Penstemon degeneri Crosswhite (Degener's beardtongue): A Technical Conservation Assessment

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Brenda Beatty, William Jennings, and Rebecca Rawlinson
CDM, 1331 17th Street, Suite 1100, Denver, Colorado 80202

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AUTHORS' BIOGRAPHIES

Brenda L. Beatty is a senior ecologist and environmental scientist with CDM Federal Programs Corporation. Ms. Beatty has over 22 years of professional experience in the environmental industry and has provided technical support for wetlands delineations, ecological surveys, threatened and endangered species surveys, ecological sampling, and ecological risk assessments throughout the country. Her experience in ecology has been used to develop species assessments, characterize biotic communities, identify sensitive ecosystems, estimate wildlife use areas, identify potential habitat for threatened and endangered species, and locate threatened and endangered species. Ms. Beatty received her B.A. in Environmental Science from California State College of Pennsylvania in 1974 and her M.S. in Botany/Plant Ecology from Ohio University in 1976.

William F. Jennings is a botanical consultant specializing in studies of rare, threatened, or endangered plant species in Colorado. Mr. Jennings regularly conducts surveys for threatened species throughout the state and is responsible for discovering several new populations of many species. His botanical emphasis is in the floristics and taxonomy of native orchids. He is the author and photographer of the book *Rare Plants of Colorado* (1997) published by the Colorado Native Plant Society and a co-author of the *Colorado Rare Plant Field Guide* (1997). Mr. Jennings received his B.S. and M.S. in Geology from the University of Colorado, Boulder.

Rebecca C. Rawlinson is an ecologist with CDM Federal Programs Corporation. Ms. Rawlinson's work has focused on the control of non-native plant invasions, conservation of native plant species, and restoration of native plant communities. She has participated in demographic monitoring of rare native plants, vegetation mapping and surveys, and restoration projects in a variety of ecosystems along the Front Range of Colorado. Ms. Rawlinson received her B.S. in Natural Resources from Cornell University in 1997 and her M.A. in Biology from the University of Colorado, Boulder in 2002.

COVER PHOTO CREDIT

Penstemon degeneri (Degener's beardtongue). Photograph by William Jennings. Reprinted with permission of the photographer.

Summary of Key Components for Conservation of *Penstemon degeneri*

Status

Penstemon degeneri (Degener's beardtongue) is a rare, endemic *Penstemon* species occurring from 1830 to 2896 meters [m] (6000 to 9500 feet [ft]) in pinyon-juniper woodlands, ponderosa pine parklands, and montane meadows in the Arkansas River valley and surrounding areas of south-central Colorado. Of the 14 occurrences of *P. degeneri* in U.S. Forest Service Region 2, five occurrences are on the National Forest System lands (Pike-San Isabel National Forest), approximately seven occurrences are on Colorado Bureau of Land Management lands, one occurrence is on Canon City lands (Royal Gorge Park), and one occurrence has unknown land ownership.

The Global Heritage Status Rank for *Penstemon degeneri* is G2, globally imperiled (NatureServe 2003). The Colorado Natural Heritage Program ranks this species as S2, imperiled (Colorado Natural Heritage Program 2003). It is on the U.S. Forest Service Rocky Mountain Region and Colorado Bureau of Land Management sensitive species lists (U.S. Bureau of Land Management 2000, U.S. Forest Service 2003).

Primary Threats

Penstemon degeneri is vulnerable because of its restricted geographic range, the small number of documented occurrences, and its vulnerability to human-related and environmental threats. Although this species occurs in a variety of habitat types and new populations have been found in recent years, the current abundance of this species is not known. Disturbances and land management activities may maintain suitable habitat for this species or negatively impact existing populations, depending on the disturbance intensity, frequency, and type. Threats to the long-term persistence of *P. degeneri* populations or habitats likely differ for each of the 14 occurrences. The most significant threats to the five occurrences on National Forest System lands may include motorized and non-motorized recreation, non-native plant invasion, grazing and trampling, extensive herbivory, succession, and global environmental changes. Populations near roads, trails, or campgrounds are at higher risk for the detrimental effects of road or trail associated activities and non-native plant invasion.

Primary Conservation Elements, Management Implications, and Considerations

The full ecological amplitude and the optimal disturbance regime for the persistence of *Penstemon degeneri* are unknown. The lack of information regarding the colonizing ability, current distribution and abundance, adaptability to changing environmental conditions, sexual and vegetative reproductive potential, and genetic variability of this species makes it difficult to predict its vulnerability. Features of *P. degeneri* biology that may be important to consider when addressing conservation of this species (i.e., key conservation elements) include its potential reliance on disturbances to create/maintain open habitat, its apparent susceptibility to herbivory, and possible outcrossing needs requiring efficient pollination. Priority conservation tools for *P. degeneri* may include assessing current distribution and abundance, identifying and protecting the highest quality occurrences, investigating the source of intense herbivory on some populations, documenting the effects of land-use practices and management activities, and monitoring population trends. Additional key conservation tools may include surveying high probability habitat for new populations, preventing non-native plant invasions, studying demographic parameters and reproductive ecology, and assessing the effects of environmental fluctuations, future management activities or changes in management direction. Identifying high-quality populations and populations that may be immediately threatened, population trend monitoring, studying herbivore dynamics, surveying for new populations, understanding the effects of management activities and disturbances, and studying basic biological traits are priorities of future research studies of *P. degeneri*.

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INTRODUCTION

This assessment is one of many being produced to support the Species Conservation Project for the Rocky Mountain Region (Region 2), U.S. Forest Service (USFS). *Penstemon degeneri* is the focus of an assessment because it is listed as a sensitive species in USFS Region 2 (U.S. Forest Service 2003). Within the National Forest System, a sensitive species is a plant or animal whose population viability is identified as a concern by a regional forester because of significant current or predicted downward trends in population numbers, density, or habitat capability that would reduce the species' existing distribution (U.S. Forest Service 1995). A sensitive species may require special management, so knowledge of its biology and ecology is critical.

This assessment addresses the biology of *Penstemon degeneri* throughout its range, all of which is in USFS Region 2. This introduction defines the goal of the assessment, outlines its scope, and describes the process used in its production.

Goal

Species conservation assessments produced as part of the Species Conservation Project are designed to provide forest managers, research biologists, and the public with a thorough discussion of the biology, ecology, conservation status, and management of certain species based on available scientific knowledge. The assessment goals limit the scope of the work to critical summaries of scientific knowledge, discussion of broad implications of that knowledge, and outlines of information needs. The assessment does not seek to develop specific management recommendations but does provide the ecological background upon which management must be based. While the assessment does not provide management recommendations, it does focus on the consequences of changes in the environment that may result from management (i.e., management implications).

Scope and Information Sources

The *Penstemon degeneri* species assessment examines the biology, ecology, conservation status, and management of this species with specific reference to the geographic and ecological characteristics of the USFS Rocky Mountain Region. Where supporting literature used to produce this species assessment originated from investigations outside the region (e.g., studies of related species), this document places that literature in the ecological and social context of the central Rockies. Similarly, this assessment is concerned with reproductive behavior, population dynamics, and other characteristics of *P. degeneri* in the context of the current environment rather than under historical conditions. The evolutionary environment of the species is considered in conducting the synthesis but placed in a current context.

In producing the assessment, an extensive literature search was performed to obtain all material focusing on *Penstemon degeneri*, as well as information on related species and on the geographical and environmental context of this species. Refereed literature (e.g., published journal articles), non-refereed publications (e.g., unpublished status reports), theses and dissertations, data accumulated by resources management agencies (e.g., Natural Heritage Program [NHP] element occurrence records), and regulatory guidelines (e.g., U.S. Forest Service Manual) were reviewed. Visits were not made to every herbarium with specimens of this species, but specimen label information provided by herbarium staff and available in NHP element occurrence records was included. Additionally, we incorporated information from studies of closely related *Penstemon* species or *Penstemon* species in USFS Region 2 or adjacent areas, and we avoided extrapolating from studies of unrelated *Penstemon* species or *Penstemon* species of drastically different environmental contexts. While the assessment emphasizes refereed literature because this is the accepted standard in science, non-refereed publications and reports were used extensively because they provided information unavailable elsewhere. These unpublished, non-refereed reports were regarded with greater skepticism, and all information was treated with appropriate uncertainty.

Treatment of Uncertainty

Science represents a rigorous, synthetic approach to obtaining knowledge. Competing ideas regarding how the world works are measured against observations. However, because our descriptions of the world are always incomplete and our observations are limited, science focuses on approaches for dealing with uncertainty. A commonly accepted approach to science is based on a progression of critical experiments to develop strong inference (Platt 1964). However, it is difficult to conduct critical experiments in the ecological sciences, and often observations, inference, good thinking, and

models must be relied on to guide the understanding of ecological relations. In this assessment, the strength of evidence for particular ideas is noted, and alternative explanations are described when appropriate. While well-executed experiments represent the strongest approach to developing knowledge, alternative methods (modeling, critical assessment of observations, and inference) are accepted approaches to understanding features of biology. In this assessment, the strength of evidence for particular ideas is noted, and alternative explanations described when appropriate.

Because of a lack of experimental research efforts concerning *Penstemon degeneri*, this assessment report relies heavily on the personal observations of botanists and land management specialists from throughout the species' range. Much of the knowledge about the biology and ecology of *P. degeneri* is based on the observations of Peterson and Harmon (1981), Anderson (1991), S. Spackman (personal communication 2003), other botanists who submitted occurrence records to Colorado NHP (Colorado Natural Heritage Program 2003), and USFS and BLM resource management specialists (E. Brekke personal communication 2003, S. Olson personal communication 2003). When information presented in this assessment is based on our personal communications with a specialist, we cite those sources as "personal communication." Unpublished data (e.g., NHP element occurrence records and herbarium records) were also important in estimating the geographic distribution and describing the habitat of this species. These data required special attention because of the diversity of persons and methods used to collect the data, and because of unverified historical information.

We also incorporated information, where available, from other *Penstemon* species endemic to USFS Region 2 or adjacent states to formulate this assessment. Any comparisons are not meant to imply that *P. degeneri* is biologically identical to these other species, but they represent an effort to hypothesize about *potential* characteristics of this species. We avoided extrapolating from studies of unrelated *Penstemon* species or *Penstemon* species of drastically different environmental contexts. As a result of limited research specific to *P. degeneri*, the biology, ecology, and conservation issues presented for this species in USFS Region 2 are based on inference from these published and unpublished (e.g., personal communications) sources. We clearly noted when we were making inferences based on the available knowledge to augment or enhance our understanding of *P. degeneri*.

Publication of Assessment on the World Wide Web

To facilitate use of species assessments in the Species Conservation Project, they will be published on the USFS Region 2 World Wide Web site. Placing documents on the Web makes them available to agency biologists and the public more rapidly than publishing them as reports. More importantly, it facilitates revision of the assessments, which will be accomplished based on guidelines established by USFS Region 2.

Peer Review

Assessments developed for the Species Conservation Project have been peer reviewed prior to release on the Web. This assessment was reviewed through a process administered by the Center for Plant Conservation, employing at least two recognized experts on this or related taxa. Peer review was designed to improve the quality of communication and to increase the rigor of the assessment.

