilia caespitosa* would also benefit other threatened, endangered, and sensitive plant species that shared the same ecosystems.

The primary objectives of the conservation agreement and strategy are threefold. The first objective is to "ensure that existing regulatory mechanisms and agency funding is available to provide for long-term management of *Gilia caespitosa*." The second objective is to "inventory for additional occurrences" and the last objective is to "identify and establish management guidelines which will ensure overall long term survivability of the species" (USDA and USDI 1996).

The strategy listed six action items and outlined which agency was responsible for conducting each of the items, as well as the budget necessary to accomplish each.

1. Assure that agencies follow existing land management policies. These policies and regulations control the collection of plants and activities that may affect its habitat. Additionally, these policies retain federal ownership of lands containing *Gilia caespitosa* and provide the feasibility of acquiring additional occupied habitat.

2. Inventory suitable habitat for *Gilia caespitosa* and determine the number of individuals in each occurrence, its habitat characteristics, and its overall distribution. Survey plans will be developed to assure that all suitable habitat is checked.

3. Establish monitoring plots to study the biology, ecology, and life history of the species. Locations and methods for monitoring are to be selected by the interagency technical team.

4. Protect *Gilia caespitosa* from international trade and commercial exploitation. Such protection includes its listing in the appendices of the Convention of International Trade in Endangered Species of Wild Fauna and Flora.

5. Fund a Center for Plant Conservation endowment for *Gilia caespitosa*. This endowment provides for seed bank collections to be made for the purpose of long-term seed storage and maintaining refuge garden populations for species that are threatened in their natural habitat. The endowment also provides for the conducting of research beneficial to the conservation and recovery of the species.

6. Develop public awareness, appreciation, and support for the conservation of *Gilia caespitosa*. This includes educating horticulturalists, specifically rock-gardeners, regarding measures needed for conservation of *Gilia caespitosa* in the wild. Some of the materials to be developed include pamphlets, audio-visual programs, and posters for use in schools, with conservation organizations, and at agency offices.

Results of the Conservation Agreement and Strategy

Agencies have taken an active role in following existing land management policies that provide protection for *Gilia caespitosa* in its natural habitat. Population occurrences have been fenced and trails have been rerouted to prevent damage from off-highway vehicle use. Federal lands occupied by *Gilia caespitosa* have been removed from potential exchange. Collection activities have been limited to those necessary for scientific study and

have been monitored by the interagency technical team.

Surveys have been completed within all conservation units, with only a few outcrops of Navajo Sandstone remaining. Prior to 1997 only 13 locations were known for *Gilia caespitosa*. These locations contained approximately 4,700 plants (Clark 1997). Surveys conducted through 2000 have documented an additional 21 population occurrences and close to 9,000 plants (Clark 1999). This has almost tripled the known number of population occurrences and plant numbers.

Surveys have provided additional information regarding the habitat characteristics of Rabbit Valley gilia. It is now obvious that there are more locations and individual plants at or above 7,000 feet elevation. Plants are found on all aspects and appear to have no preference for any particular exposure (Clark 1999). Additionally, one plant was found growing in cryptobiotic soil (Clark 1997), which had never before been observed.

Plant associations vary with changes in elevation. When all *Gilia caespitosa* sites are considered together (Table 1), no species occurs more than 71 percent of the time; however, when you divide the sites into two groups by elevation (Tables 2 and 3), a better representation of associated species can be seen. Indian ricegrass is the only species that occurs at more than 60 percent of all sites, regardless of elevation. Utah juniper occurs at 81 percent of all the sites below 6,800 feet, but at only 44 percent of the sites about 7,000 feet. Ponderosa pine occurs at 94 percent of the sites above 7,000 feet, but at no sites below that elevation (Clark 1999).

Table 1. Associated plant species occurring at 20 percent or more of all *Gilia caespitosa* sites (n = 34).

Percent of sites with *Gilia caespitosa*	Associated plant species
80–100%	0%
60–80%	71% *Stipa hymenoides* 62% *Juniperus osteosperma* 62% *Cercocarpus intricatus*
40–60%	44% *Pinus ponderosa*
20–40%	35% *Artemisia* sp. 32% *Cryptantha* sp. 32% *Pinus edulis* 32% *Shepherdia rotundifolia* 29% *Arctostaphylos patula* 29% *Erigeron* sp. 29% *Poa* sp. 26% *Arenaria fendleri* 26% *Hymenopappus filifolius* 26% *Opuntia polyacantha* 26% *Stephanomeria* sp. 25% *Gutierrezia microcephala* 25% *Penstemon* sp. 21% *Heterotheca villosa* 21% *Streptanthella longirostris*

Table 2. Associated plant species occurring at 20 percent of more of *Gilia caespitosa* sites between 5200 and 6800 feet elevation (n = 16).

Percent low-elevation *Gilia caespitosa* sites	Associated plant species
80–100%	81% *Juniperus osteosperma*
60–80%	69% *Cercocarpus intricatus* 63% *Stipa hymenoides* 63% *Shepherdia rotundifolia*
40–60%	44% *Artemisia* sp. 44% *Opuntia polyacantha* 44% *Pinus edulis*
20–40%	38% *Stephanomeria* sp. 38% *Streptanthella longirostris* 31% *Cryptantha* sp. 25% *Echinocereus triglochidatus* 25% *Ephedra viridis* 25% *Eriogonum corymbosum* 20% *Erigeron* sp. 20% *Heterotheca villosa* 20% *Festuca octoflora*

Other sensitive species have also been found during surveys for *Gilia caespitosa*: *Cymopterus beckii, Thelesperma subnudum* var. *alpinum, Astragalus consobrinus, Hymenoxys acaulis* var. *nana, Townsendia aprica,* and *Erigeron maguireii* (Clark 1997, 1999).

Monitoring studies, to date, are being conducted by Denver Botanical Gardens. Monitoring began in 1992 with two sites. Eight study sites have been monitored since 1995 (Denver Botanical Gardens 1998). Studies seem to indicate that fluctuations in recruitment are related to precipitation patterns and the availability of safe germination sites (Denver Botanical Gardens 1998). Even with large fluctuations in monitored population numbers due to recruitment and seedling mortality, statistical testing shows no significant differences between the total number of plants within each site for the first and last year of monitoring (Denver Botanical Gardens 1998). Monitoring has not shown any seedlings surviving more than 4 years (Table 4; Denver Botanical Gardens 1998).

Specific actions with regard to the Convention of International Trade in Endangered Species of Wild Fauna and Flora have not been initiated. Agencies contacted the Rock Garden Society at one of their annual meetings to educate them about the importance of *Gilia caespitosa* populations in the wild and the procedures required for its collection. The Center for Plant Conservation

Table 3. Associated plant species occurring at 20 percent or more of *Gilia caespitosa* sites between 7000 and 8000 feet (n = 18).

Percent high-elevation *Gilia caespitosa* sites	Associated plant species
80–100%	94% *Pinus ponderosa*
60–80%	78% *Stipa hymenoides*
40–60%	56% *Cercocarpus intricatus* 50% *Arctostaphylos patula* 50% *Poa* sp. 44% *Arenaria fendleri* 44% *Juniperus osteosperma* 44% *Penstemon* sp.
20–40%	39% *Gutierrezia microcephala* 39% *Hymenopappus filifolius* 39% *Erigeron* sp. 33% *Cryptantha* sp. 28% *Artemisia* sp. 28% *Artemisia ludoviciana.* 28% *Chrysothamnus nauseosus* 22% *Abronia fragrans* 22% *Heterotheca villosa* 22% *Oenothera pallida* 22% *Pinus edulis* 22% *Phlox* sp. 22% *Juniperus communis* 22% *Yucca harrimaniae*

endowment was funded through the efforts of the Denver Botanical Gardens. Seeds have been collected since 1991 when there has been sufficient seed crop. Seed collection remains a high priority, but to obtain genetically adequate samples will take many years, due to low levels of seed production (Denver Botanical Gardens 1998).

Public awareness is an important component of the conservation agreement and strategy and successful management and protection for *Gilia caespitosa*. Agencies have cooperated in the development of exhibits, flyers, and displays that include *Gilia caespitosa*. Additionally, an article was published in the Park Science Journal regarding rare plants, including *Gilia caespitosa.* The importance of protection and management of *Gilia caespitosa* has also been emphasized among staff members of the agencies involved.

Discussion

Agencies participating in the *Gilia caespitosa* conservation agreement and atrategy have actively taken part in providing the budget, labor, and expertise to promote conservation of *Gilia caespitosa* and to initiate the action items listed in the strategy over the last 4 years. To date, all but one of the items have been either fully or partially completed as a result of agency efforts. Although many of the action items have been completed, agencies are continuing to support additional efforts that will enhance the knowledge of and ability to protect *Gilia caespitosa*. The term of the conservation agreement and strategy is 10 years; however, do to initial support, the strategy will be updated with new information and new action items much earlier than anticipated.

Base knowledge has been greatly enhanced since the completion of the *Gilia caespitosa* strategy. These results have led to better species manage-

Table 4. *Gilia caespitosa* seedling survivorship.

	1992	1993	1994	1995	1996	1997
1992, 2 sites	31 alive seedlings*	12 alive 19 died	7 alive 5 died	2 alive 5 died	0 alive –	– –
1993, 3 sites	– –	1 alive seedling*	1 alive 0 died	0 alive –	– –	– –
1994, 4 sites	– –	– –	0 new live seedlings*	– –	– –	– –
1995, 8 sites	– –	– –	– –	68 alive seedlings*	2 alive 66 died	0 alive –
1996, 8 sites	– –	– –	– –	– –	17 alive seedlings*	5 alive 12 died
1997, 8 sites	– –	– –	– –	– –	– –	44 alive seedlings*

Asterisk indicates new seedlings found at additional monitoring sites. (In 1992, 31 seedlings were found at 2 sites. In 1993, only 12 of 31 individuals survived and 19 died. In 1994, of the 12 surviving individuals, only 7 individuals survived and 5 died. In 1995, of the 7 surviving individuals, only 2 individuals survived. By 1996, all the initial 31 seedlings tagged in 1992 had died.)

ment, further enhancing the ability to protect Rabbit Valley gilia and the habitat on which it depends. Cooperation between agencies has proven to be a vital factor in the ability to accomplish the measures outlined in the strategy.

Although the federal agencies have been the key players in the conservation agreement and strategy, many other groups have contributed funding, personnel, and support, including the Denver Botanical Gardens, Canon USA, the National Park Foundation, the Capitol Reef Natural History Association, Utah Valley State College, Southern Utah University, Utah State University, Northern Michigan University, and Worthington Ohio High School.

As a result of efforts associated with the *Gilia caespitosa* conservation agreement and strategy, it is obvious that Rabbit Valley gilia is more abundant than originally thought and is doing well (Figure 1). Advances in knowledge have been obtained and better management decisions are able to be made. The ability to attain the overall purpose of long-term conservation of *Gilia caespitosa* throughout its range has been greatly enhanced. The knowledge gained will continue to contribute to proactive management decisions not only for *Gilia caespitosa*, but also for other rare species that inhabit the same ecosystem.

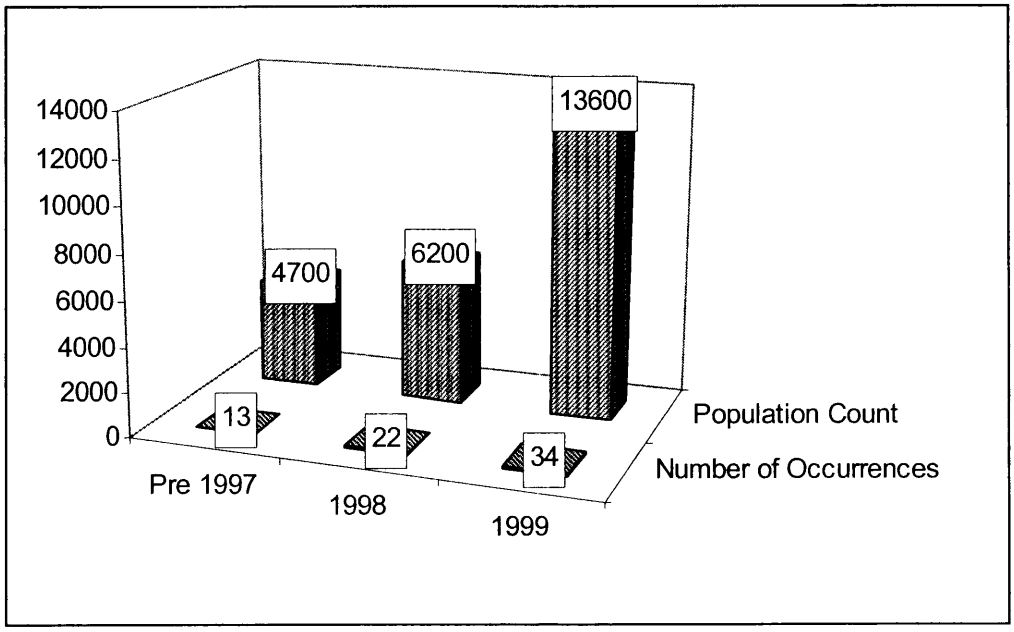


Figure 1. *Gilia caespitosa* survey results.

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Demographic Monitoring of Wright Fishhook Cactus

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Abstract: Wright fishhook cactus (*Sclerocactus wrightiae* Benson) is a small barrel cactus endemic to the San Rafael Swell in south-central Utah. It was listed as an endangered species in 1979 due to its small population size, threats of over-collecting, and development associated with oil and gas. Demographic monitoring was initiated in 1993 with the following objectives: to establish permanent plots to monitor growth, fecundity, recruitment, and mortality for at least 10 years; to identify habitat factors positively associated with cacti presence; and to identify important insect visitors and predators. Three permanent plots were located throughout the range of *S. wrightiae,* and 93 individuals were followed from 1993 to 2000. In general, diameter size class was significantly different ($P < 0.001$) for all three plots. Size classes 3 and 4 (adults) produced the greatest number of flowers and fruits. Size class 3 produced more flowers and fruits by virtue of its higher density, whereas size class 4 produced more flowers and fruits because of its larger diameter. Mortality exceeded recruitment by a 2.5:1 ratio for all plots. At Hanksville, 21 cacti (68%) were recorded dead in 1994, and the remaining 10 individuals and 5 recruits were recorded dead in 1995. No new recruits have been recorded since 1995 at Hanksville. Ord's kangaroo rats and white-tailed antelope ground squirrels were primary mortality sources at Hanksville, and the cactus-borer beetle was the primary mortality source at Giles and Mesa Butte.

Wright fishhook cactus (*Sclerocactus wrightiae* Benson) is a small, white-flowered barrel cactus endemic to the San Rafael Swell in south-central Utah. It was discovered by Dorde Wright Woodruff in 1961 "near San Rafael Ridge" in Emery County, Utah. Lyman Benson collected it in 1964 at the type location and realized that it formed a link between *Sclerocactus whipplei* and *Colorodoa mesae-verdae*. At that time the genus *Sclerocactus* consisted of just two species. In 1966, Benson expanded the genus *Sclerocactus* to six species and named the novel cactus after Mrs. Wright. Eight species of *Sclerocactus* are currently recognized in the Navajoan, Great Basin, and Mojave deserts (Benson 1982).

On October 11, 1979, *S. wrightiae* was listed as an endangered species (U.S. Fish and Wildlife Service 1979) based on its narrow distribution, its small population size, and the potential threats of commercial collecting and energy development (Mutz et al. 1985). Recent inventories (Welsh 1980, Neese 1987, Kass 1989) have extended its distribution from approximately Ferron in Emery County southwest to Hanksville in Wayne County, Utah (Figure 1).

Conservative estimates of population size range from 50,000 to 100,000 (Neese 1987, Kass 1989). As expected, the accuracy of total population counts is questionable because areas may be overlooked during inventory, and cacti may actually disappear underground during census periods (S. Welsh personal communication). Accurate counts, which are important for determining population size and dynamics, are fundamental to conservation management (Bradshaw and Doody 1978).

Local populations of *S. wrightiae* typically consist of 50–100 individuals occurring within a 1–2 hectare area. These subpopulations are often clumped on certain geologic strata and are often separated by several kilometers between strata. *S. wrightiae* is most often found on the Morrison, Curtis, and Mancos formations, and is less often found on the Summerville, Dakota, Entrada, and Carmel formations (Figure 2).

To date, the habitat characteristics of *Sclerocactus* have received little attention. Soil tests of *S. polyancistrus* habitat indicate abnormally high calcium carbonate levels (May 1979). Naumann (1989) reported that *S. mesae-verde* is limited to the Mancos Formation, but detected no differences in soil characteristics within the species range. Welsh et al. (1987) and Neese (1987) have suggested that saline or sodic soils are often associated with *S. wrightiae*. Soil surface features such as gravelly pavement may be important to the establishment and growth of *S. wrightiae* (Neese 1987, Kass 1989).

S. wrightiae is found mainly in salt desert shrub at 1378–1460 m (4200–4788 ft) elevation, growing primarily with perennial members of the

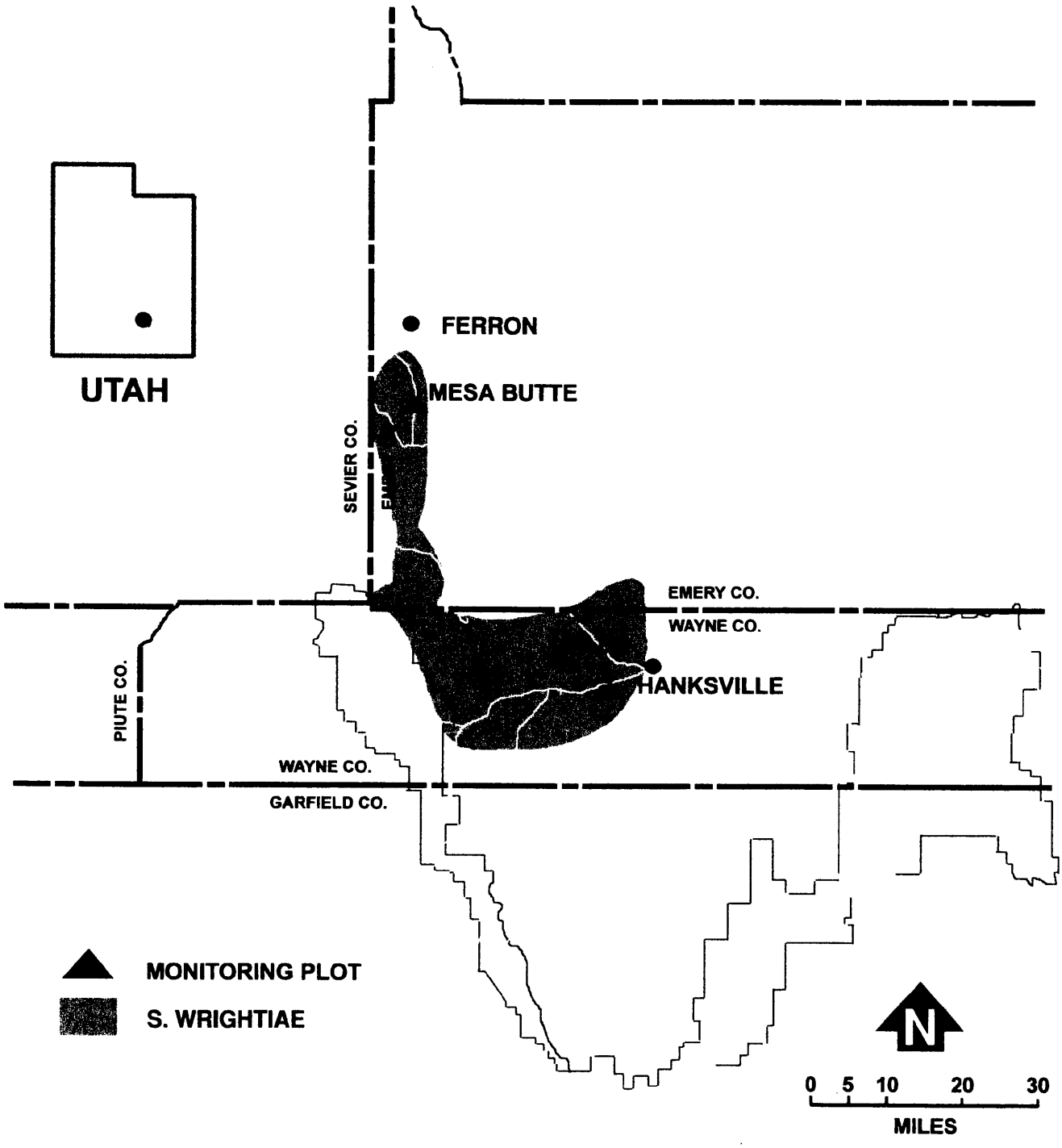


Figure 1. Distribution of *Sclerocactus wrightiae*.

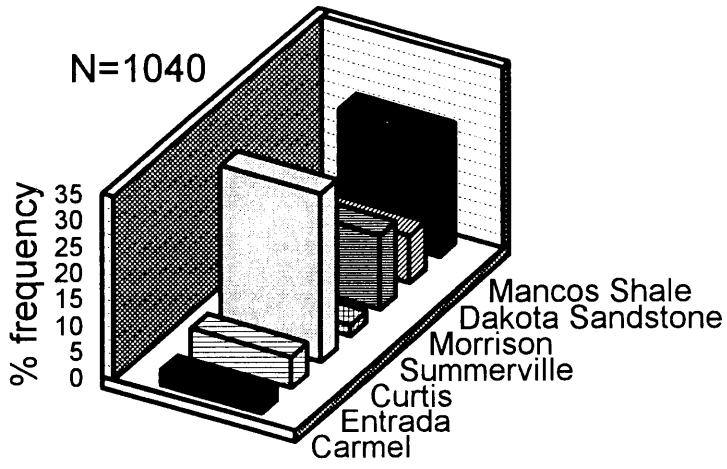


Figure 2. Percent frequency of *S. wrightiae* relative to gelogic strata.

genus *Atriplex*. It is most commonly found in association with mat saltbush (*Atriplex corrugata*), Castle Valley saltbush (*Atriplex gardneri* var. *cuneata*), and shadscale (*Atriplex confertifolia*). It also grows at the lower limits of the pinyon-juniper community at 1865–1981 m (6117–6497 ft; Table 1).

Demographic monitoring of cacti has been limited to a few short-term studies. Phillips et al. (1985) and Butterwick (1987) monitored growth and reproduction of the Peebles Navajo cactus (*Pediocactus peeblesianus* var. *peeblesianus*) in Arizona. Warren et al. (1992) monitored *Pediocactus paradinei* for 4 years on the Kaibab Plateau. In Utah, Hughes (1992) is conducting demographic monitoring of *Pediocactus sileri*. Demographic studies of *Sclerocactus* consist of those on *S. mesae-verdae* by Naumann (1989) and Culley et al. (1992) in Colorado and New Mexico, respectively.

To date, demographic information is not available for *S. wrightiae*. Sutter (1996) indicated that demographic monitoring is an essential component of rare plant conservation and is needed to precisely detect changes in populations and management over time. Age structure, establishment history, and optimal reproductive success may be inferred from demographic data (Jordan and Nobel 1982).

Long-term monitoring of *S. wrightiae* was initiated in 1993 with the following objectives: to establish permanent plots to monitor growth, fecundity, recruitment, and mortality for at least 10 years; to identify habitat factors positively associated with cacti; and to identify important insect visitors and predators. A cooperative agreement between the Bureau of Land Management (BLM) and Intermountain Ecosystems provided project funding.

Methods

Three 0.75 ha (61 x 122 m) rectangular permanent plots were selected throughout the geographic range of *S. wrightiae*. Plots varied with respect to geology, vegetation, elevation, and land use (see Table 1). Plots were selected in high-density cacti areas so the greatest number of individuals could be sampled within a manageable plot size. Eight 30 x 30 m subplots were superimposed on each 0.75 ha plot, and subplot corners were staked with rebar to facilitate location of individual plants.

Thirty-one cacti were randomly selected in each plot and marked with aluminum identification tags attached to large nails located north of each individual. Cacti were located by triangulation, with the two nearest subplot corners serving as permanent reference points.

Height, diameter, vigor, and reproduction (number of flowers and fruits) were recorded for each individual stem annually from 1993 to 2000. Seeds were collected from 20 plants each in Mesa Butte and Giles in 1995 and 1999 to determine the number of seeds per mature fruit. Plants were separated into four size classes based on diameter width. Size class 1 plants were < 2 cm wide and were considered seedlings or new recruits. Size class 2 plants were juveniles > 2 to 4 cm wide, which flowered occasionally but seldom set fruit. Size class 3 were adult plants > 4 cm to 9 cm wide that generally had slightly lower reproductive rates but a higher frequency of occurrence. Size

Table 1. General location and description of *S. wrightiae* plots in central Utah.

	Giles	Hanksville	Mesa Butte
County	Wayne	Wayne	Emery
Elevation	1371 m	1341 m	1731 m
Aspect	East	East	Southeast
Slope	0–10°	0–5°	0–10°
Geology	Mancos shale	Summerville	Mancos shale
Land use	Off-road vehicles	Cattle grazing	Cattle grazing
Vegetation	Castle Valley saltbush	Sand dropseed/galleta grass	Mat saltbush
Precipitation	12.9 cm	13.8 cm	18.5 cm

class 4 were adult plants > 9 cm wide with higher reproductive success.

Kolmogorov-Smirnov goodness-of-fit tests were used to determine if size classes in 1993 fit a normal distribution. Size class data were not normal, so the Kruskal-Wallis non-parametric analog to analysis of variance was used to test for significant differences between means. Spearman's rank correlation analysis was used to show the relationship between size class and number of reproductive structures.

Vascular plant and substrate cover (rock and bare ground) were measured along randomly placed 100 m transects. M2 quadrats were centered at 10 m intervals along the transect. The above procedures were repeated but sampling was centered on *S. wrightiae* individuals nearest the 10 m point on the transect rather than on the transect line itself. Plant-centered versus random-point locations made it possible to test the hypothesis that living cover and substrate cover are no different between cacti and non-cacti habitats. Kolmogorov-Smirnov two-sample t tests were used to test for significant differences in cover between cacti and non-cacti plots. Topographic position was recorded for each plant and was analyzed using a G test.

Three soil samples were collected from each plot (N = 9) in 1995 and analyzed for texture, pH, electrical conductivity, sodium absorption ratio, ppm nitrogen (N), and ppm sodium (Na). Soils samples were taken with an auger inserted to depth of 15 cm and placed in plastic bags. Soils were analyzed by the Brigham Young University Soil Laboratory, Department of Agronomy and Horticulture. Soil data were not tested for significant differences because of small sample size.

Results

Size class varied between sites during the first census in 1993 ($P < 0.001$) and continued to change in subsequent years (Figures 3–5). In general, the greatest number of individuals was found among size class 3 (young reproductive), followed by size class 2 (juveniles). Size class 1 (seedlings) recorded the fewest individuals, followed by size class 4 (old reproductive). Low recruitment patterns and the small number of older reproductive individuals seem to constitute a species-wide pattern.

Mortality exceeded recruitment by a 2.5:1 ratio for all plots during 1993–2000 (Table 2). After 1995, no live individuals remained in the Hanksville plot. Twenty-one cacti (68%) were recorded dead in 1994, and the remaining 10 adults and 5 recruits were recorded dead in 1995. No new recruits have been recorded since 1995 at Hanksville.

Currently, 6 individuals remain at Giles and 24 at Mesa Butte, a 68 percent decrease from the original population of 93 plants. In 1999 a rare recruitment event added 18 new individuals to Mesa Butte, a 21 percent increase in population size. As of 2000, 15 of those new recruits have survived and are responsible for the bulk of the remaining 24 individuals at Mesa Butte (Table 2).

Mean annual growth pooled for all three plots gradually increased from 1993 to 1995 and then gradually declined from 1996 to 1999, with substantial decreases in 2000. Based on observation of *S. wrightiae* in average precipitation years, seedlings and juveniles grow about 1–2 cm per year, and growth rate declines to about 0.5 cm per year for adults. From these observations, it appears that *S. wrightiae* reaches sexual maturity at about 4 years and probably has a life expectancy of 20 years.

Reproductive Effort

Spearman's rank correlation analysis showed a significant positive correlation ($P < 0.001$) between total number of flowers/fruits and stem diameter. In general, size classes 3 and 4 had the greatest number of flowers and fruits. Size class 3

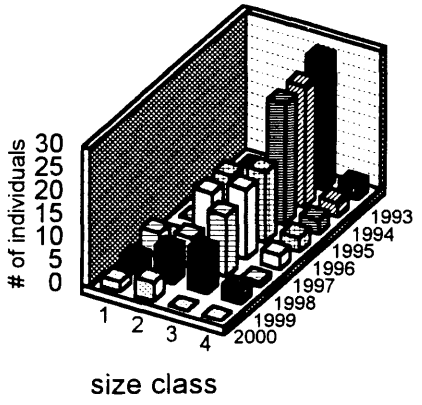


Figure 3. *Sclerocactus wrightiae* size class at Giles (n = 202).

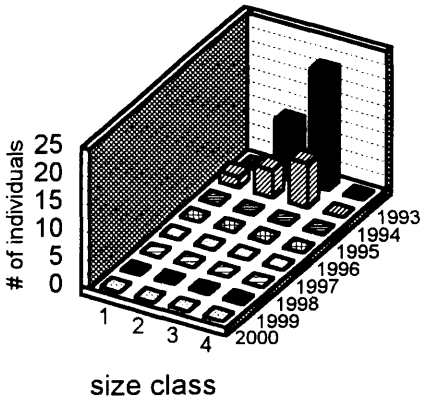


Figure 4. *Sclerocactus wrightiae* size class at Hanksville (n = 46).

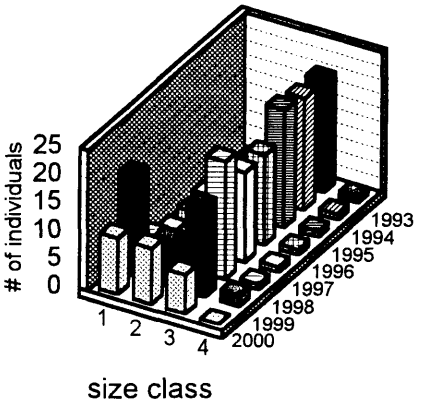


Figure 5. *Sclerocactus wrightiae* size class at Mesa Butte (n = 244).

produced more flowers and fruits by virtue of its larger numbers, whereas size class 4 produced more structures by virtue of its larger size. The reproductive effort for size class 2 was minimal and remained essentially constant throughout the years. Declines in reproductive effort for size classes 3 and 4 resulted from drought and overall mortality of the larger individuals (Figure 6).

The mean number of seeds per fruit averaged for all plots for 1995 and 1996 was 15.6 (SD 7.83). The mean number of reproductive structures per plant and mean number of seeds per plant for 1777 plants were 3.65 (SD 4.49) and 70 (SD 4.43), respectively. Flowering plants produced mature fruit on average 76.4 percent of the time.

Habitat Analysis

Shrub cover was lower and forb and grass cover was higher on cacti than non-cacti plots, but differences were not significant. Total plant cover ranged from 14.7 percent at Mesa Butte to 5.0 percent at Giles (Table 3). Bare ground was slightly higher on cacti plots and percent rock cover showed neglible differences between cacti and non-cacti plots.

The results of G tests indicated that plants are not distributed randomly with respect to topographic position ($P < 0.0001$). Plants occur on long, gradual mid-slopes (79%) and upper mid-slopes (19%) and almost never on abruptly sloping areas or slopes exceeding 11 degrees. Plants occurred on all aspects.

The results of soil analysis at Hanksville indicated electrical conductivity of 15.75 and sodium absorption ratios of 20.76, several times higher than Giles or Mesa Butte (Table 4). Nitrogen was 103.060 ppm at Hanksville, two times lower than Mesa Butte (235.56 ppm) and three times lower than Giles (301.81 ppm).

Soil alkalinity and salinity values were high at the Hanksville plot, suggesting moisture and nutrient limitation problems (Long 1981, Mengel and Kirkby 1982). Nutrient and moisture limitations may explain the smaller stature of individuals and overall poor reproductive performance compared to the other two plots in 1993 and 1994. In general, cacti are not well adapted to growing in high saline or sodic conditions (Benson 1982).

Discussion

The low frequency of occurrence in the smallest size class suggests that recruitment is a rare and episodic event. Only one significant recruitment event was observed in the last 8 years at

Table 2. Mortality and recruitment of *S. wrightiae*, 1993–2000. Values are total numbers of individuals, and values in parentheses represent annual percent mortality and recruitment. Mortality to recruitment ratio is 100:40 or 2.5:1.

Year	N	Plots	Mortality	Recruitment
1993	31	Giles	0	0
	31	Hanksville	0	0
	31	Mesa Butte	0	0
Total	93		0	0
1994	29	Giles	2	0
	15	Hanksville	21	5
	29	Mesa Butte	4	2
Total	73		27 (27)	7 (7.5)
1995	29	Giles	0	0
	0	Hanksville	15	0
	31	Mesa Butte	0	2
Total	60		15 (20.5)	2 (2.7)
1996	29	Giles	0	0
	29	Mesa Butte	2	0
Total	58		2 (3.4)	0
1997	29	Giles	0	0
	29	Mesa Butte	0	0
Total	58		0	0
1998	25	Giles	8	4
	31	Mesa Butte	3	5
Totals	56		11 (19)	9 (15.5)
1999	22	Giles	7	4
	40	Mesa Butte	9	18
Total	62		16 (28.5)	22 (39)
2000	06	Giles	16	0
	24	Mesa Butte	16	0
Total	30		32 (51.6)	0
Grand Total	100	40		

Mesa Butte, accounting for the 21 percent increase at that site. Rare and episodic recruitment patterns have been demonstrated for a number of long-lived species, especially cacti. These episodes are most likely related to precipitation events and favorable temperature regimes (Steenbergh and Lowe 1969).

The primary source of mortality at Hanksville was Ord's kangaroo rats (*Dipodomys ordii*) and white-tailed antelope ground squirrels (*Ammospermophilus leucurus*). Kangaroo rat burrows were abundant throughout the area, and antelope ground squirrel activity was observed during the day. It was not uncommon to find both seedling and adult cacti eaten at the ground level within a few nights (Kass, personal observation). Ord's kangaroo rats have been reported eating prickly pear in Idaho, and antelope ground squirrels eat seeds and fruits of cacti as a main dietary item (Zeveloff and Collett 1988). Culley et al. (1992) reported pocket gophers (*Thomomys bottae*) as a mortality source on *S. mesae-verde* in Colorado and New Mexico.

At both Giles and Mesa Butte, mortality was caused mainly by the cactus-borer beetle (*Moneilma semipunctatum*), a large, black, nocturnal, flightless beetle that ranges from the Great Basin in Nevada and western Utah, south to northern Baja California, and east to the Colorado Plateau in Utah, southwestern Colorado, northwestern New Mexico, and northern Arizona (Linsley and Chemsak 1984).

Linsley and Chemsak (1984) discussed the feeding and mating habits of the genus *Moneilema*. Adult beetles are nocturnal and become active at dusk, at which time they climb up and down the cactus stem. They feed and hide at the bases or in the crowns of stems. Mating occurs at night on top of the plant and may continue throughout the night. The female chooses a suitable ovipositor site near the base of the plant and deposits the egg. After hatching, the larvae attempt to enter the

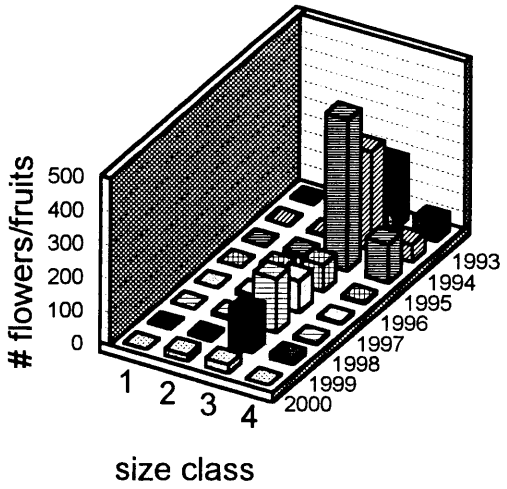


Figure 6. Reproductive efforts for all three plots (n = 1777).

plant, and during the second or third instar the larvae begin to tunnel into the plant. A pupal cell is constructed in the fall, either in the soil or within the hollowed-out stems.

It has been observed that *Moneilema* may select for larger cacti, which may explain part of the decline of larger-sized *S. wrightiae* throughout its range (see Coles and Naumann, this volume). A shift in population structure may result if larger cacti with higher reproductive rates are replaced by smaller cacti with lower reproductive rates.

Conclusions: Threats and Recommendations

Commercial collecting and vandalism are known threats to *S. wrightiae*, and several populations have been extirpated in the Hanksville area (BLM personnel, personal communication). Off-road vehicle (ORV) use is a consistent problem on two of three monitoring plots. Once every 2 years, cacti have been killed by ORVs at Giles. More important, ORVs compact the soil, probably precluding establishment of new recruits. These anthropogenic problems coupled with an overall natural mortality rate of approximately 2.5 to 1 indicate a slow decline for *S. wrightiae*.

BLM management goals for similar endangered species such as *Pediocactus sileri* in southwest

Table 3. Percent cover of vascular plants and substrate components with and without *S. wrightiae*.

	Giles		Hanksville		Mesa Butte	
	Cacti	Non	Cacti	Non	Cacti	Non
Bare ground	48.4	47.2	52.5	50.1	48.7	43.4
Rock	43.9	47.8	38.3	38.6	36.6	38.7
Shrubs	2.7	4.5	1.6	9.0	10.2	11.6
Forbs	3.6	0.5	0.3	0.0	2.5	0.5
Grasses	0.0	0.0	6.8	2.3	1.2	0.5
S. wrightiae	1.4	0.0	0.5	0.0	0.8	0.0
Totals	100	100	100	100	100	100
Live cover totals	7.7	5.0	9.2	11.3	14.7	12.6

Table 4. Mean values for selected chemical and physical parameters for all plots. Standard error shown in parentheses.

	Hanksville loamy sand	Giles loam	Mesa Butte loam
pH	8.6 (0.07)	7.8 (0.06)	7.8 (0.06)
electrical conductivity (mmho/cm)	15.75 (0.10)	2.88 (0.09)	4.35 (0.07)
Na (ppm)	2,144.1 (1.39)	96.48 (1.76)	527.36 (0.57)
N (ppm)	103.6 (0.63)	301.81 (1.23)	235.56 (1.02)
Sodium absorption ratio	20.7 (0.09)	0.97 (0.07)	5.48 (0.07)

Utah are to have about 20 percent of the population in the smallest and largest size classes (Lee Hughes, personal communication). Currently, the *S. wrightiae* smallest size class is at 6.3 percent and the largest size class is at 11.5 percent. Menges (1991) recommended that recruitment must be greater than mortality per year to maintain population viability. These goals are obviously not being met for *S. wrightiae*.

Recommendations for future research include continued monitoring to assess survival of new recruits, mortality sources, and anthropogenic impacts. Probably one of the most important biological factors affecting the narrow distribution of *S. wrightiae* is the apparent lack of long-distance dispersal. Harvester ants (*Pogonomymex* spp.) were observed carrying seeds of *S. mesae-verdae* in New Mexico (Culley et al. 1992). Most 1999 recruitment at Mesa Butte was observed around harvester ant mounds. Further research into this phenomenon would elucidate the nature of the limited distribution of these cacti.

Because members of the genus *Sclerocactus* are highly self-incompatible, identification of effective pollinators is important. Maintenance of genetic diversity appears to be totally dependent on animal pollinators in this species. Both pollinators and seed dispersers may need to be considered for the conservation and protection of *S. wrightiae*.

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Demography and Monitoring of Welsh's Milkweed (*Asclepias welshii*) at Coral Pink Sand Dunes

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Abstract: Results are presented of a 12-year monitoring program on the Coral Pink Sand Dunes and Sand Hills populations of the threatened Welsh's milkweed, *Asclepias welshii* N & P Holmgren. The species is an early seral member of the dune flora, colonizing blowouts and advancing with shifting dunes. When an area stabilizes and other vegetation encroaches, *A. welshii* is crowded out. Reproduction is by seeds and rhizomes, with the latter being more important. Three growth forms and their significance in colony dynamics are recognized. Monitoring has measured fluctuations in stem counts, vegetative competition, off-road vehicle impacts, and the general instability of the environment.

Welsh's milkweed, *Asclepias welshii* N & P Holmgren, is a herbaceous perennial sand dune endemic that was described in 1979, based on a collection made in 1978 at Coral Pink Sand Dunes in Kane County, Utah (Cronquist et al. 1984). Four populations of *A. welshii* are known, located roughly along an 80 km line paralleling the Utah-Arizona border where suitable habitats occur, at elevations ranging from 1700 to 2000 m. The colony on the eastern end of this line is about 25 km west of Page, Arizona. Another is within the Paria wilderness area straddling the Utah-Arizona border, and the largest population is on the Coral Pink Sand Dunes west of Kanab, Utah. The fourth population is about 12 km northeast of the Coral Pink Sand Dunes in the Sand Hills. The Page, Paria, and Sand Hills populations all occur in small isolated areas of suitable habitat, whereas *A. welshii* is abundant and widespread over the Bureau of Land Management administered dunes, with colonies extending to the southwest into the adjacent Coral Pink Sand Dunes State Park.

Asclepias welshii was officially listed as threatened in 1987. The major factor determining this listing was the potential threat from off-road vehicle (ORV) activity within the relatively small confines of the dunes. The dunes themselves are part of the Moquith Mountain wilderness study area. The studies reported here were therefore initiated in 1989 in part to determine the impact of ORV activity on the BLM-administered portion (approximately half) of the Coral Pink Sand Dunes, as well as on the nearby Sand Hills milkweed site.

In standard taxonomic treatments of *A. welshii* (e.g., Welsh et al. 1987, Cronquist et al. 1984) the species is described on the basis of mature specimens only. No mention is made of the fact that another growth form commonly occurs, which has narrow linear leaves, similar in appearance to those of *A. subverticillata*. Seedlings and stems arising from smaller rhizomes that may be several years old have this form, which is here designated as the "primary" stage. Primary stems may emerge among mature stems within a colony, or spread out away from existing groups of mature stems as the milkweed invades new territory.

In addition to the mature and primary growth forms there is a form that exhibits leaf shapes and sizes intermediate between the two, which we call the "secondary" stage. A casual examination of an area may cause one to overlook the stems in the primary stage, resulting in an incorrect interpretation of the existing state of *A. welshii*.

Aerial stems of *A. welshii* arise from an extensive rhizome system that may be buried from a few centimeters to several meters below the surface. Some evidence suggests that rhizomes actually penetrate the sandstone bedrock that underlies the dunes. It is possible that all of the visible stems in a colony originate from a single plant or its clones; any estimation of the total number of *A. welshii* plants in a given location is merely speculation. Therefore stem counts constitute the database for this study.

Methods

This project was initiated in 1989, when six permanent plots measuring 23 x 23 m were established. Five of the plots are on the Coral Pink Sand Dunes and one (Plot 6) is on the Sand Hills. Two plots previously established by the Bureau of Land

Management are also included in the study. Stem counts of the three growth forms have been made annually except for 1990.

The plots are assigned to one of three loosely defined habitat types:

Type I. A stable community of mixed dune shrubs and grasses with minimal sand movement (Plot 5 and BLM Plot 3).

Type II. The tops and faces of dunes where sand movement is continual, resulting in removal of large amounts of sand from the top and windward (southwest) side of the dunes and deposition of this sand on the leeward face (Plots 1, 3, 4, and 6).

Type III. Blowout areas where several meters of sand and most or all of the vegetation, including *A. welshii*, have been removed by the wind (Plot 2 and BLM Plot 2).

Other Sites. In addition to the standard plots described above, two other sites are being closely monitored. The first is a plot established in 1992 to determine the impact of competition from other species on *A. welshii* growth. This plot is adjacent to Plot 5, which acts as a control. Seven *A. welshii* stems were initially included within the plot: four in the primary growth stage and three in the secondary. Numerous stems of all three types were just outside the plot near those seven. All other vegetation was removed and continues to be weeded out annually.

The second site is a colony of *A. welshii* growing in a major ORV trail, where vehicles pass directly over the colony on a regular basis. Data have been collected since 1992.

Results

The spring of 2000 was exceptionally windy and dry. In the most exposed areas, including some of the study plots, 0.5–1.5 m of sand was moved at measured locations. Because of the weather conditions the sand was dry to greater than normal depths for that time of year. Growth, especially of primary stems, into the dryer upper sand levels was inhibited. This resulted in stem counts that were lower than those of the previous year in all plots. The results for each plot are grouped into the three habitat types described above.

Group I: Plots in Stable Areas (Plots 5 and BLM Plot 3)

Plot 5: Between 1991 and 1999 the number of *A. welshii* stems in Plot 5 has remained steady, fluctuating between 37 and 50. Primary stem numbers remain very low, an indication that competition from other species is restricting the spread of *A. welshii* (Figure 1).

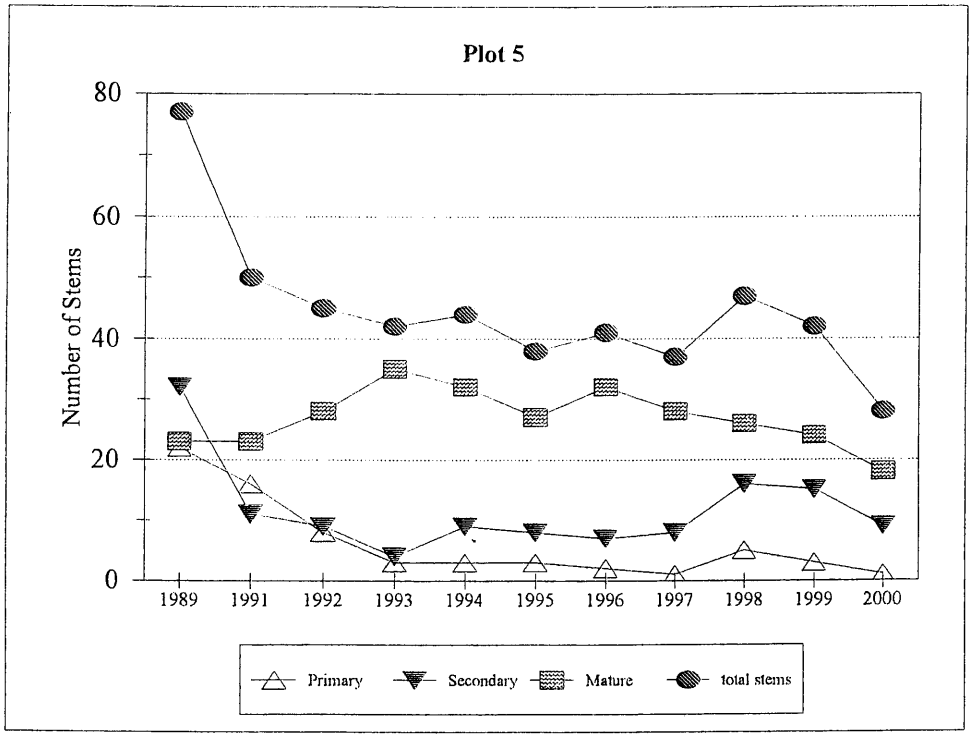
BLM Plot 3: *A. welshii* in this plot has shown a steady decline since 1989. Ground cover by other species in the plot is near maximum. The community is dominated by *Wyethia scabra, Calamovilfa gigantea, Chrysothamnus nauseosus,* and *Sophora stenophylla*. Only five *A. welshii* stems were counted in 2000. One secondary stem was growing by itself near the southwest corner of the plot. The other four stems, all mature, are part of a group growing mostly outside the plot among the *Wyethia* and under ponderosa pines. If present conditions continue, where competition is so great, this milkweed group cannot survive for many more years (see Figure 1).

Group II: Plots Where Sand Removal and Redeposition Is Continual (Plots 1, 3, 4, and 6)

Plot 1: The front of the dune upon which Plot 1 is located has advanced approximately one meter since 1989, while more than a meter of sand has been removed from the windward side. Because of a good cover of shrubs and grasses, such large-scale sand movement is not so obvious unless measured against plot corner posts. The brow and face of the dune originally bore 400 mature stems. This number has declined to less than 100. Primary and secondary stem numbers have remained steady (Figure 2).

Plot 3: This plot has also had more than a meter of sand removed from the south half of the plot and deposited on the north. The northwest corner post has been buried and the northeast post is barely protruding. The total number of stems has declined steadily since 1992, from a high of 172, to 29 this year (see Figure 2). However, the decline within this plot is not representative of the *A. welshii* population as a whole on the dune. The single largest colony of *A. welshii* at Coral Pink Sand Dunes grows here. The plot was placed on the edge of the colony and the colony is moving with the advancing dune; it is not diminishing in size. More seedlings have been observed in this area than in any other.

Plot 4: This is also on the crest of an actively moving dune. The dynamics are similar to that of Plot 3. Originally the entire plot had a good cover of blowout grass, *Redfieldia flexuosa,* but in 1990 the southwest third of the plot was blown out, resulting in the removal of the grass as well as *A. welshii.* Apparently deeply buried *A. welshii* rhizomes survived, because mature stems have returned to the



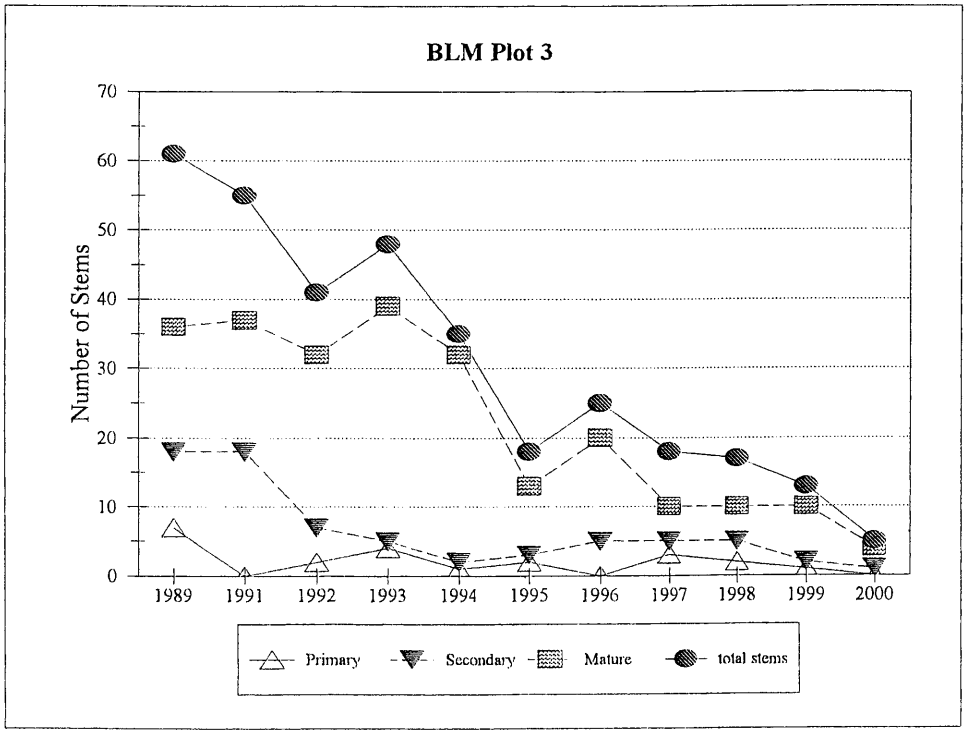
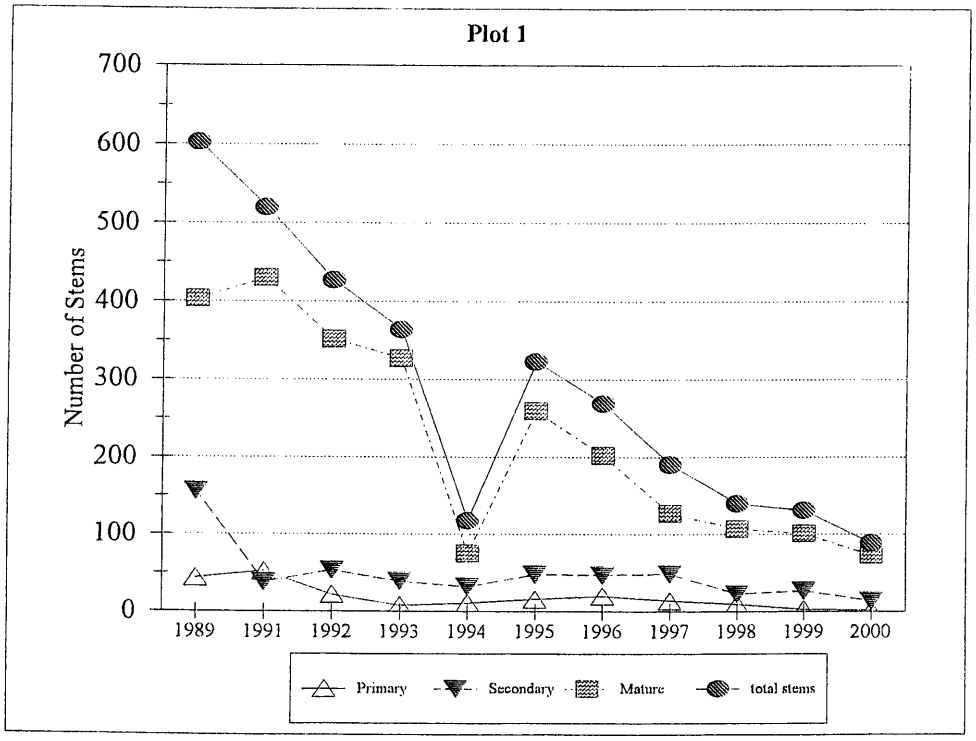


Figure 1. Habitat type I: Plot 5 and BLM Plot 3.



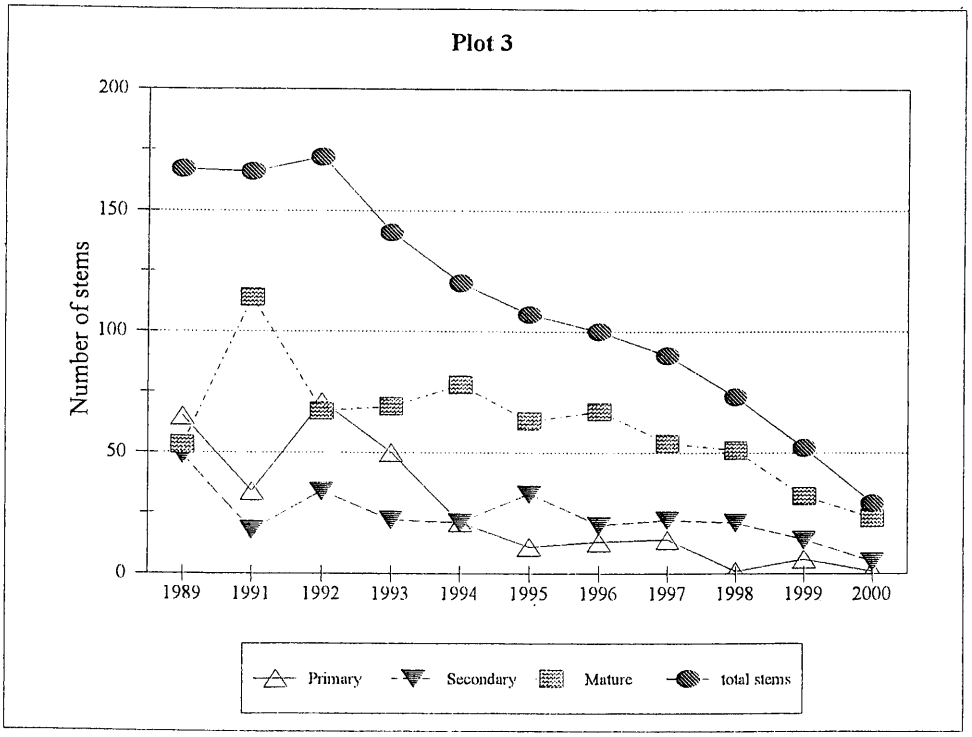


Figure 2. Habitat type II: Plots 1 and 3.

blowout site within a year of their disappearance. This could not have happened as quickly from rhizomes growing into the blowout area from the outside.

The production of primary stems is also high in this plot, especially in the areas where sand is being deposited and blowout grass is prevalent. In spite of adverse conditions, Plot 4 is one of two that up until this year has continued to show an increase in number of stems (Figure 3).

Plot 6 (Sand Hills): Plot 6 has also shown an overall increase in number of stems through 1999. After a dip in 1993 the number has climbed from 129 to 216. The plot is on the top of the dune that is home to the majority of milkweed growing in the Sand Hills. Most of the stems in this colony are located on the face of the dune outside the plot. *A. welshii* has been blown out of the south side of the plot as the sand has been removed by the wind and has been deposited on the dune face. *A. welshii* is not recovering in this blown-out area as it is in Plot 4 (see Figure 3).

Group III: Blowout Areas
(BLM Plot 2 and Plot 2)

BLM Plot 2: The plot is located on the northeast end of the dunes, on the side of a steep, formerly oak-covered dune. Large volumes of sand have been blown away and the plot area is littered with pieces of oak debris with sizes up to 20 cm in diameter and several meters long. This debris helps stabilize the sand and creates numerous pockets on the dune surface where wind effects are reduced. The total number of *A. welshii* stems in the plot has fluctuated from year to year, but continues to have a slight overall upward trend.

Plot 2: This plot is of special interest because of the nature of its population of *A. welshii*. Prior to 1989 virtually all vegetation was removed in a blowout. When the plot was established that year 805, *A. welshii* stems were counted, 680 in the primary stage and 117 in the secondary (Figure 4). Only eight mature stems were present. Many more primary stems were growing outside the plot; they were not seedlings as was first thought. With careful excavation their origins could be traced to mature stems.

Besides *A. welshii* the only other species present consisted of a few clusters of blowout grass, *Redfieldia flexuosa*. The plot seemed ideal to observe changes from a single species to a stable, mixed community of dune perennials.

The number of *A. welshii* stems increased each year until 1995, when it reached 1542 (see Figure 4). During this 7-year period the percent of stems in each of the three stages remained nearly the same. This was unexpected. It was assumed that as *A. Welshii* spread, food accumulation in the rhizome system would lead to an increase in secondary and mature stem numbers, with a relative drop in the number of primary stems. Since 1995 there has been a general decrease in stem numbers but the ratio of the three stem types has remained about the same. So far there has been no maturation of the colony, only a general decrease in stem number (see Figure 4).

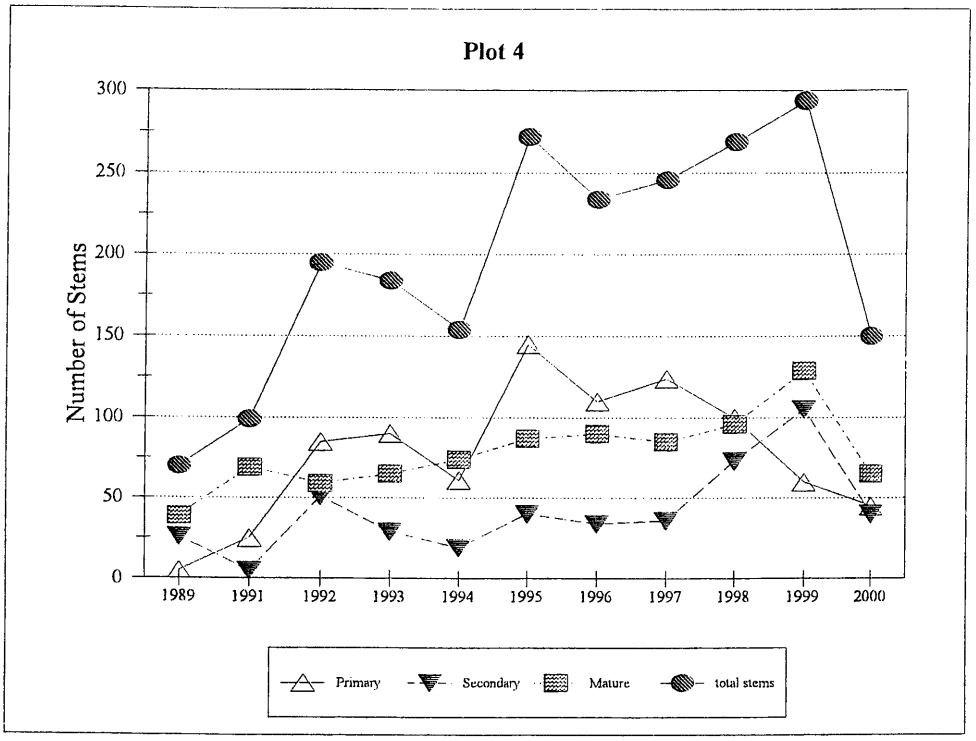
By 1995 other perennial species had become established, so a count of all the species was undertaken. As with *A. welshii*, aerial stems or clusters were counted as separate entities. The counts for rhizomatous species are subjective because each protruding stem was counted even though connections to other stems were known. In 1996, the total count of *A. welshii* as well as the combined total of all other species had decreased. In 2000 the two rhizomatous species, *Eriogonum leptocladon* and *Redfieldia flexuosa*, accounted for 86 percent of the total of all other species, with *Eriogonum alatum* accounting for another 11 percent. The non-milkweed count was more than twice that of *A. welshii* (Table 1).

Other Sites

Plant competition plot: The initial stem number of 7 in 1992 has increased to 338 in 1999 (Figure 5). Most of the increase was in the primary and secondary stages. These two growth forms are the most vulnerable to the effect of the dry windy spring. The decrease in total number of stems in 2000 was greater than in any other plot because of the higher percentage of primary and secondary stems in the plot compared to the other plots.

ORV-impacted site: *A. welshii* stems in this colony have increased steadily until this year (Figure 6). Primary and secondary stem numbers have been greater than the number of mature stems every year. This is consistent with data from other sites where competition is lacking. No other plants occur in the area, enabling the milkweed to spread freely.

Unlike the study plots that are on the crests or sides of dunes, this colony is located in a low area on the lee side of a large dune. Large-scale movement of sand is not obvious, but because of the location there is considerable movement across the site with a relatively small net change in sand deposition or removal.



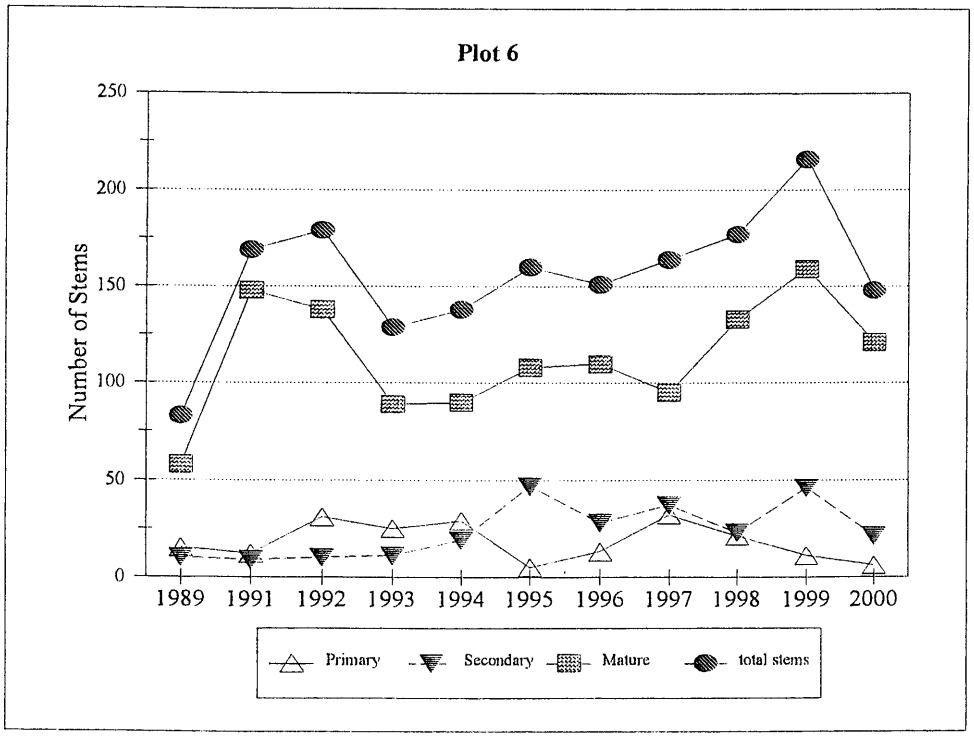
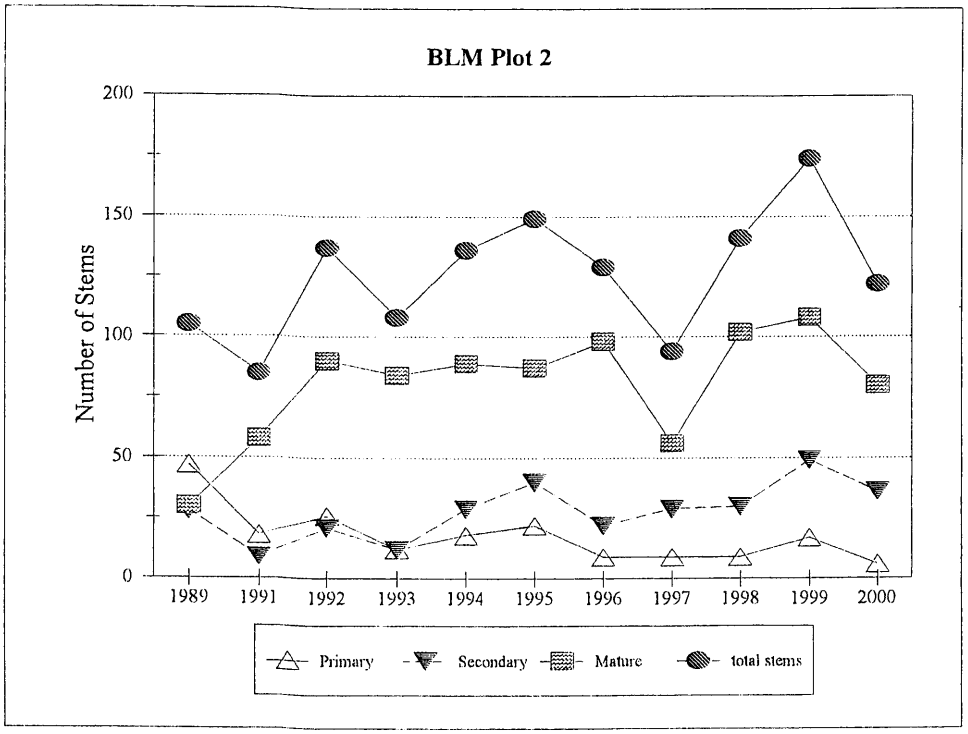


Figure 3. Habitat type II: Plots 4 and 6.



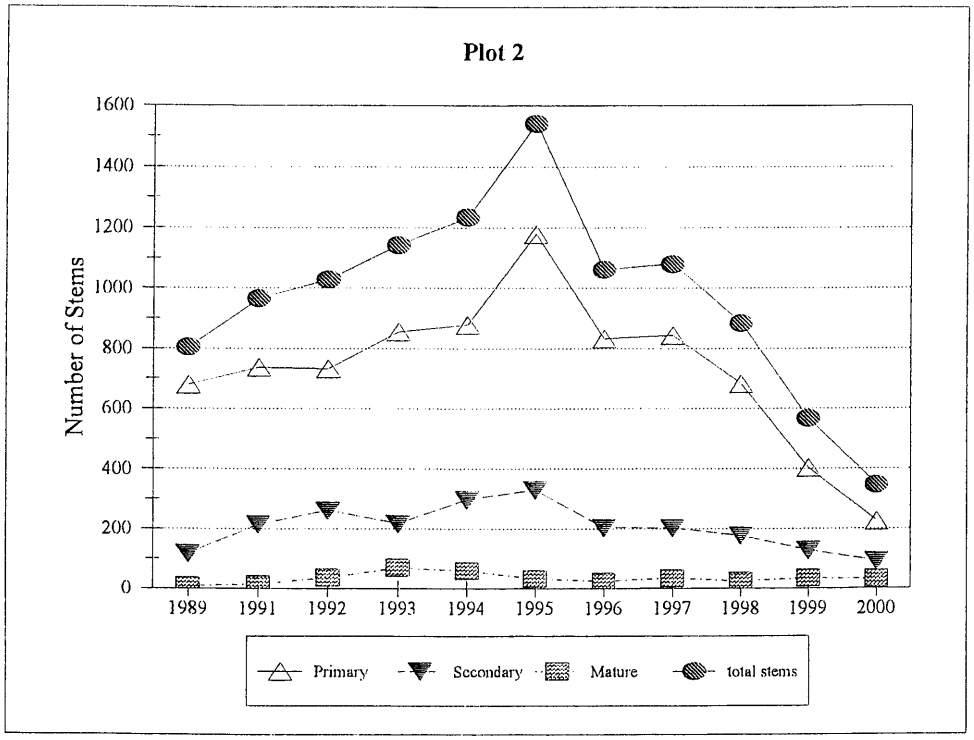


Figure 4. Habitat type III: BLM Plot 2 and Plot 2.

Table 1. Total count of all species in Plot 2 from 1995 to 2000.

Species	1995	1996	1997	1998	1999	2000
Artemisia campestris	3	3	3	2	2	3
Chrysothamnus nauseosus	1	5	3	2	4	2
Eriogonum alatum	48	18	30	17	62	87
Eriogonum leptocladon	157	45	113	108	135	136
Psoralidium lanceolatum	0	0	4	4	7	6
Wyethia scabra	6	2	5	4	4	5
Calamovilfa gigantea	0	0	0	0	0	10
Muhlenbergia pungens	0	0	1	1	1	1
Redfieldia flexuosa	117	34	126	245	229	558
Total other species	332	107	285	383	434	807
Asclepias welshii	1542	1061	1081	884	567	347

Discussion

Asclepias welshii is a pioneer or low seral species that is adapted to the constant change of active sand dunes. Its large flat seeds are rapidly buried by the drifting sand near where they drop from the fruits. They are dispersed only short distances by the wind. Temperature and soil moisture conditions are rarely suitable for widespread germination over large areas at any one time. In most years seedlings are seldom seen, but at times the number of seedlings on a specific dune may exceed 50. Attempts to determine seedling survival over more than one season indicate a survival rate of less than one percent. For example, in July of 1995 while attempting to locate a place for an additional study plot in the Sand Hills, a site was discovered where approximately 80 seedlings were found in an area of about 60 square meters. Upon returning in 1996 to establish a plot that would include the seedlings, not a single milkweed stem was present.

Rhizomes are the chief means of dispersal and survival for *A. welshii.* Clusters of mature stems arise from subterminal meristems of large rhizomes lying 16 cm or more beneath the surface. The tips of these large rhizomes do not elongate appreciably, so that clusters of stems emerge at the same location year after year. Lateral underground branches and single aerial stems having the primary, secondary, and mature forms originate from nodes and branches some distance from the apex of the larger rhizomes. Long rhizome segments exposed by the drifting sand have been found with all three stem types growing from them. Deeply buried rhizomes that escape blowouts are the source of rapid regrowth into highly disturbed areas.

These studies have produced no evidence that ORVs constitute the major threat to the existence of *A. welshii.* The plot where all other species have been removed and the colony growing in the ORV trail are both increasing in the absence of other species. The *A. welshii* population in Plot 2, once rapidly increasing as primary stems grew into unoccupied space, is on the decline as other species begin to spread through the plot.

Plot 5, on the other hand, which acts as a control for the competition plot, is barely able to support a small, static *A. welshii* population in the midst of heavy competition from other species. *A. welshii* in BLM Plot 3 has all but disappeared under extreme competition.

None of the eight plots are in areas that are normally impacted by ORVs. Plot 3 has had vehicle tracks crossing it occasionally in the past, but drifting sand and growth of blowout grass and sand buckwheat around the area have obscured the obvious trails leading to the site. Vehicle visits to the plot have been rare in the past 3 years.

Other plots slightly impacted by vehicle traffic are Plot 6 in the Sand Hills and BLM Plot 2. Plot 6 is remote and rarely visited by anyone. In 1999, however, an ORV rider discovered the dune where the plot is located and spent some time riding through it, making several trips up and down the dune face.

BLM Plot 2 is on the northeast end of Coral Pink Sand Dunes and at one time an entrance or exit trail crossed the corner of the plot. No *A. welshii* grows in the impacted area. In 1997 that end of the dunes was closed to vehicle traffic.

No evidence of ORV activity has been seen at any other plot, yet *A. welshii* populations are declining or barely increasing in all of them. This

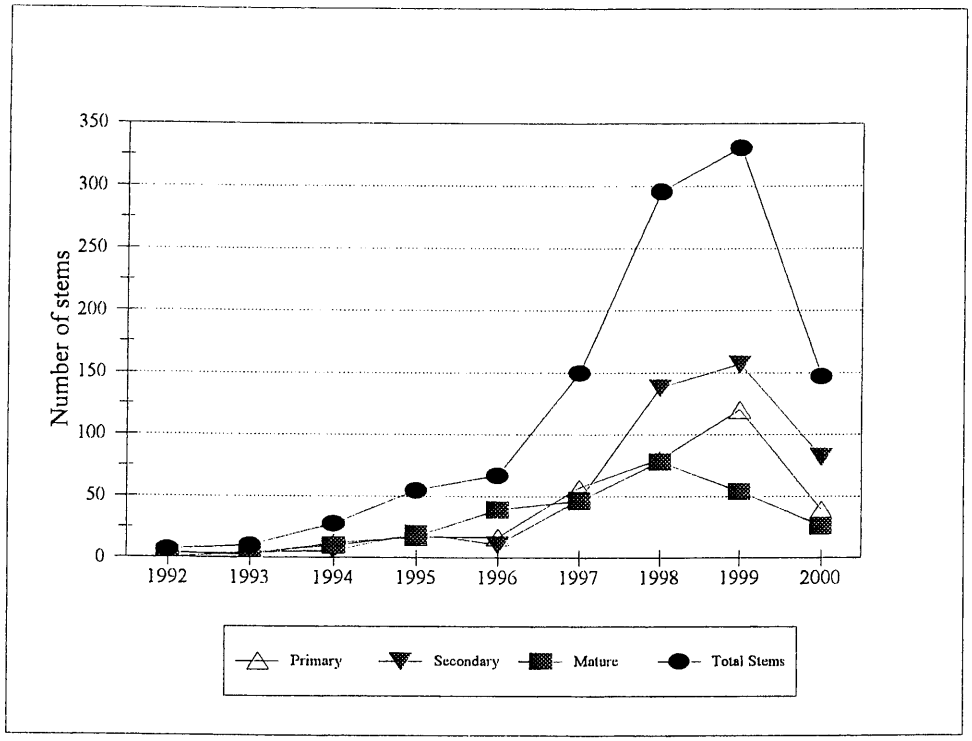


Figure 5. Stems in plot with competition removed.

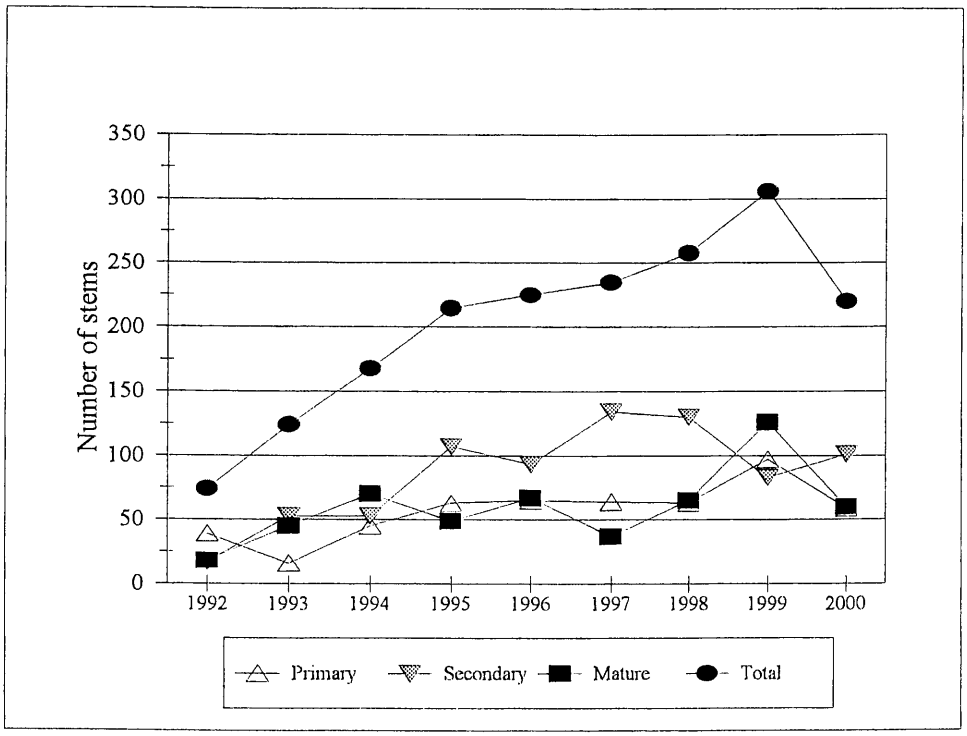


Figure 6. Stems in colony impacted by ORVs.

exemplifies the unstable nature of *A. welshii* colonies. As the habitat waxes and wanes, so does Welsh's milkweed.

Since 1980 Coral Pink Sand Dunes State Park personnel have maintained records of ORV use over the entire dunes area. From 1980 through 1984 there were fewer than 10,000 vehicles per year on the dunes. In 1986 usage peaked at 23,957 ORVs, then dropped to fewer than 7000 in 1991. Since then the numbers have fluctuated between about 6100 and 8700 per year, about a third that of 1986 (Figure 7). Moreover, not all the vehicles counted actually enter the BLM portion of the dunes.

Several factors played a role in sand dune and *A. welshii* management decisions made in the mid 1980s. First, the cost of the Model T of ATVs (all-terrain vehicles), the Honda three-wheeler, was within the budget of almost anyone who had an interest in such things. As a result ATV sales, as well as ORV numbers at Coral Pink Sand Dunes, soared (see Figure 7). At about the same time efforts to protect *A. welshii* were initiated, resulting in its official listing as a threatened species in 1987. The huge influx of ORVs resulted in the government policy statement that "ORVs constituted the single greatest threat to the survival of *A. welshii*." The Welsh's milkweed recovery plan (U.S. Fish and Wildlife Service 1992) also listed ORVs as the major threat to *A. welshii* survival.

While these events were transpiring, the sale of new three-wheeled ATVs was banned. Since few casual three-wheeler users could afford a four-wheeled ATV, the use of ORVs on the sand dunes dropped rapidly. The annual use of ORVs since 1991 has fluctuated between 6500 and 8500 vehicles.

Anyone currently traveling anywhere in southern Utah can't help but be impressed by the number of four-wheeled ATVs being transported about in trailers or pickups; it is obvious that possession of four-wheelers is no longer limited to the wealthy. It could easily be assumed that a proportionate number of these vehicles are headed for Coral Pink Sand Dunes. The figures, however, do not bear out this assumption. There has been no such increase in activity. The main reason for this is that the new four-wheelers are purchased primarily for hunting or other mountain-related activities. They are not designed for travel on sand dunes. In the higher gears they don't have the combination of power and speed necessary to traverse the high steep dunes, and in low gear excess power tends to cause them to bury themselves in the sand as they attempt to climb a dune. The two-stroke, racing-type machines perform much better on the dunes but they do not have the versatility or general appeal of the four-trax type of ATV. Consequently their use on the dunes has not increased.

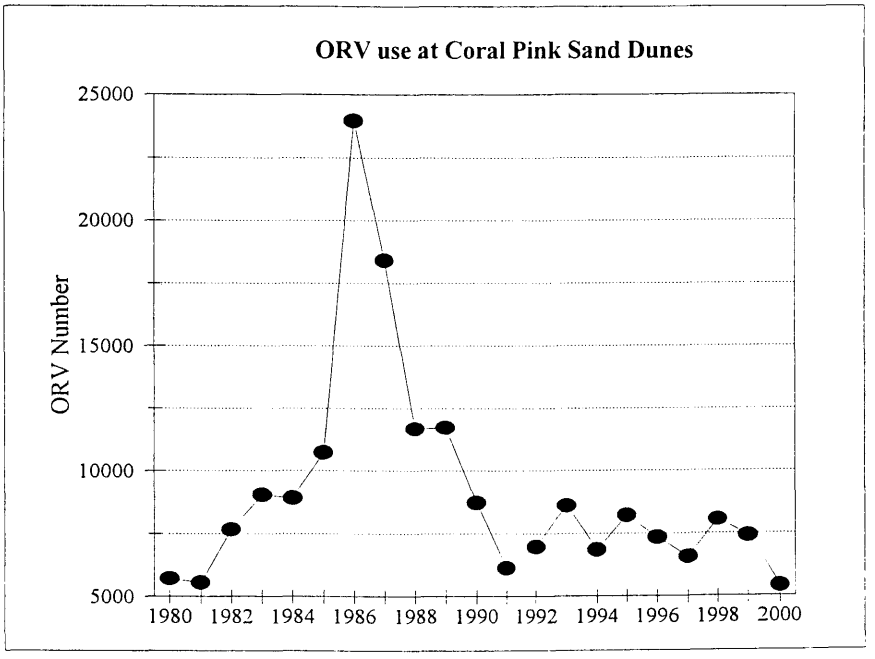


Figure 7. Annual use of ORVs at Coral Pink Sand Dunes.

For the past 4 years dune buggies have been counted separately from other ORVs, but their numbers are included in the totals. They have not shown an increase in this period, continuing to make up about 10 percent of the ORV total each year.

This study of *A. welshii* was initiated near the end of the major ORV impact period, which also coincided with a serious education and enforcement effort by state and federal agencies designed to keep riders on open areas and trails and off the dune vegetation. Twelve years of observation has shown that compliance with these objectives has improved, although some individuals still do not comply and damage to the vegetation still occurs.

In the development of a management plan for *A. welshii,* the most fundamental issue, the species' position in the sand dunes community, has not been addressed. *A. welshii* is not a component of a stable dunes community; it is a pioneer on open moving dunes, disappearing as the dunes become stabilized by shrubs and grasses. It thrives under disturbed conditions where competition is reduced or eliminated. Such conditions may be found on actively moving sand dunes or in other disturbed sites. In the Sand Hills, *A. welshii* is restricted to the still-moving front of the Sand Hills themselves, the only remaining "active" dune in the system.

The majority of *A. welshii* plants on the Coral Pink Sand Dunes are found on dune faces, dune crests, or as remnants of colonies along the edges of blown-out areas. None of these locations suggest that *A. welshii* is a member of a stable, mature dune community.

A. welshii is a "new" species; consequently, in the past its distribution and abundance was unknown and of no interest. Old photographs in the possession of Coral Pink Sand Dunes State Park show that plant cover on the dunes has increased in recent years. This could mean that *A. welshii* was more abundant in the past when there was less vegetation. Its present distribution may be simply a reflection of the adaptation of *A. welshii* to a habitat that is continuing to shrink, not because of disturbance but because of lack of disturbance. If this is the case, as these studies suggest, then a management plan that would increase the numbers of *A. welshii* must include provisions for reducing competing vegetation, possibly by chemical or mechanical weeding. Excluding man and his machines from the Coral Pink Sand Dunes, no matter how well intended, will not help solve the problem of the survival of *Asclepias welshii.*

Acknowledgments

This study has been funded through a challenge cost share agreement with the Bureau of Land Management. This support is greatly appreciated. Many thanks go to Lori Armstrong for her assistance in the field as well as her general encouragement and support, and to Ron Bolander of the Utah BLM office for his personal interest and involvement in the project. Personnel in both the Cedar City and Kanab BLM offices have also been very helpful. The help of Richard Brooksby, Kenneth Richards, Brady and Kyle Houston, and Jodi and Brian Palmer in collecting field data is also gratefully acknowledged.

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The Demography of a Small Population of Yellow Columbines in the Organ Mountains

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Abstract: Yellow-flowered columbines (*Aquilegia chrysantha* Gray) are usually found in small, isolated populations near streams and pools in mountain ranges throughout the southwestern United States. To study the long-term dynamics of these populations, which are vulnerable to extinction, we have monitored the demography of a population in Fillmore Canyon in the Organ Mountains of southern New Mexico. Annual estimates of growth, survival, and reproduction were recorded for 2,152 individuals in 15 one-meter square plots for 6 years. We estimated a seed bank survival rate from experimental plots and constructed annual size-structured transition matrices to determine population growth rates. Annual growth rates varied widely between 0.46 and 1.72 and were strongly correlated with spring precipitation. We calculated a weighted mean matrix, based on the historical frequency of spring rainfall events, resulting in a population growth rate of 1.02. The relationship between population growth rate and precipitation was used to calculate a mean growth rate from 75 years of recorded climate data and to project future growth rates under different climate conditions. These methods provide both an additional approach to modeling population persistence and a clearer understanding of the likelihood of extinction for a species dependent on mesic habitat in Fillmore Canyon.

Demographic studies often model the likelihood of population persistence based on empirical data collected from the entire life cycle of individuals and projections of population growth rate, size, or structure (Menges 2000). These projection models generally rely on a few years of data that may not adequately represent the species' population dynamics or environmental conditions (Menges 2000, Bierzychudek 1999, Damman and Cain 1998). Long-term studies have typically found considerable variation in demographic rates over time (Oostermeijer et al. 1996, Horvitz and Schemske 1995). Short-term studies, such as Beirzychudek's (1982) study of jack-in-the-pulpits, often fail to accurately project changes in population size. After revisiting her two study populations 15 years later, Beirzychudek has suggested (1999) that one possible limitation of her projection model was the limited time available to accurately capture the complete range of year-to-year environmental variability.

The feasibility of a long-term plant demography study is a concern for land managers who need to budget, plan, and justify rare plant studies. In combining demographic and rainfall data collected from a small population of *Aquilegia chrysantha* Gray (yellow columbines) in the Organ Mountains of New Mexico, we focused on reconciling some of the problems inherent in projection models that rely on just a few years of data.

Precipitation in the Southwest is quite variable. Regional correlations in precipitation are implicated in cycles of tree dynamics and shrub invasions of grasslands (Swetnam and Betancourt 1998), and at smaller scales with plant cover, seedling establishment, and primary productivity (Ernest et al. 2000, Bowers 1997, Sala et al. 1988, Beatley 1974). Population growth rates of this particular columbine population varied widely between years and were also correlated with spring precipitation. Therefore, we used a 75-year precipitation record to calculate a weighted mean matrix based on the frequency of "good" and "bad" rainfall years encountered in the present study and to check how well the past six rainfall events represent the possible range of environmental variation at our study site. We also utilized the relationship between population growth rate and precipitation to calculate a mean and median growth rate from 75 years of recorded climate data and to predict future growth rates under different climate conditions. Finally, we discuss the methods used to monitor the demography of *Aquilegia chrysantha*, a plant with a complex life history that includes dormant seeds and dormant plants.

Methods

Aquilegia chrysantha Gray (yellow columbine) is a perennial herb restricted to mesic habitats near streams, pools, and cliffs in mountain ranges

throughout the southwestern United States and Mexico. Charles Wright first collected the species in 1852 in "wet springy soil, ravines in the Organ Mountains" (Wooton and Standley 1915, Shaw 1987). Based on Wright's plant list (Shaw 1987) and a detailed description of the area by John C. Bartlett (1854) a few months later, the holotype population is probably at or near the springs in Fillmore Canyon where our study site is located.

The Organ Mountains of south-central New Mexico form a relatively small, isolated mountain range with mesic canyons that are characterized by a large number of rare and endemic plant species (Debruin 1996). A population of yellow columbines in Fillmore Canyon, which drains the central-western slope of the Organ Mountains, was censused annually beginning in April of 1995. The study site is at the springs on a north-facing outcrop of limestone at 1890 m elevation. During periods of normal late summer and winter precipitation, water seeps continuously down the moss-covered slope.

New growth of yellow columbines occurs primarily in the spring, although flowering will continue late into the monsoon season. The yellow flowers are protandrous and self-compatible, with five long petal spurs filled with nectar. The pollinators are primarily short-tongue hawkmoths (Miller 1985). The fruits have five follicles that dehisce apically, and the small black seeds lack any specialized adaptations for dispersal. One flowering stalk develops from a single rosette with four to six leaves. The following season, rosettes that produced a flowering stalk have died, and usually another rosette develops on the caudex directly below the old rosette. Older plants produce a branching, woody caudex with one to several rosettes. In dry years, the caudex can serve as an organ of dormancy, and no rosettes will develop.

Field Sampling

Two types of 1 m^2 plots were established in Fillmore Canyon in April of 1995 (Figure 1). One set of 15 plots was used to monitor the demography of *A. chrysantha* individuals. Another set of 10 plots was established to monitor the emergence of seedlings from the seed bank by removing immature fruit from plants both on and within 1 m of each plot during the first three seasons.

To select the study plots, a grid of 1 m^2 was mapped on a 30 x 10 m area of columbine plants on the north-facing slope. Eighteen transects were placed upon this grid, and 15 plots were chosen at random to monitor the demography of columbine individuals. Another 10 random plots were se-

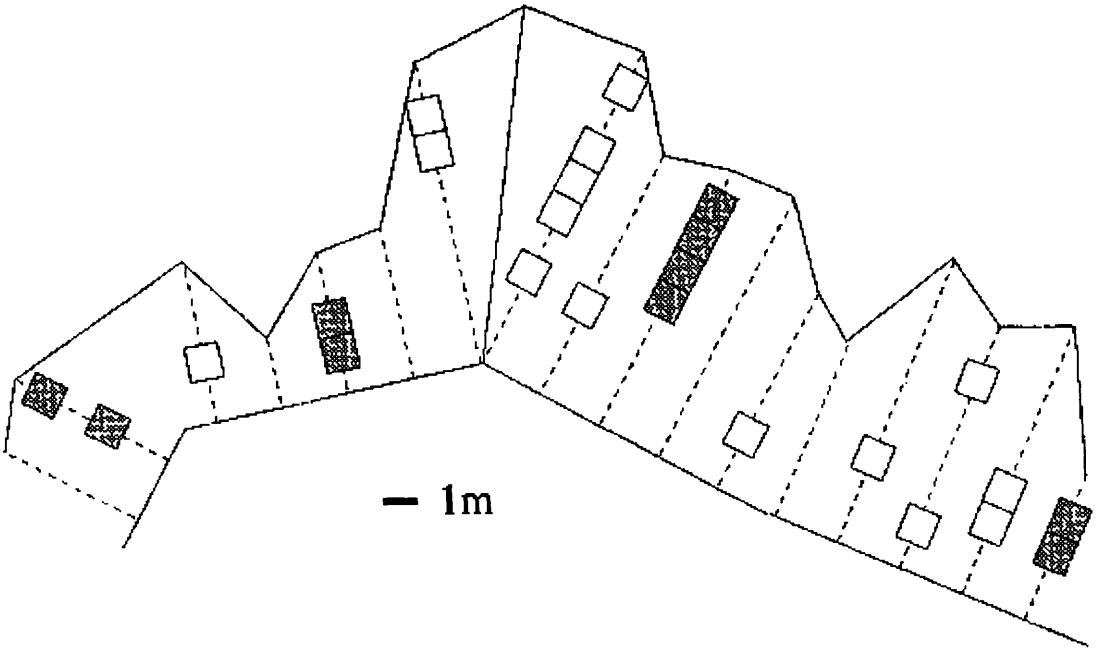


Figure 1. Map of the Fillmore Canyon population. Experimental seed rain removal plots are indicated by shaded boxes and demography plots are indicated by white boxes.

lected for the seed rain exclusion experiment, subject to the constraint that they did not fall within 2 m of the demography plots. This was intended to prevent seed movement into these plots and to minimize the effect of fruit removal on the 15 demography plots. Plot corners were marked with rebar and numbered with an aluminum tag; the dimensions of the demography plots were measured and detailed maps were made.

To obtain estimates of survival, growth, and reproduction, we conducted a complete census of each plot annually in May just before plants started producing flowers (Figure 2). The fates of individual plants were determined by relocating mapped and tagged plants in the next growing season. Large plants were marked by attaching aluminum or laminated tags around the base of the caudex with insulated telephone wire. Seedlings and small plants were marked with very small laminated tags placed on a colored plastic cocktail sword. Detailed maps of tagged plants were made in the field and later digitized to help relocate plants in subsequent years. This year, only 18 of 765 tags from the previous year were not found; in previous years the percentage of lost tags ranged from 10.9 to 24.3 percent. Individuals missing tags were identified from locations on digitized maps.

We measured two indices of plant size; total number of leaves and total number of rosettes. Because a rosette can produce a single flowering stalk, we used the number of rosettes to define size classes. Before 1998, rosette numbers were not counted, so for those early years we divided size classes into leaf number intervals based on the relationship between rosette number and leaf number (corresponding to leaf number intervals of 1–5, 6–11, 12–17, 18–23, >23 leaves). Additional size classes recognized in the life cycle of a columbine include dormant plants, seeds in the seed bank, and new recruits (plants that have germinated in the fall or spring before the annual census).

To estimate reproduction, we counted inflorescences, buds, flowers, immature fruits, and mature fruits periodically (about every 3 weeks) until the end of the summer monsoons. Mature fruits were marked with a small piece of wire, and the total number of fruits that dehisced throughout a season was used as a measure of total fruit set. Seed production per plant was estimated from seed counts of fruits collected nearby in 1995 and 1999. Note that since the size of plants was determined just prior to flowering, values for fertility in a prebreeding census also include the probability of seeds surviving to the next census (Caswell 2001).

A difficult transition to assess is the survival rate of seeds within the seed bank from year to year, because one can estimate seed fate probabilities only by experimental manipulation. We used data from the seed rain removal plots to estimate this survival rate (Strand 1997). The number of seedlings recruited into these plots, St, was measured by direct counts in each of 3 years (1995–1997). We assumed a model of geometric decay in the size of each seed bank cohort in which seeds are lost to germination at a constant rate or survive until the next year at a constant rate. The germination rate, g, was estimated as the ratio of the average number of seedlings m^{-2} that germinated from the first year's seed rain to the total seed rain m^{-2} (Figure 3). We assumed that g does not vary among plots or in time (but see Horvitz and Schemske 1995 who estimated different germination rates in "good" and "bad" years). We used the estimate of g in the following model to estimate the survivorship of seeds in the seed bank, s, and the number of seeds in the seed bank, No, from the emergence of seeds in the experimental seed rain plots, St, in a given year, t:

$$S_t = N_o [s (1-g)]^t g$$

Finally, we also assumed that g does not vary between newly produced seeds or seeds in the seed bank (both are found on the surface of the limestone in cracks or moss). This assumption was needed to estimate the relative contributions of seeds from flowering plants and seeds in the seed bank to new recruits the following year in the construction of transition matrices.

Daily rainfall data were collected and summed 6 months prior to the annual census (Dec-May) from a remote automated weather station at Dripping Springs established in 1994 (Lat 32° 19' 24" N, Long 106° 35' 12" W, elevation 1881 m) and from a cooperator network station at the Jornada Experimental Range established in 1926 (Lat 32° 31' 17 N, Long 106° 47' 50" W, elevation 1359 m).

Transition Matrix Model

We used a stage-based projection matrix model (Leftovitch 1965). The form of the model is $\mathbf{n}(t+1) = \mathbf{A}\mathbf{n}(t)$ where $\mathbf{n}(t)$ is a vector of all the individuals in the population at time t classified by stage, $\mathbf{n}(t+1)$ is the vector of the population at the next census, and $\mathbf{A}$ is a matrix of transition probabilities between different stages from time t to t + 1. When the matrix $\mathbf{A}$ is multiplied by $\mathbf{n}(t)$ and

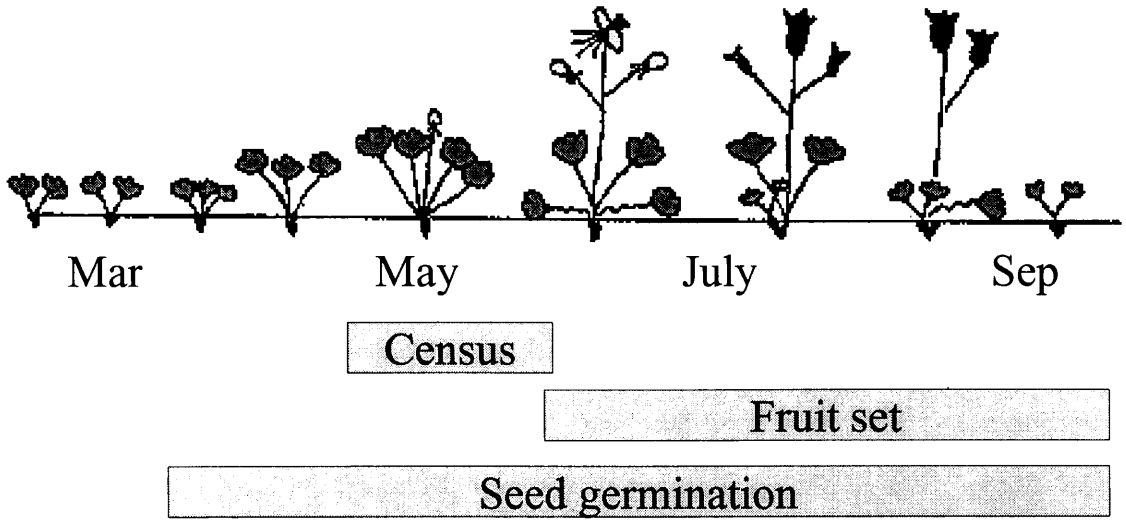


Figure 2. Diagram of *Aquilegia chrysantha* phenology and timing of the annual census, fruit set, and seed germination. Mature fruits are marked and counted about every 3 weeks until the end of fruit set.

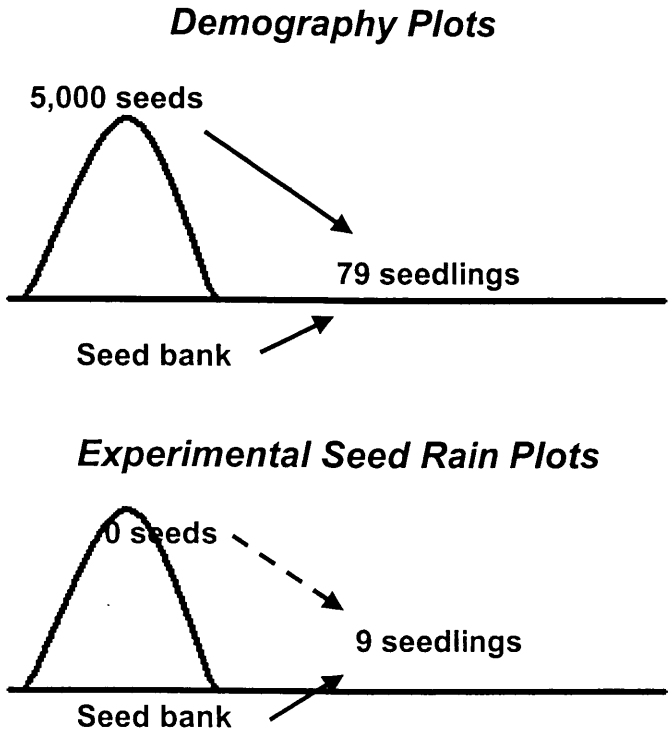


Figure 3. Diagram of the seed germination experiment in 1995. By eliminating the production of seeds falling into the seed rain plots, we estimated the relative contributions of both the seed bank and seeds released from fruits to new recruits. The germination rate is (79 – 9)/5000 = 0.014. Assuming an equal germination rate, the initial seed bank size is 9/0.014 = 9645 seeds.

subsequent products a number of times, eventually the population converges to a stable stage distribution at which time each stage is changing by a factor of λ (lambda) each time period. Lambda, or the population growth rate, quantifies the change in number of individuals through time. When $\lambda > 1$, a population is projected to increase over time; when $\lambda < 1$, a population is projected to decline.

We constructed annual, mean, and product matrices and calculated the dominant eigenvalue corresponding to the population growth rate (Caswell 2001). A weighted mean matrix was also constructed by weighting the total frequency of annual matrices in above-average rainfall years at 0.5, and those occurring in below-average rainfall years at 0.5. Annual growth rates were regressed on spring precipitation, and the resulting regression equation was used to estimate annual population growth rates from 75 years of recorded climate data. All matrix algebra was done using Numeric Python, a module of the programming language Python that we use to manipulate matrices and to generate queries to a large demography database (Python version 2.0 available at www.python.org). The regression analyses were generated using SAS/STAT software (SAS 1999).

Results and Discussion

We followed the fates of 2,152 plants in Fillmore Canyon over the last 6 years. The number of individuals within each size class varied considerably throughout the 6 years (Table 1). Flowering plants produced 577 mature fruits in 1995, followed by 252, 16, 314, and 313 mature fruits during the years 1996–1999 respectively. On average, fruits collected outside of the plots in 1995 produced 130 seeds (95% confidence interval is 110–150 seeds, Strand 1997) and 141 seeds in 1999 (n = 10, s = 54). The seed germination rate was estimated at 1.4 percent (see Figure 3). Combined with direct counts of the number of seedlings recruited into the seed rain removal plots (9, 3.6, and 0.6 recruits in 1995–1997), the seed bank decay model estimated a 12.6 percent seed survival rate and initial seed bank size of 13,100 seeds ($R^2 = 0.82$, Strand 1997).

The mean spring precipitation over the last 75 years at the Jornada Experimental Range was 6.33 cm (CV = 64%). During this study, average rainfall (6.50 cm) was recorded in spring of 1998, below-average rainfall (2.06, 2.51, and 3.43 cm) in the spring of 2000, 1996, and 1999 respectively, and above-average rainfall (9.75 cm) in the spring of 1997. Also, 78 percent of recorded observations at the Jornada weather station are within the range of conditions experienced in the last 6 years (Figure 4). However, of the 14 spring rainfall events outside this range, 10 were more extreme, and these high rainfall years may be very important for plant demography (e.g., Bowers 1997).

Population growth rates calculated from annual transition matrices varied between 0.46 and 1.72 (Table 2). Both the mean and product matrices project a population growth rate of less than one, whereas the population growth rate calculated from the weighted mean matrix was 1.02, indicating a relatively stable population. However, increasing the frequency of below-average rainfall years occurring in the weighted mean matrix to 54 percent results in a population growth rate of 1.00. Therefore, a long series of years with below-average rainfall would likely increase the risk of extinction in this small population.

The regression equation (growth rate = 0.132 precipitation + 0.331) describing the relationship between population growth rate and spring precipitation was significant (p = 0.036, Figure 5), providing further support that this population is sensitive to changes in rainfall conditions. To provide a potential long-term demography data

Table 1. Vectors of the size class distributions for *Aquilegia chrysantha* from 1995 to 2000 at Fillmore Canyon. Seeds in the seed bank were estimated from a 12 percent survival of the seed bank plus the relative contributions of seeds produced by flowering plants in the preceding year.

Size Class	1995	1996	1997	1998	1999	2000
Seed bank	9645	10684	5474	952	5263	5790
Recruit	79	15	555	394	315	9
1 rosette	360	223	75	137	220	115
2 rosettes	149	79	77	79	66	56
3 rosettes	47	29	37	37	38	34
4 rosettes	26	8	23	26	20	18
5+ rosettes	19	2	22	21	42	21
Dormant	0	41	5	0	3	83

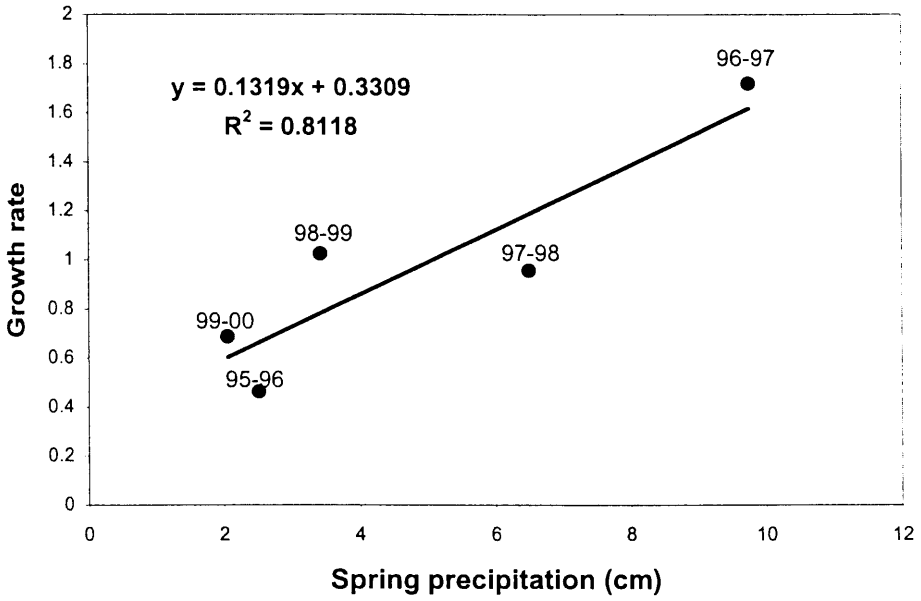


Figure 4. The relationship between spring precipitation and population growth rate at Fillmore Canyon.

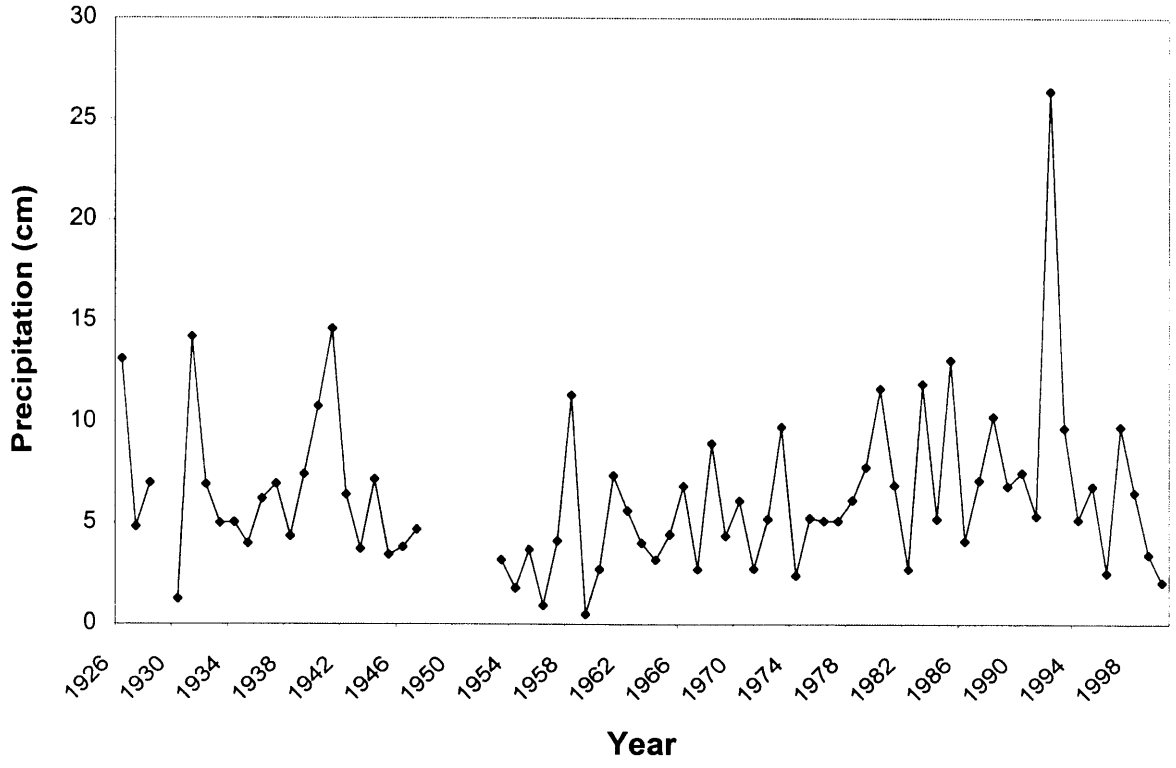


Figure 5. Spring precipitation (Dec-May) at the Jornada Experimental Range. The last six points on the graph represent the time span of the current study.

Table 2. Annual population growth rates for *Aquilegia chrysantha* from annual matrices, plus the growth rate calculated from the mean, weighted mean, and product matrix.

Transition matrix	Growth rate
1995–1996	0.464
1996–1997	1.720
1997–1998	0.957
1998–1999	1.025
1999–2000	0.688
Mean	0.963
Weighted mean	1.023
Product	0.541

set, we used the historical spring precipitation records and the regression equation above to estimate annual population growth rates at Fillmore Canyon since 1926. The distribution of these estimated growth rates is shown in Figure 6. The median growth rate of this 75-year period is 1.02 and the geometric and arithmetic means are 1.07 and 1.18 respectively, indicating a relatively stable to increasing population.

We also used the relationship between population growth rate and spring precipitation to check the effect on columbine population growth rate of weather forecasts predicting rainfall at 75 percent of normal in the Southwest for the next 30 years. As an initial approach, we multiplied the historical climate records by 0.75 and calculated new growth rates using the regression equation. The median growth rate of this new distribution is 0.85 and a geometric and arithmetic means are 0.89 and 0.96 respectively, indicating a declining population.

Finally, stochastic modeling of environmental variation typically involves calculation of annual transition matrices, which are assumed to occur independently, with equal probability, and to represent environmental conditions at a study site (Bierzychudek 1982, Menges 1990, Dammon and Cain 1998). Then, models of the distribution of population growth rates over a given time period or time to extinction (persistence times) are calculated by randomly sampling from the set of annual matrices. We plan to investigate the effects of assigning equal probability to annual matrices in typical stochastic models, and how unequal weighting of the matrices based on historical precipitation records would affect the outcome of persistence times. This approach was first used by

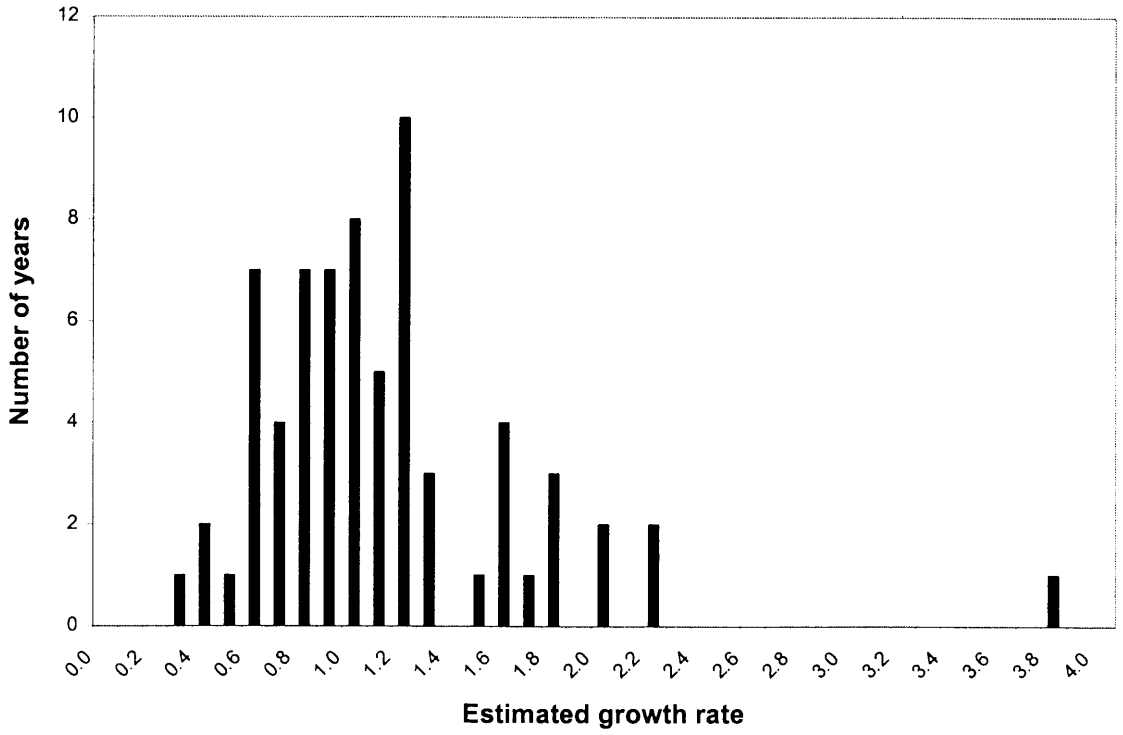


Figure 6. The distribution of annual population growth rates estimated at Fillmore Canyon since 1926. The median growth rate is 1.02 and the geometric mean is 1.07.

Aberg (1992), who modeled the stochastic growth rate of an intertidal seaweed based on frequencies taken from historical records of the amount of ice cover. These methods are particularly suited to plants in arid environments, where there is a correlation between the amount of rainfall and vital rates. Given a long-term record of precipitation and a few years of demographic data, the frequency of rainfall events can be used as the stochastic process to generate the sequence of matrices in a stochastic model.

Acknowledgments

T & E, Inc. and the Department of Biology at New Mexico State University provided funding for this study. Allan Strand recorded most of the initial field data and designed the seed germination experiment. Kelly Gallagher, Quetzal Torres, Meli Mandujano, Jordan Golubov, Tony Stout, Brie-Anne McKernan, and Bianca Tapia also provided assistance in the field.

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Monitoring Update on Four Listed Plants on the Arizona Strip

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Abstract: Four listed plants on the Arizona Strip are being monitored for various population characteristics. *Pediocactus sileri* Engelm. L. Benson and *P. bradyi* L. Benson have been monitored since 1985-86, *Asclepias welshii* N & P Holmgren since 1989, and *Cycladenia humilis* Benth. var. *jonesii* Welsh & Atwood since 1993. The two pediocactus species were monitored in plots where each cactus was tagged, measured for height or width, and mapped; how many cactus fruited and the mortality rate were also noted. *Asclepias welshii* plants were counted and mapped, and each stem was checked for follicles. Seedlings were also noted. The *Cycladenia humilis* var. *jonesii* were counted and checked for follicles in two plots. The size structure of *Pediocactus sileri* has shown a strong shift to the smaller size class from the mid-size class. *Pediocactus bradyi* has also shifted to the smaller individuals. The counts on the *Cycladenia humilis* var. *jonesii* and *Asclepias welshii* populations through the years have demonstrated ups and downs in population numbers, probably in line with precipitation amounts. Management plans have been implemented for the two pediocactus species to deal with the threats listed for the species: livestock trampling, off-road vehicle activity, mineral activity, and collection. There is a recovery plan for the *Asclepias welshii* (Welsh's milkweed), but not for the cyclad.

The Arizona Strip District of the Bureau of Land Management (BLM) has four federally listed plants. Two of the plants have management plans, one has a recovery plan, and one has no plan to prescribe management. All four have established plots that are monitored every year.

The Siler pincushion cactus *Pediocactus sileri* (Engelm.) L. Benson has been protected under an implemented Habitat Management Plan (HMP) since 1987 (BLM 1987). The Siler pincushion grows in the broad Moenkopi soil formation that ranges from St. George, Utah to the Kaibab Plateau in northern Arizona. It grows specifically on the Red and Shnabkaib members of that formation. There are 330,000 acres of habitat and potential habitat. HMP actions completed by 1990 were monitoring, placing off-road vehicle closure signs around Warner Ridge in the Utah portion of the habitat, constructing a 200 acre exclosure in the Fort Pearce part of Arizona, and placing four raptor poles in the Atkin Well allotment. The HMP for Siler pincushion cactus, which is classed by height, set a healthy near-term objective of increasing by 20 percent the size classes of 0–4 cm, 4–8 cm, 8–12 cm, 12–16 cm, and 16+ cm.

Brady pincushion cactus, *Pediocactus bradyi* L. Benson, has been managed under an HMP since 1986, and under the Marble Canyon Area of Critical Environmental Concern (ACEC) Management Plan since 1994. It grows along the Marble Canyon rim and its tributary canyon rims of the Colorado River. This plan has been aggressively implemented especially with emphasis towards off-road activity and livestock watering facilities. Due to accessible terrain along the Marble Canyon rim, signs, rock barriers, and fences have been put in place to define where not to drive and why. Interagency law enforcement has helped achieve compliance with vehicle activity restrictions. Livestock water has been relocated to prevent heavy livestock activity on the rim. Brady pincushion cactus is classed by width, rather than height. The objective for a healthy width size for all four plots of cactus is an average of 70 percent in the 0–15 mm size class and 30 percent in the 15–30+ mm size class. One plot, since establishment, has not had livetock influences on it. The other three are subject to livestock use (BLM 1994).

Welsh's milkweed, *Asclepias welshii* N & P Holmgren, is managed under a recovery plan implemented in 1992 (U.S. Fish and Wildlife Service 1992). This plant occurs in a widespread manner throughout the Paria Canyon–Vermilion Cliffs Wilderness, which contributes to the physical protection of the plant by not allowing off-road vehicle access. The Jones cyclad (*Cycladenia humilis* Benth. var. *jonesii* Welsh & Atwood) in Arizona is currently under neither a recovery nor a management plan. The Jones cyclad grows in the Chinle Formation (BLM 1999). This plant occurs on steep

slopes and it appears little threatened by livestock and off-road vehicles. The area is remote and it draws little attention from the public. However, efforts are underway to amend the Resource Management Plan for the public lands of the Arizona Strip to develop protective actions for this plant (BLM 1999).

Methods

The Brady and Siler pincushion cacti are monitored in square or rectangular plots. The plot sizes for each cactus are shown in Tables 1 and 2. Plot locations were selected using the following criteria: cactus, or other plants to be studied, are present in reasonable quantities, access is easy, and the location is in an area that shows the effects of land uses and man-induced mortality causes. All Brady and Siler pincushions are mapped and tagged at each plot. The Siler pincushion height is measured from the base of the plant to the tip of the spines at the top of the cactus; for the Brady pincushion only the width is recorded. One plot at Atkin Well is in a livestock exclosure and an adjacent plot is under the influence of livestock. The cacti are also evaluated for fruit production and mortalities and causes thereof (BLM 1987, 1994). The comparison of size classes for Brady pincushion cactus is made with a little difficulty because size classes were lumped differently in the 1980s than after 1994. The change was made because it was determined that at about the 15 mm size, the cactus begins to flower.

Welsh's milkweed is monitored by charting the plants on a map of the sand dune plot. The clump of milkweed is counted at each location, and then marked on the map with the number of plant stems, the number of stems with seed pods, and the number of seedlings. Plants are widely scattered and are easy to count (BLM 1999).

Jones cyclad is monitored in two 10 m x 10 m plots. All plants are counted, and those with follicles are counted separately. These plots occur on very steep slopes with fragile soils, so observers are prevented from marking each ramet, as working in the plot would destroy the plants. Counts are done until two consecutive counts come within a small difference of each other (BLM 1999).

Results

The size structure information given in Table 1 demonstrates that Siler pincushion cactus shifted to a large proportion of small cactus (young) from a predominantly larger size class in the 1980s. All

Table 1. *Pediocactus sileri* size structure.

Year	Height class (cm)	Number in height class	Percent in height class
Location: Yellowstone (size 30 x 45.5 m)			
1985	0–4.9	11	11%
	5–8.9	42	42%
	9–12.9	36	36%
	13–16.9	9	9%
	17+	2	2%
	Total cactus	100	
1998	0–4.9	79	60%
	5–8.9	44	34%
	9–12.9	8	6%
	13–16.9	0	0
	17+	0	0
	Total cactus	131	
Location: Atkin Well (Size of exclosure plot 444 x 360 x 330 x 468 ft; subplot 12 x 16 m. Outside plot 234 x 426 x 294 x 390 ft; subplot 17 x 17 m.) Numbers in parentheses are for exclosure cactus.			
1988	0–4.9	16 (6)	15% (8%)
	5–8.9	31 (17)	32% (22%)
	9–12.9	31 (23)	32% (29%)
	13–16.9	15 (20)	15% (29%)
	17+	4 (12)	5% (26%)
	Total cactus	96 (78)	
1997	0–4.9	42 (19)	57% (63%)
	5–8.9	8 (0)	11% (0)
	9–12.9	18 (11)	25% (37%)
	13–16.9	3 (0)	4% (0)
	17+	2 (0)	3% (0)
	Total cactus	73 (30)	
Location: Johnson Spring (Size subplot 1, 150 x 66 ft; subplot 2, 66 x 66 ft.)			
1989	0–4.9	39	71%
	5–8.9	15	27%
	9–12.9	1	2%
	13–16.9	0	0
	17+	0	0
	Total cactus	55	
1998	0–4.9	63	90%
	5–8.9	7	10%
	9–12.9	0	0
	13–16.9	0	0
	17+	0	0
	Total cactus	70	

Table 2. *Pediocactus bradyi* population structure.

Year	Width class (mm)	Number in size class	Percentage in size class
Location: Soap Creek Plot (Road closed in 1994; grazed by livestock.)			
1986	0–4.9	0	0%
	5–19.9	4	11%
	20–30.9	19	54%
	31+	12	35%
	Total cactus	35	
1998	0–15	25	19%
	15–30	91	70%
	31+	15	11%
	Total cactus	129	
Location: Badger Creek Plot (Road open to traffic; no grazing since 1980.)			
1988	0–4.9	0	0%
	5–10.9	11	15%
	11–20.9	18	26%
	21–30.9	32	46%
	31+	9	13%
	Total cactus	70	
1998	0–15	119	78%
	15–30	33	22%
	31+	1	0
	Total cactus	153	
Location: North Canyon west and east plots (Remote from roads; grazing.)			
1988	0–4.9	0, 0	0%, 0%
	5–10.9	3, 0	9%, 0%
	11–20.9	3, 19	9%, 22%
	21–30.9	22, 50	66%, 58%
	31+	5, 17	16%, 20%
	Total cactus	33, 86	
1998	0–15	19, 17	39%, 28%
	15–30	29, 41	59%, 69%
	31+	1, 1	2%, 2%
	Total cactus	49, 59	

plots for Siler pincushion have met their HMP objective for the 0–4.9 cm height class, which is to be at least 20 percent of the plot population. This is thought to be enough small and young plants to sustain the population. Siler pincushion plots now range from 60 to 90 percent for that size class. In the 1980s, only one of the three plot areas was above 20 percent for the 0–4.9 cm height class. Mortality data (not shown in the tables) reveal that the overwhelming majority of deaths of this cactus are from natural causes, mostly rabbits, old age, and insects. This continues a pattern reported by the BLM (1991) and Hughes (1992). Siler pincushion was downlisted to threatened in 1994 as a result, in part, of the above data.

The Brady pincushion data (Table 2) are encouraging in that the Badger Creek plot has met the team-generated objective in the ACEC Management Plan of 70 percent in the 0–15 mm width class and 30 percent in the 15–30+ mm width class (BLM 1994). The Soap Creek and North Canyon plots have not met that objective, but have shown significant increases in the 0–15 mm class from what the 1984–1991 readings show. The 15–30 mm class continues to predominate in these two plots. This increase in young or small plants at Badger Creek may be a 1 year in 20 type of episode. The big increase occurred in 1995.

The Jones cyclad (Table 3) has been monitored since 1993. Little change occurs with this population except for the number of ramets. The higher number of ramets probably results from well-timed precipitation. The plant generally develops only a few follicles in any one year and observations by Sipes and Tepedino (1995) and Spence (1994) have shown that no sexual reproduction occurs in this plant. The plant population occupies similar acreage year to year and reproduces vegetatively.

The Welsh's milkweed plot (Table 4) in the Coyote Buttes area of the Paria Canyon–Vermilion Cliffs Wilderness is on a large dune. The milkweed, like all plants, has higher and lower numbers in accordance with precipitation. This plant does sexually reproduce and by monitoring later in the fall, seedlings can be observed. When monitoring began, it was done in the summer after flowering. Later, fall monitoring was found to produce more fruit and reproduction data.

Discussion

Do some of the above results indicate success for the planned actions prescribed in the management plans? Have actions such as closing roads on the Marble Canyon rim, convincing the public not to drive on the rim of Marble Canyon, or putting up the raptor poles in the Siler pincushion habitat, where rabbits and others harvest the cactus, had any visible or documentable effect yet?

Road Closures

The road adjacent to the Soap Creek plot has been closed to traffic since 1994; the Badger Creek plot continues to have an authorized, open to traffic road adjacent to it and the plot was vandalized

Table 3. *Cycladenia humilis* var. *Jonesii*.

Year	Plot no.	Ramets without follicles	Ramets with follicles	No. of follicles
1993	1	180	5	9
1993	2	206	21	32
1994	1	107	10	22
1994	2	220	0	0
1995	1	101	67	0
1995	2	99	146	0
1996	1	201	NC	3
1996	2	268	NC	0
1997	1	226	FNF	
1997	2	309	FNF	
1998	1	128	1	NC
1998	2	295	4	NC

NC = not counted
FNF = follicles not formed

Table 4. *Asclepias welshii*.

Year	Number of stems	Stems with pods	seedlings
1989	240	NO	NO
1990	566	NO	NO
1993	152	NO	NO
1995	143	32 Pods	NO
1996	68	96 Pods	NO
1997	121	45	4
1998	169	55	7

NO = not observed

in 1993; and the two North Canyon plots are remote from any road since the road to them was closed in 1994. The Soap Creek Brady pincushion data in Table 2 show that the 15–30 mm size cactus continues to dominate. Badger Creek plot data show more small cactus in the Badger Creek plot than the Soap Creek plot. The North Canyon plots are remote from any road and have data similar to the Soap Creek plot. In all probability, it is too early to detect the effects of the road closures on the biological reproduction of Brady pincushion cactus. The reduction or absence of off-road tracks has been observed in the closed areas since placement of educational signs to close the areas to off-road driving. No Brady pincushions have been driven over in the plots in the late 1990s. However, four new road starts into Brady habitat were closed by signs, fences, and rock barriers in cactus habitat in the late 1990s. Educational signs explaining the need to protect the Brady pincushion, as opposed to just closure signs, appear to have had a positive effect.

Welsh's milkweed occurs totally in designated wilderness and is therefore not vulnerable to off-road vehicles. The Jones cyclad occurs on very steep slopes in an area physically inaccessible to off-road vehicles.

Raptor Poles

Four raptor poles were placed in the Atkin Well allotment as part of the Siler pincushion cactus HMP to allow raptors more opportunity to prey on rabbits, which were consuming the Siler pincushion cactus. The poles were placed near a dense population of cacti at Atkin Well, which is where the high rabbit depredation took place. Table 5 shows cacti mortality from rabbit depredation before pole placement and after the 1989 pole placement. The exclosure had the highest mortalities by rabbits of all the Siler pincushion plots. The depredation of cactus by rabbits dropped in 1989 and remained low until 1997. That year, 16 Siler pincushions in the exclosure were eaten, which was about the same depredation level as prior to the raptor pole installation; however, the level dropped in the following years. The drop in cactus depredation thus could have been facilitated by the pole placement and the subsequent raptor use of the poles.

Livestock Trampling

Two livestock exclusion areas and corresponding livestock use areas have been established for Siler and Brady pincushion cactus. The Siler pincushion Atkin Well plots, where one plot is in an exclosure and one is outside the exclosure, have been followed since 1985. To date, there is small difference between cactus size structure in the exclosure and out of the exclosure (see Table 1).

Table 5. Rabbit-caused mortality at Atkin Well exclosure pole set-up in 1989.

Year	Mortality
1985	16
1987	22
1988	15
1989	1
1990	1
1991	1
1992	NO
1993	0
1994	0
1995	0
1996	0
1997	16
1998	0

NO = not observed

The Badger Creek plot for Brady pincushion occurs in an allotment pasture that for various reasons has not been grazed since the plot was established in 1984. The plot shows a dominant presence of small cactus (0–15 mm) as compared to the Soap Creek and North Canyon plots. This is the only time in the 15 years of monitoring that the small size cactus have shown such domination in any of the plots. This, however, may be a result of an episodic reproductive event and the structure may revert to a 15–30 mm size dominance after a few years. Spence (1993) did a 2-year study on Brady pincushion in 1992-93. His size data for both years showed a population dominated by larger cacti (mean size of almost 30 mm). This size structure has continued through 1997, the last year of data collection (John R. Spence, personal communication 1999). This part of Lees Ferry has not been grazed for an unknown number of years. I have worked in the area since 1977 and have never observed livestock there; it is not designated for grazing. If livestock were the factor in trampling young, small cactus, a small sized younger population would theoretically be predominant at the Lees Ferry plots. More than likely this might indicate that young cactus predominate after an episodic reproductive event, independent of livestock absence or presence.

Welsh's milkweed occurs in an area lightly used by livestock on the Paria Plateau; however, milkweed is not a palatable forage and is not used by cattle. Its habitat is a sand dune, which often is hard for cattle to traverse, so livestock use is very light where the milkweed occurs. No damage by livestock has been observed in this population.

Jones cyclad grows on the side slopes of two canyons just west of the Kaibab Piaute Indian Reservation. The area is inaccessible in most places to livestock. In the years of doing monitoring, no cattle have been observed in the habitat.

Conclusion

The objectives and planned actions of the two management plans for the listed plants were generally to assure that enough reproduction was occurring to sustain a healthy population level. The Brady pincushion cactus has shifted slightly to the smaller, younger cactus (0–15 mm) from the 15–31+ mm size classes since the 1980s. This is a result of an apparently good germination year in 1996, when many small young cactus appeared. But the 15–31+ mm size class remains predominant in three of the four plots.

The Siler pincushion cactus populations have also shifted to the smaller, younger cactus in two of the three plot areas. Two of those plots were dominated in the 1980s and early 90s by the 5–16.9 cm size class. However, the Johnson Spring plot has always been dominated by younger and smaller cacti (the 0–4.9 cm class). This cactus has met the size class objectives for the 0–4.9 mm class of the 1987 HMP.

Welsh's milkweed had high numbers in 1990 with 566 plants counted, then dropped to 68 plants in 1996 and has since started to climb upward in number again. This population needs to be monitored for a few more years to better determine the trend and cycles of the plant.

Jones Cyclad seems not to reproduce sexually, and monitoring the number of ramets emerging seems the only indicator of trend. Judging from the numbers shown in Table 3, the number of ramets remains at strong levels during wet years, with fewer showing in dry years.

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Five-Year Monitoring Study of Siler's Pincushion Cactus (*Pediocactus sileri*) in Kane County, Utah

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Abstract: Siler's pincushion cactus (*Pediocactus sileri*) occurs primarily on Bureau of Land Management (BLM) lands in Washington and Kane Counties in southwestern Utah and across the border in northwestern Arizona. This 5 year (1993–1997) monitoring study was set up as a challenge cost-share project between Red Butte Garden and the Utah State BLM Office in Salt Lake City. A permanent study plot was established about 10 miles east of Kanab, in Kane County, to annually monitor growth, reproduction, recruitment, mortality, and threats to the species. The cactus grew an average of 0.42 cm in height and 0.33 cm in width per year. Plants were about 10 years old before they produced fruit. Four demographic patterns were observed: (1) the total number of individuals nearly doubled, (2) the average annual recruitment rate was approximately four times greater than the average annual mortality rate, (3) the population appeared young, vigorous and viable, and (4) the cactus population may have responded to above-normal precipitation at the study site. Livestock and off-road vehicle tracks were observed in the study area but apparently are not major threats to the species. The Kane County population may be the most viable of all the populations currently under study in Utah and Arizona.

Siler's pincushion cactus (*Pediocactus sileri*) has been listed as endangered by the U.S. Fish and Wildlife Service since 1979 under the Endangered Species Act of 1973 (U.S. Fish and Wildlife Service 1979). Most of the known or potential cactus habitat is managed by the Arizona Strip and Cedar City BLM Districts (U.S. Fish and Wildlife Service 1993a). It is BLM policy to implement appropriate conservation programs for endangered, threatened, and other sensitive plant species ("special status species") that occur on their lands. To accomplish that goal, the BLM has extensively studied the species in-house and under contract for 20 years (Bureau of Land Management 1985, 1987, 1990a, 1990b, Cormier 1985, Gierisch 1980, 1981, 1989, Gierisch and Anderson 1980, Hughes 1991, 1996, 1993–1998, Swapp 1985, Woodbury 1985).

Since it was listed as endangered, botanists hired by the U. S. Fish and Wildlife Service (Phillips et al. 1979) have also studied the species. After careful consideration of current information on the species, the U.S. Fish and Wildlife Service (1993a) proposed to downlist the cactus species to threatened, provided that the following five criteria could be met: "(1) known populations should be censused and mapped, (2) the BLM should establish permanent monitoring plots that are surveyed annually, (3) the BLM should develop an approved habitat management plan which includes steps to ensure the protection of the species, (4) the BLM should develop a mineral feasibility report assessing the present and potential value of the cacti's habitat for mining of gypsum, selenites and uranium and (5) the BLM should administer mining claims within known populations, mitigate adverse affects and initiate Section 7 consultations when necessary."

To meet the first two reclassification criteria listed above, the BLM entered into a cost-share agreement with Red Butte Garden to conduct an in-depth distribution and demographic survey of Siler's pincushion cactus on BLM lands in Washington and Kane Counties, Utah (Hreha and Meyer 1994). Red Butte Garden established a monitoring plot at Muggins Flat about 10 miles east of Kanab in 1993. Since the study was initiated, the U.S. Fish and Wildlife Service (1993b) has downlisted the species from endangered to threatened. This is the final summary of that monitoring study and is supplemental to the study by Hreha and Meyer (1994).

The species has been monitored at the Warner Ridge population in Washington County, southwestern Utah and in northwestern Arizona at the Atkin Well, Johnson Springs, and Yellowstone populations since 1985. However, no monitoring studies had been conducted at Muggins Flat, the only known location of the cactus in Kane County, Utah. Therefore, a permanent plot was established

at Muggins Flat to monitor cactus population parameters such as growth, reproduction, recruitment, mortality, and impacts to the species (Lesica and Steele 1997). The results of the Muggins Flat study, along with data gathered at the other monitoring plots established by the BLM throughout the range of this threatened cactus in both southern Utah and northern Arizona, will be used by the BLM to establish management guidelines for this species and its habitat.

Even after the species was downlisted, the Bureau of Land Management has continued to monitor populations on BLM lands at Muggins Flat and Warner Ridge in southern Utah and at Atkin Well, Yellowstone, and Johnson Springs in northern Arizona. Bureau of Land Management efforts are directed toward restoring habitat and stabilizing or increasing populations to the point that the provisions of the Endangered Species Act will no longer be necessary (U.S. Fish and Wildlife Service 1986, Bureau of Land Management 1987).

Methods

A 0.25 hectare plot was established at Muggins Flat about 10 miles southeast of Kanab, Utah. The plot was 50 m square and was divided into 100 subplots of 5 sq m each. Monitoring was initiated in 1993. Cacti occurring on the plot were tagged and numbered in 1994. Annual monitoring was conducted at the end of the growing season, usually at the end of September, and continued through the 1997 field season. Cactus height, width, age, vigor, reproductive status, threats, and damage were recorded annually for all tagged cacti. Vigor was assessed by subjective observation: dead, poor, fair, good, or excellent. Recruitment and mortality were also tracked for the duration of the study. New recruits were tagged and numbered the year they were first observed on the plot.

Results

Population Structure

The trend in the monitoring plot was generally toward shorter (< 1.9 cm) rather than taller (> 6.0 cm) cacti. Most (41.9%) cacti on the plot fell into the shortest height class, made up almost entirely of new recruits. The percentage of individuals in the recruitment class ranged from 28.5 to 53.3 percent of the population over 5 years. The recruitment class made up more than half (53.3%) of the population in 1995.

Most cacti (34.2%) in the plot were between 2.0 and 3.9 cm wide, and a few (5%) cacti were more than 8.0 cm wide. The remaining three width classes had about equal representation in the population at about 20 percent.

To evaluate and better compare size classes of the cacti, height and width were combined to estimate volume for each individual. Cactus volumes were calculated using the formula for a cylinder:

$$\text{Volume} = ((1/2 \text{ width})2 \times p) \times \text{height}.$$

Plant volumes were graphed as histograms on a semi-log scale to better illustrate the smallest size class and to show size distribution (from 10 to 1400 cubic cm) in the population (Figure 1).

Size class distribution was relatively stable from year to year. The general trend in cactus architecture tended to be toward short/slender rather than taller/stouter plants, representing a demographic shift toward the juvenile recruitment class and away from the mature senescent class.

The histograms show a gradual increase in size for each successive year as cohorts grew into the next size class. The smallest size class usually held the greatest proportion of the plants due to recruitment. Assuming that larger plants were generally older than smaller plants, Figure 1 also shows that the population was mostly younger rather than older plants.

Average growth rates were calculated by using increases in height and width measurements for tagged individuals on the plot. The increases in these measurements over the last 3 years of the study were tallied and an average was calculated for each parameter. Growth rates were relatively stable from 1993 through 1997. Some individuals occasionally decreased in size, probably due to shrinkage after a period of little or no rain.

Phillips and Phillips (1996) found that *Pediocactus peeblesianus* var. *peeblesianus* retracted beneath the soil surface in June after seed set and did not resurface until the fall. Hughes (1996) reported that larger individuals of *P. sileri* retracted underground less frequently than smaller individuals, but larger individuals did retract underground during long dry spells.

Cactus age classes were estimated using methods similar to those used by Culley et al. (1993) and Gibson and Nobel (1986). In both of these studies, each height class was converted into an age class based on observation of growth rates and onset of reproduction.

The average height growth rate for *P. sileri* in our study was 0.42 cm per year and the average width growth rate for cactus was 0.33 cm per year during the study. For convenience, we used the

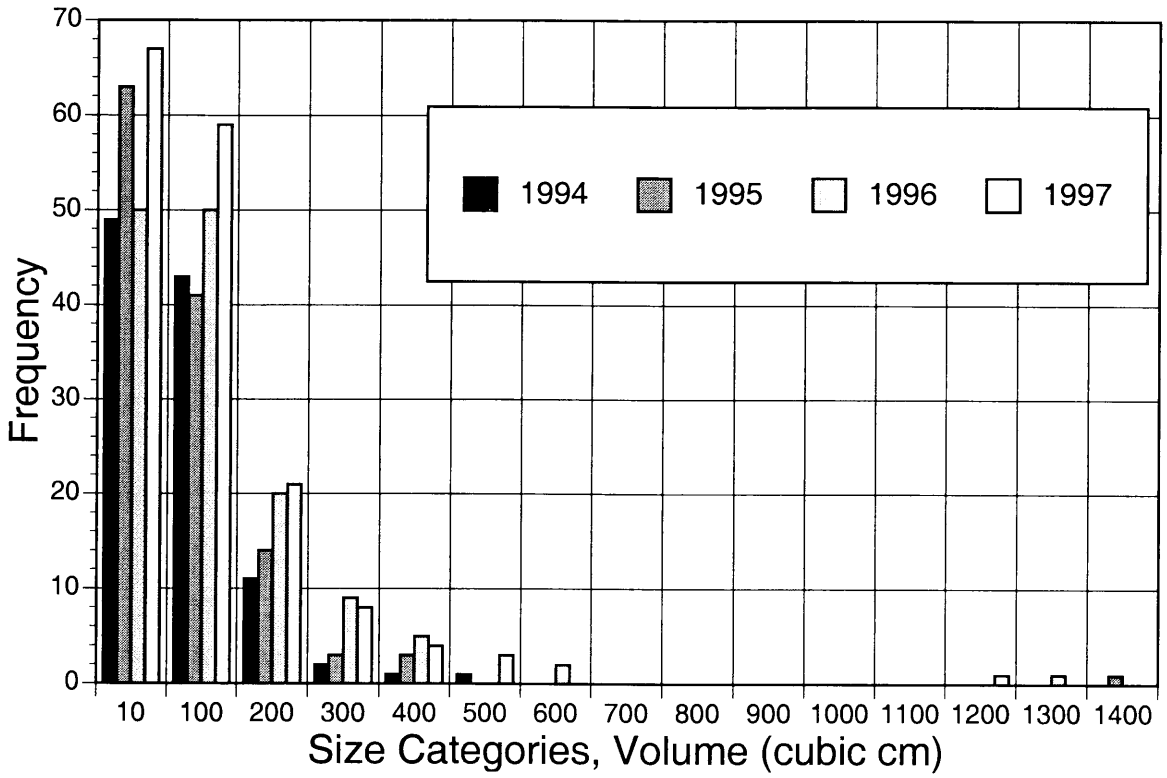


Figure 1. *P. sileri* plant size based on cylindrical volume calculated as a function of the width and height of all plants observed for each year (volume = $\pi(1/2 \text{ width})^2$ x height). The chart uses a semi-log X-axis for the smallest size category in the range of 0 to 100 cubic cm, to better illustrate that size category. Thereafter, the size categories are linear. The Y-axis shows frequency (percentage) of individual plant stems in each size category. The smallest size cohort holds the greatest number of individuals, due presumably to seedling recruitment. A single very large individual tripled in volume between 1994 and 1995.

average height growth rate of 0.5 cm per year to calculate the age estimates reported here. For example, a cactus that was 2.0 cm tall would be about 4 years old. Juveniles were probably 1–4 years old, and intermediate aged cacti were probably 4–8 years old. Mature cacti were probably more than 8 years old.

Phillips and Phillips (1996) reported that *Pediocactus peeblesianus* var. *peeblesianus* took about 8 years to reach sexual maturity. We also estimated that *P. sileri* might take 8 years to reach sexual maturity by using the shortest (4 cm) fruiting cacti on the plot. The average fruiting age was about 10 years and was calculated by using the average (5.35 cm) height of fruiting cacti on the plot. Individuals may live at least 26 years and evidently may produce fruit for about 16 years. We calculated this age by using the tallest fruiting individual (13 cm) on the plot.

We tallied almost twice as many juvenile (38.8%) and intermediate (35.8%) age cacti as mature (20.8%) cacti; nearly 75% of the population was younger, non-reproductive plants. The average recruitment rate (38.8%) of individuals into the juvenile age class was approximately 10 times greater than the average mortality rate (4.4%) observed during the study.

Reproduction

The number of fruiting plants on the plot ranged from 11 to 17, and the average over the 5-year period was 15 plants. The percentage of fruiting plants on the monitoring plot dropped from 19 percent in 1993 to 8 percent in 1997. This proportional decrease in fruiting individuals was due, however, to the increase in new recruits over the course of the study. As new recruits were added to the population, the population base number rose

and consequently the percentage of reproductive individuals in the population decreased. This shift from larger to smaller individuals suggested that the proportional reproductive potential of the species was temporarily reduced.

The actual reproductive output did not decrease, as evidenced by the fairly constant number of plants fruiting each year (about 33–50% of the reproductive plants fruited each year; 11–18 plants out of a cohort of 28 plants over the 5-year study period). As smaller (younger) individuals reach reproductive maturity, the reproductive potential of the population may gradually increase over time.

The average number of fruits produced per year on the monitoring plot was 38.6 and the average number of fruits per fruiting plant was 2.61. The number and the timing of flowering, along with differences in fruit production per individual plant, were probably due to moisture availability. Cacti may have to achieve a certain size before they have enough water to sustain flowering and subsequent fruit development (Gibson and Nobel 1986). Hughes (1996) reported that high fruit production years coincided with years of above-average precipitation.

The availability of moisture affects many stages of the reproductive cycle of cacti. Seed production may be affected by low rainfall (Gibson and Nobel 1986). Phillips and Phillips (1996) found germination to be strongly correlated with rainfall. In their study of *Pediocactus peeblesianus* var. *peeblesianus*, germination events appeared to track favorable periods of precipitation. *Pediocactus peeblesianus* var. *peeblesianus* takes advantage of both spring and summer rains and can germinate in summer or fall after favorable rainfall.

In another study, Frye (1996) was unable to correlate higher recruitment rates of *Pediocactus paradinei* on his study plots after the highest levels of precipitation recorded at the site. Apparently, even with this record moisture, the threshold necessary to produce a favorable germination response in the species was not attained. Water relations are critical during the cacti seedling stage. Jordan and Nobel (1982) found that rainfall was correlated with seedling establishment and cacti growth (height) in the Sonoran Desert. Many cacti typically germinate seeds in late summer after the monsoon season and can be killed by autumn or spring droughts. Seedlings are not tolerant of extremes in temperatures and this intolerance could be responsible for seedling mortality.

High temperatures can cause drought conditions that can limit successful cacti establishment. Seedlings not killed by extreme summertime temperatures are often killed by severe cold during winter (Gibson and Nobel 1986).

Fruiting individuals ranged from 2.0 to 13.0 cm tall and from 5.0 to 12.0 cm wide. Average fruiting plant size was 5.35 cm in height and 7.25 cm in width. Average fruiting plant volume increased from about 125 to 265 cubic cm from 1994 to 1997, respectively (Figure 2).

Average size of reproductive versus nonreproductive individuals was 214 cubic cm and 30 cubic cm, respectively. Reproductively mature individuals were about seven times larger in size (volume) than non-reproductive individuals. Larger plants tended to produce more flowers and fruits than smaller plants. Larger plants contributed the majority of resources to the reproductive effort of the species. Fruits per plant ranged from 1 on the smallest to 12 on the largest individuals. Hughes (1996) reported that larger *Pediocactus peeblesianus* var. *peeblesianus* usually produced more fruit than smaller ones. Culley et al. (1993) also reported that larger cacti were responsible for most of the reproductive effort in their study of the Mesa Verde cactus (*Sclerocactus mesae-verdae*) in Colorado and New Mexico.

Older plants in our monitoring study produced more flowers and fruits than younger plants. On average, most (78.2%) of the fruiting individuals were 8 years or older (mature age class), whereas 21.8 percent were between 4 and 8 years old (intermediate age class).

Plant Condition

Overall, cacti appeared to be in pretty good condition for the duration of the study (Figure 3). The study means for cacti vigor were excellent (43.6%), good (28.9%), fair (17.8%), and poor (4.6%). Average cactus mortality was low (4.3%) on the monitoring plot during the 5 years.

The two major threats to the study plot cacti were trampling and off-road vehicles. In 5 years, livestock trampled eight cacti and seven cacti were driven over by vehicles. Most of this damage probably occurred when ranchers entered the grazing allotment near the study site. Culley et al. (1993) and Hughes (1996) also reported that the two major threats to the cacti populations they were studying in the Southwest were livestock trampling and off-road vehicles.

Rare-plant researchers also undoubtedly impact the populations they are studying. In our study plot we were primarily concerned with

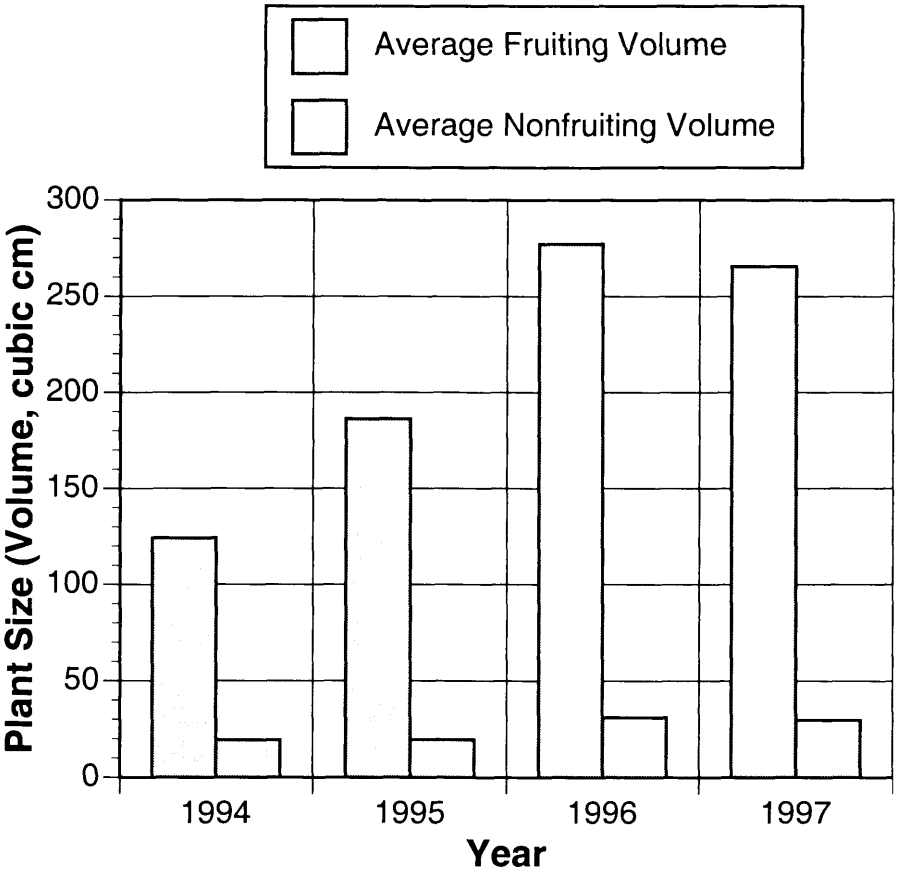


Figure 2. The entire fruiting cohort (n = 28) was averaged each year, even though not all plants in the cohort fruited every year of the study. Only two plants fruited all 5 years; their average size was 732 cubic cm over the 5 years.

disturbance of cryptobiotic crust in the cacti's habitat. During the 5-year monitoring study of this species, we attempted to walk in small, eroded ravines and on rocks, rather than on the cryptobiotic crusts, but at times it was necessary to step on crust soil. We did not evaluate the result of our impacts on the study plot and the species.

A recently reported threat to Siler's pincushion cactus was the spraying of insecticides to control grasshoppers in the cacti's habitat (Peach et al. 1993). Insecticides could indiscriminantly kill the species' pollinators and reduce their numbers. This could result in decreased pollination, fertilization, fruit production and seed set in the species. Ultimately, cacti population numbers could decline, thus threatening the species. Peach et al. (1993) recommended spraying for grasshoppers after the flowering period of the cactus, which starts the last week in March and continues through the first week in May.

Population Demographics and Trends

In 1993, we initially counted and permanently tagged 88 cacti on the monitoring plot. The population experienced a 46 percent increase in plants over the 5-year study period. The number of individuals increased to 162 cacti by 1997 (the last year of the study). The mean annual number of individuals in the population was 122 plants.

Initially, 33 percent of the subplots had cacti present in them; by the end of the study 54 percent of the subplots were observed to have cacti growing in them. Cacti frequency experienced a net increase of 21 percent.

Recruitment and Mortality

Recruitment ranged from 16 plants (1996) to 26 plants (1997) during the study. Mean annual recruitment was 21 plants on the study plot. Recruitment was recorded as zero during the first year of the study because we were unable to determine

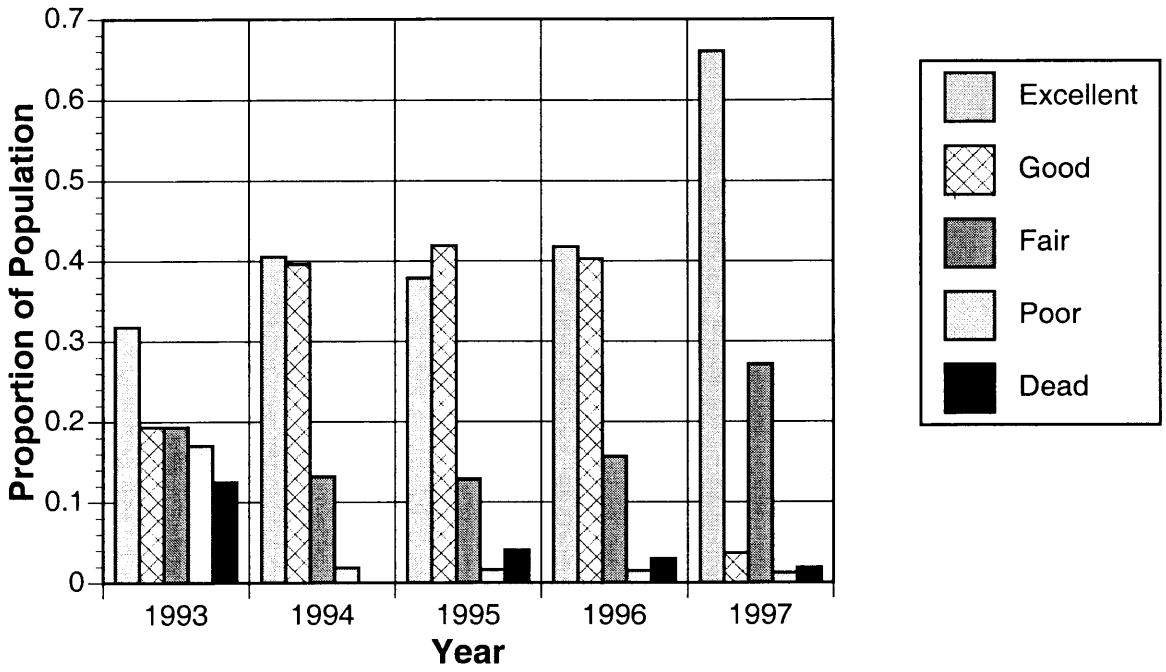


Figure 3. Vigor classes over 5 years. The 1993 "mortality" class overestimated the actual rate for the year, as it was cumulative of previous years.

the number of new recruits without data from the previous year.

Mortality ranged from 11 plants (1993) to zero (1994) during the study. Mean annual mortality was five plants on the study plot. Mortality was recorded as 11 the first year, but this number was probably high because it may have included individuals that died prior to the beginning of the study. In general, cactus mortality declined slightly during the monitoring study from 11 plants in 1993 to 3 plants in 1997. In comparison, recruitment was four times greater than mortality; this will assure that dead cacti are replaced at a ratio of 4:1.

There are many possible causes of mortality in cacti populations including rot, disease, desiccation, drought, rodent depredation, herbivory by insects, senescence (old age), off-road vehicles, and livestock trampling (Kass 1992, Culley et al. 1993).

The cause(s) of death for the cacti that died on the plot could not be determined. Some individuals simply disappeared from the plot and were not relocated. All deaths may be attributable to natural causes such as desiccation and senescence.

Most of the cacti that died belonged to the juvenile (recruit) class except for one that was mature (senescent). The very small cacti are particularly susceptible to all of the causes of mortality listed above, in particular desiccation and root rot infections from pathogenic fungi, particularly following rodent depredation, as young cacti lack central spines and are therefore poorly defended (personal observation, T. M.). Rodents, birds, and harvester ants may be responsible for herbivory of seeds and seedlings (Gibson and Nobel 1986). Excessive herbivory may contribute to mortality.

Comparison of Results with Hughes (1993–1998)

Hughes (1991) has studied *P. sileri* since 1985 and continued to record annual observations (1993–1998). Hughes (1996) also studied other members of this genus along with Butterick (1986), Frye (1996), and Phillips and Phillips (1996). Hughes's records indicate that Siler's pincushion cacti populations throughout its range have variable age distributions. Other researchers have also reported variability in population age distributions over their ranges (Culley et al. 1993, Frye 1996, Hughes 1996, Kass 1996, Phillips and Phillips 1996, Warren et al. 1993).

Hughes (1991) also reported that fruit production was variable (0–63% annually between 1985 and 1990) on his plots and that this variability probably was the result of differences in precipitation received in the cacti's habitat from year to

year. Fruiting percentages appeared to increase in years with above-normal precipitation and decrease when precipitation was low. Butterick (1986) and Hughes (1996) reported variable fruit set in the populations of *Pediocactus peeblesianus* var. *peeblesianus* that they were studying in Arizona.

Hughes (1991) also reported that *P. sileri* had variable annual recruitment (0–26 plants) and mortality (0–56 plants) from 1985 to 1990. The highest mortality (56 plants) reported in 1990 at the Johnson Springs plot was due to herbivory, probably by rabbits.

When we compared our results at Muggins Flat, Utah with Hughes's results at Johnson Springs, Arizona, we found that both sites had similar demographics during the survey period between 1993 and 1998 (Table 1). Both sites had young populations. Johnson Springs had an annual average of 86.4 percent and Muggins Flat had an average of 89.1 percent of the population in the shortest height class (0–4.9 cm).

Average annual fruit production was similar at the two sites: Johnson Springs averaged 18 percent plants fruiting and Muggins Flat averaged 11.7 percent plants fruiting per year. Average annual recruitment at Muggins Flat (16%) was nearly 10 percent higher than at Johnson Springs (6%) per year. However, average annual mortality at Muggins Flat (3%) was similar to that reported at Johnson Springs (2.3%).

The Muggins Flat cacti population, which increased from 88 to 162 plants during the study, was more than twice as large as the Johnson Springs cacti population, which fluctuated from 66 to 77 plants during the study. By the end of the study period the Muggins Flat population had approximately doubled in size and the Johnson Springs population had increased by about 6 percent.

The Muggins Flat population appeared to be more vigorous than the Johnson Springs population because of its reproductive capacity, high recruitment rate, successful establishment rate, low mortality rate, and overall population viability. Finally, when compared to the other monitoring sites for this species, the Muggins Flat site may be one of the most productive sites in the entire range of this cactus species.

Conclusions

Four general life history trends or patterns emerge from this study: (1) the number of plants increased over the 5-year study period, (2) the number of recruits was similar over the 4 years that recruits were tallied, (3) the number of dead

Table 1. *Pediocactus sileri* population monitoring results of Hughes (1993–1998, Johnson Spring) and Hreha and Meyer (1993–1997, Muggins Flat).

	1993	1994	1995	1996	1997	1998	Average
No. of plants (%) in 0–4.9 cm height class:							
Johnson Spring	55 (83.3)	54 (80.5)	55 (80.8)	75 (97.4)	—	63 (90.0)	60.4 (86.4)
Muggins Flat	79 (89.7)	101 (95.3)	114 (91.9)	111 (82.8)	139 (85.8)	—	109 (89.1)
No. of plants (%) producing fruits:							
Johnson Spring (F)	11 (16.7)	2 (3)	25 (36.8)	—	—	11 (15.7)	12 (18)
Muggins Flat	17 (19.3)	11 (10.4)	16 (12.9)	16 (11.9)	13 (8)	—	15 (11.7)
No. of recruits (%) in population:							
Johnson Spring	7 (11)	2 (3)	5 (7)	7 (9)	—	0	4 (6)
Muggins Flat	—	18 (16.9)	24 (19.4)	16 (11.9)	26 (16)	—	21 (16)
No. of deaths (%) in population:							
Johnson Spring	4 (6)	1 (2)	1 (1)	1 (1)	—	1 (1.4)	2 (2.3)
Muggins Flat	11 (12.5)	0	5 (4)	4 (3)	3 (1.9)	—	5 (3)
Total no. of plants in plot for the year:							
Johnson Spring	66	67	68	77	—	70	
Muggins Flat	88	106	124	134	162	—	

Johnson Spring data from annual reports on *Pediocactus sileri* by Lee Hughes (1993–1998).

plants decreased slightly over the 5 years that mortality was counted, and (4) the number of recruits was about four times greater than the number of plants that died each year in the plot.

The 100-year average precipitation for a region is typically positively correlated with elevation. In Figure 4 we regressed average annual precipitation spanning the 5 years of our monitoring study, as well as the 100-year average precipitation, versus elevation for the weather stations nearest our monitoring plot. The data was from the five nearest regional weather stations collected by the Utah State Climate Center (Ashcroft 1992, Utah State University 1999). We calculated total annual precipitation from May through April of the following year as our "water year" because we assumed that this would be the precipitation cycle impacting the current growth and flowering. The regression equation was

$$Y = 124.65 + 0.0864\ (X)$$

where Y is the predicted rainfall in millimeters and X is the elevation in meters. The R^2 of the regression of 100-year average precipitation vs. elevation was 0.18; therefore, elevation accounts for only 18 percent of the variation in rainfall. The chart demonstrates that the Kanab weather station registered higher precipitation for the 5 years of the study than would normally be predicted on the basis of either elevation or long-term weather patterns. The higher value was due primarily to very high precipitation in the early months of our study, and to a single month, September 1997, that registered 232 mm precipitation (9 inches) at the station.

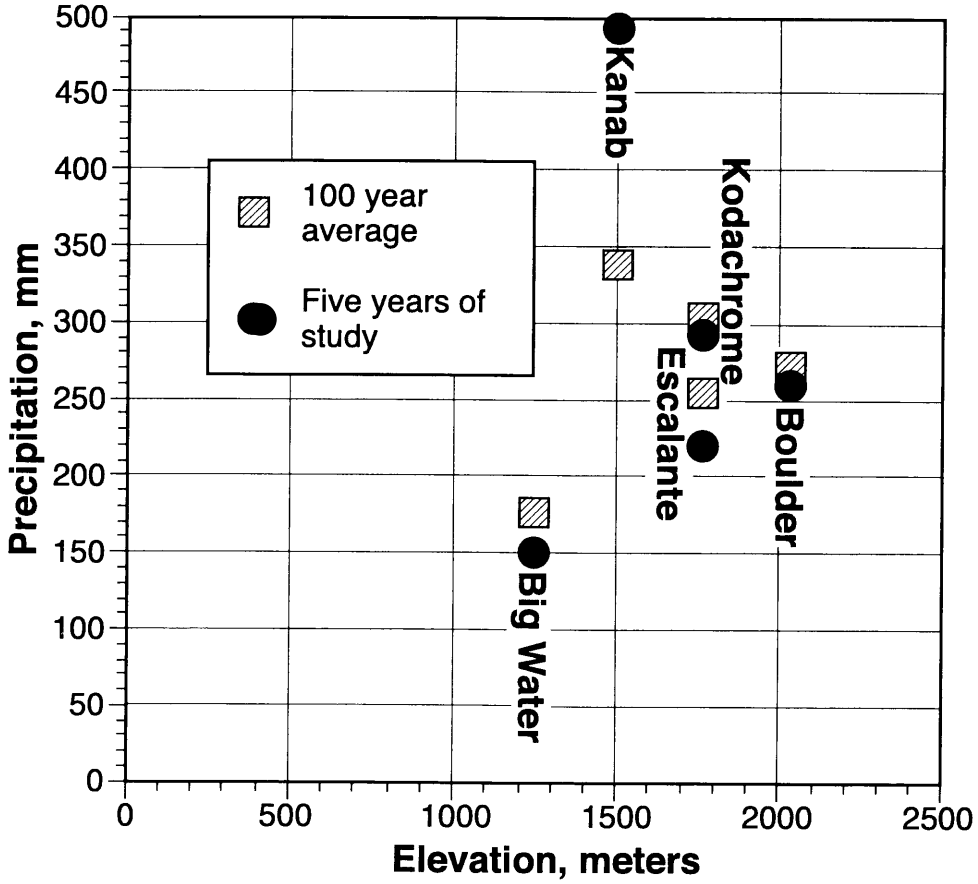


Figure 4. Regression of average annual precipitation during the 5 years of monitoring, as well as the 100-year average precipitation, versus elevation for the weather stations nearest our monitoring plot. Data from the five neareste regional weather stations, Utah State Climate Center (USU 1999). We calculated total annual precipitation from May of one year through April of the following year as the "water year," assuming that to be the precipitation cycle impacting current growth and flowering.

Although high, the precipitation records were included because we assumed they were accurate. During the study, Escalante and Big Water were slightly below their 100-year averages, whereas Kodachrome and Boulder were quite close to their 100-year averages.

We used the long-term weather records of Kanab, Utah for our *P. sileri* site, as it was geographically closest and at a similar elevation. Kanab receives an average (100-year norm) 337.5 mm (13.5 inches) of precipitation per year (Pope and Brough 1996, Utah State University 1999).

This Siler's pincushion cactus population may have responded to above-normal precipitation at the study site, which was favorable for recruitment and may be a major driving force in population growth (Figure 5). The above-normal (4 years out of 5) precipitation over the course of the study may also account for the slight drop in mortality.

Major weather events occur over the whole area and individual storms may be spotty in distribution, especially in summer, resulting in differences in precipitation and temperature between Kanab and the study site. By refining our study design (cf. Phillips and Phillips 1996), it may be possible to correlate weather data with cactus population data such as seedling establishment, recruitment events, age classes, and mortality.

Several authors have discussed population viability analysis (PVA) and minimum viable pop-

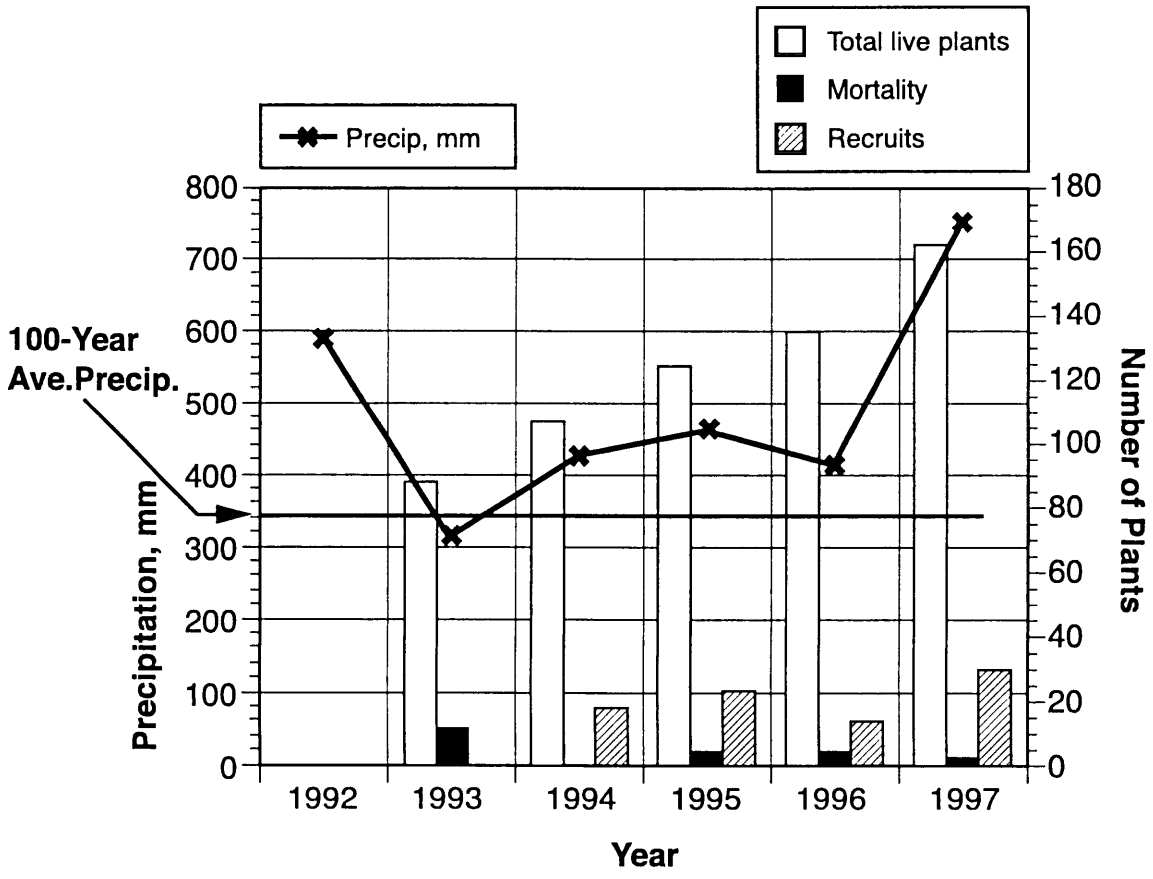


Figure 5. Demographic trends in *Pediocactus sileri* and precipitation. Precipitation (mm, left Y-axis) plotted next to numbers of plants in three life stages: total live plants, mortality, recruits (also included in total live plants column). As in Figure 4, precipitation "water year" is calculated from May through following April. Average precipitation 1992–1997 (not shown): 492 mm, which is 155 mm (6 inches) above 100-year average.

ulation (MVP) size in conjunction with rare plant populations (Boyce 1992, Crone and Gehring 1998, Gilpin 1989, Menges 1986, 1990, 1991, Nunney and Campbell 1993, Shaffer 1981). Menges (1990) was probably the first to bring a rare plant case study to the forefront when he reported his findings on Furbish's lousewort (*Pedicularis furbishiae*).

Height and width measurements, as well as age, reproduction, and vigor observations, may be used to assess population viability (Hughes 1991, Menges 1991). Both height and width distributional patterns remained constant over the 5 years of this study.

Hughes (1991) reported that a healthy cactus population should have as many smaller, younger recruits as larger, older (senescent) individuals. The study plot had about eight times as many younger (39%) recruitment size plants than older (5%) senescent plants.

There was relatively equal representation (19–34%) in each width class except the largest, which averaged only 5 percent of the population.

The 1997 *P. sileri* population size class distribution is consistent with the habitat management plan objectives set for the species (Bureau of Land Management 1987). Nearly 75 percent of the population were juvenile or intermediate in age (< 8.0 years old). Younger (juvenile) plants are usually healthier than older (senescent) individuals. The vigor of about 75 percent of the population on the monitoring plot was observed to be excellent or good. Vigorous plants are usually healthier and more viable.

Potential causes of extinction in plant populations include environmental, demographic, and genetic stochasticity, plus natural catastrophes (Shaffer 1981). To this list we can add man-made alterations to their habitats such as fragmentation, introduction of alien flora and fauna, and disruption of ecosystems from pollution or spraying of insecticides.

Impacts to a species and changes in its population dynamics may be detected at the habitat level, the population level, and the individual level (Menges and Gordon 1996). To detect variations in rare plant populations, population parameters need to be monitored annually to ascertain demographic trends. The simplest way to assess population viability is to measure the population's growth from one year to the next over a period of several years for at least 10 years but preferably for 20 years (Menges 1986). A viable population is usually stable if recruitment equals mortality and increasing in size through time if recruitment exceeds mortality.

Menges (1991) noted that recruitment should be greater than mortality per year to maintain population viability. Reproduction was successful on the monitoring plot, producing about 20 new recruits per year. Recruitment was four times greater than mortality on the plot.

According to Frye (1996), even with very low mortality rates a population with little or no recruitment would most likely decline. A population that lives for 25 years may need one or two good years of reproduction to replace itself. A short-term sampling period (less than 10 years) might miss a favorable reproductive year and thus overestimate the risk of extinction.

The Muggins Flat cacti population appears young, vigorous, and viable. This population may enjoy optimal site conditions for cactus growth and survival, possibly in contrast to the remainder of its range. However, the duration of this study did not capture any environmental catastrophes such as drought, fire, temperature extremes, and excessive depredation by rodents, herbivory by insects, or plant disease. In managing rare plant populations we often have to make decisions using incomplete data sets. Therefore, our ability to use the available data effectively is critical to our success as managers of rare plant species such as *P. sileri* (Crone and Gehring 1998).

Management Recommendations

1. Continue to protect the monitoring plot near Muggins Flat. Make sure grazing activities in the vicinity of the site do not threaten the species or its habitat.

2. Refine the monitoring study to include precipitation data for Kanab, Utah and correlate precipitation data at the site with demographic data for the cactus population.

3. Continue to monitor the Muggins Flat population every year or at least every other year starting in 2000.

4. Continue to compare the Muggins Flat population demographics with the other BLM sites monitored by Lee Hughes (BLM, Arizona Strip Field Office, St. George).

5. Monitor the timing of spraying for grasshoppers. Spraying insecticides to control grasshoppers in the cacti's habitat could kill the species' pollinators. According to Peach et al. (1993), spraying for grasshoppers should be later than the flowering period of the cactus, which starts the last week in March and proceeds through the first week in May.