MANAGEMENT STATUS AND NATURAL HISTORY

Penstemon degeneri is an endemic species known from 14 occurrences in the Arkansas River valley and surrounding areas of south-central Colorado within USFS Region 2 (**Figure 1**, **Table 1**). This section discusses the special management status, existing regulatory mechanisms, and biological characteristics of this species.

Management and Conservation Status

Federal status

The Endangered Species Act of 1973 was passed to protect plant and animal species placed on the threatened or endangered list. The listing process is based on population data and is maintained and enforced by the U.S. Fish and Wildlife Service (USFWS). In 1980, *Penstemon degeneri* was ranked as a Category 2 species, a taxa for which proposal as endangered or threatened is appropriate, but conclusive data on biological vulnerability and threats are not currently available (U.S. Fish and Wildlife Service 1980). After discovering several new populations during a status

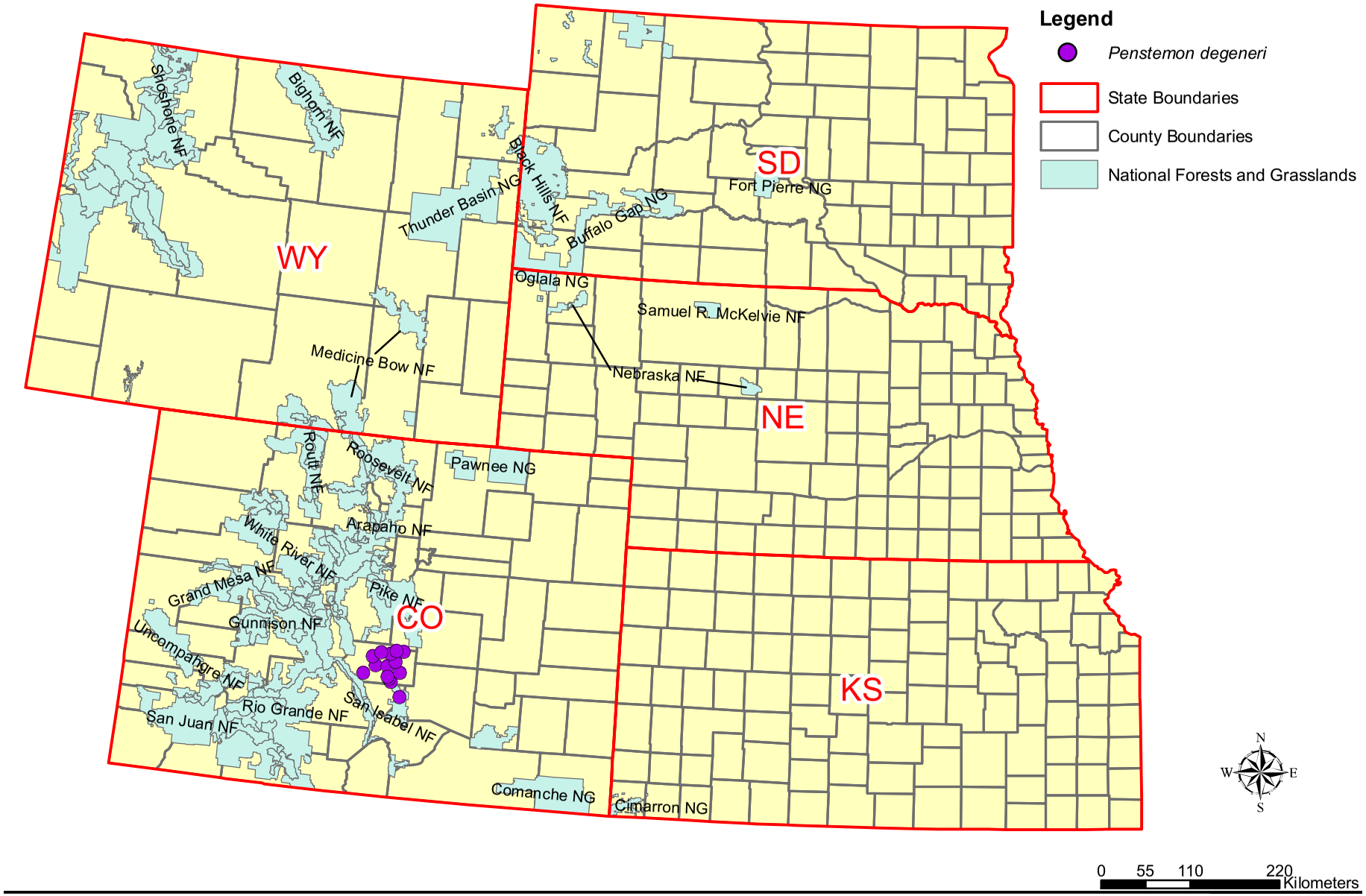

Figure 1. Map of U.S. Forest Service (USFS) Region 2 illustrating *Penstemon degeneri* occurrences in Fremont and Custer counties, Colorado. Each occurrence may include one to several populations. Refer to document for abundance information. Source: Colorado Natural Heritage Program, Fort Collins, Colorado (2003); Rocky Mountain Herbarium, Laramie, Wyoming (2003); University of Colorado Herbarium, Boulder, Colorado (2003).

Table 1. Summary information for *Penstemon degeneri* occurrences in U.S. Forest Service Region 2. Includes county in Colorado, number of occurrences, Natural Heritage Program (NHP) occurrence identifier, date of recorded observations, estimated abundance, estimated area, and land management context (? – indicates uncertainty). Sources: Colorado Natural Heritage Program, Fort Collins, CO (2003); Rocky Mountain Herbarium, Laramie, WY (2003); University of Colorado Herbarium, Boulder, CO (2003).

County	NHP Occurrence Identifier	Date of Recorded Observations	Estimated Abundance	Estimated Area (acres)	Management Area/Ownership
Custer (1 occurrence)	016	2000	25+	0.5	Pike-San Isabel National Forest (may extend onto U.S. Bureau of Land Management (BLM) or private lands)
Fremont (13 occurrences)	001	1954, 1984, 1998	300+ (1984); 25 to 50 (1998)	Not Available (NA)	BLM
	004	1967, 1983, 1990, 1995	<25 (1990); "hundreds" (1995)	NA	Royal Gorge Park (may extend onto BLM lands)
	005	1988, 1990	Not Available (NA)	NA	BLM
	006	1989	NA	NA	BLM
	007	1989	NA	NA	Pike-San Isabel National Forest
	008	1989, 1990, 2001	"hundreds/ thousands" (2001)	5	Pike-San Isabel National Forest
	013	1989, 1998, 2000	1000+ (2000)	5 to 8	Pike-San Isabel National Forest
	014	1989, 1998	200 (1989); 25 (1998)	NA	Pike-San Isabel National Forest
	Not included in NHP records	1998	1	NA	BLM
	Not included in NHP records	1998	NA	NA	BLM
	Not included in NHP records	1998	NA	NA	BLM, State of Colorado?
	Not included in NHP records	1998	NA	NA	BLM
	Not included in NHP records	1872	NA	NA	?

survey, Anderson (1991) recommended that this species be downranked to Category 3C. The category program was eliminated by the USFWS in 1996, and those species are no longer being considered as candidate species (U.S. Fish and Wildlife Service 1996). Therefore, *P. degeneri* is not currently ranked under the Endangered Species Act. *Penstemon degeneri* is listed as a sensitive species by USFS Region 2 and Colorado Bureau of Land Management (BLM) (U.S. Bureau of Land Management 2000, U.S. Forest Service 2003).

Heritage program ranks

Natural Heritage Programs store information about the biological diversity of their respective states and maintain databases of plant species of concern. Due to its limited abundance and distribution, the Global Heritage Status Rank for *Penstemon degeneri* is G2, globally imperiled (NatureServe 2003), and the Colorado NHP ranks it as S2, or imperiled (vulnerable to extirpation; endangered or threatened in the state) (Colorado Natural Heritage Program 2003).

Penstemon degeneri is not known to occur in the other four states of USFS Region 2 (i.e., Kansas, Nebraska, South Dakota, or Wyoming) and is thus not currently listed or ranked in those states (Kansas Natural Heritage Inventory 2000, Nebraska Natural Heritage Program 2001, Fertig and Heidel 2002, South Dakota Natural Heritage Program 2002).

Existing Regulatory Mechanisms, Management Plans, and Conservation Practices

Known populations of *Penstemon degeneri* occur in a variety of land ownership and management contexts in Colorado. There is considerable uncertainty regarding the exact location of several of the sites; inferences about land management are made from location descriptions and mapping exercises. In addition, *P. degeneri* occurrences can extend over a large area of potential habitat and can include lands with different ownerships. Of the 14 occurrences of *P. degeneri* in USFS Region 2, five are on the Pike-San Isabel National Forest (San Carlos Ranger District), approximately seven are on Colorado BLM lands (Royal Gorge and Canon City Field Offices), one is on Canon City Parks and Forestry Department lands (Royal Gorge Park), and one has unknown land ownership (**Table 1**).

Although *Penstemon degeneri* has been identified as a species of special concern, there are few specific regulatory mechanisms at the federal or state level to regulate its conservation. This species was previously considered a USFWS Category 2 plant (U.S. Fish and Wildlife Service 1980, U.S. Fish and Wildlife Service 1996), but there is no legal protection for this species, especially with the elimination of the category program. *Penstemon degeneri* is currently designated as a USFS Region 2 and Colorado BLM sensitive species, and it may obtain some protection under various conservation strategies designed to protect plants and animals within federal lands (U.S. Forest Service 1995, U.S. Bureau of Land Management 1996a). While managing lands for multiple use, the USFS and BLM are directed to develop and implement management practices to ensure that sensitive species do not become threatened and endangered (U.S. Forest Service 1995, U.S. Bureau of Land Management 1996a). For example, the National Environmental Policy Act requires an assessment of impacts to the environment from any proposed federal project (U.S. Congress 1982), and USFS policies require Biological Evaluations to determine the impacts of USFS projects to sensitive species (U.S. Forest Service 1995). The BLM Manual 6840 (Special Status Species Management) states that, "The BLM shall carry out management, consistent with multiple use, for the conservation of candidate species and their habitats and shall ensure that actions authorized, funded, or carried out do not contribute to the need to list any of these species as Threatened or Endangered.'' (U.S. Bureau of Land Management 1996a). BLM regulations help minimize negative effects on special status species, especially by designating certain zones as Areas of Critical Environmental Concern, altering livestock grazing patterns, restricting off-highway vehicle (OHV) use, and limiting mineral operations (U.S. Bureau of Land Management 1996a). There is a proposed Research Natural Area (RNA) in Pike-San Isabel National Forest that is adjacent to an area with several known occurrences of *P. degeneri* (S. Olson personal communication 2003). Although there are no known occurrences of *P. degeneri* within the proposed RNA, potential habitat and undiscovered populations of this species may exist there. If this area is approved as an RNA in the next planning cycle, then any populations of this species would be protected as part of a national network to preserve representative areas for research, education, and maintenance of biological diversity (U.S. Forest Service 1997). In addition, USFS and BLM policies prohibit the collection of any sensitive plants without a permit (U.S. Forest Service 1995, U.S. Bureau of Land Management 1996a). USFS and BLM travel management plans also protect some rare species by restricting OHV use to established roads only (U.S. Bureau of Land Management 1996b, Arkansas

Headwaters Recreation Area 2001, U.S. Forest Service and U.S. Bureau of Land Management 2000). The Arkansas Headwaters Recreation Area is cooperatively managed by BLM and the State of Colorado's Division of Parks and Outdoor Recreation, with additional partnership by the USFS and the State of Colorado's Division of Wildlife. The Arkansas River Recreation Management Plan is an effort to manage recreation resources and activities along 148 miles of the Arkansas River from Leadville to Pueblo Reservoir. For example, the plan stipulates that surveys must be completed prior to construction activities near populations of sensitive species (Arkansas Headwaters Recreation Area 2001).