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Tracking Rare Orchids (Orchidaceae) in Arizona

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Abstract: Twenty-six native orchid species occur in Arizona, and 14 are considered rare with fewer than 100 occurrences in the state. The author is conducting three studies covering four of the wild orchids: *Stenorrhynchos michuacanum, Hexalectris revoluta, Malaxis porphyrea,* and *M. tenuis*. The studies are ongoing so only interim results are available. Interim results indicate that plants of *S. michuacanum* and *H. revoluta* do not bloom every year, and in the latter case do not come up every year. The study on *Malaxis* is looking at recovery rates in damaged habitat, but is still in its first year.

Twenty-six native orchid species in 13 genera occur in Arizona. Fourteen are considered rare in the state, using the Nature Conservancy's ranking of relative rareness, with rankings of S1, S2, or S3 being considered rare. A ranking of S1 implies 5 or fewer occurrences in the state; S2 implies 6 to 20 occurrences; and S3 implies 21 to 100 occurrences. A list of all of the native orchids in Arizona and their rarity ranking is in Table 1. I am conducting multiyear studies on 4 of the 14 rare taxa, looking into population dynamics, flowering sequences, dormancy patterns, and recovery trends. None of the studies is complete, so only partial results are reported here, and only interim conclusions can be drawn at this stage.

Stenorrhynchos michuacanum, Hexalectris revoluta, Malaxis porphyrea, and *M. tenuis* were selected for this study for multiple reasons. Proximity to the University of Arizona in Tucson was a major reason. All of the colonies under study are less than a 2.5 hour drive from Tucson, and thus can be visited multiple times during the flowering season. A second reason was that all of these taxa are rare in the United States, and very little is known about their blooming and reproductive patterns. A third reason, although it did not apply to all the species selected, is threat of habitat destruction due to development (*H. revoluta*) or recreational (*M. tenuis* and *M. porphyrea*) use.

Methods and Results

Stenorrhynchos michuacanum (Lexarza) Lindley blooms between late September and late October on an inflorescence between 25 and 58 cm tall, with 10–30 pale green flowers with dark green stripes on the sepals, petals and lip. It grows between 1,500 and 2,134 m elevation in Madrean evergreen woodland, primarily in association with alligator juniper (*Juniperus deppeana* Steud.) A blooming plant has either three or four leaves, from 15 to more than 20 cm long and up to 3 cm wide. Plants that do not bloom the following year are often reduced in size to one or two leaves under 10 cm in length. A common companion, essentially an indicator plant, is *Milla biflora*.

Stenorrhynchos michuacanum is distributed widely in Mexico, and it is named after the Mexican state of Michoacan. It is historically rare in the United States, occurring only in Big Bend National Park in Texas and in the southeastern Arizona counties of Cochise, Pima, and Santa Cruz.

I staked and numbered a total of 50 plants in four different colonies and have been monitoring them since 1995. The objective of this study is to determine flowering frequency and the effect flowering has on the plants. The plants are observed several times each year, and size, vigor, and bloom status are recorded.

The survey started in 1995 with 30 plants and was expanded to 50 plants in 1996 upon the discovery of additional colonies. Thirty-three plants have attempted to bloom in the 6 years the study has been ongoing, with a total of 59 blooming attempts. A blooming attempt is defined as the initiation of an inflorescence, which may or may not survive to maturity, due primarily to herbivory before anthesis. Only about 40 percent of the plants that attempted to bloom each year also tried to flower the following year, as shown in Table 2.

Seven plants bloomed 2 years in a row; three bloomed 3 years in a row, and one plant bloomed 4 years in a row. One plant that bloomed 3 years in a row and the one that has bloomed 4 years in a row bloomed in the year 2000. It is possible that successive blooms may continue in these individuals. Gaps between blooming attempts are as great as 5 years, as one plant bloomed only in the first year of the survey.

Hexalectris revoluta Correll blooms from late May to early June in canyon bottoms and on sides

Table 1. Relative rarity of Arizona's native orchids.

Species	Relative rarity*
Calypso bulbosa var. *americana*	
Coeloglossum viride	AZ
Corallorhiza maculata	
Corallorhiza striata	
Corallorhiza wisteriana	
Cypripedium parviflorum	AZ
Epipactis gigantea	
Goodyera oblongifolia	
Goodyera repens	AZ
Hexalectris revoluta	W
Hexalectris spicata var. *arizonica*	
Hexalectris spicata var. *spicata*	AZ
Hexalectris warnockii	W
Listera convallarioides	AZ
Malaxis corymbosa	US
Malaxis porphyrea	W
Malaxis soulei	
Malaxis tenuis	US
Platanthera limosa	US
Platanthera purpurascens	
Platanthera sparsiflora	
Platanthera zothecina	W
Schiedeella arizonica	
Spiranthes delitescens	W
Spiranthes romanzoffiana	
Stenorrhynchos michuacana	US

AZ = rare in Arizona
US = rare in United States
W = rare throughout its range

Table 2. Repeat bloom attempts for *Stenorrhynchos michuacanum*.

Year	Number attempting bloom	Percent attempting repeat bloom in next year
1996	20	30
1997	8	50
1998	12	42
1999	10	40
Avg repeat bloom attempts		40.5

of canyons between 1370 and 1525 m elevation, under oaks and mesquite, often in association with Arizona walnut. Like all members of *Hexalectris* Rafinesque, it is a mycotrophic plant that appears above ground only to bloom. Up to 20 tan to pinkish flowers appear on a slender spicate, sparsely flowered, pale cream to tan leafless stem that ranges from 20 to more than 50 cm tall. Four to five bracts sheath the stem. Each flower is approximately 2 cm x 2 cm. The sepals and petals are free and spreading and are rolled back along the outer third of their length to form a tight circle, a feature that can be used to distinguish it from any of the other *Hexalectris* in Arizona and New Mexico. The three-lobed lip is whitish tan to rose tan. The lateral lobes have distinct purple veining. The central lobe has five to seven raised purple ridges running its entire length, from near the column to the apex.

Hexalectris revoluta is extremely rare throughout its range, which is limited to portions of northern Mexico, the Big Bend area of Texas, and southeastern Arizona. It was discovered only relatively recently in Arizona. Voucher specimens of *H. revoluta* from Pima County deposited at the University of Arizona Herbarium in Tucson were collected in Baboquivari Canyon by Toolin and Reichenbacher in 1981 and in McCleary Canyon by McLaughlin in 1986. Both were originally identified as *H. spicata* based on keys in published floras of Arizona available at the time. The flowers of *H. spicata* and *H. revoluta* are similar and dried specimens are sometimes difficult to distinguish. After studying fresh material in the field, the plants were identified as *H. revoluta* (Coleman 1999). There are now three documented locations of *H. revoluta* in Arizona, although the plant has not been observed at the Baboquivari location since the original discovery, despite repeated searches.

The discovery of *H. revoluta* in Arizona represents a western range extension of approximately 290 miles (483 km) and a northern range extension of approximately 210 miles (350 km) from Big Bend National Park in Brewster County, Texas. It is not known from New Mexico. *Hexalectris revoluta* is not currently a candidate for federal endangered species status, but should be considered for listing due to rareness across its range. The McCleary Canyon location was included within the boundaries of land being considered for trade from the Forest Service to a mining developer, but that trade was not completed.

I have been studying blooming patterns at two sites of *H. revoluta* since 1996: the McCleary Canyon site in Pima County, and the Sawmill Canyon site in Santa Cruz County. The number of plants appearing above ground fluctuates widely from year to year as shown in Table 3, but has been going monotonically downward since 1997. Rarely does a plant bloom 2 years in a row. The reason for the decreasing number of plant appearances could possibly be the lack of winter rainfall over the past several years. Other mycotrophic orchids in the

Table 3. Blooming patterns of *Hexalectris revoluta* at two sites in Arizona.

	1996	1997	1998	1999	2000
Site 1	1	19	9	2	1
Site 2	–	30	12	8	0

Note: Site 2 not found until 1997.

southwestern United States are also down significantly over that same period.

Five species of the genus *Malaxis* Swartz grow in the southwestern United States. All five appear above ground after the onset of the summer monsoon rains and bloom from about mid-July to early September. *Malaxis wendtii* Salazar has the smallest penetration into the United States, occurring only in the Big Bend area of Texas. *Malaxis soulei* L. O. Williams is the most numerous and widespread. It occurs in west Texas and in mountainous regions of New Mexico and Arizona, often in dense colonies. In the United States *M. corymbosa* (S. Watson) Kuntze occurs only in southeastern Arizona, but it is more widespread in Mexico. The remaining two species in the Southwest, *M. porphyrea* (Ridley) Kuntze and *M. tenuis* (S. Watson) Ames, are the subjects of a study initiated in the spring of 2000.

Malaxis porphyrea shows up in current floras as *M. ehrenbergii* (Reichenbach f.) Kuntze. Todsen (1997) established that the correct name is *M. porphyrea*. The 15–35 cm tall plants have a single ovate, acute leaf partway up the stem and a terminal spicate inflorescence. The purple flowers are the smallest orchid flowers in Arizona. The sepals, petals, and lip are covered with tiny raised bumps, or half-spheres. The sagittate lip has a cream to whitish yellow central portion, with the margins purple. The tiny translucent petals are wispy and all but invisible to the unaided eye.

Malaxis porphyrea grows in northern Mexico and in Arizona and New Mexico in mixed oak, fir, and pine forest between 2100 and 2800 m elevation. Its most common habitat is near damp, mossy, or grassy places in slightly open areas in the forest and on the edges of meadows, usually in association with iris species.

Malaxis tenuis grows in the same habitat as *M. porphyrea*, but is much more restricted in distribution. *Malaxis tenuis* occurs only in the Catalina and Chiricahua mountain ranges in Arizona, and only from three historical locations in New Mexico. Two of the New Mexico locations are probably extirpated, with only a few plants at the remaining location in Catron County. Its situation in Arizona is only slightly more secure. There are less than two dozen plants in the Santa Catalina Mountains, although there are several hundred in the Chiricahua Mountains.

Malaxis tenuis gets up to 18 cm tall with a single ovate leaf about 6 cm from the ground. The spicate terminal inflorescence is cylindrical, 3–5 cm in length. Most of the tiny green flowers are held horizontally with the lip pointing outward, but others face up, down, and sideways. The flowers are about 1 cm long, but only 2 mm wide. The sagittate lip has four dark green stripes, one on each edge and two toward the middle. The dorsal sepal is solid green, but the lateral sepals have faint dark green striping. The tiny petals are filiform and translucent, and they fold behind the dorsal sepal.

The greatest concentration of both *M. porphyrea* and *M. tenuis* in the United States is in the Chiricahua Mountains in Cochise County, Arizona. I have monitored the plants there every year since 1995. One of the meadows near the burn limit of the Rattlesnake Canyon fire had the highest concentration of these two species in the United States. In 1998 I observed campers parked on the meadow with their vehicle, tent, and equipment directly on top of the area with the highest density of plants. In late summer of 1999 that same area was significantly damaged, most likely by foraging deer or human excavation, with 20–30 cm of top soil removed from several square meters of meadow, and slightly less, but still major damage to adjacent square meters of the orchid colony. The plants had not been counted prior to the damage so the number lost is not known. I estimate that nearly half of the colony was lost, approximately 100 plants.

The Coronado National Forest granted permission to establish a study plot at the site. The objectives of the study are to determine recovery rates in the damaged area, and to try to deduce information on the rate of spread of the orchids. I staked out a double perimeter, with the inner perimeter enclosing the area of total damage, and the outer area partial damage. The total damage

area had top soil removed to a depth greater than 4 cm, greater than the depth of the orchids' rhizomes, so no orchids could have survived. The outer perimeter marked the area where the soil was disturbed, but not to as great a depth, so orchids may have survived. An undisturbed area will also be monitored as a control.

In the summer of 2000 only one orchid came up in the study area, and it did not bloom. This may indicate that the area of total damage is much larger than first estimated. However, orchids take a long time to reproduce, and it will be many years before results are available from this study on *M. porphyrea* and *M. tenuis*.

Discussion

Except for the long-term study on *Spiranthes delitescens* conducted by the Nature Conservancy on their Canelo Hills Reserve (McClaran and Sundt 1992), orchids in the Southwest have received little formal study. Given the rarity of orchids in this fragile environment, more studies such as those reported here should be undertaken. These preliminary monitoring studies will identify blooming patterns and recovery rates in damaged areas. These data should prove of value for making land management decisions.

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A Preliminary Population Study of Alcove Bog Orchid (*Platanthera zothecina*) at Navajo National Monument, Arizona

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Abstract: This study on *Platanthera zothecina* (alcove bog orchid) was initiated by the National Park Service after a recent threatened and endangered species survey at Navajo National Monument. It is listed as Category 2 (species of special concern) by the U.S. Fish and Wildlife Service, and Category 3 (likely to become endangered) by the Navajo Nation. Because *P. zothecina* is a fairly new taxon, and little is known about its ecology, this baseline study documents population size, number of basal leaves, flowering plant height, number of flowers, and fruit set rates for a 2-year period (1999 and 2000) at Betatakin Canyon. Population size dropped from 1,944 to 1,151 plants by the second year. Average number of basal leaves was three. Flowering plant height averaged 23 cm with the tallest measuring 60 cm. Number of flowers per spike averaged 5 with a high of 20. The flowering rate declined from 33 to 22 percent by the second year. Average number of seed capsules was four. Fruit set rate decreased from 81 to 61 percent in the plants that flowered. The proportion of the population to set fruit was down from 9 to 7 percent by the second year. Herbivory was quite high and appeared to affect fruit set rates and possibly long-term recruitment.

Platanthera zothecina (Higgens and Welsh) Kartesz & Gandhi (Orchidaceae; alcove bog orchid) is in a group of species that have been placed in three different genera over time: *Habenaria, Limnorchis,* and *Platanthera* (Colorado Native Plant Society 1997, Atwood et al. 1991). At Navajo National Monument, the first collection was made in 1935 by John Wetherill in Betatakin Canyon (Rothman 1991). Welsh et al. (1987) described and named *P. zothecina* based on a specimen from Grand County, Utah. Before their description, it had been considered a variant of *P. sparsiflora* (Hevly 1961).

Platanthera zothecina is easily distinguished from *P. sparsiflora* based on several morphological characteristics (Figure 1). Leaves are dimorphic on *P. zothecina* with basal leaves more oval with obtuse leaf tips and the leaves are more clustered near the bottom of the stem than on *P. sparsiflora* (Spackman et al. 1997). The lip of *P. zothecina* is usually linear elliptic, whereas the lip of *P. sparsiflora* is linear. The most distinctive feature of *P. zothecina* is the long spur that protrudes stiffly out the back of the flower. Its length is 1.5–2.5 times the length of the lip (Spackman et al. 1997). In *P. sparsiflora,* the spur ranges from slightly shorter than the lip to 1.5 times as long.

The germination ecology of *P. zothecina* is unknown, but is assumed to be similar to other orchids. Germination requires a symbiotic relationship with mycorrhizal fungi in the soil (Cronquist 1981). The fungus *Rhizoctonia* sp. has been associated with several orchid species (Bjugstad-Porter 1993). Pollination is required for seed production and seed establishment is required for recruitment of new individuals (Bowles 1983). *Platanthera* individuals regenerate vegetatively during the growing season by forming a new tuber and perennating bud, which then gives rise to a new shoot the following season (Dressler 1981).

Orchids generally have two distinct life states, vegetative and flowering, but the length of time in each of these states appears dependent on environmental conditions (Mehrhoff 1989). Exposure to environmental stressors can influence not only first-year survival, but subsequent years as well (Lesica and Steele 1994). For *Platanthera,* flowering may be related to precipitation (Bowles et al. 1992). In one study, the most significant factor influencing the number of *Platanthera praeclara* (western fringed prairie orchid) was soil moisture (Hull-Sieg 1997). At Betatakin Canyon, *P. zothecina* was found only in areas with moist soils.

Orchids are also considered to be long-lived species with erratic flowering patterns and periods of dormancy (Bowles 1983). However, when Hull-Sieg and Wolken (1997) excavated orchids from their plots that appeared to be dormant, they found that *P. praeclara* had very high mortality and a shorter life span than previously thought. Furthermore, after an orchid disappeared, it rarely reappeared (Hull-Sieg and King 1995). For many orchid species, a dormancy period of 3–4 years may be the upper limit (Falb and Leopold 1993). It

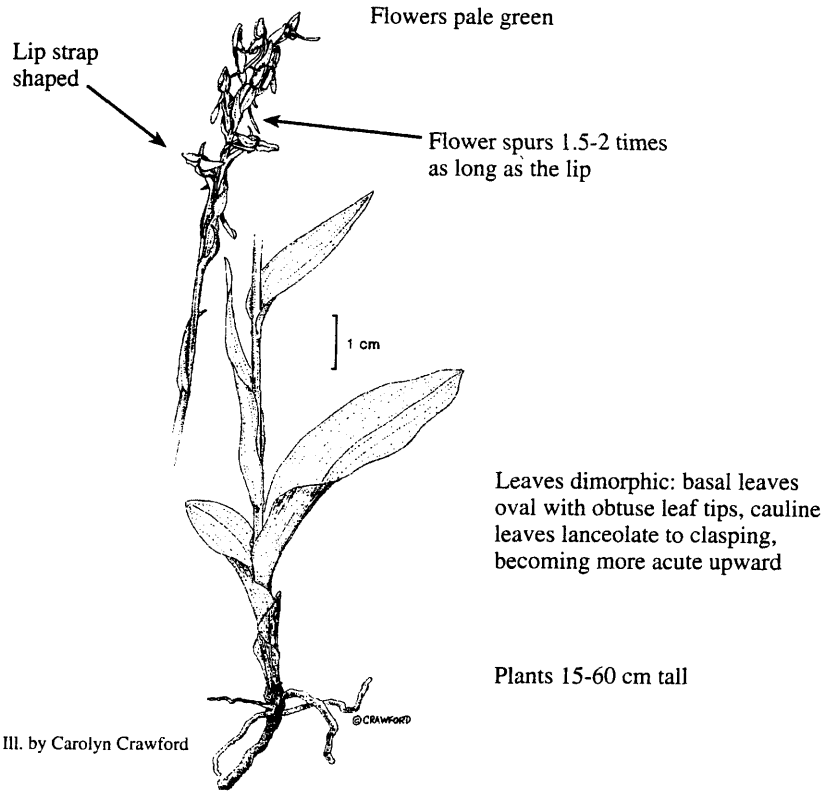


Figure 1. Diagram of *Platanthera zothecina*, the alcove bog orchid.

is unknown whether *P. zothecina* also displays episodic aboveground growth due to dormancy, drought, flooding, or death.

Despite some general information on orchids, and specifically *Platanthera*, we still do not know much about the biology or phenology of *P. zothecina*. In addition, because it is listed as Category 2 (species of special concern) by the U.S. Fish and Wildlife Service, and Category 3 (likely to become endangered) by the Navajo Nation, the National Park Service initiated this study to gather baseline data to better understand the status of this orchid species. This study documents *P. zothecina* population size, number of basal leaves, flowering plant height, number of flowers, and fruit set rates for a 2-year period in Betatakin Canyon.

Area Description

Platanthera zothecina appears to be confined mostly to the upper Colorado River watershed in southeastern Utah, northeastern Arizona, and extreme western Colorado (Colorado Native Plant Society 1997). Data from herbarium collections and other publications from Arizona, Colorado, and Utah suggest that *P. zothecina* is restricted to an elevational range between 1300 and 2700 m (Drost 2000, Spackman et al. 1997, Welsh et al. 1987). At Navajo National Monument, the orchids are located within this elevational range at Betatakin Canyon (2056 m).

The geology of Betatakin Canyon generally consists of Navajo Sandstone, which is porous and allows percolation into the Kayenta Formation, where seeps occur. Exfoliation of the sandstone above the seeps causes the formation of alcoves (Holiday 1998). Vegetation assemblages around the alcoves in Betatakin Canyon consist of *Quercus gambelii*, *Ribes cereum*, and *Prunus virginiana* (Holiday 1998). The alcove seeps in Betatakin Canyon are unique communities dominated by *Aguilegia micrantha* and *Mimulus eastwoodiae* (Holiday 1998). *P. zothecina* was found in Betatakin Canyon along alcove seeps and in the oak terrace community only where moisture was present.

Climatic conditions around Betatakin Canyon are classified as arid with cold winters and hot summers (Holiday 1998). Weather data analyzed by Holiday (1998) from 1978 to 1995 showed that the daily average temperature was 10° C; temperatures varied from highs of 34–38° C in July to lows of –23 to 13° C in the winters. The frost-free season averaged about 155 days. Precipitation in the

canyon was variable with a range of 17.3–47.7 cm annually. Most of the precipitation was during infrequent monsoon rain events. It appeared that the 2 years of this study (1999 and 2000) were relatively dry at Betatakin Canyon, with most of the precipitation occurring in the month of August (R. Best, personal communication).

Methods

In the first-year survey, five workers systematically surveyed one small alcove drainage within Betatakin Canyon. A second survey was done by the author and another biological technician to verify total population size and locations. The entire drainage is approximately 76 m wide (west to east) and 152 m long (north to south). We started the survey inside the alcove, working our way downhill, including a survey of both east and west side slopes. We identified four main populations, marked study site parameters with rebar, described habitat type, slope, aspect, elevation, and microsite vegetation, and photographed study sites (Table 1).

Sites 1 and 2 are located on two separate seeps inside Betatakin Canyon alcove. Site 1, the highest seep, is 4.6 m long. Site 2 is along a seep below Site 1 and is 6.9 m long. Site 3 is along the eastern sideslope starting just outside the alcove, on the uphill side of a maintained hiking trail. Site 3 has one section where a small spring flows downhill, disappears underground, and reappears again at Site 4. Due to the size of this population, Site 3 was subdivided into 5 m sections with a total length of 55 m. Each square subsection included all visible orchids uphill from the trail (5 m long x 1.5 m wide). Site 4 is south and downhill from the alcove in an accumulation zone where debris is left after major rain or rockfall events. Site 4 is 12 m long and is directly on the spring that reappears after going underground near Site 3. Site 4 included all visible orchids along both sides of the spring in squares 12 m long x 0.5 m wide.

On 24 June 1999 and 15 July 2000, we counted the total number of plants of *Platanthera zothecina* on all four study sites. Other data collected consisted of the number of basal leaves, flowering plant height, and number of flowers. During the fall survey, 6 September 1999 and 15 September 2000, we counted the number of seed capsules with seeds present or obviously released (fruit set). Navajo National Monument personnel were contacted throughout the summer to determine when certain life stages (green-up, spike growth, flowering, seed capsule development, seed dispersal, and dormancy) were occurring. Averages were calculated for each year for the number of basal leaves, flowering plant height, and number of flowers. Proportion of plants to flower, proportion of flowering plants that set fruit, and fruit set rate for the entire population was determined. We also documented any disturbances for each study site, such as herbivory, trampling, flooding, and rockfall.

Results

In approximately mid-May, the orchids began their growing season. A complete count of all orchids on all four sites totaled 1,944 individuals for 1999 and 1,151 for 2000 (Table 2). On average, there were three basal leaves per plant for both years. Spike growth occurred throughout May and June. Average flowering plant height was 23 cm

Table 1. Study site description for *Platanthera zothecina* at Navajo National Monument.

Study site	Location and habitat type	Slope ratio, aspect, and elevation	Microsite vegetation (in order of dominance)
1	Sandstone wall; alcove seep	1:1 SE 2056 m	*Aguilegia micrantha, Mimulus eastwoodiae, Carex* spp., *Pinus edulus*
2	Sandstone wall; alcove seep	1:1 SE 2054 m	*Aguilegia micrantha, Mimulus eastwoodiae, Carex* spp., *Pinus edulus, Quercus gambelii*
3	Outside of alcove; vertical side canyon	1:2 E 2042 m	*Oenothera elata, Rosa woodsii, Shepherdia rotundifolia, Acer negundo, Taxicodendron rydbergii, Elymus canadensis, Phragmites australis, Penstemon barbatus, Juncus arcticus, Astragalus ceramicus, Quercus gambelii, Pinus edulus*
4	Below alcove; *Quercus gambelii/Juniperus osteosperma;* sides of year-round spring	1:4 S 1962 m	*Heterotheca villosa, Geranium caespitosum, Cornus sericea, Onopordum acanthium* (Scotch thistle), *Elymus canadensis, Elymus elymoides, Acer negundo*

Table 2. Two-year population data on *Platanthera zothecina* at Navajo National Monument.

	Site 1		Site 2		Site 3		Site 4	
	1999	2000	1999	2000	1999	2000	1999	2000
Number of ramets	43	21	320	*266	1019	627	562	237
Mean number of basal leaves (SD)	3.3 (0.76)	2.7 (0.58)	3.7 (0.69)	2.8 (0.44)	3.7 (2.42)	2.5 (0.53)	3.8 (3.04)	2.4 (0.84)
Mean spike height in cm (SD)	19.6 (7.82)	22.9 (6.4)	21.7 (4.70)	16.3 (4.93)	23.9 (7.52)	24.5 (8.1)	21.0 (5.82)	28.9 (7.36)
Mean number of flowers (SD)	4.3 (2.97)	5.5 (3.51)	2.6 (2.35)	3.7 (1.53)	6.4 (5.80)	8.3 (3.69)	3.8 (1.74)	6.9 (3.58)
No. of plants to flower	35	48	13	2	74	22	9	17
Mean number of seed capsules per plant (SD)	4.1 (1.5)	2.7 (2.1)	2.0 (1.8)	1.0 (0)	5.3 (3.0)	4.4 (3.1)	**0	6.2 (2.4)
Percent of flowering plants that set fruit (SD)	75	75	83	100	84	60	**0	10
Percent of total plants to set fruit	9	14	5	1	12	11	**0	2

*Rockfall covered a small section of Site 2 in the winter of 1999.
**Flood debris covered Site 4 in August of 1999.

for both years with a high of 60 cm on Site 3. Flowering began approximately in early July and lasted into mid-August. The average number of flowers per plant was 5, with a high of 20 on Site 4. Flowering for 1999 was quite variable and ranged from 74 percent on Site 3 to 9 percent on Site 4. This variability was still evident for 2000 with 48 percent on Site 1 and 2 percent on Site 2. The average for flowering on all sites went down from 33 percent in the first year to 22 percent for the second year.

Fruit set began in mid-August and extended into early September; seeds finished dispersing generally by mid-September. The average number of seed capsules was four for both years, with a high of nine. Of the plants that did flower in 1999, 81 percent successfully set fruit (excluding Site 4, see below) with 61 percent success for 2000 (including Site 4). The proportion of the total number of plants to actually set fruit was 9 percent for 1999 and 7 percent for 2000. Dormancy was observed to occur in mid to late September (yellowing of leaves). In both years, we documented herbivory and some trampling for all four sites. About 85 percent of the spikes were eaten or broken in both years of the study. In addition, in August of 1999, flood debris and sediment buried Site 4 and no further data were collected. By the second year, Site 4 appeared to have recovered well, but it had about half of the original population of orchids. On Site 2, a large rock came down some time during the winter of 1999 and covered a small section of the study area.

Discussion

During the first year of data collection, one of the most important observations we made in the field was the extensive herbivory of spikes and flowers. Intense disturbances that remove seed heads are detrimental to long-term recruitment (Bowles 1983). Damage to flowering in just one year may revert a plant back to a vegetative state or even cause mortality (Falb and Leopold 1993). Rabbit herbivory explained much of the long-term demographic fluctuations found in a study on the small white ladyslipper (Falb and Leopold 1993). The sites at Betatakin Canyon had several pack-rat dens in the vicinity, as well as evidence of deer, squirrels, and rabbits near the study sites. When considering the proportion of plants that flowered (33% down to 22%), the proportion of those that flowered and then set fruit (81% down to 61%), and the proportion of the total population to set fruit (9% down to 7%), it appears that herbivory may play an important role in flowering, fruit set, and long-term recruitment.

Total population size was lower in 2000 (down from 1,944 to 1,151 plants), which may have been caused by the previous year's disturbances (herbivory, trampling, flooding, and rockfall). Yet, certain disturbances such as grazing, flooding, and fires can provide open microsites or regeneration niches for orchids (Bowles 1983). Increased light and decreased competition could stimulate growth and flowering in terrestrial orchids, assuming that the appropriate amount of moisture is available (Stoutamire 1974). If this were the case at Betatakin Canyon, we would expect to see an increase of orchids on Site 4, which flooded in August of 1999. However, there was not an increase, but a decrease in population size from 563 plants in 1999 to 237 on this site in 2000. Other vegetation, such as *Heterotheca villosa* and *Onopordum acanthium*, quickly dominated Site 4 in the spring of 2000, possibly outcompeting the orchids for light, growing space, and moisture.

Annual climate patterns, such as several dry years in a row, may have also been a factor in the decline of this orchid population, but recent weather records were not analyzed for this study. Soil moisture is considered another determining factor in orchid numbers (Hull-Sieg 1997). Although soil moisture was not measured directly for this study, it was observed that all four sites were moist throughout both years. It is possible that this decline in population size might also involve the unknown amount of dormancy that is common to most orchids (Bowles 1983), but individual plants were not tagged nor excavated, so we were not able to track this phenomenon. Another issue altogether is whether we accurately counted individual plants. Hull-Sieg and King (1995) found that there can be two or three ramets arising from one individual *Platanthera praeclara* plant. It is unknown if this is a characteristic of *Platanthera zothecina*.

Due to its unknown distribution and low numbers in northern Arizona, the National Park Service and the Navajo Nation are concerned about the alcove bog orchid population. Because its habitat appears to be limited to seeps and springs, it is important to continue surveying for other populations where water is found and to monitor the sites already identified. The results from this 2-year study suggest a need to better quantify the impacts of herbivory and to determine whether dormancy is an issue with this species. Future monitoring should include tagging individual plants to provide more detailed phenologic and demographic data to better understand recruitment over the long term. It would also be helpful to identify pollinators and determine seed viability and the number of viable seeds that are incorporated into the seed bank. The addition of measurable hydrologic variables, with annual climate patterns and soil moisture being the most logical, is extremely important in this arid environment where seasonal moisture fluctuations may determine the long-term stability of these orchids.

Acknowledgments

I would like to thank Dr. Carolyn Hull-Sieg and Ron Coleman for their time spent explaining orchid biology to me and reviewing an earlier version of this article. I would also like to thank the superintendent of Navajo National Monument, James Charles, and the National Park Service for providing me with the funding and the personnel to implement this project.

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The Influence of Interplant Distance and Number of Flowers on Seed Set in Dwarf Bear-Poppy (*Arctomecon humilis*)

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Abstract: Samples from three isolated populations of the dwarf bear-poppy (*Arctomecon humilis* Cov.) demonstrate that both flower pollination (fruit set) and seed set per fruit decline as interplant distances increase and the number of flowers per plant declines. Interplant distance and number of flowers per plant tend to interact with reproduction. Seed set per plant is most impaired on plants that produce few flowers and are far from other flowering, conspecific individuals. Such data warn that the number of surviving individuals alone is not a safe criterion for evaluating reproductive health of a plant population. Population density (number of individuals per unit area) strongly influences the reproductive success of this species. Other studies suggest that large reductions in the pollen deposited on stigmas may eliminate competition among pollen grains for access to ovules and adversely affect the vigor of the next sporophyte generation.

The dwarf bear-poppy is a local endemic confined to gypsiferous soils in Washington County, Utah and the adjacent edge of Mohave County, Arizona (McDougall 1973, Welsh et al. 1993). The species is formally listed as endangered by the U.S. Fish and Wildlife Service (1979).

It is a low-growing (rarely over 2 cm tall in flower), evergreen herb that usually survives for only 5 or 6 years. The dwarf bear-poppy flowers in April and early May and produces as many as 200 flowers per plant. Individual flowers are white and about 4 cm in diameter: Each flower displays a mass of numerous, bright yellow anthers at its center for a few hours after opening. Flowers remain attractive and reproductively receptive to pollen for 2 or 3 days (Nelson 1989). As many as 8 or 10 new flowers open each day and flowering individuals are rendered even more conspicuous by retention of petals indefinitely after anthesis. The shriveled, off-white petals enfold the developing fruit and are abscised with it at maturity.

The dwarf bear-poppy was pollinated in presettlement time by two native, solitary bees, species of *Perdita* and *Synhalonia* (Borror et al. 1976, Buchmann and Nabhan 1996). The domestic honeybee (*Apis mellifera*) has also become a regular pollinator of the species. In fact, our observations suggest that the honeybee is currently the most frequent visitor to dwarf bear-poppy flowers. Pollinator visits appear to be rewarded with pollen only: Nectar is apparently not produced by the flowers.

Our earlier work has shown that the dwarf bear-poppy is highly self-incompatible (Harper et al., unpub. data). Plants enclosed in mesh cages rarely produce fruits, whereas plants open to natural pollinators show high percentages of fruits set per flower (consistently over 90% in dense populations). More than 85 percent of the ovules in fruits produced in dense populations produced viable seeds in a sample taken at the Red Bluff (Washington County, Utah) monitoring site in 1997, a year of better than average precipitation.

The dwarf bear-poppy displays large variations in population size at all known sites of occurrence. The population at Red Bluff has been monitored annually since 1987. During that period the population varied from a high of 425 plants per 0.1 ha in April of 1993 to a low of 19 plants per 0.1 ha in October of 1987 (Harper et al. 2000).

In this study, we have attempted to determine the effect of variable interplant distances on seed set for *Arctomecon humilis*. Because interplant distances inescapably increase as population density declines, one might expect this insect-pollinated species to reproduce less effectively when pollinators are forced to commute greater distances between plants. However, little information exists concerning the effects of interplant distances on the behavior of common pollinators of the dwarf bear-poppy. Likewise, the influence of interplant distance on frequency of pollinator visits or the number of pollen grains that are deposited on individual stigmas after a single visit is not known

for this bear-poppy. Other studies have demonstrated that many plant species rarely produce maximum seed set after a single visit from a pollinator (Primack and Silander 1975, Silander 1978, Rathcke 1983). Such studies have also shown that pollinators differ widely with respect to their ability to effect high seed set after a single visit to flowers of any specific species.

Methods

To obtain data that are broadly representative of the influence of interplant distance on seed production of the dwarf bear-poppy, we have drawn our sample from three separate populations of the species. Allphin et al. (1998) have shown that the three populations sampled show genetic differences from each other in respect to allele frequencies at selected loci.

The Red Bluff population that we sampled is near the community of Bloomington and north of the Virgin River. We have also sampled the White Dome and the Beehive Dome populations. The White Dome population is roughly 10 km south of St. George and almost on the Utah-Arizona border. Beehive Dome is approximately 15 km southeast of St. George, near the Arizona border, on Warner Ridge.

All of the sample sites occur on the Shinabkaib member of the Moenkopi Formation at about 875 m elevation. The Shinabkaib shales are strongly impregnated with gypsum, 25–50 percent by weight (Nelson and Harper 1991). Annual precipitation averages about 200 mm across the sample area. The mean annual temperature at St. George is 16.8° C (Nelson and Harper 1991).

The annual precipitation is both highly variable over these study areas and of critical importance for seed germination, seedling establishment, and seed production for the dwarf bear-poppy. The coefficient of variation for annual precipitation at St. George is almost 32 percent over the 100 years that the station has operated (National Oceanographic and Atmospheric Administration 2000). Perhaps more pertinent is the fact that annual precipitation has ranged from a low of 90.2 to a high to 425.5 mm during the period of record at that station. To more accurately document influential climatic variables for seed production by this bear-poppy, we have determined precipitation at the St. George station for the 7 months preceding sampling dates for seed production. That period includes the coolest months of the year at this location, so most of the precipitation falling during the period enters the soil and is available for flowering and fruiting of the dwarf bear-poppy, which occurs in April and early May.

Samples were collected from approximately 20-ha plots at each of the three sites. Ten sample points were taken within each study plot; they were positioned at the intersections of a grid across the surface of each study area. Grid lines were 50 m apart. At each intersection a peg was pushed into the ground and the area around that point was divided into four quadrants of equal size (90° angles). These points became centers for the quarter method, a distance method used to sample plant populations in which individuals are often far removed from each other.

The quarter method provided a crude estimate of poppy density at each site and quantified the degree to which plants were aggregated in space; it also provided an objective method for selecting plants to evaluate the effects of interplant distance on pollination and seed set (Cottam and Curtis 1956). Operationally, a point positioned at a grid intersection became the center for four quadrants erected around the point. The distance from the point to the nearest object of interest (in this case, the nearest bear-poppy) was recorded for each quadrant. In a population of randomly dispersed objects, the average point-to-object distance provides an accurate estimate of the square root of the mean area per individual in the population (when area and distance are recorded in the same basic units—e.g., in m^2 and m, respectively). We have used the ratio of average point-to-object distance and the variance of that value as an estimator of population aggregation, because statisticians have long known that the ratio approaches 1.0 for randomly dispersed objects (Steel and Torrie 1960).

The nearest poppy plant in quadrants 1–3 became the base plant for interplant distance analyses. In each quadrant, the closest plant was taken as the base plant if it was flowering. If the nearest plant was not flowering, the nearest flowering individual in the quadrant was located and the nearest flowering poppy to that plant was chosen for analysis. The distance between those two individuals was recorded and the nearest neighbor individual was studied for number of flowers produced and number of developing fruits. Finally, one of the larger fruits present on the nearest neighbor plants was harvested and placed in a 5 cm x 10 cm paper envelope, which was sealed. Plant number and collection site were recorded on the envelope. Thirty randomly chosen plants were thus inventoried at each of the three sites.

In the laboratory, fruits were opened and the number of well-filled, apparently viable seeds was recorded. The numbers of aborted seeds (shriveled) and unexpanded ovules in the fruit were also recorded. Ultimately, percent pollination (percent of flowers that produced expanded fruits) and percentage of seed set (the proportion of ovules in each fruit that produced filled seeds) was correlated with the interplant distance associated with individual inventory plants. Preliminary analyses suggested that the number of flowers produced by inventoried plants was interacting with interplant distance to determine percentage pollination and seeds set per fruit of individual plants. Accordingly, the joint effects of interplant distance and flower number on flower pollination and fruit set were evaluated using multiple regression (Steel and Torrie 1960).

Results

The spatial distribution of bear-poppy plants at the three study sites is considered in Table 1. The average point-to-plant distances obtained using the quarter method show that plants in all populations are widely spaced and highly aggregated. Small, disjunct subpopulations are widely separated from other subpopulations. Plants appear to prefer tops and southern exposures of ridges in the gently undulating terrains that develop on weathered exposures of Moenkopi shale. Because all populations show strong aggregation of individuals into small, variably spaced subpopulations, reliable estimates of plant density are not possible; such estimates are based on the assumption that all objects sampled are randomly dispersed in space. We do know the exact number of plants on a 0.07 ha monitoring site at Red Bluff—that area contained 74 plants (~106 plants per 0.1 ha) in October of 1999. Using the assumption that the average point-to-plant distance (2.78 m in Table 1) equals the square root of the mean area per plant for randomly dispersed objects (Cottam and Curtis 1956), one would estimate approximately 129 plants per 0.1 ha. Thus, even though the distances obtained with the quarter method are not randomly dispersed about their mean, they do permit an estimate of population density that is reasonably close to actual density values observed on a portion of the larger sample area. It should be noted, however, that poppy populations at Beehive Dome and White Dome are much more aggregated than at Red Bluff. Thus point-to-plant distances could be expected to yield less reliable estimates of true density.

Table 1. Population characteristics for dwarf bear poppies at three sample sites.

Site	Average point-to-plant distance (m)	Aggregation Index*
Red Bluff	2.78	9.9
Beehive Dome	9.54	50.0
White Dome	11.78	37.9

*The aggregation index is the ratio of each average point-to-plant distance divided into the variance for that average.

The extreme aggregation within the bear-poppy populations provides a wide variation in interplant distances. Both pollination and seed fill are strongly influenced by interplant distance and number of flowers per plant (Table 2). The data suggest that for the dwarf bear-poppy and the pollinators involved in our area, pollination is not adversely affected by interplant distance until it exceeds 10 m. The effect is slight for plants that produce more than 30 flowers, but becomes progressively more influential as flower number declines. The effects of flower number and interplant distances on seed fill were strong even when interplant distances were less than 3 m. When distances exceeded 10 m, plants with less than 10 flowers filled less than 20 percent of potential seed, on average.

Table 2. Percent pollination and seed fill for 90 randomly selected plants separated into classes based on flower number and distance to nearest flowering conspecific. Sample size (n) is given for each compartment. Data are based on a sample taken in year 2000.

Interplant distance classes (m)	Number of flowers per plant		
	1–10	11–30	≥ 31
Percent Pollination			
≤ 3.0	96.4 ± 2.83 (12)	92.6 ± 3.72 (11)	95.9 ± 1.58 (13)
3.1–10.0	93.5 ± 4.37 (7)	92.6 ± 4.05 (6)	90.4 ± 3.25 (16)
≥ 10.1	56.9 ± 14.01 (6)	64.9 ± 13.79 (4)	89.6 ± 2.70 (15)
Percent Seed Fill			
≤ 3.0	51.3 ± 9.92 (12)	66.7 ± 7.53 (11)	72.5 ± 6.67 (13)
3.1–10.0	41.3 ± 13.48 (7)	49.8 ± 11.00 (6)	71.5 ± 5.73 (16)
≥ 10.1	19.4 ± 12.29 (6)	35.2 ± 20.36 (4)	67.1 ± 6.52 (15)

Pollination success and seed fill appear to be dependent on the conspicuousness of the floral flag. Increasing distance or fewer flowers per plant both appear to reduce the attractiveness of the floral signal for foraging pollinators, effectively reducing the number of pollinator visits. Pollination appears to be less sensitive to the number of pollinator visits than percentage seed fill. The results of multiple regression analyses (Table 3) demonstrate that interplant distance and number of flowers per plant both exert statistically significant effects on pollination and seed set. For pollination the interaction between distance and number of flowers per plant was significant.

Because we have preliminary interplant distance data, and we know its influence on pollination and seed fill from Red Bluff for reproductive year 1997, a year of far better moisture relations than 2000, we can make a rough evaluation of the relative impacts of abiotic resources (water availability) and interplant distances on pollination and seed fill. During the 7-month period (October 1996–April 1997) preceding flowering and fruiting of the dwarf bear-poppy in 1997, 196.3 mm of precipitation fell at the St. George, Utah weather station (137.8% of the long-term mean for that period). The pollination percentage was 93.9 at the Red Bluff site, and the seed set percentage averaged 84.5 in 1997. When results for 2000 are averaged across all interplant distance and flower number classes, pollination averaged 82.0 percent and seed fill was 52.8 percent. Precipitation for the preceding 7 months in 2000 was only 65.5 mm (46.0% of the long-term average).

These data demonstrate that resources do exert a strong impact on flower pollination and seed fill in developing fruits of the dwarf bear-poppy. Nevertheless, the year 2000 results demonstrate significant effects of interplant distance and flower number on pollination and seed fill independent of those of abiotic resources.

Discussion

Our results demonstrate that the number of surviving plants alone is not an adequate indicator of the reproductive health of rare plants. When interplant distances become too great, both percentage pollination and percentage seed fill can be expected to decline. That decline may be especially great for species that produce few or inconspicuous flowers. Results for interplant distance will undoubtedly vary with pollinators. Flowers ser-

Table 3. Multiple regression results of the combined (above) and independent (below) effects of number of flowers per plant and interplant distance on percentage fruit set (pollination) and percentage seed fill. The interaction of number of flowers per plant and distance between flowering plants on percentage of flowers setting fruit or filling seeds is also tested.

Source of variation	Degrees of freedom	Sum of squares	Mean sum of squares	Probability of F value	Larger F
Pollination combined effects					
Model	8	10,171.78	1,271.47	6.25	<0.0001
Error	81	16,490.85	203.59		
Corrected total	89	26,662.63			
Pollination independent effects					
Distance	2	7,861.35	3930.67	19.31	<0.0001
No. flowers per plant	2	1,815.46	970.73	4.46	0.0146
Distance-flower interaction	4	4,200.77	1050.19	5.16	0.0009
Seed fill combined effects					
Model	8	22,072.64	2,759.08	3.42	0.0019
Error	81	65,275.25	805.87		
Corrected total	89	87,347.90			
Seed fill independent effects					
Distance	2	6,577.33	3,288.67	4.08	0.0205
No. flowers per plant	2	17,705.08	8,852.54	10.99	<0.001
Distance-flower interaction	4	2,759.21	689.80	0.86	0.4941

viced by pollinators that habitually make long commutes between floral resources and nesting sites would probably be less handicapped by large reductions in density than plants serviced by pollinators less prone to search large areas.

Because seed production is the product of percentage pollination times percentage seed fill, reductions in these processes can have large effects on seed production per plant in any given year. For the bear-poppy considered here, small plants that were far removed from other flowering individuals experienced reductions in potential seed set of more than 75 percent.

Windsor et al. (2000) have demonstrated that maximum seed set in the desert vine, *Cucurbita foetidissima*, was never achieved after a single pollinator visit. Maximum fertilization was dependent upon multiple visitations. They further demonstrated that pollen competition occurred in the species when it received abundant pollen. Progeny tests demonstrated that seedlings emerging from seed produced by heavily pollinated fruits consistently showed greater vigor for several characteristics than seedlings from fruits that received insufficient pollen to experience pollen competition. Their results suggest that not only may seed set suffer when population density falls below a critical level among reproductively active plants, but vigor of individuals in the next generation may also be eroded. That hypothesis is supported by studies that show a significant correlation between vigor of gametophyte and sporophyte generations in several species. (See Mulcahy et al. 1983 and Willson 1979 for reviews of pollen tube competition and its potential effects on sporophyte genotype and vigor.)

Acknowledgments

Donna Barnes and Dianne Carter provided invaluable field assistance in 2000. Janet Cooper has repeatedly assisted in field monitoring work. Field work was partially funded by the Dixie Resource Area of the Bureau of Land Management, United States Department of the Interior.

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The Effects of Canopy Openings and Population Size on the Persistence of Southwest Columbines at Risk of Extinction

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Abstract: The habitat associated with riparian, understory, rare and endangered plant populations of the Southwest includes rocky places in high-altitude canyons, mostly along shady streams, pools, and dripping cliffs. The composition of these insular plant populations, which are separated by intervening desert, is influenced by several local environmental conditions. The understory light environment, which is influenced by canopy cover, is a key determinant of vegetation patterns; it varies spatially within and among populations, and is determined by intermediate closure and light availability. Light availability could directly affect individual fitness (via affecting photosynthetic, micro-climatic, and transpirational processes) and subsequently could indirectly affect plant population size and persistence. We examined the environmental influences of canopy cover and light availability in seven populations of herbaceous, perennial yellow columbines (genus *Aquilegia*) in the Southwest. *Aquilegia* populations exhibit many of the characteristics, particularly isolation and relatively small population size, associated with at-risk populations. For example, *Aquilegia chaplinei*, or Chapline's columbine, is currently protected under the New Mexico Endangered Plant Species Act. Canopy cover and understory light environments were quantified from the view each plant has of the sky, measured via vertical photography. These images were analyzed to investigate the percentage of sky versus canopy cover, as well as the relationship of canopy cover and within- and among-population traits. Overall, these ecological assessments will help expand our understanding of environmental influences and may be important in regard to the conservation, persistence, and recovery of small, isolated plant populations.

Historically, the main criterion for identifying threatened and endangered plant species has been the scarcity of individuals or populations. Recently, however, scientists and managers have recognized the need to assess rarity and vulnerability based on biological processes in addition to patterns of geographic distribution (Holsinger and Gottlieb 1991). Reduced geographical distribution or population size could be the result of, and could potentially be affected by, three important types of processes: genetic, demographic, and environmental. The performance of plant individuals and populations hinges on the integration of these types of processes. The focus here is on one environmental factor that potentially influences at-risk columbine (*Aquilegia*) populations in semiarid ecosystems of the U.S. Southwest. (For a discussion of the importance of understanding plant evolutionary genetics and demography see Milligan, and Stubben and Milligan, this volume).

Semiarid woodland ecosystems in the Southwest are especially sensitive to changes in vegetation due to habitat degradation (Schlesinger et al. 1990) and drastic climate changes (Neilson 1986). Climate change in particular has caused profound reductions in the ranges of Southwestern woody vegetation since the Pleistocene (Stephenson 1990). Changes in such overstory functional types directly affect the understory light environment. Previous studies have shown that woody overstory canopy patterns affect the understory by altering solar radiation and soil moisture (Breshears et al. 1997), seed germination and seedling performance (Caccia and Ballare 1998), ectomycorrhizal associations (Zhou and Sharik 1997), and species richness (Vetaas 1997), as well as desert grasslands being invaded by woody mesquite (Warren et al. 1996). Our study is unique in that it examines the direct relationship between overstory, woody canopy openings and the vegetative and reproductive outputs (directly or indirectly affecting fitness) of understory plant individuals whose populations are considered at risk of extinction.

Understory light (1) is influenced by canopy openings, (2) varies spatially within and among understory populations, (3) is often the most limiting factor, and (4) could influence vegetative and reproductive outputs for understory herbaceous plant functional types. Martens et al. (2000) clearly demonstrated the relatively strong, negative relationship between percent canopy cover and photosynthetically active radiation (PAR); as percent canopy cover increases, PAR decreases. Because PAR is the only light source available to plants,

fitness-related plant traits could be reduced as the degree of canopy opening becomes greater. Specifically, we predicted a negative relationship between overstory canopy gap and both vegetative and reproductive outputs for understory *Aquilegia* individuals.

To comprehend the relationship between light and understory plant distribution and performance, we must accurately quantify light availability through space. There are many techniques to measure the canopy, but photography of the overstory canopy closure, or the proportion of the sky hemisphere obscured by natural structures when viewed from a single point, is preferred for quantifying forest structure and its causal force on the understory light environment (Jennings et al. 1999, Robison and McCarthy 1999).

Methods

The genus *Aquilegia* (Ranunculaceae) is composed of at least 70 North Temperate herbaceous perennials (Munz 1946, Whittemore 1997). The *Aquilegia* populations in the Southwest exhibit many of the characteristics, particularly isolation and relatively small population size, associated with at-risk populations. This is exemplified by the conservation status of *Aquilegia chrysantha* var. *chaplinei* (Chapline's columbine) and its limited distribution within Eddy County, New Mexico. Chapline's columbine is currently protected at the state and federal levels, and is a U.S. Forest Service Sensitive Species.

The habitat associated with many Southwest *Aquilegia* consists of rocky places in canyons, mostly along streams and dripping cliffs; therefore, the biogeographical range of *Aquilegia* is among montane "islands." The woody overstory for such *Aquilegia* typically includes some combination of maple (*Acer* spp.), ash (*Fraxinus* spp.), and cottonwood (*Populus* spp.). The persistence of *Aquilegia* populations may depend on woody overstory; specifically, changes in the overstory structure could cause *Aquilegia* population size decline.

Previous genetic analyses of closely related Southwest *Aquilegia* suggest a limited among-population gene flow within and among mountain ranges in the Southwest (Hodges and Arnold 1994, Strand et al. 1996). As a result, the population structure of *Aquilegia* enables comparisons among geographically and genetically isolated "island" populations. Additionally, principal components analysis (PCA) for several floral traits of these *Aquilegia* implies indistinguishable taxonomic boundaries (unpublished data). This understanding of Southwest *Aquilegia* population isolation and of its possible dependence on woody overstory, regardless of historical taxonomic treatment, is fundamental for investigating the natural association between overstory canopy openings and understory *Aquilegia* population performance.

Study Sites

To empirically test our prediction that understory population size is affected by the degree of overstory canopy openings, we sampled populations that exhibit a range of numbers of individuals (Table 1). Population size estimates entailed counting the number of adult plants and estimating numbers of seedlings and juveniles. Sample sizes range from 20 to 160 individuals, depending on the population.

Vegetative and Reproductive Outputs

Data recorded for each individual plant consisted of stem height, rosette number, leaf number, and leaflet width for one of the basal leaves. Reproductive outputs quantified for each individual were the number of flowers and fruits produced per individual.

Canopy Opening

To assess the effect of the light environment on plant phenotypes, we quantified light availability from the view each plant has of the sky. Above each sampled plant, sky and canopy photographs were taken with an Olympus OM camera, a 28 mm, wide-angle lens, and Fuji 400 ASA black-and-white film. A blue filter (Tiffen 80B) was used to increase the contrast between foliage and sky. For each photograph, the camera was aligned with true north, and a level was used to ensure that the camera was positioned horizontally. A Hewlett Packard Scan Jet IIcx was used to scan the resulting images. Computerized image processing software (Open Visualization Data Explorer, available

Table 1. Sampled populations, locations, and estimated population sizes.

Aquilegia population	Location	Estimated population size
Caballero Canyon	Sacramento Mtns, NM	75
Pine Canyon	Chisos Mtns, TX	100
Cattail Falls	Chisos Mtns, TX	200
Dripping Springs	Organ Mtns, NM	235
McKittrick Can.	Guadalupe Mtns, NM	375
Maple Canyon	Chisos Mtns, TX	500
Ash Springs	San Andres Mtns, NM	3000

online at http://www.research.ibm.com/dx) was then used to express sky and foilage areas to calculate the fraction of open sky per image.

Data Analyses

All statistical analyses were performed with JMP IN7 statistical software (SAS 1996). The distribution of response variable data were checked for deviations from the normal distribution using the univariate procedure of a Shapiro-Wilks W test (a = 0.05; SAS 1996). In the event that these data possessed non-normal distributions or unequal variances, the data were log transformed or we used non-parametric statistical tests to rank responses for comparison (Pratt and Gibbons 1981, Sokal and Rohlf 1987, Sprent 1989). Further, to examine the relationships between the percent open canopy and a suite of plant traits, we used a regression of each of six traits, or response variables on the degrees of percent open sky (Sokal and Rohlf 1987). For statistical significance, the alpha level was set at $P < 0.05$.

Results

With regard to differences in canopy openings among populations, Figure 1 indicates that the distributions vary and the means differ across populations. However, there are possible *statistically* significant differences among the populations. The Wilcoxon/Kruskal-Wallis rank sums results (Table 2) show statistically significant differences in 16 of 21 total pairwise comparisons, prompting an investigation into whether the population-level differences in canopy opening played a role in influencing the number of surviving individuals in each population.

Because the degree of average canopy opening depends on the population, and because our sampled populations vary in the number of individuals, we investigated whether there is a direct, detectable relationship between the degree of open canopy and *Aquilegia* population size. The relatively low, non-significant Spearman's correlation coefficient value (rho = 0.1429; prob > |rho| = 0.7872) illustrates that *Aquilegia* population size is not directly dependent on the degree of open canopy. Although the degree of overstory canopy opening does not *directly* influence the numbers of individuals in the understory *Aquilegia* populations, it may have an *indirect* affect on *Aquilegia* population size if our data support a relationship between the degree of canopy opening and certain plant traits.

Ideally, we strove to determine whether differences in population-level averages of percent open canopy influence differences in population-level averages for a suite of plant traits. Table 3 shows the regression coefficients and describes the

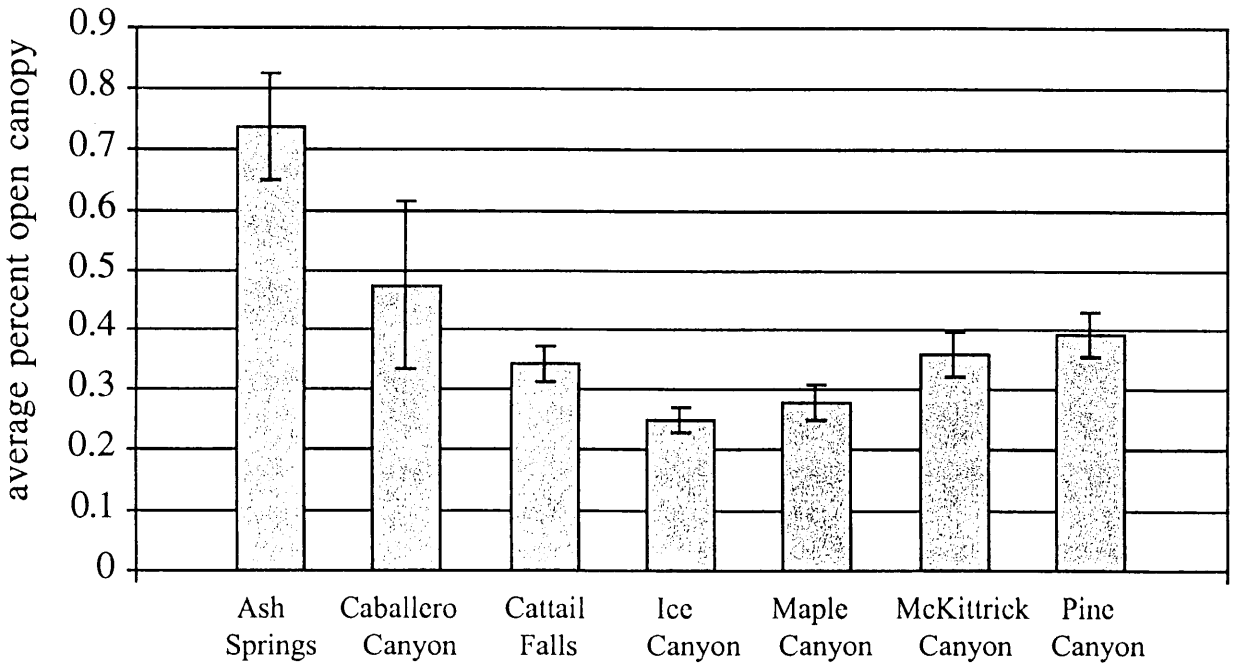


Figure 1. Population profile for average percent open canopy (with 95% confidence intervals).

Table 2. Wilcoxon/Kruskal-Wallis rank probabilities (Prob > χ^2).

	Ash Springs	Caballero Canyon	Cattail Falls	Ice Canyon	Maple Canyon	McKittrick Canyon	Pine Canyon
Ash Springs		0.045*	**	**	**	**	**
Caballero Canyon			0.087	**	0.011*	0.043*	0.387
Cattail Falls				**	0.012*	0.386	0.015*
Ice Canyon					0.547	0.002*	**
Maple Canyon						0.374	**
McKittrick Canyon							0.042*
Pine Canyon							

*prob < 0.05; **prob < 0.001.

Table 3. Regression coefficients describing the effect of open sky on a suite of fitness-related *Aquilegia* traits.

	Number flowers	Number fruits	Leaflet width	Number rosettes	Number leaves	Stem height	Stems
Ash Springs	0.1128*	0.1637*		0.0100	0.0242		0.0754
Caballero Canyon	0.0002	0.0507*	0.0161	0.0382	0.0301*	0.0705	0.0118
Cattail Falls		0.1439	0.2351*	0.0090	0.0042		
Ice Canyon	0.0270*	0.0420*	0.0258	0.0200*	0.0088*	0.1112*	0.1192*
Maple Canyon	0.0232	0.0005	0.0823	0.0177	0.0011	0.2548	0.0011
McKittrick Canyon	0.0274*	0.0009	0.0002	0.0082*	0.0005	0.0236	0.0006
Pine Canyon		0.1508*	0.2135*	0.0366	0.0149	0.3019	0.1357*

Empty boxes indicate missing data; *p < 0.05.

population-level relationships between the effects of open canopy and six plant traits per individual. We can then ask, if there are detectable relationships between the degree of canopy opening and plant traits, whether the regression coefficients, or slopes of the regression lines, differ across populations. In other words, does the expression of plant traits depend on the *interaction* between the population and canopy opening? The highly significant effect test results for five of the six plant traits (Table 4) illustrate that the influences of overstory canopy opening on these particular *Aquilegia* individual traits are remarkably dependent on the population.

Discussion

Our study represents a unique approach to account for the particular environmental influence of overstory canopy openings and estimates of light availability. Our results demonstrate that there exists considerable among-population differentiation in canopy openings, and that there is no detectable causal relationship between the degree of canopy opening and population size. Further, we gauged the impacts of open canopy on fitness-related traits of *Aquilegia* individuals within populations. Although our data for *Aquilegia* populations suggest that the degrees of canopy openings do slightly influence certain plant vegetative and reproductive outputs, this relationship may not be very strong, as evidenced by some of the weak regression coefficients. This is not surprising, given that variance in the mean understory light is often a curvilinear function of cover such that the photosynthetically active radiation (PAR) variance is highest at intermediate values of canopy and is dependent on the spatial pattern (Martens et al. 2000). Further, given the complex nature of the relationships between wavelengths of light affecting photosynthetic processes and the allocation of vegetative and reproductive outputs, there may be tradeoffs depending on the life histories of each population (Bazzaz 1996).

Another cause of the relatively weak relationships between percent open sky and certain plant traits may be due to time lags in understory response to changes in canopy cover, either within the lifetime of an individual or between generations. This phenomenon has been observed in other studies of this nature (e.g., Thomas et al. 1999) and is applicable to this study, especially due to the relatively long generation times of

Table 4. Effect test results for the expression of plant traits dependent on the interaction between the population and canopy opening.

Response variable (Y)	F Ratio	Prob > F
Number of flowers	1.767	0.105
Number of fruits	6.997	< 0.001*
Number of rosettes	3.554	< 0.001*
Number of leaves	3.951	< 0.001*
Stem height	5.376	0.003*
Lower leaflet width	3.536	< 0.001*

Aquilegia that would, in turn, cause a relatively slow rate of response to selection. Elucidation of a time lag could be resolved if demographic analyses are employed to determine plant growth rates (e.g., Pearcy 1983). Therefore, although most of the regression coefficients explaining the variation in traits due to canopy opening have low values, they afford potentially useful information for other analyses.

Future Objectives

Canopy images not only provide information regarding canopy openings, they also provide detailed quantitative descriptions of the forest canopy, such as leaf area index (LAI) , leaf angle distribution, and vertical distribution of leaves. These descriptions are necessary when studying the effects of overstory cover on the understory light environment (McIntyre et al. 1990). We intend to use our images to further characterize the structure of the overstory canopy and to quantify other environmental parameters such as the photosynthetically active radiation (PAR) available to *Aquilegia* individuals.

Although this paper focuses on one particular environmental process affecting at-risk plant populations, one of our aims is to integrate the environmental knowledge with our understanding of quantitative genetic factors that influence plant traits (Milligan, this volume). In particular, our quantitative genetic study seeks to determine the relative contributions of genetic versus environmental influences. Although the data presented in Table 2 suggest that vegetative and reproductive outputs for *Aquilegia* plant individuals are minimally influenced by one particular environmental parameter—the understory light environment—this information will play a significant role in our larger study.

In addition to the effects of open canopy on vegetative and reproductive outputs for perennial plants, the effect of open canopy is an integral factor in demographic processes. For example, theoretical (Pons 1992) and empirical (Caccia and Ballare 1998) studies have demonstrated that the understory light environment influences at least one particular demographic factor: seedling recruitment. Counts of recruited seedlings and of adult reproductive plants from ongoing studies on *Aquilegia* populations (Stubben and Milligan, this volume) provide essential demographic information, such as effective population sizes (Nunney and Elam 1994, Nunney 1995). Additionally, the precipitation available to each of the sampled *Aquilegia* populations has been quantified, showing that the amount of precipitation strongly influences fluctuations in population growth rate (Stubben and Milligan, this volume). Therefore, because we have obtained both demographic and environmental data, and considering that the associations of population size and persistence largely depend on the coupled effects of demographic processes and environmental influences, we have the potential to predict future population growth or decline. Therefore, the integration of genetic, demographic, and environmental influences could play a powerful role in the cause of understory *Aquilegia* population growth or decline.

Conclusion

This study evaluated overstory distribution patterns and the relationship between understory light environments and plant fitness. The importance of this project includes the utilization of photographic techniques and image analyses as powerful tools to estimate the degree of overstory canopy openings, as well as regression-based approaches to assess the relationship between the degree of canopy openings and quantitative traits in *Aquilegia*. Further, the overstory canopy data could be utilized to answer questions regarding other understory plant taxa associated with the Southwest *Aquilegia*, or the photographic methodology and image analyses could be widely applicable to gauging the effects of overstory, open canopy composition, or density on a variety of understory taxa. Ultimately, we intend to collectively examine the interrelationships among evolutionary genetics, demography, and the environment. This knowledge will elucidate a connection between the effects of open canopy and effective population size and persistence, and this will in turn aid our understanding and implementation of effective conservation strategies.

Acknowledgments

We wish to thank Chris Stubben, Julie Smith, and Annette Turrentine for their help in the field. Additionally, we appreciate funding from the Wildlife Society, the New Mexico Chapter of Sigma Xi, the Scientific Research Society, the New Mexico State University Department of Biology, and T & E., Inc. Research Grants for Conservation Biology.

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The Status of *Lepidospartum burgessii* (Burgess Broomshrub or Gypsum Broomscale)

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Abstract: *Lepidospartum burgessii* is designated a Species of Concern by the U.S. Fish and Wildlife Service. This shrub is endemic to gypsum soils in north Culberson County, Texas and southern Otero County, New Mexico. In 1991-92 the condition and number of plants in New Mexico were examined but otherwise little was known about the ecology or biology of this species. Our objectives were to define its habitat characteristics and status. We found that *L. burgessii* colonizes more diverse habitats than previously thought. In New Mexico the plants generally grew on stabilized, microbiotic-covered, gypsum soils with approximately 5 percent basal vegetation–litter cover. In Texas, and at one site in New Mexico, shrubs grew on mobile gypsum dunes with an average of 20 percent basal vegetation–litter cover. In 1997 plants were counted in seven colonies in New Mexico. Approximately 15 percent of the individuals counted within those colonies in 1991-92 were dead in 1997 and the number of juvenile plants had declined. Recruitment was only by clonal propagation. No seeds formed, although there were abundant flowers. Involucre length was significantly longer from plants in Texas than from those in New Mexico, which suggests genetic diversity between the two populations. Two potential disease problems were identified: *Corythuca marmorata* (Tingidae, Hymenoptera), a known pathogen of some Asteraceae species, caused leaf loss and stem necrosis, and *Alternaria alternata* (Dematiaceae, Monilialales), a potential pathogenic fungus, was observed within some flowers.

Lepidospartum burgessii (Burgess broomshrub or gypsum scalebroom) has been identified by the U.S. Fish and Wildlife Service, Region 2, as a Species of Concern. It is a silvery-white shrub belonging to the Asteraceae (Compositae) family. It was described in 1977 and was considered to be a local endemic in extreme western Texas, although the number of plants growing in Texas was never accurately determined. In 1982 it was discovered in extreme southern Otero County, New Mexico, on a few small alkaline playas. Even though these discoveries somewhat expanded its range it still remains a rare endemic to this approximately 420 sq mile area. The plants occur singly or in scattered colonies on the tops of stabilized gypsum sand dunes. In May of 1996 the Bureau of Land Management (BLM) proposed to designate the area within the Caballo Resource Area that encompassed the majority of plants known in New Mexico as an Area of Critical Environmental Concern (ACEC; Bureau of Land Management 1997).

Lepidospartum burgessii is found only on gypseous soils at the fringe of the northern Chihuahuan Desert. Dick-Peddie (1992) designated the region Chihuahuan desert scrub. Some authorities have regarded the whole area as part of the desert plains grassland (Humphrey 1958). The latter designation may be more appropriate for the relatively small areas where *L. burgessii* occurs because creosote bush, which is the dominant shrub of the Chihuahuan desert scrub vegetation type, does not occur with *L. burgessii*. The climate in this area is relatively extreme with summer temperature highs of 34–41° C and winter temperatures ranging from lows of –2° C to highs of 14° C. Freezing is common at this time. Precipitation comes primarily during the summer (ranging from 131 mm to 468 mm). However, substantial spring rains have been reported and there is a high degree of year-to-year variability, which is characteristic of most arid and semi-arid climates (Noy-Mier 1973). In 1997 local residents reported that there had been very little precipitation over the Alkali Lakes during the last few years.

There are two other species in the genus *Lepidospartum* but neither are sympatric with *L. burgessii* (Munz 1974). It is noteworthy that *L. burgessi* has been mistaken for a species of *Chrysothamnus*, but the three rounded bracts of the involucre on the heads clearly distinguish it from that genus. The biological relationships of *L. burgessii* with its surrounding community are poorly understood and the habitat preferences of the plant are known at only a general level. One critical biological concern for *L. burgessii* is its lack of reproduction. Seed

set (sexual reproduction) appeared to be absent or extremely low, and clonal propagation appeared to be infrequent. This project consisted of three integrated objectives: to define the habitat characteristics and status of the plant in New Mexico, to determine the range of the species and its status in west Texas, and to determine the cause of the apparent absence of reproduction of the species. This paper reports on the habitat characteristics and status of the species.

Methods

Field work for this project was conducted during eight visits in 1997. Visits to the ACEC and Dell City were made July 14 –19, August 4–8 and 15–19, August 29–September 2, September 7–12 and 18–20, October 20–24, and November 20–21. *Lepidospartum burgessii* flowers from June to October with the peak during late July through early September. More than 10 years ago, three *L. burgessii* plants had been transplanted from private land in Texas to a garden in front of commercial offices in central Dell City. These plants comprise the Dell City site. The surveys in Texas were all conducted September 7–12, 1997.

Surveys outside the ACEC were conducted only in Texas. Surveys were conducted on foot by two or three field botanists. Potential habitat was targeted but some areas that had marginal habitat (e.g., very mobile dune fields) were also examined. Permission was obtained from the respective landowners in Texas before any survey was undertaken. Guadalupe Mountains National Park granted us permission to survey National Park Service (NPS) land to relocate historic occurrences within the Guadalupe National Park boundary. Permission was also granted by the Nature Conservancy to survey Gypsum Dunes Preserve land and by one local ranch owner. One other ranch manager said he had no objection to our surveying portions of his land through binoculars from the road. Two discrete populations 1–2 miles apart were located on private land. The southernmost population has since been acquired by the National Park Service.

Most of the studies on *L. burgessii* were conducted on plants within the ACEC on BLM land. Previous data collected by BLM and New Mexico State University (NMSU) personnel (Huenneke 1991) were used to re-locate the sites, and these data were also used for comparison to assess the current status of the plants. Approximately 18 months prior to this study the BLM erected livestock exclosures around at least seven colonies of plants. Livestock grazing is permitted within the ACEC outside of the exclosures. We studied 12 clusters of plants (sites) within a 10 m^2 area in detail. Six sites were within livestock exclosures and six were unfenced within the ACEC. Nine sites were within larger BLM-designated colonies (Bureau of Land Management 1988). The sites in exclosures were designated 41, 45, 43, 31, 29, and 20. Unfenced sites were designated 40, 42, 47, 30, 30B, and 25.

Measurements were taken to characterize the habitat occupied by *L. burgessii.* Plots within the ACEC were established within the chosen sites by selecting a plant at random and measuring a 10 x10 m area with the selected plant at the center of the square. Ground cover and number of *Lepidospartum* plants within each 100 m^2 plot were recorded during the first visit in July, 1997. The amount of dead wood on each plant and indications of disease were also recorded. Samples of leafless branch tissue were taken and stored in ethanol (70%). In Texas, two 100 m^2 plots were established by selecting a plant at random in both the northern (private land) and southern (newly acquired NPS land) populations, and measurements were made in September similar to those on the plants in the ACEC.

Soil samples taken within 2 m of a *Lepidospartum* shrub and at a depth of 15–20 cm were used to determine soil pH. Seven samples were taken from the ACEC and four from Dell City. Soil (4–6 g) from each sample was measured in the laboratory and stirred for 10 minutes with 12–18 ml distilled water (1:3 parts soil:water weight/volume). After filtering through Whatmans no. 3 filter paper, the filtrate was measured using a pH meter.

In addition to the measurements within the plots, measurements similar to those taken in 1991 and 1992 (Huenneke 1993) were made on the plants in colonies 14, 20, 25, 29, 31, 43, and 45. The total number of plants were counted and their heights, maximum and perpendicular diameter, phenological state, and distance to the nearest neighbor were measured so that comparisons between the years could be made.

Flower size was quantified by measuring the height (length) of the involucre. A total of 459 flowers from Dell City, Texas private land (from which the Dell City plants originated), and the ACEC were measured using a ruler and a microscope on return to the laboratory.

For studies on the reproductive organs, flowers were placed in preservative solution (70%

ethanol: acetic acid 3:1) in vials that were stored in ice chests in such a way that the contents did not freeze. The tissue was transferred to 70% ethanol (aqueous) solution after 24 hours. The vials were transferred to the refrigerator on arriving back at the laboratory. After refrigerated storage, the flowers were rehydrated and dissected. The gynoecia were placed in 0.8 M sodium hydroxide in a 60° C water bath for approximately 35 minutes to clear. Gynoecia were rinsed with double distilled water and placed in 1.0 mg/ml aniline blue in 0.1 M K_3PO_4 buffer overnight (Martin 1959). The tissue was then put on a slide with some clear phosphate buffer and examined under light and fluorescent light (395–440 nm) with a Zeiss Axioskop microscope. Examination of the carpels was made at 200x and 400x magnification.

Fifteen seed heads were taken from 33 shrubs that had more than 300 flowers for viability analysis. To avoid collecting immature seeds, the seed heads were taken only when the pappus was brown and fully emerged and the receptacle fully open and dry. The flower heads were examined and there did not seem to be any filled seeds. However, 20 seeds that appeared to be partially filled were taken from plants from 10 colonies, including one on Texas private land. In the laboratory half the seeds were surface sterilized by stirring in a 5% aqueous Chlorox™ (5.25% sodium hypochlorite) solution to which one drop of Tween 80 had been added. All the seeds were then rinsed with double distilled water and placed on moist germination paper in petri plates (10 seeds per plate). The plates were wrapped in aluminum foil and kept at approximately 22° C. In addition, 60 seeds were planted in a gypsum–potting soil (1:1) mix and kept in a greenhouse. Approximately one year elapsed between seed harvest and testing the germination rate.

Many of the data, even after appropriate transformations, violate the assumptions that permit use of the analysis of variance (ANOVA). Therefore to determine the level of statistical significance, values were statistically analyzed by non-parametric methods (Kruskall-Wallis and Mood Median Tests). However, because it frequently helps to have mean values to appreciate the biology, mean values are often presented along with the standard error or standard deviation of the mean, which are good indicators of the variability encountered. A simple linear regression model was used to estimate the rate of decline of the population using 1997 and 1991-92 data.

Results

Historic records indicate that *L. burgessii* grew immediately west of the Guadalupe Mountains in Texas. A thorough pedestrian survey was conducted on the Nature Conservancy preserve and in the general area where the historic records indicated that *Lepidospartum* was found in Guadalupe Mountains National Park; however, none were found on either property. The area within the National Park boundaries was very sandy and the most prominent shrub was *Poliomintha incana*. It may be that the authors of earlier reports found small gypsum outcrops that were missed during our survey or that the earlier locations were not accurately mapped.

Lepidospartum plants were found in Texas near the National Park on private land on which we had permission to survey. There were two general areas approximately 1–2 miles apart. There were 576 plants in the first, northern, area distributed among 13 colonies that ranged in size from groups of 3 to 205 individuals. A colony is defined as a group of plants isolated by at least 20 m. Most of the plants were in good condition and we noted only five that appeared to be dead. The plants grew on both microbiotic-stabilized gypsum soils and more mobile sandy dunes. It was from this population that the flowers were taken to compare the size to those on BLM land and in Dell City. Since this survey was made in 1997 the National Park boundaries have been extended and now include a second (southern) population of *Lepidospartum* plants that were originally on private land. Within this area there were 446 plants distributed among 11 colonies that ranged in size from 1 to groups of 113 individuals.

Morphology

Lepidospartum burgessii shrubs varied in size from small single-stemmed plants to large shrubs with high amounts of dead wood. The single-stemmed plants appeared relatively young and were probably clones of adjacent plants. An exposed root on private land in Texas indicated that *Lepidospartum* is capable of producing innumerable suckers.

Single-stemmed plants were particularly evident on the private land. The number of flowers per shrub was variable; from one flower head to literally hundreds of flower heads were counted on any given shrub. There did not appear to be a close relationship between the size of the plant and the number of flowers, which was not surpri-

sing because the largest shrubs were often in a decadent (> 50% dead wood) condition (Table 1). Some of the shrubs, e.g., at site 41, did not flower all season.

Habitat

The majority of *Lepidospartum* shrubs grew on stabilized gypsum soils with a well-developed microbiotic crust. However, they were also found on more mobile sandy gypsum soils both in Texas and in one area in New Mexico. The species was observed to be in as good, and perhaps in an even more vigorous condition, on the more mobile soils as on the stabilized soils.

Lepidospartum burgessii habitat was initially characterized by 5 percent vegetation cover comprising *Tiquilia hispidissima, Commicarpus scandens, Sporobolus airoides, L. burgessi,* and *Yucca elata* (Soreng 1986). However, our studies have shown that *L. burgessii* grows in a greater variety of habitat. Shrubs and sub-shrubs associated with *L. burgessii* included *Atriplex canescens, Opuntia leptocaulis,* and *Yucca elata,* as well as *Tiquilia hispidissima.* In Texas, *Poliomintha incana* was a common associate. *Allenrolfia occidentalis* was also observed within one of the plots in Texas. Associated grasses included *Bouteloua breviseta, Sporobolus neeleyi,* and *Sporobolus airoides. Gaillardia multiceps, Mentzelia* sp., *Isocoma* sp., and *Senecio warnockii* were common forbs associated with *L. burgessi* although their contribution to the ground cover was very low.

There was more vegetation cover in the regions occupied by *L. burgessii* in Texas than in New Mexico. In the former, litter and basal vegetation was approximately quadruple (20% vs. 5%) that of the latter region and vascular plant canopy cover was also significantly higher. The total shrub canopy cover was, on average, approximately 6 percent in the ACEC and 34.5 percent in Texas. In both areas, *L. burgessii* canopy contributed approximately half the total shrub canopy cover. The average *L. burgessii* canopy cover was only 3.4 percent of the total plot (100 m^2) area on the ACEC but was 19 percent on the Texas land. In the ACEC, grass canopy was less than 2 percent on average and forb cover approximately one tenth of the grass cover. In Texas, grass canopy was variable, ranging from 2 to 23 percent, but forb cover was always less than 3 percent. The difference in time of year (early summer compared to fall) may account for slight differences, especially in the grass and annual forb cover, but it is most likely that the differences reflect a more vegetated habitat on the Texas land. The reason for the differences in vegetation cover was not immediately obvious. Greater groundwater availability or differences in local precipitation or microclimate may be speculated. The heights of the *Lepidospartum* plants were similar among all populations but, as the canopy cover suggests, the plant volumes were larger in Texas, especially on the private land (Table 2). Litter was mainly around the base of living plants in all regions. Basal vegetation–litter cover ranged from 2 to 20 percent in the ACEC and 10–30 percent in Texas. At many of the sites in the ACEC more than 70 percent of the soil was covered by a complex microbiotic flora. As would be expected, the dunes (colony 20) had significantly less microbiotic cover. Total lichen cover, rather than total microbiotic cover, was estimated for three of the four plots in Texas

Table 1. The number of buds and open flowers on a sample of randomly selected *Lepidospartum burgessii* shrubs within the ACEC, New Mexico.

Date	Site in the ACEC	Plant number	Total flowers	Number of flowers		Percent flowers open	Shrub height (m)	Shrub volume* (m^3)
				open	pre-emergent			
8/17/97	29	29-10	316	29	287	10	1.05	1.42
8/17/97	29	29-a	132	36	96	38	0.84	0.79
8/17/97	28	28-b	—	76	not measured	—	1.00	1.50
8/17/97	28	28-c	—	56	not measured	—	0.66	0.37
8/17/97	28	28-d	—	30	not measured	—	1.00	0.56
8/18/97	43	43-11	684	181	503	36	1.05	1.18
8/18/97	43	43-10	90	12	78	15	0.84	0.30
8/18/97	30B	30B-C	210	39	171	23	0.97	0.73
8/18/97	30B	30B-a	121	17	104	16	0.71	0.46
8/18/97	30B	30B-b	132	36	96	38	0.82	0.66
8/30/97	20	20-265	96	70	26	73	0.61	1.08

*Volume was estimated as though the shrubs were rectangular as in 1991-92 (Huenneke 1993).

Table 2. The average height, volume, and number of *Lepidospartum burgessii* plants observed to suffer from branch dieback on 100 m^2 plots within the ACEC, on Texas private land, and in the newly acquired National Park Service land.

Location	Number of plants	Average height (median)	Average volume	Average deadwood/shrub (median)*	Number of plants with dieback
ACEC	69	0.62 m (0.6)	0.63 m^3	22.0% (15) a	51
Texas land – NPS	23	0.67 m (0.6)	1.63 m^3	37.6% (30) b	21
Texas land - private	32	0.79 m (0.7)	5.77 m^3	13.7% (10) a	20**

*Values followed by the same letter are not significantly different (P = 0.000).
** Significantly less dieback using the Moods median statistical test (P = 0.046).

due to changes in survey personnel. From considering one plot in Texas and the plots on the ACEC (where survey personnel remained the same) it was estimated that the amounts of total microbiotic cover are approximately 38 percent higher than lichen cover. A substantial unidentified algal component and a very small moss component accounts for the difference. Therefore, even allowing for this underestimate, due to considering lichen cover only, there was significantly less microbiotic cover on the plots chosen at random on the Texas land. This was likely due to the more mobile nature of the soils. Colony 20 in the ACEC has the most similar habitat and plant morphology to that observed in Texas.

A southeastern aspect appeared to be most common but a strong preference for a particular aspect was not observed. The pH of the soil in Dell City and in six of the colonies within the ACEC was measured from soil samples within 2 m of a *L. burgessii* shrub. The pH was, on average, slightly (but significantly) higher in Dell City (pH 7.78, variance 0.02, n = 4) than on the ACEC (pH 7.38, variance 0.03, n = 7).

Comparison of Status, 1991-92 and 1997, in the ACEC, New Mexico

These results directly pertain only to colonies 14, 20, 25, 29, 31, 43, and 45, as all plants in the ACEC could not be counted in the time available. However, these colonies were distributed throughout the ACEC and it is likely that they are representative of the other colonies in the ACEC. In total, 557 plants were counted in 1997, compared to 570 in 1991-92. Therefore, 13 plants were unaccounted for in 1997. The phenotypes of the plants were designated as juvenile (J), mature (M), decadent (greater than 50% dead wood, D), and fully dead (DD). In all years surveyors were unsure if some plants were mature or decadent and notes were made to that effect. These plants were scored MD. Therefore, two statistical analyses were made, one considering the plants in question as mature, and the second considering the plants as decadent. The phenotype scores for each colony are tabulated in Table 3. Because the data violated many of the assumptions for the ANOVA, nonparametric methods were applied to determine if differences existed between years. Phenotypic classes were statistically analyzed by the Kruskall Wallis and Mood Median tests. There were appreciably more dead plants (100% dead wood) in 1997 than in 1991-92 and fewer juveniles (Figure 1). In the first analysis, where questionable (MD) plants were rated "mature," all the median phenotypes in both years were mature except for colony 43 in 1997 where the median value was decadent. When the MD plants were designated "decadent," the median values remained the same for all colonies and years. However, the variation observed in colony 43 was such that there were no statistically significant differences between years, which suggests that all those MD plants in 1991-92 were in fact decadent. (Totally dead plants in 1991-92 = 0, in 1997 = 24; MD plants in 1991-92 = 22, in 1997 = 1; Decadent in 1991-92 = 16, in 1997 = 40; Mature in 1991-92 = 55, in 1997 = 37; and Juvenile in 1991-92 = 1; in 1997 = 1.)

The nearest neighbor distance was significantly more in 1997 (median = 1.25 m) than in the previous years (median = 0.46 m) which is consistent with the higher number of dead and unaccounted for plants in 1997. Particularly, colonies 20, 25, and 43 all showed significantly greater distances between plants in 1997 than in the previous years (see Table 3).

If the decline in the number of total plants, the number of mature plants, and the number of juveniles is assumed to be linear, a simple prediction can be made as to when the three classes of indi-

Table 3. The phenotype status of the *Lepidospartum* plants in selected colonies within the ACEC in 1991-92 and 1997.

Colony (Site) in the ACEC	Date	Median nearest neighbor distance (m)	Number of plants					Total live plants	Total plants
			D	MD	M	J	DD		
14	09/14/97	0.6 ab	4	0	27	0	2	31	33
20	09/13/97	1.2 a	44	20	165	7	42	236	278
25	09/08/97	1.5 a	15	0	53	2	5	70	75
29	09/14/97	1.5 a	0	0	10	0	1	10	11
31	09/14/97	1.6 a	4	0	22	1	1	27	28
43	09/14/97	1.2 a	40	3	37	1	22	81	103
45	09/14/97	2.0 a	1	0	19	7	2	27	29
Total	1997	1.25	108	23	333	18	75	482	557
14	02/09/92	0.35 ab	0	0	25	0	0	25	25
20	11/17/91	0.41 b	54	11	207	53	1	325	326
25	10/24/91	0.61 b	0	0	67	1	0	68	68
29	02/22/92	1.30 ab	0	0	10	0	0	10	10
31	02/23/92	1.05 ab	0	0	26	1	0	27	27
43	02/23/92	0.50 b	16	22	55	1	0	94	94
45	08/21/91	1.61 a	0	0	15	5	0	20	20
Total	1992	0.46	70	33	405	61	1	569	570

*Values followed by the same letter are not significantly different; Mood median test, P = 0.000.

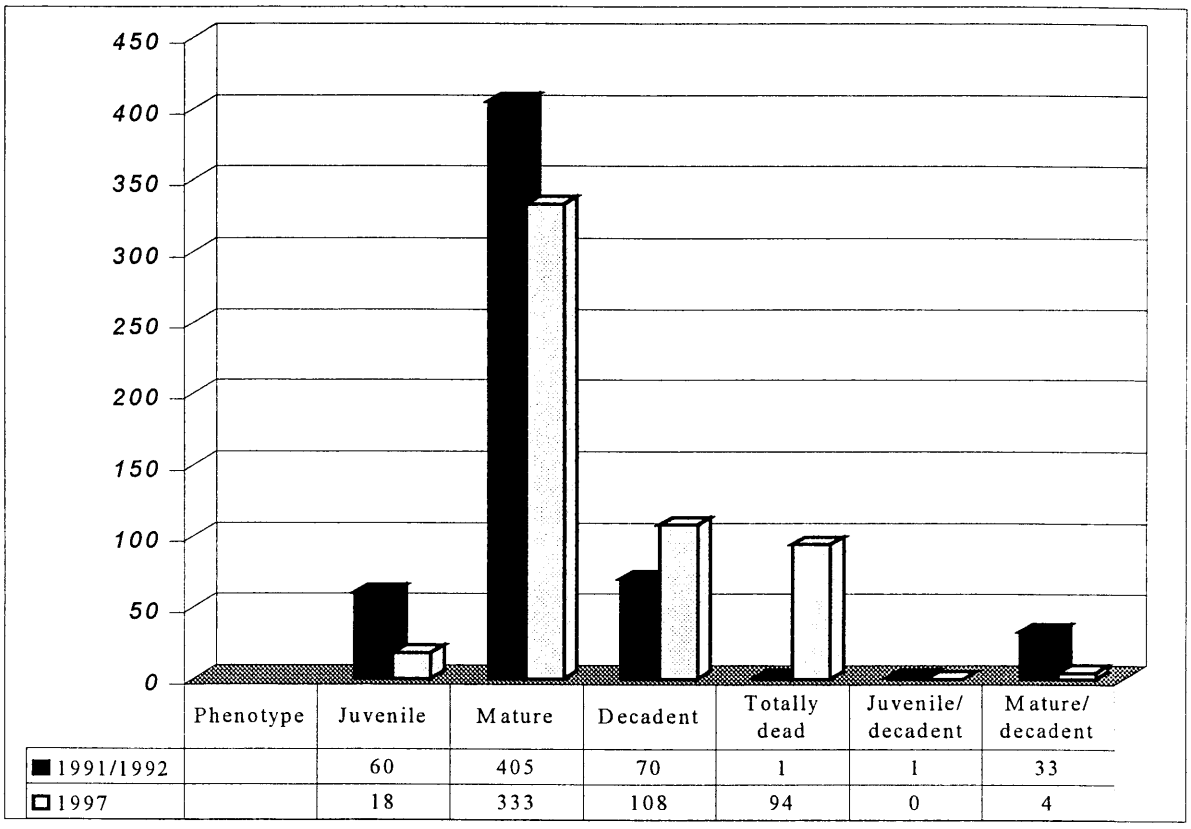


Figure 1. The number of *Lepidospartum burgessii* plants (y-axis) in each of the phenotype classes in 1997 and 1991-92 combining the data from all colonies.

viduals will reach zero (Figure 2): For total plants it is 33 years, for mature plants 35 years, and for juveniles only 10 years. Supposing the rate of death is also linear, then after 31 years all 463 individuals would be dead. Obviously a linear model is too simple and from only two points in time predictive power is very limited. For example, considerable precipitation may be required for successful reproduction and seedling emergence. In this region precipitation is highly variable and years of high precipitation are likely relatively few. However, further consideration of these data may provide insight to the behavior of this population, which appears to be declining relatively rapidly.

Flower Size Differences, Private Land in Texas and ACEC

The flowers on the Dell City plants were noticeably larger than those on the plants within the ACEC. I initially ascribed the difference to the frequent irrigation and fertilization that plants in Dell City received. However, when surveying the lands in Texas it seemed that the flowers on plants on the private land were as large as those in Dell City. Therefore, a limited number of flowers were taken from plants in Dell City, the Texas private land, and the ACEC, and the length of the receptacles was measured. The mean and median lengths of the receptacles from both the Texas populations were significantly larger (Table 4).

Observations on Disease

Two notable observations were made on the disease status of the *L. burgessii* plants. Microscope observations of the flowers and pollen showed that a common fungal spore was frequently present on the stigma surface (Figure 3) and that sometimes the spore germinated to form a tangle of mycelium on some of the stigmas (Figure 4). The

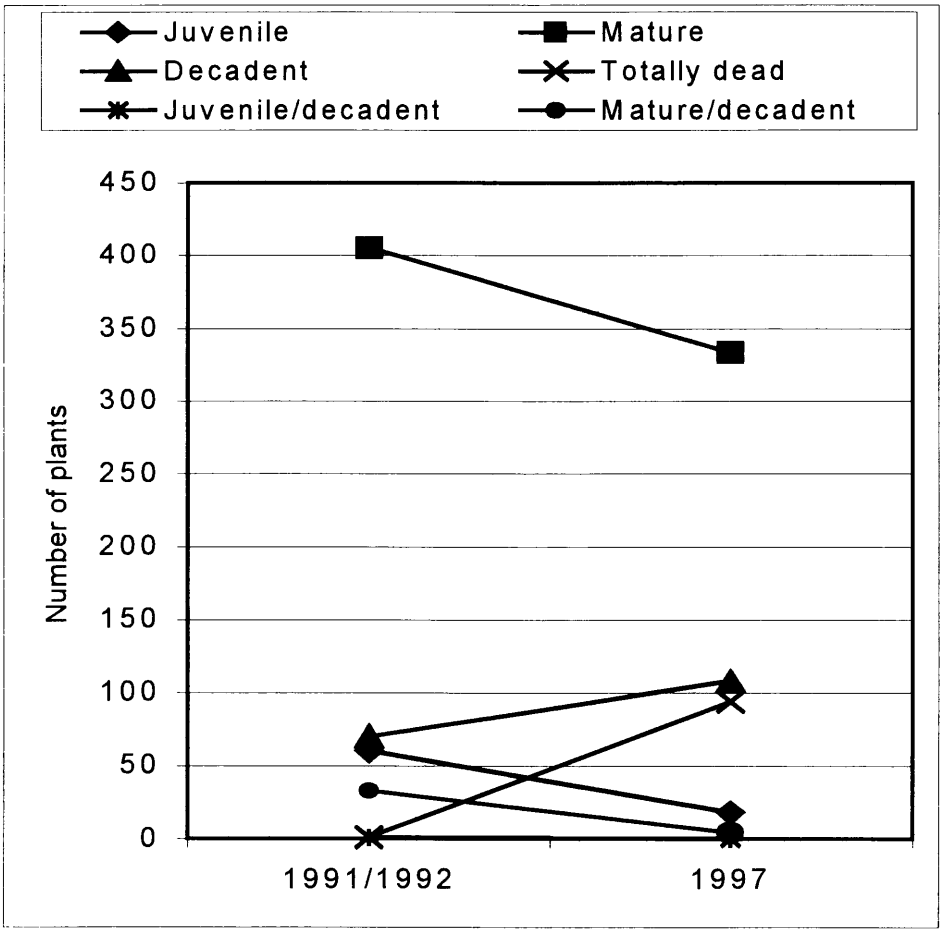


Figure 2. A graphical description of the changes observed in the phenotype classes between 1991-92 and 1997.

Table 4. The size of flower involucres in New Mexico and Texas populations.

Location	No. of flowers	Mean (1/32 inch)	Median (1/32 inch)
ACEC	375	10.3	10
Dell City	56	12.6	12.5
Texas Land	28	12.3	12.5

spore was identified as a species of *Alternaria*, probably *A. alternata* (Dr. Natalie Goldberg, plant pathologist, New Mexico State University, personal communication).

In the field the presence of branch tip dieback was scored as present or absent on individual plants. Branch tip dieback was observed on many of the plants in the ACEC and on the land in Texas. The condition appeared to be negligible on the plants in Dell City and less severe on plants on the Texas private land. In addition, there were significantly fewer individuals with any tip dieback on the private land in Texas (see Table 2). When using a hand lens or dissection scope the branch surface seemed to be a little "bumpy," but it was not obvious what was causing the leafless brown branches. However, a few weeks after the leafless branches were put in 70% ethanol, numerous little insects were found in the solution. No insects were found in the solution in which leafy tissue had been placed. These insects were identified as a type of lace bug (*Corythuca marmorata*, Tingidae family). They are known to particularly infest members of the Asteraceae, notably goldenrod and asters. They also cause severe damage to chrysanthemums (Richard Fagerland, entomologist and IPM specialist, University of New Mexico, personal communication). No information is readily available on their relationship with *Lepidospartum* species.

Scale was also noticed but it was primarily on the four-wing saltbush (*Atriplex canescens*) that was growing amongst or intertwined with the *Lepidospartum* shrubs. Unlike the other two pathogenic organisms, this infection does not seem to pose a serious threat to *Lepidospartum*.

Seed Germination

Forty-two petri plates (with 10 seeds per plate) from nine colonies in the ACEC and from six plants in Texas were examined. There were an equal number of plates with sterilized and non-sterilized seeds. All of the seeds looked poorly formed but were judged to be in relatively "good" condition. The petri plates were observed after 2, 4, and 8 weeks. Fungal contamination began to be observed on some of the seeds after only 2 days. After 10 weeks an average of 6.7 seeds per petri dish (std dev 2.6) had fungal mycelial growth, but only 1.7 sterilized seeds per petri dish (std dev 2.3) had fungal contamination. Therefore, the surface sterilization procedure did inhibit molding of the seeds. However, no seeds from either treatment were observed to germinate. Similarly no seedlings have been observed in the pot experiment at the time of writing. It may be that the length of time (approximately one year) between harvest and testing germination ability contributed to the poor germination results.

Discussion

The depletion of groundwater within the last 150 years must have had a major effect on the area hydrology. An amateur local historian and member of a long-time ranching family in the area reported that extensive changes had taken place in the Alkali Flats region over the last 150 years (Mrs. Isobel Gilmore, personal communication, 1997). For example, in 1858 Crow Springs and an adjacent well were important sources of water for settlers in the area. Mrs. Gilmore described how 1,000–1,500 head of cattle were commonly watered at a single time in 1889 and 1890. At the turn of the century the springs were used extensively by the Butterfield Stage Coach. Apparently by 1928, or 1929, 35 springs in the general area around Alkali Flats had gone dry from overuse. The intensive irrigated farming practices first adopted in Dell City in 1948 also took their toll on groundwater availability. In the 1940s the wells in Dell City were approximately 10 feet deep, by the 1950s potable water was to be found only at about 60 feet, and then a decade or so later the wells had to be at least 90 feet deep. Now, many of the wells on her extensive properties are yielding only saline and undrinkable water. The impact of this situation on *L. burgessii* cannot be judged. Whether the receding water table has influenced the availability of water to the plants in some regions is unknown.

A significant cause for concern is the infestation of *Corythuca marmorata* (Tingidae wasps) on the plants, which causes dieback of the stems and branches. This was especially unmistakable on the plants in the ACEC although it was also evident on all the plant colonies except those in Dell City,



Figure 3. A photomicrograph of *Alternaria* spores amongst the stigmatic hairs of *Lepidospartum burgessi*. The photograph was taken at 400x with black and white Kodak 5052 TMX film.



Figure 4. A photomicrograph of *Alternaria* spores and dense mycelial growth on the stigmatic surface of *Lepidospartum burgessi*. The photograph was taken at 400x with black and white Kodak 5052 TMX film.

which were receiving water from a garden irrigation system. Although these insects were also found on a number of branch tips that were examined during the one visit in 1998, the plant population was closely observed during only one year and it may be that this level of infestation is in a state of equilibrium for this species. Monitoring the progress of this infestation over the next several years is the only reliable way to determine the importance of this infestation. A problem with field observations is that the insects themselves are not very evident and the stems need to be soaked in ethanol to release the insects.

The other potential pathogen is the fungus *Alternaria* which seemed to target the flowers, although it is apparently more typically a leaf pathogen (Rotem 1994). However, seed infection has been reported to be common to all *Alternaria* species and is a variation of quiescent infection. In all cases the infection of the seeds starts with infected flowers (Rotem 1994). It is unclear how significant this observation is to either the overall health or the absence of reproduction of *L. burgessii.*

Harper (1977) summarized why populations may be small as follows: (a) The carrying capacity of the site may be low. (b) The available sites are few and separated by distances beyond the species' normal dispersal ability. (c) The habitability of the site is of short duration because of successional displacement. (d) Colonization is in its early stages, and full exploitation of the site has not occurred.

It is likely that the carrying capacity of the Alkali Lakes region is low and this condition may be partially responsible for *L. burgessii* rarity. Available sites may also be few but when the apparent potential habitat is considered it appears that there is room for greater exploitation of the Alkali Flats area by *L. burgessii.* There is no indication that successional displacement is a significant restriction on the species, and the state of the plants indicates that *L. burgessii* is not in early stages of colonization. It may be that this species is restricted to relatively small refugia owing to an environmental change that precipitated a genetic bottleneck, which is a single event in time that describes a sharp reduction in the genetic diversity of the species (Barrett and Kohn 1991). Such a bottleneck event would add to a loss of diversity that could result in lowered resistance to disease and an inability to adapt to a changing environment. Not only has a very low level of clonal propagation been observed, but genetic variability is likely low in these populations given that field observations over many years have suggested no or low seed production (Michael Howard, personal communication). During 1997 no filled seeds developed and none of the partially filled seeds that we collected germinated. However, there was a statistically significant 1 mm difference between the average size (length of the involucre) of flowers on shrubs in Texas (private land) and in New Mexico (BLM). This latter observation implies a genetic variation in flower size, which suggests that the different populations may have significant genetic differences.

Although data from only two seasons, 6 years apart, were used to evaluate population trends, it does appear that *L. burgessi* is declining to extinction. One way to increase the robustness of the populations may be to make crosses between the plants in Texas and New Mexico to obtain viable seed and make small local plantings throughout the Alkali Flats region.

Acknowledgments

It is a great pleasure to acknowledge the Species at Risk Program of the USGS Biological Research Division, the Las Cruces Field Office of the Bureau of Land Management, and T & E Inc. for their financial support of this project. The fieldwork of Nancy Monteith, Yvonne Chauvin, Tanya Cole, and Anneke Swineheart is also gratefully acknowledged.

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Implications of Managing the Timing and Intensity of Herbivory for Conservation of Arizona Leatherflower

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Abstract: For rare plants, the question of whether and to what extent wild and domestic herbivores influence growth, reproduction, and survival can be critical to preservation. The sensitive species, *Clematis hirsutissima* var. *arizonica*, grows on Forest Service lands where cattle, elk, mule deer, and numerous small mammals forage. In a 3-year clipping experiment, I examined the impact of season and intensity of herbivory on reproduction and growth. Vegetative reproduction was not influenced by year, season, or intensity of herbivory; however, sexual reproduction was influenced by year and season of herbivory. Spring-clipped plants produced significantly fewer seeds than mid or late-season clipped plants in 1996 and 1997. Once clipped in the spring, plants had reduced seed set in subsequent years. Natural levels of herbivory were significantly higher on unprotected than caged plants, especially when cattle were present. Unprotected plants tended to produce fewer flowers but differences were not significant. Overall sexual reproduction was very low in the light-limited study site. Conserving northern Arizona populations will require limiting detrimental early season activities, such as grazing and controlled burns, and increasing understory light reception.

Coordinating multiple use activities while simultaneously enhancing forest health and protecting biodiversity within a forest ecosystem is the challenge facing land managers. Although some conservationists would like to eliminate multi-use activities, such as grazing, on public lands (Noss 1994), others have argued that the role of the conservation scientist is to conduct research that can help ameliorate management actions (Brussard et al. 1994). Control rather than complete removal of domestic and wild grazing animals has been suggested as a way to improve long-term regeneration of woodlands, and it may be a more realistic approach (Mitchell and Kirby 1990). However, empirical data supporting specific prescriptive strategies for managing herbivores, while enhancing plant populations, are lacking (Mitchell and Kirby 1990).

There is disagreement about the impacts of domestic and wild animal grazing on plant populations and communities. Some argue that domestic grazing can be detrimental to plant populations and communities (Painter and Belsky 1993, Papanastasis et al. 1995), and has reverberating negative effects throughout the ecosystem (Fleischner 1994), especially in the semi-arid conditions of the western United States (Bartolome 1993). However, others argue that modifying the timing and intensity of pasture use can enhance vegetation (Savory 1988, Hester et al. 1996). Similarly, wild ungulate browsing has been shown to have negative impacts on vegetation (Kay 1997, Patten 1993, Lowenberg 1994, Motta 1996), yet not all plant species decline when exposed to browsing (Hernandez and Silva-Pando 1996). Some believe that vegetation decline attributed to wild herbivores may have been caused by other factors, such as changes in climate (Singer et al. 1994). Small mammals can also affect plant population dynamics and be significant plant mortality factors (Palmisano and Fox 1997). Thus, a priori predictions of the impact of domestic and wild animals on rare plant species in a forest understory are not necessarily obvious.

Ecological theory helping to predict the impact of herbivory on a given plant species illustrates the complexity of plant-herbivore interactions (e.g., Coley et al. 1985, Whitham et al. 1991, Rosenthal and Kotanen 1994). Plants can contend with herbivores by avoidance or tolerance (Crawley 1983, Rosenthal and Kotanen 1994), but they often lose the fitness battle (Crawley 1993). Plants can avoid herbivores through escape in time or space or through a battery of chemical, mutualistic, phenological, or structural defenses (e.g., Coley and Aide 1991) or a plant may tolerate herbivory by regrowing or compensating for loss of tissue. A plant's ability to compensate from herbivory depends upon many factors, including frequency and intensity of herbivory, population history, life history, nutrient availability, and presence of competitors (e.g., Maschinski and Whitham 1989, Painter et al. 1989, Rosenthal and Kotanen 1994). Therefore, intrinsic and extrinsic factors influence

the impact of herbivores on plants, but even knowing many of these factors may not allow absolute predictions that grazing or browsing will be detrimental to a species.

This study addressed whether herbivory by wild and domestic mammals influenced the reproduction and growth of the rare forest understory plant species, *Clematis hirsutissima* var. *arizonica*. Because woody perennials growing in resource-limited environments are predicted to undercompensate from herbivory (Whitham et al. 1991), I predicted that herbivory would be detrimental to *C. hirsutissima* var. *arizonica*. Yet, it is possible that controlling the season of use and intensity of herbivory could modify impacts on the plant, as has been seen in other plant species (e.g., Turnipseed 1972, Smith and Bass 1972, Maschinski and Whitham 1989, Paige 1992). I specifically asked four questions related to the management of herbivores and the conservation of *C. hirsutissima* var. *arizonica*: (1) Does the intensity of herbivory influence its growth and reproduction? (2) Does the season of herbivory affect its growth, reproduction, and survival? (3) Is it being eaten by large or small mammals? (4) Is it capable of compensating from herbivory?

Methods

The regionally rare herbaceous understory species, Arizona leatherflower (*C. hirsutissima* var. *arizonica*), is a categorized as a Forest Service Sensitive species. The variety is known from high elevations (2300–2800 m) near Flagstaff and Tusayan, Arizona, the Chuska Mountains on the Navajo Nation in northern Arizona, and the Zuni Mountains in New Mexico. Populations in New Mexico are associated with oak woodlands; however, in northern Arizona, where the largest populations exist, the species grows preferentially on north-facing limestone outcroppings in ponderosa pine (*Pinus ponderosa*) forests. Recent taxonomic review of the genus has lumped this variety with the more widespread *C. hirsutissima* var. *hirsutissima*, which has a distribution that extends from Arizona to British Columbia (Pringle 1997). The U.S. Fish and Wildlife Service consequently removed the species from candidate 1 status, but the Coconino National Forest maintains the variety as a Species of Concern. The populations in northern Arizona are patchily distributed and rare understory components. Throughout this paper, I have used the name *Clematis hirsutissima* var. *arizonica* to clarify that I am discussing the northern Arizona population.

C. hirsutissima var. *arizonica* is a 10–50 cm tall herbaceous perennial that has pinnately compound leaves on stems arising from a woody caudex (Kearney and Peebles 1960). Individuals can produce 1–50 stems, though most of the individuals in northern Arizona produce fewer than 6 stems (Maschinski et al. 1997). Solitary purple, bell-shaped flowers on the ends of stems and lateral shoots bear 18–30 achenes with plumose styles 1–6 cm in length, but the quality of seeds is influenced by environment and outcrossing (Maschinski 1989). Most plants produce fewer than eight flowers that set seed (Maschinski et al. 1997). Although flowers can set some seed without outcrossing, preliminary tests indicate that selfed seed has reduced viability in comparison to outcrossed seed (Maschinski 1989). Germination of outcrossed seed after long periods of stratification under greenhouse and field conditions is less than 1 percent (Maschinski, unpublished data). Shoots elongate from a perennial caudex in early May, usually flower by the beginning of June, and set seed by August. In the fall, after seeds are shed, aboveground vegetation dies back.

A major anthropogenic factor believed to threaten the species is herbivory. In pastures where *C. hirsutissima* var. *arizonica* grows on the Coconino National Forest, cattle herds graze on a rest-rotation grazing system. In addition, approximately 1500 elk (*Cervus elaphus nelsonii*) and less abundant numbers of mule deer (*Odocoileus hemionus*) utilize the area (Arizona Game and Fish Department 1993). Other potential mammalian herbivores in the vicinity are golden mantle ground squirrels (*Spermophilus lateralis*), pocket gophers (*Thomomys bottae*), voles (*Microtus mexicanus*), deer mice (*Peromyscus maniculatus*), and cottontails (*Sylvilagus audubonii* ssp. *warreni*). Observations made from 1989 to 1995 of natural levels of herbivory indicated that *C. hirsutissima* var. *arizonica* experienced two different degrees of mammalian herbivory: light herbivory, where only flowers were eaten, and heavy herbivory, where all but 4 cm of stems were eaten (Maschinski 1996). In 5 years of observation, there was no consistent spatial pattern of herbivore use on *C. hirsutissima* var. *arizonica* that suggested any preferential site or genotype that received heavy or light herbivory (Maschinski 1996, Maschinski et al. 1997). In Arizona, wild mammals are managed by the Arizona Game and Fish Department, whereas cattle are managed by permittees under U.S. Forest Service guidelines. Hence, the agency responsible for economic or management deci-

sions linked to the preservation of *C. hirsutissima* var. *arizonica* may change depending upon the herbivore utilizing the plant.

I conducted these studies in the vicinity of Lake Mary, 26 km southwest of Flagstaff, Arizona (2118 m elevation). The study area has cold winters and variable precipitation throughout the year (Figure 1). Yearly mean temperature is 7° C; freezing temperatures can occur any month of the year. Precipitation is minimal or absent in May and June; monsoon rains usually begin in July and last through September. From 1995 to 1997, the duration of this experiment, there was significant variation in annual precipitation (see Figure 1). Total annual precipitation was 66.3 cm, 46.25 cm, and 67.54 cm in 1995, 1996, and 1997, respectively. Between October 1995 and June 1996, less than 14 cm of precipitation fell, the lowest recorded in the past 100 years.

Clipping Experiments

To evaluate the impact of the timing and intensity of herbivory on *C. hirsutissima* var. *arizonica*, I selected 366 plants for the experiment in the spring of 1995. All plants were growing on limestone outcroppings. Canopy cover of experimental plants ranged from 22 to 39 percent of full sun and forest litter ranged from 10 to 15.5 cm in depth. I caged all plants with 1.6 m tall hog-wire and chicken-wire fencing that excluded large herbivores known to graze in the vicinity (elk, deer, and cattle), but did not exclude small mammals. Because there are only approximately 1500 individuals in the Flagstaff area, the plants used in this and the second experiment represented 27 percent of the existing plants. As a Forest Service sensitive species, actions that may have harmed the continued existence of the species were rigorously controlled. Because it was not known whether treatments would kill plants, the number of plants I was able to use in this study was restricted.

To address whether the intensity of herbivory influenced *C. hirsutissima* var. *arizonica* growth and reproduction, I mimicked previously observed natural levels of herbivory with a clipping treatment. I assigned plants randomly to one of three clipping treatments: light herbivory where only the first centimeter below the flower bud was clipped, heavy herbivory where plants were clipped to 4 cm above the ground, or controls with no clipping treatment. To determine whether the season in which herbivory occurred influenced plant reproduction and growth, I assigned clipping treatment and control plants randomly to one of three seasons of herbivory: early season herbivory was simulated by clipping in May, mid-season herbivory was simulated by clipping in July, and late-season herbivory was simulated by clipping in September-October. Thus, plants were assigned to one of seven treatments: light clipping in May, heavy clipping in May, light clipping in July, heavy clipping in July, light clipping in September-October, heavy clipping in September-October, and caged controls with no clipping treatment. Plants were clipped 22–27 May, 21–25 July, and 25 September–20 October of 1995; 10–23 May, 24–30 July, and 3–10 September of 1996; and 6–7 May, 1–3 July, and 2–4 Sept of 1997. I noted the number of successful and unsuccessful flowers or dried buds, the total number of stems, and the total stems eaten on all individuals. To assess potential compensation for clipping, I measured the numbers of lateral shoots produced by each stem and the reproductive condition of lateral shoots. In all figures the numbers of flowers and stems reflect the fall condition before the plant received the clipping treatment. I included only plants that survived for all 3 years of the experiment.

During the course of this experiment, no cattle were present at the study site in 1995, 520 cows and calves were present in July of 1996 for 28 days, and 250 cows and calves were present for 31 days in August 1997.

To compare the impact of timing and intensity of clipping across years, I analyzed vegetative reproduction and sexual reproduction for September-October 1995, 1996, and 1997 using SYSTAT's General Linear Model repeated measures analysis of variance (SPSS 1996), which had two fixed main effects: season of clipping (early, mid, and late) and clipping intensity (low, high, and none); and the repeated measure was year (1995, 1996, and 1997). I log transformed reproductive measures to normalize the data. To account for multiple measures on experimental units, I used a Bonferroni adjustment for alpha levels (Snedecor and Cochran 1980). In addition, I assessed reproductive failure across years and groups by comparing the percent of dried buds on main stems and lateral shoots using the Kruskal-Wallis test (Zar 1984).

Natural Levels of Herbivory

To examine the impact of natural levels of herbivory, I compared vegetative reproduction, sexual reproduction, and the number of stems eaten of 35 unprotected plants and 69 caged con-

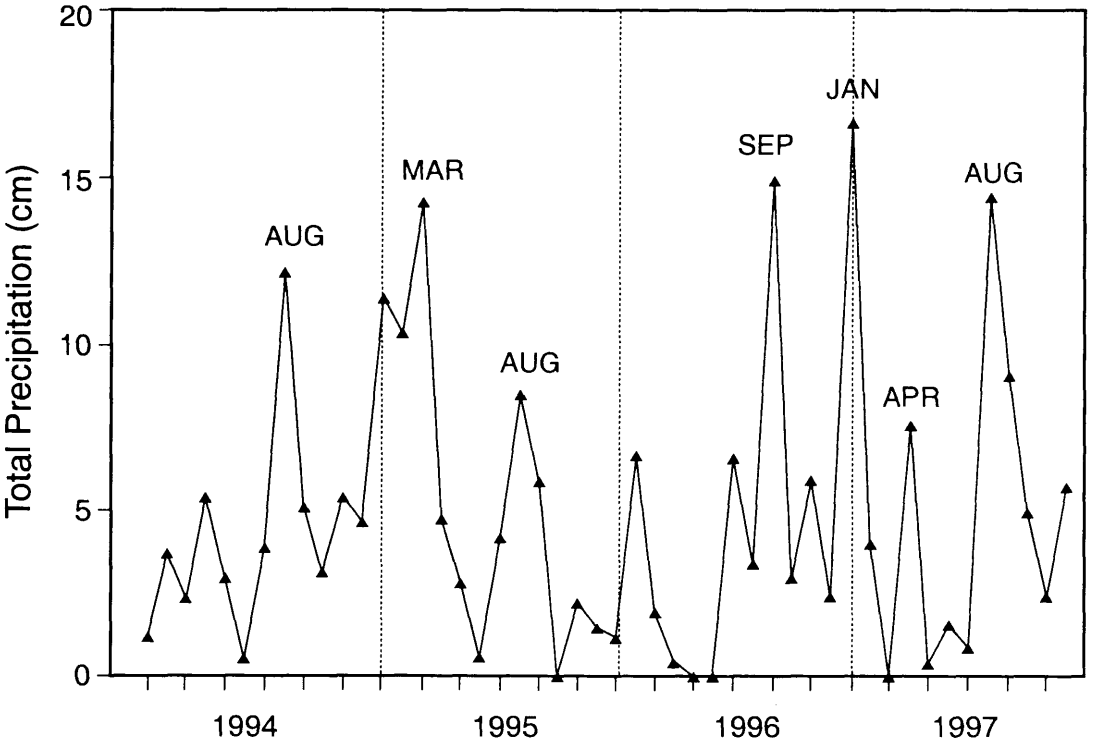


Figure 1. Annual precipitation from 1994 to 1997 in Flagstaff, Arizona.

trols over the 3 years of the study. I measured the same plant characteristics as above and compared these data using a repeated measures analysis of variance, where caging was the fixed effect and year was the repeated measure. Within each year, I examined natural levels of herbivory across the seasons using analysis of variance.

Results

Clipping Experiment – Effects of Season of Clipping

The number of *C. hirsutissima* var. *arizonica* stems and lateral shoots produced did not vary significantly with season of clipping (Table 1). Although there was a tendency for early season clipped plants to produce more lateral shoots than late season plants, this difference was not significant (Figure 2).

Season of clipping did significantly affect the number of *C. hirsutissima* var. *arizonica* flowers that set seed (see Table 1). In 1996 and 1997, late-season clipped plants produced 67–59 percent more flowers that set seed than early season clipped plants (Figure 3). As the growing season progressed, plants had more time to produce flowers; thus plants in the late-season clipped treatment groups had the greatest opportunity to produce flowers before the clipping treatment, regardless of the intensity of herbivory (see Figure 3). Early season clipping was the most detrimental to sexual reproduction in 2 of 3 years (see Figure 3).

Clipping Experiment – Effects of Clipping Intensity

Neither vegetative nor sexual reproduction varied significantly across intensities of clipping treatments (see Table 1). There was no significant effect of clipping on plant survival regardless of intensity.

Clipping Experiment – Effects of Year

The number of stems and lateral shoots produced did not vary significantly in any year (see Table 1). Despite climatic variation, both lateral and main stem production were relatively stable across years (Figure 4).

Table 1. Repeated measures analysis of variance for total number of stems and lateral shoots, and total flowers on main and lateral stems that set seed in three seasons (early, mid, and late), for three intensities of clipping (low, high, and none), measured in September 1995, 1996, and 1997.

	Total number of stems and lateral shoots				Total flowers that set seed on main and lateral stems			
Source	df	MS	F	p	df	MS	F	p
Season	2	12.69	0.45	0.64	2	0.356	5.45	0.02
Intensity	2	12.78	0.45	0.64	2	0.002	0.025	0.98
S x I	4	18.26	0.65	0.63	4	0.072	1.099	0.36
Error	357	28.21			338	338	0.065	
Year	2	7.38	0.57	0.57	2	O.168	6.008	0.01
Y x S	4	13.46	1.03	0.39	4	0.066	1.854	0.12
Y x I	4	11.65	0.89	0.47	4	0.070	1.956	0.10
Y x S x I	8	13.06	1.00	0.43	8	0.027	0.745	0.65
Error	676				714	0.036		

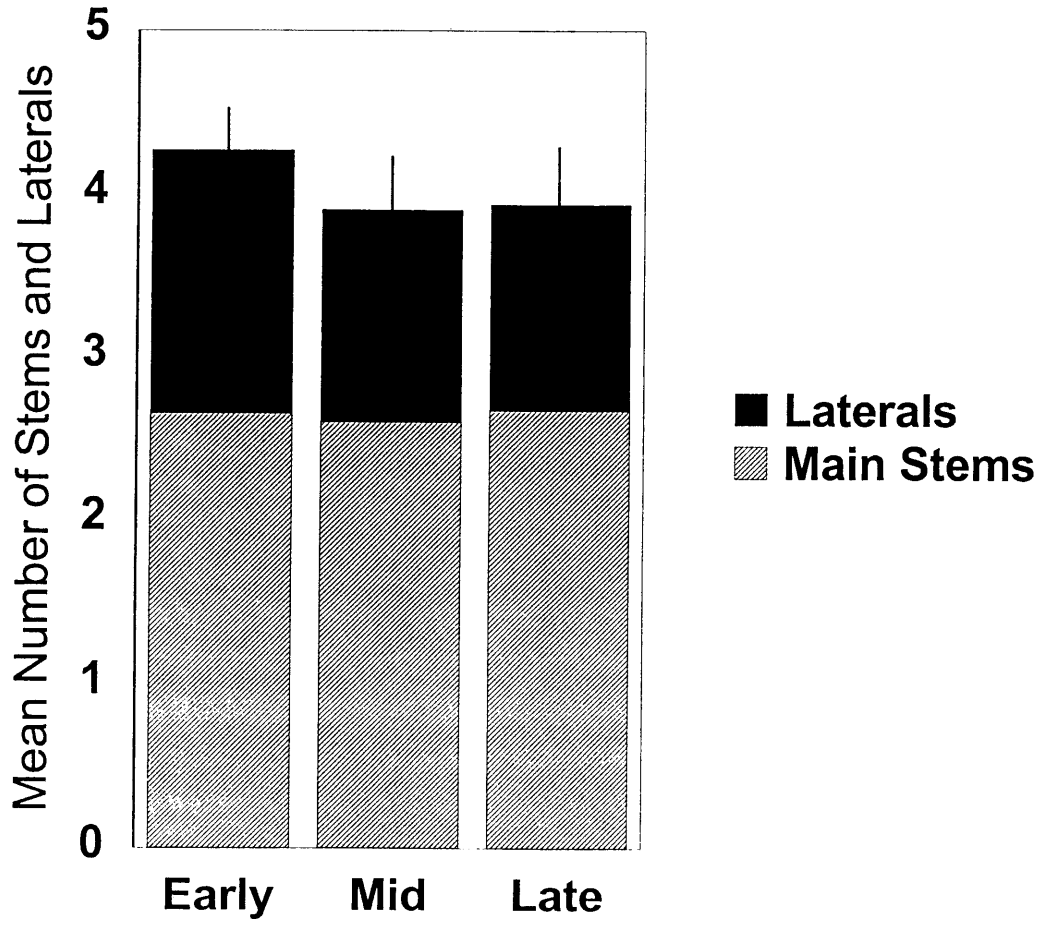


Figure 2. Vegetative reproduction of *Clematis hirsutissima* var. *arizonica* in early, mid, and late clipping groups averaged over 1995, 1996, and 1997. Early groups received clipping treatment in May, mid groups received clipping treatment in July, and late groups received clipping in September-October. Means ± 1 SE are indicated.

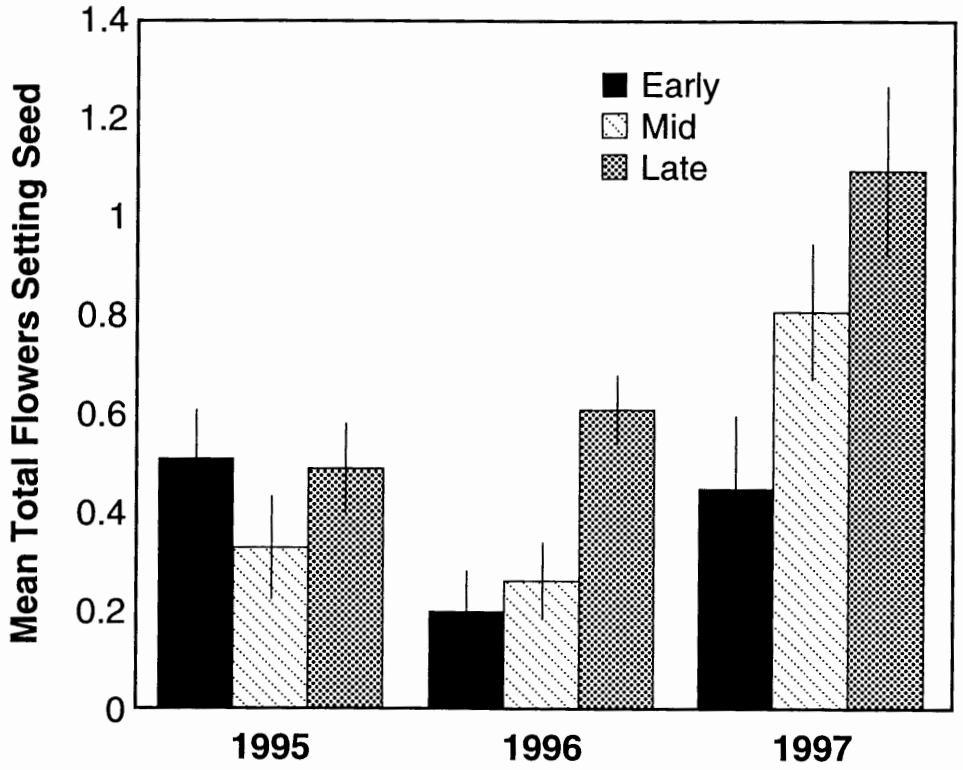


Figure 3. Sexual reproduction of *Clematis hirsutissima* var. *arizonica* in early, mid, and late clipping groups in 1995, 1996, and 1997. Early groups received clipping treatment in May, mid groups received clipping treatment in July, and late groups received clipping in September-October. Means ± 1 SE are indicated.

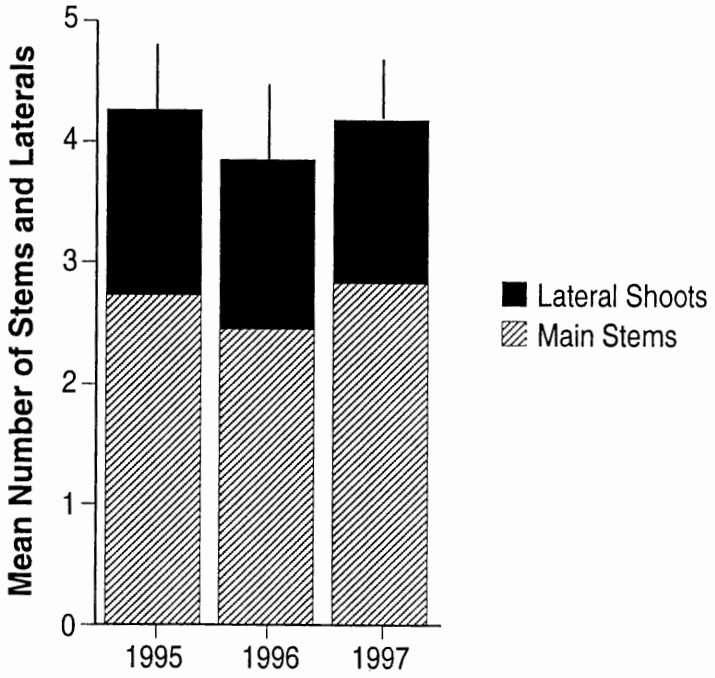


Figure 4. Vegetative reproduction of *Clematis hirsutissima* var. *arizonica* in 1995, 1996, and 1997. Means ± 1 SE are indicated.

In contrast, sexual reproduction was significantly affected by year. The greatest total flower production occurred in 1997 (Table 1, Figure 5). In most clipping intensity/season groups, total flower production increased in 1997; however, the exceptions are noteworthy (Figure 6). Both the low and high intensity, early season clipped plants produced fewer flowers that set seed in 1997 compared to 1995 or 1996. This indicates a long-term negative impact from early season herbivory on reproduction. Plants in the early season treatment did not recover as the other treatment groups did even in the comparatively wet year of 1997.

The only way that *C. hirsutissima* var. *arizonica* stems could compensate for loss of flowers or portions of stems after the clipping treatment was through production of lateral shoots, which in turn produced flowers. The contribution to flower production from lateral shoots varied with year (Year $F_{2,714} = 4.86$, $p < 0.001$, see Figure 5). For most groups, lateral shoot contribution to reproduction was greatest in 1997 (see Figure 6). However, there was no significant effect of season or intensity on the number of lateral flowers that successfully set seed (Season $F_{2,357} = 0.172$, $p > 0.05$; Intensity $F_{2,357} = 0.517$, $p > 0.05$). Although *C. hirsutissima* var. *arizonica* attempted to compensate for the loss of flowers by producing lateral shoots, no group completely replaced or compensated for flowers lost to clipping.

Experiment 2 – Natural Levels of Herbivory

In comparison to caged controls, unprotected plants that were exposed to both small and large herbivores experienced significantly more herbivory ($F_{1,102} = 22.83$, $p < 0.01$, Figure 7). In 1995, 1996, and 1997, unprotected controls experienced 40, 55, and 92 percent more herbivory than caged plants. Small mammals account for all herbivory on caged controls, as large mammals were excluded. The greatest herbivory on caged plants occurred in 1996.

The timing of natural herbivory within each year increased as the season progressed (1995 $F_{1,102} = 14.29$, $p < 0.001$; 1996 $F_{1,102} = 22.45$, $p < 0.001$; 1997 $F_{1,102} = 40.47$, $p < 0.001$). The greatest amount of herbivory occurred late in the season in all years with little or no herbivory occurring in the spring (see Figure 7). The exception to this pattern was in 1996, the driest year, when both caged and unprotected plants experienced herbivory in the spring. In 1996 and 1997, when cattle were present at the site, uncaged plants experienced significantly higher levels of herbivory than in seasons or years when cattle were not present. Because cattle were not present in 1995, wild animals account for herbivory that year. Similarly, wild animals accounted for spring 1996 herbivory, because cattle were not present on the study site until mid-season.

Protecting plants from large herbivores with caging did not significantly influence stem, lateral shoot, or seed production, despite the fact that uncaged plants had greater levels of herbivory (Table 2). For all characters, there was a trend for higher production with caging, however none of these comparisons was significant (Stem $F_{1,102} = 0.6$, $p > 0.05$; Lateral $F_{1,102} = 0.4$, $p > 0.05$; Seed $F_{1,102} = 0.58$, $p > 0.05$).

Discussion

Regardless of climatic variation across years, or the timing or intensity of herbivory, vegetative reproduction of *C. hirsutissima* var. *arizonica* was stable, whereas seed production was very sensitive to season of herbivory and climate. Clipping treatments may have removed biomass, but this did not influence total stem production in subsequent

Table 2. Comparison of the number of flowers setting seed, stems, and lateral shoots of caged versus uncaged *Clematis hirsutissima* var. *arizonica*. Neither year or caging significantly influenced any character.

Character	Year	Caged	Uncaged
No. of flowers setting seed	1995	0.44 ± 0.15	0.49 ± 0.21
	1996	0.39 ± 0.10	0.23 ± 0.14
	1997	0.71 ± 0.20	0.40 ± 0.28
Stems	1995	2.65 ± 0.25	2.49 ± 0.34
	1996	2.67 ± 0.24	2.06 ± 0.34
	1997	2.28 ± 0.20	2.37 ± 0.28
Lateral shoots	1995	1.30 ± 0.25	0.57 ± 0.34
	1996	1.39 ± 0.41	1.74 ± 0.41
	1997	1.09 ± 0.25	0.94 ± 0.36

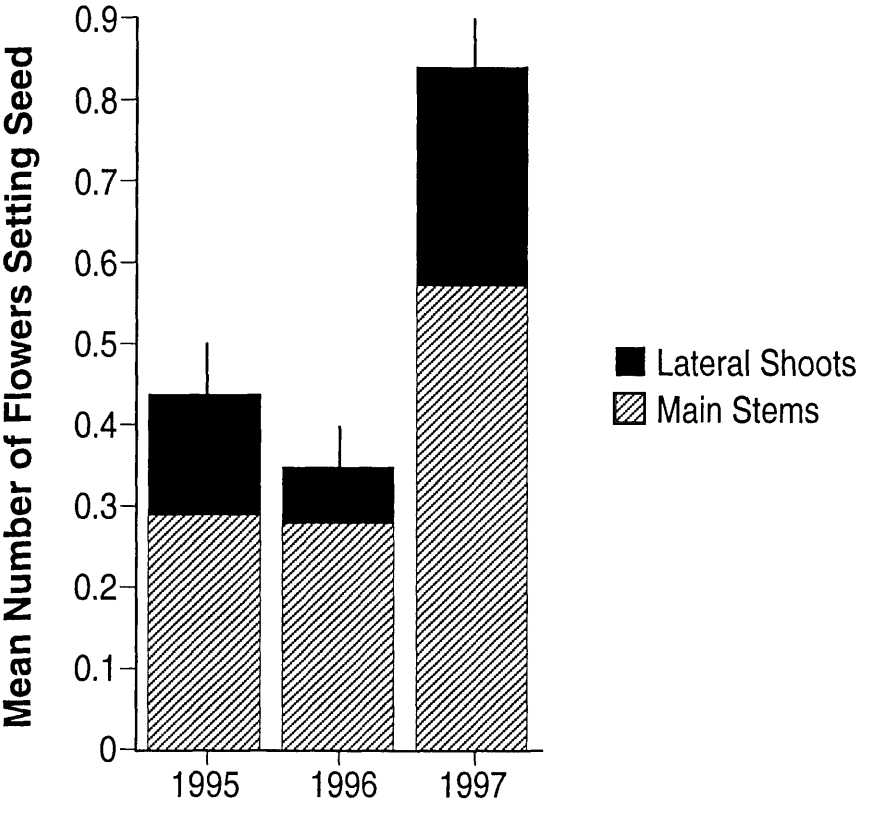


Figure 5. Mean number of flowers setting seed on main and lateral stems of *Clematis hirsutissima* var. *arizonica* in 1995, 1996 and 1997. Means ± 1 SE are indicated.

years. Neither low nor high intensities of clipping induced consistent, substantial lateral shoot growth.

Conversely, sexual reproduction was influenced by climatic variation and the timing of herbivory. Early-season herbivory reduced seed set within the year of treatment and in subsequent years, whereas late-season herbivory had little effect on sexual reproduction within or across years. This finding contrasts to previous studies on other herbaceous species indicating early season herbivory was less detrimental because plants had more time to recover within a single growing season (i.e., Maschinski and Whitham 1989). Apparently early-season herbivory on *C. hirsutissima* var. *arizonica* depletes a carbohydrate reserve that is not replaced within the season and compensatory flower production cannot occur.

The second experiment comparing caged versus unprotected controls demonstrated that both small and large mammals feed upon *C. hirsutissima* var. *arizonica*. The number of stems eaten was always significantly higher on uncaged versus caged plants, indicating that large mammals were responsible for most herbivory on natural populations of *Clematis*. The highest levels of herbivory occurred when cattle were present on the pasture (in July 1996 and August 1997) and when precipitation was low. The greatest amount of spring herbivory inside and outside cages occurred following the prolonged drought in 1996 when less understory vegetation was available for all herbivores.

Although caged plants experienced significantly less herbivory, this did not result in significantly greater seed production (see Table 2). The overall low reproduction of plants can explain this finding. Many stems and lateral shoots did not produce successful flowers regardless of whether they were browsed or not.

The general reproductive success of the species is problematic and is probably related to both climate and overall forest health. Sexual reproduction was extremely low overall, such that the mean number of flowers setting seed per individual was < 1 in most groups in 1995 and 1996. In 1997, the mean number of flowers setting seed increased to ≥ 1 in most groups except early season. Arid con-

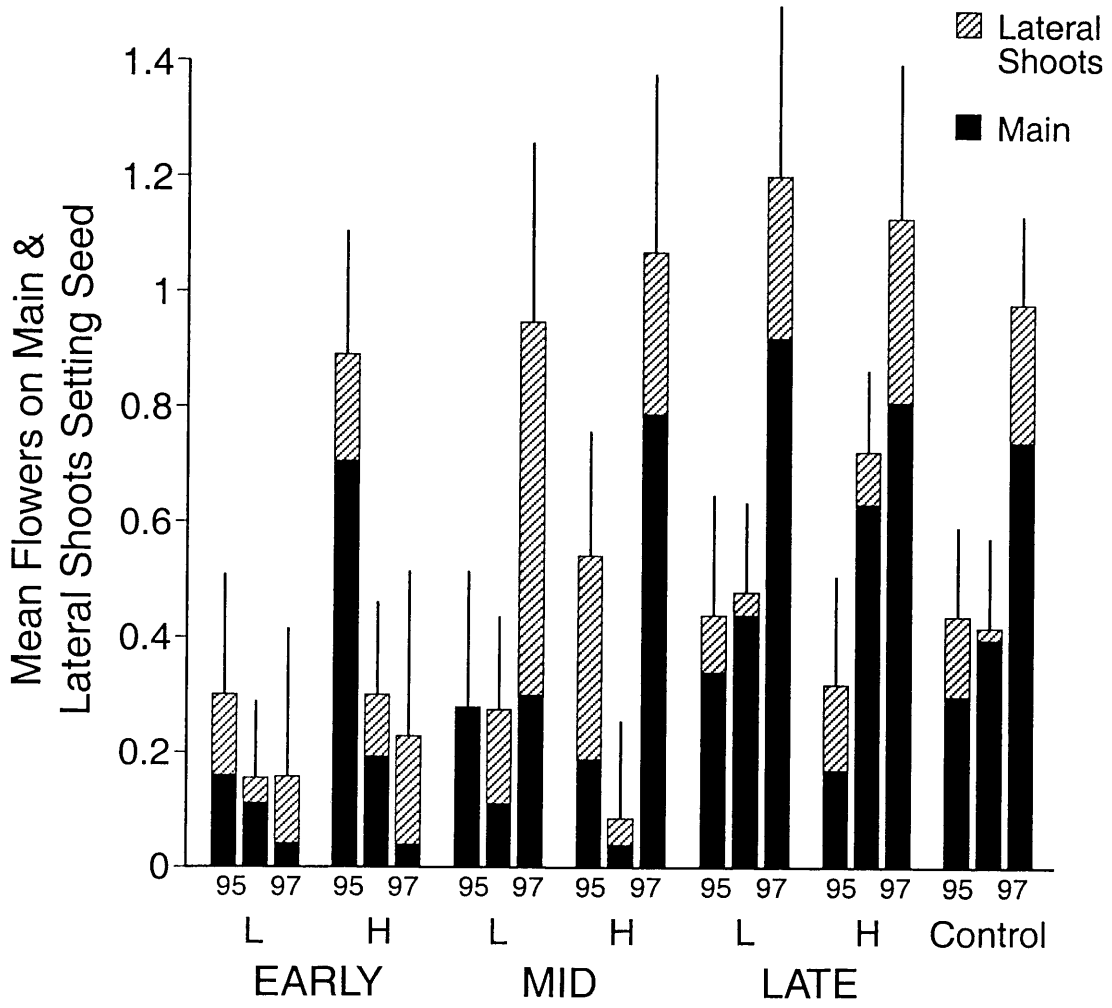


Figure 6. Mean number of *Clematis hirsutissima* var. *arizonica* flowers that set seed on main and lateral shoots for treatment groups. Measurements taken in September 1995, 1996, and 1997 are reported in adjacent columns for each treatment group. L and H signify light and heavy clipping treatments. Control group received no clipping treatment. Early groups received clipping treatment in May, mid groups received clipping treatment in July, and late groups received clipping in September-October. Means ± 1 SE are indicated.

ditions coupled with unpredictable freezes may contribute to high percentages of flower and bud death, as is seen with many blooming plants in the region. In addition, previous studies have shown that the reproductive success of *C. hirsutissima* var. *arizonica* is significantly greater in canopies with approximately 50 percent light (Maschinski et al. 1997). At light levels greater than 75 percent, plants suffer from high bud mortality, low seed viability, low seedling establishment, low mid-season water potentials, and high exposure to competing grasses. At light levels less than 40 percent plants had low seed and stem production and low photosynthetic rates (Maschinski et al. 1997). Because the mean light levels received by plants in this study were 22–39 percent light, plants were light-limited. The reason for the light-limitation is probably related to disrupted patterns of fire frequency in *Pinus ponderosa* forests of this region. Fire suppression, which began as early as 1908 in the Flagstaff area, has had ecosystem-level effects resulting in overstocked patches of saplings and pole-sized trees, greater canopy closure, reduced tree growth, stagnated nutrient cycles, and decreased on-site water balance (Covington and Moore 1994). The low productivity of the study site contributed to the low reproductive success of the species and to the relatively lower influence of

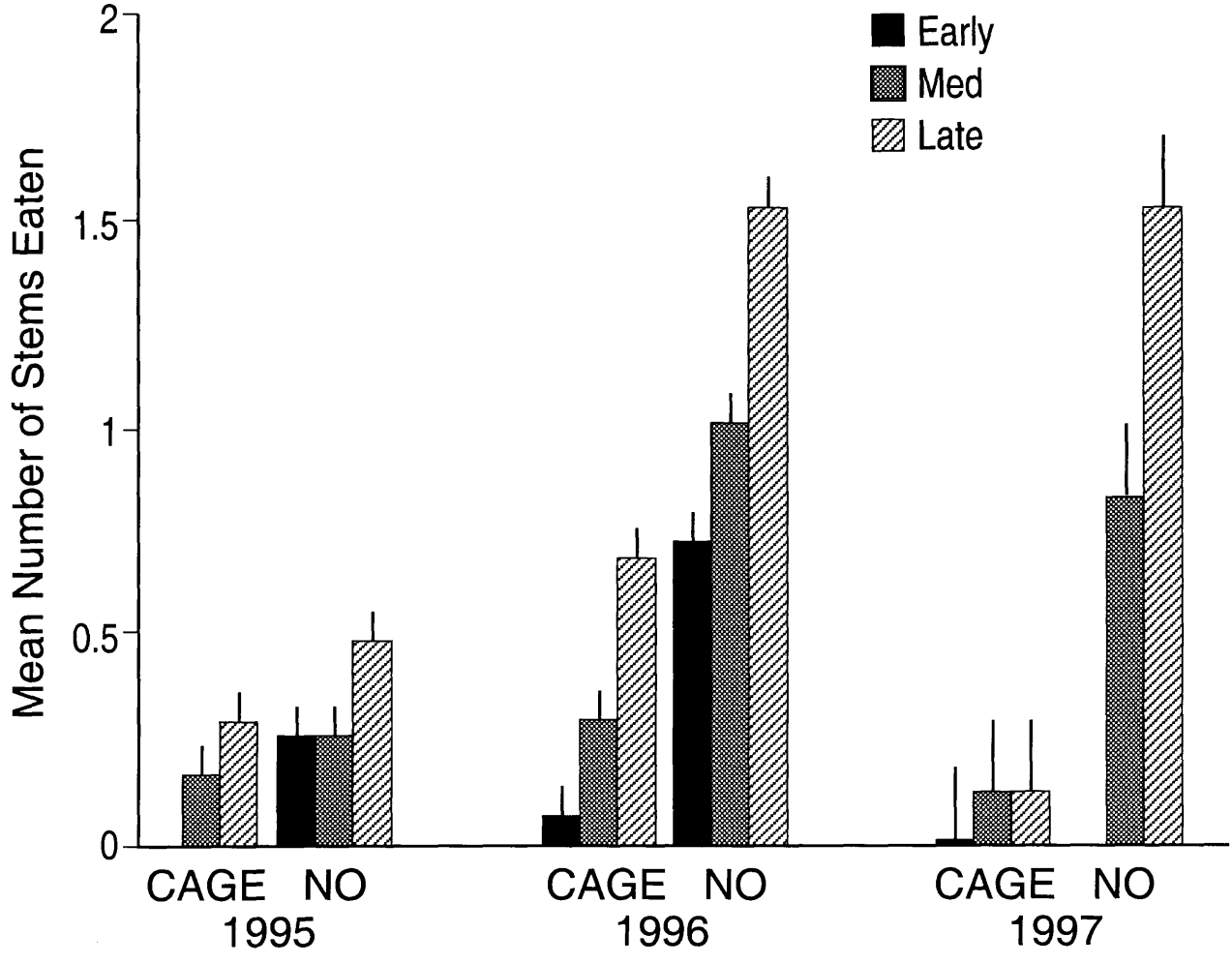


Figure 7. Comparison of the mean number of *Clematis hirsutissima* var. *arizonica* stems eaten by mammals in early, mid and late season in 1995, 1996 and 1997 on caged and unprotected plants.

herbivores on sexual reproduction, as has been seen in other systems (John and Turkington 1995).

The results of this study have management implications for the conservation of *C. hirsutissima* var. *arizonica*. Early-season cattle grazing in *C. hirsutissima* var. *arizonica* pastures would be very detrimental to this species. Therefore it would be advisable to limit cattle use of pastures where *C. hirsutissima* var. *arizonica* grows to the late summer and fall after plants have shed seed. It is likely that other management activities, such as controlled burns, would also be detrimental to *C. hirsutissima* var. *arizonica* early in the season. Because the reproductive success of the species is so limited, any management activity that enhanced wild or domestic herbivores would be inadvisable. These management suggestions can be considered as one piece in the overall puzzle of managing the diversity of the entire forest.

Acknowledgments

Thanks to Joanne Baggs, Mary Beach, Cheryl Casey, Stephanie Galgon, Karen Hueston, Kenric Kesler, Kai and Mira Petersen, Jeff Peterson, Ron Popowski, Nigel Sparks, Beth Williams, and Al Zalfini for field assistance. Barbara Phillips and Heather Green of the U.S. Forest Service provided logistical support for these studies. This study was funded by Section 6 cost-share contracts from the Arizona Department of Agriculture through the efforts of Bruce Palmer, Angie Brooks, and Jim McGinnis.

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Response of a Rare Endemic, *Penstemon clutei*, to Burning and Reduced Belowground Competition

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Abstract: *Penstemon clutei*, a rare perennial beardtongue endemic to the ponderosa pine forest of the Sunset Crater volcanic field of northern Arizona, presents an opportunity to test the hypothesis that restoration of historic ecosystem conditions may enhance the sustainability of a rare species. We tested prescribed burning and root trenching treatments as proxies for the surface fires and reduced tree densities characteristic of historic ponderosa pine ecosystems in a study area at O'Leary Peak, part of the Sunset Crater volcanic field (Coconino National Forest, AZ). Prescribed burning killed many mature *P. clutei* plants and negatively affected density for at least 3 years post-burn. In contrast, trenching to cut root competition of overstory trees led to a 1200 percent increase in *P. clutei* plants. Precipitation influenced the response. Seed germination experiments showed that *P. clutei* does not have innate dormancy. Germination rates in the lab ranged from 5 to 70 percent under a range of environmental and fire-related conditions (i.e., cold stratification, light, exposure to ash, NH_4), but these factors were not statistically significant. Tested seedling establishment rates in situ were very low (0.4%). These experiments suggest that the observed *P. clutei* population increase following severe wildfires (1973 Burnt fire, 1996 Hochderffer fire) may have been due primarily to the removal of tree competition rather than to direct fire effects. Further experimentation is suggested to develop ecological information for thoughtful integration of ecosystem restoration with the habitat needs of rare plants.

Rare plant species present fundamental challenges for the management of forest ecosystems. Conservation of native biological diversity is central to management of public resources, as mandated by the Endangered Species Act and other legislation, but often little is known about the ecology of rare species (National Plant Conservation Initiative, 1995). The very fact of rarity limits our ability to adequately sample or experimentally study species to obtain the types of ecological information needed to support management decisions (Palmer 1987, Owen and Rosentreter 1992). In the absence of information, the conservative position is to minimize management action in the hopes of avoiding habitat degradation. This approach may be the best we can do in many settings, but it may be useless or even counterproductive in others. Many ecosystems are currently in conditions far removed from the structural and disturbance patterns characteristic of the environment in which native species evolved. These altered conditions may be an underlying reason for the present rarity of some species and perpetuation of these conditions through "no-action" management may unintentionally contribute to further loss of habitat.

Penstemon clutei, a rare perennial beardtongue endemic to the ponderosa pine (*Pinus ponderosa*) forest of the Sunset Crater volcanic field of northern Arizona, presents an opportunity to test the hypothesis that restoration of historic ecosystem conditions may enhance the sustainability of a rare species. Changes in ponderosa pine ecosytems have been well documented (Weaver 1951, Cooper 1960, Covington and Moore 1994, Arno et al. 1995, Swetnam and Baisan 1996, Fulé et al. 1997, Moore et al. 1999). Briefly, the historic regime of frequent low-intensity fires was disrupted by livestock grazing and fire suppression beginning around 1870–1880. Extensive timber harvesting and snag cutting removed a major fraction of the old-growth trees, but dense stands of young trees form continuous fuels across landscapes and vertically within stands. Heavy tree competition causes reduced productivity and increased mortality of old-growth trees (Biondi 1996, Stone et al. 1999, Mast et al. 1999) and reduced understory plant productivity (Riegel et al. 1995, Covington et al. 1997), and affects a host of ecosystem attributes including nutrient cycling and wildlife habitat (Covington et al. 1997). Wildfire size, intensity (crownfires), and severity (overstory and understory mortality) have increased throughout the ponderosa pine range (Swetnam and Betancourt 1998). As a result, the restoration of historic eco-

system characteristics, especially though thinning and burning, is a management strategy receiving great attention (U.S. General Accounting Office 1998).

Although ecosystem restoration may be an appropriate "coarse-filter" strategy for ponderosa forest management (Kaufmann et al. 1994), it is challenging to integrate large-scale treatments with the "fine-filter" approach usually adopted for biological conservation of rare species. The ponderosa pine–*Penstemon clutei* forest provides a good test system for several reasons: (1) The species receives special management consideration, but it is not a federally listed threatened species. (2) Penstemons and many other taxa in the Scrophulariaceae are early successional species, logically adapted to frequent disturbance. (3) The Coconino National Forest, which encompasses almost all of the *P. clutei* range, must deal with management issues in *P. clutei* habitat on a continuing basis, including pipeline and road expansion, recreational site development, off-road vehicle use, timber and mineral resource extraction, and fire management.

The Burnt Fire in November of 1973 burned a portion of the *Penstemon clutei* habitat west of Sunset Crater National Monument. Goodwin (1979) reported that *P. clutei* plants proliferated in the burned area with vigorous growth and abundant reproduction. He concluded that *P. clutei* was a pioneering species requiring periodic disturbance by fire. Vigorous plants and prolific regeneration were also observed after the intense Hochderffer fire in 1996 in the northwestern portion of the *P. clutei* range (P. Z. Fulé, personal observation, 1997 and 1998). Disturbance created by an unusual tornado and subsequent timber salvage (1992–1994) was also associated with increased *P. clutei* abundance (Crisp 1996). After Goodwin's (1979) observations, two prescribed burning studies were carried out by the Forest Service. The first study, in 1982, was conducted under wet conditions and gave inconclusive results (Nagiller 1992). The second study, in 1991, was hampered by a lack of replication and also gave preliminary results of an inconclusive mix of mortality and regeneration (Nagiller 1992).

Beginning in 1992, we initiated studies to quantify *P. clutei* response to prescribed burning and to understand seed germination requirements. Germination response to a range of treatments has been studied extensively in a variety of western penstemons (e.g., Kitchen and Meyer 1991, Raeber and Lee 1991). In commercial production of *P. clutei*, moist chilling for 90 days results in 70–80 percent germination (Plants of the Southwest, Santa Fe, New Mexico, personal communication 1992). Studies on the closely related *Penstemon palmeri* have demonstrated that it is a relatively nondormant species in comparison to other penstemons, but dormancy and requirements for moist chilling and light are variable (Kitchen and Meyer 1991, 1992). Moist chilling at winter temperatures induced secondary dormancy in approximately half of a sample of *P. palmeri* seeds (Meyer and Kitchen 1992). The secondary dormancy was removed by warm summer temperature treatment, suggesting that *P. palmeri* has a strategy of cyclic seed dormancy, dividing seeds into spring and autumn germination groups (Meyer and Kitchen 1992). Seed collected from a recently burned site exhibited primary dormancy an order of magnitude higher than seed from other collections (Meyer and Kitchen 1992). *Penstemon* species from cold, high-elevation habitats required more extensive moist chilling to remove primary dormancy (Kitchen and Meyer 1992, Meyer 1992). The low-elevation species *P. parryi* exhibits little response to moist chilling (Raeber and Lee 1991). Viability of *P. palmeri* seeds in storage remains 83 percent after 2 years and reduces to 50 percent after 15 years (Stevens et al. 1981). Given its ecological characteristics intermediate between *P. parryi* and *P. palmeri*, *P. clutei* might be expected to have an intermediate moist chilling requirement and long seed viability.

Plant regeneration following fire is not necessarily through seed germination and establishment. *Penstemon haydenii* in Nebraska was found to reproduce primarily vegetatively (Flessner and Stubbendieck 1992). A study of disturbance effects by fire and pocket gophers on *Penstemon grandiflorus* in Minnesota showed that plants that survived fire resprouted and displayed no increased reproductive output (Davis et al. 1991a). Even though fire appeared to have a negative impact on individual *P. grandiflorus* plants, the population as a whole was dependent on fire and gopher disturbance to maintain a suitable, open habitat (Davis et al. 1991b). *Ipomopsus aggregata*, a species associated with *Penstemon clutei* that displays a similar growth form, resprouted following fire in northern Arizona, although growth and vigor were reduced in burned plants (Paige 1992). Seedling establishment of *I. aggregata*, however, increased 116-fold over controls (Paige 1992). Vose and White (1987) found that reproduction of several understory species, including *Penstemon virgatus*, following fire in northern Arizona occurred

from residual seed or seed rain from surviving plants, rather than from buried seed populations. In an investigation of the regeneration of several understory species following fire in California chaparral, Keeley et al. (1985) distinguished several reproductive strategies. Herbaceous perennials tended to resprout, whereas annuals divided into an opportunistic class with varying germination requirements and a fire-dependent class that displayed strong germination response to heat or the presence of charred wood (Keeley et al. 1985).

In 1997, after evaluating negative results from the prescribed burning experiment described below, we investigated the hypothesis that the vigorous *P. clutei* responses seen after the Burnt and Hochderffer fires and the 1992 tornado were due to the mortality of overstory trees, thereby removing root competition. Competition with overstory vegetation may affect understory plants either through light interception or through the relatively greater ability of trees to extract water and nutrients from the soil. Southwestern ponderosa pine forests have relatively open canopies (40–65% canopy cover by vertical projection at sites across northern Arizona, Fulé et al. 1997 and unpublished data). Riegel et al. (1995) tested the effects of light versus root competition on understory species composition and cover in an Oregon ponderosa pine forest. Both factors were significant, but trenching to remove tree root competition increased the cover and density of 60 percent more understory species than in the canopy-reduction treatment (Riegel et al. 1995).

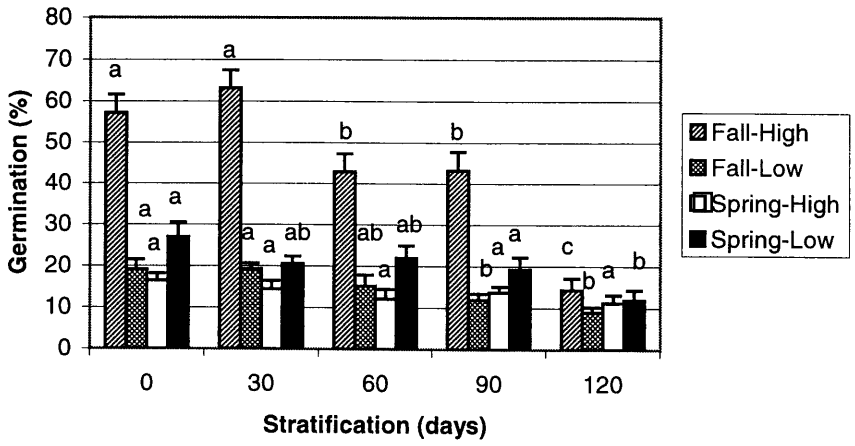
From 1992 to 2000, we conducted the following studies on *P. clutei*: (1) We measured germination response to a variety of environmental factors in lab and field settings. (2) We tested the hypothesis that prescribed fire would increase *P. clutei* density by removing litter and competing vegetation. (3) We tested the hypothesis that cutting root competition through trenching would increase *P. clutei* density.

Methods

P. clutei was described by Nelson (1927) and named after the original collector, Willard N. Clute. The plant was classified as a subspecies of *Penstemon pseudospectabilis* by Keck (1937), then reclassified as an independent species by Clokey and Keck (1939) who considered it intermediate between *P. pseudospectabilis* ssp. *connatifolius* and *P. palmeri*. *Penstemon clutei* falls between these species in size and appearance, attaining heights of more than 1 m with pink to purple flowers (Goodwin 1979, specimens at Deaver Herbarium, Northern Arizona University, Flagstaff). Goodwin (1979) and Phillips et al. (1980) described the habitat of *P. clutei* as limited to about 65 sq km in the cinder hills around Sunset Crater on soils covered with up to 25 cm of raw volcanic cinders of alkaline olivine basalt formed in the most recent volcanic eruption (A.D. 1046). An apparently disjunct population is located in cinder hills around Indian Flat, about 20 km northwest of Sunset Crater. *Penstemon clutei* is distributed in patches, with the greatest occurrence in areas of sparse herbaceous vegetation, past logging disturbance (stumps, skid trails), and recently killed snags (Phillips et al. 1992, Crisp 1996). The dominant vegetation is ponderosa pine, with scattered *Pinus edulis* and *Juniperus osteosperma*. Understory species commonly associated with *P. clutei* include *Chrysothamnus nauseosus, Fallugia paradoxa, Penstemon barbatus,* and *Verbascum thapsus.* An intensive survey of the southern habitat region by Phillips et al. (1992) also found *Rhus trilobata* occurring frequently with *P. clutei,* although no associated species were reliable *P. clutei* indicators. Because the age of the oldest *P. clutei* plants was estimated at 5 to 10 years, maintenance of a soil seed bank could be important for the regeneration of such short-lived plants (Phillips et al. 1992). The presence of a root-boring insect larva that could reduce the life span of the plants was also noted (Phillips et al. 1992). Pollination by both hummingbirds and bees has been observed in *P. clutei* (Phillips et al. 1980) and the closely related *P. pseudospectabilis* (Reid et al. 1988, Lange and Scott 1999). Phillips et al. (1992) summarized the legal protection history and status of *P. clutei;* it is currently considered a sensitive species with the USDA Forest Service (Arizona Game and Fish Department 1997).

The experimental studies described here were conducted on Coconino National Forest lands at O'Leary Peak, adjacent to Sunset Crater National Monument (Figure 1). The elevation of the study area is approximately 2100 m. Soils are cindery and deep, well-drained Vitrandic Ustochrepts and Typic Ustorthents (USDA Forest Service 1995). Weather records from Sunset Crater National Monument, 1 km south of the study area, show a bimodal precipitation pattern typical of southwestern forests. Annual precipitation averages 43.9 cm (1969–1993), occurring in winter and during the summer monsoon (July–September), but precipitation has varied widely in recent decades from 23.6

(a)



(b)

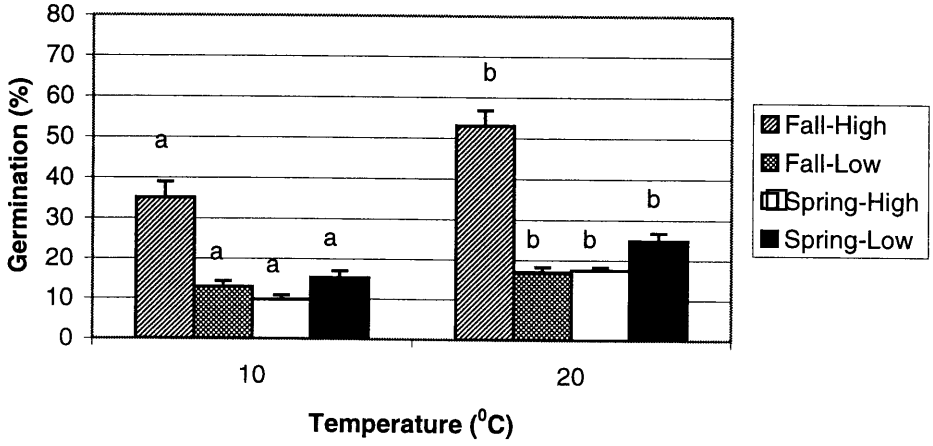


Figure 1. (a) Germination percentages of four *P. clutei* seed lots (fall/spring seasons, high/low elevations) stratified for different periods. Different superscript letters indicate significant differences between stratification periods within seed lots. Standard error bars shown. (b) Germination percentages of four *P. clutei* seed lots at two temperatures (all stratification periods combined). Different superscript letters indicate significant differences between temperatures within seed lots.

cm in 1989 to 66 cm in 1992. The average minimum temperature in January is –11° C and the average maximum temperature in July is 29° C.

Seed Germination Studies

Seed lots were collected from *P. clutei* plants on May 18 and October 18 in 1993. The May collection (spring) was from seed capsules that matured in 1992, and the October collection (fall) was from 1993 seed. Seeds were collected below and above 2,290 m elevation (low and high elevation, in the vicinity of O'Leary Peak, Coconino National Forest). A seed predatory insect was encountered in 70 percent of seed collections from 20 separate plants in May of 1996. The insect was identified by the USDA Sytematic Entomology Laboratory as *Kleidocerys ovalis* Barber (Hemiptera: Lygaediae), a seed bug. Subsequent informal examinations of *P. clutei* seed capsules have shown the bugs to be present every year but at lower rates of infestation than that observed in 1993.

Two lab germination experiments and a field seeding trial were conducted. The first lab study followed a fractional factorial experimental design for an exploratory test of multiple factors that were associated with triggering germination in other fire-adapted plant species. The defining relation for the 28-2V design was I = ABCDG = ABEFH = CDEFGH. The alias of any effect can be found by multiplying the effect by the words in the defining relation (Montgomery 1984:342), so the alias structure of C, for example, was C = ABDG = ABCEF = DEFGH. Study factors at high/low or presence/absence levels were (a) heat pulse, 70° C for 5 minutes which mimics low seedbank temperature average from California chaparral (Keeley et al. 1985, Keeley 1987) and New Jersey grass studies (Cheplick and Quinn 1988); (b) ammonium-nitrogen, 77 ppm, based on post-fire NH_4^+ concentration in ponderosa pine (Covington and Sackett 1992); (c) charred litter (Keeley et al. 1985, Keeley 1987); (d) collection elevation, which is related to genetic diversity; (e) charred *P. clutei* litter; (f) nitrate-nitrogen, 40 ppm, based on post-fire NO_3^- concentration in ponderosa pine (Covington and Sackett 1992); (g) light, 12-hour photoperiod presence/absence (Meyer and Kitchen 1992); and (h) collection date, which is related to primary dormancy. Groups of 25 *P. clutei* seeds were placed on moistened filter papers in covered (not sealed) pyrex petri dishes and allowed to germinate in a Percival growth chamber at 15° C and 60 percent relative humidity. Germinated seeds were counted and removed weekly for 5 weeks, beginning January 21, 1994. Analysis of the design was done with Yates' algorithm (Montgomery 1984:337). The alpha level for all analyses was 0.05.

The second lab germination study tested *P. clutei* seeds from the four seed lots collected in 1993. Seeds were stored in paper bags at approximately 20° C until germination tests were conducted in 1997. Germination tests were conducted in climate-controlled incubators (Percival model I37-LL). Five cold stratification periods (0, 30, 60, 90, and 120 days) and two germination temperatures (10 and 70° C) were tested. For cold stratification treatments, seeds were soaked in deionized water for 24 h, drained, placed in plastic bags, and stored in the dark at 3–4° C for the length of the treatment period. At the end of the stratification period, 20–50 seeds were placed in petri dishes on moistened filter paper. Five dishes were used per treatment combination (seed lot X stratification X temperature). Two germination chambers were used and conditions were set at 30 percent relative humidity, 10 h of light exposure, and a constant temperature of either 10 or 20° C.

Seeds were counted every 3 days and the number of germinated seeds was recorded until germination was complete (i.e., no additional seeds germinated between successive counts). Seeds were considered to have germinated when emerging radicals reached at least 2 mm in length. Germination (%) was calculated as the maximum number of seeds counted per dish divided by the total number of seeds present. Factorial analysis of variance (ANOVA) was used to test for main effects due to stratification period and growth chamber temperature. Analyses were conducted separately for individual seed lots. Data were square root transformed when necessary to meet analytical assumptions (normal distribution and similar variance). Main effects were tested at an alpha level of 0.05.

A field seeding trial was conducted as part of a mitigation effort for a natural gas pipeline project. The factors were disturbance and seeding at two levels each (presence/absence), applied in a split-plot design implemented on April 27, 1993, with 10 blocks consisting of two quadrats of 1 sq m each in the disturbed right-of-way and two in the adjacent undisturbed forest. Seeding with 50 stratified seeds was assigned randomly to one quadrat in each of the disturbed and undisturbed sites. The blocks were distributed at approximately 900 m intervals along the 11 km transect where the pipeline passed through *P. clutei* habitat. No

seedlings were found on quadrat inventories in June and September, so the experiment was repeated on October 2, 1993, using unstratified seeds from a September, 1993, seed collection along the pipeline. One hundred seeds per sq m were placed in new quadrats adjacent to the original locations. Quadrats were inventoried in June and August of 1994.

To minimize mortality to the species, the role of vegetative propagation in *P. clutei* was not assessed directly. Several dead *P. clutei* were excavated and found to have long rhizome-like roots. However, the small "seedling" *P. clutei* plants observed on the plots each summer appeared to be actual seedlings starting with cotyledons.

Prescribed Burning

An experiment on the effects of prescribed burning on the *P. clutei* community was established in 1994. Forty *P. clutei* plant-centered plots were established between July 29 and August 1 of 1994 at the same sites described for seed collection in the first germination studies. Because the sample plots were centered on existing plants, a technique often used in rare-plant studies (Travis and Sutter 1986), all data were calculated in terms of plants per plot and the actual absolute density of *P. clutei* and other species (plants per ha) in the study sites was unknown. Each plot was a 2.5 m radius circle (area = 19.6 sq m) centered 0.3 m northwest of an existing *P. clutei* plant. All species were tallied within each plot. *P. clutei* was tallied in four categories: seedling, second-year plant, mature plant, and dead. Field experience indicated that the distinctions between the living plant categories were approximate. Fuels were measured on two perpendicular planar transects established SE-NW and SW-NE on each plot following the methods of Brown (1974) and Sackett (1980). Plots were randomly selected for burn or control treatments. Burning was conducted on September 26, 1994, between 9:30 AM and 2:30 P M. Temperatures ranged from 21.1 to 23.9° C, winds averaged 8.5 km per hour (max 13.6 km/h), and relative humidity decreased from 26 to 20 percent during the burning period. Flame lengths averaged 29.1 cm, corresponding to an average fireline intensity of 17.7 kW per m (Agee 1993). Burn season effects were tested on a second experimental site immediately north of the lower elevation fall burning site. Forty new plots were established April 6–7 of 1995. Twenty randomly selected plots were burned on April 27, 1995, between 9:30 and 11:30 AM. Temperatures ranged from 12.8 to 16.1° C, winds averaged 8.5 km per hour (max 17 km/h), and relative humidity decreased slightly from 28 to 27 percent during the burning period. Flame lengths averaged 34.7 cm, corresponding to an average fireline intensity of 25.9 kW per m (Agee 1993). The fall burn plots were remeasured on July 10–11, 1995. All 120 plots, including spring and fall burns, were remeasured August 28–September 4, 1996, August 5–7, 1997, and August 20–25, 1998.

Changes in *P. clutei* density, species richness, and fuels were analyzed with repeated measures analysis of variance (Systat 8.0, SPSS Science, Chicago). Data were square-root transformed to meet ANOVA assumptions. Community data were assessed with nonmetric multidimensional scaling, a nonparametric ordination procedure (PC-Ord 4.0, MjM Software, Gleneden Beach, Oregon). Indicator values were calculated for individual species based on relative abundance and relative frequency. A Monte Carlo procedure with 1000 iterations was used to assess the probability of encountering indicator values by chance.

Belowground Competition

In 1997 (October 1–10) we established eight new experimental plots within the low-elevation burning study area, each paired with a nearby control plot from the original burn experiment. The belowground effects of tree removal were simulated by digging a narrow trench approximately 1 m deep around each plot. Trenches were located 50 cm outside the plot boundary to avoid physical disturbance within the measured area and were lined with plastic sheeting to minimize tree root regrowth (Milne 1979). Trenches were backfilled immediately after lining. Plots were remeasured on August 25, 1998, September 1, 1999, and August 15, 2000. *P. clutei* density, species richness, fuels, and community data were analyzed as described for the prescribed burning study above.

Results

Seed germination in the fractional factorial experiment ranged from 8 to 80 percent. Analysis of variance for main effects and two-way interactions indicated that only the pre-existing elevation and collection date factors were statistically significant, with fall seeds and high-elevation seeds germinating best. Tests of statistical significance in the fractional factorial design rely on the assumption that higher-order interactions may be considered as error, in the absence of a pure error term, so the ANOVA p values should be treated with caution. Because the collections were not

replicated, the identification of "elevation" and "season" as causal factors of differences between seed lots is tenuous.

The second germination experiment showed that cold stratification significantly affected *P. clutei* germination for three of the four seed lots (Figure 1). In all cases, mean germination decreased as cold-stratification period increased from 0 to 120 days. Decreases were most dramatic for the fall high-elevation collection, which had consistently higher germination than the other seed lots under all treatment conditions. Germination for this lot decreased almost 50 percent as the stratification period was increased from 0 to 120 days. Although during stratification seeds were kept in the dark and at temperatures just above freezing (3–4° C), germinated seeds were observed in the stratification bags at 120 days. Temperature significantly affected germination of all seed lots (Figure 2). On average, germination was increased by 9.7 percent when germination temperature was kept at 20° C compared with a constant 10° C. Similar to cold-stratification tests, the difference in germination between the two temperature regimes was most dramatic for the fall high-elevation seed lot compared with the other collections.

The field seeding trial resulted in extremely low seedling establishment. No seedlings were established following the April 1993 seeding. Seedlings established on only three seeded quadrats and no unseeded quadrats following the October 1993 seeding. The total establishment rate was 0.6 percent on the disturbed pipeline quadrats and 0.1 percent on the undisturbed quadrats. These values were considered too low for meaningful statistical analysis.

Prescribed Burning

Contrary to expectations, burning caused a significant decline in *P. clutei* density, dropping from an average of 6.5 plants per plot before burning to 1.6 plants per plot at the end of the first growing season after the fire, a 75 percent reduction (Table 1). Season of burning (fall/spring) and site elevation (low/high) were not significant factors. *P. clutei* densities also declined over the study period in two of the three control sites. The low-elevation fall control declined by 53 percent and the low-elevation spring control declined by 75 percent between 1994-95 and 1998. Only the high-elevation fall control maintained a nearly constant *P. clutei* density (2% decline). Coupled with a recovery of *P. clutei* densities in the burned plots, *P. clutei* densities in burned and control plots differed by less than 1 plant per plot by 1998, averaging 2.1 and 3.0 plants, respectively. Litter (total of freshly fallen as well as decomposing material) declined significantly in the burned plots, with an average reduction of 2.0 cm, and the litter depth remained constant through 1998. Species richness was not significantly affected by the burning treatment. Plant community ordinations indicated minor shifts between treatments and years. Burn treatment plots tended to group together by year, whereas control plots were generally clustered.

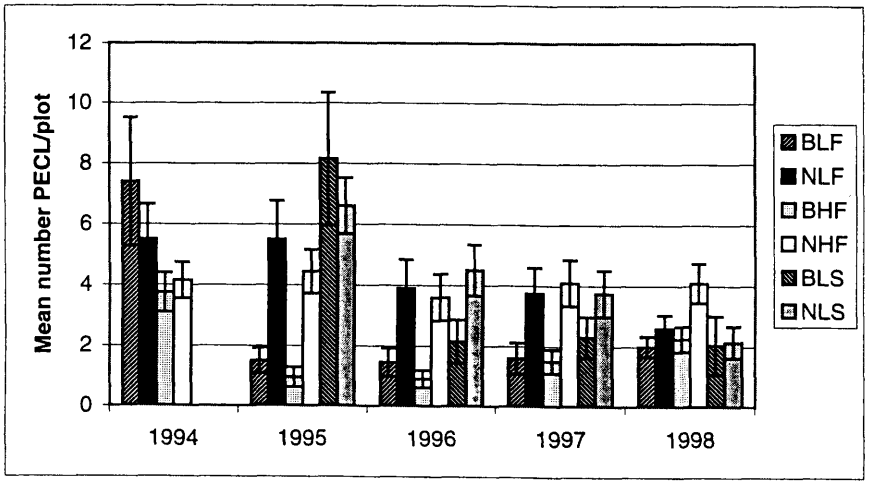


Figure 2. Changes in burn and control plots from 1994 through 1998. B = burn, N = no-burn (control), L = low elevation, H = high elevation, F = fall burning season (September 1994), S = spring burning season (April 1995). Standard error bars shown.

Table 1. Density of *P. clutei* (PECL, number per 19.6 sq m plot), species richness, litter depth, and woody fuel. N = 20 in each category, N/A = not available. Data shown are mean, (standard error), and min-max. The pretreatment year (Year 1) was 1994 for the fall burn and 1995 for the spring burn, so the fall burn sites have 5 years of data (1994–1998) whereas the spring burn sites have 4 years of data (1995–1998).