The Colorado NHP has classified *Penstemon degeneri* as a species of special concern due to its regional endemic status (Colorado Natural Heritage Program 2003). NHP databases draw attention to species potentially requiring conservation strategies for future success. However, these lists are not associated with specific legal constraints, such as limiting plant harvesting or restricting damage to critical habitats. *Penstemon degeneri* is one of 600 plants in the Center for Plant Conservation's (CPC) National Collection of Endangered Plants. As a result, seeds and other living material have been collected and are maintained by the Denver Botanic Gardens and National Genetic Resources Program (NGRP). These living collections represent opportunities for scientific study of life cycles and *ex situ* conservation.

Existing regulations do not appear adequate to conserve *Penstemon degeneri* over the long term, considering that the current abundance and distribution of this species are not well known and that specific populations may be threatened by trail use, recreation development, or grazing.

Biology and Ecology

Classification and description

Systematics and synonymy

Penstemon degeneri Crosswhite is a member of the genus *Penstemon* of the family Scrophulariaceae (Figwort or Snapdragon) of phylum Anthophyta (flowering plants) (Crosswhite 1965a). *Penstemon* is one of the largest genera of the Scrophulariaceae family in North America (approximately 270 species), stretching from Alaska to Guatemala, and the main center of diversity for this genus is Intermountain North America (Zomlefer 1994, Meyer et al. 1995, U.S. Department of Agriculture, Natural Resources Conservation Service 2003). The genus *Penstemon* has been the focus of extensive research and horticultural efforts concerning germination, pollination, and genetics although no research to date has focused on *P. degeneri*.

Penstemon degeneri belongs to the subgenus *Habroanthus*, section *Penstemon*, subsection *Humiles*, series *Gracilis*, and alliance *Oliganthi* (Crosswhite 1965a, Nold 1999). Common names for *P. degeneri* include Degener's beardtongue, Degener beardtongue, or Degener penstemon. Plants of the *Humiles* subsection are found in the Rocky Mountains and westward, are glandular-pubescent with a loose inflorescence, and tend to be smaller than other penstemons (Nold 1999). The other *Penstemon* species of Alliance *Oliganthi* include *P. griffinii* of Colorado and *P. inflatus*, *P. oliganthus*, and *P. pseudoparvus* of New Mexico. There are no known synonyms for *P. degeneri*, but there is some question that *P. inflatus* of northern New Mexico may not be separable from *P. degeneri* based on observations of herbarium specimens (Jennings 1998). Similar synonymy issues have also been raised concerning the segregation of *P. griffinii* (Colorado) and *P. oliganthus* (New Mexico) (Harrington 1954, Peterson and Harmon 1981).

History of species

Crosswhite described *Penstemon degeneri* in 1965 based solely on herbarium specimens, specifically one collected by Otto and Isa Degener (undated specimen) from Fremont County, Colorado (Crosswhite 1965a). He named the species after the Degeners in honor of their penstemon collection and interests in conservation. *Penstemon degeneri* was likely first collected by Redfield (5981) in 1872; other early specimens include Harrington (7517) in 1954, and Weber (13360) in 1967. The holotype specimen (Degener & Degener 27041) is housed at the University of Wisconsin Herbarium (Madison, WI), and additional specimens are at the University of Colorado Herbarium (Boulder, CO), Colorado State University Herbarium (Fort Collins, CO), Rocky Mountain Herbarium (Laramie, WY), and Missouri Botanical Garden Herbarium (St. Louis, MO).

In 1981, J.S. Peterson and W. Harmon wrote a *Penstemon degeneri* status report for the Colorado Natural Areas Program based on five known populations at the time. O'Kane (1988) described this species as rare until further inventories took place. J. Anderson collected specimens in 1989, discovered several new population locations and habitat types, and prepared a status report for this species on behalf of the Colorado

Natural Heritage Program in 1991 (Anderson 1991). The Arkansas River drainage was the focus of a floristic survey by the Colorado NHP and master's thesis work by Tim Chumley in 1998, during which several new populations of *P. degeneri* were found (Chumley 1998, Colorado Natural Heritage Program 2003, Rocky Mountain Herbarium 2003). Ten of the fourteen occurrences have been discovered or re-observed since 1995. No in-depth demographic, ecological, or biological studies of this species have been initiated.

Morphological characteristics

Members of the family Scrophulariaceae are characterized by colorful, zygomorphic flowers, which often have a sympetalous tube with petals flaring outward at the end. *Penstemon* species exhibit a wide variety of floral morphologies and colors, and the genus is arranged into different sections based largely on these characteristics (Meyer et al. 1995).

Penstemon degeneri is a perennial herb from 25 to 40 centimeters (cm) tall with five or more, slender (1.0 to 2.5 millimeters [mm] diameter at base), leafy, short-pubescent stems and a suffrutescent caudex (**Figure 2**) (Crosswhite 1965a, Peterson and Harmon 1981, Spackman et al. 1997, NatureServe 2003). The basal leaves are lanceolate, entire, and up to 6 cm long and 16 mm wide (Spackman et al. 1997). The cauline leaves are more linear, more pubescent, and more sessile. The unleafy, sparingly glandular inflorescence is 3 to 10 cm high, with 2 to 10 tubular flowers at the ends of the stems. The dark blue to violet corolla of the flower is gradually inflated, 14 to 19 mm long and 4 to 5 mm wide at the mouth. The corollas are slightly two-ridged on the floor and have straight, reddish guidelines and sparse yellow hairs in the corolla throat. The staminode is also bearded with sparse golden hairs for about half its length. The anther sacs are 2.0 mm across the connective and are longer than wide. The papery calyx is persistent and the dehisced capsules are 7 to 9 mm long, with small, dark brown, irregularly angled seeds (Peterson and Harmon 1981).

The characteristics used to distinguish *Penstemon degeneri* from other penstemons include leaf morphology, the size of the anther sacs, the color and density of hairs in the corolla throat, growth form, and geography. *Penstemon degeneri* can be easily confused with other *Penstemon* species that may overlap in distribution (i.e., *P. gracilis*, *P. virens*) (Spackman personal communication 2003). *Penstemon gracilis*, of Colorado's eastern slope, has finely toothed leaves, a pale blue corolla, and whitish corolla hairs (Jennings 1998). *Penstemon virens* has a corolla 10 to 25 mm long and totally glabrous stems; it tends to grow in patches or mats with numerous stems, whereas *P. degeneri* tends to grow more singly and has minutely pubescent stems (Weber and Wittmann 2001). *Penstemon degeneri* generally lacks a basal rosette when in flower, but there can be conspicuous basal or low cauline leaves that make this characteristic confusing (Nold 1999). *Penstemon radicosus* is found in north-central Colorado (Peterson and Harmon 1981). The strongly two-ridged corolla floor and staminode of *P. inflatus* (New Mexico) have such dense yellow hairs that the corolla throat is sometimes closed (Jennings 1998). *Penstemon griffinii* is found to the west of Fremont County, from Park County to Mineral and Conejos counties (Anderson 1991). Contrary to *P. degeneri*, *P. griffinii* retains a basal rosette throughout its flowering period, has smaller stem leaves (2 to 3 cm long and 2 cm wide), a slightly larger corolla, and dense golden hairs in its throat (Anderson 1991, Spackman et al. 1997, Weber and Wittmann 2001). Several observers noted other individual variations in *P. degeneri*, including smaller stature, few-flowered, whitish hairs in the flower throat, and lavender or magenta flowers (Colorado Natural Heritage Program 2003). Whenever possible, it is best to obtain a specimen of *P. degeneri* for identification verification (Spackman personal communication 2003).

Technical descriptions of this species are presented in Crosswhite (1965a) and Peterson and Harmon (1981). Keys to *Penstemon* in Colorado are available in Weber and Wittmann (2001) and Jennings (1998). Photos and illustrations are available in Spackman et al. (1997).

Distribution and abundance

Distribution

Penstemon degeneri is known only from Fremont and Custer counties in south-central Colorado (**Figure 1**, **Table 1**; Crosswhite 1965a, Anderson 1991, Spackman et al. 1997, Colorado Natural Heritage Program 2003). This species is found in and around the Arkansas River corridor, from Cotopaxi to Canon City, mainly in the Royal Gorge area. It is also known from the Wet Mountains south of Canon City to Phantom Canyon north of Canon City. There are nine known occurrences reported by Colorado NHP (2003) and five additional herbarium records that are not included in the CNHP database (Rocky Mountain Herbarium 2003, University of Colorado Herbarium 2003). Herbarium specimens generally only have brief descriptions, and the herbarium specimens collected from before 1960 have ambiguous location information. In addition, the

(A)

Photographs by William Jennings. Reprinted with permission from the photographer.

(B)

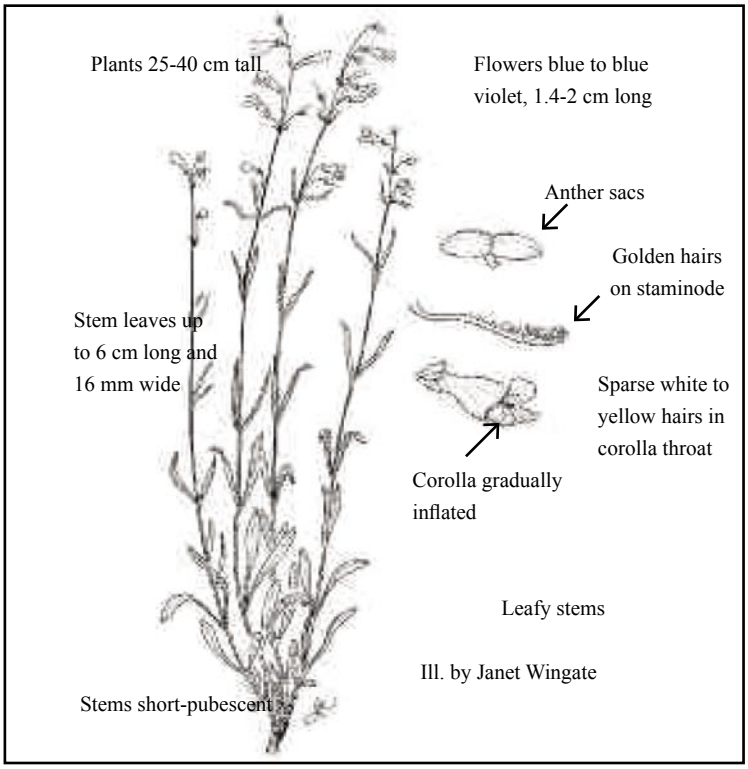

Illustration by Janet Wingate. Reprinted with permission from the artist.