	Pretreatment (Year 1)	Year 2	Year 3	Year 4	Year 5
Low-Elevation Fall Burn					
PECL density	7.4 (2.1) 1-34	1.5 (0.4) 0-6	1.5 (0.5) 0-8	1.6 (0.5) 0-8	2.0 (0.3) 0-5
Spp. richness	6.1 (0.4) 3-10	4.6 (0.5) 2-9	8.0 (0.8) 3-14	7.5 (0.7) 3-14	6.4 (0.5) 2-10
Litter (cm)	2.6 (0.4) .6-6.2	0.9 (0.1) .1-2.0	0.9 (0.2) 0-3.2	0.6 (0.1) 0-2.1	1.0 (0.2) .1-2.7
Low-Elevation Fall Control					
PECL density	5.5 (1.2) 1-22	5.5 (1.3) 0-18	3.9 (1.0) 0-14	3.8 (0.8) 0-13	2.6 (0.4) 0-7
Spp. richness	6.2 (0.4) 2-9	4.9 (0.3) 1-8	7.7 (0.8) 3-12	7.7 (0.8) 0-13	6.7 (0.5) 2-10
Litter (cm)	2.9 (0.3) .8-6.4	2.6 (0.3) .7-5.8	2.5 (0.4) .5-5.8	1.9 (0.3) .2-5.1	2.0 (0.3) .3-5.6
High-Elevation Fall Burn					
PECL density	3.8 (0.7) 1-12	1.0 (0.3) 0-6	0.9 (0.3) 0-5	1.5 (0.4) 0-7	2.3 (0.4) 0-7
Spp. richness	7.0 (0.5) 3-11	4.6 (0.4) 0-7	8.5 (0.8) 0-15	8.8 (0.7) 1-13	7.8 (0.7) 0-11
Litter (cm)	2.6 (0.5) .4-8.2	0.6 (0.1) .1-1.6	0.6 (0.1) .1-1.5	0.5 (0.1) .2-1.2	0.4 (0.1) 0-1.7
High-Elevation Fall Control					
PECL density	4.2 (0.6) 1-11	4.5 (0.7) 1-12	3.6 (0.8) 0-14	4.1 (0.8) 0-13	4.1 (0.6) 0-9
Spp. richness	7.6 (0.4) 5-12	6.2 (0.3) 4-8	9.3 (0.8) 4-16	9.1 (0.9) 4-15	7.8 (0.5) 3-12
Litter (cm)	3.2 (0.4) .4-6.7	2.6 (0.3) .8-6.7	3.4 (0.6) .6-8.8	2.6 (0.4) .7-6.1	2.2 (0.4) .2-5.4
Low-Elevation Spring Burn					
PECL density	8.2 (2.2) 1-36	2.2 (0.7) 0-13	2.3 (0.7) 0-11	2.1 (1.0) 0-15	N/A
Spp. richness	N/A	7.7 (0.7) 2-15	7.4 (0.6) 4-14	5.8 (0.5) 2-10	
Litter (cm)	2.3 (0.4) .2-6.3	0.6 (0.1) 0-1.7	0.6 (0.1) 0-1.5	0.5 (0.1) 0-1.7	
High-Elevation Spring Control					
PECL density	6.6 (0.9) 1-14	4.5 (0.8) 1-16	3.8 (0.8) 0-14	2.2 (0.5) 0-8	N/A
Spp. richness	N/A	6.3 (0.6) 1-11	6.5 (0.6) 2-11	4.8 (0.5) 1-8	
Litter (cm)	2.6 (0.4) .5-6.8	2.0 (0.3) .6-5.5	1.7 (0.3) .4-5.7	1.9 (0.4) .2-7.4	

Removing annual species from the analysis eliminated differences in treatment patterns, suggesting that the shifts were related to annual climatic variation (Table 2). Indicator species for the burn and control treatments are identified in Table 3.

Belowground Competition

P. clutei density in the eight trenched plots (average 7.9 plants per plot) was higher than that of the eight nearest control plots (3.4 plants per plot) even prior to treatment in 1997, but the difference was not statistically significant (Figure 3). By 1998, the trenched *P. clutei* density averaged 8 plants but the control density dropped to 2.5 plants, a significant difference. In 1999, *P. clutei* densities increased sharply in both trenched and control plots, but the rise was much steeper in the treated plots (104.9 plants) than the controls (14.0 plants). The monsoon season in 1999 was the wettest of the 1992–2000 study period, with 37.2 cm of precipitation from June through September (Table 2). The 1999 monsoon also comprised the highest proportion (78%) of annual precipitation during the study period. In 2000, a dry year, *P. clutei* densities declined to an average of 30.6 plants in the trenched plots and only 1.5 plants in the controls. No notable *P. clutei* increase occurred on the disturbed trench areas outside the plots. Community ordination indicated a minor separation between the trenched and control plots, but with considerable overlap. Indicator species for trenched plots are shown in Table 1.

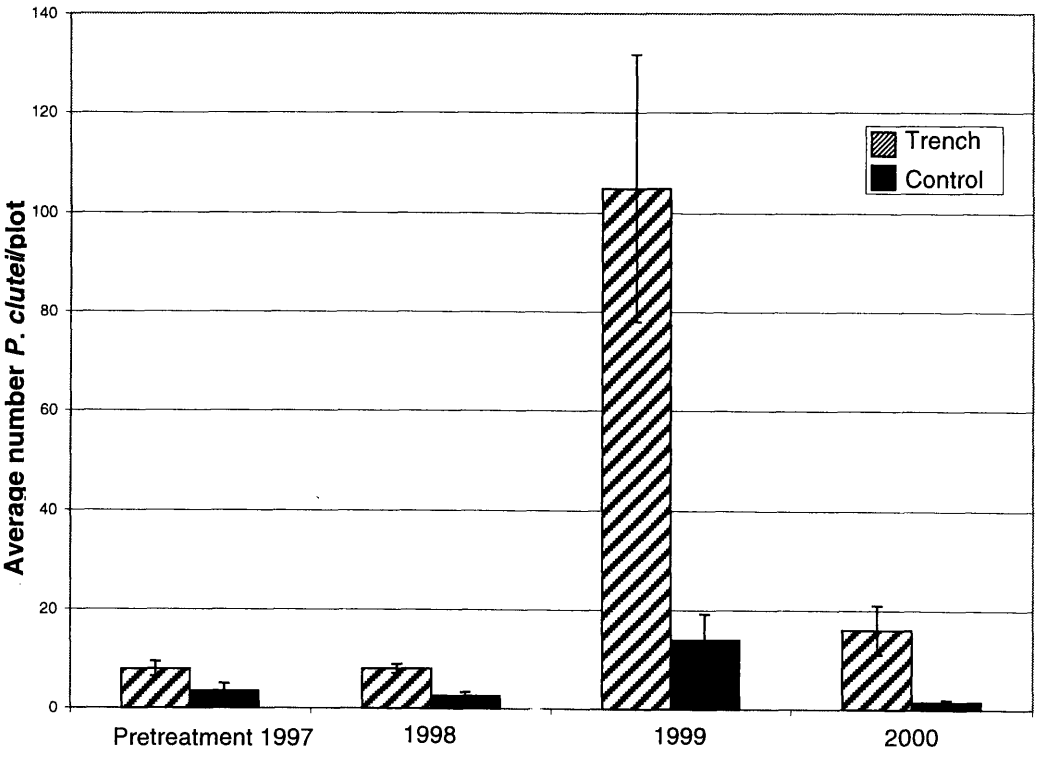


Figure 3. *P. clutei* density increased substantially in 1999—a year with excellent growing season moisture—in both trenched and control plots, but the increase in the trenched plots was eight times greater than in the controls. *P. clutei* densities declined sharply in 2000, a dry year, but trenched densities remained significantly higher than controls.

Discussion

The reasons why *P. clutei* is sparsely distributed in nature were not completely clarified by this set of studies. *P. clutei* germinated readily with moisture under lab conditions with little or no innate dormancy necessary. Increasing periods of stratification, in fact, decreased germination, contrary to the experience of Plants of the Southwest (Santa Fe, New Mexico). These germination characteristics are adaptive in light of the fact that warm, moist soils are typically present during the monsoon season (late June through September) in the Sunset Crater area and that we have observed most seedling regeneration to occur in the monsoon season, rather than the spring. However, in contrast to the high lab germination rates, field establishment of the species on seeded quadrats was dismal (0.4%). The long-term demographic data (1993–2000) from the burning and trenching control plots also show a general decline in *P. clutei* numbers over time, and no counteracting increase in *P. clutei* density was observed outside the permanent plots. Variability in germination among seed lots collected at different dates and elevations suggests that genetic or environmental factors may influence germination.

Trenching was the only experimental treatment that resulted in highly significant increases in *P. clutei* density, but our approach had many limitations due to the small scale of the experiment (N = 16). The control plots started out with a lower average density than the trenched plots and we did not quantify differences in soil moisture, physiological processes, plant vigor, biomass, flowering, pollination, seed production, viability, predation, soil seed bank, or plant herbivory.

Table 2. Annual and monsoonal (June–September) precipitation at Sunset Crater National Monument from 1992 through 1999. Data from National Climatic Data Center, Asheville, NC.

	1992	1993	1994	1995	1996	1997	1998	1999
Annual (cm)	66.0	47.0	41.1	29.5	32.3	51.8	47.3	47.4
June–Sept (cm)	18.2	12.8	23.1	11.6	21.6	26.7	25.2	37.2

Table 3. Species found in burning and trenching experiments. Species found on burn plots only are shown with *, species found on trench plots only are shown with **. Species identified as strong and significant treatment indicators, based on relative abundance and relative frequency, are shown with the indicator value (maximum 100) and p value.

Family	Species	Indicator burn	Indicator control	Indicator trench
Burn	Indicator			
Control	Indicator trench			
Amaranthaceae	*Amaranthus albus*			
Asclepiadaceae	*Asclepias subverticillata*			
Asteraceae	*Agoseris* sp.**			
	*Artemisia dracunculus**			
	Bahia dissecta			
	Brickellia chlorolepis			
	Brickellia grandiflora			
	Chrysothamnus nauseousus			
	*Cirsium wheeleri**			
	Conyza schiedeana			
	Erigeron sp.			
	*Helianthus petiolaris***			
	*Heterosperma pinnata**			
	Hieracium fendleri			
	Lactuca serriola			
	*Machaeranthera canescens***			
	*Senecio spartioides**			
	Solidago sp.**			
	Tragopogon dubius			
Berberidaceae	*Berberis fremontii**			
Brassicaceae	*Arabis fendleri*			
	Physaria newberryi			
	Schoencrambe linearifolia		30.0 / .02	
Cactaceae	*Opuntia* sp.*			
Caryophyllaceae	*Drymaria leptophylla***			
Chenopodiaceae	*Chenopodium album**			
	*Chenopodium desiccatum**			
	Chenopodium graveolens			
Commelinaceae	*Commelina dianthifolia*			
Euphorbiaceae	*Chamaesyce revoluta*			
	Chamaesyce serpyllifolia			
	Euphorbia albomarginata			
	Euphoriba lurida			
Fabaceae	*Phaseolus angustissimus*			
Fumiariaceae	*Corydalis aurea***			
Geraniaceae	*Geranium caespitosum*			54.3 / .006
Grossulariaceae	*Ribes cereum*			
Hydrophyllaceae	*Nama dichotomum*			
	Phacelia crenulata			
Lamiaceae	*Monardella odoratissima*			
Loasaceae	*Mentzelia collomiae*			
Molluginaceae	*Molluga cerviana*			
Nyctaginaceae	*Mirabilis decipiens*	29.3 / .004		
	Mirabilis linearis			

Table 3 (continued)

Family	Species	Indicator burn	Indicator control	Indicator trench
Onagraceae	*Oenothera caespitosum*			
Pinaceae	*Pinus edulis***			
	Pinus ponderosa			
Poaceae	*Aristida arizonica**			
	*Bouteloua gracilis**			
	Elymus elymoides			
	Muhlenbergia minutissima			
	Muhlenbergia montana			
	*Poa fendleriana**			
	Stipa comata			
Polemoniaceae	*Ipomopsis arizonica**			
Rosaceae	*Fallugia paradoxa*			
Rubiaceae	*Galium wrightii**			
Scrophulariaceae	*Linaria dalmatica*			
	Verbascum thapsus			
	Penstemon barbatus			
	Penstemon clutei		57.6 / .001	85.7 / .001
Solanaceae	*Physalis hederifolia*			

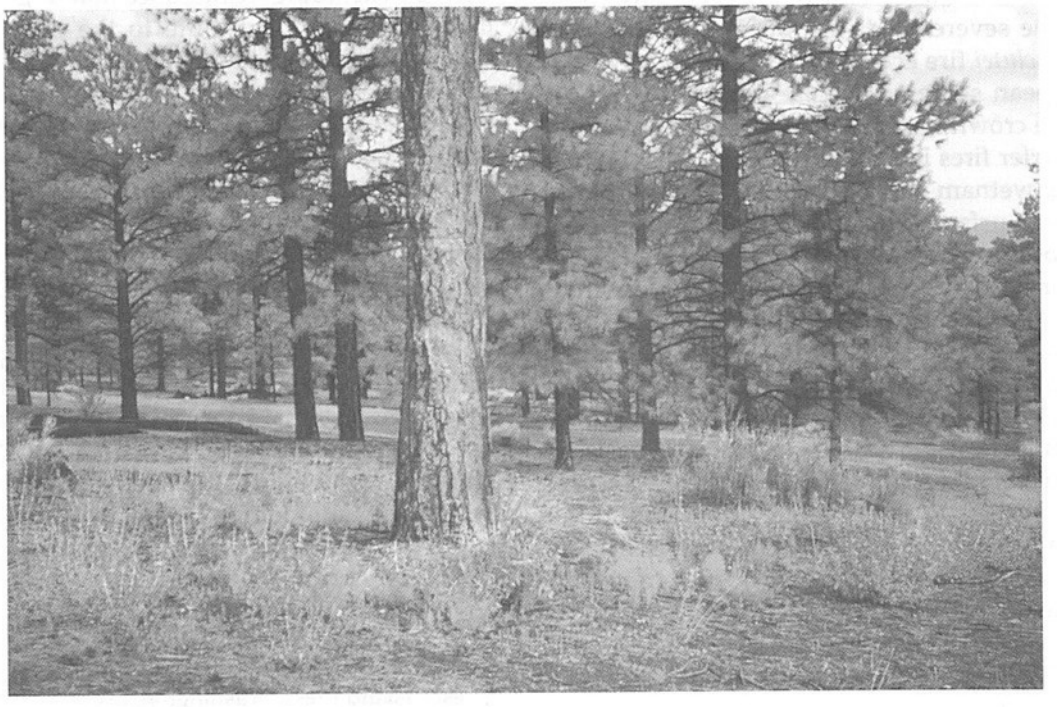


Figure 4. Vigorous *P. clutei* plants growing around the base of a mature ponderosa pine tree that died around 1997–1998 in the lower elevation study area (photo Oct. 1999). This example of *P. clutei* response to the removal of tree competition may be a natural analog to the effects of the trenching experiment.

Therefore the mechanisms underlying the increase remain uncertain and further research will be useful. The trenching process itself and the plastic liner may have affected plot hydrology apart from simply cutting root competition, but the effect may have been just as likely to keep water out as to keep it in. Three preliminary conclusions were drawn from the trenching study: (a) cutting root competition has a significant positive effect on *P. clutei* reproduction, (b) the trenching effect was more pronounced in a year with favorable climate (1999) but was also evident in a less-favorable year (1998) and was sustained into a dry year (2000), and (c) root competition appears to be much more important for *P. clutei* response than light competition, consistent with the results reported by Riegel et al. (1995). We did not manipulate the light environment, but still had a highly significant population increase.

Although prescribed burning decreased *P. clutei* density, contrary to the initial research hypothesis, the historic role of fire in the ponderosa pine ecosystem may not have been adequately simulated in our experiment. The prescribed fires were of low intensity and did not kill any trees, unlike the severe wildfires that led to questions about *P. clutei* fire ecology in the first place. Prior to European settlement there is no evidence for extensive crown fires at the scale of the Burnt and Hochderrfer fires in southwestern ponderosa pine forests (Swetnam and Baisan 1996). But naturally occurring surface fires in relatively undisrupted ponderosa and related forests do create patchy tree mortality at scales ranging from individual trees to a few hectares (Fulé and Covington 1997, Fulé et al., unpublished data). These patches of fire-caused mortality and other tree deaths from windthrow, insects, pathogens, or lightning may have comprised important disturbance patterns that facilitated *P. clutei* regeneration. Figure 4 shows vigorous *P. clutei* regeneration around the base of a recently deceased mature ponderosa pine tree, possibly a natural analog to the trenching experiment.

Management Recommendations

The high year-to-year variability in *P. clutei* densities and the general trend in the control plots toward declining *P. clutei* density are issues of concern for sustaining this rare species. Results from this study and others (Goodwin 1979, Phillips et al. 1992, Crisp 1996) support a positive relationship between *P. clutei* abundance and disturbance, within certain parameters.

Low-intensity surface fire alone appears unlikely to benefit *P. clutei*, although there are other valuable reasons for burning in the forest environment. However, more intense prescribed fires that kill some trees or a combination of thinning trees and burning may be promising treatments that could facilitate *P. clutei* regeneration and simultaneously meet other ecosystem management goals, such as restoring historic forest structure and fire disturbance regimes. Other methods of simply killing overstory trees, such as snag creation through cutting cambium or inducing insect attack, may also benefit *P. clutei* regeneration.

Even severe ground disturbance may create environments that benefit *P. clutei* vigor and reproduction. Many *P. clutei* plants observed on the Transwestern pipeline and on roadcuts were among the most vigorous in the region. However, repeated physical impacts that destroy established plants, such as off-road vehicle use in the Cinder Hills, appear to reduce *P. clutei* populations.

The management of a rare species that is adapted to disturbance is difficult because "protection" by excluding disturbance that might damage the plants may contribute to the decline of the species. The Coconino National Forest has had a proactive management policy of encouraging experimentation and monitoring of the species. Further management-level experiments focusing on restoration of historic disturbance patterns and understanding the mechanisms of *P. clutei* response would be valuable.

Acknowledgments

We thank Sandy Nagiller, Barb Phillips, Linda Farnsworth, Allen Farnsworth, and Peter Gordon (Coconino National Forest), Joyce Maschinski (The Arboretum at Flagstaff), Graydon Bell (Northern Arizona University), M. Lacey-Theisen (USDA Systematic Entomology Laboratory), and students and staff of the Ecological Restoration Institute (Northern Arizona University).

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Pollination Ecology of the Rare Orchid, *Spiranthes diluvialis*: Implications for Conservation

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Abstract: We examined the pollination ecology of *Spiranthes diluvialis* Sheviak, Ute ladies-tresses, a federally listed, threatened orchid species known only from small, isolated populations in the western United States. The pollinator composition, male and female reproductive success, and demography of *S. diluvialis* populations were examined in 1995, 1997, and 1999. *Spiranthes diluvialis* sets fruit only when visited by pollinators and observations indicate that native bees, predominantly bumblebees (*Bombus* spp.), are the most important pollinators. Comparisons of male and female reproductive success were made between populations and years. Significant declines in fruit production and pollinia removal that occurred in 1999 in the Diamond Fork population may be related to changes in pollinator composition. Significant increases in fruit production were recorded in the Brown's Park population, an area in which native pollinators were released in 1999. Management plans to conserve this threatened orchid must provide for the pollinators, their nesting habitat, and pollen-producing plants (*S. diluvialis* provides no pollen to pollinators). We identified important pollen sources for pollinators in the Diamond Fork population and supplied several types of semi-natural nesting materials to promote nesting by *Anthophora terminalis*, another species thought to be an important pollinator. Successful preservation of this threatened orchid requires a community-level conservation plan.

Evolutionary ecologists have hypothesized that as an outcrossing common plant species becomes rare, its attraction to pollinators and its dependence on conspecifics for sexual reproduction also declines (Tepedino 1979, Kruckeberg and Rabinowitz 1985). Such rare species are expected to be characterized by high levels of self-compatibility, autogamy, and possibly even agamospermy (Tepedino 1979). However, recent studies of the reproductive biology and pollinator composition of more than two dozen rare plant species in the western United States (Tepedino 2000) have provided compelling evidence that rare plant species are as dependent upon pollinators as common plants are, and that native bees are their primary pollinators.

Spiranthes diluvialis (Orchidaceae), a federally listed, threatened orchid species known only from small, isolated riparian populations in the western United States, provides a unique opportunity to examine such questions about rare plant pollination ecology. The floral morphology, presence of pollinia, and lack of pollen rewards for insect visitors combine to facilitate studies of pollination. Flowers of *S. diluvialis* are arranged spirally on a single spike, with flowering commencing at the bottommost flower and proceeding upward sequentially. Like most orchid species, *S. diluvialis* flowers have male and female parts fused into a column, with the stigmatic surface on the ventral side of the column and the single anther containing pollinia (packages of pollen) on the dorsal side. Each flower has a pollinarium composed of two joined pollinia attached to a viscidium, which when touched releases a sticky substance that promotes its removal. The large size of the pollinarium makes removal easy to census. Pollinia are bright yellow and can be detected on an insect's body from up to 2 m away (Sheviak 1984, Sipes 1995).

Previous studies of *S. diluvialis* have shown it to depend upon insect pollinators for sexual reproduction (Sipes and Tepedino 1995). Flowers are neither autogamous nor agamospermous. Primary pollinators are bumblebees (*Bombus* spp.) and solitary bees of the genus *Anthophora*, which carry the pollinia glued to their mouthparts, which they incidentally pick up while foraging for nectar (Sipes and Tepedino 1995). Of these species, *A. terminalis* Cresson was shown in 1995 to be a more effective pollinator than other insect visitors (Sipes and Tepedino 1995): Fruit production in areas where

A. terminalis was present displayed a three-fold increase over areas where it was absent.

All bee species have high nutritional and energetic needs. Adults primarily use nectar as fuel, but they collect pollen and nectar to feed their progeny. Because *S. diluvialis* offers only nectar as a reward to its pollinators, bees must visit other flowering species to collect pollen. These supplementary pollen sources must be identified to encourage their continued presence in *S. diluvialis* habitat.

In addition to pollen and nectar, bees require particular kinds of nesting materials in a matrix of appropriate habitat. Bees in general use a range of nesting habitats, but the behavior of individual species is quite stereotypical. The nesting requirements for important pollinators of *S. diluvialis* must be determined to enhance management efforts to augment nest sites as well as to support pollinator transplantation. Preservation of habitat for pollinator nesting is vital to the preservation of *S. diluvialis*.

Our objectives were (1) to further survey the insect species that pollinate *S. diluvialis* in Diamond Fork Canyon, Utah and to compare these with pollinators observed in previous studies (Sipes and Tepedino 1995, Kuta et al. 1997); (2) to compare the efficiency of pollinators observed visiting *S. diluvialis*; (3) to determine the primary pollen source for *A. terminalis* and other important pollinators; (4) to describe patterns of male and female reproductive success as measured by pollinia removal and fruit set; and (5) to characterize the nesting requirements for pollinators of *S. diluvialis* and to determine if semi-natural habitats and nesting materials can be tailored to promote nesting of these pollinators.

Methods

The main study area was located in Diamond Fork Canyon, Utah County, Utah, where 36 colonies of *S. diluvialis* occur along the Diamond Fork River. In July of 1999 we selected colonies 1, 14, 21, and 35 for most of our experiments (Figure 1). These sites were selected because of population sizes and accessibility, and because they allowed comparison with results from Sipes and Tepedino (1995) and Kuta et al. (1997). Colonies 4, 9, 15, and 25 were also visited to obtain estimates of final reproductive success. Two additional visits were made to the Brown's Park population located on Forest Service (USDA) land along the Green River in Daggett County (see Figure 1).

We analyzed the data on two spatial scales. First, data from Diamond Fork colonies were pooled for comparison with Brown's Park. Second, data from the Diamond Fork colonies were compared among demes.

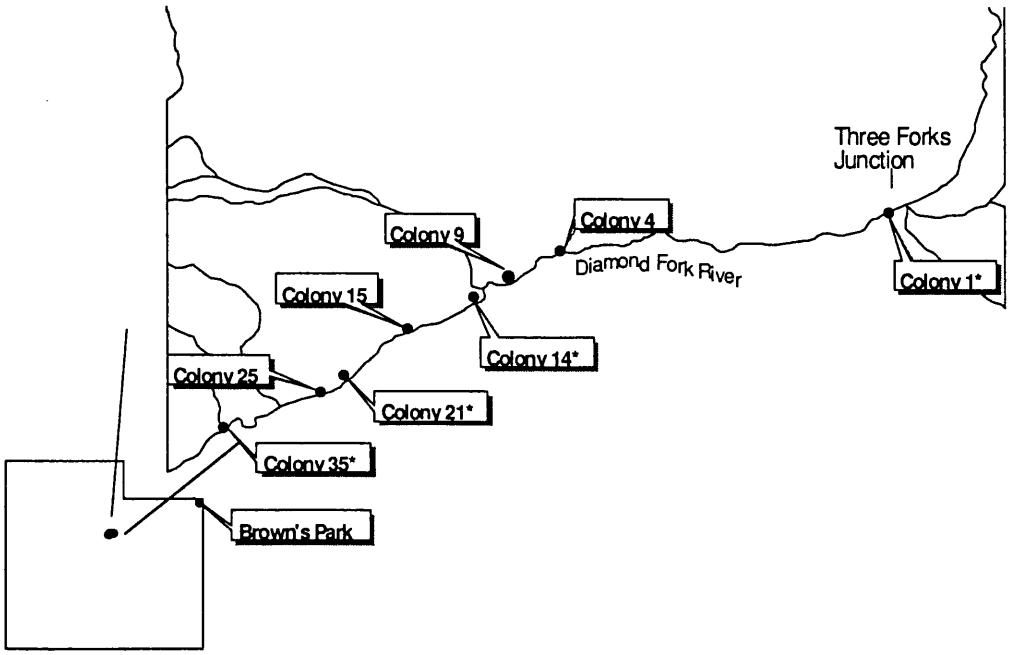


Figure 1. Distribution of *Spiranthes diluvialis* colonies in Diamond Fork Canyon and Brown's Park, Utah. Colonies used in pollination observation studies and reproductive trend studies indicated by an asterisk.

Pollinator Observation and Collection

Observations of floral visitors to *S. diluvialis* were made in colonies 1, 14, 21, and 35 throughout the flowering season. To estimate insect visitation rates and to determine pollinator species, we observed large patches of flowering *S. diluvialis* individuals for several 30-minute intervals daily between 0700 and 1800 hours. During observation intervals we recorded the taxon of the visitor (when possible), its foraging behavior on the inflorescence (acropetal or non-acropetal movement), the number of inflorescences visited, and whether or not the visitor carried pollinia of *S. diluvialis*. Several specimens of each taxon observed visiting *S. diluvialis* were collected for mounting and identification.

To test for the incidence of night pollination, 10 *S. diluvialis* individuals were marked and caged prior to floral bud initiation. Plants were caged during the day (dawn until dusk) and uncovered in the evening for the duration of flowering. Flowers were examined each morning for pollinia removal and pollen deposition. Plants remained caged for several weeks following these experiments to allow fruit development.

Comparison of Pollen Sources

A pollen reference collection was prepared by collecting pollen from all co-blooming plant species in colonies 1, 14, 21, and 35. Pollen from each species was stained on microscope slides with basic fuchsin gel (Beattie 1971).

Potential pollen sources for *S. diluvialis* pollinators were sampled by capturing insects visiting flowers of contemporaneously blooming plant species during scheduled intervals, and dabbing their bodies with a fuchsin-infused cube of gelatin that was then melted onto a microscope slide. Several transects were made through each slide, and pollen was identified and counted by comparison with the reference collection.

Nesting Requirements

We compared the efficacy of three types of semi-natural nesting materials in promoting the establishment of *A. terminalis*. Cut lengths of *Populus angustifolia* James logs (120 cm in length, 25 cm in diameter) were used to simulate downed wood. Twenty-five holes (15 cm deep, 8 mm diameter) were drilled in each end of the log. Elderberry twigs (*Sambucus* sp.) drilled with 8 mm diameter holes were used in short bundles (6 twigs per bundle, 15 cm in length) and as solitary uprights (45 cm in length). Open areas and ecotone areas (defined as the junction of open and wooded areas) were selected for placement of materials. Five logs were placed in each selected colony (two in the open, three in the ecotone). Elderberry bundles were attached with heavy gauge wire to shrubbery in the ecotone and to upright sticks in the open where they were placed along transects at 5 m intervals. Single upright elderberry twigs were driven approximately 10 cm into the ground and placed along transects at 10 m intervals beginning in the open and continuing through the ecotone. Nesting materials were placed in colonies 1, 14, 21, and 35 in Diamond Fork Canyon and at the Brown's Park population.

All semi-natural nesting materials were collected following the completion of the *S. diluvialis* flowering season. All nesting materials except the logs were x-rayed to examine the nesting inhabitants.

Anthophora terminalis individuals found nesting in elderberry twigs in 1998 were released in the bundles at the Brown's Park population. These individuals were collected from the Brown's Park population in 1998 and were returned to the population in 1999.

Reproductive Success and Trends

The final reproductive success of individuals from colonies 1, 4, 9, 14, 15, 21, 25, and 35 was measured during the height of fruit set (September 13–23, 1999). To randomly select *S. diluvialis* individuals, a transect tape was placed through the colony and the closest individual to each meter mark was identified (Sipes and Tepedino 1995, Kuta et al. 1997). For each individual, we recorded the following information: the height of the inflorescence, the number of flowers per inflorescence, the presence or absence of pollinia for each flower, the production of fruit, the gender of those flowers that remained open, and the distances to the three nearest blooming conspecific neighbors. Final male and female reproductive success can be measured because floral parts and unremoved pollinia persist during fruit production.

The Brown's Park population was visited during the fruiting stage of *S. diluvialis* (Sept. 25, 1999). A transect was placed through the center of the colony and individuals were selected as above. We recorded inflorescence height, number of flowers, fruit set, pollinia removal, and the distance to the three nearest conspecific neighbors.

The number of flowers per inflorescence, inflorescence height, percent fruit set, and percent

pollinia removal were compared between the Diamond Fork colonies and the Brown's Park population for 1995 (Sipes and Tepedino 1995), 1997 (Kuta et al. 1997), and 1999 by using the Kruskal-Wallis non-parametric comparison (PROC NPAR1WAY, SAS Institute 1999). Data from the Diamond Fork colonies were pooled for comparisons between populations and years. The Diamond Fork data were also analyzed separately by colony to compare reproductive trends between colonies and between years (PROC NPAR1WAY, SAS Institute 1999). When significant differences between years occurred, post hoc Wilcoxon tests for unequal variances were used to explore these differences (PROC, NPAR1WAY WILCOXON, SAS Institute 1999).

Regression analyses (PROC REG, SAS Institute 1999) were used to determine if fruit set or pollinia removal were related to inflorescence height, number of flowers per inflorescence, or nearest neighbor distance. Data from the Diamond Fork colonies were pooled to compare years. These Diamond Fork data were also analyzed separately by colony to compare reproductive trends between colonies and between years. We used paired t-tests to test the null hypothesis that percent fruit set equaled percent pollinia removal within populations and colonies (PROC TTEST, SAS Institute 1999).

Results

Pollinator Observation and Collection

As in prior studies (Sipes and Tepedino 1995, Kuta et al. 1997), visitors to the flowers of *S. diluvialis* were seldom observed (Table 1). In more than 43 hours of survey, only 54 insects were seen visiting *S. diluvialis* flowers. Most visits were between 0900 and 1600 hours and the mean visitation rate for all visitors pooled was 0.41 (± 0.65 std dev) visits per plant per hour, and 2.86 (± 4.11 std dev) visits per plant per day.

Previously in Diamond Fork Canyon, Sipes and Tepedino (1995) found *A. terminalis* to be the most abundant and efficient pollinator of *S. diluvialis*. They also recorded *A. bomboides* and *A. urbana* as visitors. In 1999, however, we observed only two *Anthophora* individuals (both *A. terminalis*) within the entire Diamond Fork population. As in other years and at other *S. diluvialis* populations, we found bumblebees (*Bombus* spp., Table 1) to be the most abundant pollinators (Sipes and Tepedino 1995). Of these, *B. griseocollis* appeared to be the most abundant pollinator of *S. diluvialis*. We also found much higher visitation by honeybees, *Apis mellifera*, than in previous years.

Table 1. Insect visitors of *Spiranthes diluvialis* in 1999. All observations are from Diamond Fork Canyon.

Taxon	No. of observ.	Pollinia carried	Foraged bottom-up
Hymenoptera			
Anthophora terminalis	2	yes (2)	yes (2)
Apis mellifera	13	yes (6)	yes (3)
Bombus appositus	2	yes (1)	yes (1)
Bombus griseocollis	12	yes (6)	yes (6)
Bombus bifarius	3	yes (3)	yes (2)
Bombus rufocinctus	3	yes (2)	yes (2)
Bombus occidentalis	2	yes (1)	yes (1)
Colletes sp.	1	no	no
Halictus sp.	1	no	no
Osmia sp.	1	no	yes (1)
Vespula maculata	2	no	no
Vespula sp.	1	no	no
Lepidoptera			
Unidentified skipper	1	no	no
Diptera			
Syrphidae	4	no	no

Insects were scored for acropetal foraging behavior, number of conspecifics visited after first perceived *S. diluvialis* visit, and the presence or absence of pollinia on the mouthparts. The two *A. terminalis* individuals, all *Bombus* spp., and some honeybees carried pollinia and foraged acropetally, indicating that they were accomplishing cross-pollination (Table 1). Other insect visitors at Diamond Fork did not pollinate the flowers (Table 1). Among these were unidentified wasps, syrphid flies, one *Osmia* bee species, halictid bees, and a butterfly. During these visits, nectar appeared to be appropriated without pollination.

Bumblebees exhibited greater fidelity to *S. diluvialis* flowers than did honeybees. On average, bumblebees visited 4.83 (± 2.58) successive *S. diluvialis* spikes until visiting a co-blooming species; honeybees visited an average of 2.25 (± 1.38) spikes. This difference was significant ($t = 3.03$, $df = 15$, $p < 0.01$).

The number of pollinia on bee bodies was also compared between bumblebees (mean = 1.55) and honeybees (mean = 1.50). No significant difference was observed ($t = 0.13$, $df = 10$, $p = 0.44$).

We collected 21 specimens of the insect species visiting *S. diluvialis* (relatively few were collected to minimize the impact on pollinators). Although none of these specimens had full pollen loads when collected, we were able to sample small

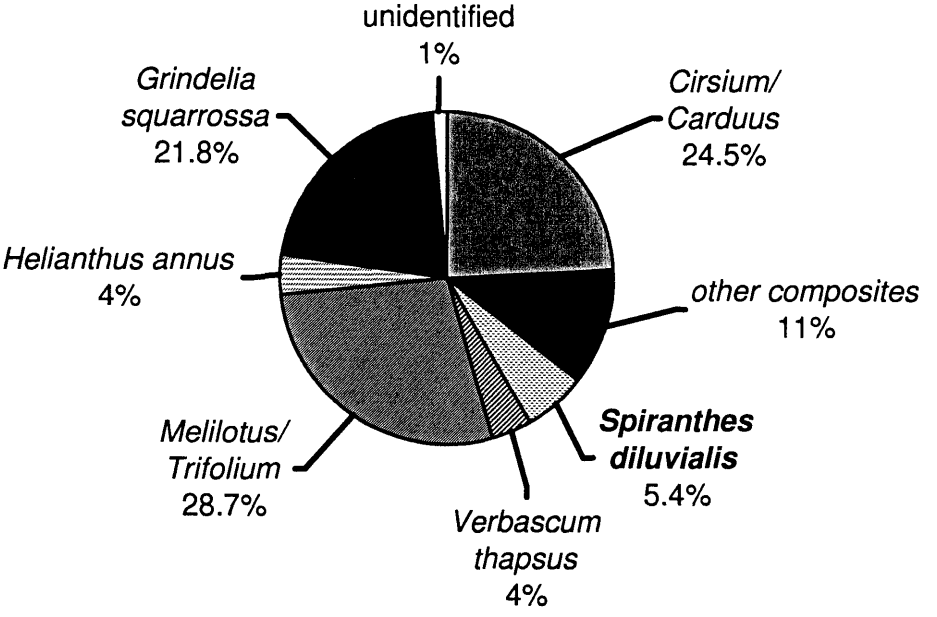


Figure 2. Identity of pollen grains from all *Spiranthes diluvialis* visitors (n = 21).

amounts of the pollen they carried. Figure 2 summarizes the average pollen load from all flower visitors of *S. diluvialis*. Most of the pollen from these bees was from *Cirsium/Carduus* (24.5%), *Melilotus/Trifolium* (21.7%), and *Grindelia squarrosa* (21.8%). Loose pollen grains from *S. diluvialis* were found on most bees. The average percent of *S. diluvialis* pollen carried was much less in 1999 (5.4%) than in 1995 (15.9%).

Nocturnal Pollination

No incidence of night pollination was observed. No pollinia were removed from the flowers of individuals uncaged at night, nor was any visible pollen observed on their stigmata. To test for the possible presence of unseen pollen, plants remained caged for several weeks following this experiment, but no fruits developed. Thus, *S. diluvialis* is not being visited on a regular schedule by nocturnal pollinators.

Comparison of Pollen Sources

The co-flowering species most abundant in *S. diluvialis* populations included *Aster hesperius, Carduus nutans, Cirsium arvense, Cirsium vulgare, Grindelia squarrosa, Helianthus annus, Melilotus officinalis, Solidago occidentalis,* and *Verbascum thapsus*. Several small flowered species were also locally abundant but may not have provided the copious amounts of pollen required by many bee species. These species included *Gayophytum diffusum, Descurania sophia, Sisyrinchium idahoensis,* and *Veronica anagallis-aquatica*. In total, we identified 31 native species and 20 exotics.

We observed these plant species to determine which were used for pollen by *Anthophora*, bumblebees, honeybees, and other insect visitors. Table 2 summarizes the co-occurring species visited by *S. diluvialis* pollinators. Not all *S. diluvialis* pollinators were observed on surrounding vegetation.

Table 2. Pollen sources for insect visitors of *Spiranthes diluvialis* in 1999. All observations are from Diamond Fork Canyon. Exotic species denoted by an asterisk.

Taxon	No. of Observ.	Additional Species Visited
Apis mellifera	15	*Aster hesperius, Grindelia squarrossa, *Carduus nutans, *Cirsium arvensis, *Medicago sativa, *Gutierrezia sarothrae*
Bombus appositus	3	**Carduus nutans, *Cirsium arvense, *Cirsium vulgare*
Bombus griseocollis	9	*Aster hesperius, Carduus nutans, *Cirsium arvense, Prunella vulgaris, Helianthus anuus, Grindelia squarrossa, *Melilotus officinalis*
Bombus bifarius	3	**Cirsium arvense, *Carduus nutans*
Bombus rufocinctus	1	**Melilotus officinalis, *Carduus nutans*
Bombus occidentalis	1	**Carduus nutans, *Cirsium arvense*

Nesting Requirements

Despite the diversity of semi-natural nesting materials employed at Diamond Fork Canyon to attract *A. terminalis* and other bees, few nests were made. Indeed *A. terminalis* produced only one nest, in an elderberry upright in the ecotone, and it contained only two very unhealthy looking cells. In general, elderberry uprights and bundles were not much used in either population. The use of nesting material by *A. terminalis* was higher at Brown's Park, where one elderberry upright (9 cells) and one twig bundle (4 cells) were obtained. In contrast, many nests were constructed in logs by the bees *Megachile pugnata, M. inermis,* and *M. relativa,* and *Isodontia* and other unidentified wasps. Unfortunately, none of these species were pollinators of *S. diluvialis.*

Reproductive Success and Trends

Patterns of reproductive success convey important information about the population dynamics of both Diamond Fork and Brown's Park populations of *S. diluvialis.* Female reproductive success, as measured by percent fruit set, was significantly greater in the Diamond Fork population than at Brown's Park in all years measured (Table 3, Figure 3; Sipes and Tepedino 1995, Kuta et al. 1997). Within the Diamond Fork population, percent fruit set varied significantly among years (Table 3). A significant increase in percent fruit was observed between 1995 and 1997 (Wilcoxon $Z = 3.92$, $p < 0.0001$), but this was followed by a significant decrease in 1999 (Wilcoxon $Z = 4.89$, $p < 0.0001$ from 1995 to 1999 and Wilcoxon $Z = 7.28$, $p < 0.0001$ from 1997 to 1999). An opposite trend was observed for Brown's Park, where percent fruit set increased significantly from critically low levels to an encouraging 27.7 percent in 1999 (Wilcoxon $Z = 5.35$, $p < 0.0001$ from 1995 to 1999 and Wilcoxon $Z = -3.56$, $p < 0.001$ for 1997 to 1999).

Male reproductive success, measured by percent pollinia removed per inflorescence, had patterns of variation between years and populations that were similar to fruit set (Table 3). As with fruit set, the percent pollinia removed was significantly greater in the Diamond Fork population than in Brown's Park in all years measured (Table 3, Figure 3; Sipes and Tepedino 1995, Kuta et al. 1997). Within Diamond Fork, the percent of pollinia removed varied between years (Table 3) with a significant decrease in 1999 (Wilcoxon $Z = 4.73$, $p < 0.0001$ from 1995 to 1999 and Wilcoxon $Z = 5.06$, $p < 0.0001$ from 1997 to 1999). In contrast, the percent of pollinia removed within Brown's Park did not significantly differ between years (Table 3).

Across-year trends similar to those found for the Diamond Fork population were also found within the individual colonies between years. Significant declines in percent fruit set were found for all colonies ($p < 0.01$ for all) except colony 21.

Table 3. Comparisons of reproductive and morphological data for *Spiranthes diluvialis* collected in 1995, 1997, and 1999 at the Diamond Fork and Brown's Park populations (Sipes and Tepedino 1995, Kuta et al. 1997). Data in bold indicate a significant difference among years (Kruskal-Wallis non-parametric comparison). Means with the same superscript are not significantly different (Wilcoxon $p > 0.10$). Means with different superscripts are significantly different ($p < 0.01$).

	Brown's Park				Diamond Fork			
Character	1995	1997	1999	p	1995	1997	1999	p
Flowers per inflorescence	12.9 (5.2)^a	14.2 (5.0)^a	15.1 (5.8)^a	0.10	19.1 (7.1)^a	18.6 (7.3)^a	19.6 (5.8)^a	0.30
Height of inflorescence	22.9 (6.3)^a	21.5 (5.42)^a	29.5 (7.8)^b	**< 0.001**	25.8 (7.5)^a	30.1 (7.3)^b	33.3 (9.2)^c	**< 0.001**
Percent fruit set	0.03 (0.10)^a	0.07 (0.12)^b	0.27 (0.23)^c	**< 0.001**	0.75 (0.20)^a	0.83 (0.21)^b	0.61 (0.22)^c	**< 0.001**
Percent pollinia removed	0.17 (0.16)^a	0.16 (0.18)^a	0.18 (0.14)^a	0.40	0.55 (0.24)^a	0.58 (0.27)^a	0.40 (0.21)^b	**< 0.001**
Avg distance to 3 nearest neighbors (cm)	102.7 (71.3)^a	79.7 (40.6)^a	128.9 (156)^a	0.60	167 (183)^a	94.8 (67.03)^b	93.2 (87.9)^b	**< 0.001**

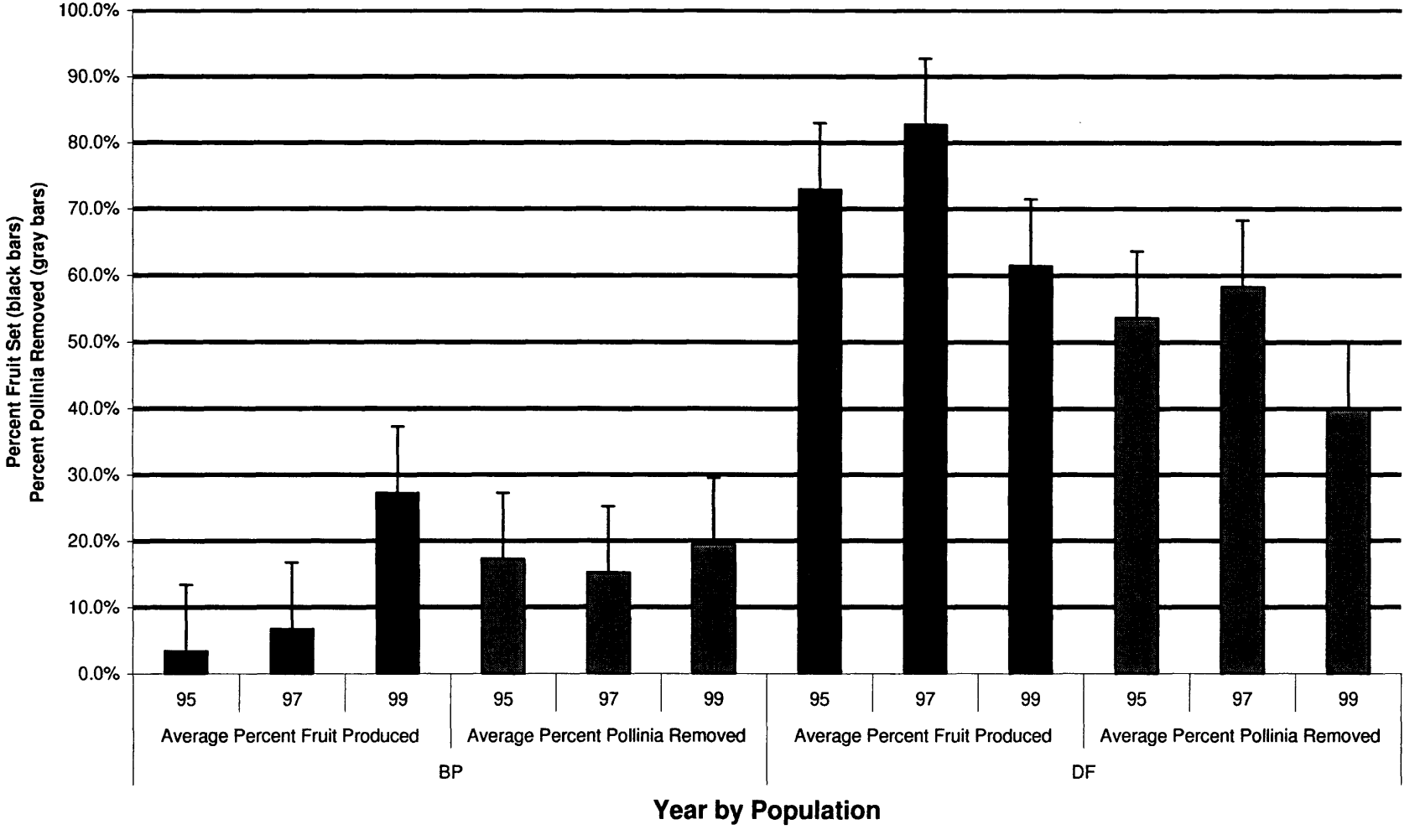


Figure 3. Comparison of percent fruit set and pollinia removal for *Spiranthes diluvialis* individuals in 1995, 1997, and 1999 in Diamond Fork and Brown's Park populations.

Percent of pollinia removal per inflorescence was also significantly lower at individual colonies in 1999 (Pierson and Tepedino 2000).

As observed in previous years (Sipes and Tepedino 1995, Kuta et al. 1997), we found a positive relationship between the number of fruits per plant and the number of flowers produced for both populations in 1999. The relationship at Diamond Fork was strong ($R^2 = 0.54$, $p < 0.0001$). It was weaker at Brown's Park ($R^2 = 0.33$, $p < 0.001$), but was still much higher than that recorded in 1995 ($R^2 = 0.09$; Sipes and Tepedino 1995). Significant, positive relationships between the number of fruits and the number of flowers were found for colonies 15, 21, 25, and 35 ($p < 0.01$ for all), but not for colonies 1, 4, 14, and 15 ($p > 0.10$).

A positive relationship between number of pollinia removed and number of flowers per inflorescence was found for the entire Diamond Fork population ($R^2 = 0.32$, $p < 0.001$) and for colony 25 in Diamond Fork ($R^2 = 0.61$, $p < 0.0001$), but not for any of the others. This relationship was not significant for Brown's Park ($p = 0.23$).

Perhaps more interesting, pollinia removal appeared to be at least partially decoupled from fruit set. At both Brown's Park and Diamond Fork populations, mean percent fruit set was significantly higher than mean percent pollinia removal per inflorescence (Brown's Park $t = 2.78$, $df = 23$, $p < 0.01$; Diamond Fork $t = 12.87$, $df = 203$, $p < 0.0001$). Comparisons were statistically significant ($p < 0.001$) for all colonies within Diamond Fork as well. These findings are important because they suggest that each pollinia fertilizes, on average, more than one fruit. This is possible because whole pollinia are not inserted onto a *S. diluvialis* stigmata; rather, grains of pollen are brushed off the pollinia and deposited individually.

We compared the density of populations at Diamond Fork and Brown's Park by measuring distances from focal plants to the three nearest neighbors. No significant difference was found between Diamond Fork and Brown's Park populations (Table 3; Wilcoxon $Z = 1.25$, $df = 1$, $p = 0.20$). However, the average distance to the three nearest conspecific neighbors did differ significantly among the colonies of Diamond Fork (ranging from 56.20 cm to 158.35 cm, Kruskal-Wallis $df = 7$, $p < 0.0001$). We found no evidence that mean distance to the nearest neighbor influenced the mean percent of fruit produced. Comparisons between Brown's Park and Diamond Fork populations, as well as among the Diamond Fork colonies, yielded no statistically significant relationships ($p < 0.10$ for all).

Insect visitation and reproductive success are often thought to be positively related to the size and density of the floral display (Heinrich 1979, Schemske 1980, Rodriguez-Robles et al. 1992). Thus, factors such as inflorescence height, floral density (as measured by distance to nearest neighbor), and number of flowers per inflorescence may increase plant attractiveness. These variables were measured in 1999 from Brown's Park and Diamond Fork populations to determine if they were significantly correlated with the percent fruit produced or pollinia removed per inflorescence. No significant correlations between percent pollinia removed per inflorescence with height, distance to nearest neighbor, or number of flowers per inflorescence were found for Diamond Fork or Brown's Park (all comparisons $p > 0.10$). It is therefore unlikely that the size of the inflorescence and the close proximity of conspecific neighbors influenced the number of pollinator visits.

Discussion

Pollinator Visitation

The diversity and abundance of pollinators of *S. diluvialis* appears to fluctuate between populations and years. Bumblebees (*Bombus* spp.) were found to be the most important pollinators for both the Diamond Fork and Brown's Park populations in 1991 and 1992 (Sipes 1995, Sipes and Tepedino 1995), but in 1995 *A. terminalis* was most abundant and likely the most efficient pollinator for the Diamond Fork population (Sipes et al. 1996).

In 1999, only two *Anthophora* individuals (both *A. terminalis*) were seen visiting the flowers of *S. diluvialis*, whereas a variety of other pollinator taxa, such as bumblebees (*Bombus* spp.), honeybees (*Apis mellifera*), solitary bees, syrphid flies (Syrphidae), and wasps (*Vespula* spp.), were observed visiting these flowers (Table 1). Of the these, only bumblebees and honeybees appeared to serve as pollen vectors. The occurrence of such large fluctuations in native bee populations is well known (Bohart and Knowlton 1953, Tepedino and Stanton 1980, 1981), though the reasons for such changes are not well understood.

Bumblebees have been shown to be among the most important pollinators of *Spiranthes* in several other studies (Ames 1921, Luer 1975, Catling 1983, Larsen and Larson 1990, Sipes and Tepedino 1995).

Of the several species observed visiting *S. diluvialis* in 1999, *B. griseocollis* (Degeer) appeared to be the most efficient pollinator at Diamond Fork. Although *B. griseocollis* carried no more pollinia or pollen on their bodies than did other species, individuals consecutively visited significantly more *S. diluvialis* spikes than did honeybees, and therefore were likely responsible for a greater number of pollinations. In contrast, honeybees may waste pollinia in deposition on non-orchid hosts because they more commonly switch from *S. diluvialis* to other flower species. Thus, honeybees are unreliable as primary pollinators of *S. diluvialis*, although they could be valuable as supplementary pollinators when native pollinators are scarce.

The two visits to the Brown's Park population provided insufficient time to identify pollinators in 1999. The significant increase in fruit production in 1999 may have been the result of many factors. Among those, an increase in pollinator abundance or diversity is the most intriguing possibility. Efforts to transplant individuals of *A. terminalis* into Brown's Park should continue and should be augmented by attempts to build up bumblebee populations by providing nest boxes.

Nesting Requirements

Anthophora terminalis used few of the artificial nesting materials provided at Diamond Fork, undoubtedly because of its low abundance. Low numbers may have been due to excessive overwinter mortality or perhaps to a previously unsuspected life cycle, common to some species, that requires 2 years to complete (Torchio and Tepedino 1982). The poor success observed in 1999 should not hinder future attempts at pollinator augmentation or transplantation into this isolated population. Given a better year, nest recruitment of *A. terminalis* could be much higher: such nesting material has been heavily used by *A. terminalis* in the past in Grand Teton National Park (Parker and Tepedino, unpublished report). Research efforts should detail the success of *A. terminalis* within this population and also attempt to confirm its role in fruit set. These findings could then be utilized to design transplantation efforts in larger populations such as at Diamond Fork. Future efforts should also attempt to attract a wider range of native pollinators, especially bumblebees.

Reproductive Success and Trends

The reproductive success of *S. diluvialis* fluctuates greatly between populations, between demes within populations, and between years (Table 3; Pierson and Tepedino 2000). A significant overall decline in percent fruit set was observed for Diamond Fork in 1999 (Table 3, Figure 3) compared with 1995 and 1997 (Sipes and Tepedino 1995, Kuta et al. 1997). The percent of pollinia removed at Diamond Fork also declined significantly (Table 3, $p < 0.001$) in 1999 compared with previous years (Figure 3; Sipes and Tepedino 1995, Kuta et al. 1997). As in previous years, percent fruit set significantly exceeded percent pollinia removed at Diamond Fork (Figure 3), indicating that pollen from each pollinia is reaching more than one flower (Sipes and Tepedino 1995, Kuta et al. 1997).

Previously, Sipes and Tepedino (1995) hypothesized that the abundance of *A. terminalis* was responsible for the high fruit set observed in Diamond Fork in 1995. If *A. terminalis* does play such an important role in the pollination of *S. diluvialis*, then its virtual absence in 1999 might help explain why fruit set was significantly lower that year than in 1995 and 1997. The overall reduction in male reproductive success (lower percent pollinia removal) could further suggest that the pollinators observed in 1999 may either prefer the flowers of other plants more than those of *S. diluvialis*, or be less efficient at pollinating *S. diluvialis* flowers than those observed in 1995. At this point, we know only that *A. terminalis* shares its role as an important pollinator with bumblebees.

An opposite and encouraging trend for reproductive success was observed for Brown's Park, where a three-fold increase in fruit set was recorded from 1997 to 1999 (Kuta et al. 1997; Figure 3). Fruit set in 1999 was also dramatically greater than the dismal 3.3 percent recorded in 1995 ($df = 1$, $p < 0.0001$; Sipes and Tepedino 1995), although it fell short of the 37 percent recorded for this population in 1991 (Sipes 1995).

Surprisingly, the increase in percent fruit set was not accompanied by an increase in the percent pollinia removed, which did not differ between the years investigated ($df = 2$, $p = 0.40$, Table 3, Figure 3). Again, percent pollinia removed was significantly lower than percent fruit set ($p < 0.0001$), solidifying the finding that pollinia commonly pollinate more than one flower if moved by effective pollinators. The program to monitor reproductive success at Brown's Park should be continued so that we may judge our progress toward augmenting this population.

Not unlike previous years, the factor that may be limiting reproduction by *Spiranthes diluvialis* at

Diamond Fork is herbivory by voles (Sipes and Tepedino 1995, Sipes et al. 1996, Kuta et al. 1997, Black personal communication, Pierson and Bowlin personal observation). Herbivory by voles has also been reported in the *S. diluvialis* population in Boulder, Colorado, where *Microtis* sp. were primarily responsible for inflorescence destruction. In 1999, voles damaged inflorescences in most colonies and their runways were obvious. Voles tunneled under wire and mesh exclosures to attack protected inflorescences. Future studies should estimate vole population size and the impact of vole herbivory on the reproductive and vegetative success of *S. diluvialis*.

Implications for Conservation

To successfully conserve the existing populations of *S. diluvialis*, a community-based management plan is essential. Given the dependence of *S. diluvialis* on pollinators for sexual reproduction (Sipes and Tepedino 1995), an appropriate management plan must provide for the overall preservation of pollinating species and must incorporate their nutritional, provisional, and nesting needs. Understanding the biology of these species is vital to their preservation as well as to the continued conservation of *S. diluvialis*. Many efforts can be made to encourage the establishment of such bees within the ecosystem.

As outlined in Sipes and Tepedino (1995), the long activity period of bumblebees (spring to early autumn), renders their populations vulnerable to management decisions throughout the growing season. Populations of bumblebees are annual with only the young mated queens produced in late summer–early fall capable of overwintering or hibernation. The production of entire new colonies the following year is dependent upon the survival of these queens over winter. In spring, these queens will forage until the first progeny reach workerhood (Michener 1974, Alford 1975). The application of insecticides during these foraging and mating periods could prevent formation of entire colonies and could also jeopardize the health of a colony. Workers can become vectors of contaminated nectar or pollen. Because bumblebees can forage great distances (up to 3 miles), insecticide applications must be prohibited over distances much greater than the mandated 500 foot buffer around water courses.

Conservation of native pollinators not only requires minimizing the potential detrimental effects of management but also requires promoting and preserving the factors critical to their survival. By providing for the nesting requirements and nutritional needs of these bee species, maintenance of native pollinators is possible.

The nesting and foraging requirements of the pollinators of *S. diluvialis* are varied. *Bombus griseocollis* prefers to nest in dry aboveground locations such as downed logs, abandoned sheds, or farm buildings (Eshelman and Plowright 1972), whereas other species (*B. appositus, B. rufocinctus,* and *B. bifarius*) typically nest in belowground burrows or in abandoned rodent nests (Medler and Carney 1963, Hobbs 1965, 1966). *Bombus occidentalis* prefers to nest in open west-southwest slopes bordered by poplar trees and sites connected to the surface with downward-sloping tunnels (Hobbs 1968). These species are often attracted to legumes such as *Melilotus, Medicago,* and *Trifolium,* and members of the Asteraceae including *Solidago* and *Aster* (Plath 1927, Medler and Carney 1963, Hobbs 1965, 1966).

Because the pollinators of *S. diluvialis* appear to fluctuate from year to year and site to site, a larger scale conservation plan to preserve and encourage the establishment of all native pollinators would be extremely beneficial. Efforts to encourage the establishment of *A. terminalis* should be continued. Nesting sites such as logs, snags, shrubs, and downed wood should be encouraged rather than disturbed. Augmenting populations with such nesting material may also prove beneficial to the populations of *A. terminalis*. Bumblebees should be encouraged to establish or colonize areas surrounding the *S. diluvialis* populations. Subterranean nesting boxes that have been designed to promote ground-nesting bumblebees (Alford 1975) could be employed in the more mesic areas surrounding *Spiranthes* colonies. Additional nest-building material such as cotton batting, dried moss, or old bird nests could be provided to encourage colonization by such species. Bumblebees have also been observed nesting at ground level when large accumulations of dried moss or fine grass are available (Alford 1975).

Although *B. morrisoni* and *B. fervidus* were not observed visiting the flowers of *S. diluvialis* in 1999, their importance as pollinators has been noted previously (Sipes 1995, Sipes and Tepedino 1995). Conservation efforts should incorporate the needs of these pollinators as well. Recommendations for increasing successful nesting and preservation of these species are outlined in Sipes and Tepedino (1995).

In addition to providing for the nesting requirements of these native pollinators, manage-

ment plans must consider the importance of co-occurring vegetation. Pollinators cannot use *S. diluvialis* pollen and must therefore seek their pollen elsewhere. We have provided a list of specific pollen resources (Table 2) used by *S. diluvialis* visitors. Many of the pollinators of *S. diluvialis* currently appear to depend upon the pollen of non-native vegetation for survival, and managers should not seek to eradicate these species without parallel efforts to return native vegetation to the area.

A detailed list of native entomophilous vegetation usable in revegetation efforts and to support populations of native pollinators is provided in Table 4. Of these, members of the mint family (Lamiaceae) and figwort family (Scrophulariaceae) are attractive to bees (*A. terminalis* and many *Bombus* spp.) and are also valuable for revegetation. Plants should be spaced to promote wide pollinator movement and foraging throughout the entire flowering region. Finally, plants selected for revegetation efforts should flower not only when *S. diluvialis* does, but throughout the growing season to promote long-lived populations of native pollinators.

Table 4. Native entomophilus plant species useful for revegetation efforts.

Species	Family	Flowering time
Allium sp.	Liliaceae	Early spring
Aster spp.	Asteraceae	Late sum–fall
Linum perenne L.	Linaceae	Spring
Gutierrezia sarothrae Pursh	Asteraceae	Late sum–fall
Helianthella uniflora	Asteraceae	Mid-late sum
Helianthus annus L.	Asteraceae	Late sum–fall
Heterotheca villosa (Pursh) Shinn	Asteraceae	Mid sum
Mentha arvensis L.	Lamiaceae	Mid-late sum
Mertensia ciliata (James) G. Don	Boraginaceae	Spring
Monarda spp.	Lamiaceae	Spring–sum
Penstemon spp.	Scrophulariaceae	Variable
Penstemon palmeri Gray	Scrophulariaceae	Late spring
Polemonium spp.	Polemoniaceae	Variable
Polemonium viscosum Nutt.	Polemoniaceae	Mid summer
Prunella vulgaris L.	Lamiaceae	Mid summer
Rosa woodsii Lindl.	Rosaceae	Mid late sum
Salvia reflexa Hornem.	Lamiaceae	Mid summer
Scutellaria spp.	Lamiaceae	Mid-late sum
Senecio spp.	Asteraceae	Variable
Solidago spp.	Asteraceae	Variable
Stachys plaustris L.	Lamiaceae	Mid-summer

We hope that the foregoing has shown that conservation efforts for *S. diluvialis* must be designed and implemented at a community or ecosystem level to be successful. Healthy populations of *S. diluvialis* will be realized not simply by protecting riparian habitat; in addition, managers must be cognizant of the natural nesting habitat and floral needs of the bee pollinators that make reproduction and continued existence of this rare plant possible.

Acknowledgments

We thank the USDA Forest Service (Uinta National Forest) and the Central Utah Water Conservancy District for funding this study and the Uinta National Forest for camping accommodations and technical support. Also, we would like to thank the U.S. Fish and Wildlife Service for their cooperation and support. Assistance in the field was provided by S. Enright, K. Konen, and B. Bowlin. E. Klomps and J. L. Harris provided assistance in the lab. T. L Griswold, O. Messinger, and W. Hansen identified insect specimens.

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Seed Ecology of a Rare Sage, *Salvia dorrii* ssp. *mearnsii*

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Abstract: Although related taxa occur throughout the western United States, *Salvia dorrii* ssp. *mearnsii* is endemic to central Arizona. In part, its narrow distribution may be attributed to its limited fruit production, low seedling establishment, and germination requirements. Heavy herbivory pressures decreased the numbers of mature fruits in populations in two different vegetation zones and soil origins, desertscrub (limestone origin) and chaparrral (sandstone origin). The percentage of mature fruits was higher in populations from soils of limestone origin in desertscrub vegetation than from soils of sandstone origin in chaparral vegetation. Little in situ evidence of seedling establishment was observed during three field seasons. Germination experiments were conducted to test the effects of water, soil origin, light, and scarification. Greenhouse results suggest that *Salvia dorrii* ssp. *mearnsii* has few restrictions for germination. This taxon does not appear to have complex dormancy mechanisms, as it germinated readily without scarification. Germination occurred independent of soil origin except that germination did not occur at all in potting soil. Excessive water and direct light appear to inhibit germination. Maximum germination occurred at low water levels.

During the life of a plant, there are critical phases of its development that have the potential to limit its "tolerance range for a particular factor in the environment" (Gates et al. 1951). Often the first susceptible phases in a plant's life history are seed germination and seedling establishment. These are influenced by many factors, including restriction to specific soils (Thompson 1981), dependence on certain amounts of precipitation (Thompson 1981, Kadmon 1993, Bowers 1994), season (Harper 1977, Thompson 1981), temperature (Meyer et al. 1997), competition (Hallmark and Allen 1975), inhibitory compounds (Hallmark and Allen 1975), genetics (Meyer et al. 1989, Cabin 1996), and the availability of "safe sites" where seeds can readily germinate (Thompson 1981).

Germination requirements of woody members of the genus *Salvia* vary widely. Love (1989) found that cool-moist stratification for 8 weeks allowed maximum germination of *Salvia dorrii*. *S. mellifera* seeds are fire-adapted and germinate only when exposed to charcoal (Keeley 1986). Without any prior treatment, seeds of *S. vermiculata* germinate at a rate of 70 percent and remain viable for 7 years of low-temperature storage (Kay et al. 1988). Seeds of *S. reflexa* germinate better in soils with low osmotic potential (Weerakeen and Levett 1986). Some species of *Salvia* require scarification, cold stratification, or gibberellin treatment to induce germination and break dormancy (Love 1989, Young and Young 1992).

Seed characteristics and germination requirements have not been previously investigated in *Salvia dorrii* ssp. *mearnsii*. Limited numbers of mature fruits, low seedling establishment, and specific germination requirements may restrict its distribution in central Arizona. This subspecies is a long-lived, perennial shrub that displays no evidence of vegetative reproduction and very few seedlings in its natural environment (personal observation). It is distributed in disjunct patches in central Arizona along the Verde River from Perkinsville to Camp Verde (Figure 1) and grows in limestone- and sandstone-based soils in three vegetative zones: pinon-juniper, chaparral, and desert grassland. Its distribution is restricted as a result of many factors but does not appear to be strictly constrained by soil characteristics.

The U.S. Forest Service lists *Salvia dorrii* ssp. *mearnsii* as a sensitive species because of this limited distribution and threats to its survival. The rapid development of the Verde Valley potentially threatens the plant and its habitat. If not protected, *S. dorrii* ssp. *mearnsii* may not persist in nature. Specific activities that threaten this taxon are mining, land trades, and other development projects.

Several questions are addressed here: Does herbivory affect fruit production in *Salvia dorrii* ssp. *mearnsii*? Is fruit production of *S. dorrii* ssp. *mearnsii* different in plants from different soil origins? Is germination of this subspecies affected by soil origin, watering level, or light availibility? Knowledge of the germination requirements will aid in the conservation of this rare sage.

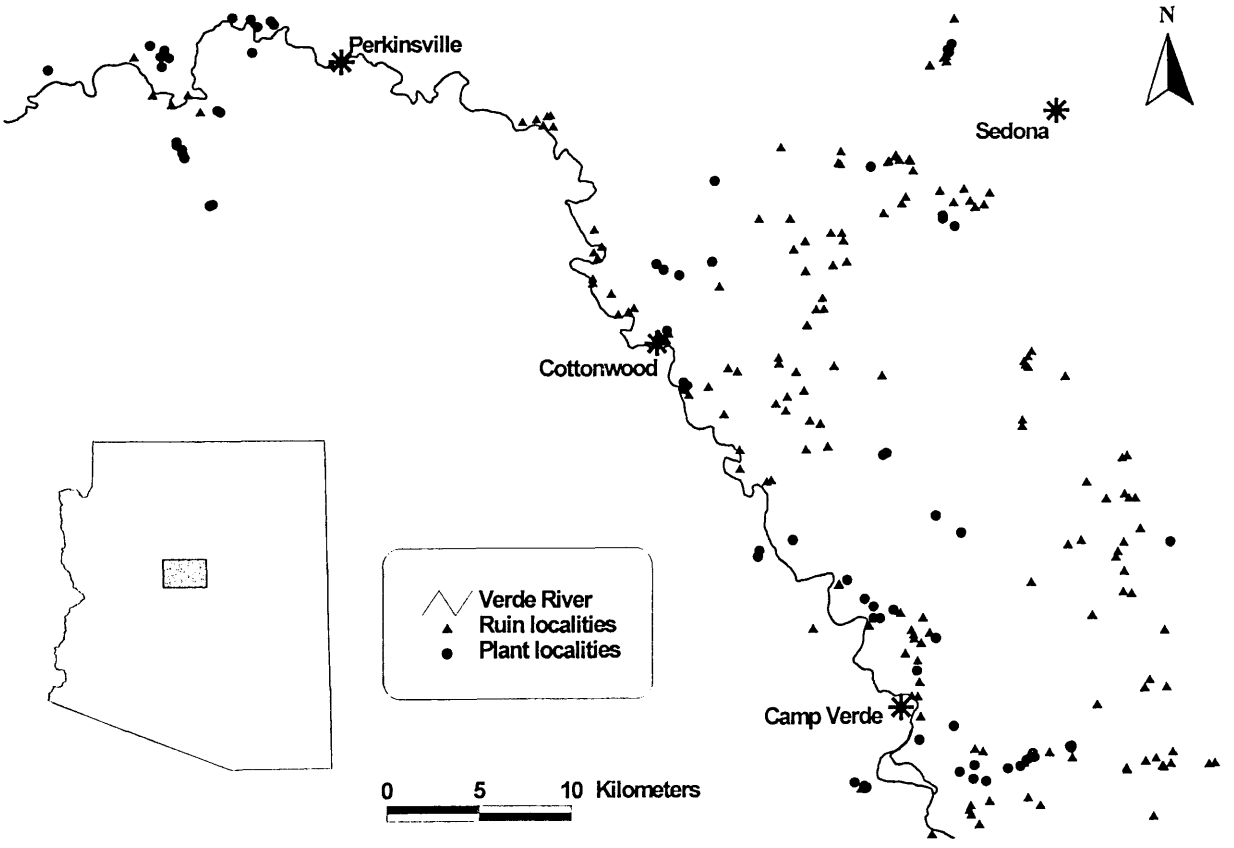


Figure 1. Distribution of *Salvia dorrii* ssp. *mearnsii* in the study area. Inset is study area on Arizona map.

Distribution and Taxonomy

Salvia dorrii ssp. *mearnsii* is one of two subspecies in the *Salvia dorrii* complex. *Salvia dorrii* ssp. *mearnsii* is geographically isolated from *S. dorrii* (Kellogg) Abrams ssp. *dorrii* (Strachan 1982). It is also morphologically distinct from *S. dorrii* ssp. *dorrii* due to its reduced stature (15–30 cm vs. 10–50 cm), narrow leaves (1.5–3 mm wide vs. 6–10 mm wide), and low number of verticels per branchlet (1–3 vs. 2–5). *Salvia dorrii* ssp. *mearnsii* is limited to central Arizona whereas the other subspecies, *S. dorrii* ssp. *dorrii*, and its varieties, var. *dorrii*, var. *clokeyi* Strachan, var. *carnosa* (Douglas ex Greene) Cronq., and var. *pilosa* (A. Gray) Strachan and Reveal, are widespread throughout the western United States and into Mexico. *Salvia pachyphylla* Epling ex Munz is closely related as well, occurring in disjunct populations in northern Arizona and Baja California. Current molecular genetics studies (Robin Taylor, unpublished data) will aid in the interpretation of the phylogenetic relationships between members of the *Salvia dorrii* complex and *S. pachyphylla*.

Geological History and Site Specificity

The Verde Valley is a northwest-trending basin that was formed by movement along the Verde fault (Cassell 1980, Nations 1981). Depositional environments in this basin led to the development of the Verde Formation, named by Jenkins (1923) because of its many limestone, sand, clay, and saline sediments.

Many of the known populations of *Salvia dorrii* ssp. *mearnsii* inhabit the eroded mesas and hills of the Verde Formation on substrates of limestone,

siltstone, and gypsum (Mahard 1949, Twenter and Metzger 1963, Cassell 1980, Nations 1981). These substrates are generally white to brown in color, hard in texture, relatively resistant to weathering, and composed of fine particles that form rough, hard conglomerations of limestone and clay. Other sedimentary substrates inhabited by *S. dorrii* ssp. *mearnsii* include iron-rich, coarse sandstones. Of the 48 known populations, 30 occur on the limestone deposits of the Camp Verde and Cottonwood regions, 4 populations inhabit the sandstone deposits near Sedona, and 14 populations occur in the Perkinsville area on interfacing soils of limestones, siltstones, and mudstones.

Plant Distribution Patterns

Although most of the Verde Valley is a depositional basin of limestones, siltstones, sandstones, basalts, and gravels, the distribution of *Salvia dorrii* ssp. *mearnsii* is limited to specific areas. At every site where the plant occurs, the population boundaries are distinct yet confounding. This subspecies is absent in adjacent areas that seem optimal. Some of the populations grow in close proximity to one another but have dramatically different soil characteristics (particle sizes, water holding capacities, and colors). The distribution of *S. dorrii* ssp. *mearnsii* cannot be completely explained by a certain chemical, physical, or biological element within these soils (Baskin and Baskin 1988).

Lacking fossil and pollen records for this subspecies, the paleodistribution of *Salvia dorrii* ssp. *mearnsii* cannot be pinpointed. According to J. Dale Nations (personal communication) and Carr (1986), there was no major structural change in the landscape of western Arizona after a drying trend (2–4 million years ago), which could have affected a continuous population of *Salvia* (Nations 1981). However, changing climatic conditions may have contributed to the isolation and evolution of *S. dorrii* ssp. *mearnsii*.

The closest relative of *Salvia dorrii* ssp. *mearnsii* is assumed to be *S. dorrii* ssp. *dorrii*. It grows in the mountains of western Arizona and California and may have extended into central Arizona in the past. Anderson (1986, 1996) noted that other basins of central Arizona similar to the Verde Valley exhibit similar floristic patterns (concentration of endemics, similar species, patchy distributions), indicating that major plant migrations have occurred across this range. Populations of plants could easily have been reproductively isolated due to climate change, causing speciation at the subspecies level (Mayr 1982, Grant 1981, Watts 1984, Price 1996).

Furthermore, palynological studies indicate that the paleoenvironment of Lake Verde consisted of many fluctuating pools of water from several inches to a few feet (Hevly 1974). This wetland environment supported reeds, rushes, cattails, and marshland algae. Surrounding this depositional basin were evergreens, low-growing shrubs, perennial herbs, and grasses (Hevly 1974). Aridland plants like *Salvia dorrii* ssp. *mearnsii* and other species similar to present-day plants inhabited the dryer slopes around Lake Verde during this time (Hevly 1974). As central Arizona slowly dried out 2–4 million years ago, this slope-upland vegetation likely colonized the lakebed deposits of the Verde basin (Dean Blinn and J. Dale Nations, personal communication) as it does today.

Materials and Methods

Herbivory and Fruit Production

To assess the impacts of floral herbivory and to ensure the collection of an adequate number of nutlets (one-seeded, indehiscent fruit) for germination experiments, inflorescences of *Salvia dorrii* ssp. *mearnsii* were wrapped with cheesecloth. When nutlets began maturing, the verticels were covered with cheesecloth and secured with twist ties. Some fruits had been damaged, so only inflorescences without evidence of herbivory were chosen. A second criterion for covering an inflorescence was the presence of at least five maturing nutlets. A total of 125 verticels were covered on plants from limestone soils and 159 were covered on plants from sandstone soils.

Mature nutlets were collected in mid June. An equal number of uncovered inflorescences were collected from the same plants for assessing herbivory. After analysis, potentially viable nutlets were stored in a refrigerator (4.5° C) for 90 days. In total, 604 viable nutlets from both covered and uncovered inflorescences were collected from plants growing in soils of limestone origin and 306 viable nutlets were collected from plants growing in soils of sandstone origin. Data from each site were pooled by soil origin, sandstone and limestone.

Chi-square tests were used to compare the numbers of mature and damaged fruits between covered and uncovered inflorescences. A mature fruit was classified as an ovary that was fertilized and swollen to some degree even if the seed inside was not fully mature and viable. An immature fruit was categorized as a fruit that collapsed

under pressure or one that had evidence of herbivory. These comparisons were conducted independently of soil type.

Soil and Fruit Production

The effects of soil origin on the floral and seed ecology of *Salvia dorrii* ssp. *mearnsii* were analyzed only for uncovered verticels. Analyzed values included the percentage of mature fruits and the percentage of fruits with evidence of herbivory (damaged). They were compared between plants from soils of different origins (sandstone and limestone) to determine if site characteristics (soil origin, elevation, temperature, precipitation) affected these variables.

Germination Experiments

Experiments were conducted to investigate how various factors affect germination in *Salvia dorrii* ssp. *mearnsii*. Greenhouse studies were conducted because it was not feasible to observe germination in the field. Soil and fruits collected from five distinct plant localities were used to test the effects of scarification, watering level, light availability, and soil origin on germination percentage.

Sample sizes were small because of the limited supply of fruits. Each treatment was allotted 36 fruits divided into 12 pots (3 inch, 250 cm^3) so that there were 3 fruits per pot (or petri dish). Closed petri dishes were used to assess the effects of scarification (eliminating other variables); the fruits were placed on wet, sterilized filter paper. All nutlets planted in soil were placed approximately 0.6 cm below the soil surface. The pots were stored in a greenhouse at 20–24° C (evening-day) and watered daily. When testing the effect of watering level, the low-water treatment pots received 10 ml of water each per day and the high-water treatment pots received 50 ml of water each per day. Fruits were placed on top of or 0.6 cm below the soil surface to test the effects of light availability, using 18 pots with 4 fruits each. When germination occurred (up to 32 days), tallies were taken. In the petri dishes, germination was determined to be successful when the cotyledons reached 0.6 cm long. Fruits that were planted in soil were considered germinated when the cotyledons appeared above the soil surface. Chi-square analyses were conducted using the total number of fruits germinated in all pots and means were used for the ANOVA comparisons. The data were not transformed.

Soil Analyses

Field moisture content and percent rock were assessed in soils of limestone and sandstone origin where *Salvia dorrii* ssp. *mearnsii* is located. Soil was collected to 8 inches deep three times throughout two field seasons. Due to the rocky nature of these soils, a shovel was used to collect the soil instead of a soil corer. Soils were weighed immediately after collection, dried for 5 days at 40.6° C, and reweighed to determine the field moisture content. The following equation was used to determine moisture for each sample: [(weight of soil before drying (g)) – (weight of soil after drying (g))/ (weight of soil before drying (g))] x 100. Percent rock was measured as athe percentage of soil weight that was occupied by particles greater than 4.75 mm. All soil was then stored at room temperature until used in germination experiments.

Results

Herbivory and Fruit Production

Herbivory negatively affected fruit production of *Salvia dorrii* ssp. *mearnsii*. Fruits from covered verticels had proportionally lower levels of herbivory (17%) than those from uncovered (64%) verticels (Chi square = 110.33, $p << 0.001$, Figure 2). The covered verticels also had a higher proportion of mature fruits (50%) than uncovered (35%) verticels (Chi square = 83.861, $p << 0.001$, Figure 3).

Soil and Fruit Production

The percentage of mature fruits was significantly different for plants from different soil origins and vegetation communities; however, herbivory was not significantly different. Plants from soils of sandstone origin in chaparral vegetation had 23 percent of fruits mature, whereas plants from soils of limestone origin in desertscrub vegetation had 43 percent of fruits mature (Chi square = 354.5, $p << 0.001$, Figure 4). Although not significantly different, the proportion of damaged fruit was 57 percent for plants from soils of limestone origin in desertscrub communities and 78 percent for plants from soils of sandstone origin in chaparral communities (Chi square = 2.537, $p > 0.05$).

Germination Experiments

Scarification did not significantly affect germination percentages of *Salvia dorrii* ssp. *mearnsii* fruits. Analyses were conducted independently of what type of soil origin in which the plants were

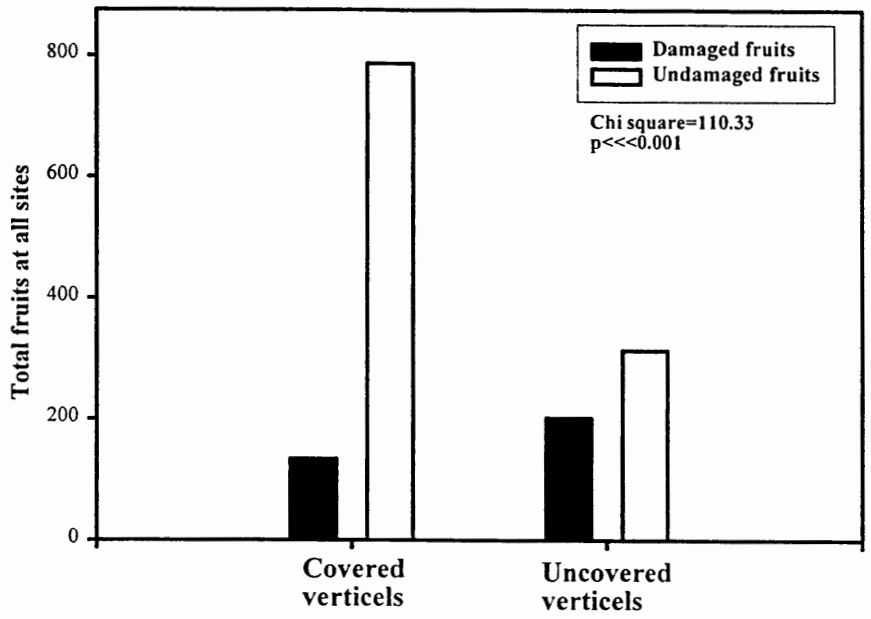


Figure 2. Herbivory negatively affects the fruits of *Salvia dorrii* ssp. *mearnsii*. Verticels that were covered with cheesecloth had significantly lower herbivory (17% of fruits damaged) than verticels that were not covered (64% of fruits damaged).

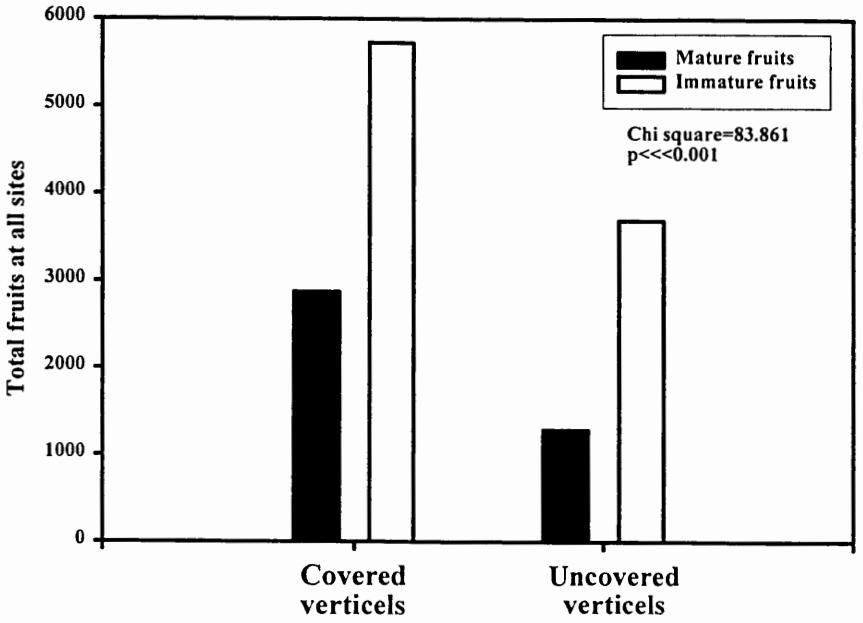


Figure 3. Fruit set in *Salvia dorrii* ssp. *mearnsii* plants was negatively affected by herbivory in all soil types. A significantly lower proportion of fruits matured in verticels that were uncovered than in those that were covered.

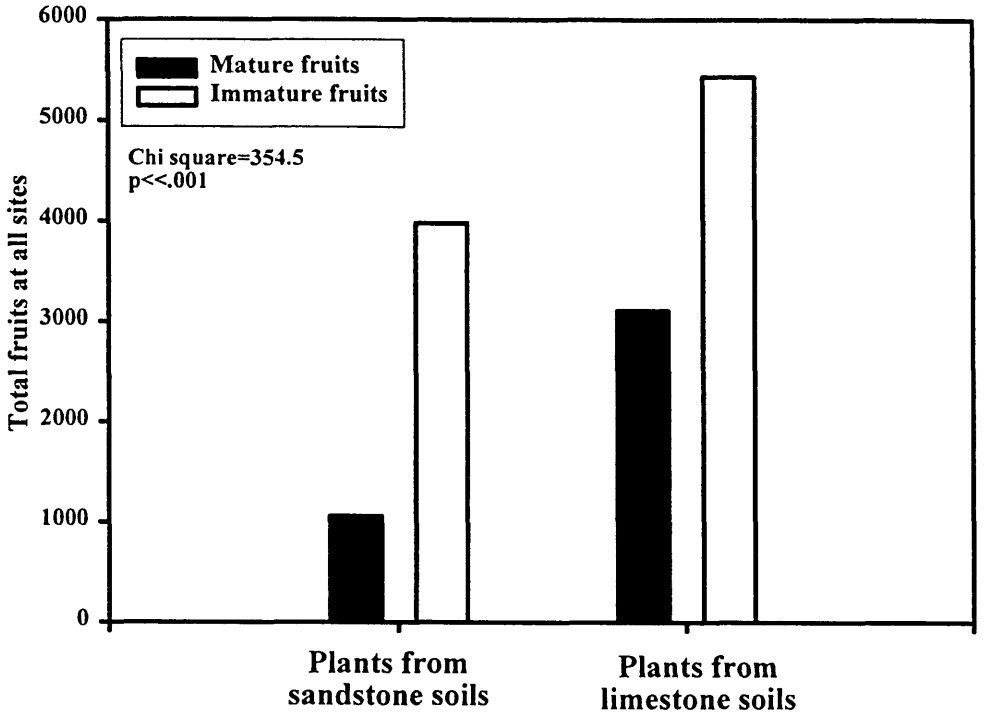


Figure 4. Fruit set varied on plants from different soil origins (limestone vs. sandstone). A significantly lower proportion of fruit was set in plants on soil of sandstone origin than plants on soil of limestone origin.

growing. Seventy-one percent of scarified fruits germinated and 66 percent of unscarified fruits germinated (Chi square = 0.1662, $p > 0.05$).

Regardless of scarification treatment, overall germination was maximized when conducted in petri dishes. Eighty-eight percent of fruits from plants in soils of sandstone origin germinated and 55 percent of fruits from plants in soils of limestone origin germinated. Chi-square analyses confirmed that these percentages were significantly different (Chi square = 12.261, $p << 0.001$).

Fruits in petri dishes had higher germination than fruits planted in soils. After 32 days, only 1 fruit of 72 from both types of soils germinated in a standard potting soil mix. When the fruits were planted in their native soils and watered heavily, fruits from sandstone soils in chaparral vegetation germinated less often (2.8%) than fruits from limestone soils in desertscrub vegetation (13.9%). Chi-square analyses indicated that planting fruits in native versus foreign soil did not affect germination percentages (Chi square = 0, $p > 0.1$). Chi-square analyses indicated that planting fruits in on-site soil versus off-site soil did not affect germination percentages (Chi square = 0, $p > 0.1$).

Soil origin and watering level significantly affected germination percentages. Fruits from plants in soils of limestone origin germinated at significantly higher percentages at low (mean = 50%) and high (mean = 22.2%) watering levels (ANOVA, Figure 5) than fruits from plants in soils of sandstone origin. Fruits from plants in soils of sandstone origin germinated similarly at low (mean = 5.6%) and high (mean = 5.6%) watering levels (ANOVA, see Figure 5).

The amount of light reaching the fruits (placement) did not significantly affect their germination. In this particular trial, soil origin was a covariate to eliminate the effect of soil in the analysis. At both watering levels, mean germination percentage was higher, although not significantly, for fruits that were placed on top of the soil surface than those that were buried 0.6 cm under the soil surface (ANOVA, $p = 0.069$, Figure 6). This experiment reiterates the results that fruits germinate more frequently at low watering levels (ANOVA, $p = 0.001$, see Figure 6), as shown above.

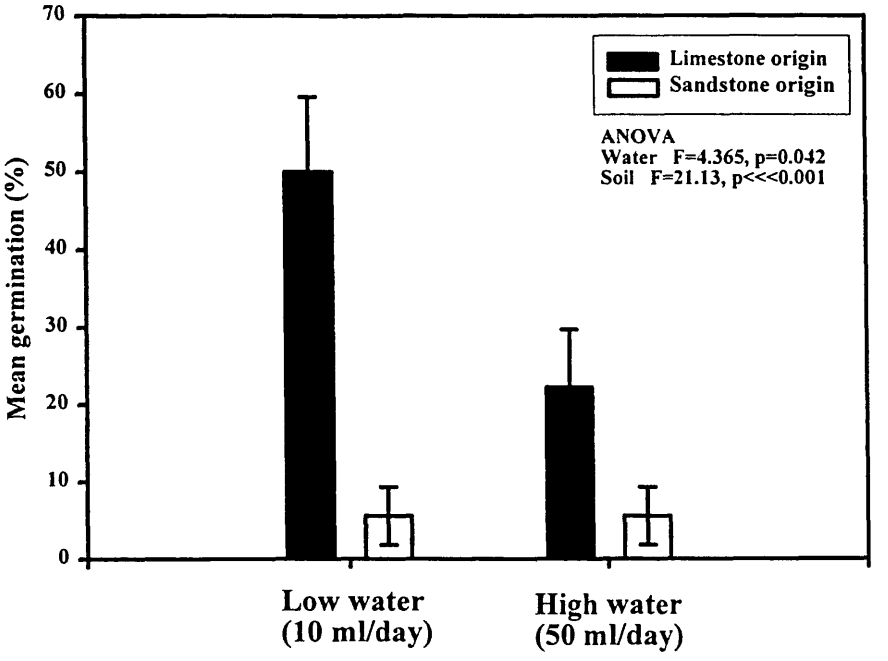


Figure 5. Germination experiments tested the effects of watering level and soil origin (seeds were germinated in different soils). Seeds from plants on soils of limestone origin had significantly higher percent germination than plants on soils of sandstone origin at both low and high watering levels. Germination percentages were similar for plants on soils of sandstone origin at both watering levels.

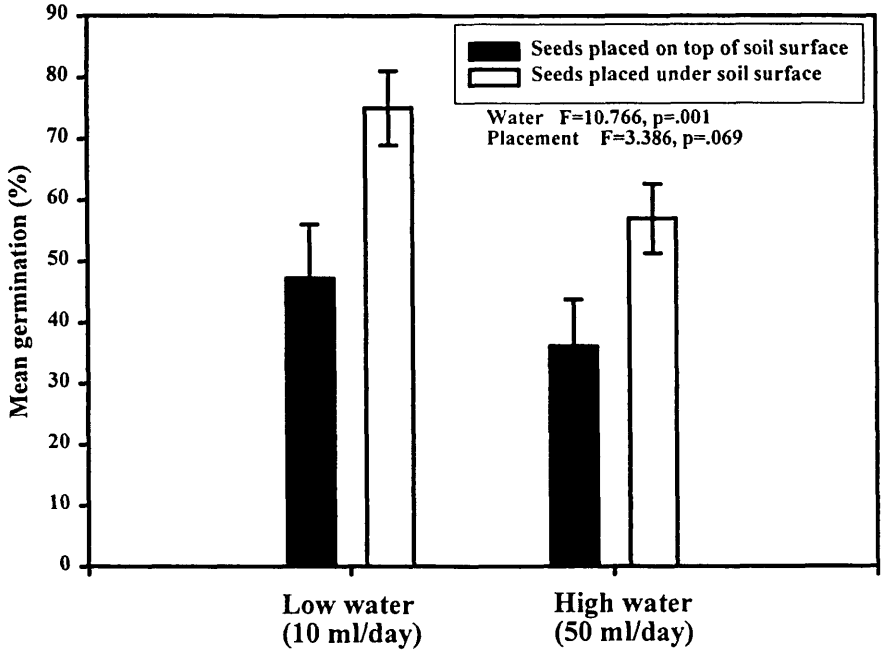


Figure 6. Germination experiments tested the effects of light availability and watering level. Soil origin (limestone vs. sandstone) was included as a covariate to eliminate its effects on germination. Note that watering level significantly affects germination although the placement of the seeds (top vs. under soil) is not a significant variable.

Soil Analyses

The percent of field water content varied for different soils of different origin. In all months of collection, soils of limestone origin (mean = 3.3%) had significantly lower field water content on average than soils of sandstone origin (mean = 11.4%; ANOVA, $F = 10.187$, $p << 0.001$). The percent of rock did not vary significantly between soils of sandstone origin (mean = 34%) and soils of limestone origin (mean = 44%; ANOVA, $F = 2.444$, $p > 0.07$).

Discussion

Herbivory and Fruit Production

Fruits of *Salvia dorrii* ssp. *mearnsii* are adversely affected by herbivory. Although other herbivores may have an effect, the most dominant herbivore observed was a caterpillar from the order Lepidoptera (Peter Price, personal communication). Exact identification could have been obtained through examination of the adult butterfly but that was beyond the scope of this study. The caterpillars were large enough that the cheesecloth covers effectively isolated them from the maturing fruits. The covers decreased herbivory pressure, which allowed more fruits to mature; however, some of the fruits were still damaged. It is likely that caterpillars were inside of these verticels when they were covered. Although uncovered verticels had the potential for additional pollination and fertilization, heavy herbivory adversely affected them. This was seen in plants from both limestone and sandstone soils, suggesting that fruit herbivory in this taxon is independent of soil and microsite characteristics.

Herbivory appears to be one cause of unviable fruits. However, some ovules (though pollinated) were unviable due to early collection; all verticels on one branchlet were collected at one time. In addition, the cheesecloth covers may have affected fruit maturation by changing the temperatures of the maturing fruits.

Soil and Fruit Production

Herbivory affects fruit production in this subspecies of *Salvia* in all environments. Overall, plants from soils of sandstone origin in chaparral vegetation had fewer mature fruits than plants from soils of limestone origin in desertscrub vegetation. The relatively dense chaparral vegetation (soil of sandstone origin) may support a greater number and variety of herbivores that feed on the aromatic fruits of *Salvia dorrii* ssp. *mearnsii*. In contrast, the sites on soils of limestone origin are more open and do not support as much nutrient-rich vegetation that is favorable to herbivores (Janzen 1974, Coley et al. 1985). Coley et al. (1985) also suggested that nutrient-poor soils, like those of limestone origin in the Verde Valley, support fewer herbivores because of limited resources in the plants on these soils. Water availability, varying greatly in soils of different origins, is also likely to affect the number and quality of fruits produced in the chaparral and desertscrub communities of central Arizona.

Germination Experiments

The timing of germination is a key element in the survival of a plant; it varies in different habitats and with different life history characteristics (Harper 1977, Silvertown 1981, Venable and Brown 1988, Meyer et al. 1989, Meyer and Kitchen 1994). Platt (1951) found that seeds of several species readily germinated on shale barrens in Virginia during the spring months but that seedling establishment was rare due to the extreme heat and dryness of the summer months. The germination of *Salvia dorrii* ssp. *mearnsii* follows similar patterns. Although fruits are mature in May or June, germination in the field does not occur until September or October. Clearly, the dry months, June and July, are too stressful for seedling establishment to occur. Even when precipitation is heavy in central Arizona, during August and September, fruits of *S. dorrii* ssp. *mearnsii* germinate relatively sparsely in their natural habitat. The drought that follows the fall rains probably limits its germination and seedling survival (Keeley 1986, Bowers 1994).

Scarification treatments did not increase germination percentages in fruits of *Salvia dorrii* ssp. *mearnsii*. Young and Young (1992) reported that many members of the genus *Salvia* require scarification or cold treatments for germination. Love (1989) found that scarification was not as effective as alternating temperatures for maximum germination in *S. dorrii* ssp. *dorrii*. However, this subspecies does not appear to depend on scarification for germination. This suggests that aridland plants may not have complex dormancy mechanisms. Meyer et al. (1989) have proposed that nondormant species have evolved in the Great Basin Desert because they do not have the risk of premature summer germination that areas of excessive summer rain have.

Interestingly, fruits from soils of sandstone origin germinated more often than fruits from

soils of limestone origin in petri dishes but less often in soil. This suggests that fruits from plants on soils of sandstone origin are extremely viable and able to germinate but that characteristics of the native soil may inhibit germination. However, these results may also be an artifact of container versus *in situ* experimentation. Low water availability in soils of sandstone origin due to rapid drainage may also limit germination. In addition, some plants such as creosote bush (*Larrea tridentata*) release inhibitory compounds that hinder germination of other seeds (Hallmark and Allen 1975). Such compounds from other plants or within the soil may limit germination, as seen in the overall low germination percentages in soils.

Excessive amounts of water appear to be inhibitory to the germination in this taxon, given that the highest levels of germination were in the pots with low-water treatments (10 ml per day). At high water levels, a high solute load, especially in soils of limestone origin, may inhibit germination. In addition, it appears that germination in *Salvia dorrii* ssp. *mearnsii* is adapted to low precipitation environments. Fruits in wet pots may have rotted. Watering regimes in these germination trials may have poorly represented the scattered, inconsistent precipitation that is characteristic of central Arizona. Furthermore, germination experiments in soils amended with perlite, vermiculite, or peat moss are likely to give different results.

Germination was strikingly similar in native, foreign, and off-site soils. If climatic and biotic conditions were favorable, *Salvia dorrii* ssp. *mearnsii* could germinate in these marginal soils and potentially expand the range of individual populations. However, under natural conditions the boundaries of this distribution are very distinct. This suggests that factors other than soil, such as competition, herbivory, and ant frugivory—evidenced in the fruits by the presence of a polysaccharide coating when imbibed with water—limit the expansion of *Salvia dorrii* ssp. *mearnsii* (Beattie 1985, Keeler 1989, Horvitz 1991).

Although *Salvia dorrii* ssp. *mearnsii* grows in high light environments, high light availability does not appear to be a requirement for germination. In fact, fruits that were placed under the soil surface germinated at higher percentages than fruits that were placed on top of the soil surface. Water availability is a more significant factor in controlling germination in *S. dorrii* ssp. *mearnsii*.

Soil Analyses

During the greenhouse germination experiments, differences were noticed in the water drainage of soils of limestone and sandstone origin. Soils of sandstone origin were completely dry in 1 day on average, whereas soils of limestone origin tended to remain moist for at least 2 days. However, these observations contradict the findings on field moisture content that showed soils of limestone origin having significantly lower percent moisture contents. This probably reflects the differences in precipitation over an elevational gradient and differences between greenhouse and field conditions. Although pots were watered every day, drying of soils, especially the fast-drying soils of sandstone origin, potentially limited germination in the greenhouse.

Conclusion

It is extremely difficult to pinpoint the factors that contribute most to the disjunct distribution of *Salvia dorrii* ssp. *mearnsii*. As Kruckeberg and Rabinowitz (1985) stated, "Organisms do not occur where they cannot, but often they do not occur where they might." This accurately describes the distribution of this subspecies. It occurs only in certain areas that are disjunct from one another and the populations are sharply defined from the surrounding vegetation. Areas where the plant occurs are not noticeably different from areas where it is absent. In addition, the soil on and off of *Salvia dorrii* ssp. *mearnsii* sites is similar and probably does not limit its occurrence. However, there are clear differences in germination of fruits from plants growing in soils of different origins. Fruits from plants in soils of limestone origin may be better adapted to the environmental conditions found in central Arizona and therefore may germinate more readily.

In addition, the polysaccharide coating on the seeds (when imbibed with water) indicates that ant dispersal may play a role in expanding populations of this subspecies (Brad Blake, personal communication, Keeler 1989). Ants are known to be important for seed dispersal in xeric environments (Keeler 1989). Although they do not disperse seeds over long distances, they do usually cache the seed in a well-fertilized area (Keeler 1989). As in some species of *Viola* and *Datura*, ant caching helps to perpetuate plant populations where seed herbivory is high (Keeler 1989).

Throughout the course of this study, many factors that may contribute to the failure or success of germination in *Salvia dorrii* ssp. *mearnsii* were elucidated. Germination percentages were highest when the fruits were watered at low levels. Under natural conditions, the water-holding capacity of the soil and adaptability of this taxon to dry environments may limit germination and seedling establishment. The plants are certainly found in higher abundance in lower elevation sites on soils of limestone origin.

Acknowledgments

I thank my thesis committee: Dr. Tina Ayers, Dr. Randy Scott, Dr. George Koch, Dr. Mike Kearsley, and Phyllis Hogan. Those who assisted with field work made the project a success: Gabe Martinez, Leslie Brandt, Tina Ayers, Randy Scott, Phyllis Hogan, Kambria Beck, and Melissa Jurgenson. I thank Dr. Neil Cobb, Elaine Zamora, Peter Pilles, Barbara Phillips, Jean Searle, Tracy Murphy, Dr. Marc Baker, Brad Blake, and Jeff Schively for advice and assistance. The National, Pacific Region and State Councils of Garden Clubs, the Orchid Society of Arizona, the Arizona Ethnobotanical Research Association, and the NAU Ecological Restoration Institute provided partial funding for this project.

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From the Greenhouse to the Field: Cultivation Requirements of Arizona Cliffrose (*Purshia subintegra*)

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Abstract: Central to the conservation of the federally endangered *Purshia subintegra* (Arizona cliffrose) is development of an understanding of its cultivation requirements. This knowledge will enable us to augment declining or threatened populations as well as preserve genotypes impacted by human activities. We studied seed and stem cutting propagation of *P. subintegra*. The highest success rate for rooted stem cuttings of *P. subintegra* that were collected wild was 34 percent. The stem cuttings of *P. subintegra* survived best when they were taken in the fall, rooted in perlite with Hormex 8, and watered once daily. Stem cuttings can take from 1 to 11 months to root depending on treatment and time of cutting. Propagation from seed was much more successful (88%) when we used fresh seed sown in perlite with cold stratification for 4 weeks. Seeds did not require native soil to germinate, nor did seedlings require native soil to survive. This means that *P. subintegra* can propagate and survive under conditions far different than it experiences in the field. Because road construction is destroying *P. subintegra* and its habitat, transplanting propagules to unoccupied habitat may prove to be an important avenue for conserving genotypes. Following our successful propagation trials, we introduced *P. subintegra* into its natural habitat in the Verde Valley in February 2000. We tested whether irrigating plants for 5 months increased survival and found that supplemental water was important to the survival of transplanted plants. For rare plants, we need a much greater knowledge base on how to grow and transplant them. This process is time consuming, but will be necessary as more and more species that are impacted by human disturbance must be conserved ex situ.

Both in situ and ex situ conservation can be important components of rare plant conservation (Frankel et al. 1995). Although plant conservation in the wild is most important for maintaining a population, ex situ populations can serve many purposes. Knowledge gained from ex situ cultivation will enable us to augment declining or threatened populations, to restore or transplant individuals impacted by disturbance, to conduct experiments on ecological requirements of the species, and to germinate seeds from in-house or long-term storage.

Several propagation methods are available to grow plants in a greenhouse setting. Ex situ seed banks are standard practice to conserve the genetic diversity of a species and safeguard it against the demise of the wild population. Germination studies are needed to determine seed viability and proper propagation techniques to successfully germinate and establish seedlings so that ex situ seed banks can be used if necessary for species recovery. Rooting stem cuttings is another propagation technique that can be used to preserve genotypes.

The federally endangered shrub *Purshia subintegra* (Kearney) Henrickson is threatened by rapid development of its habitat in the Verde Valley. Road expansion, new road construction, and land sales will eliminate about 600 individuals; therefore transplanting individuals may be an important mitigation solution. The recovery plan clearly states that restoration or transplantation should be considered a mitigation solution only if successful propagation techniques to grow and transplant *P. subintegra* are determined (U.S. Fish and Wildlife Service 1994). The ability to grow *P. subintegra* from seed or stem cuttings may provide an avenue to conserve genotypes as impacts and disturbances to its natural habitat continue to occur.

Purshia subintegra is a rare soil endemic. It is typically restricted to nutrient-poor, lacustrine limestone deposits (Anderson 1986, 1993). Four populations are known from central Arizona. We are interested in the largest population in the Verde Valley outside of Cottonwood. In the Verde Valley, the distribution of *P. subintegra* overlaps with the distribution of *P. stansburiana*. Plants that have characteristics of both parents have been observed, leading to some taxonomic questions about *P. subintegra* (see U.S. Fish and Wildlife Service 1994 for discussion). Using the descriptions

and definitions from the Arizona Cliffrose Recovery Plan, we refer to plants outside the definition of *P. subintegra* as the introgressed form.

Our two goals were to determine the best method to propagate *P. subintegra* from both seeds and stem cuttings, and to determine the feasibility of transplanting or relocating propagules. Maintaining plants ex situ in a greenhouse is not a feasible long-term solution with these large evergreen shrubs. Our intent was therefore to learn to grow *P. subintegra* for preservation and reintroduction of threatened genotypes.

Past Propagation Trials

Seeds

Previous seed germination studies reported little or no success with propagation of *P. subintegra*. We therefore examined germination studies conducted with the common cliffrose, *Purshia stansburiana* (Torr.) Henrickson. *Purshia stansburiana* requires cold-moist stratification to break dormancy, but germination success is related to length of stratification and temperature (Alexander et al. 1974, Young and Young 1986). A germination success rate of 55 percent occurred after 2 weeks of stratification at 5° C with incubation temperatures (night/day) at 10/20, 10/25, 10/30, and 15/25° C (Young and Young 1992). Even better germination success (88%) occurred when seeds were incubated at 21° C with light, and germination success was 76 percent with 3 months of cold stratificaiton (Deno 1993). Seeds have remained viable for up to 7 years in dry storage (Young and Young 1986). These studies of *P. subintegra* and *P. stansburiana* suggested that we should examine seed for viability before germination trials and implement a cold-moist stratification treatment.

The germination of *P. subintegra* has critical implications for its survival in the Verde Valley. First, we need to understand the methods of seed propagation for *P. subintegra* in the event that plants must be grown from seed that had been stored ex situ as a method to conserve genotypes. In addition, knowledge about its germination requirements will help us understand the biology of *P. subintegra*. In the Verde Valley, *P. subintegra* occurs in a restricted habitat that can also be occupied by the introgressed form. The germination requirements of *P. subintegra*, *P. stansburiana*, and the introgressed form may help explain the distribution of each taxa as well as competition in the natural habitat.

Stem Cuttings

Previous studies on the cultivation of *P. subintegra* from stem cuttings had variable and low success (Asplund 1989). Results from a trial to root stem cuttings from 1986 to 1989 found that cuttings collected in summer (June-July) had a higher rooting rate than cuttings collected during other seasons. Hormex 3 and Hormex 8 treatments had a higher rate of rooting than Dip 'N Grow or Wood's Rooting Compound. Intermittent mist also increased the success rate. After the cuttings rooted, they were transplanted to pots using standard potting mix. None survived transplanting (Asplund 1989).

The Arboretum at Flagstaff tried to root *P. subintegra* cuttings in 1990 and 1991 with varying success. In 1990, 51 percent of the stem cuttings rooted that were collected in October. All of the rooted cuttings were planted in potting mix, but none survived more than 4 months (Maschinski 1990). In 1991, only 3 percent of the stem cuttings collected in December rooted. However, the plants were potted in native soil and two large plants still survive to date.

In June through September 1996, the Arboretum at Flagstaff collected stem cuttings of *P. subintegra* and the introgressed form. Rooting trials in germination mix (8 perlite: 1 vermiculite: 1 peat) with Hormex 3 had 35 and 53 percent rooting success for *P. subintegra* and the introgressed form. In comparison, perlite and Hormex 8 had a success rate of 18 percent with *P. subintegra*, whereas the introgressed form success was only 8 percent.

In general, time of year, site of cutting, nutrient status, rooting hormone, amount of light, and juvenility have been shown to affect rooting success (Macdonald 1986, Dirr and Heuser 1987). We examined the influence of woodiness of stem, time of collection, propagation technique, and rooting hormone on stem cuttings of *P. subintegra*. In addition, we determined how to keep seedlings and rooted cuttings alive after they were transplanted to pots.

Materials and Methods

Seeds

Using the cold stratification period recommended for *P. stansburiana*, we investigated the effects of the propagation media on germination and compared the rate of germination of *P. subintegra*, *P. stansburiana*, and the introgressed form. We used three propagation media: perlite, germination mix (8 perlite: 1 vermiculite: 1 peat), and

native soil mix (2 soil: 1 perlite: 1 sand). We collected native soil in the Verde Valley in an area where *P. subintegra* grows and passed the soil through a sieve to remove large rocks. We planted each taxon in each of the three propagation media.

We sorted seeds visually for viability with about 40 percent of the collected seeds appearing viable. In January 1998, we planted five seeds in each individual pot. Only five seeds could be used due to the limitations of working with an endangered species. We planted 30 pots of each species divided equally among the three propagation media. The seeds then received a cold-moist treatment at 5° C for 4 weeks in dark plastic bags. We placed the pots in the passive solar greenhouse at the Arboretum at Flagstaff and watered by mist. Due to differences in the propagation media, we misted seeds in perlite and germination mix for 16 seconds every 64 minutes during the day, and we misted seeds in the native soil mix once daily. The greenhouse had daily fluctuations from 10 to 35° C during this period. We monitored seedlings every 3 to 4 days to measure germination and survival. Germination began 4 days after the pots were placed in the greenhouse and continued for 24 days. We counted a seed as germinated when the hypocotyl elongated.

We analyzed the percentage of seed germination (arcsin transformed) with a two-factor analysis of variance with all assumptions met (SYSTAT 6.0 – GLM). We calculated the percentage of seeds germinating as the total number of seeds that germinated in a pot over the 24-day period divided by the total number of seeds per pot. The two factors were species and propagation media. Not all seedlings survived the 24 days and we recorded mortality for the seeds that germinated.

Stem Cuttings

Because previous propagation trials with cuttings had low success, we examined whether the condition of plants, the age of stem cuttings (woodiness), different propagation techniques, or time of year influenced rooting success. Although we experimented with many propagation techniques, we used some standard procedures in all the experiments. The factors that vary from the standard procedure are propagation media, rooting hormone, watering treatment, and bottom heat (Table 1). They are described in detail in the following sections. Stem cuttings were approximately 10 cm long and were stripped of the lower half of their leaves. We were careful not to damage the stem when removing leaves. Before inserting the ends of stem cuttings, we soaked them in 10 percent bleach solution for 10 minutes and then applied a small amount of rooting hormone to the cut end. We maintained the cutting flats in the passive solar greenhouse at the Arboretum at Flagstaff. We also needed to determine how much time a cutting would need to root; we therefore monitored the stem cuttings for up to 1 year as long as the cuttings maintained green leaves. After cuttings had developed roots, we marked the date and transplanted the cuttings to pots to be used in later greenhouse experiments.

Origin of Cuttings

To determine whether the origin of cuttings influenced rooting success, we collected stem cuttings from both wild plants and greenhouse-grown plants (Table 1). We took wild stem cuttings from both the rare *P. subintegra* and the introgressed form from September 1996 to November 1996. During the same period, we took cuttings from two large *P. subintegra* plants that survived 1996 propagation trials and that are maintained in the greenhouse at the Arboretum at Flagstaff. These plants are well watered, healthy, and robust. We treated all the stem cuttings with our standard procedures as described. We applied Hormex 8 to the cuttings before placing them in perlite.

Woodiness

We used greenhouse-grown plants as material for cuttings in order to classify cuttings based on amount of lignification or woodiness. New tissue, less than a month old, is pliable, whereas older tissue quickly becomes woody. We took cuttings (n = 126) from greenhouse-grown *P. subintegra* and scored them for woodiness in September of 1996. We classified cuttings in four categories: new, where terminal growth was green and pliable; early, where stems had begun to lignify but were still pliable; 1 year, where the stem was completely woody and 1 year old; and old, where stems had woody growth greater than 1 year in age. We applied Hormex 8 to the cuttings before placing them in perlite (Table 1). We analyzed the proportion of rooted cuttings for each category using Pearson chi-square analysis.

Propagation Techniques

Previous trials of propagating stem cuttings suggested that propagation techniques could affect the success of rooting cuttings. The main difficulty was getting cuttings to root before they rotted. We performed three trials that manipulated

Table 1. Details of each propagation trial with stem cuttings.

Trial	Date	Taxa	Origin	Propagation medium	Rooting hormone	Watering treatment	Bottom heat	Other
Origin of cutting	Sept.–Oct. 1996	*P. subintegra*	wild and greenhouse	perlite	Hormex 8	once daily	no	
Woodiness	Sept. 1996	*P. subintegra*	greenhouse	perlite	Hormex 8	once daily	no	age of stem
Propagation techniques								
1.	Oct. 1996	Introgressed	wild form	germination mix	Hormex 8	once daily	no	
				perlite	Hormex 8	once daily	no	
				perlite	Hormex 8	once daily	yes	
				perlite	Hormex 8	mist every 32 min	no	
2.	March 1997	Introgressed form	wild	perlite	Rootone	once daily	yes	
				perlite	Hormex 3	once daily	yes	
				perlite	Hormex 8	once daily	yes	
				germination mix	Rootone	once daily	yes	
				germination mix	Hormex 3	once daily	yes	
3.	Sept. 1997	*P. subintegra*	wild	perlite	Hormex 3	once daily	no	
				perlite	Hormex 8	once daily	no	
Time of collection	variable	*P. subintegra*	wild	perlite	Hormex 8	once daily	as needed	
		Introgressed form	wild	perlite	Hormex 8	once daily	as needed	

propagation medium, rooting hormone, and watering treatment (Table 1). We used three rooting hormones: Rootone (Black Leaf Products, Louisville, KY 40222), Hormex 3, and Hormex 8 (Brooker Chemical Corporation, P.O. Box 9335, N. Hollywood, CA 91609). We also used two propagation media to root cuttings: perlite and germination mix (8 perlite: 1 vermiculite: 1 peat).

In the first trial we examined the differences of propagation media and watering treatment. In October of 1996 we collected cuttings of the wild introgressed form of *Purshia* (n = 191). We compared four treatments: germination mix watered once daily, perlite watered once daily, perlite watered once daily with bottom heat of 20° C, and perlite misted at 32 minute internals for 16 seconds for 3 months. Because of low temperatures in the greenhouse, we placed all of the cutting flats on heating mats during week 13. We analyzed the proportion of rooted cuttings after 1 year for each treatment using Pearson chi-square analysis.

In the second trial we compared propagation media and rooting hormone. In March of 1997 we collected stem cuttings from the introgressed form (n = 171). We used two rooting media: perlite and germination mix. In perlite, we compared the three rooting hormones, Rootone, Hormex 3, and Hormex 8. In germination mix, we compared rooting hormones Rootone and Hormex 3. We placed all cuttings on heating mats at 20° C and watered once daily. We did not perform a statistical analysis because most treatments had no success.

In the third trial we examined the effect of the rooting hormones Hormex 3 (n = 705) and Hormex 8 (n = 699) in perlite on stem cuttings of *P. subintegra* we collected in September of 1997 from the Verde Valley. We placed the stem cuttings in perlite and watered once daily. We analyzed the proportion of rooted cuttings for each rooting hormone using Pearson chi-square analysis.

Timing of Wild Collection

Previous results indicated that the season in which wild cuttings are taken is important; we took cuttings systematically over the year to determine the optimal time to take cuttings for the

greatest success. We collected stem cuttings of *P. subintegra* in fall 1996 (October and November), winter 1997 (March), spring 1997 (May), and fall 1997 (September) and the introgressed form in summer 1996 (June), fall 1996 (October and November), winter 1997 (February and March), and spring 1997 (May). We treated the stem cuttings using our standard procedures as described previously. We placed the cuttings in perlite after treating them with Hormex 8 (Table 1). We watered the cutting flats once daily and placed them on bottom heat as the low temperatures in the greenhouse required for 12 months. Using Pearson chi-square analysis, we compared rooting success in the four seasons for each taxon.

Greenhouse Plants

Little is known about the cultural requirements of soil endemics. Previous trials suggested that *P. subintegra* required native soil even in a greenhouse situation; however, native limestone soil is difficult to use in pots because it resembles concrete after a few weeks. We therefore tested the success of growing *P. subintegra* in different pot sizes and media. The container sizes tested were 3.25 inch square pots (volume 500 ml), 10 inch seedling tubes (volume 650 ml), and 1 gallon pots (volume 3.0 L). We also tested three types of potting media: standard potting mix (8 Supersoil, Rod McLellan Co., 914 S. Claremont St., San Mateo, CA 94402, 4 perlite: 1 sand), native soil mix (2 limestone soil: 1 sand: 1 perlite), steam-sterilized native soil mix (2 limestone soil: 1 sand: 1 perlite), and a mix of equal parts of the native soil mix and our standard potting mix. When stem cuttings had rooted or seedlings were large enough, we transplanted them to pots. In 1 gallon pots, we usually planted three stem cuttings per pot. We calculated survival after 6 months from the time of transplant. We maintained potted plants in the passive solar greenhouse and research greenhouse at the Arboretum at Flagstaff.

Reintroduction Trial

One of our main goals was to reintroduce plants to the wild as a conservation measure for the species, so we relocated plants generated from cuttings or seeds into the Verde Valley to determine the optimal method for transplanting success. Initially, we were interested in the amount of care necessary to ensure survival of the plants. We therefore chose to water half the plants for 5 months in this initial trial and the other half for 1 month.

We selected 98 plants propagated from seeds and cuttings of *P. subintegra* from the Verde Valley to use for the reintroduction. All of the plants had been established in the greenhouse for approximately a year in 1 gallon pots in standard potting mix. On February 25, 2000, we transplanted them into the Verde Valley in wash bottoms and the sides of washes where *P. subintegra* grows naturally. We thought the sides of the large washes would give the plants the best chance of survival due to higher soil moisture. We dug holes 25 cm deep x 25 cm wide and wetted the hole with approximately 2 gallons of water before planting. After transplanting, we gave the plants additional water until saturation. We installed a drip irrigation system to deliver approximately 1 gallon of water per week to 49 of the plants for 5 months. The remaining 49 plants received water for 3 weeks by hand and then received no additional water.

We monitored survivorship from February to August 2000. We will continue to monitor monthly for a year and then seasonally for the next year. We analyzed survivorship of each treatment with a Pearson chi-square test at 6 months.

Results

Seeds

Purshia subintegra, P. stansburiana, and the introgressed form germinated after 4 days in each propagation medium. Germination varied between species and media treatment (Table 2). All taxa had their highest germination in perlite and lowest in the native soil mix (Figure 1). The introgressed form had the lowest germination rate in all of the propagation media, whereas *P. subintegra* and *P. stansburiana* had similar germination rates.

All three taxa had the highest mortality in native soil (Table 3). In perlite and germination mix, mortality was less than 10 percent, but in native

Table 2. Analysis of variance on the proportion of the total number of seed germinated (arcsin transformed) for species (*Purshia stansburiana, P. subintegra,* and introgressed form) and propagation media (perlite, germination mix, and native soil mix).

Source of variation	DF	MS	F-value	p-value
Species	2	0.89	3.70	0.0291
Propagation media	2	2.81	11.72	< 0.0001
Species * propagation media	4	0.21	0.89	0.4759
Error	81	0.24		

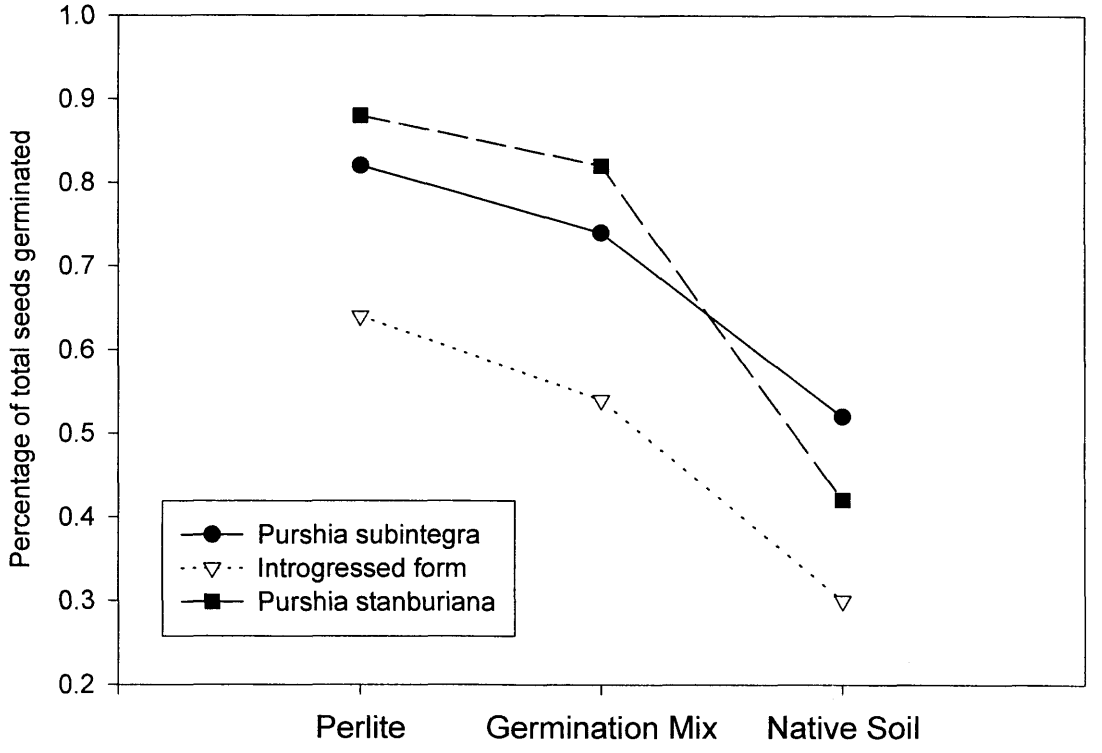


Figure 1. Percentage of total seeds germinating in each propagation medium for the species *Purshia subintegra, P. stansburiana,* and the introgressed form.

soil mortality ranged from 44 to 68 percent. Mortality was due to several causes. Many seedlings began to germinate but never developed enough to shed the seed case from the cotyledons. Other seedlings wilted or damped off at the surface layer.

Stem Cuttings

Origin of Cutting

The success rate varied as a function of the origin of the cutting (Table 4). Wild cuttings taken in September to November 1996 had an overall success of 34 percent for *P. subintegra* and 19 percent for the introgressed form. Stem cutting success from greenhouse-grown *P. subintegra* plants was much greater at 81 percent. Wild-collected cuttings took 8 to 31 weeks to root, whereas cuttings from greenhouse-grown plants took 8 to 25 weeks.

Woodiness

The woodiness of stems did not significantly influence rooting success (Table 4, $\chi^2 = 3.347$, df = 3, p = 0.34). The oldest woody cuttings had lower rooting success than the other classifications. The trend is similar to what is observed with wild-collected cuttings. Stem cuttings that rooted most successfully were from the early growth (where stems had begun to lignify but were still pliable). All cuttings rooted in 8 to 24 weeks with no difference between categories in the length of time needed to root.

Propagation Techniques

In the first trial, propagation techniques significantly affected the proportion of stem cuttings rooted (Table 5, $\chi^2 = 58.6$, df = 3, $p < 0.0001$). Cuttings with bottom heat were most successful at 60 percent after 13 weeks, whereas cuttings in perlite

Table 3. Mortality of seedlings for each species and each propagation media.

	Perlite	Germination mix	Native soil mix
P. stansburiana	2%	6%	44%
P. subintegra	5%	2%	61%
Purshia hybrid	10%	0%	68%

Table 4. Results of propagation trials with stem cuttings examining the origin and woodiness of cutting. Values are listed as percentage of stem cuttings that rooted.

	Purshia subintegra	Introgressed form
Origin of cutting (Sept.–Oct. 1996)		
Wild collected	34%	19%
Greenhouse grown	81%	
Woodiness (Sept. 1996)		
Terminal new growth	76%	
Branch still pliable	87%	
Woody about 1 year old	70%	
Woody > 1 year old	68%	

that were watered daily rooted between weeks 4 and 12, with only 14 percent success. In February (week 13), we placed all cuttings on heating mats due to low temperatures in the greenhouse. It was only after placement on the heating mats that the cuttings in the misting treatment began to root, increasing the success rate to 43 percent between weeks 17 and 39. Cuttings in germination mix also developed roots from week 16 to week 24, achieving a success rate of 14 percent after we placed cuttings on the heating mats.

The March 1997 (second) trial had very low success rates with no difference between treatments (Table 5), and cuttings of *P. subintegra* and *P. stansburiana* during this period were unsuccessful. Cuttings with the germination mix and Rootone treatment were most successful at 12 percent, but they also took a longer time to root, from week 16 to week 41.

In the third trial, to examine the effect of the rooting hormone on *P. subintegra*, we compared rooting success with Hormex 3 and Hormex 8 (Table 5, September 1997). Cuttings treated with Hormex 8 had a success rate of 27 percent compared to 16 percent for cuttings treated with Hormex 3 ($\chi^2 = 24.97$, df = 1, $p < 0.0001$). Most cuttings rooted within 11 to 31 weeks, with a few rooting as late as week 43.

Timing of Wild Collection

To determine whether the season the cuttings were taken in was important for their rooting success, we collected stem cuttings of *P. subintegra* and the introgressed form during different seasons (Table 6). Using Pearson chi-square analysis, we compared rooting success in the four seasons. Cuttings had significantly greater rooting success in the fall (*P. subintegra*: $\chi^2 = 30.40$, df = 3, $p < 0.0001$; introgressed form: $\chi^2 = 41.61$, df = 3, $p < 0.0001$). The success rate of cuttings for *P. subintegra* was similar in fall 1996 and fall 1997 even though the years were very different; 1996 was a drought year and 1997 had adequate rain in both winter and spring.

Table 5. Results of trials of different propagation techniques with stem cuttings. Values are listed as percentage of stem cuttings that rooted.

Propagation media	Rooting hormone	Watering treatment	Bottom heat	*Purshia subintegra*	Introgressed form
October 1996					
Perlite		Daily	no		14%
		Daily	yes		60%
		Misted	yes		0% (43%)
Germination mix	Hormex 8	Daily	yes		0% (14%)
March 1997					
Perlite	Rootone	Daily	yes		0%
	Hormex 3				4%
	Hormex 8				7%
Germination mix	Rootone				12%
	Hormex 3				0%
September 1997					
Perlite	Hormex 3	Daily		16%	
	Hormex 8			27%	

Table 6. Results of propagation trials examining the timing of wild collection of stem cuttings. Values are listed as percentage of stem cuttings that rooted.

Time of wild collection	*Purshia subintegra*	Introgressed form
Summer 1996		8%
Fall 1996	34%	39%
Winter 1997	23%	7%
Spring 1997	7%	18%
Fall 1997	27%	

Greenhouse Plants

The survival of rooted cuttings and seedlings varied with pot size and media used after transplanting. Transplants were most successful in native soil mixes that included additional sand and perlite (Table 7). Rooted cuttings actually survived the best in sterilized native soil mixes but grew very slowly. The plants grew fastest in potting mix, but had higher mortality. Seedlings transplanted to 3.25 inch pots survived best in native soil mix compared to our standard potting mix.

When plants were large enough, we transplanted them into 1 gallon pots. Survival was similar to the previous results, with the greatest survival in native soil mixes (93%) and lowest survival (73%) in the standard potting mix.

Reintroduction Trial

Irrigation was important to the survival of transplanted plants. After 1 month only 2 percent of the transplants died regardless of treatment (Figure 2). After 3 months the transplants that were not watered had a much higher rate of mortality until the fifth month. The watered group had significantly greater survival after 6 months (χ^2 = 27.88, df = 1, $p < 0.001$). After the irrigation was discontinued from the watered group, five plants died in both groups between the fifth and sixth months. In this experiment we saw mortality due only to transplanting and environmental stress and not herbivore or pest damage.

Table 7. The mortality rate of transplanted rooted cuttings and seedlings of *Purshia subintegra* in different pot sizes and potting media.

Pot type	Native soil mix	Potting mix	Sterile native soil mix	Half and half*
Rooted Cuttings				
3.25 inch pots	85%	72%	90%	
Seedling tubes	56%	78%		
Gallon pots	78%	60%		70%
Seedlings				
3.25 inch pots	94%	67%		

*Half native soil: half potting mix.

Discussion

Seeds

Germination of *P. subintegra* seeds requires the use of fresh good seed in perlite with a cold stratification treatment for 4 weeks. Inviable seed of *Purshia* is flat in appearance and easily detectable; viable seed appears plump and is larger than inviable seed. We performed the experiments with seed that had been stored for 6 months under cool and dry conditions. Tests will need to be performed to determine the length of time that *P. subintegra* seed can be stored. Cold moist stratification of seed is a common requirement for many native plants. We suggest using perlite as the rooting medium because seedling growth was usually faster in perlite than in germination mix.

Neither *P. subintegra, P. stransburiana,* nor the introgressed form required native soil to germinate in the greenhouse. In fact, seedlings sown in native soil had the highest mortality in comparison to seeds grown in perlite or germination mix. This contrasts with the fact that the best survival for rooted cuttings was in native soil. The difference can be attributed to the difficulty encountered in using native soil to germinate seeds. Regulating water to keep the soil moist without rotting the seedlings was difficult.

Several factors may explain the increased mortality of seedlings in native soil. Conditions differ for plants grown in pots and greenhouses than in the field. The greenhouse for this experiment had a high humidity level, usually greater 70 percent, and can experience large daily fluctuations in temperature (up to 40° F). We initially over-watered the seedlings in native soil and many seedlings died. When we reduced the amount of water, the survival of seedlings improved. Because of the pot effect, seedlings in native soil experienced more extremes with the drying and wetting of the soil.

Stem Cuttings

Successful propagation of *P. subintegra, P. stansburiana,* and the introgressed form requires proper timing, media, hormones, heat, and time. The main challenge was to encourage stem cuttings to root before they died or rotted. The wild-collected stem cuttings of both *P. subintegra* and

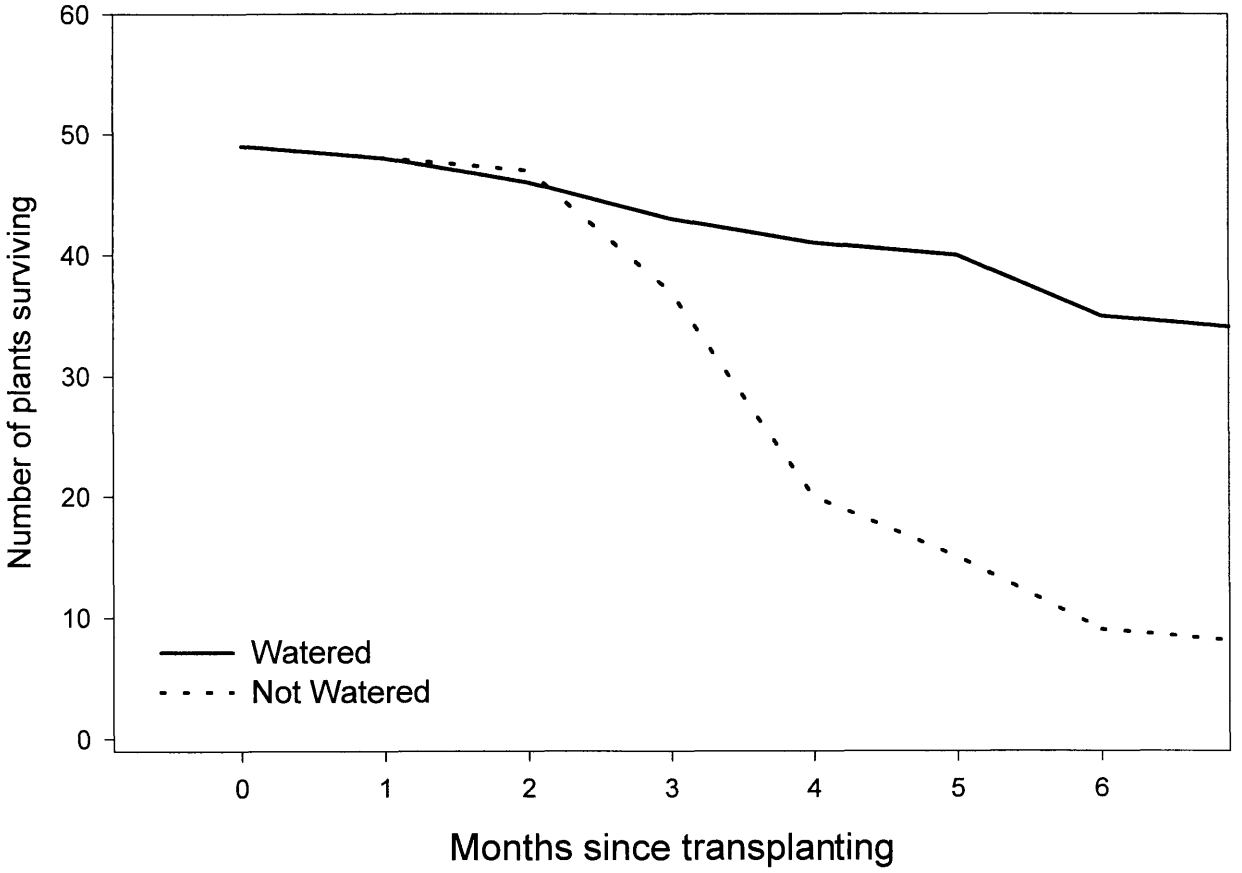


Figure 2. Number of plants that have survived since transplanting on February 25, 2000. All plants were watered for 3 weeks; 49 were watered for a total of 5 months.

the introgressed form survived best when they were taken in the fall, rooted in perlite with Hormex 8, and placed on heating mats. These techniques also produced roots in the least amount of time. The results from trials using the age of the cutting and the season suggest that cuttings taken from the current year's growth at the end of the growing season have the highest rate of success. The differing success rate through the year may be a result of either the time that cuttings are taken from the wild or the conditions in the greenhouse. In the fall, the plants may have a better physiological condition in response to the monsoons or a hardening off of growth with a buildup of storage products (Macdonald 1986, Dirr and Heuser 1987). Greenhouse-grown plants had the highest success rate. Plants from greenhouses have better nutrient and water status and often have high rates of rooting success (Dirr and Heuser 1987). An ex situ population of rare plant stock would enable experiments on its biology and would provide genetic material for experimental reintroduction without compromising the wild population.

Greenhouse Plants

To establish an ex situ population, you must also be able to grow plants in a greenhouse situation. We found that *P. subintegra* will grow in a variety of media, but each has its drawbacks. In potting mix the plants grew faster but were far more finicky in their water needs. The soil dried easily and would stress the plants. For soil mixes with native soil, the plants survived at a higher rate but grew slower than in other potting media. Obtaining native limestone soil can also prove problematic. We are still examining whether the success of plants transplanted in the wild will vary with size or potting mix. Plants potted in the native soil are already inoculated with the native soil flora, including arbuscular mycorrhizae.

We experimented with both seed germination and rooting stem cuttings to determine the cultivation requirements for *P. subintegra*. Although we had some information about congeners, we still had to experiment with this species. At the Arboretum, our results with rooting stem cuttings of *P. subintegra* are actually much better than with *P.*

stansburiana. Initial results suggested that *P. subintegra* required its native soil to survive even in the greenhouse. Further work showed that this was not the case. Using knowledge from congeners helped, but there is still a vast need for horticultural and cultivation information on rare species.

Reintroduction Trial

We thought that our transplanting procedures were adequate with almost no mortality in the first month and only 18 percent mortality in the group that received 5 months of water after transplanting. The drip irrigation was very successful even though the time involved to install and to maintain the system was great. A four-person crew could set up the system in 8 hours, but the system had to be checked weekly. Irrigation drip emitters would clog with dirt or would need to be adjusted based on their location on the landscape and the irrigation line. Surprisingly, we saw only minimal damage to the irrigation lines by animals. We will continue to monitor these plants for long-term survival and reproduction for another year. Other transplant trials are underway to examine the timing of transplanting, effect of propagation techniques, and microsites.

These results have implications for the success of future *P. subintegra* reintroduction trials and trials of other desert species. We recommend using plants generated from cuttings or seeds for transplantation or reintroduction. Because *P. subintegra* is a deep tap-rooted shrub, manipulating cultivated plants instead of digging up plants is more feasible. Digging up individual plants would be destructive to the old and new habitat and would be difficult with large plants. Growing plants from seeds or cuttings would also allow more flexibility in determining the number of plants and genotypes needed.

Because precipitation can be variable and the timing and amount can affect the outcome of transplant trials, it is necessary to supplement transplants with a constant, dependable source of water during establishment. We recommend watering for 5 months or more. It is important to note that the time involved for the care of transplants is significant and may mean that a reintroduction requires multiple years.

Finally, despite the additional expenditure in time and money, monitoring should be considered an important part of any transplant experiment (Sutter 1996). Monitoring is necessary to increase the knowledge base about reintroductions, and monitoring also provides managers with reasonable expectations of the cost and time involved for a successful reintroduction.

Acknowledgments

This work was funded by the Arizona Department of Transportation. We greatly appreciate Janice Busco's assistance and advice on propagation and plant care. We would also like to thank Ted Martinez, Julie Giguere, Becca Cammack, Wendy Thompson, Drew Callihan, Mira Petersen, Richard Libengood, Scott Winter, Jackie Campbell, Karen Hueston, Susannah Carney, Elaine Ferris, Charlot Root, Mike Gibson, Suzanna Hubbard, Loni Shapiro, and Patrice Morrow for help with field and greenhouse studies.

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Quantitative Genetics in Natural Populations: Means of Monitoring Natural Biological Processes

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Abstract: One of the goals of conservation biology is to maintain the integrity of natural processes in populations of rare plants. In the short term one of the main concerns is often whether the mating system of rare plants is disrupted, for example, by fragmentation. In the long term one of the main concerns is often whether small isolated populations maintain enough genetic variation to respond to selection due to human-induced environmental changes. Management of rare plant populations would, therefore, be supported by tools enabling the effective monitoring of these and similar processes. Unfortunately, direct measures are often difficult, time consuming, or expensive to obtain and therefore not useful for monitoring efforts. We are developing some simple genetic-based methods for quantifying both mating systems and the expected response to selection. They rely on joint genetic and phenotypic data obtained from field-collected samples and obviate the need for intensive breeding designs and common gardens that typify quantitative genetic studies. As a result, they will be directly applicable to monitoring populations of rare plants, and will enable better efforts directed toward maintaining the integrity of natural resources.

The practice of conservation biology often focuses attention on the numbers of individuals present in populations. This is particularly true of most listing efforts, which trigger concern when the number of individuals or populations has fallen to a low level (Wilcove et al. 1993); it is also characteristic of much monitoring effort, which typically seeks to quantify through time the number or density of individuals or populations. This focus on population size results in part from the view that genetic information is at best only indirectly useful in assessing a population (Lande 1988, Menges 1986, Schemske et al. 1994). Inherent in this focus is the assumption that all individuals are equivalent to each other with regard to fitness and that high-quality status information cannot be obtained through assessing status in ways that do not assume that all individuals are equivalent.

Other areas of conservation biology do, in fact, recognize that all individuals are not equivalent. For example, concern among conservation biologists about inbreeding depression or the ability of small populations to respond to selection are founded on the notion that individuals differ in their genetic composition, which may influence their performance. Further, the focus of conservation genetics is on using differences among individuals to provide information on the geographic or taxonomic partitioning of diversity (Avise and Hamrick 1996). Unfortunately, as emphasized by Lynch (1996), there are neither abundant direct empirical connections between such measures of genetic diversity and the processes of primary concern—including mating systems, inbreeding depression, and response to selection—nor strong theoretical expectations of such connections. Consequently, many practitioners of conservation biology are disenchanted with genetic information.

Nevertheless, it is clear that to maintain the integrity of rare plant populations, natural processes must be maintained in both the short and long term. One process of direct relevance in the short term is the mating system. If it is disrupted by habitat fragmentation or by changes in pollinator abundance, for example, plant populations may respond in detrimental ways due to enhanced inbreeding or simply lack of mating opportunities. Further, changes in the mating system must precede any numerical changes in population size due to the mating system, because at a minimum they are detectable in a parental generation whereas abundance cannot change until at least the offspring generation if not much later, especially for perennials.

One process of direct relevance to long-term management is the ability of a rare plant population to respond to selection. In a changing environment, such as induced by human activities, persistence is dependent on an ability to either colonize new habitats or evolve in situ; the latter of course depends directly on the genetic basis of adaptive traits. Because of the direct importance of these processes, management of rare plant populations would be enhanced by tools enabling the ef-

fective monitoring of these and similar processes.

Unfortunately, direct measures of plant mating systems are often difficult, time consuming, or expensive to obtain and therefore not useful for monitoring efforts. For example, to directly monitor mating systems requires tracking pollen from a source flower to a fertilized ovule. This can be done in part through the use of dyes applied to anthers, but many colors of dye are required to differentiate among source plants, it is extremely labor intensive in the field, and selection at the fertilization stage is always neglected (Kearns and Inouye 1993). Quantifying the genetic basis of an ecologically important trait is at least as difficult, and typically requires extensive breeding and culturing facilities; it may not even be possible for rare plants of immediate concern.

Clearly, there is a need for methods that enable managers to obtain information on the status of a population that is as closely related as possible to the processes of mating and the ability to respond to selection. The remainder of this paper serves as an introduction to some methods that accomplish this. Of necessity, to focus attention on the importance of applying these methods to assist natural resource management, just an overview of the detailed quantitative genetics is given. It is hoped that the main point—that genetic information can be used effectively in conservation biology—remains clear and that managers interested in pursuing these methods will initiate collaborations to apply them to practical problems of interest.

Quantitative Genetics

Quantitative genetics (Lynch and Walsh 1998) focuses on disentangling the relative importance of genetic factors to determine the phenotype of traits with a complex basis involving both genetic and environmental influences. Essentially, all traits of interest to conservation biologists are of this sort. For example, morphological traits that influence pollinator response likely involve the interaction of many genes and many environmental factors; fitness and life history traits can be regarded as measurable phenotypes influenced by both genetic and environmental factors. Thus, the tools of quantitative genetics are of direct relevance to the problem of assessing the mating system and the response to selection in rare plant populations.

Quantitative genetics is based on the premise that genetically related individuals will exhibit greater phenotypic similarity than unrelated individuals, and further that a quantitative relationship exists between genetic relatedness and phenotypic similarity (Jacquard 1974).

Relatedness

In the traditional development of quantitative genetics, the relationship between a pair of individuals is described by a set of coefficients, $\Delta = (\Delta_1, \Delta_2, \Delta_3, \ldots \Delta_9)$, each of which represents the probability of the four alleles at a single locus in two diploid individuals sharing a particular pattern of identity by descent (Jacquard 1974). In a large, non-inbred population, only Δ_7, Δ_8, and Δ_9 are nonzero; consequently, any pattern of relationship between two individuals can be described by that set of three coefficients. A useful summary of the degree of relationship described in more detail by these three coefficients is the coefficient of coancestry (Jacquard 1974, Lynch and Walsh 1998),

$$\theta = \frac{1}{2}\Delta_7 + \frac{1}{4}\Delta_8,$$

which quantifies the probability that two individuals will produce an inbred offspring were they to mate.

Molecular genetic data provides information on the patterns of identity-in-state, for example, which nucleotide sequence is present at each of the four alleles in the two individuals. The pattern of identity in state is determined by the allele frequencies in the population and by the genetic relatedness of the two individuals:

$$\Pr(S) = \sum_{i=1}^{9} \Pr(S|S_i')\Pr(S_i') \qquad (1)$$

where S is a particular pattern of identity-in-state (e.g., all four alleles are a specific nucleotide sequence), S_i' is a particular pattern of identity-by-descent, and the coefficients of relatedness $\Delta_i = \Pr(S_i')$. Equation (1) is the likelihood equation (Edwards 1992) for the Δ_i and can be used to estimate the relatedness between pairs of individuals given information obtainable from genetic markers on their genotypes.

As with any estimator of genetic relatedness, the quality of the estimate depends on the amount of available genetic information. Typically, both the number of loci for which genetic information is available and the number of alleles segregating at those loci have strong influences on the variance of the estimate of relatedness. Table 1 illustrates how these parameters affect the variance in the estimate of relatedness based on equation (1). It is evident that precision of the estimate increases with increasing numbers of either loci or alleles per locus.

Table 1. Dependence of the variance in relatedness (θ) on available genetic information. The variance was obtained from 1000 simulations with the corresponding number of loci, alleles, and type of marker expression under the assumption that the three coefficients of relatedness are equal: $\Delta_7 = \Delta_8 = \Delta_9$. In each case the alleles are assumed to be equally frequent.

Loci	Alleles	Expression	Var (θ)
50	2	Codominant	0.007815
50	16	Codominant	0.001701
500	2	Codominant	0.000863
500	16	Codominant	0.000169
50	2	Dominant	0.005432
500	2	Dominant	0.000515

Another major factor influencing the estimation of relatedness from genetic marker information is the phenotypic expression of the markers on a gel. For example, it is much easier to obtain genetic data from hundreds of loci using molecular technology that detects dominant markers, such as RAPDs (Hadrys et al. 1992, Williams et al. 1993) or AFLPs (Lin and Kuo 1995, Vos et al. 1995), rather than using more traditional techniques such as RFLPs or DNA sequencing. Unfortunately, dominant phenotypic expression also typically reduces the amount of genetic information available for estimating relatedness between individuals (Lynch and Milligan 1994). Table 1 also illustrates the effect of dominance on the variance of relatedness. Again, more as opposed to fewer dominant markers provide a better measure (lower variance) of the degree of relatedness. In this case, there is little if any increase in variance for dominant compared to codominant markers, but this is not likely to be a completely general result because of the inherent loss of information due to dominance (Milligan and McMurry 1993). However, these results indicate that at least under some conditions, dominant markers may remain useful for estimating relatedness.

Quantitative Genetics

Traditional approaches to quantitative genetics rely on manipulating or otherwise knowing the degree of relatedness between pairs of individuals, measuring the degree of phenotypic similarity, and using mathematical models (Jacquard 1974) to determine the extent to which genetic variation is responsible for variation in the phenotypic trait. Given that relatedness between a pair of individuals can be estimated using molecular marker data, however, it is possible to estimate the extent of genetic variation from joint marker and phenotypic data, because they are determined by the pattern of relatedness and the degree of genetic variation. Specifically, the joint molecular marker and phenotypic data can be modelled as an extension to equation (1):

$$\Pr(S,Z) = \sum_{i=1}^{9} \Pr(S|S_i')\Pr(Z|S_i')\Pr(S_i') \qquad (2)$$

where Z represents the phenotypic information, and S and S′ are, as before, a particular pattern of identity-in-state and a particular pattern of identity-by-descent. Note that equation (2) is essentially the same as equation (1) with the addition of a term for the phenotype Z. Given the joint marker (S) and phenotypic (Z) data, one can estimate both the relatedness (Δ) and the degree of genetic variation, which is often quantified by the additive genetic variance and appears in equation (2) as a parameter of $\Pr(Z|S_i')$.

Figure 1 illustrates an example of jointly estimating the additive (V_A) and environmental (V_E) variance components, along with relatedness. Although there is some variation in the estimates, there is no obvious statistical bias. The approach to estimating the genetic basis of a quantitative trait from joint molecular and phenotypic data is feasible.

Applications to Conservation Biology

The previous section briefly outlines methods for addressing quantitative genetics in the field and estimating properties of natural populations that are relevant to conservation biologists. However, the application of these methods may not be transparent from an introduction to the theory.

To monitor mating systems, one must be able to quantify the pattern of relatedness between individuals. Ideally, that quantification would be carried out periodically to provide insight into how the patterns change through time as a result of environmental conditions, pollinator interactions, or human activities. As outlined above, the necessary information consists solely of a collection of genetic marker data (e.g., allozyme- or DNA-based genotypes) for each individual sampled. Ideally, many loci would be studied, but markers exhibiting either codominant or dominant expression are useful, as are mixtures of the two. In many cases, it will only be possible to obtain information on a few codominant loci and many dominant ones. For each pair of individuals sampled, the methods outlined earlier provide estimates of how closely related are they. Conse-

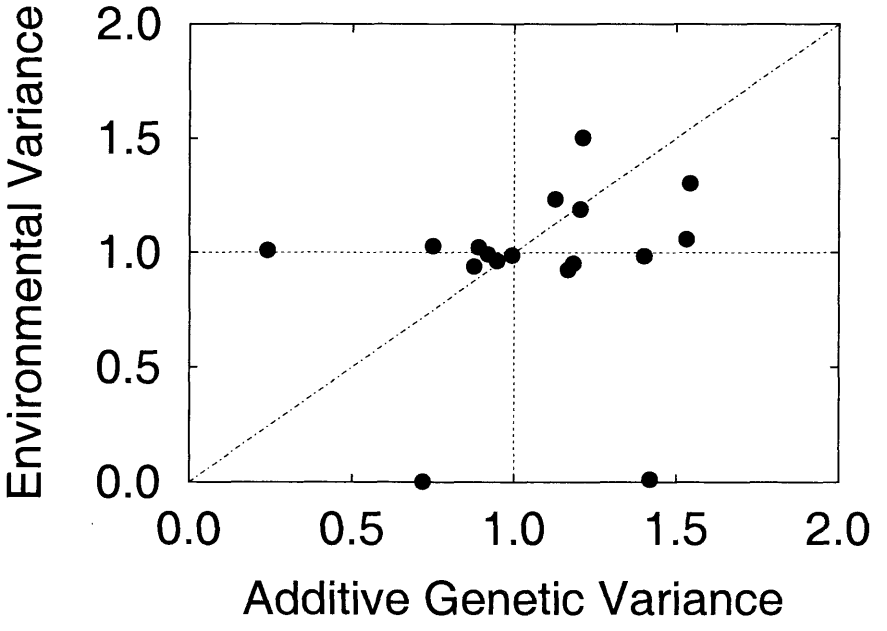


Figure 1. Estimation of variance components. Each point represents the estimate obtained from a single replicate simulation under the assumption of $V_A = V_E = 1.0$; those two parameter values are signified by the vertical and horizontal dotted lines. The dashed line represents values of the variance components corresponding to heritability = $h2 = \frac{V_A}{V_A + V_E} = 0.5$.

quently, a large sample of individuals provides a picture of the distribution of pairwise relatedness found in the population at the time it was sampled. Comparisons of such distributions across a temporal sequence of samples provides information on such things as whether the mean relatedness is increasing as might be expected in a small, inbreeding population, or whether the variation is expanding as might be expected if some individuals are able to attract pollinators from distant pollen sources and the remainder largely mate with nearby relatives or self. Such knowledge can provide an early indication of biological effects that later could influence persistence.

To monitor the ability of a population to respond to selection, one must be able to quantify the components of variance contributing to phenotypic variation among individuals. In the simplest case, this involves disentangling the additive genetic (V_A) from the environmental (V_E) variance for each trait of interest. Again, this quantification would ideally be carried out periodically to identify changes in the genetic basis of important traits such as fitness, floral morphology, or drought tolerance. In addition to the genetic marker data described above, measurements of each relevant phenotype must be obtained for each individual. The joint marker-phenotype data yield estimates of both relatedness and the variance components. Comparisons of the variance components across a temporal sequence of samples provides information on such things as whether the additive genetic component, which determines the response to selection (Lynch and Walsh 1998), is declining as might be expected in small populations losing genetic variation. As with knowing how relatedness changes through time, this knowledge of how genetic variation for adaptive traits changes can provide an early indication of biological effects that will increase in importance through time.

Discussion

Although the direct relationship between molecular marker data (e.g., allozyme diversity, RFLPs, or DNA sequences) and factors that affect risk of extinction for plant populations is unclear (Lynch 1996), quantitative genetics approaches can provide more direct measures of risk factors such as changing mating systems or reduced ability to respond to selection.

To take advantage of the approaches to conservation genetics outlined here, studies must be designed to provide both genetic and phenotypic information. Marker data alone can be used to

determine the patterns of genetic relatedness, which in turn are important in monitoring mating systems. In conjunction with phenotypic data on the same individuals, however, one can monitor the degree of underlying genetic variation for ecologically important traits. These traits include the fitness components themselves, as well as morphological traits that influence pollinator interactions or physiological traits the determine growth rates, drought stress, or disease resistance. Thus, it is important for managers to become aware of these possibilities and design their research appropriately.

A number of benefits arise from monitoring biological processes through the use of quantitative genetics. The most significant of these is that the processes being monitored are of direct importance to rare plant populations. For example, by monitoring patterns of relatedness between individuals one may detect the effects of fragmentation or altered pollinator fauna, which affect mating patterns. Effects on the mating system will undoubtedly be detectable long before the population has changed in size or otherwise responded in a way that is visible by non-genetic means.

Another example is that, by including quantitative genetics within a monitoring program, one may be able to track the ability of a plant population to respond to selection. This is particularly critical because the persistence of rare plant populations necessarily involves one of two options: colonize new habitats or evolve in situ. By estimating such quantities as additive genetic variance, one can ascertain whether or not the second option remains viable as a long-term persistence mechanism. One could also determine whether ex situ preservation efforts maintained, for example, by botanical gardens or germplasm storage facilities are reducing an accession's ability to adapt when it is reestablished in natural habitat.

One very large advantage of the quantitative genetics approaches introduced here is that they can be applied to natural, unmanipulated field situations. The estimates obtained apply directly to the population under study and there is no need to manipulate the mating system of individuals. These features are particularly attractive for studies of rare plants, because it is often impossible for either managment or ethical reasons to manipulate them to the extent typically required by traditional quantitative genetics.

At the very least, this paper illustrates that it is possible to quantify, in natural populations, biologically important processes of relevance to conservation biology. By expanding the scope of monitoring to consider the fact that all individuals within a population are not equivalent, and to use that as a source of important information, one gains the ability to detect changes long before they might otherwise be visible. Even though the tools of quantitative genetics may be complex to the uninitiated, they can provide an excellent means of using genetic data to enhance understanding and management.

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Preliminary Report on the Reproductive Biology of the Threatened Chisos Mountain Hedgehog Cactus

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Abstract: The Chisos Mountain hedgehog cactus (*Echinocereus chisoensis*, Cactaceae) is a narrow endemic restricted to an approximately 100 square mile area in Big Bend National Park, Texas. It was listed as threatened in 1987 as *Echinocereus chisoensis* var. *chisoensis*. An investigation of the reproductive biology and pollination ecology conducted in 1999 and 2000 revealed the taxon to be homogamous, self-incompatible, xenogamous, and heavily dependent upon the cactus oligolectic bee, *Diadasia rinconis* (Anthophoridae) for pollination. Despite infrequent bee visitation, fruit set from open pollination is high and fruits produce large numbers of seeds. Predation in 2002, probably from rodents as a result of severe drought conditions, was severe on plants, flower buds, and fruits.

The Chisos Mountain hedgehog cactus, or Chisos pitaya (*Echinocereus chisoensis* W. Marshall), is 1 of 20 threatened or endangered cacti listed by the U.S. Fish and Wildlife Service for Region 2 (http: // ecos. fws.gov/ webpage/ webpage_lead.html? lead_region=2&type=L&listings=1). In 1987 it was added to the federal lists (53 FR 38453) of endangered and threatened wildlife and plants as threatened because of its restricted distribution, low numbers, loss of viability in existing populations, vulnerability to private and commercial cactus collectors, and habitat disruption (U.S. Fish and Wildlife Service 1993). As with other protected cacti, the lack of basic scientific information about the species is limiting the ability of conservation agencies to evaluate the limiting factors and to prescribe management activities. This study, which is part of a long-term investigation of the taxon's life history, presents a description of the pollination ecology and breeding system of *E. chisoensis* and a discussion as to how these features relate to the species' fitness.

Echinocereus chisoensis, a small cylindrical cactus, is restricted to flat alluvial fans and terrace deposits in Big Bend National Park in Brewster County, Texas at elevations of 650–750 m in well-developed desert hardpan of the Chamberinos, Pantera, and Upton-Nickel soil associations (USDA Soil Conservation Service 1985). Plants are typically found growing either under or within dominants of the lowland desert shrub community. Common associates are dog cholla (*Opuntia schottii* G. Engelmann), creosote (*Larrea tridentata* (DC) Cov.), ratany (*Krameria grayi* Rose & Painter and *K. erecta* C. von Willdenow ex J. A. Schultes), whitethorn acacia (*Acacia constricta* A. Gray), tasajillo (*Opuntia leptocaulis* DC.), ocotillo (*Fouquieria splendens* K. Kunth), leatherstem (*Jatropha dioica* V. de Cervantes), lechuguilla (*Agave lechuguilla* J. Torrey), and ceniza (*Leucophyllum frutescens* (J. Berlandier) I. M. Johnston). An earlier study (Hendershott et al. 1992) did not show specific *E. chisoensis*–nurse plant associations, but rather showed associations as a consequence of soil conditions that provide a hospitable environment for a diversity of species or the exploitation by *E. chisoensis* of conditions that are provided by the presence of any nurse plant. The *E. chisoensis* habitat is shared with several other cacti, including blind prickly pear (*Opuntia rufida* Engelm.), purple prickly pear (*O. macrocentra* Engelm.), brown-spine prickly pear (*O. phaeacantha* Engelm.), strawberry cactus (*Echinocereus stramineus* (G. Engelmann) F. Seitz), rainbow cactus (*E. dasyacanthus* G. Engelmann), devil's-head cactus (*Echinocactus horizonthalonius* C. Lemaire, *Echinomastus warnockii* (l. Benson) C. Glass & R. Foster), and coryphantha (*Coryphantha macromeris* R. O. Baird, *C. echinus* (G. Engelmann) N. Britton & Rose)).

Material and Methods

Data were collected over a 2-week period in mid-March 1999 and 2000 at two sites, designated as S1 and ET, that are approximately 4 miles apart. In 2000 additional observations were made approximately every 3 days until April 22. In 1999 *E. chisoensis* plants at the two sites were mapped and individual plant locations were marked with numbered metal tags for subsequent identification of individual plants. In 2000 additional plants were marked at each site to increase sample sizes. Observations and crossing experiments were made

with these plants (1999 S1, n = 50; 2000 S1, n = 84; 1999 ET, n = 34; 2000 ET, n = 70), and additional observations of insect visitors were made on unmarked plants.

Phenology

Floral phenology was determined by daily observation of marked plants. Events noted consisted of the time of day the flower opened and closed, flower longevity, pre-pollination and post-pollination floral behavior, the time of anther dehiscence, and the relative position of floral parts. The number of open flowers by individual plant was recorded each day. The status of buds, flowers, and fruits was monitored for each plant throughout the study.

To determine stigma receptivity, bagged flowers (n = 18) were cross pollinated and self-pollinated by hand at 1 hour intervals beginning at 1000 hrs CDT and continuing to 1500 hrs. Between 0800 and 0915 hrs the following morning, styles were excised and preserved. They were then stained and the stigmas were examined for pollen tube growth with a fluorescence microscope (Martin 1959). Four of the flowers with excised stigmas were marked for later evaluation of seed set. In another test, pollen germination was compared between cross and self-pollinated flowers (n = 16). For this investigation, either plants having two open flowers were used with one flower receiving cross pollen and the other flower receiving self-pollen, or for plants with only a single open flower, half of the stigma received cross pollen and the other half was self-pollinated. Stigmas were collected 2 hours after treatment; they were preserved, stained, and examined for pollen tube growth using a fluorescence microscope (Martin 1959).

Breeding Systems

The breeding system of *Echinocereus chisoensis* was defined through a series of crossing experiments. Pollination was controlled throughout the life of the flower by covering flowers, beginning with mature buds, with insect exclusion bags made of bridal veil fabric. Individual flowers were color coded by treatment with either plastic cable ties or yarn to track fruit development. To determine the role of self-pollination or apomixis, flowers (n = 28 in 1999, n = 16 in 2000) remained covered. Self-compatibility was tested by hand pollinating flowers (n = 37 in 1999, n = 37 in 2000) with their own pollen. In cross-compatibility tests in 1999, flowers (n = 55 in 1999) were hand pollinated using pollen harvested from at least three distant plants. In 2000, cross pollinations (n = 60) were made with pollen from only a single plant, and for 38 of the crosses the distance between the parents was measured. For comparison, fruit set from open pollinated flowers (n = 143 in 1999, n = 71 in 2000) was obtained by marking flowers that were not caged. In 1999 a sample of fruits (n = 63) was harvested for each treatment from each site, and they were sent to the Desert Botanical Garden in Phoenix where the numbers of seeds per fruit were counted. Results from the remaining treatments were recorded as either aborted fruit or set fruit. Chi-square tests (Sokal and Rohlf 1981) were used to determine if significant differences exist among treatments or between populations for fruit set. An analysis of variance was used to determine if the number of seeds produced per fruit was significantly different by treatment or by site. A pollen/ovule ratio and an outcrossing index (Cruden 1977) were prepared as another means of predicting the breeding system.

Attractants and Rewards

The presence of nectar was determined by observing the behavior of insect visitors and by using microcapillary tubes to probe flowers that were protected from insect visitors. Pollen production was estimated by placing all of the anthers of a single flower in a known volume of 3:1 lactic acid/glycerine solution, macerating the anthers to liberate the pollen, and then shaking the suspension with a Vortex Junior Mixer for 30 seconds. A small sample of the pollen suspension was removed with a pipette and placed on a hemocytometer. Pollen grains in the four corners and center square of the hemocytometer were counted, with repetitive counts made for each flower (n = 6). The number of pollen grains for the flower was estimated through the known volume of suspension (Dafni 1992). The number of ovules was determined by dissecting a mature ovary, and with the aid of magnification, counting the ovules.

Flower color was described using the *Naturalist's Color Guide* (Smithe 1975). Floral insect colors and patterns were determined by photographing the flowers, along with a gray scale for comparison, with Tri-X black-and-white film using a series of monochromatic filters (Kodak 35, 61, 48, 25, 65, 18). The resulting photographs were analyzed using Kevan's (1978, 1983) trichromatic technique for insect vision.

Pollen Vectors

Pollinators were determined through observation of flowers and visitors' intrafloral behavior. Voucher specimens of pollinators (i.e. those exhibiting appropriate floral behavior) were collected and sent to appropriate experts for identification.

Results

Phenology

Echinocereus chisoensis flowers have on average a 61.5 mm (SD ± 11.3) outside diameter, ranging from 34 to 85 mm (n = 28). The inside diameter is on average 35.7 mm (SD ± 9.6), ranging from 26 to 46 mm (n = 23). The degree of tepal reflex is determined by environmental conditions, but flowers usually remain cup shaped at full anthesis. The tricolored tepals are showy. The outer tips of the tepals are magenta-rose with a mid-circle of white followed by a band of deep magenta at the tepal base. The time of flower opening and closing varies with ambient temperature, sunlight, and wind, but typically during the peak flowering period flowers open between 0900 and 0930 hrs CDT (ranging from as early as 0800 hrs to as late as 1100 hrs) and close at approximately 1630 hrs (ranging from 1330 hrs to 1730 hrs). Most flowers last a single day, with rare individuals lasting two days. Anther dehiscence closely coincides with time of flower opening. Stamens are numerous and are attached to the bottom and along the curved sides of the floral cup. As a result anthers achieve different heights, with those nearest the style the shortest and those attached on the outer circle, the tallest. At first the stamens are bunched around the style. Shortly after the flower opens or with the first visitation, the stamens become vertical and no longer crowd the style. The anther mass is from 5 to 12 mm (μ = 9.1 ± 1.3 mm, n = 28) below the stigma. The green stigma is multi-lobed (ca. 10–17) with surface diameter ranging from 4 to 17 mm (μ = 8.9 mm ± 3.4, n = 18). The lobes of the stigma may be vertical, spread horizontally, or spread with the tips erect. Regardless of initial position, the lobes do not change position appreciably during the life of the flower.

Pollen germination commences approximately 2 hours after cross pollination regardless of time of pollen deposition (1000 hrs CDT, 1100 hrs, 1200 hrs, 1330 hrs), suggesting similar stigma receptivity throughout the life of the open flower. Stigmas harvested approximately 17 hours after pollination did not interfere with seed production, indicating rapid pollen tube growth through the style. Results were inconclusive concerning pollen germination on self-pollinated stigmas.

Flower production begins around March 12 followed by a 2-week peak flower production. At S1 in 2000 the 84 plants observed produced a total of 273 flowers (including 17 flowers that had opened prior to the observation period) from shortly before March 12 to April 8, with 95 percent of the flower crop expended by March 24 (Figure 1). Likewise, in this period, 85 percent of the plants had completed flowering. In comparison, the ET population showed a slight delay in flowering with only 2 of the 169 flowers appearing before March 12. By April 10, 95 percent of the flowers had been produced and 85 percent of the 70 plants under observation had completed flowering (Figure 2). The percentage of flower completion at ET is skewed slightly because of the April 1 production of 21 flowers, 15 of which were produced on two plants. Flower production follows mast cycling with flowers appearing for 2 or 3 days followed by a day or more of no or few flowers (Figures 1 and 2). For the 2 study years, early March to mid-April defines the flowering period. On a few occasions, new flower buds were formed late in the flowering period. In years with adequate rainfall, the flowering period may be prolonged beyond what was observed during the droughty study period.

Of the 154 plants observed for flower production, 25 failed to produce flowers (Figure 3). At ET the cause was predation of flower buds (14) or, in one case, the death of the plant. At S1 plants either did not produce buds, buds stopped development, or they were eaten. Most plants (125) produced four or fewer flowers; 29 of the plants produced five or more flowers (Figure 3) with the record number of 17 flowers produced by an ET plant having seven stems. Generally, plants producing more than four flowers were multi-stemmed or multi-headed plants (3.16 average number of stems per head for plants with five or more flowers versus 1.46 for plants with fewer flowers).

Unsuccessful crosses result in abortion of the ovary approximately 1 week after flowering. When the ovary falls, there is a distinct depression surrounded by white cottonly trichomes on the stem where the ovary was attached. Fruits take approximately a month to mature, with little change in coloration. The dry fruits dehise longitudinally.

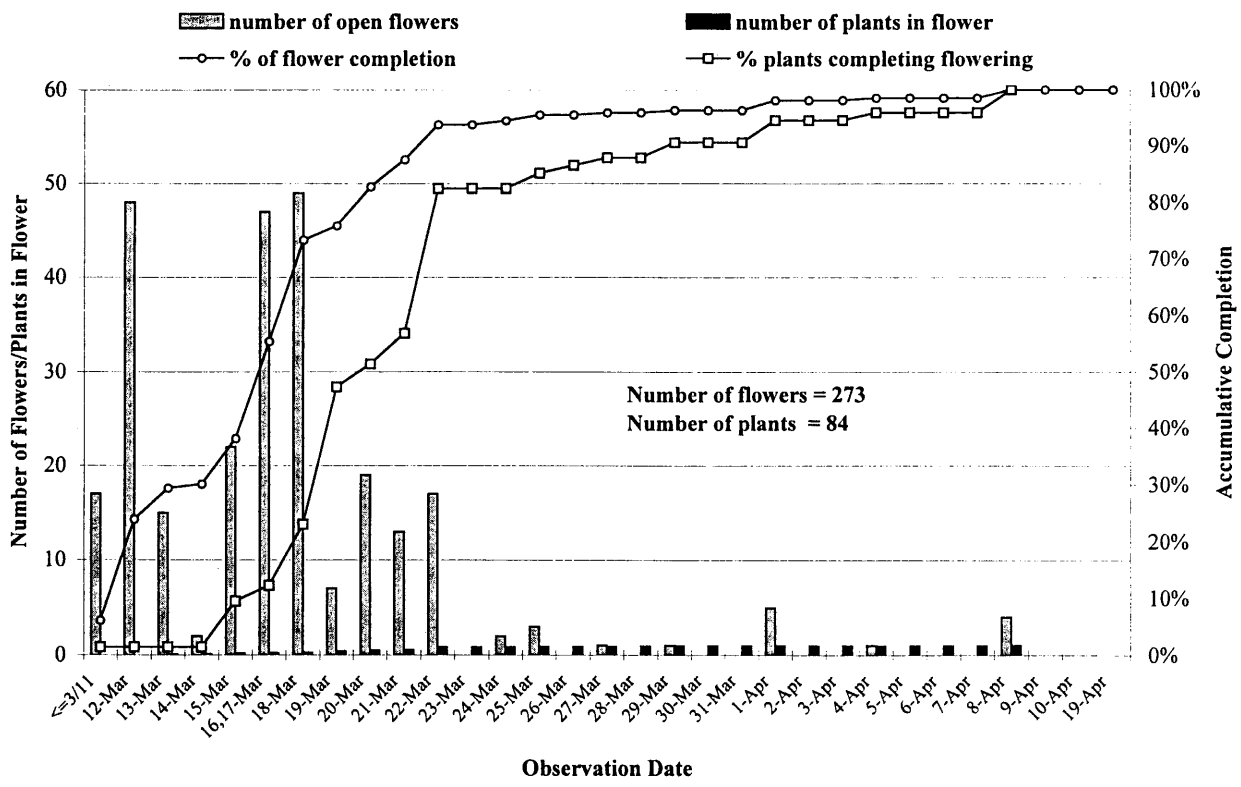


Figure 1. Flower production for S1 in 2000 with the bars showing the number of open flowers each day and the number of plants that produced flowers each day. The lines show accumulative completion of flower production as a percentage of flowers produced and by the percentage of plants completing flower production.

Breeding System

Results from non-manipulated and self-pollination tests were similar with few of the 44 non-manipulatechd flowers (1999, 11%; 2000, 0) or the 74 self-pollinated flowers (1999, 8%; 2000, 5%) forming fruits (Table 1). Chi-square tests showed no significant difference between sites or years (all $p > 0.05$). In 1999 fruit production was high for both the cross-pollinated (93%) and open-pollinated flowers (90%). There was no significant difference between the treatments.

In 2000 many of the ovaries from the cross-pollination (67%) and open-pollination (63%) tests were eaten. Fruit set data for non-manipulated and self-pollinated treatments were less affected because failure to set fruit is typically marked by abortion of the ovary about a week after flowering (Table 2). To use data from the 2000 crossing experiments, a Kruskal-Wallis non-parametric one-way analysis of variance was used to compare the number of days from treatment to result, with the result being defined as abortion, eaten fruit, or mature fruit. Results for self-pollinations were compared with cross and open pollinations. Because this analysis showed a significant difference (x^2 approximation = 54.6, df = 1, $p < 0.01$) between the two treatments, it is likely that ovaries that remained on the plant longer than the average for self-pollinations were forming seeds and being recorded as set fruit. Based on this assumption, comparisons between years showed no marked difference in regard to treatment or site (Table 1).

Based on breeding study results, *E. chisosensis* is self-incompatible, requires a pollinator, and is xenogamous. This is supported by a pollen/ovule ratio of 1416.7 which is within the range for facultative xenogamy (Cruden 1977). An outcrossing index of four also defines *E. chisosensis* as an outcrossing species (Dafni 1992).