Figure 2. *Penstemon degeneri* photographs in its natural habitat (A), and illustration of the vegetative and reproductive structures (B).

one occurrence in Custer County lacks an associated herbarium specimen, and this location should be re-visited in order to verify the identification of *P. degeneri* (Spackman personal communication 2003). For the purposes of this assessment, all of these occurrences, including historical or unverified ones, are considered in the discussion of this species. There is uncertainty regarding the exact location of several of the sites and the land management at those locations; inferences are made from location descriptions and mapping exercises. In addition, *P. degeneri* occurrences can extend over a large area of potential habitat and include lands with different ownerships. Of the 14 occurrences of *P. degeneri* in USFS Region 2, five are on Pike-San Isabel National Forest, approximately seven are on Colorado BLM lands, one is on Royal Gorge Park lands, and one has unknown land ownership.

The occurrence information for *Penstemon degeneri* presented in **Table 1** is a summary of Colorado NHP element occurrence records, herbarium specimen information, maps of population clusters provided by Anderson (1991), and survey records. An occurrence, as defined by the Colorado NHP (2003), is a metapopulation that is separated by sufficient distance or a barrier from a neighboring population. If two groups exist in suitable habitat within 2 miles of each other (1 mile in unsuitable habitat), then they are collectively considered one occurrence or part of the same metapopulation, especially because further surveying may yield additional groups in the area. Thus, each occurrence record may represent a location with several suboccurrence population clusters. Because *P. degeneri* has a wide ecological amplitude, one metapopulation can span a wide area and/or elevational range.

Within USFS Region 2, *Penstemon degeneri* has not been discovered in Kansas, Nebraska, South Dakota, or Wyoming and is thus not currently listed or ranked in those states (Kansas Natural Heritage Inventory 2000, Nebraska Natural Heritage Program 2001, Fertig and Heidel 2002, South Dakota Natural Heritage Program 2002).

Abundance

The number of *Penstemon degeneri* individuals varies drastically from population to population. Depending on location and habitat, some suboccurrence populations had 25 to 50 individuals, while other populations had hundreds or thousands of individuals (**Table 1**; Colorado NHP 2003). Colorado NHP (2000) estimated a total of 1,550 individuals from four occurrences. Anderson (1991) found that this species was actually more common and more abundant at the higher elevation locations within its range than the pinyon-juniper woodlands of its type locality. Spackman (personal communication 2003) also noted that *Penstemon* species can fluctuate dramatically in abundance from year to year.

Each occurrence of *Penstemon degeneri* is associated with an element occurrence rank based on population abundance, perceived habitat quality, and potential threats (Colorado Natural Heritage Program 2003). Of six ranked occurrences, one was ranked as an "A" occurrence (1,000 or more individuals; occurrence has excellent likelihood of long-term viability; occurs in a high-quality environment), three were ranked as "B" occurrences (100 or more individuals; occurrence should have good likelihood of long-term viability; occurs in an environment fragmented or impacted by humans), and two were ranked as "C" occurrences (15 to 100 individuals; occurrence may be less productive; occurs in a somewhat degraded environment). The C-ranked occurrences were generally small populations found next to trails and roads (Colorado Natural Heritage Program 2003). Specifically, the four ranked occurrences on USFS lands included one C-ranked occurrence, two B-ranked occurrences, and one occurrence ranked A to C (Colorado Natural Heritage Program 2003).

Population trends

Although population sizes of *Penstemon degeneri* have been estimated, multi-year population or demographic monitoring has not been initiated for any site, and no population trend data exists. In general, the size and extent of the metapopulations are not well defined due to the scattered nature of suboccurrence populations, making it difficult to extrapolate population trends from the information presented in the occurrence records. The recorded abundance of *P. degeneri* has increased dramatically since 1981 as a result of newly discovered locations. Several occurrences appear to have drastically declined and show evidence of intense herbivory (Colorado Natural Heritage Program 2003). It is also possible that additional populations may exist in areas that have not been thoroughly surveyed (Anderson 1991). Thus the abundance could be overestimated or underestimated, depending on the full spatial extent of the species, undiscovered populations, potentially misidentified occurrences, and the effects of environmental influences.

Habitat characteristics

Penstemon degeneri was originally only known from the type locality in pinyon-juniper woodlands at an elevation of 1830 to 2042 meters (m) (6000 to 6700 feet [ft]). This species has since been collected at elevations ranging from 1830 to 2896 meters [m] (6000 to 9500 feet [ft]) from pinyon-juniper woodlands, ponderosa pine parklands with oak brush and bunchgrasses, and montane meadows (**Table 2**; Anderson 1991, Colorado Natural Heritage Program 2003, NatureServe 2003). All available notes from herbarium specimen labels and element occurrence records are presented in **Table 2** (Colorado Natural Heritage Program 2003, Rocky Mountain Herbarium 2003, University of Colorado Herbarium 2003). Based on these habitat descriptions, we classified the vegetation communities or vegetation alliances in areas with *P. degeneri* using the classifications of Grossman et al. (1998). This process is associated with uncertainty. In addition, one metapopulation can extend for several miles and include several populations along an elevational gradient of different habitat types (Anderson 1991, Colorado Natural Heritage Program 2000).

The *Penstemon degeneri* type specimen (Degener & Degener 27041) was collected from pinyon-juniper habitat from 1830 to 2042 m (6000 to 6700 ft) elevation in the Royal Gorge area. The vegetation here, *Pinus edulis* – (*Juniperus* spp.) Woodland Alliance (II.A.4.N.a.18), is generally characterized by open canopies of *Pinus edulis* and *Juniperus* spp., and a mixed understory of scattered shrubs, forbs, and grasses (Grossman et al. 1998). Associated species reported with *P. degeneri* in these areas include *Arabis divaricarpa*, *Artemisia frigida*, *Atriplex canescens*, *Bouteloua gracilis*, *Bromus japonicus*, *Carex stenophylla*, *Eriogonum jamesii*, *Grindelia squarrosa*, *Gutierrezia* spp., *Heterotheca horrida*, *Juniperus monosperma*, *Lesquerella montana*, *Opuntia phaeacantha*, *Opuntia* spp., *Oryzopsis* spp., *Pinus edulis*, *Poa* spp., *Quercus gambelii*, *Ribes* spp., *Sitanion longifolium*, *Stipa* spp., *Symphoricarpos* spp., *Verbena bracteata*, and *Yucca* spp. (Colorado Natural Heritage Program 2003).

Penstemon degeneri is also known from elevations of 2073 to 2743 m (6800 to 9000 ft) in montane grasslands, shrublands, and parklands (Colorado Natural Heritage Program 2003, Rocky Mountain Herbarium 2003, University of Colorado Herbarium 2003). The vegetation here is generally of the *Pinus ponderosa* Woodland Alliance (II.A.4.N.a.32) with influence from other tree, shrub, and grass species depending on elevation, substrate, topography, and geography (Grossman et al. 1998). *Penstemon degeneri* occurs in shrublands (elevation 6800 to 7200 ft) with *Antennaria rosea*, *Artemisia* spp., *Cercocarpus montanus*, *Eriogonum* spp., *Ipomopsis aggregata*, *Liatris punctata*, *Pinus edulis*, and *Quercus gambelii*. Other occurrences are in shrubby montane parks (elevation 7360 to 7440 ft) with *Abies concolor*, *Antennaria* spp., *Atragene* spp., *Campanula* spp., *Coriflora* spp., *Eriogonum jamesii*, *Fragaria* spp., *Galium* spp., *Geranium* spp., *Iris* spp., *Juniperus* spp., *Lathyrus* spp., *Lupinus* spp., *Opuntia imbricata*, *Penstemon virens*, *Picea engelmannii*, *Pinus* spp., *Poa pratensis*, *Populus* spp., *Ptelea trifolata*, *Pseudotsuga menziesii*, *Quercus gambelii*, *Ribes* spp., *Rosa* spp., *Sedum* spp., *Thalictrum* spp., *Thermopsis* spp., *Trifolium* spp., and *Vicia* spp. *Penstemon degeneri* also grows in the ecotone between high quality montane grasslands and surrounding forests (elevation 8150 to 9040 ft) with *Antennaria* spp., *Erysimum* spp., *Geranium* spp., *Oxytropis* spp., *Poa* spp., *Potentilla* spp., *Quercus gambelii*, *Pinus ponderosa*, *Pinus strobiformis*, *Pseudotsuga menziesii*, *Sedum* spp., and *Stipa* spp.

Finally, the highest elevation occurrences of *Penstemon degeneri* are from 2804 to 2896 m (9200 to 9500 ft) in mountaintop meadows (Colorado Natural Heritage Program 2003, Rocky Mountain Herbarium 2003, University of Colorado Herbarium 2003). One occurrence is located in a meadow with *Danthonia parryi* herbaceous vegetation association (V.A.5.N.h.5; Grossman et al. 1998). *Penstemon degeneri* also extends to the meadow edge and downslope into scattered forests with *Pinus ponderosa*, *Populus* spp., and *Pseudotsuga menziesii* (Colorado Natural Heritage Program 2003). Associated species include *Achillea* spp., *Antennaria* spp., *Artemisia frigida*, *Carex* spp., *Lupinus* spp., *Muhlenbergia montana*, *Thermopsis montana*, and other penstemons (e.g., *Penstemon virens*).

Penstemon degeneri inhabits a variety of microhabitats. It can occur in the cracks of large rock slabs, in rocky areas at the rim of a canyon, in deep grassy meadows, in pine needle duff, in oak brush, along trails, or at the ecotone between meadows and forests (Anderson 1991, Peterson and Harmon 1981, Colorado Natural Heritage Program 2003, Rocky Mountain Herbarium 2003, University of Colorado Herbarium 2003). The parent material in these areas includes igneous rocks from the Miocene-Pliocene, basalt flows and associated tuff, breccia, conglomerate, migmatitic gneiss, schist, and granitic bedrock. The soil is generally poorly developed and dry, and the soil types range from sandy loams to granite mineral soils to gravels to bedrock (Center for Plant Conservation 2003, Colorado Natural Heritage Program 2003, Rocky Mountain

Table 2. Habitat information for *Penstemon degeneri* occurrences in U.S. Forest Service Region 2. Includes county in Colorado, Natural Heritage Program (NHP) occurrence identifier, elevation range, general habitat description, associated plant species, slope/aspect, and substrate. Source: Colorado Natural Heritage Program, Fort Collins, CO (2003); Rocky Mountain Herbarium, Laramie, WY (2003); University of Colorado Herbarium, Boulder, CO (2003).

County	NHP Occurrence Identifier	Elevation Range (ft)	General Habitat Description	Associated Plant Species	Slope/Aspect	Substrate
Custer (1 occurrence)	016	6,800 to 7,200	Mountain shrubland; tree cover 10%, shrub cover 75%, forb cover 70%, graminoid cover 30%, moss/lichen cover 0%, bare ground cover 50%	*Antennaria rosea*, *Artemesia* spp., *Cercocarpus montanus*, *Eriogonum* spp., *Ipomopsis aggregata*, *Liatrus punctata*, *Pinus edulis*, *Quercus gambelii*	East-facing; 10% straight slope; open exposure; upperslope; dry	Decomposed granite/mineral soils; sandy loam
Fremont (13 occurrences)	001	6,000 to 9,500	Scattered in pinyon-juniper woodland on steep slope	*Artemisia* spp., *Bouteloua gracilis*, *Cylindropuntia imbricata*, *Gutierrezia* sp., *Juniperus* spp., *Opuntia* sp., *Oryzopsis* sp., *Pinus* spp., *Stipa* spp., *Yucca* sp.	North-facing; 10-50 degree slope; partly shaded	Migmatitic gneiss
	004	6,480 to 6,740	Pinyon/juniper woodland; in open *Juniperus* forest; little else under canopy; mainly in rocky areas near rim of the canyon; in duff under *Pinus edulis*	*Arabis* sp., *Juniperus* spp., *Lesquerella* spp., *Pinus edulis*, *Pinus* spp., *Poa* spp., *Ribes* spp., *Symphoricarpos* spp.	North-facing	Precambrian; sandy soil; reddish soil
	005	6,700 to 7,200	Canyonside; growing under pinyon/ juniper/oak with grass understory	*Eriogonum jamesii*, *Juniperus* sp., *Opuntia imbricata*, *Penstemon virens*, *Pinus edulis*, *Ptelea trifoliata*, *Quercus gambelii*, *Symphoricarpos* spp.,	Not Available (NA)	Not Available (NA)
	006	8,150	Small montane meadow in Douglas-fir/ ponderosa pine forest	*Pinus ponderosa*, *Poa* sp., *Pseudotsuga menziesii*, *Stipa* spp.	NA	NA
	007	6,850	Oak brush	*Cercocarpus montanus*, *Pinus edulis*, *Pinus ponderosa*, *Pseudotsuga menziesii*, *Quercus* spp.	NA	NA
	008	9,200	Large montane grassland surrounded by montane forest; open montane meadow; along meadow edge under scattered aspen/ponderosa; scattered pine & fir at meadow edge; forb cover 50%, graminoid cover 50%; dominant grass is *Danthonia parryi*	*Achillea* sp., *Antennaria* sp., *Artemisia frigida*, *Carex* sp., *Danthonia parryi*, *Lupinus* spp., *Muhlenbergia montana*, *Penstemon griffinii*, *Penstemon virens*, *Penstemon* spp., *Pinus ponderosa*, *Populus* spp., *Thermopsis montana*	South- or southeast-facing; 0-6% slope; open exposure; dry	Decomposed granite with pine duff in areas; loam
	013	7,360 to 9,450	Pinyon/juniper/oak forest; spruce/fir along streamside trail; open forest dominated by *Abies concolor*, *Pinus ponderosa*, and *Quercus gambelii*; montane park surrounded by pine, aspen, Douglas fir and spruce forest; total vegetation cover 90%, tree cover 5-10%, shrub cover: 25%, forb cover: 50%, graminoid cover 15%, moss/lichen cover <10%, bare ground cover 25%	*Abies concolor*, *Antennaria* spp., *Atragene* spp., *Campanula* spp., *Coriflora* spp., *Fragaria* spp., *Gallium* spp., *Geranium* spp., *Iris* spp., *Juniperus* spp., *Lathyrus* spp., *Lupinus* spp., *Penstemon virens*, *Pinus* sp., *Pinus ponderosa*, *Pinus* spp., *Poa pratensis*, *Populus* spp., *Pseudotsuga menziesii*, *Quercus gambelii*, *Rosa* spp., *Ribes* spp., *Sedum* spp., *Thalictrum* sp., *Thermopsis* spp., *Trifolium* spp., *Vicia* spp.	South-, north-, and west-facing; 20% straight slope; open exposure; dry	Granitic bedrock; gravel/rocky; pine needle duff

Table 2 (concluded).

County	NHP Occurrence Identifier	Elevation Range (ft)	General Habitat Description	Associated Plant Species	Slope/Aspect	Substrate
	014	9,000 to 9,050	Large montane meadow within montane forest, mostly in ecotone between grassland and forest; high quality grassland with mixed forbs and patches of oak surrounded by ponderosa pine-white pine-Douglas fir open forest	*Antennaria* spp., *Erysimum* spp., *Geranium* spp., *Oxytropis* spp., *Pinus ponderosa*, *Pinus* spp., *Potentilla* spp., *Pseudotsuga menziesii*, *Sedum* spp., and other native bunch grasses	NA	NA
	Not included in NHP records	Not Available (NA)	Growing at base of granite outcrop in barren granite gravel	Not Available (NA)	55 degree slope	Granite
	Not included in NHP records	NA	Not Available (NA)	NA	NA	NA
	Not included in NHP records	NA	On north face of mountain; along creek	NA	NA	NA
	Not included in NHP records	NA	On south slopes and stream gulches	NA	NA	NA
	Not included in NHP records	NA	NA	NA	NA	NA

Herbarium 2003, University of Colorado Herbarium 2003). Although the soils tend to drain rapidly, there can often be a thick litter layer of pine needle duff on the soil surface that may hold in moisture. Peterson and Harmon (1981) found the highest density of individuals at Royal Gorge Park in disturbed or gravelly soils. Slopes vary from 0 to 50 percent, with a variety of aspects. Based on qualitative estimates by botanists, the bare ground cover ranges from 25 to 50 percent; the dominant understory is comprised of grasses, forbs, or shrubs at 50 to 75 percent cover; and tree cover is sparse, ranging from 5 to 10 percent (Colorado Natural Heritage Program 2003, Rocky Mountain Herbarium 2003, University of Colorado Herbarium 2003). *Penstemon degeneri* occurs in both full sun and shaded conditions. The factors restricting *P. degeneri* to a small geographic area of occurrence despite being a relative habitat generalist are unknown (Anderson 1991). In addition, the microclimate requirements and barriers to dispersal for this species are unknown, especially as presumably suitable sites near existing populations have been surveyed and lacked this species (Spackman personal communication 2003).

Reproductive biology and autecology

Reproduction

Details concerning the breeding system of *Penstemon degeneri* are largely unknown. In this section, we mainly present information from congeners in the subgenus *Habroanthus* in an effort to elucidate potential reproductive mechanisms for *P. degeneri*.

Penstemon degeneri produces an inflorescence with 2 to 10 blue, tubular flowers from mid-June through July and sets seed a few weeks later, with annual fluctuations in the phenology (Peterson and Harmon 1981, Ryke et al. 1994, Colorado Natural Heritage Program 2003). In one year, plants with only a few flowers left were observed on July 10; in another year, all plants were in mature fruit by July 7 (Colorado Natural Heritage Program 2000). Often, the plants hold onto the previous year's fruit (Colorado Natural Heritage Program 2003).

There is no information concerning the extent of vegetative reproduction. One observer noted that the *Penstemon degeneri* was present both as "spreading clumps" as well as single plants (Colorado Natural Heritage Program 2003), suggesting that some vegetative growth may occur. *Penstemon haydenii* (on sandy blowout habitats) and *P. debilis* (on loose shale scree) reproduce primarily by rhizomes as a response to replace ramets that are damaged by continuously shifting terrain (Flessner 1989, McMullen 1998). Although *P. degeneri* does not inhabit similar shifting substrates, it is possible that this species may also reproduce vegetatively.

Many *Penstemon* species exhibit both self- and cross-pollination, but it is unknown if *Penstemon degeneri* is partially or wholly self-incompatible. For example, *P. debilis*, *P. haydenii*, *P. lemhiensis*, and *P. penlandii* are largely outcrossers with some self-pollination, whereas *P. procerus* is mainly self-pollinated (Flessner and Stubbendieck 1992b, McMullen 1998, Tepedino et al. 1999). There have also been no studies on other vital aspects of *P. degeneri* reproduction, such as which insect species are effective pollinators, germination requirements and success, demographic parameters, or genetic aspects of reproduction.

Observations of *Penstemon degeneri* indicate that most populations had a mix of vegetative, flowering, or fruiting individuals. The proportions of each depended on the date of the observation; the reported percentage of flowering individuals ranged from 1 to greater than 90 percent at different sites and dates (Colorado Natural Heritage Program 2003). Many observers have concluded that reproduction is generally successful based on evidence of populations persisting for over 20 years, locally abundant and dense populations, and records of populations with 100 percent of the individuals producing fruit (Colorado Natural Heritage Program 2003).

Life history and strategy

There have been no studies on the life history, demography, or longevity of *Penstemon degeneri*. In general, this species is a perennial forb that grows in dry, disturbed or rocky environments. The hypothesized life cycle of this perennial plant is depicted in **Figure 3**. The rates of growth, survival, recruitment, dispersal, and longevity are unknown. Nold (1999) has found that penstemon individuals of the subgenus *Habroanthus* can persist for 5 to 10 years in garden environments.

Based on vegetation strategies described by Grime (1979), *Penstemon degeneri* could be considered a stress-tolerant, or s-selected, species with potential capabilities to exploit ruderal environments. Plants with a perennial life history, an ability to withstand harsh and unproductive environments, and the capability to access resources with well-developed roots are considered stress-tolerant (Grime 1979, Barbour et al. 1987). Ruderal species can exploit low stress, high disturbance