Seeds per fruit ranged from 0 to 758, with an average of 399 (n = 73). For fruits with one or more seeds, there was no significant difference (F = 2.03,

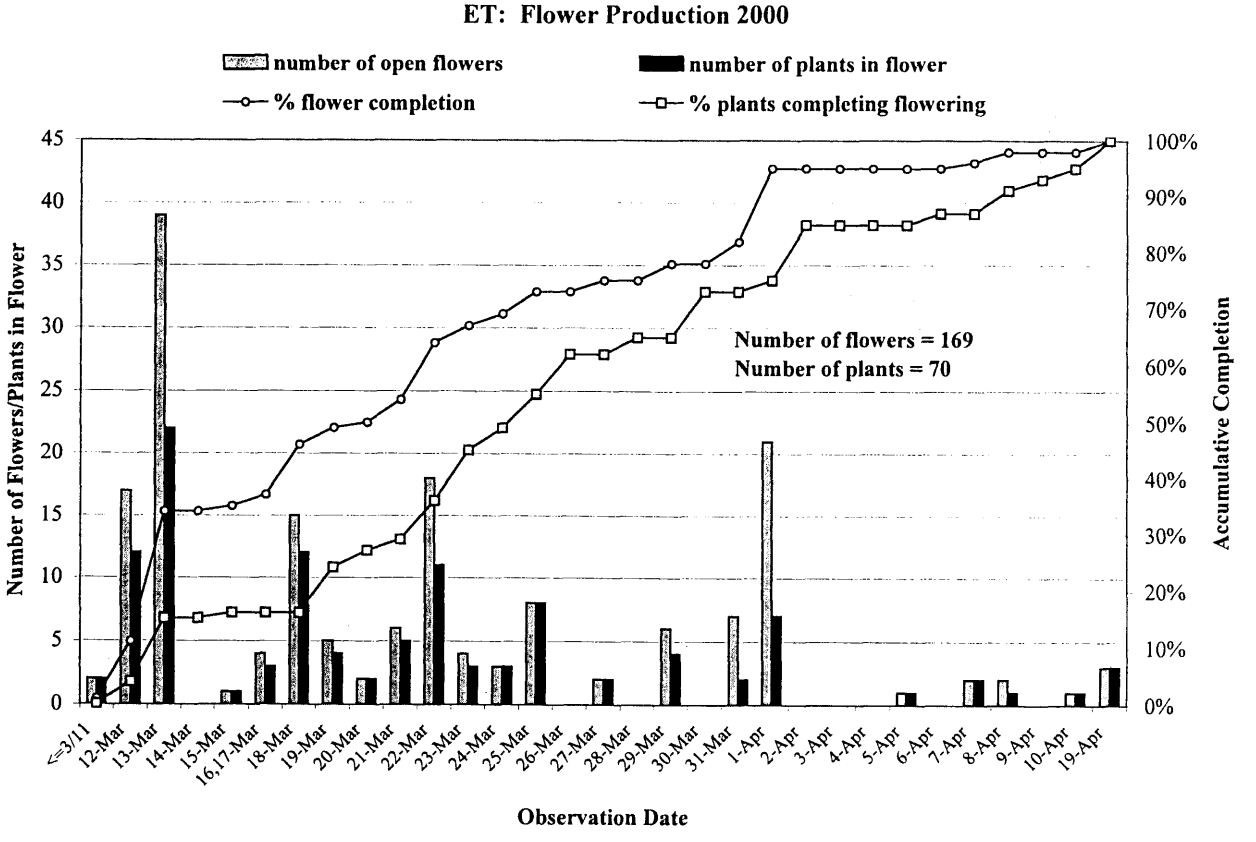


Figure 2. Flower production for ET in 2000 with the bars showing the number of open flowers each day and the number of plants that produced flowers each day. The lines show accumulative completion of flower production as a percentage of flowers produced and by the percentage of plants completing flower production.

df = 3, 63, p = 0.11) in the number of seeds formed at each site or between treatments (Table 3). Because of the rarity of fruit formation for the non-manipulated and self-pollinated treatments, only three fruits were harvested for each of these treatments and these six fruits are probably a result of experimental contamination. The bridal veil exclusion cages must be loosely attached to the cactus to prevent damaging the plant and are occasionally partially dislodged by the wind, allowing insect access. Self-pollinations conducted on three of the six plants in 2000 did not result in fruit formation.

In 2000, cross pollinations were made between parents separated by distances ranging from less than a meter (3 dm) to 157 meters. Only one of the flowers (2.7 m) failed to initiate fruit development (seed counts could not be evaluated because of high loss of fruits to predation). Based on these limited data, the distance between pollen donor and seed plant is not a limiting factor in successful reproduction. This study also involved only a single pollen donor for each cross, as compared to the use of three or more in 1999 cross pollinations. The high success with one pollen donor suggests

Table 1. Results from breeding experiments. Fruit set for cross- and open-pollinated treatments for 2000 are estimates. Due to predation, fruit set was based on how long fruit remained on the plant following treatment rather than mature fruits, as in 1999.

Treatment	N / Number of fruits formed	Percentage fruit set
1999		
Non-manipulated	28/3	11%
Self-pollinated	37/3	8%
Cross-pollinated	55/51	93%
Open-pollinated	143/129	90%
2000		
Non-manipulated	16/0	0%
Self-pollinated	37/2	5%
Cross-pollinated	60/54*	90%
Open-pollinated	71/70**	99%

*Six fruits aborted, 15 partially eaten, and 25 completely eaten.
**One fruit aborted, 5 partially eaten, and 40 completely eaten.

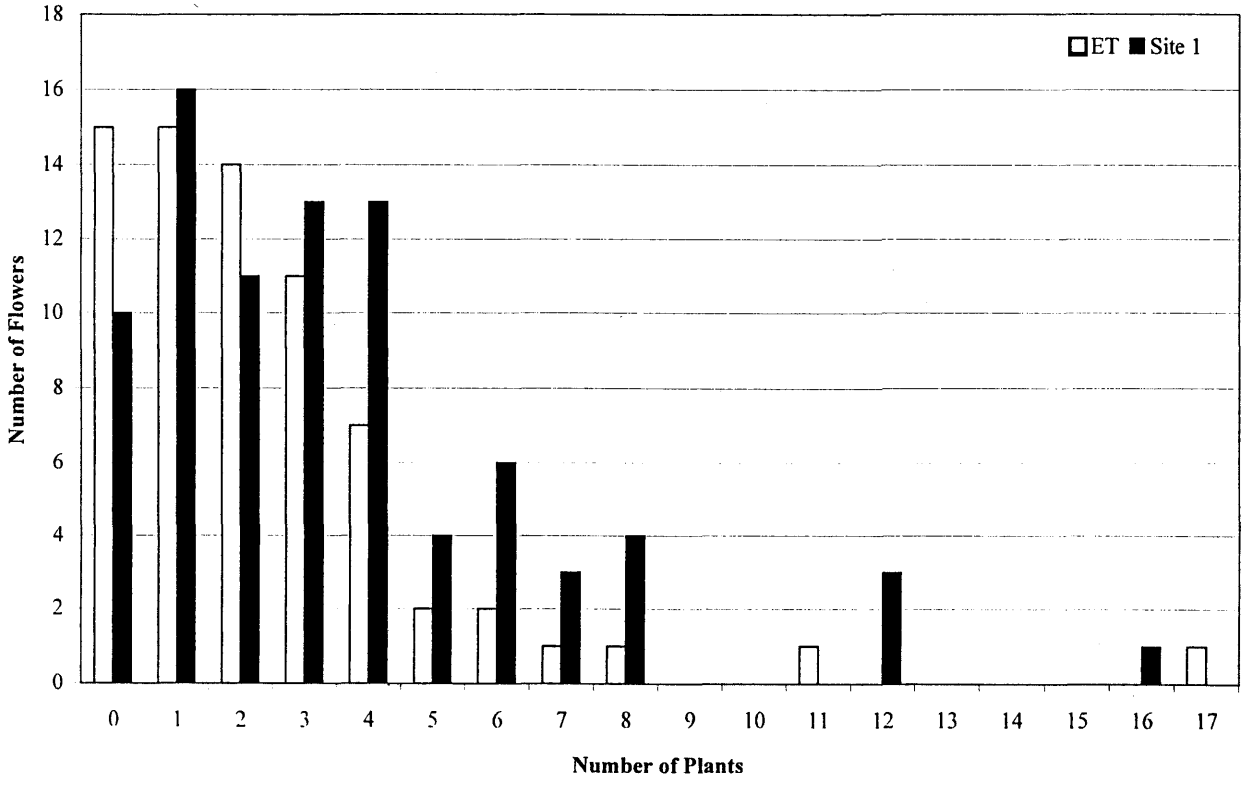


Figure 3. Number of flowers produced by each of the marked plants in 2000.

that pollinators may be equally successful even with short foraging distances or limited diversity in pollen loads.

Floral Attractants and Rewards

Insect visitors were observed harvesting pollen and foraging for nectar. However, nectar production is scanty, at best, because none could be collected using microcapillary tubes on protected flowers at any time during the day. Copious amounts of large, spiny, yellow pollen are produced in each flower (μ = 495,833 ± 185,133 per flower, n = 6). Flowers have a faint sweet aroma. The color pattern for bees is similar to that for humans. The tepals are tri-colored: insect green at the tips followed by a mid-circle of insect yellow, then insect red at the tepal base. The anthers are insect red-orange and the stigma is insect blue-purple. Studies comparing pre- and post-pollination colors and population variation are not complete.

Pollen Vectors

The frequency of all floral visitors was low (i.e. one visitor approximately every 30 min). Diversity of potential pollinators was also low with only three species of bees, *Megachile sidalceae* (Megachilidae), *Dialictus* sp. (Halictidae), and *Diadasia rinconis* (Anthophoridae) collected from the flowers. *Megachile sidalceae* was a rare visitor. The small polylectic *Dialictus* sp. bees were more frequent but ineffective pollinators because they entered and exited the flower without coming in contact with the stigma. The most frequent flower visitor was the mid-sized bee *Diadasia rinconis*. Males foraged for nectar and hunted for females while females visited the flowers for nectar and pollen. Floral arrivals and departures for both males and females occurred on and from the stigma. A single foray within the styles by a *Diadasia* resulted in a liberal dusting of pollen on the bee's body, the inner surface of the tepals, and, upon departure,

Table 2. The average number of days with the standard deviation from the day of flowering in 2000 by treatment to result, with result being defined as aborted fruit, eaten fruit, or harvested fruit. Data for the two sites are combined.

Treatment	Average number of days to result	N
Non-manipulated	8.7 ± 4.5	18
Self-pollinated	11.3 ± 7.6	36
Cross-pollinated	32.1 ± 7.0	59
Open-pollinated	32.4 ± 4.2	72

Table 3. Results from seed counts for 1999 by treatment.

Treatment	No. fruits counted	Range seeds per fruit	Avg seeds per fruit
Non-manipulated	3	457-599	545 ± 77
Self-pollinated	3	14-749	261 ± 423
Cross-pollinated	29	141-758	395 ± 162
Open-pollinated	38	158-735	401 ± 123

the stigma. Subsequent visits to other flowers resulted in pollination.

Diadasia is oligolectic on Cactaceae, especially *Opuntia* (Hurd 1979, Ordway 1987). *Diadasia rinconis* has been listed as an important pollinator or floral visitor for several cacti, including *Echinomastus erectrocentrus* var. *acunensis* (Johnson 1992), *Echinocereus engelmannii* var. *acicularis* (Johnson 1992), *Opuntia phaeacanth*ha (Osborn et al. 1988), *Echinocereus dubius* and *E. stramineus* (Breckenridge and Miller 1982), *Opuntia lindheimeri, O. discata* (Grant et al. 1979), and *Opuntia basilaris* var. *treleasei* (Grant and Grant 1979a). In central Texas, Neff and Simpson (1992) reported *D. rinconsis* visiting flowers of *Opuntia engelmannii* var. *lindheimeri, O. leptocaulis, O. macrorhiza, Echinocereus reichenbachii,* and *Ferocactus setispinis*. When described, the intrafloral behavior for *D. rinconis* in these cacti is similar to what was observed in *E. chisoensis*.

Discussion

Echinocereus chisoensis displays the features characteristic of Southwestern Cactaceae flowers: medium to large brightly colored bowl-shaped flowers, copious yellow pollen, large stigma, and little to no nectar. It differs from other *Echinocereus* species (Breckenridge and Miller 1982, Johnson 1992, Leuck 1980, Grant and Grant 1979b) in having a flower that lasts a single day rather than 3–4 days. It is homogamous, a feature it shares with members of the *E. viridiflorus* complex, differing from the protandry of other Southwestern *Echinocereus* studied thus far. It is obligately xenogamous and heavily dependent upon the primary pollinator, the oligolectic cactus bee, *Diadasia rinconis*. Despite infrequent insect visitation, at least from the perspective of a human observer, there is no evidence of pollinator limitation as shown by the high percentage of open fruit set and no significant difference between hand cross-pollinated and open-pollinated seed set. Based on these first observations, the taxon's precarious existence does not appear to be directly related to its breeding system or pollination ecology.

Several caveats must be mentioned. The two populations studied thus far are the largest known for the species. These populations are large enough to attract sufficient numbers of pollinators. There is also apparently enough variability present in the population to prevent self-incompatibility from reducing seed set. Many *E. chisosensis* plants occur in small, isolated populations, some containing fewer than a dozen plants. Reduced population size, especially for an obligate xenogamous species, can have dramatic effects on reproductive output (Petanidou et al. 1995). Pollinator behavior and the number of pollen grains transferred are influenced by the geometry (i.e. size, density, shape) of a plant population (Handel 1983). Future studies will compare the reproductive success of the small populations with the larger ones and define the genetic variation for both small and large populations.

Abundant seed was produced in 1999 and would have again in 2000, except for predation caused by dry conditions. Without seed viability tests, we cannot evaluate the value of the seed rain and cannot totally eliminate the breeding system as a possible factor in poor recruitment. Very few seedlings have been observed in the field, albeit they are difficult to find with the nurse plant association. Future studies will address seed viability, germination requirements, and seed and seedling predation.

Another condition to consider is the drought of 1999 and 2000. Rainfall during both of the study years was less than average. In 1999, Rio Grande Village (RGV) and Panther Junction (PJ), the two nearest rainfall collection sites to the populations, showed a respective 27 percent and 31 percent decline in rainfall from 14-year averages of 9.41 (RGV) and 14.30 (PJ) inches (Big Bend National Park Communications Center Weather Data). Other than cacti, few species were in flower at either site. In years with more rainfall, floral resources will be more diverse. Leuck (1980) suggested that reproductive output in the *Echinocereus viridiflorus* complex may be higher during inclement conditions because the cactus flowers are virtually ignored in the presence of taxa with more substantial nectar rewards. However, the primary pollinators reported for *E. virdiflorus* flowers were solitary halictid bees rather than a cactus oligolege. Regardless, both polylectic bees with marked flower preferences and oligolectic bees are known to change floral species in dry years when their preferred hosts are rare or absent (Hurd and Linsley 1975).

If there is a strong dependency upon a single species of pollinator, such as suggested in this 2-year observation, fruit set will be more precarious because undoubtedly pollinator availability will differ from year to year. For example, in their discussion of partial bivoltinism in central Texas, Neff and Simpson (1992) observed 2 years in which *Diadasia rinconis* populations had low densities, despite abundant and appropriate floral resources. They concluded that this may reflect a pattern of skipping years in which a significant proportion of the *D. rinconis* population apparently spends 2 years rather than the usual single year in diapause.

Of particular interest is the continued study of the reproductive relationship between *E. chisoensis* and the other cacti, particularly the *Opuntia*, that share the habitat. *Diadasia rinconis* is a cactus oligolege but perhaps with a preference for *Opuntia* (Neff and Simpson 1992). When there is direct competition for pollinators, one species often competes more successfully than the other (Mosquin 1971). Small populations of rare species, particularly those less effective in attracting pollinators, may be prone to reduced seed set (Petanidou et al. 1995). The flowering period of *E. chisoensis* appears to begin about a week before the sympatric *Opuntias*. Does an earlier flowering time reduce competition between *E. chisoensis* and the *Opuntia*? With the vagarious nature of desert weather, timing of flowering of the cacti in the community is rarely absolute. In years with overlap in flowering times, does *E. chisoensis* produce as many fruits? Does *E. chisoensis* provide resources for the initial *Diadasia* populations which are then available to pollinate the later flowering *Opuntias*, providing pollination facilitation (Petanidou et al. 1995) or sequential mutualism (Mosquin 1971)? These are a few of the questions to be addressed in future years.

Acknowledgments

We thank Kelly McCoy, Angelo State University, for statistical assistance; Kathy Rice, Desert Botanical Garden, for seed counts; Terry Griswold, Utah State University, for bee identifications; Big Bend National Park (BBNP) for allowing the research to be conducted; and the Angelo State "hedgehog crew" of Sam Lightsey, Jason Neil, Mark Pourner, John Shelton, Larisa Watson, and Jody Davila (BBNP) for help in the field. The research was supported in part with a Beta Beta Beta Undergraduate Research Grant and an Angelo State University Carr Undergraduate Research Scholarship awarded to C. Vassiliou. Research was conducted under U.S. Fish and Wildlife Service permit TE006210-0 and Big Bend National Park permits BIBE-98-15 and BIBE-2000-017.

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Dalmatian Toadflax, an Invasive Exotic Noxious Weed, Threatens Flagstaff Pennyroyal Community Following Prescribed Fire

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Abstract: Many noxious weed infestations are initiated or increased by soil disturbance. With the recent emphasis on reintroduction of fire into natural ecosystems there has been increased interest in the effects of noxious weeds following fires. This paper discusses the effects of fire on Flagstaff pennyroyal, a Forest Service Region 3 sensitive plant, and the subsequent infestation of the project area by Dalmatian toadflax (*Linaria genistifolia* ssp. *dalmatica*).

Flagstaff pennyroyal (*Hedeoma diffusum* Greene) grows on Kaibab limestone soils adjacent to Flagstaff where forest restoration and fuel reduction projects are planned or underway. A prescribed burn study conducted on the Coconino National Forest from 1989 to 1995 showed that after burning, Flagstaff pennyroyal produced larger plants with more abundant flowers and had increased seedling recruitment and survivorship due to increased soil nutrients and reductions in duff, needle litter, and canopy closure.

During a follow-up reconnaissance of the Flagstaff pennyroyal prescribed burn area in 1999 we found that the burned area had been invaded by the noxious weed Dalmatian toadflax (*Linaria genistifolia* ssp. *dalmatica* [L.] Maire and Petitmengin), a member of the Figwort family (Scrophulariaceae). Recent post-fire vegetation studies in Southwestern ponderosa pine forests have shown dramatic increases in total cover of exotic plants in both moderate and high-severity burn areas (Crawford et al. unpublished data, Foxx 1996). In their studies of three 1996 wildfires in northern Arizona (Bridger Knoll, Pot, and Hochderffer), Crawford et al. found the highest cover of exotic species on the Hochderffer fire in high-severity burn areas. In both the Pot and Bridger Knoll fires, there was also an increase of exotic species in the moderately burned areas. The exotic plant cover occurred only in trace amounts in unburned patches.

Native to the Mediterranean regions of western Asia and Europe, Dalmatian toadflax is a fire-adapted species in its southeastern European homeland and has become prevalent on the Coconino National Forest, invading an estimated 80,000 ha. This perennial weed, found mainly in the northeastern and western United States and western Canada, was brought to the west coast of North America as an ornamental about 1874. The root system can reach a depth of 2 m or more; lateral roots can extend 3 m from the parent plant. Each plant can produce up to a half million seeds and it also produces vegetative root buds, each of which can produce a new and independent plant (Lajeunesse et al. 1995). When established, the plants are very competitive and difficult to eradicate.

Flagstaff pennyroyal is a small, prostrate, perennial member of the mint family (Labiatae) that is currently a U.S. Forest Service Southwestern Region (R3) sensitive species. It was nominated for listing as a threatened species with the U.S. Fish and Wildlife Service in the Federal Register on June 29, 1983. After further investigation (Phillips 1984, Boucher 1984), the species was found to be more abundant and more widely distributed than initially thought and listing was not warranted (Phillips et al. 1992). In 1984, the Coconino National Forest developed a management plan for Flagstaff pennyroyal (Boucher 1984) to mitigate potential problems that might occur due to management activities within its habitat.

Observations by various field personnel have suggested that increasing amounts of litter cover and tree canopy might be affecting the species ability to grow in certain places (Goodwin 1983, Fletcher 1984). A prescribed burn study conducted on the Coconino National Forest from 1989 to 1995 (Galeano-Popp 1989, Dudley 1989a, 1989b, Dudley et al. 1989, Phillips et al. 1992, Crisp 1997) had four objectives: (1) Determine whether any beneficial or adverse effects (increases or decreases in plant densities or vigor) occur in *Hedeoma diffusum* populations following fire treatment. (2) Assess the importance of fire intensity and fire timing

(season of burn) on *Hedeoma diffusum* plants. (3) Assess the effects of ground cover on the plants following fire treatment. (4) Evaluate the potential role of climatic factors on plants following fire treatments.

Methods

The prescribed burns were conducted in two comparatively flat and easily accessible sampling locations at the center of the Mormon Lake Ranger District on the Coconino National Forest (Dudley et al. 1989). The areas were selected because there were sufficient numbers of *H. diffusum* plants to provide for adequate samples for pre- and post-monsoon burn plots and controls with two densities of ground cover. Area 1 (A1) had a small amount of ground cover (5–30%). Area 2 (A2) had ground cover in the range of 10–53%. In Area 2, eight plots are located on a broad limestone ridge and two plots are 500 m disjunct to the northeast. Hot and cool intensity pre-monsoon, hot and cool intensity post-monsoon burn blocks, and control blocks were designated in areas 1 and 2.

We established two plots within each block in June of 1989. Each circular plot has a steel fence post at its center and a radius of 1.8 m. We took pre-burn samples in June, and we placed a galvanized nail adjacent to each plant found in the 20 plots. Fire lines were constructed around each 0.2–0.4 ha burn block to prevent the spread of the fire into the adjacent forest (Phillips et al. 1992). The plots were burned at the designated time and intensity. However, plots A1S4D2 and A2S3D3 burned cooler than planned. Therefore, the pre-monsoon hot burn in area 1 and post-monsoon hot burn in area 2 are represented by only one plot each, and the pre-monsoon cool burn in area 1 and the post-monsoon cool burn in area 2 are represented by three plots each (Table 1).

The plots were counted each year from 1989 through 1995. Each year different colored nails were used for new plants. Mortality was assessed based on the number of nails present without plants. This method of marking and counting plants was used until 1992. After 1992, plants were divided into two categories, adults and seedlings.

In 1999 we returned to the sites to locate the plots with a Global Positioning System unit, rephotographed each plot, and recorded the associated species and percent ground cover in each plot. At that time we noted that Dalmatian toadflax was invading several of the plots in Area 2. We organized a weed pull that summer and removed the stems only outside the plots within the immediate vicinity.

We decided to take this opportunity to investigate whether Dalmatian toadflax might have invaded the area, or existing populations of it within the area might have expanded, due to disturbances associated with the burn study. We also investigated whether the presence of Dalmatian toadflax in the plots appeared to have any correlation with the timing (pre- and post-monsoon) and intensity (hot and cool) of the burns. In August and September of 2000 we counted the number of Dalmatian toadflax plants within the invaded plots, and recorded the number of Flagstaff pennyroyal plants present in the Area 2 plots. We did not count the plants in Area 1 because only one Dalmatian toadflax was observed in Area 1 and it was pulled. We also walked the Area 2 fire lines to assess the spread of Dalmatian toadflax within and outside of the project area. We then looked for the presence of Dalmatian toadflax

Table 1. *Hedeoma diffusum* prescribed burn study plot design.

	Area 1 Low Ground Cover		Area 2 Medium Ground Cover	
Treatment	Plot number	Date burned	Plot number	Date burned
Pre monsoon hot	A1S4D1	5/16/90	A2S2D1	6/19/90
			A2S2D2	6/19/90
Pre monsoon cool	A1S3D1	5/16/90	A2S4D1	6/19/90
	A1S3D2	5/16/90	A2S4D2	6/19/90
	A1S4D2	5/16/90		
Post monsoon hot	A1S1D1	8/29/89	A2S1D1	10/30/89
	A1S1D2	8/29/89		
Post monsoon cool	A1S2D1	8/29/89	A2S1D2	10/30/89
	A1S2D2	8/29/89	A2S3D1	10/30/89
			A2S3D2	10/30/89

outside the project area to determine its overall distribution in the habitat and to evaluate whether it was present before 1989 or might have been brought in during the project burns.

Results

The numbers of total live *Hedeoma diffusum* plants for each year from 1989 to 1995 is shown in Table 2. Plant numbers generally increased during the study. However, the number of plants on some individual plots decreased. The hot burn treatments provided the greatest increase in plant numbers. However, when individual plots are examined, two plots had large increases in plants, whereas plant numbers on the other four plots actually decreased. The cool fire treatments provided more consistent increases until 1995.

An analysis of litter depth and tree canopy with habitat, burn intensity, and timing did not show any strong correlations (Crisp 1997). Needles cast from the trees stressed by the fires replaced the duff and needles consumed. Shallow roots and, in some cases, whole trees were killed by the hot fire treatments. Today many ponderosa pine trees are dead or dying from the stress of the fire treatments and drought, which will gradually expose the understory plants to more light and less needle litter over time.

The percent survival for each treatment is shown in Table 3. Percent survival in 1990 was most variable in the post-hot treatment (27–65%). Survival in the other treatments was generally higher, but still variable (post-cool 53–80%, pre-hot 63%, pre-cool 67–93%, and control plots 51–112%). Recruitment was generally low until 1992, when it increased dramatically on most plots . Recruitment ranged from 10% on one post-hot treatment to 89% on another post-hot treatment plot. The high rate of recruitment caused a large population increase in 1992. Recruitment was much lower on most plots in 1993 than in 1992, and then it increased in 1994 and 1995 on most plots. Most plots showed high survival in 1991, 1992, and 1994. Survival was lower in 1993 and 1995. Flagstaff pennyroyal plants in the burned areas were much larger and had many more flowers per plant than normal for several years after the burns.

The post-hot treatment and the pre-hot treatment mean percent increase in total live plants for 1989–1995 (Table 3) was 172% and 69%, respectively. The post-cool, pre-cool, and control treatments showed some increase from 1989 through 1995 but not as great. The post-cool mean percent change was 17%, the pre-cool had a 15% increase, and the control had a 6% increase.

The numbers of Flagstaff pennyroyal and Dalmatian toadflax present in the Area 2 plots in September 2000 are shown in Table 4. The numbers of

Table 2. Total live plants on *Hedeoma diffusum* fire plots, 1989–1995.

Treatment	1989	1990	1991	1992	1993	1994	1995
Post hot	170	111	112	703	398	460	463
Post cool	1036	899	1089	2209	1589	1242	1210
Pre hot	325	106	219	532	486	609	548
Pre cool	562	287	553	1876	775	822	645
Control	532	528	578	1083	1093	693	564

Pre and post refer to before and after monsoon rains.

Table 3. Mean percent change in *Hedeoma diffusum* fire plots, 1989–1995.

Year	Post hot	Post cool	Pre hot	Pre cool	Control
1989–1990	–34.71	–13.22	–38.96	–14.58	–0.75
1990–1991	0.90	21.13	106.60	92.68	–11.17
1991–1992	527.68	102.85	142.92	239.24	12.98
1992–1993	–43.39	–28.07	–8.65	–58.69	0.92
1993–1994	15.58	–21.84	25.31	6.06	–36.60
1994–1995	0.65	–2.58	–10.02	–21.53	–18.61
1989–1995	172.35	16.80	68.62	14.77	6.02

Pre and post refer to before and after monsoon rains.

Table 4. Observations of Flagstaff pennyroyal and Dalmatian toadflax in *Hedeoma diffusum* fire plots area in 1989, 1995, and 2000.

Plot	*Hedeoma* 1989	*Hedeoma* 1995	*Hedeoma* 2000	*Linaria* 2000	Notes
Post hot burn					
A2S1D1	86	48	23	0	disjunct
Post cool burn					
A2S1D2	79	8	35	0	disjunct
A2S3D1	76	48	32	0	
A2S3D2	90	73	82	0	
Pre hot burn					
A2S2D1	36	17	22	19	June burn
A2S2D2	126	110	66	6	June burn
Pre cool burn					
A2S4D1	167	99	82	18	June burn
A2S4D2	59	81	60	24	June burn
Control burn					
A2S5D1	108	83	19	18	
A2S5D2	195	205	76	0	

Pre and post refer to before and after monsoon rains.

Hedeoma diffusum plants in each of the plots had declined, in some cases substantially, from those recorded in 1989 and 1995. Dalmatian toadflax was noted as an associated plant species on some of the plots. The species had not occurred on the plots during the annual counts from 1989 through 1995. Five of the eight plots occurring on a ridge in Area 2 had been invaded by Dalmatian toadflax by September of 2000. Four of these infested plots (hot and cool) were burned on June 19, 1990. The infested control plot is immediately adjacent to infested pre-cool plots. None of the plots (hot or cool) that were burned after the monsoons on October 30, 1989 had been invaded by Dalmatian toadflax by September 2000.

By September of 2000 Dalmatian toadflax occurred on approximately 0.5 ha and extended east of the eight ridge plots to a site near the disjunct A2S1 plots. No Dalmatian toadflax plants were observed outside of the fire lines on the north, west, or south sides of the main project ridge where the native grasses and herbs are very dense. A couple of large mature toadflax plants were found below the ridge approximately 45 m west of the fire lines, growing under mature ponderosa pine trees.

Discussion

The invasion of Area 2 by the noxious Dalmatian toadflax was an unexpected result of this prescribed burn study. Steve Dudley (personal communication 2000) remembered seeing Dalmatian toadflax in Area 2 when conducting the June 1990 burns. He remembered that there were some toadflax plants on the eastern cliff-face below plots A2S4D1 and A2S4D2 (pre-cool) and A2S5D1 (control), and some plants in plot A2S2D1 (pre-hot). A photograph of fire ignition shows a Dalmatian toadflax present in plot A2S2D1, so there is also visual documentation.

Dudley's observations and the photograph were from June 1990, so it is unknown whether Dalmatian toadflax was present before any work was done in Area 2 or whether the noxious weed came in when the fire lines were established in late summer 1989 prior to the October burning. Some disturbance to the habitat would have occurred as the fire lines were scraped down to the mineral soil.

The start of this prescribed burn study was several years before noxious weed awareness and inventories were begun on the Coconino National Forest. However, some practices were followed in implementing the prescribed burn study that are considered important for noxious weed prevention (Phillips et al. 1998). Vehicles were parked on the road south of the project area; no vehicles were allowed to drive across the meadow below the plots. Shovels and chain saws were used to establish the fire lines. No heavy equipment such as bulldozers was used (Dudley, personal communication 2000).

All of the plots (hot and cool) burned in mid-June have become infested by Dalmatian toadflax whereas none of the plots (hot or cool) burned after the monsoons in late October have been invaded. This could indicate that timing of the burn is a more important factor than intensity of the burn for seedling establishment. Adult Dalmatian toadflax responds positively to fire because root buds are not killed and removal of top growth can stimulate production of vegetative shoots (Sheley and Petroff 1999).

According to Sheley and Petroff (1999), Dalmatian toadflax seedlings are vulnerable to dehydration and competition from other species and have difficulty getting established. They are easily outcompeted by plants in areas with good groundcover, and in particular by well-adapted perennials (Robocker 1970). This could explain why the Dalmatian toadflax has not yet invaded the areas surrounding the burn study area where the grasses are very dense.

The enhanced seedling recruitment and increased vigor of Flagstaff pennyroyal plants observed in this study support the belief that this rare plant is adapted to a frequent fire regime. Monitoring (U.S. Forest Service unpublished data, Crisp 1997) has shown that the Flagstaff pennyroyal is a short-lived perennial, with most plants living for 5 to 8 years. This is similar to the fire recurrence interval proposed for the ponderosa pine forests in the Flagstaff area (Swetman 1990, Sackett et al. 1994 a, 1994b).

Extreme drought conditions also affect Flagstaff pennyroyal survival. Most of the years from 1989 to 1995 had normal or above normal precipitation and the numbers of plants in the plots were still quite high at the end of the study. The year 1996, however, was one of the worst drought years on record (Crisp 1997), and the winter of 1999–2000 was also very dry. By August of 2000 there were substantially fewer Flagstaff pennyroyal plants in 9 of the 10 plots in Area 2. Three of the five permanent *Hedeoma diffusum* plots that were monitored in 1985, 1989, and 1996 (Boucher 1984) showed substantial decreases in plant numbers by June of 1996. One exposed plot located on a large limestone slab in full sunlight had declined by 99 percent (U.S. Forest Service unpublished data, Crisp 1997).

This prescribed burn study illustrates that urban interface and forest restoration efforts to reduce the risk of catastrophic fire could expand noxious weed infestations toward the outlying forests, which currently are less disturbed and less infested with noxious weeds. Several noxious weed species, including yellow starthistle (*Centaurea solstitialis*), diffuse knapweed (*Centaurea diffusa*), Scotch thistle (*Onopordum acanthium*), Mediterranean sage (*Salvia aethiops*), bull thistle (*Cirsium vulgare*), and others, in addition to Dalmatian toadflax, are expanding explosively in northern Arizona, especially in the urban interface (Crawford et al. in review, Griffis et al. 2001, Moser and Phillips 2000). Unless appropriate preventative and control measures for noxious weeds are undertaken during the urban interface and forest restoration efforts, noxious weeds could cause serious impacts to the biodiversity of these ecosystems.

According to recent literature and research on fire and exotic species (D'Antonio 2000, Foxx 1996, Crawford et al. unpublished data), fire in most ecosystems tends to promote rather than discourage introduced species, including in many ecosystems where fire has been an important force prior to European colonization. Research on the effects of fire in rare plant habitats must address invasive plants before these treatments are used on a landscape scale in ponderosa pine ecosystems (Moir, personal communication 2000, Neary et al. 2001).

Acknowledgments

Greg Goodwin provided the initial observations and ideas for both the fire study of *Hedeoma diffusum* and the initiation of the noxious weed program on the Coconino National Forest. Renee Galeano-Popp, Heather Green, and Steve Dudley were instrumental in developing the *Hedeoma* burn project and conducting pre-burn and initial monitoring. The Mormon Lake Ranger District fire crew conducted the burns. Numerous Forest Service personnel and volunteers read the plots each year. Laura Moser, Will Moir, and Julie Crawford provided ideas and discussions about the effects of various burn intensities on the spread of noxious weeds.

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Extinction Risk of *Ipomopsis sancti-spiritus* in Holy Ghost Canyon With and Without Management Intervention

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Abstract: Small populations are threatened with deterministic and stochastic events that can drive the number of individuals below a critical threshold for survival. Long-term studies allow us to increase our understanding of processes required for their conservation. In the past 7 years, the population of the federally endangered Holy Ghost ipomopsis (*Ipomopsis sancti-spiritus*) in Holy Ghost Canyon has fluctuated widely from 2047 to 372 plants. Metapopulation analysis of average Leslie matrices suggested that *I. sancti-spiritus* has a high probability of extinction; 60 percent of the demographic transects have negative growth rates. Transects with the greatest likelihood of remaining occupied, the highest λ values, and the greatest source of new propagules for maintaining the species in Holy Ghost Canyon are in the sunny lower part of the canyon. In comparison, transects at the top of the canyon have fewer individuals and lower probability of remaining occupied. With management intervention to disperse propagules from more fecund to less fecund areas of the canyon, metapopulation modeling indicated decreased (but still a high) risk of extinction within the next 50 years. Thus, although seed augmentation and habitat improvement can improve the chances for *I. sancti-spiritus* persistence in Holy Ghost Canyon, the species remains at high risk of extinction.

Small populations are threatened with deterministic and stochastic events that can drive the number of individuals below a critical threshold for survival (Shaffer 1987, Holsinger 2000). Climatic variation, habitat changes, impacts of exotic species, and inherent reproductive limitations have dramatic and exaggerated impacts on small populations. Through long-term studies of small populations, we can increase our understanding of the processes required for their conservation.

The federally endangered Holy Ghost ipomopsis (*Ipomopsis sancti-spiritus* Wilken & Fletcher) is threatened by events that plague all small populations. Believed to be a newly derived taxa having arisen within the last 10,000 years (Wolf et al. 1991), it was first described in 1988 (Wilken and Fletcher 1988) and very little was known about its biology. Growing along a 1.3 mile stretch of road cut through mixed conifer forests of Holy Ghost Canyon (elevation 2350–2500 m) in northern New Mexico, Santa Fe National Forest, *I. sancti-spiritus* seems to be an early successional species, like many of its congeners. Nearly 80 percent of the population grows on west-facing steeply cut Terrero limestone slopes along the road in the canyon. It is associated with open areas with low densities of ponderosa pine (*Pinus ponderosa*), Douglas fir (*Pseudotsuga menziesii*), quaking aspen (*Populus tremuloides*), Gambel oak (*Quercus gambelii*), mountain mohagany (*Cercocarpus montanus*), Woods' rose (*Rosa woodsii*), poison ivy (*Toxicodendron rydbergii*), Indian hemp (*Apocynum cannabinum*), western yarrow (*Achilliea millefolium*), white ragweed (*Hymenopappus newberryi*), and *Erigeron speciosa*. It does not co-occur with grasses.

In 1991, Robert Sivinski of New Mexico Forestry and Resources Conservation Division estimated the *I. sancti-spiritus* population size to be between 1250 and 2500 individuals. It was listed as endangered in 1994 (U.S. Fish and Wildlife Service 1994). Because the majority of the population occurs along cut and fill slopes of one road, it was hypothesized that management practices, which eliminated natural disturbances (i.e., fire and erosion), shifted the dependence of the species to man-made disturbance for suitable habitat. Incursions of exotic grasses smooth brome (*Bromus inermis*) and Kentucky bluegrass (*Poa pratensis*) may have excluded *I. sancti-spiritus* expansion within the canyon. The extremely narrow geographic distribution of the species and its lack of competitive ability make it extremely vulnerable to activities related to road maintenance, exotics, and activities that suppress moderate disturbance (U.S. Fish and Wildlife Service 1994).

In 1994, I established long-term demographic plots in Holy Ghost Canyon to assess the population viability of the endangered species. I treated the demographic plots as a metapopulation—a system of local populations connected by dispers-

ing individuals and gene flow, where colonization and extinction play significant roles in the dynamics and persistence of the species (Hanski 1998). Examining an entire corridor where the species occurred allowed me to examine patterns of patch extinction and colonization. Thrall et al. (2000) have argued that a metapopulation approach to conservation biology is likely to provide one of the most useful tools for developing management strategies that optimize among-population processes critical for the persistence of many natural systems.

Methods

To determine population viability of the *I. sancti-spiritus*, I established ten 13 X 5 m randomly selected transects numbered 1 through 10 from the top of Holy Ghost Canyon to the bottom. All transects had adult *I. sancti-spiritus* present in 1994. I tracked location, plant size, reproductive output, and survival of individuals in plots each year from 1994 through 2000.

In each transect, I measured the amount of light with a photometer to determine PPFD (photosynthetic photon flux density) and estimated the total hours of solar radiation received by plants in each transect.

Using RAMAS Metapop (Akcakaya 1998), I modeled population viability analysis of all 10 transects in Holy Ghost Canyon. Three stages were represented in the model: seedling, rosette, and adult. I generated a Leslie matrix for each transect from the means and variances of the past 6 transition years. I calculated reproductive values by dividing the number of seedlings by reproductive adults in each transect in each transition year, then derived the mean and variance for the 6 transition years. I assumed that populations had ceiling Allee density dependence with carrying capacities 1.5 times greater than population numbers seen in the last 7 years. I assumed that dispersal of seeds would be most likely to be unidirectional from the top of the canyon to the bottom. Transects separated by < 0.1 mile (0.16 km) had higher probabilities of dispersal than transects separated by > 0.5 mile (1.2 km). I assumed demographic and environmental stochasticity and included parameters in the model.

There were local and regional level catastrophes during the 7 years of monitoring. In some transects, local "catastrophes" were created by vehicles crushing plants, gophers burying plants, and erosion or landslides eliminating sections of a plot. I estimated the probabilities for local catastrophe by reviewing the evidence of disturbance in the plots over the past 7 years. For example, disturbance in 1 out of 7 years yielded a probability of 0.14 of a local catastrophe for that plot. Regional level catastrophes due to climatic conditions affected all plots. I assigned a probability of 0.14 for regional catastrophe, because severe drought has occurred once in the past 7 years of monitoring. The model ran 50 replicates for 100 years.

To examine whether management intervention could help conserve the species, I tested the impact of increasing dispersal throughout Holy Ghost Canyon on persistence of the species. The second model simulates moving seeds uphill and dispersing to all transects. I assumed dispersal of 5 percent of seeds in any given year to all uphill transects. The model ran 50 replicates for 100 years.

Results

The majority of seedlings required 1–3 years to achieve reproductive maturity. Although the range was between 1 and 6 years, mean maturation time was 1.86 years. Seeds often germinated with the onset of monsoon rains and had several true leaves by September.

The lower portion of the canyon received significantly more sun and had more fecund populations with greater numbers of individuals than the upper portion of the canyon. Upper transects 1–4 received approximately 2 hours of sunlight. The filtered sunlight was approximately 20 percent of full sun. Transects at the lowest part of the canyon received approximately 10 hours of full sun, with less than 5 percent shading.

There was significant variation in survival and reproduction across years. Most transects experienced good seedling establishment in 1996. In contrast, the lowest population numbers occurred in 1995, 1999, and 2000, which were comparatively dry years (Table 1). I observed no extinction within transects, although some transects consistently maintained few individuals (Table 1).

Population viability analysis of mean Leslie matrices over 6 transition years indicated that 40 percent of the transects have positive growth rates ($\lambda > 1.0$, Table 1 and 2), whereas 60 percent have negative growth rates ($\lambda < 1.0$). Not surprisingly, metapopulation analysis indicated that occupancy of *I. sancti-spiritus* in any transect has a probability of zero within 44 years (Figures 1 and 2) and that within the next 10 years only 2 of the 10 transects will be occupied. The model estimated a median of 16.8 years for the numbers of individuals in all

Table 1. Total number of individuals in each transect for the 7 years of monitoring. Mean λ values were determined from the average of six matrices. Total individuals in all transects are indicated for each year in the bottom row.

Site	1994	1995	1996	1997	1998	1999	2000	Mean λ
1	38	54	65	38	81	52	77	1.24
2	79	66	112	43	34	39	45	0.788
3	12	4	4	12	12	9	16	0.562
4	21	13	15	26	18	10	12	0.973
5	34	21	70	24	22	14	6	0.901
6	34	27	42	106	99	69	40	0.791
7	76	59	453	247	213	144	52	1.312
8	53	27	321	141	104	38	12	1.513
9	142	54	243	140	57	15	7	0.908
10	130	89	722	566	530	206	105	1.265
Total	619	414	2047	1343	1170	596	372	

Table 2. Mean probabilities for stage transitions across 6 transition years at each transect.

	Transects in Holy Ghost Canyon									
Stage	1	2	3	4	5	6	7	8	9	10
Seedling–rosette	0.5	0.63	0.35	0.55	0.42	0.55	0.51	0.40	0.40	0.63
Seedling–adult	0.28	0.09	0.31	0.24	0.06	0.15	0.24	0.37	0.28	0.09
Rosette–rosette	0.46	0.42	0.22	0.44	0.26	0.29	0.24	0.22	0.17	0.32
Rosette–adult	0.24	0.35	0.32	0.35	0.41	0.39	0.33	0.38	0.44	0.37
Reproductive value	3.556	0.909	0.50	1.585	2.51	1.08	4.298	4.66	1.596	4.8

transects to fall to zero (Figure 2). Transects 1, 7, 8, 9, and 10 have the greatest likelihood of remaining occupied, have the highest λ values, have the highest variation of occupancy, and represent the greatest source of new propagules for maintaining the species in Holy Ghost Canyon (Figure 3).

The second model, which simulated the management intervention of dispersing seeds from lower canyon transects to upper canyon transects, showed a significant impact from dispersal; local occupancy of all transects increased dramatically (Figure 4). Most important, the upper range of time steps increased from < 15 steps to > 40 steps for transects 1–8. With human-aided uphill dispersal, the estimated time to extinction and the upper range of persistence increased (Figure 5), as did the metapopulation occupancy (Figure 6). Without uphill dispersal, the estimated occupation time for 10 transects was less than 5 years, whereas with uphill dispersal the estimated occupation time increased to 26 years (Figure 6). Uphill dispersal increased the probability of species persistence in the individual transects and in the entire canyon.

Discussion

Wide fluctuations of growth rates within the metapopulation of *I. sancti-spiritus* in Holy Ghost Canyon are endangering the species. During the past 7 years, *I. sancti-spiritus* experienced both favorable and unfavorable climatic conditions. Even though years with good precipitation produced good seedling recruitment, this did not translate to good adult survival and reproduction in subsequent years. Similarly, years when the numbers of adults were comparatively great did not yield good seedling establishment in subsequent years. Even stable or increasing populations will suffer decline with high year-to-year variability in population growth rate, regardless of whether the variation is caused by the environment or rare catastrophic events (Holsinger 2000).

The metapopulation analysis indicated that persistence of the species in Holy Ghost Canyon does not look promising without management intervention. Six of 10 transects are declining and have low solar exposure. The analysis predicted a high risk of extinction for the species. Holsinger (2000) admonished that populations with negative

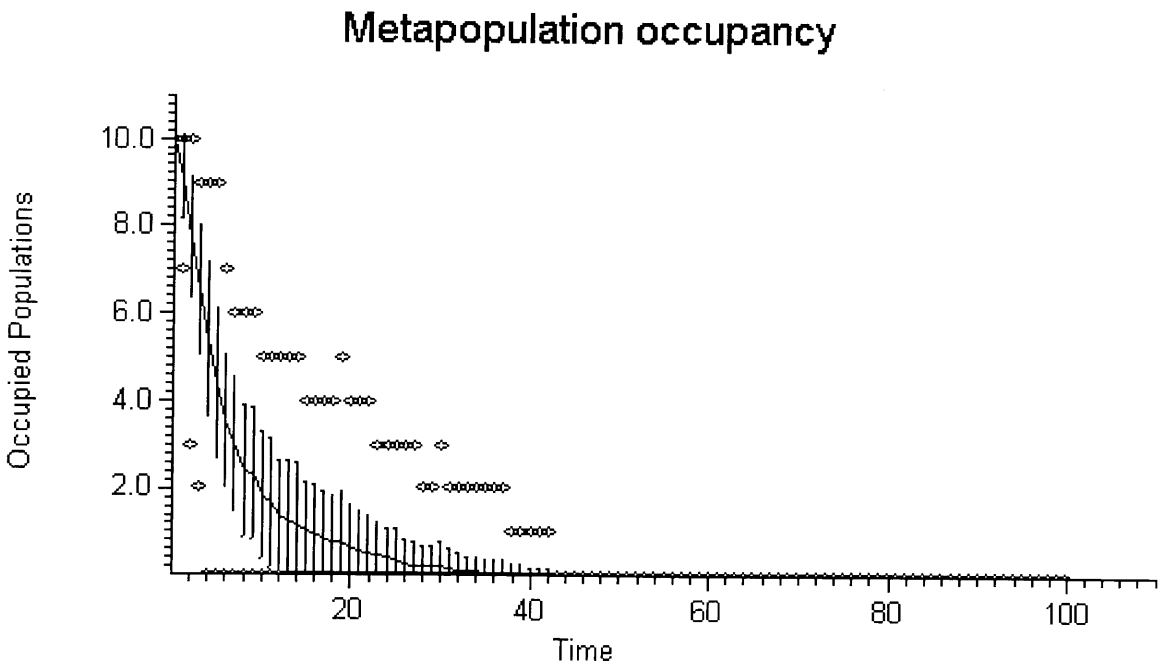


Figure 1. Summary of expected occupancy of *Ipomopsis sancti-spiritus* metapopulation through time. The average ± standard deviation, minimum and maximum number of extant populations are indicated. The model used average matrices (indicated in Table 2) and assumed dispersal downhill only to adjacent transects.

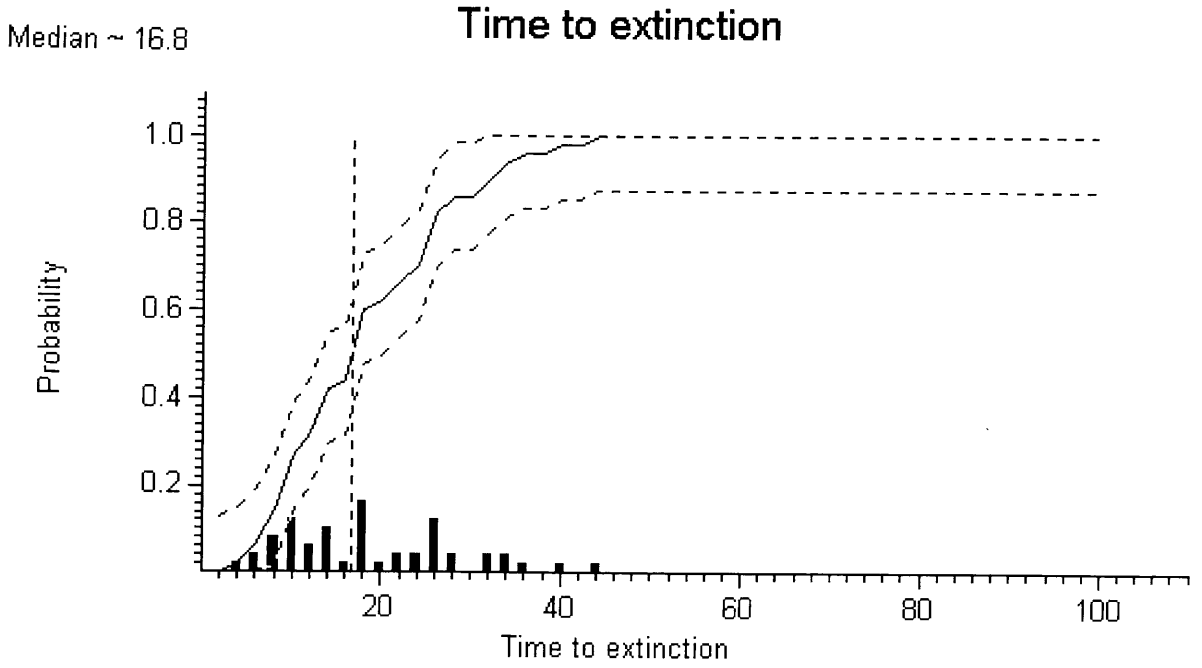


Figure 2. Time to extinction projected by the model using average matrices indicated in Table 2. The dotted vertical line indicates that the median of the distribution is 16.8 years. The histogram shows the probability that the metapopulation size will fall below or increase above zero exactly at the time step. The continuous line is the cumulative probability distribution. It shows the probability of the metapopulation falling below zero at or before a specific year; after 44 years the probability of extinction is 1.0. The model assumed dispersal downhill only to adjacent transects.

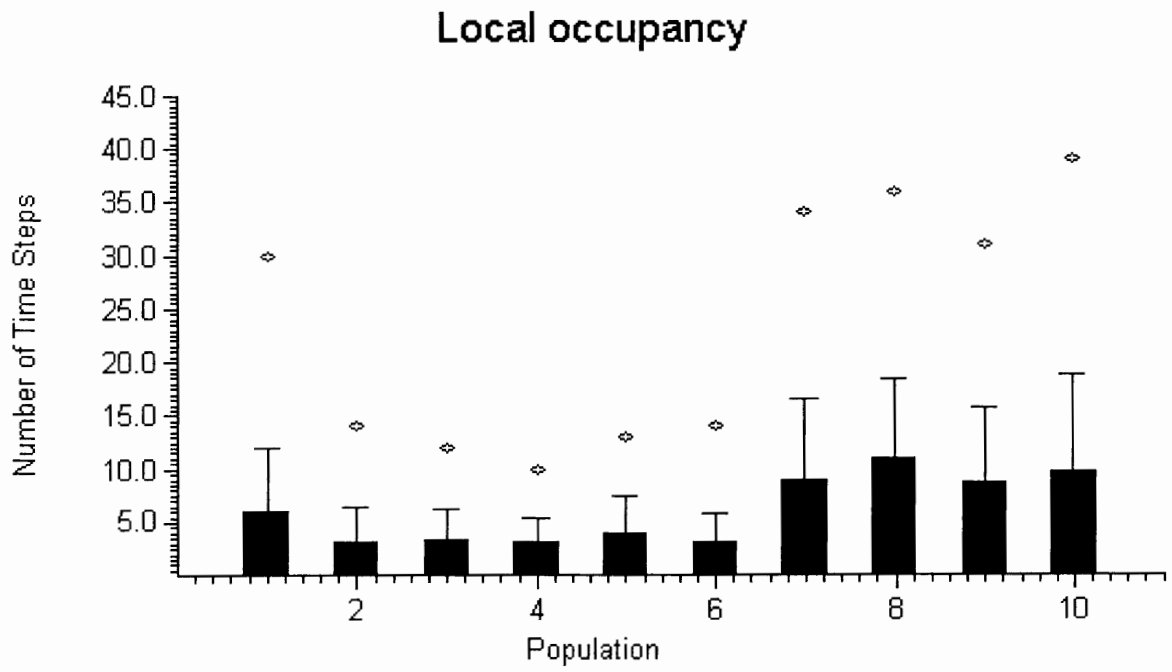


Figure 3. Statistical summary of the proportion of time that patches of *Ipomopsis sancti-spiritus* will remain occupied. The average ± 1 standard deviation, minimum and maximum number of years that each population has remained extant is indicated. The model used average matrices (see Table 2) and assumed dispersal downhill only to adjacent transects.

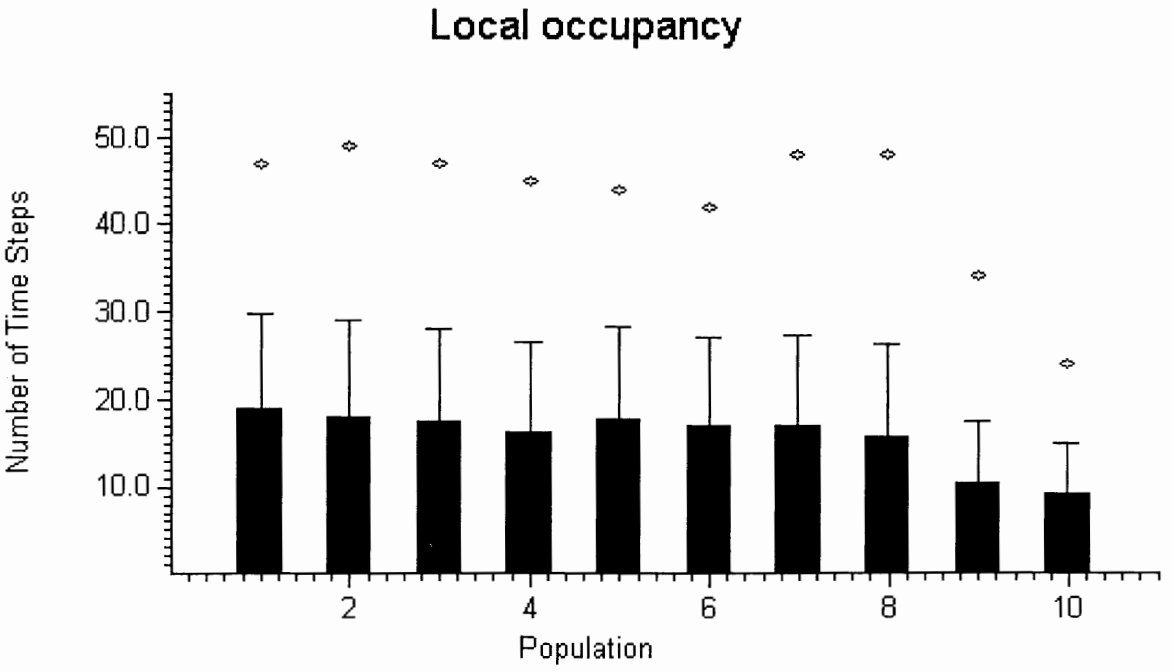


Figure 4. Statistical summary of the proportion of time that patches of *Ipomopsis sancti-spiritus* will remain occupied. The model used average matrices (indicated in Table 2) and assumed human-aided dispersal uphill to all transects. The average ± 1 standard deviation, minimum and maximum number of years that each population has remained extant is indicated.

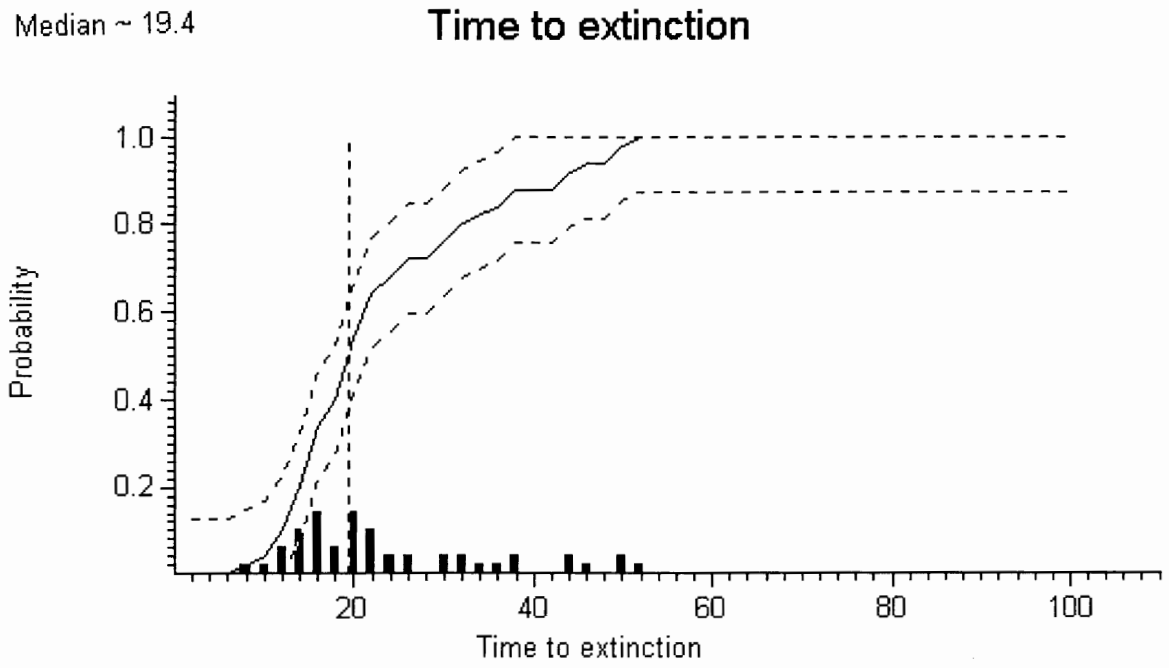


Figure 5. Time to extinction projected by the model using average matrices (indicated in Table 2) and assuming human-aided dispersal uphill to all transects. The dotted vertical line indicates that the median of the distribution is 19.4 years. The histogram shows the probability that the metapopulation size will fall below or increase above zero exactly at the time step. The continuous line is the cumulative probability distribution. It shows the probability of the metapopulation falling below zero at or before a specific year; after 52 years the probability of extinction is 1.0.

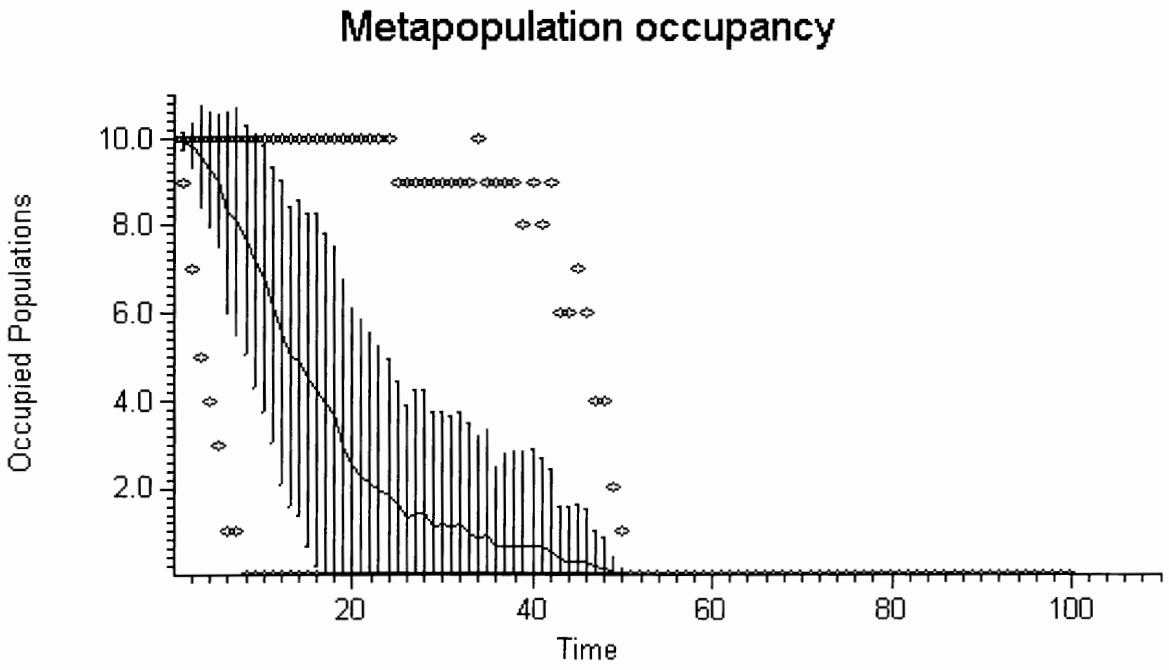


Figure 6. Statistical summary of the proportion of time that patches of *Ipomopsis sancti-spiritus* will remain occupied. The average ± 1 standard deviation, minimum and maximum number of years that each population has remained extant is indicated. The model used average matrices (see Table 2) and assumed human-aided dispersal uphill to all transects. Note the greater variance and range than in Figure 3.

long-term growth rates will require constant management and frequent supplementation to prevent their extinction. Because all populations are ultimately ephemeral, colonization processes must be preserved for any species to have a long-term future (Thrall et al. 2000). Colonization is naturally limited by the canyon topography; therefore any action that would increase options for dispersal and colonization would help preserve the species. This is supported by the metapopulation analysis, which indicated that species preservation would be favored with uphill dispersal. Therefore, a potential management strategy for conserving the species is to disperse seeds from transects 7, 8, 9, and 10 to uphill transects. However, there is a cost for dispersing seeds away from the "best" transects. The uphill dispersal model indicated that removing 45 percent of the seeds from transect 10 would decrease its longevity (Figure 4). A better option for preserving the Holy Ghost metapopulation would be to augment transects from *ex situ* seed sources, including the common garden currently being cultivated by Robert Sivinski, New Mexico Forestry and Resources Conservation Division, in Santa Fe, New Mexico.

A second management strategy is to increase light and decrease competition where *I. sancti-spiritus* grows. Although the amount of sunlight reaching the ground is constrained by topography in the upper canyon, selective timber harvest could open up canopies and favor *I. sancti-spiritus* establishment there. Manual exclusion of aggressive herbaceous competitors could also favor *I. sancti-spiritus* establishment throughout the canyon.

Even with these management actions, *I. sancti-spiritus* remains a species with a high risk of extinction in Holy Ghost Canyon. Recovery actions underway to establish populations in new locations certainly are supported by these analyses.

Acknowledgments

I am grateful to the U.S. Fish and Wildlife Service, Otto and Gallina Franz, and Ron Horn for their generous support of this research. Diana Warr, Mira Petersen, Charlie McDonald, and Karen Hueston have kindly assisted with field research in Holy Ghost Canyon.

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The Threat of Increasing Hybridization of an Endangered Plant Species, *Purshia subintegra*, in the Verde Valley, Arizona

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Abstract: The existence of the endangered shrub *Purshia subintegra* may be threatened by hybridization with the more common *P. stansburiana*. In the Verde Valley, the range of the rare *P. subintegra* overlaps with the range of *P. stansburiana*, allowing introgression to occur. Although *P. subintegra* and *P. stansburiana* have many distinguishing characteristics, there are plants in the Verde Valley that have a combination of characteristics, making them difficult to identify. Using discriminant function analysis, we found that the parents and introgressed forms had detectable morphological differences that could be used to classify individuals, but only to 87 percent accuracy. Examining phenological and ecological differences increased our ability to detect introgressed forms. *Purshia subintegra, P. stansburiana,* and the introgressed forms overlap in their time of flowering in the spring, but *P. stansburiana* and plants showing characteristics of introgression can also bloom again in the summer. Comparing the presence of both parents and the introgressed forms in the Verde Valley in undisturbed limestone soil, roadsides, and washes, we found a significant difference in the habitat distributions of *P. subintegra, P. stansburiana,* and introgressed forms. *Purshia subintegra* showed no habitat preference; however introgressed forms occurred more frequently along washes and roadsides than in undisturbed habitat and *P. stansburiana* occurred in washes and on undisturbed limestone soil, but not along roadsides. Increased road construction and human disturbance in the rare *P. subintegra* habitat may favor the spread of introgressed forms along roads and increase the likelihood of more introgression. This has grave implications for the conservation of this rare species.

Arizona cliffrose, *Purshia subintegra* (Kearney) Henrickson, is a rare soil endemic that was listed as an endangered species in 1984 (U.S. Fish and Wildlife Service 1984). It is known from four disjunct populations across central Arizona (Figure 1) in the upper Sonoran desert on Tertiary lakebed limestone deposits: Burro Creek in Mohave County (Kearney 1943), Bylas in Graham County (Pinkava et al. 1970), near Horseshoe Lake in Maricopa and Yapavai Counties, and in the Verde Valley near Cottonwood, Yapavai County (Anderson 1986). The largest, healthiest, and most morphologically variable population grows in the Verde Valley outside of Cottonwood, where its range overlaps with the more common cliffrose, *Purshia stansburiana* (Torr.) Henrickson, and there is introgression or hybridization (Anderson 1986, Reichenbacher 1994, U.S. Fish and Wildlife Service 1994).

The morphological variability of *P. subintegra* has led to confusion regarding its taxonomy and the degree to which introgression occurs in the species. Like other members of the genus, *Purshia subintegra* forms fertile hybrids in nature (Stutz and Thomas 1964, Koehler and Smith 1981), and it is often difficult to determine the taxonomic identity of the shrubs. Three scenarios to explain the variability of *P. subintegra* morphology have been suggested. The first hypothesis is that the population at Bylas is a rare form (named *P. pinkava*) and the other three populations are hybrid races of *P. pinkava* x *P. stansburiana* (Schaack 1987a, 1987b). The second hypothesis poses that *P. stansburiana* once extended further south, possibly overlapping with the range of *P. subintegra*. The variability in the Burro Creek and Horseshoe Lake populations is due to past introgression with *P. stansburiana*, whereas in the Verde Valley the phenotypic variability is due to past and current hybridization with *P. stansburiana*, which extends down into the desert floor from the surrounding foothills (Anderson 1986). The third hypothesis is that the four populations are *P. subintegra*, but gene exchange may have occurred in the past between *P. subintegra* and *P. stansburiana* in the Verde Valley, resulting in plants that are difficult to classify (Reichenbacher 1994). Genetic studies have neither supported nor refuted any of these hypotheses (Phillips et al. 1988). Currently, the Arizona cliffrose recovery plan recognizes that *P. subintegra* is phenotypically plastic in response to climatic and environmental conditions and forms an introgressing hybrid

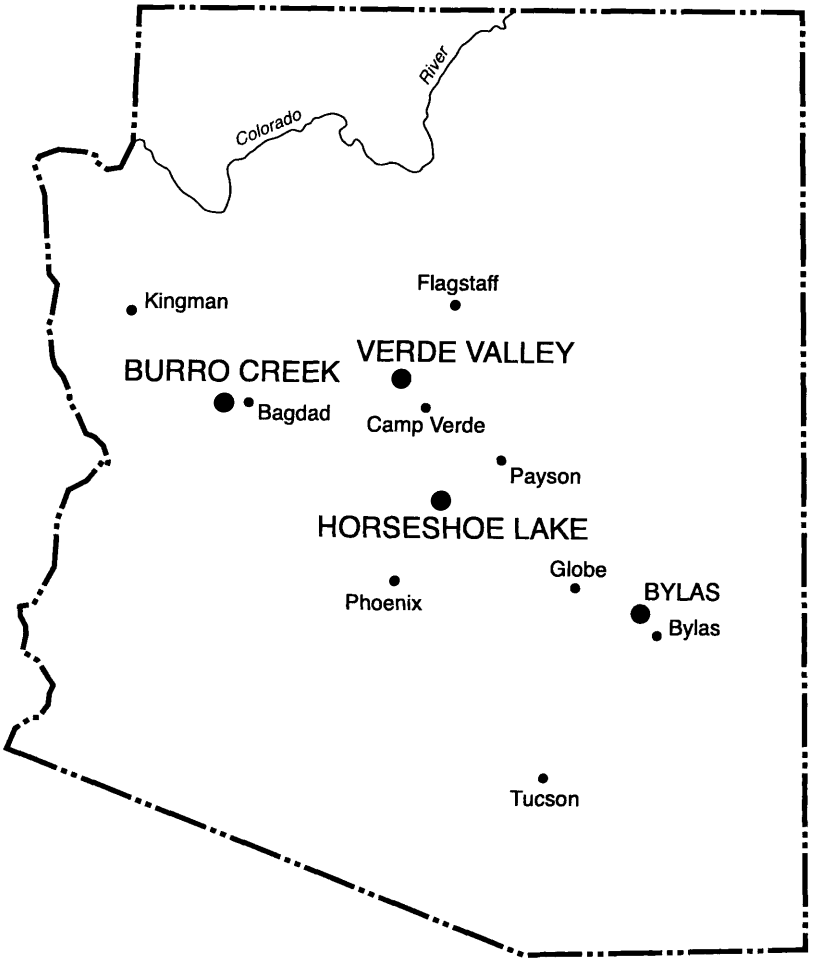


Figure 1. Map of Arizona with the four populations of Arizona cliffrose. Map is modified from U.S. Fish and Wildlife Service (1994).

swarm with *P. stansburiana* in the Verde Valley (U.S. Fish and Wildlife Service 1994).

The Verde Valley population is threatened by habitat destruction, road construction, and land sales. A planned new road will bisect the population, destroy about 10 percent of the known individuals, and degrade available and potential habitat. Development along the road will most likely lead to the additional loss of *P. subintegra* habitat. In addition, roads can fragment the population, increase disturbance and human use of the area, alter the physical and chemical environment, and provide corridors for weed invasion (reviewed in Trombulak and Frissell 2000, Parendes and Jones 2000). Roadsides have been associated with the introduction and spread of hybrids within the genus *Purshia* (Koehler and Smith 1981) and other genera (Brochmann 1984, Bramwell 1990).

We are concerned about the impact of disturbance associated with road building on the genetic diversity and integrity of *P. subintegra* in the Verde Valley. It is possible that the road construction and associated disturbance may create corridors for introgressed forms, bringing them spatially closer to stands of "pure" *P. subintegra* and therefore impacting the population dynamics of *P. subintegra*. To address these concerns we first determined which morphological characters could be used to distinguish between *P. subintegra*, *P. stansburiana*, and introgressed forms. To determine if roads would favor introgressed forms, we examined the habitat preferences of *P. subintegra*, *P. stansburiana*, and introgressed forms in washes, roadsides, and limestone outcrops.

Methods

Because of discrepancies in classification of the introgressed forms, our first goal was to determine a set of characters to identify plants in the field. We grew putative *P. subintegra*, *P. stansburiana*, and the introgressed form from rooted stem cuttings in greenhouses at the Arboretum at Flagstaff. Using these greenhouse-grown plants and plants from Burro Creek and Horseshoe Lake, we determined easily identifiable morphological characteristics to use in the field to make identifications. To account for the phenotypic variation of *P. subintegra*, we selected 57 plants for inclusion in the analysis: 16 *P. subintegra*, 10 *P. stansburiana*, and 11 introgressed forms that represented the known range of plants in the Verde Valley, and 5 plants each from the Burro Creek and Horseshoe Lake populations. Note that *P. stansburiana* does not currently grow in the vicinity of the Burro Creek or Horseshoe Lake populations.

Characteristics from previous treatments that were known to be useful in identifying the *P. subintegra* complex were leaf shape, impressed-punctate glands on leaves, hypanthium-pedicel glands, hypanthium-pedicel length, and young twig pubescence (Table 1, Reichenbacher 1994, U.S. Fish and Wildlife Service 1994). We considered everything between the descriptions of *P. subintegra and P. stansburiana* to be the introgressed form. We used these descriptions to make the a priori determination of taxa from which we took cuttings in the field.

To measure the morphological characteristics of the greenhouse-grown plants, we used only the vegetative characteristics because floral characteristics were not available for all individuals when grown in the greenhouse (Table 2). We scored five leaves and the young stems for each plant. We analyzed our ability to identify the different taxa with discriminant function analysis (SYSTAT 8.0).

Table 1. Morphological characteristics used to distinguish *Purshia subintegra*, *P. stansburiana*, and introgressed form in the field. (Modified from Reichenbacher 1994, U.S Fish and Wildlife 1994.)

Morphological characteristics	*Purshia subintegra*	Introgressed form	*Purshia stansburiana*
Leaf shape	Entire to 1 to 2 lobes	1 to 5 lobes	3–5 deep lobes
Impressed-punctate glands on leaves	Absent	Absent/present	Present
Leaf pubescence	Loosely to densely arachnid-pubescent	Glabrous to densely pubescent	Glabrous
Young twigs	Tomentose, red-brown color	Tomentose to glandular	Red, not tomentose, and stalked glands
Hypanthium pubescence	Tomentose	Tomentose or with stalked glands	Stalked glands

Table 2. List of vegetative characteristics used in discriminant function analysis. The values of each morphological characteristic for each taxon as determined by the discriminant function analysis is listed.

Morphological characteristics	Values	*Purshia subintegra*	Introgressed form	*Purshia stansburiana*
Number of leaf lobes	Number of lobes; entire leaf is 1	1 to 3	1 to 3	3 to 5
Leaf pubescence	0 – no hairs to 5 – densely arachnid-pubescent	1 to 5	0 to 4	0 to 2
Impressed punctate glands on leaves	Presence/absence	Absent	Present or absent	Present
Stalk glands on young stems	Presence/absence	Absent	Present or absent	Present

Using phenological data, we refined our list of characteristics to easily identify these taxa in the field. We visited the Verde Valley throughout the year and recorded plant location, vegetative characters, and patterns of flowering, especially for plants that flowered out of their typical season. We used these factors to refine the determination of parental or introgressed status.

In May and June of 1999 we monitored *P. subintegra*, *P. stansburiana*, and introgressed forms in three different habitats in the Verde Valley: washes, disturbed roadsides with limestone soils, and undisturbed limestone soils. We located five sites of each habitat with *Purshia* and picked a random starting plant. We then walked through the habitat and determined the characteristics and taxa of the first 25 plants encountered. We determined taxa using the vegetative characteristics listed in Table 2 and a floral characteristic, the presence of stalked glands on the hypanthium. We analyzed the number of each taxa found in the five sites in each habitat with a chi-square test (Snedecor and Cochran 1989).

Results

Using the morphological characteristics in Table 1, the discriminant function analysis classified *Purshia subintegra*, *P. stansburiana*, and their introgressed forms with 87 percent accuracy (Table 3). Our identification of *P. subintegra* and *P. stansburiana* was correct, but identification of the introgressed forms was only 55 percent accurate. The analysis classified putative hybrids as *P. stansburiana* based on the presence of stem glands.

We found that leaf shape was an extremely plastic character and therefore not the best one to use to distinguish *P. subintegra* from *P. stansburiana* or the introgressed form. Cuttings collected from the field that had entire or slightly lobed leaves (our conservative criteria for being classified as *P. subintegra*) grew new leaves with two or more lobes in the greenhouse. We found that the best taxonomic characters were presence or absence of glands on the leaves, stems, and hypanthia, because they were less plastic.

To help resolve the identification of the introgressed form, we examined the phenological differences of plants in the Verde Valley (Figure 2). *Purshia subintegra* and *P. stansburiana* differ in their timing of flowering but have a 2-week period of overlap. *Purshia subintegra* blooms in early spring from April to late May, whereas *P. stansburiana* blooms from late spring (May to late June) until September, if water is available. Individual plants showing some, but not all of the morphological characteristics of *P. stansburiana* have two blooming periods: in the spring 2–3 weeks after *P. subintegra* begins to bloom and again in August and September in response to monsoon precipitation (Figure 2). We have observed plants that show characteristics of introgression and characteristics of *P. stansburiana* blooming only in late summer in the Verde Valley. The exact timing depends on the microsite and yearly climate. Thus, biseasonal flowering phenology is a useful character for determining whether a plant is introgressed.

We found a significant difference ($\chi^2 = 22.8$, df = 4, p = 0.0001) between the distribution of *P. subintegra*, *P. stansburiana*, and the introgressed forms in three habitats in the Verde Valley (Table 4). *Purshia subintegra* did not show a habitat preference, but *P. stansburiana* was more likely to be found in washes and was almost never found along roadsides. Roadsides and washes contained significantly more plants of introgressed form than expected.

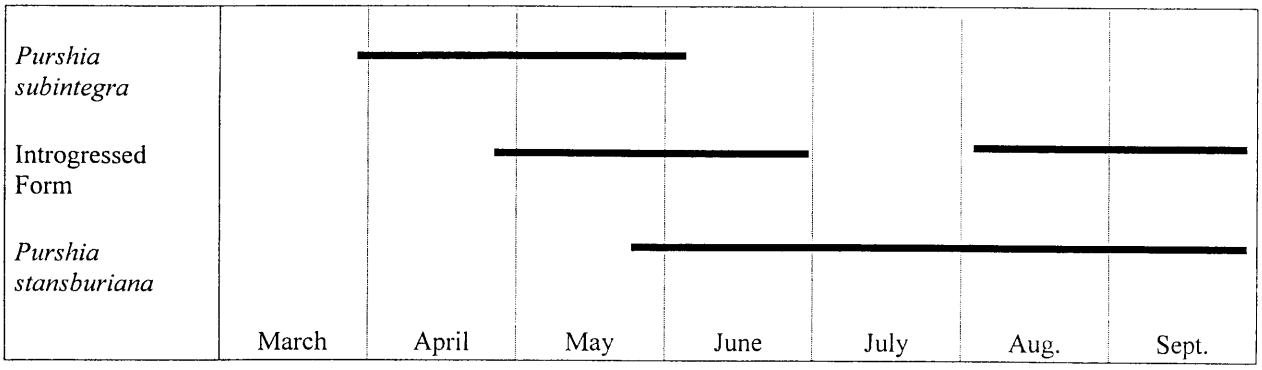


Figure 2. Timing of flowers in the Verde Valley.

Table 3. Results of the discriminant function analysis. Original identification was from the field-collected plants using characteristics in Table 1.

Original Identification	Post-hoc classification			
	P. subintegra	Introgressed form	*P. stansburiana*	Percent correct
P. subintegra	25	1	0	96
Introgressed form	2	6	3	55
P. stansburiana	0	0	10	100
	27	7	13	87

Table 4. The expected and observed values for the number of plants for each taxon and habitat using a χ^2 test. Numbers in italics indicate pairs with the greatest differences (standardized deviates greater than 1).

	Purshia subintegra		Introgressed form		*Purshia stansburiana*	
Habitat	Expected	Observed	Expected	Observed	Expected	Observed
Undisturbed	52	50	60	60	13	15
Wash	52	49	*60*	*52*	*13*	*24*
Road	52	56	*60*	*68*	*13*	*1*
Total		155		180		40

Discussion

In the Verde Valley the hybrid swarm and associated parental species are distributed in a non-random pattern. *Purshia subintegra* is distributed mostly on limestone outcrops, but also occurs naturally in first-order drainages and larger washes and along roads (Figure 3). *P. stansburiana* encounters *P. subintegra* along washes within the valley and on the southwestern edge of the range. The introgressed forms occur in all the habitats, but significantly more than expected were found along roadsides at the southwest edge of the *P. subintegra* range. One possible reason for this pattern is that roadsides are preferred habitat for introgressed forms.

Alternatively, the occurrence of introgressed forms along roadsides may be an artifact of roads being built through existing hybrid swarms rather than creating them. Roads have been built only on the edges of the distribution of Arizona cliffrose, where the two parent species overlap (Figure 3). The new road being built through the *P. subintegra* habitat will provide an opportunity to research these two alternate hypotheses.

Roads and other disturbances can cause the breakdown of ecological barriers between species by providing habitats and movement corridors for hybrids (Bramwell 1990, Levin et al. 1996), thereby increasing the rate of introgression. The proposed road bisecting the *P. subintegra* population could provide such a corridor for introgressed forms to make contact with the densest and most fecund stand of pure *P. subintegra*. In the center of the population on the undisturbed limestone outcrops, *P. subintegra* exists without close contact with the introgressed form or *P. stansburiana*. However, the proposed road differs from other roads in the area because it will bisect the population, crossing washes and other areas containing the introgressed form, thereby increasing the likelihood of introgression.

Increased introgression or hybridization has several consequences for the population dynamics of *P. subintegra*. When a rare species comes into contact with an abundant widespread species, genetic assimilation or swamping can occur, potentially causing outbreeding depression or a loss of unique gene combinations in the rare species (Rieseberg 1991, Levin et al. 1996). Our studies showed that hybrids had greater opportunities for pollen transfer and seed set, because they have two bouts of flowering and seed set. Because the flowering period of the introgressed forms overlaps with the flowering periods of *P. subintegra* and *P. stansburiana*, they likely will cross-pollinate with pure parental species (see Figure 2). Previous

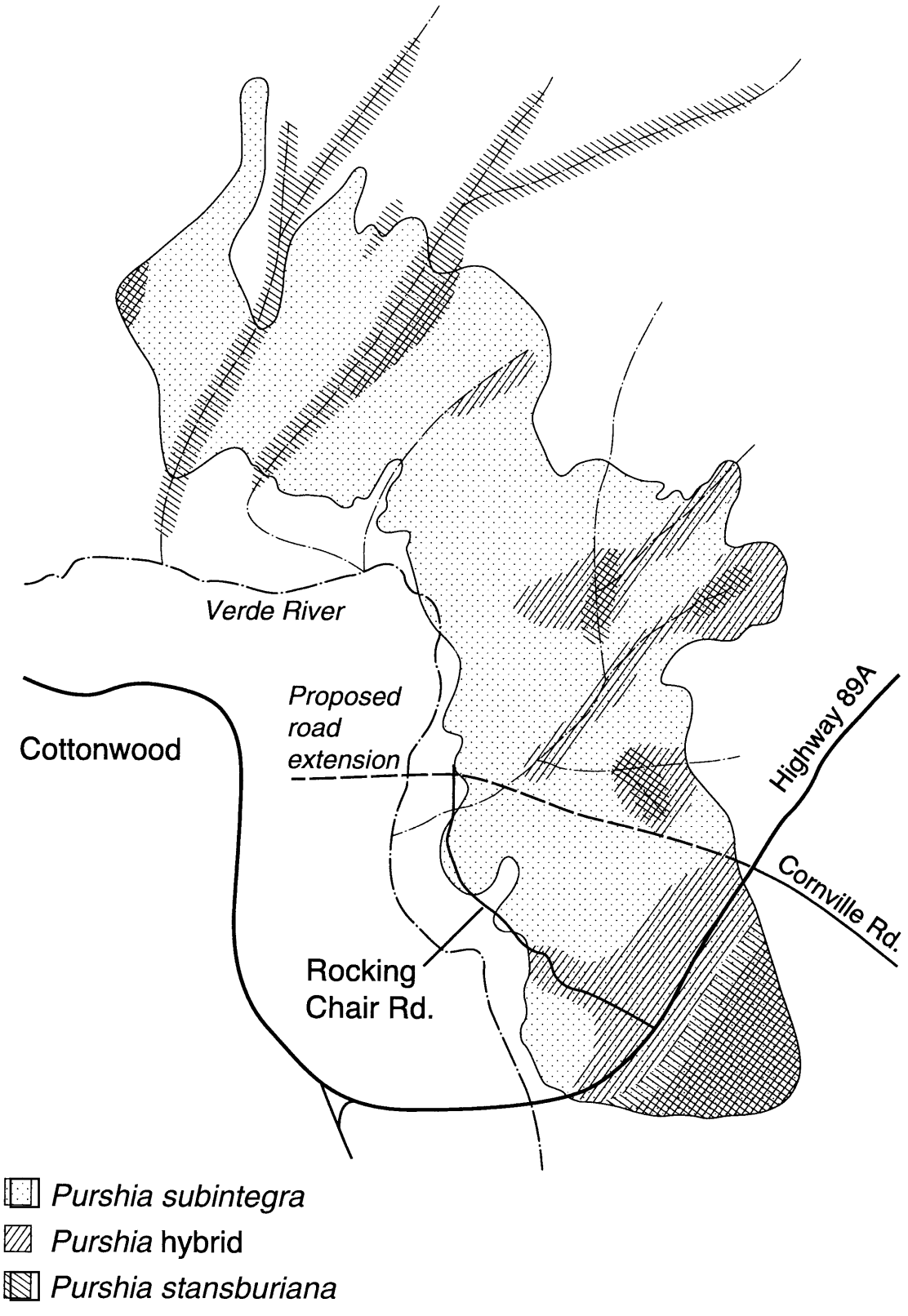


Figure 3. Map of *Purshia subintegra, P. stansburiana,* and the introgressed forms in the Verde Valley with the proposed Mingus Avenue extension. The distribution of each taxa is based on our results, U.S. Fish and Wildlife (1994), and Denham and Fobes (1994).

studies have shown that *P. subintegra* and the introgressed form can cross and produce fertile seed (Baggs and Maschinski this volume, Fitts et al. 1992); therefore through interference competition introgressed forms limit the chance for pure *P. subintegra* pollen to reach pure *P. subintegra* stigmata. In addition, a longer season of flowering and seed production gives introgressed forms a competitive advantage for responding to unpredictable rainfall and a greater seed rain. Our studies showed that introgressed forms grew on a wide range of habitats, suggesting that they are good competitors and may outcompete parental species for seedling microsites and limited resources. Conversely, *P. subintegra* grows in restricted habitats and has variable seed production that is positively correlated to the previous winter's precipitation (Baggs and Maschinski 2000). Following winter drought, *P. subintegra* is not likely to set flowers or seed in the spring and will lose a year of seed production.

Yet hybrid or introgression zones can be important for diversity and evolution (Stebbins 1959). Hybrid origins have been proposed for several rare species (Rieseberg 1991) including species of *Purshia* (Stutz and Thomas 1964). Introgression may in fact provide a mechanism to introduce genetic variability and new characters into a population of rare plants to allow its continued survival and adaptation into new environments and sites (Rieseberg 1991, Stebbins 1959), a positive aspect of hybridization in the management of rare species (Whitham and Maschinski 1996). This scenario has also been suggested for many species in the genus *Purshia* (Stutz and Thomas 1964, Anderson 1993). Yet there is concern about losing the unique characters of this rare species as a consequence of hybridization (Anderson 1993).