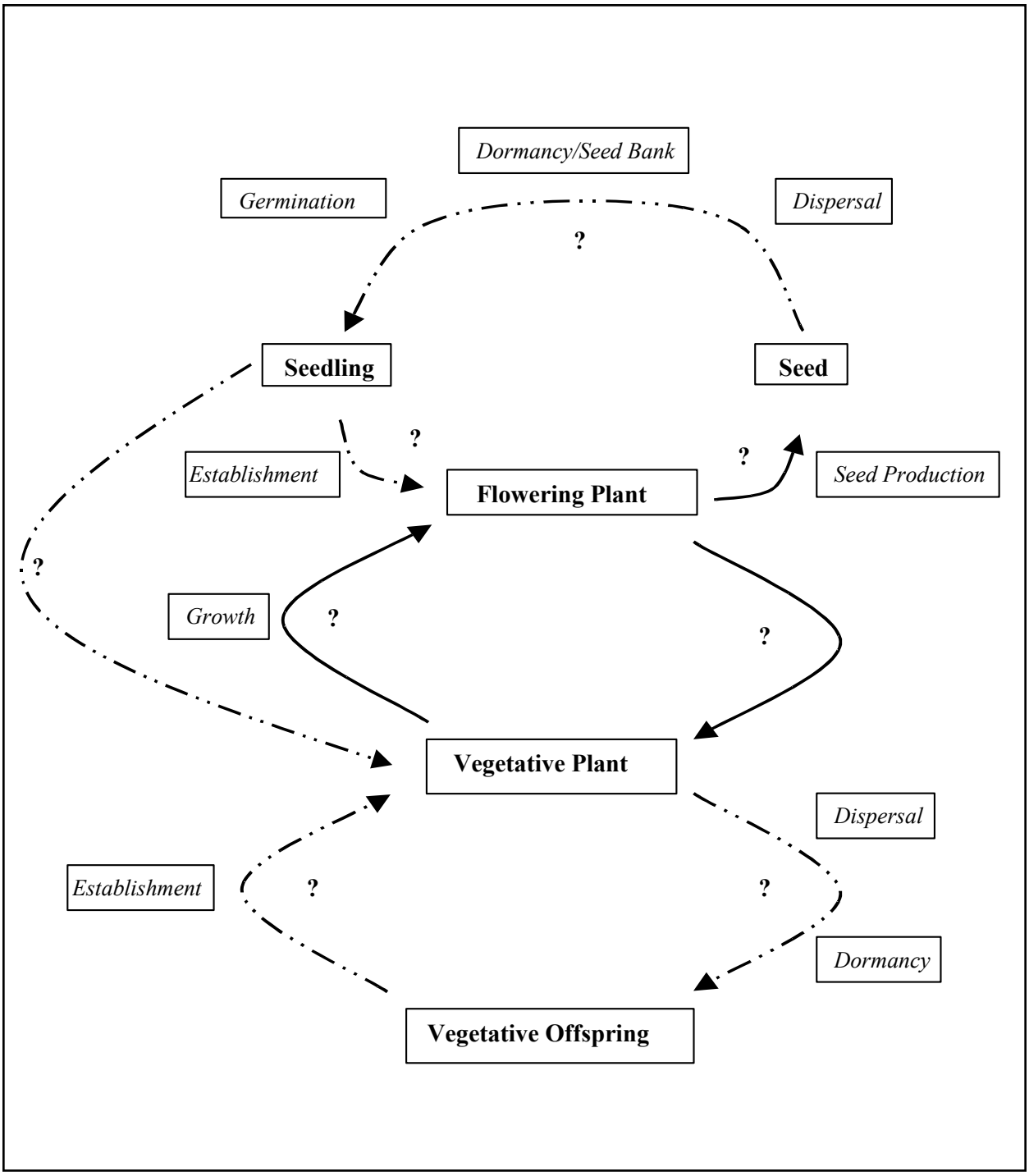

Figure 3. Schematic representation of the hypothesized life cycle of *Penstemon degeneri*. There is not sufficient information about this species to create a more specific diagram. Dotted lines indicate juvenile phases of the life cycle and solid lines indicate mature phases of the life cycle. The extent of sexual and vegetative reproduction is unknown for this species. Rates of growth, dispersal, and seed production are also unknown (indicated by "?"). Figure adapted from Grime (1979).

environments by minimizing vegetative growth and maximizing reproductive output (Grime 1979, Barbour et al. 1987). Although *P. degeneri* inhabits disturbed areas in Royal Gorge Park (Peterson and Harmon 1981), the extent to which this species can actually colonize disturbed areas is unknown. This species occurs in other areas with potential for disturbance, such as livestock trampling and trail use, but the actual effects of disturbance on the habitat or the ability of this penstemon to tolerate continuous disturbances are also unknown. The persistent woody caudex of *P. degeneri* presumably aids this plant to anchor it in loose soil, to store resources, and to access water, and mediates the effects of disturbance and perhaps functions in vegetative reproduction. Davis et al. (1991) discovered that older *P. grandiflorus* individuals with larger caudices were more capable to tolerate stresses, such as fire, soil disturbances, herbivory, and competition with other species. Heidel and Shelley (2001) found that development of a caudex by *P. lemhiensis* seedlings was essential for moisture absorption and stress tolerance.

Pollinators and pollination ecology

The pollination biology of other *Penstemon* species has been studied in a multitude of field and greenhouse studies (e.g., Scogin and Freeman 1987, Reid et al. 1988, Flessner and Stubbendieck 1992b, Clinebell and Bernhardt 1998, Mitchell et al. 1998, Nielson 1998, Lange and Scott 1999, Nold 1999, Tepedino et al. 1999, Mitchell and Ankeny 2001, Reed 2002), but the specific pollination mechanisms for *P. degeneri* are unknown.

In general, penstemons are well equipped with colorful, tubular flowers to attract pollinators such as hummingbirds, butterflies, bees, wasps, moths, and flies. Although there are exceptions, red penstemon flowers with narrow corollas are generally associated with hummingbird pollination while blue, pink, or purple penstemon flowers with wide-lobed corollas tend to be insect pollinated (Tepedino et al. 1999). *Penstemon degeneri* is most likely insect pollinated because it consists of several blue, bilaterally symmetric flowers on an erect stem. It is likely that *P. degeneri* would be visited by a variety of pollinators as a result of its varied habitat and elevation. Common visitors to *Penstemon* flowers in Colorado and Nebraska (e.g., *P. debilis*, *P. glaber*, *P. haydenii*, *P. harringtonii*, *P. strictus*) include a wide variety of bees (e.g., *Osmia* spp. of family Megachilidae), wasps (e.g., *Pseudomasaris vespoides* of family Masaridae), flies, butterflies, and beetles (McMullen 1998, Nielson 1998, Nold 1999, Tepedino et al. 1999). However, the most consistent and effective pollinators, those that actually transport pollen to contact reproductive structures, included bees of the Megachilidae family (e.g., *Osmia* spp.,), Apidae family (e.g., *Bombus* spp.), and one pollen-collecting wasp species of the Masaridae family (*Pseudomasaris vespoides*). Some of these bee species appear to specialize on visiting blue and purple flowers of *Penstemon* species (Crosswhite and Crosswhite 1966, Nielson 1998, Tepedino et al. 1999). *Pseudomasaris vespoides* is considered an oligolege on *Penstemon* species because it has behavioral and morphological specializations to collect pollen and efficiently pollinate *Penstemon* flowers (Tepedino et al. 1999). The *Penstemon* species cited above generally have larger, more open flowers than *P. degeneri*. Based on flower morphology, the most consistent and effective pollinators for the smaller *P. degeneri* flowers may be smaller insects than for those other *Penstemon* species. Effective pollination also depends on the timing of reproductive maturity of anthers and stigmas, activity and behavior of pollinators, and flower and insect morphologies. We presume that *P. degeneri* is not limited by effective pollinators because it has successful seed production. Studies on other *Penstemon* species in USFS Region 2 and adjacent areas have found that reproductive success is generally not limited by pollinators (McMullen 1998, Nielson 1998, Tepedino et al. 1999, Reed 2002).

Important issues related to the pollination of rare plants that have yet to be researched for *Penstemon degeneri* include the identity and effectiveness of pollinators, the role of plant density on pollinator behavior, annual fluctuations in pollinator activity and timing of flowering, and genetic implications of pollination. For example, the reproductive timing of flowers fluctuates from year to year and may not always match the abundance of different species of pollinators (Nielson 1998, Tepedino et al. 1999). As a result, conservation of the full complement of pollinators is an important feature of a rare plant species conservation plan. In addition, researchers have discovered that pollinators may be attracted to dense floral resources but densely aggregated plants can potentially suffer from resource competition (Nielson 1998, Mitchell and Ankeny 2001). The effect of density on *P. degeneri* is not known although it does occur with other flowering species, including other *Penstemon* species. In addition, several researchers observed that the flowering phenology of *P. degeneri* is earlier than other species (Colorado Natural Heritage Program 2003).

Dispersal mechanisms

Details of seed dispersal mechanisms or adaptations in *Penstemon degeneri* are not known. *Penstemon degeneri* capsules split open at maturity and probably drop seeds near the parent plant when jostled by wind or animals, as seen with other *Penstemon* species (Nielson 1998, Heidel and Shelley 2001). The small seeds may be dispersed downslope or downwind by erosion, wind, or water, but it is likely that the majority of seeds remain within one meter of the parent plant (Heidel and Shelley 2001). Heidel and Shelley (2001) hypothesized that animals such as insects, birds, or small mammals, could possibly disperse *P. lemhiensis* seeds through collection or consumption. Presumably, dispersal success depends on wind patterns, topographic heterogeneity, precipitation amount and frequency, animal uses, and availability of suitable "safe" sites for seed germination.

Seed viability and germination requirements

Because *Penstemon* species are desirable horticultural species, much work has been performed with the germination requirements of these showy ornamentals (e.g., Flessner and Stubbendieck 1989, Kitchen and Meyer 1992, Meyer and Kitchen 1992, Meyer and Kitchen 1995, Meyer et al. 1995, Nielson 1998, Nold 1999). However, little information is available concerning the fertility, seed viability, and germination requirements of *P. degeneri* in the field.

In general, penstemons are easy to grow in the garden and are prolific seed producers (Nold 1999). *Penstemon* species appear to have evolved habitat-specific germination regulation strategies, such as moist cold stratification to break dormancy for high elevation species and scarification to remove thick coats of seeds in buried seed banks (Flessner and Stubbendieck 1989, Kitchen and Meyer 1992, Meyer and Kitchen 1992, Meyer and Kitchen 1995, Meyer et al. 1995). Horticultural experience indicates that *P. degeneri* can be germinated by sowing seeds on a planting mix with barely any cover for 8 weeks at 4 ºC (40 ºF) and then moving to 10 ºC (50 ºF) with light (Swayne 2000). An online database on rock garden plants notes that *P. degeneri* has been cultivated in mesic, sunny sites in moist, rich, drained soils with some humus (Slaby 2001). This species can be seeded in the spring or propagated from cuttings taken in late summer. *Penstemon degeneri* is also listed in the Denver Botanic Gardens living collections database (Denver Botanic Gardens 2003). Studies by the Denver Botanic Gardens in conjunction with the CPC found that there was 80 percent germination for seeds stored from 1990 to 2002 (Grant personal communication 2003). The seeds were cold stratified for 2 months and then moved into the greenhouse. Seeds that were not cold stratified but were kept in pots on a warm bench with periodic mist did not germinate (DePrenger-Levin personal communication 2003). Several plants are now growing in the Denver Botanic Gardens "Western Panorama" public garden, and they have flowered and persisted successfully for one year (DePrenger-Levin personal communication 2003, Grant personal communication 2003). Transplanted seedlings were used in a *P. haydenii* recovery program because direct seeding into suitable habitat was not successful (Stubbendieck et al. 1993).

Phenotypic plasticity

Phenotypic plasticity is demonstrated when members of a species vary in morphology, phenology, or other attributes, with change in light intensity, latitude, elevation, or other macrosite or microsite characteristics. Observations suggest that *Penstemon degeneri* can vary in growth morphology ("spreading clumps" or single plants), flower color (bluish violet to magenta), and corolla hair color (yellowish to whitish) (Colorado Natural Heritage Program 2003). In addition, flowering phenology and reproductive success may be affected by annual fluctuations in moisture conditions, elevational effects on temperatures and length of growing season, or microsite conditions (e.g., shading).

Cryptic phases

Cryptic phases during the life cycle of *Penstemon degeneri* could include overwintering seeds in the soil or dormant mature individuals. It is unknown if mature individuals of *P. degeneri* can go dormant during suboptimal conditions, storing resources in the persistent caudex. It is also unknown whether a persistent seed bank exists or the extent of seed dormancy for *P. degeneri*. Seed dormancy can be an important adaptation by which plant populations exploit favorable conditions in harsh environments (Kaye 1997). Seedbank studies of *P. lemhiensis* in Montana discovered that population trends of this species are well buffered by the existence of seedbanks (Meyer 1996). Seeds of *P. lemhiensis* have two levels of dormancy (Meyer 1996). A large proportion of the seeds responded to chilling and germinated in the spring after exposure to winter conditions, while the other proportion did not respond to chilling and could remain dormant in the soil for up to 6 years, perhaps responding to disturbance events (e.g., fire) or moisture conditions (e.g., wet growing seasons). The germination response differed for populations of

P. lemhiensis in different habitat types, suggesting that there may be local adaptations and genetic differences between populations.

Mycorrhizal relationships

The existence of mycorrhizal relationships with *Penstemon degeneri* was not reported in the literature. Flessner and Stubbendieck (1992a) investigated the mycorrhizal associations with *P. haydenii* on sandy prairie soils of Nebraska. They discovered that mycorrhizal levels were naturally low in the shifting sands and concluded that maintaining mycorrhizal associations was a low conservation priority for this species. *Penstemon degeneri* also grows in poorly developed soils, but the pine litter layer commonly incorporated in the surficial soils might retain moisture and provide habitat for associated mycorrhizae.

Hybridization

There were no reported occurrences of hybridization with *Penstemon degeneri* although the ranges of other *Penstemon* species (e.g., *P. gracilis*, *P. virens*) overlap with that of *P. degeneri*. However, the extent to which observers were looking for hybrids in areas where *Penstemon* species co-occur is not known. In addition, the flowering phenology for these species has not been researched in order to assess the potential for synchronous flowering and possible hybridization between these species.

Current and historical hybridization (leading to speciation) has been demonstrated for other *Penstemon* species, including species from different sections (Crosswhite 1965b, Wolfe and Elisens 1994, Wolfe and Elisens 1995, Wolfe et al. 1998a, 1998b, Chari and Wilson 2001, Wilson and Valenzuela 2002, Glenne 2003). The genus *Penstemon* has the second largest number of hybrids of any genera in the Intermountain Region of the United States (Ellstrand et al. 1996). Glenne (2003) identified several areas in Nevada where the rare *P. bicolor* hybridizes with the more common *P. palmeri*. Disturbances and the spread of *P. palmeri* by human-related activities have increased the contact between these two species and potentially threaten the existence of *P. bicolor* through hybridization. Hybridization, whether natural or anthropogenic, can lead to rare species extinction when a more abundant congener genetically swamps the rare species, when hybrid offspring outcompete the rare parent species, or when the production of hybrid seed reduces reproductive success of the rare species (Glenne 2003). Because *P. degeneri* does come in contact with more common *Penstemon* species at some locations, the occurrence of hybridization or the existence of pre-zygotic or post-zygotic isolating mechanisms is an important area of research for this species.

Demography

Life history characteristics

There is no information regarding population parameters or demographic features of *Penstemon degeneri*, such as metapopulation dynamics, longevity, recruitment, and survival.

Life cycle diagram and demographic matrix. Demographic parameters, such as recruitment and survival rates, have not been investigated for *Penstemon degeneri*, and so there are no definitive data regarding the vital rates that contribute to species fitness. Although stage-based models based on population matrices and transition probabilities can be used to assess population viability (Caswell 2001), adequate quantitative demographic data are needed for input into the model. A life cycle diagram is a series of nodes that represent the different life stages connected by various arrows that represent the vital rates (i.e., survival rate, fecundity). The specific events in the life cycle or longevity of *P. degeneri* are unknown. Both *P. grandiflorus* and *P. lemhiensis* exist as seedlings, then develop into rosettes with well-developed caudices within the first few years, and then mature to produce flowering stalks in subsequent years. In suboptimal conditions, these species can be dormant, relying on resources stored in the woody caudex (Davis et al. 1991, 1995, 1997, Heidel and Shelley 2001). For *P. degeneri*, the stages that could potentially be incorporated into a demographic matrix include seed, seedling, vegetative individuals (rosettes), reproductive mature individuals, and dormant mature individuals (**Figure 3**).

The percentage of each age class in populations, the rates of survival, and the factors affecting demographic rates are unknown for this species. Presumably, there are seeds or propagules in the soil at existing population locations of *Penstemon degeneri*. The probability of germination and subsequent establishment depends on the longevity of these propagules and whether appropriate environmental conditions exist for germination and growth. Seeds that germinate will grow into seedlings, assimilate resources, become rosettes, and eventually become mature, established plants. Growth rates may be influenced by the intensity and frequency of disturbance and by the availability of resources, such as space,

light, moisture, and nutrients. The time to maturity is unknown. If appropriate conditions exist, then mature individuals in the population can produce flowers. Davis et al. (1991) found that larger, more established *P. grandiflorus* individuals were more likely to flower than smaller individuals. Successful seed set will depend on the rates of pollen and ovule formation, pollination, fertilization, and embryo development. Fecundity rates depend on the production of seeds and the percentage of those seeds that overwinter and survive to germinate the next year.

Population viability analysis . In order to initiate a population viability analysis for *Penstemon degeneri*, the rates of germination, fecundity, survival, and other important parameters require additional study.

Ecological influences on survival and reproduction

No information exists about the ecological factors affecting growth and establishment of *Penstemon degeneri*. The long-term persistence of this species at a location most likely depends on a range of ecological influences on reproduction and growth, including climatic fluctuations, microsite conditions (e.g., moisture), availability of suitable germination sites, pollinator activities, herbivory levels, disturbance patterns, and interspecific competition. Refer to **Figure 4** for an envirogram outlining resources potentially important to *P. degeneri*. Heidel and Shelley (2001) discovered that early summer mean monthly precipitation and late summer mean maximum monthly temperatures were key climatic factors influencing the germination, flowering, and mortality of *P. lemhiensis* in Montana. There is no information on the capabilities of *P. degeneri* to disperse, colonize, and establish new populations around the landscape. The establishment of new populations most likely depends on barriers to dispersal and the availability of suitable germination sites.

It is unclear what type, size, intensity, and frequency of disturbance regime or what microhabitat features are important for *Penstemon degeneri*. Disturbances in mountainous environments can include erosion, rockslide, fire, blowdowns, frost heaving, wind scouring, small mammal activity, grazing/trampling, and human influences (e.g., grazing, timber harvesting, thinning, mining, prescribed fire, or trail use) (Zwinger and Willard 1996). Depending on intensity and location, a disturbance could simultaneously play a role in creating suitable habitat throughout a landscape and in directly impacting an existing population. For example, several populations of *P. degeneri* are thriving in "disturbed" areas in Royal Gorge Park, but these could also be negatively affected by direct trail-related damage, such as trampling or soil movement. Several populations exist near trails and could be affected by any trail-related damage, such as trampling or soil movement (e.g., erosion and deposition).

Penstemon degeneri may require periodic fires to open the understory and canopy of its woodland habitats (Colorado Natural Heritage Program 2000). The optimal fire return intervals for persistence of *P. degeneri* are not known, but the cycles most likely vary for different habitat types and elevations. A prescribed burn is being considered within the next few years for one area near a *P. degeneri* occurrence (S. Olson personal communication 2003). We were unable to obtain detailed information concerning specific timber management or thinning protocols on parcels with *P. degeneri*. In general, pinyon-juniper woodlands, especially on steep or rocky slopes, are not priorities for timber harvest, thinning, or grazing activities (Arkansas Headwaters Recreation Area 2001, Brekke personal communication 2003). Livestock grazing has historically occurred on one USFS allotment with *P. degeneri*, but that allotment is currently vacant (Colorado Natural Heritage Program 2003, Olson personal communication 2003). The effects of grazing on this species or its habitat have not been studied. Refer to the Community Ecology section for further discussion.

Spatial characteristics

The factors affecting the spatial distribution of *Penstemon degeneri* have not been studied. Characteristics that could influence the spatial distribution of this rare species include disturbance patterns, seed dispersal patterns, competition with other vegetation, overstory configuration, and landscape and microsite heterogeneity.

Despite a highly restricted geographic range, *Penstemon degeneri* has locally abundant coverage in a variety of habitats. The size and extent of populations are difficult to define because one metapopulation can stretch for many miles over a range of habitat types and elevations (Colorado Natural Heritage Program 2003). In contrast, some populations were small (e.g., 25 individuals) and clustered in one area, despite seemingly suitable habitat all around (Spackman personal communication 2003). One account reported that *Penstemon degeneri* was the dominant understory forb, while another described *P. degeneri* as being very scattered (Colorado Natural Heritage Program 2003).

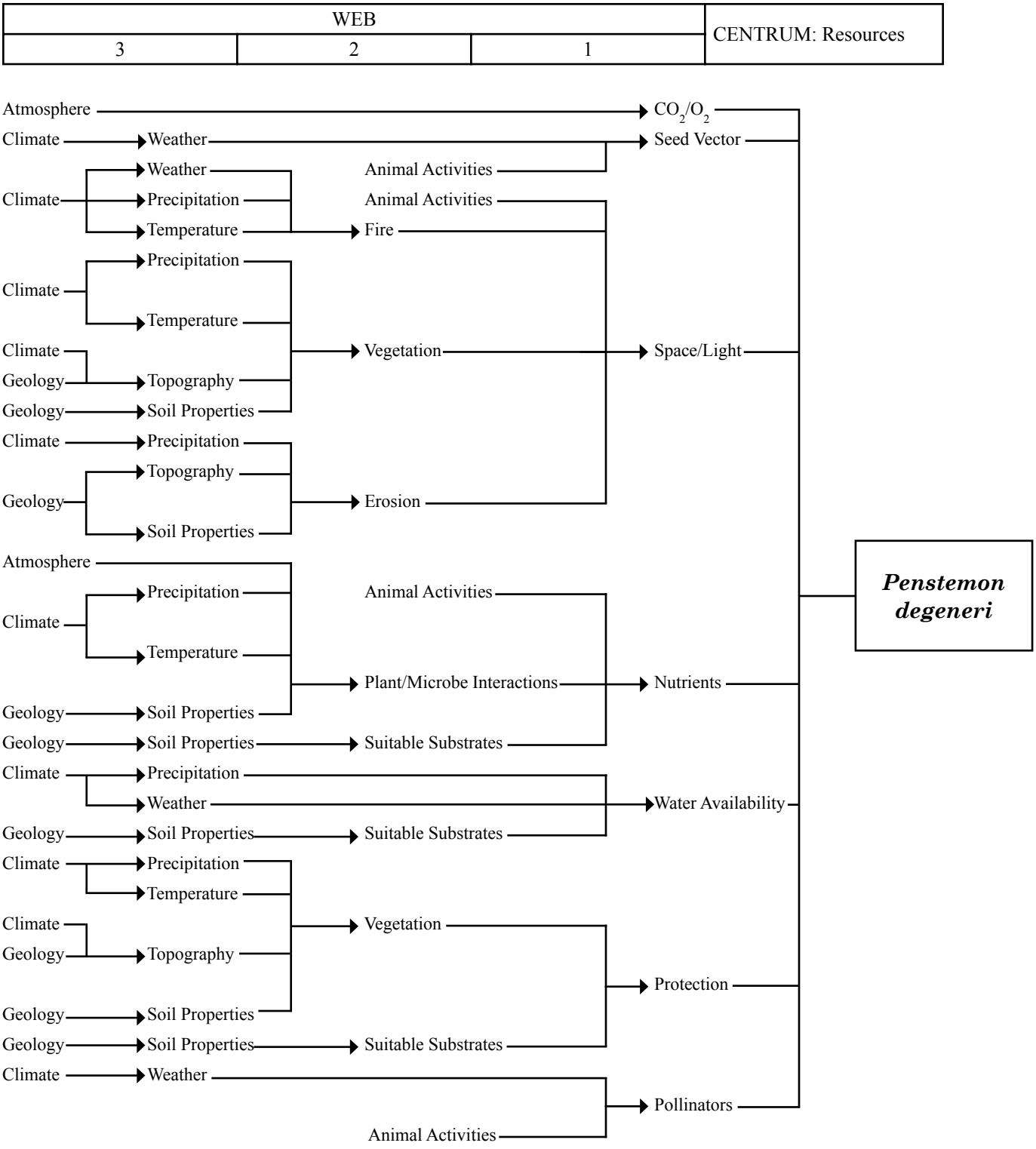

Figure 4. Envirogram outlining potential resources for *Penstemon degeneri*.