There are many possibilities for future research. We are continuing to research the genetic relationship of *P. subintegra, P. stansburiana,* and introgressed forms through common garden experiments and genetic analysis. In addition, the new road construction will allow us to examine the impacts of road construction on a rare soil endemic. Because roadsides can provide habitat for both *P. subintegra* and the introgressed forms, recruitment and establishment into the roadsides of *Purshia* can be monitored. The road will also bisect the population so that continued monitoring can help us understand the effect of the road on the population dynamics of *P. subintegra* in the Verde Valley.

Acknowledgments

This research was funded by the Arizona Department of Transportation. We would like to thank Barbara Phillips, Jan Busco, Drew Callinan, and Julie Giguere for their assistance with this part of the project.

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Distribution of Paradine Plains Cactus in Pinyon-Juniper Woodland on the North Kaibab Ranger District, Kaibab National Forest

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BARBARA G. PHILLIPS, and DIEDRE WEAGE

Abstract: Surveys for Paradine plains cactus (*Pediocactus paradinei* B. W. Benson) conducted for the Kaibab National Forest, North Kaibab Ranger District in 1992-94 qualitatively showed a fairly substantial population of scattered individuals in the pinyon-juniper woodland, and indicated that there might be a correlation between plant distribution and dripline of trees. This project was initiated in 1999 to test that possibility. Field surveys in July of 2000 showed an apparent sharp decrease in numbers of cacti since 1994, probably due to conditions caused by a drought from 1998 to the summer of 2000. The plants that were located showed no statistical correlation between dripline and distribution when both tree species were considered together; however, there was a positive correlation between juniper and *Pediocactus* distribution on the dripline, and a negative correlation between pinyon and *Pediocactus* on the dripline. Mycorrhizal association may be responsible for the positive correlation of juniper and *Pediocactus*. The small sample size due to low numbers of plants makes these conclusions preliminary.

Paradine plains cactus is a small endemic plant whose entire range is on the middle and lower eastern slopes of the East Kaibab Monocline. Its rarity has long been recognized, and it was a candidate for listing by the U.S. Fish and Wildlife Service for many years. It was proposed for threatened status in the Smithsonian Petition published July 1, 1975 (U.S. Fish & Wildlife Service 1975), and was reclassified as a Category 1 Candidate in the 1980 Notice of Review (U.S. Fish and Wildlife Service 1980, Phillips et al. 1981). This classification was maintained through the 1993 Notice of Review (U.S. Fish & Wildlife Service 1993), after which it was removed from USFWS consideration. It continues to be included in the Region 3 USDA Forest Service Sensitive Plants List.

In 1995-96 an interagency team prepared a conservation assessment for the species (USDA Forest Service 1996). The document was signed by the Kaibab National Forest, the Arizona Strip District–Bureau of Land Management, and the U.S. Fish and Wildlife Service in 1998. The Conservation Strategy section of the document called for annual monitoring and expanded research activities to better understand the biology and ecology of the species. This project was designed and funded to better understand aspects of the distribution and ecology of the species. Further information on the biology, ecology, and management of the species may be found in the conservation assessment.

Surveys for Paradine plains cactus were conducted by the senior author of this report in 1992-94 along the East Side Game Road (FR 220) and elsewhere within and adjacent to its known range (Phillips 1992-94) to prepare environmental assessments for road maintenance and grazing allotment reviews. It has long been known that the plant occurs in somewhat dense, isolated colonies on small islands of suitable habitat, often in openings in sagebrush along broad, open drainages. It also occurs as isolated, widely separated individuals or small groups in upland habitats with Colorado pinyon (*Pinus edulis*) and one-seed and Utah juniper (*Juniperus monosperma* and *J. osteosperma*). The 1992-94 surveys led to the thesis that overall, more plants occurred in woodland sites than in dense colonies in open habitats. Moreover, there appeared to be a correlation between the dripline of pinyon and juniper trees and the distribution of cacti. The purpose of this project was therefore to examine and evaluate the distribution patterns of Paradine plains cactus within the woodland.

Methods

The surveys carried out in 1992-94 were not quantitative; in most cases, presence of the species and mapping were the objectives. At any given site, after presence was established the surveyors moved on to the next site. Within areas where the plants were present, two observations were made: (1) the plants were more common than previously

reported, with individuals found at perhaps every third tree on average; and (2) where plants were present they favored the dripline around the outer edge of the tree canopy.

To test this correlation, a sampling design was developed to randomly select six blocks of trees within the known range, then randomly select a starting point within a selected block, and sample 20 consecutive trees from selected points. The number of trees necessary would be determined by testing for an adequate sample in the first block.

Two belts would be surveyed around each selected tree: one belt 1 m wide with its inner edge at the dripline, and a second belt 0.7 m wide concentric with and beyond the first belt (with a small buffer zone between the belts to prevent overlap). This would provide a survey around each tree of approximately equal area on and outside the dripline. Figure 1 shows a diagram of the survey method. Surveyors were provided with meter sticks, and the dripline was defined as the point where tree-related duff ends; this is usually an abrupt change. The number of cacti found in each belt was recorded, along with the species of tree (pinyon or juniper).

Because the plants were much less common than expected during the July 2000 surveys (see below), some modifications in the sampling method were necessary. It was not possible to run a test for adequate sample size, as there were no places with enough trees with plants for an adequate sample. The method used was to stop at random places within areas where the plants had been found during the earlier surveys, and for three people to fan out looking for plants. When or if anyone found plants, all surveyors converged at that point, and data collection commenced. Consecutive trees were sampled using the technique described above. A minimum of eight trees was included at each site, and sampling continued until cacti were no longer found. The number of trees in each sample was therefore different.

The data were analyzed using several t-tests, which (1) compared the mean values of cacti per tree on the dripline and outside the dripline, and (2) tested the correlation of cacti with each species of tree. The data from the five survey blocks were arranged in a single database, which included tree species and number of *Pediocactus paradinei* on and outside the dripline. A total of 81 trees was included in the first t-test, and the mean value of cacti per tree was calculated for each belt (Table 1). A second t-test was performed in which the survey block that contained the highest occurrence of cacti and the block that contained the lowest occurrence of cacti (0) were excluded (Table 1). The purpose of the second test was to eliminate extreme values that could reflect a skewed distribution and mean. Analysis of a 20 percent trimmed mean reduced the impact of very large and very small values on the mean, and allowed for a more reliable measure of the central value for the sample set (Ott 1993).

A third t-test was performed in which the mean value of cacti on the dripline of pinyon was compared to the mean value of cacti on the dripline of juniper, and the mean values of cacti outside the driplines of each species was compared, in order to test the correlation of cacti with tree species (Table 1). All of the trees included in the survey were grouped by species and numbered,

Table 1. Summary of distribution of *Pediocactus paradinei* with respect to driplines of pinyon and juniper together, just pinyon, and just juniper.

	On Dripline			Outside Dripline		
	N (Pepa)	Mean/tree	SD	N (Pepa)	Mean/tree	SD
T-text #1 Compare mean values Sample size: 81 trees	42	.5185	1.352	40	.4938	1.628
T-test #2 Compare 20% trimmed mean values Sample size: 62 trees	15	.2419	.5635	12	.1935	.5680
T-test #3 Compare mean values by species Sample size: 15 pinyon	3	.2000	.7746	13	.7333*	1.580
Sample size: 15 juniper	11	.8667*	2.6421	4	.2667	.7988

*Indicates significant correlation.

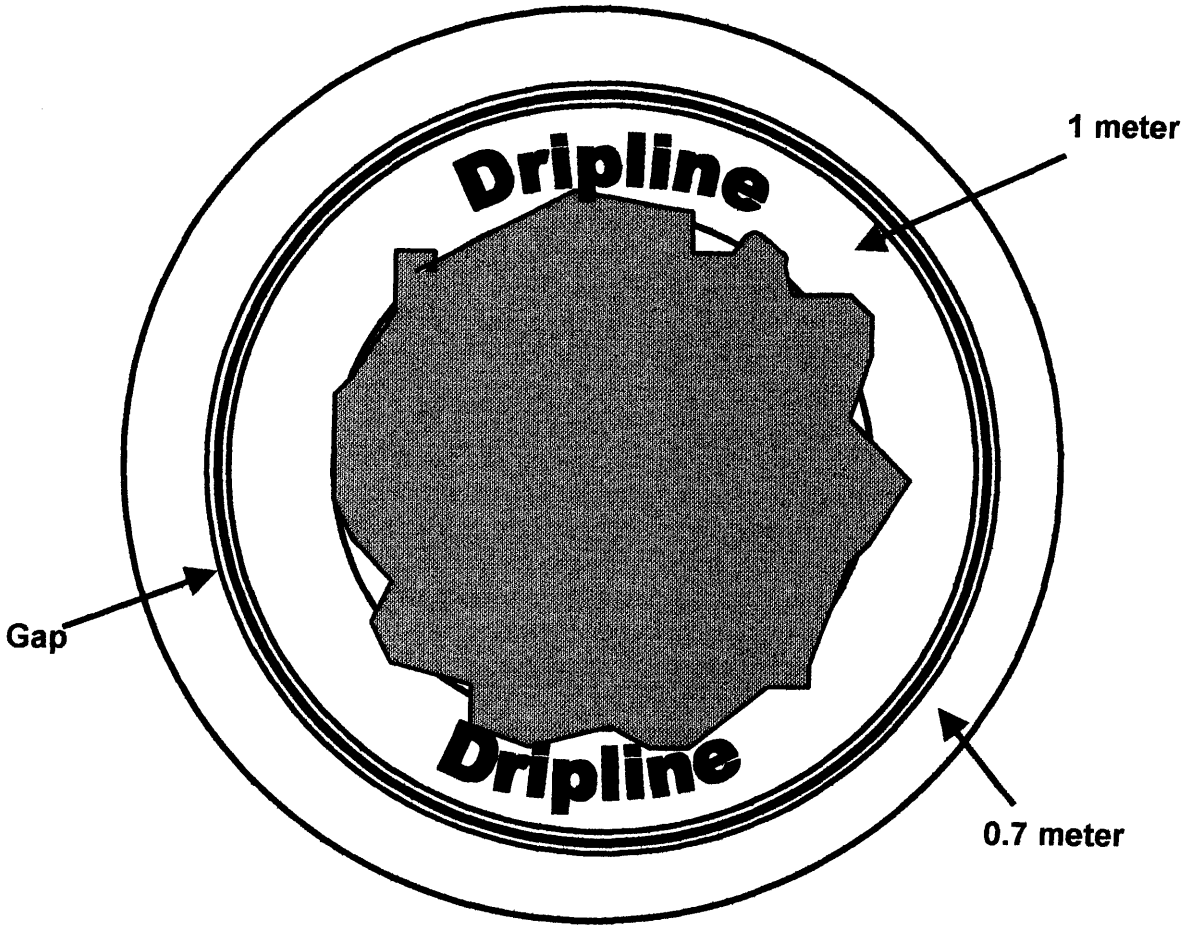


Figure 1. Diagram depicting the survey method used to search for *Pediocactus paradinei* on and outside the dripline around pinyon and juniper trees.

and using a random number generator, 15 trees of each species were selected for analysis. Equal sample sizes were chosen to approximate equal variance between each (Ott 1993).

The null hypothesis for the comparison of mean values of cacti on the dripline and cacti outside the dripline (for both the entire database and the 20% trimmed mean) was that the mean value of cacti on the dripline equals the mean value outside the dripline (H_0: $M_1 - M_2 = 0$). The null hypothesis for the comparison of mean values of cacti on the dripline of pinyon and cacti on the dripline of juniper was that the mean value of cacti on the dripline of pinyon equals the mean value on the dripline of juniper (H_0: $M_p - M_j = 0$). The same null hypothesis was used for the comparison of mean values of cacti outside the driplines of each tree species.

Results

During the first field trip in 2000 it became apparent that population levels of Paradine plains cactus were much reduced from their 1992-94 values. Although the previous surveys were neither quantitative nor comprehensive, they were sufficient to suggest consistent, if scattered, distribution in several areas of the woodland.

In early July of 2000, searches were carried out for six person-days at 12 locations along the East Side Game Road, and a total of three plants was found, each in a different area. In late July, surveys were continued for eight person-days with searches at 15 sites, four of which were positive for plants. Surveys using the method described above were completed around 8–30 trees at each site.

Statistical analysis was performed on data collected at five sites (including one that was nega-

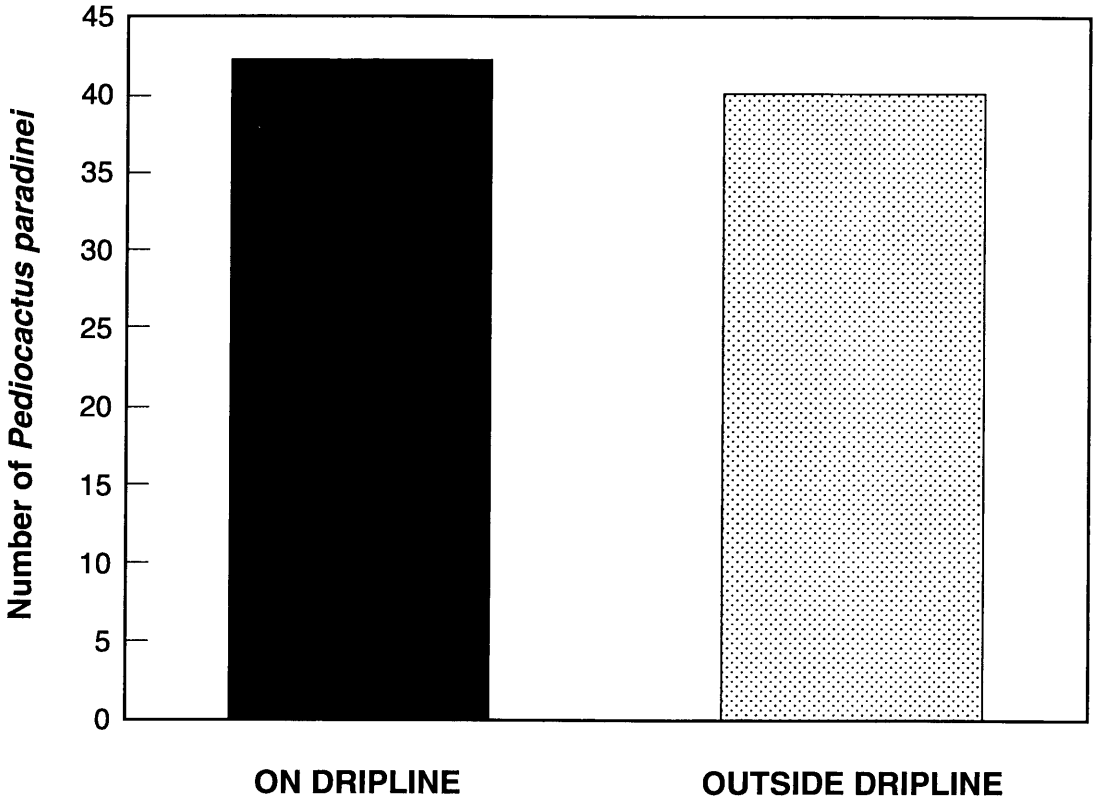


Figure 2. Number of *Pediocactus paradinei* on the dripline and outside of the dripline of pinyon and juniper trees at five sites.

tive). There were probably several reasons for the reduction in population, including severe drought for the preceding 2 years, herbivory by various rodents and rabbits due to lack of other available forage and water, and covering of plants by sheetwash during a severe storm the day before surveys commenced on the first trip. Paradine plains cactus plants retract below the surface of the ground by shrinking the size of the plant body, accordion-style, during times of protracted water stress. This makes them more difficult to locate, and after a storm resulting in sheetwash they may be covered with silt until sufficient moisture is available for the plants to swell and extend above the ground surface. The effects of these factors, and possibly other unknown factors causing a population reduction during the proceeding 6 years, are unknown. The previous surveys were conducted from late May to early September, so seasonal differences alone should not account for the reduction. The number of plants located during the first trip was not sufficient to obtain data for analyzing the dripline theory. During the second trip data were collected using the method described.

Statistical Analysis

The results reported here must be considered preliminary because the number of trees where cacti were found was too small a sample for adequate statistical evaluation. Statistical tests were performed to determine trends, and cannot be considered definitive.

The two t-tests, which compared the mean value of cacti on the dripline and the mean value of cacti outside the dripline, showed no statistically significant difference in mean values, and the null hypothesis was therefore accepted (Figures 2 and 3). The t-test comparing the mean value of cacti on and outside the dripline of pinyon trees with the mean value of cacti on and outside the dripline of juniper trees showed a statistically significant difference in mean values of cacti both on

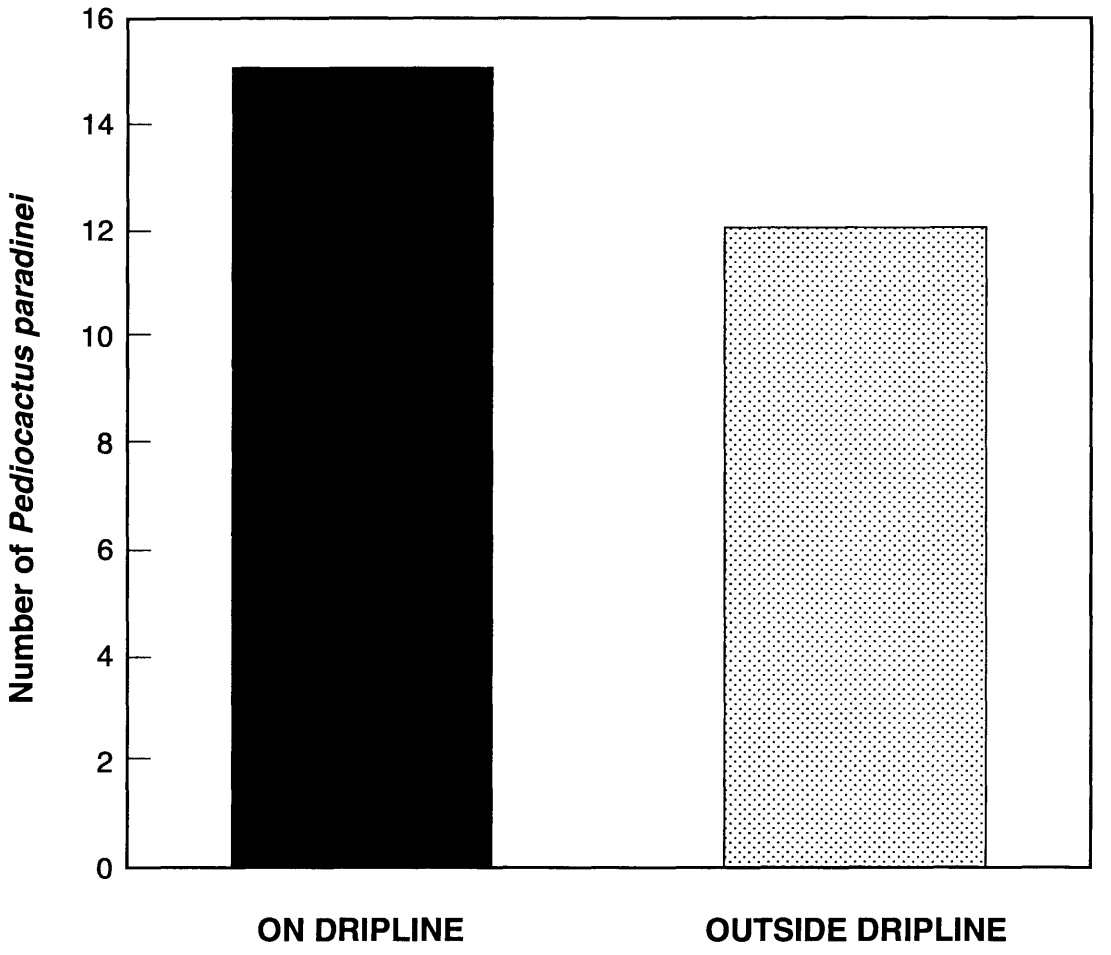


Figure 3. Number of *Pediocactus paradinei* on the dripline and outside of the dripline of pinyon and juniper trees at three sites.

and outside the dripline (Figure 4). Therefore, the null hypothesis was rejected.

The results of the statistical analysis indicate no significant association of Paradine plains cactus with the driplines around pinyon and juniper when the data are combined for associated tree species. However, when the association of pediocacti with pinyon and juniper was analyzed separately, the results indicate that the association of cacti on the dripline of juniper is significantly stronger than that of cacti on the dripline of pinyon. Additionally, the association of cacti outside the dripline of pinyon is significantly stronger than that of cacti outside the dripline of juniper.

Mycorrhizal Association

All species of *Pediocactus* except *P. sileri* are mycorrhizal; that is, their roots are colonized by vesicular-arbuscular mycorrhizae (VAM), fungi associated with the roots of certain plants that benefit the plants by enhancing nutrient absorption and water uptake (Milne 1987 and references cited by Milne). The association with mycorrhizae may enhance the ability of plants to live in harsh environments, such as the rocky, droughty soils where pediocacti are frequently found. Juniper, grasses, and pediocacti are among plants that are endomycorrhizal; pinyons are not. The indication is that pediocacti may be preferentially associated with juniper in the pinyon-juniper woodland because both cacti and junipers are endomycorrhizal.

Conclusions

1. The small number of cacti found in woodland habitats during this study is cause for concern, and is a trend that has also been noted in monitoring plots in the past 2 years. Drought is probably an overall causative factor resulting in the death of some pediocacti; cactus predation is a secondary effect caused by the stress of drought on rodents and rabbits. Because surveys were not conducted between 1994 and 2000, it is not known

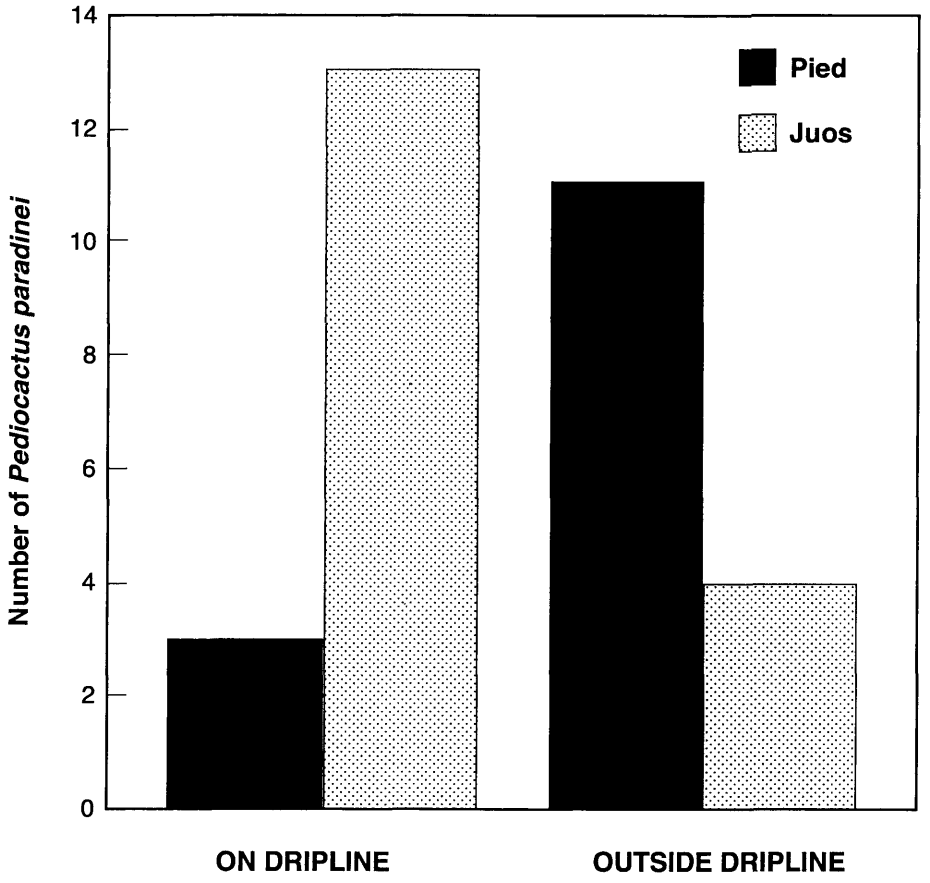


Figure 4. Number of *Pediocactus paradinei* on the dripline and outside of the dripline of a random sample of 15 pinyon and 15 juniper trees.

when the population decline may have started in the woodland.

2. Seasonal effects have had an unknown impact on the apparent rarity of the cacti. Because they tend to retract into the soil during periods of water stress, and then may be covered with soil by sheetwash during severe storms, it is possible that some plants were not visible during these surveys. This should be investigated during the next spring growing season that follows a winter with adequate precipitation.

3. Due to the small number of plants that could be located, the sample size is too small to be statistically significant, and the results reported here indicate only trends and not firm conclusions. A larger sample should be examined during a time of more favorable weather conditions to ascertain whether the population has decreased, as this survey suggests, or whether the plants were simply invisible. A larger sample is also needed to confirm the indication that there is no statistical correlation of Paradine plains cactus with pinyon and juniper taken together, and that the cacti are preferentially associated with the dripline around junipers.

4. The apparent decrease in numbers of such a rare plant is cause for concern about its status. If this is confirmed, the Conservation Assessment and Strategy should be amended, and management actions should be initiated to ensure the stability of the remaining population.

Acknowledgments

The authors thank Dr. Ward Brady, Environmental Resources Program, Arizona State University East in Mesa, for assistance in developing the study design. Field work was conducted July 9–13, 2000 by A. Phillips and D. Kennedy, and July 28–31, 2000 by A. Phillips, D. Weage, and B. Phillips. Statistical analysis was performed by D. Kennedy. Funding was provided by a purchase order issued to A. Phillips by the Kaibab National Forest.

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Cultural Influence As a Factor in Determining the Distribution of a Rare Sage, *Salvia dorrii* subspecies *mearnsii*

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Abstract: Although related taxa occur throughout the western United States, *Salvia dorrii* ssp. *mearnsii* is endemic to central Arizona. In part, its narrow distribution may be attributed to prehistoric human influences. A spatial analysis was used to determine the relationship of archaeological sites and populations of *S. dorrii* ssp. *mearnsii*. In the lower Verde Valley, approximately 89 percent of the plant populations were spatially related to archaeological sites. Plant populations from a different geographic area in the upper Verde Valley were also spatially related to known archaeological remains, although only 75 percent of the time. Consultations with traditional scholars of three indigenous tribes, the Hopi, Paipai, and Kumiai, were conducted to gain a better understanding of the cultural significance of the plant and to aid in the interpretation of plant–archaeological remain relationships. The consultants indicated that certain taxa in the genus *Salvia* (*S. dorrii* var. *dorrii* and *S. pachyphylla*) are used in ceremonies and as medicine. These plant–archaeological site associations may be the result of prehistoric plant husbandry systems including trade and dispersal of seeds via Native American clan travel.

Cultural factors affecting plant distribution have been discussed by many researchers in the past (Clark 1968, Yarnell 1973, Minnis and Plog 1976). It is well accepted that some plants have received special care by people, a practice known as plant husbandry (Winter and Hogan 1986, Anderson and Nabhan 1991, Minnis 1992, Smith 1992, Ford 1997). Generally, indigenous peoples were managing the entire ecological landscape in which they lived (Nabhan 1997) although in some cases, evidence of this management is ephemeral or completely absent. As Ford (1978) has discussed, there is a spectrum of plant husbandry techniques that includes activities such as tolerating or eliminating weeds, pruning, thinning, transplanting, tending, burning, cultivation, and domestication (Table 1).

Some plant husbandry techniques have significantly altered the distribution of certain plant species. Minnis and Plog (1976) concluded that the elevational range of *Agave parryi* had been increased by human movement. Other studies have discussed plant–archaeological site relationships for genera such as *Opuntia, Lycium, Cleome, Pinus, Juglans,* and *Malus* (Gilmore 1931, Mosely 1931, Zeiner 1946, Yarnell 1965, Clark 1968, Minnis and Plog 1976, Frison 1978). These relationships are difficult to interpret using modern ideas about human ecology and plant dispersal patterns. Consideration of ethnobotanical uses, characteristics of archaeological sites, cultural migration, and history of the study area should be included in analyses of such associations.

The distribution of *Salvia dorrii* ssp. *mearnsii* in central Arizona lends itself to an investigation of plant–archaeological site relationships. It is distributed in disjunct patches along the Verde River from Perkinsville to Camp Verde (Figure 1). The plants are often found adjacent to archaeological sites, although not all of the populations show this pattern. They appear to inhabit unique substrates (limestones, sandstones, mudstones) but are not limited to one vegetation type. Plants are found in desertscrub, chaparral, and pinon-juniper communities.

The ethnobotanical value of plants in the genus *Salvia* is useful in interpreting a plant–archaeological site relationship. Some taxa in the genus *Salvia* have been used for medicine by North American tribes such as the Diné (Navajo), Hopi, Kumiai, Northern Paiute, Paipai, Shoshone, Washoe, and Kawaiisu (Whiting 1939, Train et al. 1941, Zigmond 1981, Moerman 1986, Fowler 1989; and Teodora Cuero, Theodora Homewytewa, Benito Peralta, and Robin Taylor, personal communication). *Salvia dorrii* ssp. *mearnsii* may have been used by people living in central Arizona in the past. Traditional scholars from several tribes (Hopi, Kumiai, Paipai) have been consulted; they have indicated that relatives of this subspecies (*Salvia dorrii* ssp. *dorrii* and *S. pachyphylla*) are used extensively for stomach-aches, headaches, and

Table 1. The spectrum of plant husbandry techniques (Smith 1992, Ford 1997).

Least intensive management	Toleration of weeds
	Weeding
	Pruning
	Thinning
	Active encouragement
	Active selection of certain traits
	Burning
Most intensive management	Gardening
	Management of trees/nuts
	Cultivation
	Domestication

other medicinal uses, and that *S. dorrii* ssp. *mearnsii* was probably used in central Arizona in the past as an alternative to plants that people knew from different geographical areas for similar medicinal and ceremonial reasons (Homewytewa and Taylor, personal communication).

I investigated whether human influence was a factor in the distribution of *Salvia dorrii* ssp. *mearnsii* by analyzing the spatial relationship between archaeological sites in central Arizona and the culturally significant plant, *Salvia dorrii* ssp. *mearnsii*. I addressed the following two questions: Are archaeological sites and populations of *Salvia dorrii* ssp. *mearnsii* in the upper and lower Verde Valley spatially independent? How can we use modern distributions of plants to interpret past human influence on the distribution of plants? This study is unique because it analyzes the relationship between plants and archaeological sites using spatial statistics. In addition, I consulted traditional scholars to better understand the cultural importance of this subspecies and plant husbandry systems in the Southwest and to verify historical writings and biological patterns.

Taxonomy and Description

Salvia dorrii ssp. *mearnsii* is one of two subspecies in the *S. dorrii* complex. *Salvia dorrii* ssp. *mearnsii* is geographically isolated from *S. dorrii* (Kellogg) Abrams ssp. *dorrii* (Strachan 1982). It is

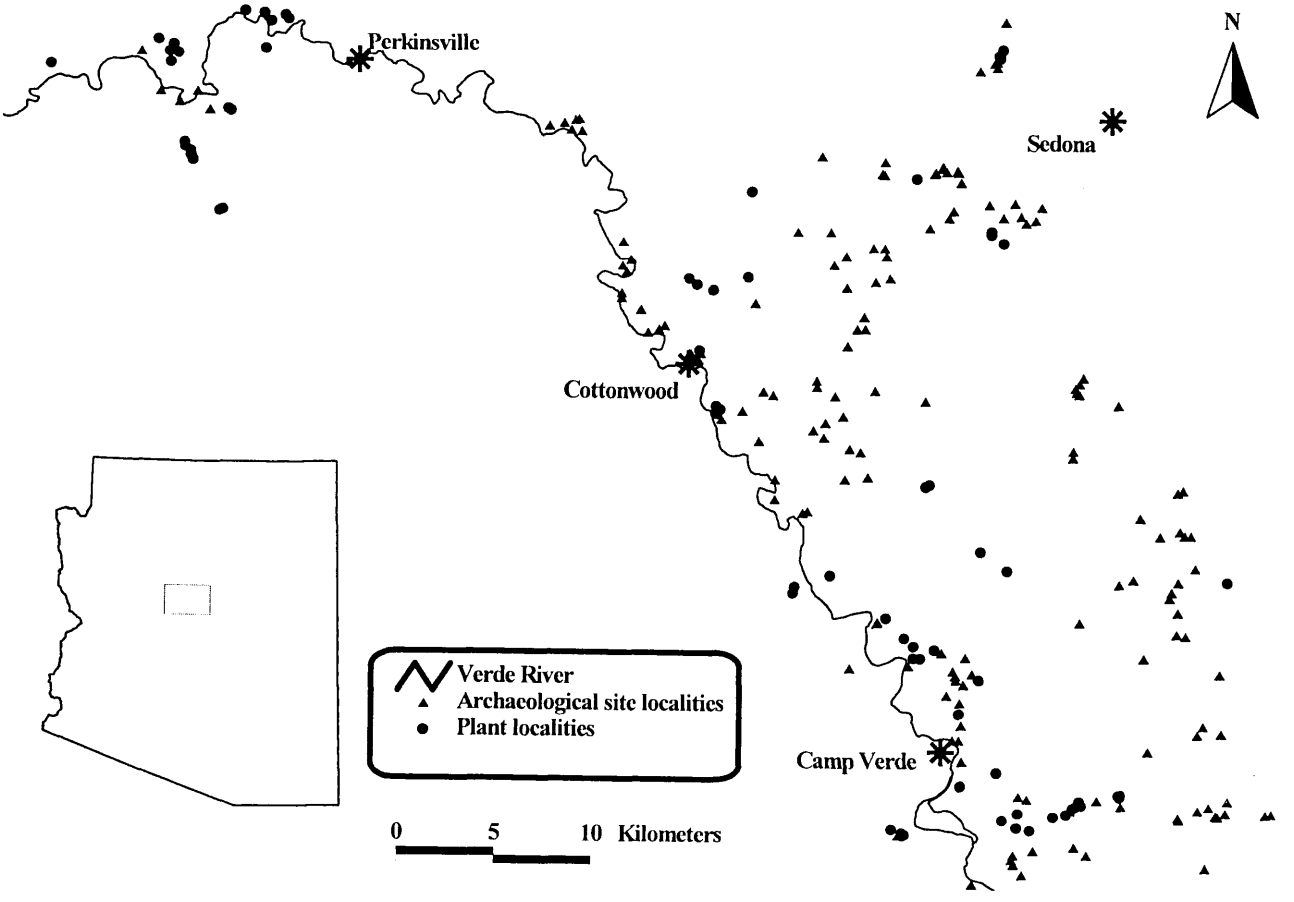


Figure 1. Distribution of *Salvia dorrii* ssp. *mearnsii* and archaeological sites in the study area. Inset is study area on Arizona map.

also morphologically distinct from *S. dorrii* ssp. *dorrii* by its reduced stature (15–30 cm vs. 10–50 cm), narrow leaves (1.5–3 mm wide vs. 6–10 mm wide), and low number of verticels per branchlet (1–3 vs. 2–5). *Salvia dorrii* ssp. *mearnsii* is limited to central Arizona, whereas the other subspecies, *S. dorrii* ssp. *dorrii*, and its varieties, var. *dorrii*, var. *clokeyi* Strachan, var. *carnosa* (Douglas ex Greene) Cronq., and var. *pilosa* (A. Gray) Strachan & Reveal, are widespread throughout the western United States and into Mexico. *Salvia pachyphylla* Epling ex Munz is closely related to members of the *S. dorrii* complex and occurs in disjunct populations in northern Arizona, California, and Mexico (Strachan 1982).

The U.S. Forest Service lists *Salvia dorrii* ssp. *mearnsii* as a sensitive species because of its limited distribution and threats to its survival. The rapid development of the Verde Valley potentially threatens the plant and its habitat; specific activities that endanger this taxon are mining, land trades, and other development projects. If not protected, *Salvia dorrii* ssp. *mearnsii* may not persist in nature.

Cultural History of Central Arizona

Not only is central Arizona in the midst of a biological transition zone, it is a cultural transition zone as well (Gummerman and Johnson 1971, Pilles 1981). The upland habitats of the Colorado Plateau and the desert scrub and grassland habitats of the Sonoran Desert merge in a valley used by many groups of people (Table 2). The most essential resources required for human survival were all available: water for irrigation and consumption, wild plants and animals for food and medicine, building material, salt, clays and ores for paints, and fertile soil for agriculture. Based on archaeological remains, written histories, and oral tradition, many cultural groups (Table 2) with different lifestyles are known to have lived in this area since 12,000 B.C. (Fish and Fish 1977, Pilles 1981, Fish and Fish 1984, Macnider et al. 1989, Downum 1992). The many types of archaeological sites in the Verde Valley, including caves, large and small pueblos, pithouses, fieldhouses, cliff dwellings, ballcourts, roasting pits, and forts, give evidence of distinct lifestyle differences, time periods, and cultural groups.

Table 2. Cultural history of central Arizona (Fish and Fish 1977, Fish and Fish 1984, Pilles 1981, Macnider et al. 1989, Downum 1992).

Date*	Period and cultural group	Lifestyle and other notes
12,000–8000 B.C.	PaleoIndian	Little evidence because of alluvium deposits; hunters likely to be present
8000 B.C.–1 A.D.	Archaic	Migratory hunters and gatherers
1–800 A.D.	San Pedro Cochise/ Basketmaker II	Hunters, seasonal use, and beginnings of agriculture
ca. 1–900 A.D.	Early Sinagua and Anasazi	Puebloan farmers
ca. 700–1100 A.D.	Hohokam	Irrigation farmers
1100–1300 A.D.	Southern Sinagua	Farmers
ca. 1200 A.D. (1300–1450 A.D.)	Pueblo IV (Tuzigoot, Montezuma Castle)	Hopi clans travel through on the way to the mesas; claim ancestral land here
1000–1275 A.D.	Prescott/Cohonina	Puebloan farmers
ca. 1500–1850s (to present on reservations)	Yavapai	Hunters & gatherers with some irrigated farming
ca. 1500–1800s	Apache	Hunters & gatherers with some irrigated farming
1500–1650s	Spanish	Scientists and military
1860s	American	Miners, beaver trappers, and first settlements

* Dates vary according to the author and geographical area; earliest and latest hypothesized dates are noted.

Most of the remains in the Verde Valley area are from the Southern Sinagua and Hohokam cultures, found in this area from approximately 700 to 1300 A.D. (Pilles 1981, Fish and Fish 1977, Fish and Fish 1984, Downum 1992). Evidence of these two groups appears near Perkinsville, although most of the remains in this region are of the Prescott and Cohonina cultures. Due to the lack of archaeological studies on the Prescott culture, their ancestry is unknown. However, the Prescott-Yavapai, Zuni, and Hopi tribes claim direct ancestry with the Prescott people (USDA 1996, Elaine Zamora personal communication) and the Hualapai and Havasupai are also thought to be related to the people who once lived in the upper Verde Valley (Schwartz 1955, Dobyns 1956, Heueh 1974, Manners 1974, Dobyns and Euler 1976, Euler 1981, Weber and Seaman 1985).

Materials and Methods

Identification of Plants and Archaeological Sites

Plant locality information for *Salvia dorrii* ssp. *mearnsii* was collected using two methods. Sixteen distinct sites of the plant were mapped using a portable GPS. Due to time constraints and accessibility to certain plant populations, the remaining sites were gathered from the Heritage Database Management System at the Arizona Game and Fish Department, which contains 48 point localities of *Salvia dorrii* ssp. *mearnsii*; 27 of the 48 sites were observed during this study. To obtain accurate statistical results, the study area was divided into two distinct geographical areas, the upper and lower Verde Valley, in accordance with their actual locations in Arizona (Figure 1).

Archaeological site locality information was gathered for all geographical areas where populations of *Salvia dorrii* ssp. *mearnsii* are known to occur. Information describing each archaeological site was collected from records at the U.S. Forest Service and from the archives at the Museum of Northern Arizona in Flagstaff. Map coordinates for the archaeological sites, their descriptions, and their approximate dates of occupation were used to subdivide the archaeological remains into logical categories that aided in determining which archaeological sites were appropriate for spatial analysis (Table 3).

Two separate spatial analyses were conducted for each geographical area because some archaeological remains are more indicative of past environments than others. If people were manipulating the growth and reproduction of *Salvia dorrii* ssp. *mearnsii*, it follows that the plants would be found more frequently on or near old home sites than near petroglyphs or lithic scatters. In each geographical area, the first analysis included only habitation sites such as pueblos, caves, and pithouses. The second analysis was more inclusive, using all habitation sites as well as other archaeological remains that may have been associated with homes, such as ballcourts or irrigation canals (Table 3). In addition, it should be noted that the archaeological sites analyzed in this study are from a wide variety of cultural groups from different time periods. This analysis does not distinguish between the different time periods due to the difficulty of interpretation based solely on limited archaeological records.

Table 3. Classifications of archaeological remains.

Habitations only *
Temporary campsite, structure
Pithouse, fieldhouse
Cliff dwelling
Pueblo
Unspecified habitation
Cave structure
Habitations and other archaeological remains *
Rock alignment
Stone area (possibly houses)
Terrace, irrigation canal
Old field
Ballcourt
Yavapai-unspecified structure with rooms
Other archaeological remains **
Plant or food processing area
Artifact scatter, lithics
Roast pit
Burial
Manos and metates
Historic remains
Petroglyphs

* Remains that were used in the statistical analysis.
** Remains that were not used in the statistical analysis

Plant–Archaeological Site Associations

Scatter plots relating individuals of *Salvia dorrii* ssp. *mearnsii* to archaeological sites did not determine whether the components were spatially related; therefore, spatial statistics were employed. Duncan's spatial analysis software was used to investigate spatial independence between two components. This program calculates a value $K_{12}(t)$ using x,y coordinates for two variables, in this case plants and archaeological sites (Lotwick and Silverman 1982, Diggle 1983, Upton and Fingleton 1985, Duncan 1991, Duncan and Stewart

1991, Duncan 1993). The value is calculated using the formula $K_{12}(t) = \lambda_2^{-1} E$ [number of type 2 events within distance t of an arbitrary type 1 event], where t = 0, (t) is the distance, lambda (λ) is the mean number of type 2 events per unit area, and E is the expectation (Lotwick and Silverman 1982, Diggle 1983, Upton and Fingleton 1985). The null hypothesis is that the two components are spatially independent and randomly distributed. The null is rejected if the $K_{12}(t)$ values fall above or below a 99 percent confidence interval whereby the two variables could be attracted (positively associated) or repulsed (negatively associated), respectively.

Every point on the graph represents a $K_{12}(t)$ value calculated every 20 m up to 1200 m. The program compares the actual positions of the components to 99 simulated combinations of a random distribution pattern. When these data points fall between the lower and upper confidence limits, the two variables exhibit a random distribution and are spatially independent. However, when the observed data points fall outside of the lower and upper confidence limits, there is spatial dependence.

The percentage of plant populations of the total that could be associated with archaeological sites was determined from the raw data. All plant localities that occurred within the distances of spatial dependence (see results) were included in the total percentage of plants associated with archaeological sites.

Results

In the lower Verde Valley, 34 *Salvia dorrii* ssp. *mearnsii* populations, 137 habitation sites, and 25 non-habitation sites were used in the analysis; in the upper Verde Valley, 14 *Salvia dorrii* ssp. *mearnsii* populations, 44 habitation sites, and 4 non-habitation sites were used.

Archaeological sites and populations of *Salvia dorrii* ssp. *mearnsii* are spatially dependent. As explained above for spatial analyses, two components are positively associated when the data points lie above the upper confidence interval limit. At distances between 500 and 1200 m, populations of this subspecies (n = 34) and archaeological sites that are old home sites (n = 137) in the lower Verde Valley are spatially dependent (99% CI; Figure 2a). Similarly, when other archaeological remains (Table 3; n = 162) are included in the analysis, plants and archaeological sites at distances between 500 and 950 m are spatially dependent (99% CI; Figure 2b). This relationship with archaeological sites is representative of 89 percent of the plant populations found in this area.

Similarly, in the upper Verde Valley, Duncan's spatial analysis indicates that archaeological sites and populations of *Salvia dorrii* ssp. *mearnsii* are spatially dependent. The plants (n = 14) and sites that were old habitations (n = 44) are spatially dependent at distances between 1100 and 2000 m (99% CI; Figure 3a). Similarly, when other types of archaeological sites are included (n = 48), plants and sites in the upper Verde Valley are spatially dependent at distances between 1000 and 2000 m (99% CI; Figure 3b). This relationship with archaeological sites is representative of 75 percent of the plant populations found in this area.

Populations of the subspecies are found away from archaeological sites up to 25 percent of the time. This lends support to the hypothesis that *Salvia dorrii* ssp. *mearnsii* was present in central Arizona before humans inhabited the area. The statistical analyses provide clues as to why *Salvia* appears to be on archaeological sites more often than not, but does not explain why it is found in areas without archaeological sites. However, through time, associations between plants and archaeological sites may diminish as plant husbandry traditions cease (Karen Adams, personal communication).

Discussion

It is extremely difficult to determine why *Salvia dorrii* ssp. *mearnsii* is not more widespread in central Arizona. Spatial statistics provide a means of analyzing relationships that may not be evident using scatter plots and standard statistics. The positive spatial relationship of *S. dorrii* ssp. *mearnsii* with archaeological sites (75–89%) lends support to the theory that this subspecies was cared for by people. It appears that humans have, at least in part, had a role in its dispersal and reproduction. Brooks and Johannes (1990) reported that "positive [vegetative] indications include the presence of plants brought to, or raised at specific sites for express purposes, usually nutritional or ceremonial." In addition, consultations with traditional Hopi scholars and medicine people have indicated that *Salvia dorrii* ssp. *mearnsii* was probably used as a medicine and in ceremonies, and people were probably involved in its care and dispersal (Homewytewa and Taylor, personal communication).

Manipulation of *Salvia dorrii* ssp. *mearnsii* by people may have altered its abundance and its range. It is well known that plant husbandry

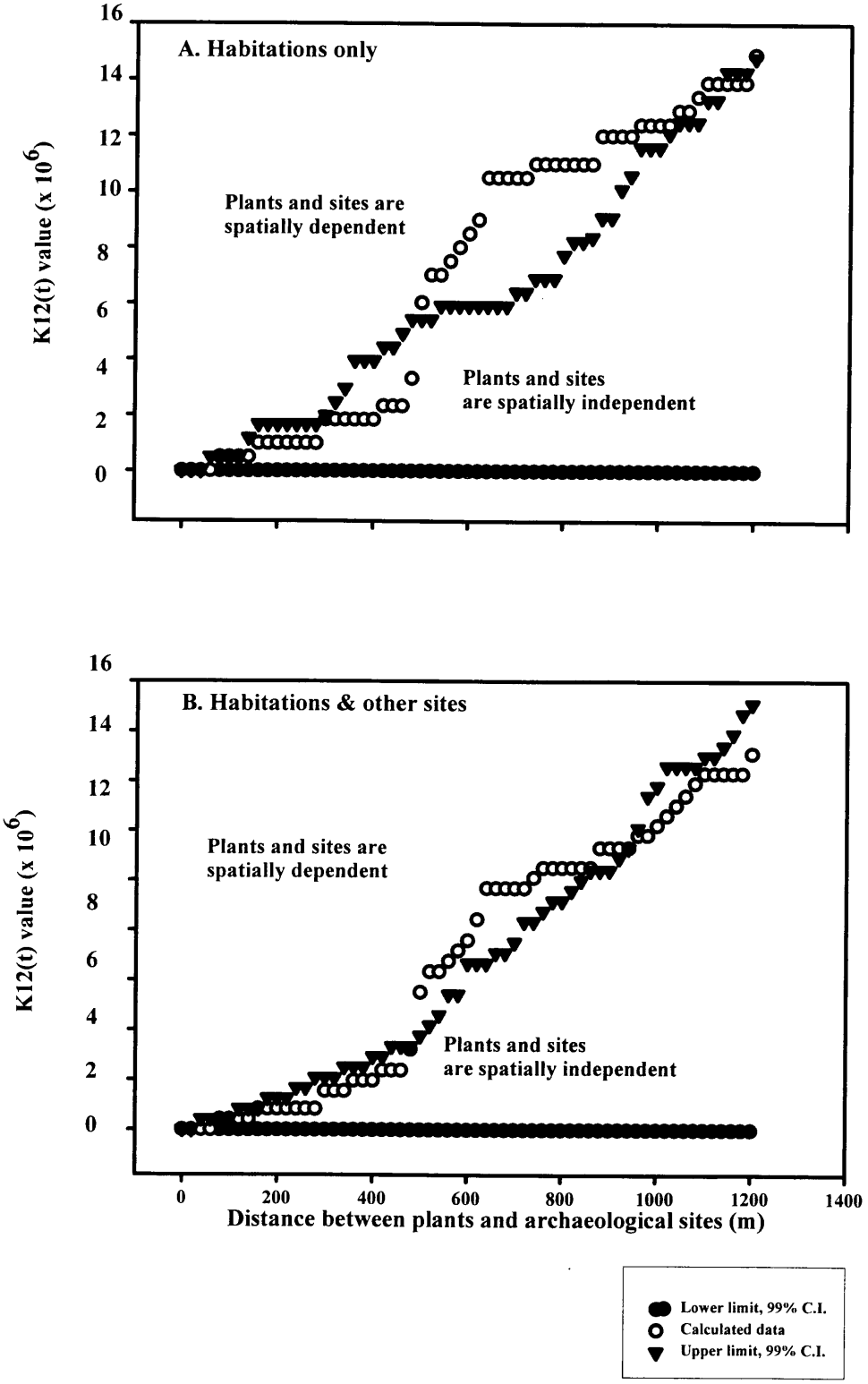


Figure 2. Populations of *Salvia dorrii* ssp. *mearnsii* in the lower Verde Valley and archaeological sites are spatially dependent at distances between (a) 500 and 1200 m when habitations were included in the analysis, and (b) 500–950 m when habitations and other archaeological sites were included in the analysis.

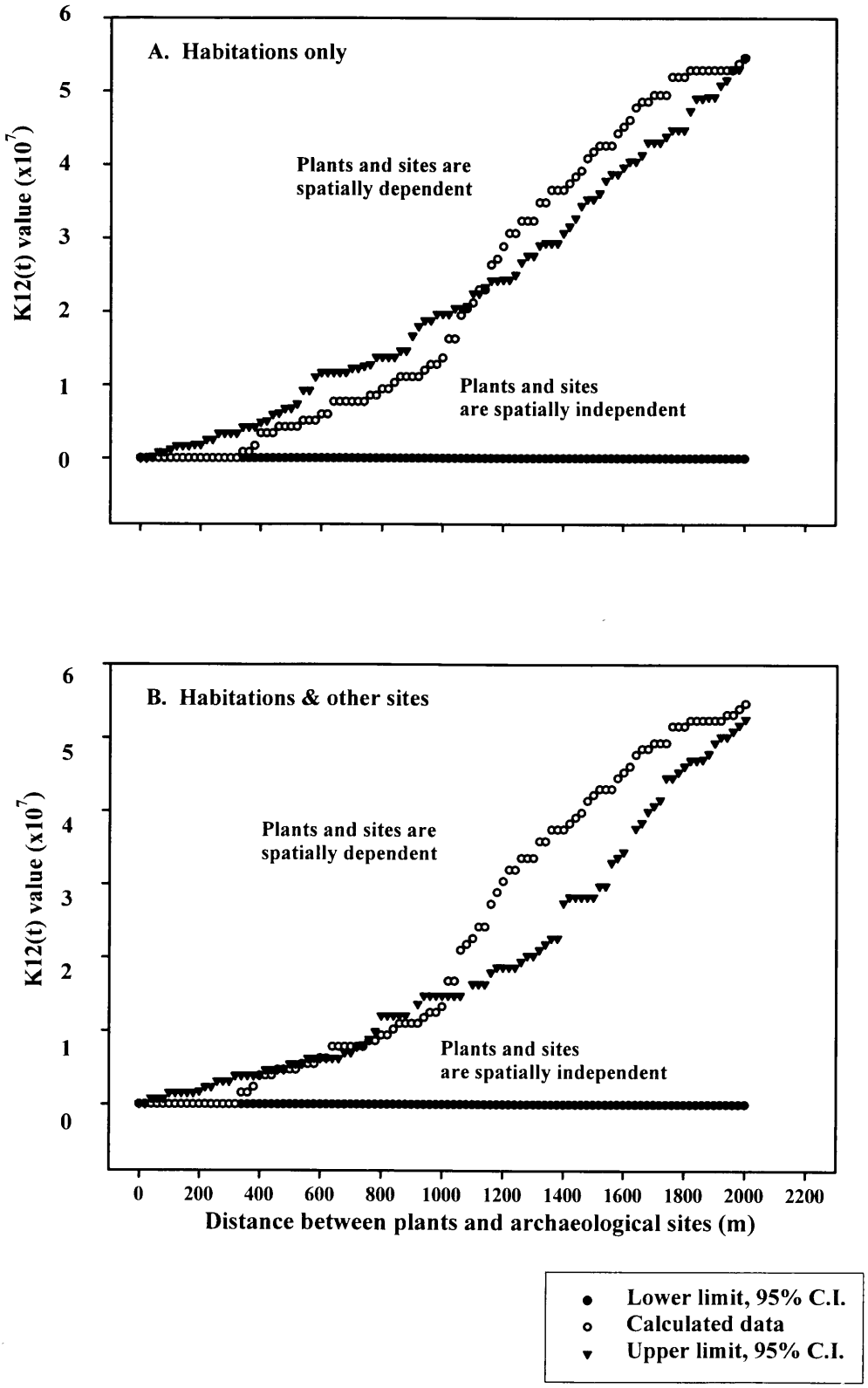


Figure 3. Populations of *Salvia dorrii* ssp. *mearnsii* in the upper Verde Valley and archaeological sites are spatially dependent at distances between (a) 1100 and 2000 m when only habitations are included in the analysis, and (b) 1000–2000 m when habitations and other archaeological sites are included.

activities have affected the present-day abundance and distribution of other species (Whiting 1939, Wells 1959, Winter and Hogan 1986; and Hogan and Taylor, personal communication). For example, pruning of shrubs and trees affects the abundance of fruits desired for harvest. Similarly, pruning of *Salvia dorrii* ssp. *mearnsii* may have been a technique to stimulate new growth of fresh leaves.

Trade is also an important component when discussing the movement of plants. Ford (1984) has hypothesized that plants were traded over long distances as well as within localized exchange systems. Trade routes can function as mechanisms for overcoming geographical barriers, enabling new subspecies to develop (Brooks and Johannes 1990). Traders carry seeds of many plants from place to place (Young 1990, Slifer and Duffield 1993, Hill 1995; and Hogan, Homewytewa, and Taylor, personal communication) and trade of *Salvia* species between people in the western United States and Mexico is likely to have occurred. Extensive trading of the seeds, leaves, and flowers of this taxon may have resulted in a human-mediated founder effect that allowed the morphologically distinct plants to become established in central Arizona.

Furthermore, whole groups of migrating people, called clans, brought plants from their homelands to new places of habitation (Lowie 1929, Herrington 1939, Sherer 1965, Lynch 1987). This theory has been validated on several accounts through consultations with clan leaders, herbalists, and medicine people from indigenous American groups such as the Hopi and Diné (Navajo) that are still organized in clans (Hogan, Homewytewa, and Taylor, personal communication). For example, important plants such as tobacco have been carried by some tribes (whole plants or seeds) for centuries (Homewytewa and Taylor, personal communication). In fact, it is logical to assume that "any group of people accustomed to using these plants might be inclined to bring them along when traveling" (Black 1978).

Significant plants used for certain medicines or ceremonies may have been important enough to transport and replant in new settlements. *Salvia* may have been one of these plants. One Kumiai medicine woman, Teodora Cuero (personal communication), noted that *Salvia pachyphylla* was one of her most revered plants. The establishment of new populations of *S/ dorrii* ssp. *mearnsii* as people moved around central Arizona is likely. The collection of seeds from this plant may have enhanced its distribution in some areas, especially in disturbed sites like habitation areas.

Without human-mediated dispersal, *Salvia dorrii* ssp. *mearnsii* is not equipped to disperse itself over large distances. Although many seeds are adapted for animal, wind, and water dispersal (Lidicker and Caldwell 1982, Swingland and Greenwood 1983), this plant has large seeds that are not adapted for these types of dispersal. However, its seeds have a polysaccharide coating when imbibed with water, and may be dispersed by ants (Beattie 1985, Horvitz 1991). Ant dispersal does not explain the disjunct populations of *Salvia dorrii* ssp. *mearnsii* that are more than 100 miles from the closest populations of its relative *Salvia dorrii* ssp. *dorrii*.

In addition, *Salvia dorrii* ssp. *mearnsii* is not easily established in undisturbed, untended areas in nature. It is not considered to be a weedy plant although it can flourish in disturbed areas, such as old mine sites. Old mine sites provide optimal colonization sites for many plants due to the high degree of disturbance and increased levels of available minerals in the soil (Bradshaw and McNeilly 1981, Brooks and Johannes 1990). In fact, *Salvia dorrii* ssp. *mearnsii* has become established at one major mine site near Perkinsville (upper Verde Valley). Archaeological sites are also highly disturbed and may therefore provide an optimal habitat for *Salvia dorrii* ssp. *mearnsii*.

Conclusions

Many factors affect the unique distribution of the endemic sage, *Salvia dorrii* ssp. *mearnsii*. After 3 years of study and through consultations with traditional scholars, I believe that *Salvia dorrii* ssp. *mearnsii* was tended by people in central Arizona, changing its natural distribution. It is an important plant in medicine and in ceremonies, and a high percentage of plant populations occur near archaeological sites. Current molecular genetics studies (Taylor, unpublished data) will aid in the interpretation of the distribution and phylogenetic relationships between members of the *Salvia dorrii* complex and *Salvia pachyphylla*.

As Gary Nabhan (1997) has suggested, vegetation distribution and change must be viewed by incorporating both environmental and cultural influences when studying ecological systems. Each set of data can provide supporting information in explaining ecological patterns. As scientists we must consider the knowledge that indigenous people hold about their environments and collaborate with them in our studies of the ecological relationships between plants and animals (Nabhan 1997).

Many researchers believe that Native American land management practices acknowledged and considered rare species (Nabhan 1997). Anderson and Nabhan (1991) suggested that "Native Americans not only were stewards of major food resources, they also protected certain plants and animals that were too rare to have ever been valued on utilitarian grounds alone." *Salvia dorrii* ssp. *mearnsii* is a plant that was probably more important to people living in central Arizona than can be gathered through a spatial statistical analysis. Each piece of information about this taxon, ecological or cultural, adds a new perspective on its unique distribution.

Acknowledgments

I would like to thank my thesis committee: Drs. Tina Ayers, Randy Scott, George Koch, and Mike Kearsley, and Phyllis Hogan. Special thanks to Teodora Cuero, Theodora Homewytewa, Josefina Ochurte, Benito Peralta, Michelle Sockwyma, Dalton Taylor, and Max Taylor for their willingness to discuss the cultural significance of this plant. Thanks to those who assisted with fieldwork: Kambria Beck, Leslie Brandt, Melissa Jurgenson, Gabe Martinez, Dr. Neil Cobb, Elaine Zamora, Peter Pilles, Barbara Phillips, Jean Searle, Tracy Murphy, Marc Baker, Brad Blake, and Jeff Schively; all assisted with design and statistical analysis. The National, Pacific Region, and State Councils of Garden Clubs, the Orchid Society of Arizona, NAU's Ecological Restoration Institute, and the Arizona Ethnobotanical Research Association all provided support for this project.

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Distribution and Taxonomic Discussion of *Tetraneuris verdiensis*, an Apparently Rare Edaphic Endemic from the Verde Valley of Arizona

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Abstract: *Tetraneuris verdiensis* was first published in 1996. It appears to be closely related to *Tetraneuris acaulis* var. *arizonica*. The closest known location of *T. acaulis* var. *arizonica* is approximately 7 miles northwest of the known *T. verdiensis* locations, which are 5 miles east of Camp Verde. *Tetraneuris verdiensis* is significant in that no other entirely discoid populations, or series of populations, of *Tetraneuris* have been reported. *Tetraneuris verdiensis* populations are consistently discoid, which separates them from *T. acaulis* var. *arizonica*. The type locality is on the top of a low hill of a gypsum stratum of the Late Tertiary Verde Formation. Denham and Turner (1996) stated that additional populations occur on the tops of the adjacent small hills within this stratigraphic unit. Results of a survey of all of the similar gypsum hills and mesas in this area east of Camp Verde are presented, along with population sizes for each gypsum hill where this species occurs. The morphological similarities and differences between *T. verdiensis* and *T. acaulis* var. *arizonica* are discussed, as well as the taxonomic status of *T. verdiensis*.

During recent investigations of rare plant distributions for the Arizona Rare Plant Field Guide (in preparation), a recently named species from the Late Tertiary Verde Formation of central Arizona was first investigated by this author. *Tetraneuris verdiensis* R. A. Denham & B. L. Turner is a dwarf scapose perennial species with densely pilose basal leaves and discoid yellow flower heads (Figure 1). At the time of its discovery in the winter of 1993–1994, this species was known only from the tops of a few small localized gypsum hills within the lacustrine limestone deposits of the Verde Formation. It has been well documented that the lacustrine deposits of the Verde Valley contain several species of endemic, disjunct, and relict plants from different floristic communities (Anderson 1996, Denham and Turner 1996).

To understand the floristics of the Verde Valley's lacustrine deposits, it is important to look at the geologic and climatic history of that region. The Verde Valley is in an area of central Arizona where the northern limits of the Sonoran Desert come into contact with the Transition Zone. The Transition Zone is a relatively narrow geologic province below the Mogollon Escarpment that consists of closely spaced mountain ranges with narrow basins (Anderson 1996, Titley 1984). Approximately 15 million years ago, this geologic province was formed during the mid-Miocene Basin and Range Disturbance, which initially resulted in the formation of a series of sub-Mogollon enclosed basins through tectonic uplifting and subsidence, as well as volcanic activities. During the Late Tertiary period, these enclosed basins subsequently filled with large quantities of water, where lacustrine deposits with interbedded ash flows were laid down into limy tuffs (Anderson 1996, Damon et al. 1984, Denham and Turner 1996). The Late Tertiary Verde Formation was created during this process, as well as several other geologic lacustrine formations in disjunct sub-Mogollon basins (Anderson 1992, 1996). See Figure 2 for a map of the Transition Zone and the formerly enclosed basins, where lacustrine deposits formed during the Late Tertiary Period.

During the Pleistocene glacial periods that occurred approximately 11,000 years ago, as subsidence ceased and precipitation increased, stream throughflow between basins increased and caused erosion to occur. In the Verde Valley area, this erosional activity exposed the undeformed lacustrine deposits of the Late Tertiary Verde Formation, allowing plant species to colonize the area (Anderson 1996, Nations et al. 1982). Floristic communities within these deposits vary drastically with changes in the substrates of this formation. The upper portion of this formation, near Cottonwood, consists of narrow interbedded layers of limestones, mudstones, and marls. The lower end of the formation, from near Camp Verde and extending to the south and east, was formed in the deepest parts of the prehistoric lake. This area consists primarily of larger limestone deposits and evaporites, such as gypsum and deposits of salts (Anderson 1992, Denham and Turner 1996). In this portion of the Verde Valley, numerous narrow bands of peculiar soils running in a northeast-southwest direction are exposed. In this area one



Figure 1. *Tetraneuris verdiensis*.

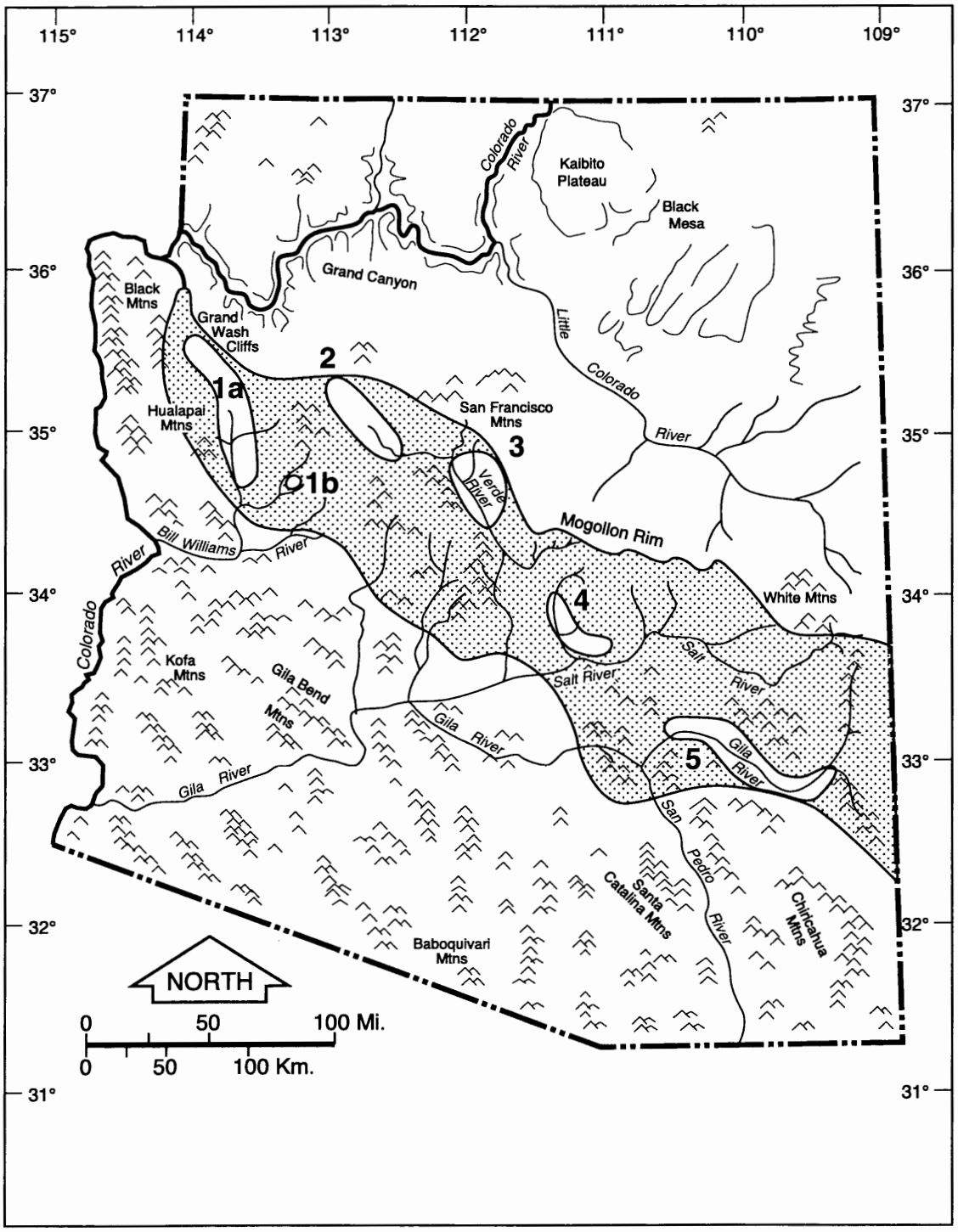


Figure 2. The Transition Zone geologic province of Arizona (shaded area). 1a = Hualapai Valley, 1b = Burro Creek, 2 = Chino Valley, 3 = Verde Valley, 4 = Tonto Valley, 5 = San Carlos Basin.

can go from areas of limestone to areas of gypsum and marl, and eventually to areas of volcanic tuff. Each of these substrates accommodates a unique floristic community. *Tetraneuris verdiensis* apparently occurs only on these gypsum marl soils of the lower end of the Verde Formation.

The Verde Valley is approximately 300–450 m higher in elevation than any of the other Transition Zone basins and is the closest of these basins to the Mogollon Rim. As in all of the other Transition Zone basins, the climate is more equable than the surrounding desert areas. This equable climate exhibits a biseasonal precipitation pattern of 25 cm or more of annual precipitation, a moderate mean annual temperature, and a relatively small difference between the annual high and low temperatures as compared to other areas in the surrounding deserts (Raven and Axelrod 1978, Axelrod 1979, Anderson 1996). The combination of these climatic characteristics causes the climate to be similar to the more mesic climate of the Miocene in the Southwest (Axelrod 1979, Anderson 1996).

The Verde Valley Transition Zone basin is located within the *Larrea tridentata–Canotia holacantha* series of the Arizona Upland Subdivision of the Sonoran Desertscrub biotic community (Brown 1994). However, the relatively infertile soils of the lacustrine deposits within the Verde Valley form a sharp edaphic contrast and generally exclude species that are typically dominant in this biotic community, including *Larrea tridentata* (DC) Coville, *Parkinsonia microphylla* Torr., and *Canotia holacantha* Torr. This opens the way for the occurrence of disjunct, endemic, and relict species by reducing competition for soil moisture. The number of elevationally and geographically disjunct species, as well as endemic and relict species, is higher in the Verde Valley than in any of the other Transition Zone basins (Anderson 1996). Apparently, the sharp edaphic contrast of the lacustrine deposits compared to the typical volcanic and metamorphic soils found in the Sonoran Desert has been the most important factor in the establishment and continued existence of the endemic, disjunct, and relict species that are found there (Gankin and Major 1964, Anderson 1996).

Climatic changes in the Southwest have provided the sources of these floristic curiosities in the Verde Valley area. Through studies of pack rat middens, it has become clear that the Verde Valley contained pine-oak-juniper woodland with chaparral as recently as the Late Tertiary period. This vegetation arrived in that area as a result of Pleistocene glacial cycles, which caused pinyon-juniper woodlands to extend southward into the lower elevation deserts of the Southwest, including areas that today contain the modern Sonoran and Chihuahuan Deserts (Betancourt 1986, Van Devender 1977, Van Devender and Spaulding 1979, Van Devender and King 1971, Lanner and Van Devender 1981). At the end of the most recent Wisconsin glaciation, approximately 11,000 years ago, the climate of the Southwest became warmer and drier, causing pinyon-juniper woodland to retreat from these lower deserts (Anderson 1992). The relatively infertile soils of the Verde Valley's lacustrine limestone deposits have apparently offered refugia for many genera that historically occurred in the area. Because of the biseasonal precipitation pattern and relatively equable climate, and the fact that many of the species dominant in the modern Sonoran Desert do not grow on these infertile soils, the lack of competition for soil moisture has enabled genera typically associated with pine-pinyon-juniper vegetation to remain in the Verde Valley (Anderson 1992, 1996). The genus *Tetraneuris* is no exception, as it typically occurs at higher elevations in the Great Plains, Great Basin, and Rocky Mountains (Denham and Turner 1996).

Distribution of *Tetraneuris verdiensis*

The distribution of *Tetraneuris verdiensis* and the sizes of each population segment of this apparently rare plant were investigated and documented during this study. This research was conducted in May of 1999 and 2000. Based on Denham and Turner's (1996) description of the habitat and distribution of this species and on personal observations of the habitat of the type location, all suitable and similar habitats within a 3-mile radius of the type locality were surveyed for this species. This habitat consists of the tops of low chalky hills composed of gypsum crystals, gravel, and marl, occupied by a dwarf sub-shrub community of numerous perennial species (Figure 3). The dominant species of the type location include edaphic endemic species, such as *Eriogonum ericifolium* Torrey & A. Gray var. *ericifolium*, *Salvia dorrii* (Kell.) Abrams subsp. *mearnsii*, and *Lesquerella cinerea* S. Wats., as well as *Hymenopappus filifolius* Hook., *Penstemon thompsoniae* (Gray) Rydb., *Krameria erecta* Willd. ex J. A. Schultes, *Melampodium leucanthum* Torr. & A. Gray, *Townsendia incana* Nutt., *Thymophylla acerosa* (DC) Strother, *Frasera albomarginata* S. Wats., *Houstonia rubra* Cav., and *Castilleja chromosa* A. Nels. Other less dominant species present at the type location include Arenaria eastwoodiae Rydb. var. adenophora Kearney

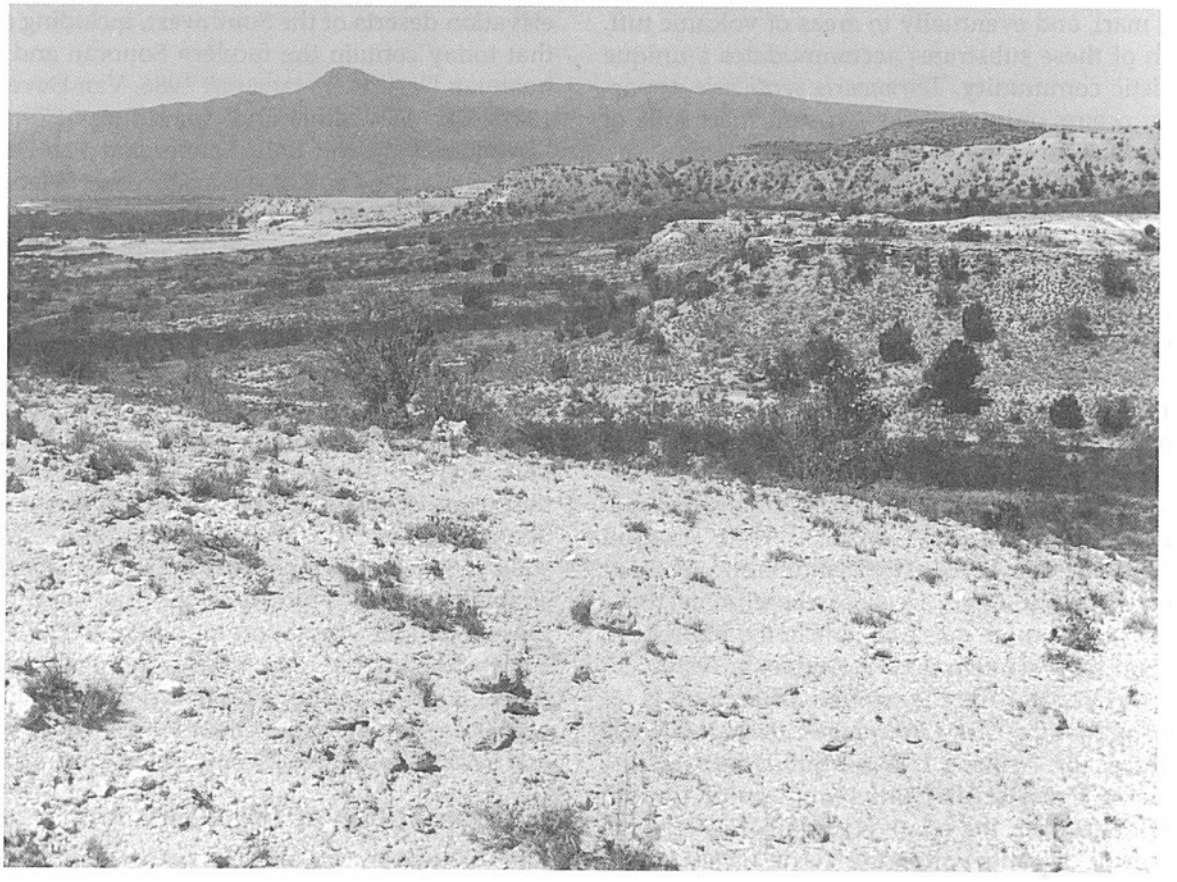


Figure 3. *Tetraneuris verdiensis* habitat.

& Peebles *Polygala alba* Nutt., *Ceanothus greggii* Gray, *Echinocereus engelmannii* (Parry ex Engelm.) Lem., *Ephedra torreyana* S. Wats., *Lepidium* sp., *Purshia stansburyana* (Torr.) Henrickson, *Rhus trilobata* Nutt., and *Juniperus coahuilensis* (Martinez) Gaussen ex R. P. Adams.

In total, 18 low hills and mesas in the nearby area were searched for the presence of this species, based on soil characteristics and the presence of similar vegetation. Each of these areas contained sub-shrub communities with many of the same species found at the type location. Of the 18 study areas, only 10 appeared to contain the same mix of gypsum, marl, and gravel substrates as the type location. These unique gypsiferous soils of the type location are limited to the southeastern portion of the Verde Valley, where the deepest portions of the ancient lake were located.

Tetraneuris verdiensis was found only on the tops of four low hills: the type location and three low hills adjacent to it. The distribution of this species was patchy, and primarily limited to the tops of the hills or on gently sloping areas at the edges of the tops. Steeper sides of these hills, and areas at the base of these hills with very similar soils and sub-shrub communities, were conspicuously lacking this species. In addition, this species was not found in areas on the same hilltops where thicker shrub communities and more gravelly or cobbly soils were present.

This taxon occurred in seven distinct population segments on these four low hills. The number of plants present in each of these population segments was estimated (Table 1), and each population segment was sampled with 5 m wide transects of variable length. Five transects were sampled in each of the smaller population segments, which covered nearly the entire distribution of the segments and the very specific habitat each occurred in. In the two largest population segments, where

Table 1. Population estimates for each population segment of *Tetraneuris verdiensis*.

Population segment no.	No. transects sampled	No. plants per sq m	Size of area sampled in sq m	Estimated no. plants
1	8	0.39	4,621	1,808
2	5	0.08	532	43
3	5	0.11	550	62
4	8	0.28	2,148	602
5	5	0.36	926	341
6	5	0.07	789	58
7	5	0.31	1,224	384
Totals			10,790	3,298

the amount of suitable habitat was more abundant, eight transects were surveyed for this species and approximately half of the area in those population segments was sampled. The average number of plants per square meter was determined for these transects, and a population estimate was made based on the total area covered by the population segment and the total number of plants per square meter in the sampled transects.

The total number of plants is approximately 3,298. It should be noted that the exact number of plants is difficult to determine with this species, as multiple underground stems are commonly associated with one plant. The estimated total area of suitable habitat occupied by this species was 10,790 sq m (1.08 hectares). Based on the transects sampled for this study, the overall average of plants per square meter is estimated to be 0.23. By far, the largest population segment can be found at the type location, where approximately 1,808 plants occur. Several of the population segments occurred on small patches of suitable habitat, which supported less than 100 plants. Only in the largest population segment was the phenology of this species examined. An estimated 51% of plants within that population segment were blooming. The only insect pollinator observed was a bee fly (Family Bombyllidae).

Taxonomic Discussion of *Tetraneuris verdiensis*

The genus *Tetraneuris* was first described in 1898 by E. L. Greene and is part of the *Hymenoxys* complex (Asteraceae: Helenieae). In the past century, various botanists have encountered difficulties when attempting to understand generic delimitation within the *Hymenoxys* complex. In light of these challenges, several different treatments of this group have been published. This complex includes taxa referable to *Dugaldia* Cass., *Hymenoxys* Cass., *Macdougalia* A. Heller, *Phileozera* Buckley, *Picradenia* Hook., *Plummera* A. Gray, *Rydbergia* Greene, and *Tetraneuris* Greene. Various taxonomic treatments have recoginized *Tetraneuris* at the generic level, including Rydberg (1914), Robinson (1981), Bierner (1994), and Bierner and Jansen (1998). Others have submerged the genus *Tetraneuris* into *Hymenoxys* (Turner and Powell 1977, Kearney and Peebles 1960, Lehr 1978).

After analysis of the chromosome numbers, chemical characters, and morphological characters of taxa within the *Hymenoxys* complex, Bierner (1994) determined that a reasonable case could be made for either submerging all of the genera in this complex into *Hymenoxys* or for splitting them into the eight genera mentioned above. More recent studies of DNA restriction site variation in *Hymenoxys* and *Tetraneuris* taxa have clearly separated the taxa referable to *Tetraneuris* into a separate branch of the DNA phylogenetic tree from all of the other taxa that were evaluated within the *Hymenoxys* group. These findings were consistent within the taxa studied, with the exception of *Hymenoxys texana*, which produced a phenogram that placed it with *Tetraneuris* (Bierner and Jansen 1998, Spring et al. 1994). Although *Tetraneuris* is a genus closely related to *Hymenoxys*, Bierner and Jansen (1998) discovered that the taxa referable to *Tetraneuris* that they studied formed a monophyletic clade supported by the presence of 40 shared characters and a boot strap value of 100%. This research appears to merit recognition of *Tetraneuris* at the generic level.

The apparently closely related taxon, *Tetraneuris acaulis* (Pursh) Greene var. *arizonica* (Greene) K. L. Parker also occurs in the Verde Valley, where it can be found on the lacustrine limestone deposits and adjacent Mesozoic sandstones. This taxon, common in northern Arizona and southern Utah, reaches the southernmost extent of its range in the Verde Valley, where it has been documented by Denham and Turner (1996) near the town of

Cottonwood and in the Middle Verde Road area by Anderson (1996). The Middle Verde Road population is approximately 7 miles from the known locations of *Tetraneuris verdiensis* but the two have not been documented as occurring together, possibly because of the lack of suitable habitat between them. The most important characteristic distinguishing these two species is the consistently discoid flower heads of *Tetraneuris verdiensis*. Denham and Turner (1996) also stated that *T. verdiensis* differs from *T. acaulis* var. *arizonica* in its dwarf habit, long pilose vestiture, and relatively short broad leaves. However, observations of the latter species in the Middle Verde Road area reveal a population of *T. acaulis* var. *arizonica* that does exhibit a dwarf habit, long pilose vestiture, and relatively short broad leaves (Figure 4). Although the degree of hairiness in this population of *T. acaulis* var. *arizonica* is not as severe as it is in *T. verdiensis*, the characters that these plants exhibit appear to provide evidence of intergradation and intermediate forms between the two taxa.

Discoid individuals have been documented elsewhere in taxa referable to *Tetraneuris*, such as in the case of populations of *Tetraneuris acaulis* Greene var. *acaulis* in Wyoming. There, discoid individuals have been documented within the population as isolated individuals that only differed from the typical form of this species in their rayless condition. Those plants were the basis of *T. eradiata* A. Nelson, but are currently considered to be deviant forms of *T. acaulis* var. *acaulis* (Denham and Turner 1996). Other than *T. verdiensis*, no completely discoid populations or series of populations have been documented within this genus.

Discussion

The results of this research indicate that *Tetraneuris verdiensis* has a severely limited range and very specific habitat requirements. Of 18 hills searched, this species was documented only on the tops of four adjacent hills in the Verde Valley, occurring in seven distinct subpopulations. A total population estimate of 3,298 plants, covering approximately 10,790 sq m (1.08 hectares), was revealed during this study. This taxon is apparently very sensitive to slight changes in soil characteristics, degree of slope, and competition from other plants. Even on the same hills as known populations, this species was not found in areas of more dense shrub cover or in more gravelly-cobbly situations. On the steeper slopes of the sides of these hills, where soils and sub-shrub communities appeared to be very similar, this species could also not be found. Some very small patches of seemingly similar habitat on nearby hills were not occupied by this species at the time of this study, and appear to be available for colonization by this species in the future.

Taxonomically, this species appears to be very closely related to *Tetraneuris acaulis* var. *arizonica*. The two taxa both occur in the Verde Valley, but known locations of these two taxa are separated by a distance of 7 miles and occur in different habitats. The nearest location of *T. acaulis* var. *arizonica* occurred on gently sloping areas in the bottom of the valley, where somewhat more dense shrub communities with less gypsiferous soils were present. Meanwhile, *T. verdiensis* occurred only on the tops of low hills. The entirely discoid flower heads of *T. verdiensis* were consistently observed in all plants and all sub-populations, and not as isolated individuals. In addition, all plants observed in the nearest *T. acaulis* var. *arizonica* population contained ray flowers. However, the long pilose vestiture and dwarf habit of plants within the nearest location of *T. acaulis* var. *arizonica* appeared to be intermediate between the degree of those characters found in *T. verdiensis* and the typical more northern form of this taxon.

Recent genetic studies of the genus *Tetraneuris* by Bierner (1994) and Bierner and Jansen (1998) did not include *T. verdiensis*. To further understand the taxonomy of the species, genetic studies appear to be necessary. It appears possible that *T. verdiensis* would be best treated as a discoid variety of *T. acaulis*. However, without genetic analysis of this taxon, that recognition cannot be made at this time.

Currently, all known occurrences of this species are located on lands owned by the Coconino National Forest. However, privately owned land can be found directly south of the hills occupied by *T. verdiensis*, and some of the hills on that land are currently being mined for gypsum. Although at least one of the hills containing this species is accessible to all-terrain vehicles, the degree of disturbance within the occupied habitat is currently minimal. Protection of these hills would not only benefit *T. verdiensis*, but would also benefit other edaphic endemic species (*Eriogonum ericifolium* var. *ericifolium*, *Salvia dorrii* subsp. *mearnsii*, and *Lesquerella cinerea*) as well as populations of several disjunct species. Simply by retaining these lands under the current Coconino National Forest ownership and management regime, this unique taxon and the rare combination of substrates and



Figure 4. *Tetraneuris acaulis* var. *arizonica*.

vegetation that makes up its specific habitat will be protected. It is possible that more populations are present that were not detected during this survey. Further investigations into the distribution of this plant within the Verde Valley may uncover new populations in the future.

Acknowledgments

I am especially grateful to John Anderson for his guidance and helpful information, both in the field and in reviewing this manuscript. Special thanks to Mark Bierner, who first made me aware of the existence of this taxon, and whose recent research on the *Hymenoxys* complex has helped immensely in understanding the taxonomy of *Tetraneuris*. Also appreciated are Sabra Schwartz of Arizona's Heritage Data Management System and Ken Houser of SWCA Inc., for allowing me to spend time studying this rare plant while under their supervision. And last, but definitely not least, I would like to thank my wife Sarah for her support and understanding during the many hours I spent putting this paper together.

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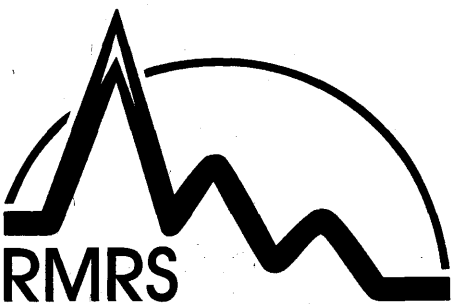
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