The spatial juxtaposition of *P. degeneri* to other plants has not been studied, but this species has been observed in moderately shaded areas, such as in a cluster of pinyon trees or at the ecotone between meadow and forest (Spackman personal communication 2003).

In Royal Gorge Park, *Penstemon degeneri* clusters appear to be densest where the soil substrate is more gravelly or disturbed. Reported densities in this area range from 0.01 to 0.12 individuals per square foot (Peterson and Harmon 1981). The densities of other populations were not noted.

Genetic characteristics and concerns

In general, the genetic status, including issues related to hybridization, polyploidy, and genetic variability, is largely unknown for *Penstemon degeneri*. A base chromosome count of 2n = 16 is common for species within the *Penstemon* genus, including several species in Colorado (i.e., *P. eriantherus*, *P. glaber*, and *P. virens*) (Freeman 1983). Polyploidy is relatively infrequent and has been observed in only 20 percent of the species within the genus *Penstemon*. Issues related to gene flow, inbreeding, and genetic isolation could affect the demography, ecology, and management considerations for this species. For example, *P. haydenii*, an endangered species in Nebraska, has virtually nonexistent interpopulation gene flow, but it has maintained enough genetic variability to avoid detrimental inbreeding depression (Caha et al. 1998). The genetic variability and the extent to which gene flow occurs between populations of *P. degeneri* are unknown. Peterson and Harmon (1981) hypothesized that this species may have large genetic potential, as evidenced by its broad range of adaptability, and this genetic potential may help maintain viable populations over the long term.

Factors limiting population growth

Population growth or establishment of *Penstemon degeneri* could be limited by competition with other species (e.g., invasive species), inadequate pollinators, excessive herbivory or trampling disturbance, or inappropriate environmental conditions for germination or growth. The rate at which colonization and establishment of new, persistent populations occurs is unknown.

Community ecology

Herbivores and relationship to habitat

Several *Penstemon degeneri* populations showed evidence of extensive herbivory although the identity of the grazer or browser was unknown (Peterson and Harmon 1981, Colorado Natural Heritage Program 2003). In the populations that were suffering from severe grazing pressures, all the individuals in the population showed browsing effects, and the population size was drastically smaller than in previous years (Colorado Natural Heritage Program 2003). One occurrence record specifically noted that extensive herbivory was attributed to native herbivores and not livestock grazing. Possible herbivores in *P. degeneri* habitat include cattle, bighorn sheep, mule deer, elk, rabbits, grasshoppers, and/or other insects (Colorado Natural Heritage Program 2003). The specific identity of these herbivores and the effects of extensive herbivory on population dynamics and reproductive success of these populations would be an important area of future research for *P. degeneri*.

Of the five occurrences of *Penstemon degeneri* on USFS lands, one is located within a currently vacant allotment that was historically grazed and has the potential for future grazing (Olson personal communication 2003). The element occurrence record for that occurrence described that the *P. degeneri* clusters were located near stock ponds and that a large cattle herd with calves was nearby at the time of the observation. The populations of this species on non-USFS lands could also possibly occur in areas with livestock grazing (Brekke personal communication 2003). The extent of trampling or grazing and the possible direct impacts of such activity on the *P. degeneri* in these areas is not known. There have been no declines of this species specifically attributed to the direct impacts of livestock grazing or trampling. In addition, the possible indirect impacts of grazing activities on *P. degeneri* habitat, such as importation of invasive weed seeds, soil erosion or compaction, or destruction of pollinator habitat, have not been studied. It is possible that grazing could either create suitable habitat throughout a landscape or directly impact an existing population, depending on frequency, intensity, size, and location of the grazing disturbance.

Herbivory is also not uncommon for other western *Penstemon* species. Some *Penstemon* species are known to be palatable to livestock and are heavily grazed (e.g., *P. palmeri* planted to supplement feral horse diets) (Glenne 2003, Tepedino personal communication 2003). *Penstemon lemhiensis* is also a highly palatable *Penstemon* species of Montana, and mule deer, elk, and cattle graze the tall inflorescences and leafy rosettes. A summer livestock grazing rotation caused all of the flowering inflorescences to be eaten before seed set (Heidel and Shelley 2001). In Colorado, many *P. penlandii* fruits were eaten by ground squirrels (*Spermophilous elegans*) (Tepedino et al. 1999), but ground squirrels (*Spermophilous lineatus*) and chipmunks (*Eutamius uintahensis*) did not eat the fruits of *P. debilis* (McMullen 1998). A prairie penstemon, *P. grandiflorus*, was susceptible to root herbivory by pocket gophers (*Geomys bursarius*) (Davis et al.1991, 1995, 1997). While many *Penstemon* species can be susceptible to fruit predation by insects, *P. debilis* did not experience significant fruit predation (McMullen 1998). A significant number of fruits and seeds of *P. digitalis* were destroyed by micro-lepidopterans (Tortricidae), and many inflorescences were damaged by stem and bud feeding caterpillars (Mitchell and Ankeny 2001). Small melyrid beetles fed on the nectar of *P. bicolor* by entering the flowers or sucking nectar from holes in the corolla (Glenne 2003).

Some Intermountain *Penstemon* species produce secondary metabolites (e.g., iridoid glycosides), which may possibly function in plant defense by reducing palatability to some herbivores (Stermitz et al. 1993, Franzyk et al. 1998). The production of secondary plant compounds by *P. degeneri* is unknown. In addition, the age of the individuals in a population (and possibly plant size and root growth) and the time since establishment may mediate the effect of herbivory or other disturbances. Fire and gopher activity differentially affected the growth of *P. grandiflorus* individuals; larger (2 year) individuals with well-developed caudices were more likely to survive the effects of disturbance and flower earlier than smaller individuals (Davis et al. 1991).

Competitors and relationship to habitat

The interactions of *Penstemon degeneri* within the plant community are not well known. This penstemon is found with a wide range of associated species and overstory species, including grasses, shrubs, and trees. It inhabits sparsely vegetated disturbed soils, rocky areas, well-developed grasslands, the ecotone between grasslands and forests, and the forest understory. Some populations grow in microhabitats characterized by full sun exposure, and other populations grow within shaded microhabitats of dense pinyon/juniper. *Penstemon degeneri* is scattered in some locations and prolific in other locations. It is not possible to ascertain to what extent this species competes for resources with other species or is able to tolerate stressful environments.

The interactions among interspecific competition, succession, disturbances, germination requirements, and flowering needs for *Penstemon degeneri* are not known. Some of the lower-elevation pinyon-juniper woodlands in the Arkansas River corridor are described as "not meeting vegetation standards" because the trees are dense, and as a result, understory plants lack vigor and seedling establishment (Arkansas Headwaters Recreation Area 2001). The status of any *P. degeneri* populations in these areas has not been ascertained. The germination, growth, and flowering needs of *P. degeneri* are not known in enough detail to understand competition dynamics or the effects of shading. As discussed previously, disturbances such as fire and grazing may possibly play a role in creating or maintaining suitable open areas for *P. degeneri* by reducing competition with shrub and grass species. The optimal fire return intervals for persistence of *P. degeneri* are not known, but the cycles most likely vary for different habitat types and elevations. Brekke (personal communication 2003) explained that lightning-started wildfires are relatively uncommon in the region and any fires tend to be small (less than one acre), especially due to fire suppression activities.

Fire has proved to be important for reducing shrubby encroachment and litter accumulation and for creating suitable germination conditions in *Penstemon lemhiensis* habitat in Montana. After a fall prescribed burn treatment, recruitment levels for this species increased by up to 6400 percent, new seedling mortality decreased, and transition time from seedlings to rosette stages decreased compared to pre-fire average rates (Heidel and Shelley 2001). In Colorado, a flush of *P. virens* was observed two years after a fire that crown-burned and left all trees dead in ponderosa pine habitat (Crawford personal communication 2003). The fires probably served to reduce interspecific competition, to provide a flush of nutrients, to stimulate germination, and to potentially prolong the growing season. *Penstemon grandiflorus* also relies on disturbances from pocket gopher activity and fire to reduce woody encroachment and to open areas for germination and establishment (Davis et al. 1991, 1995, 1997). *Penstemon harringtonii* inhabits areas within *Artemisia tridentata* canopies as well as open areas (Nielson

1998). The average number of seeds produced per *P. harringtonii* plant was the same for plants in open areas and plants within *A. tridentata* canopies. However, for the *P. harringtonii* plants that were growing closely with *A. tridentata*, the uppermost, exposed flowers of the plants produced significantly more seeds than the lower, more hidden flowers (Nielson 1998).

Many non-native, invasive plant species can invade disturbed (e.g., roads, trails) or undisturbed sites, form dense, monospecific stands, and outcompete native species by using space, nutrients, and water (Cronk and Fuller 1995, Luken and Thieret 1997, Mack et al. 2000). Although there are no reports of invasive plant species negatively affecting *Penstemon degeneri*, invasive species such as *Poa pratensis* (Kentucky bluegrass) and *Bromus japonicus* (Japanese brome) have been found with *P. degeneri* (Colorado Natural Heritage Program 2003). Other species, such as *Linaria vulgaris* (yellow toadflax) and *Acroptilon repens* (Russian knapweed) have been increasing in the Arkansas River corridor (Arkansas Headwaters Recreation Area 2001). These noxious perennial species can invade disturbed or undisturbed sites, reproduce vegetatively, form dense, monospecific stands, and outcompete native species. Along the railroad line in the canyon, exotic annual weeds such as *Kochia scoparia* (kochia), *Salsola iberica* (Russian thistle), *Ambrosia artemisiifolia* (ragweed), and *Melilotus officinalis* (biennial yellow sweet clover) are also prevalent and may spread to adjacent communities. Weeds have invaded this area as a result of soil disturbance related to road construction, recreation site development, increased recreation use, and OHV use (Arkansas Headwaters Recreation Area 2001). *Centaurea maculosa* (spotted knapweed) is proving to be a management concern for the conservation of *P. lemhiensis* in Idaho (Mosely et al. 1990). Both species grow in open, bare soil communities often found along roadsides, but herbicide application to control the knapweed can potentially harm the native penstemon. The occurrence of weed control activities in areas with *P. degeneri* was not reported.

Parasites and disease

There is no evidence of parasites or diseases on *Penstemon degeneri* (Colorado Natural Heritage Program 2003).

Symbiotic interactions

Insect pollination of flowering plants is an example of an important symbiotic interaction. Plants lure insects to a pollen or nectar reward, and the insects carry pollen to other flowers, thus, helping to cross-fertilize. Specific details concerning pollination ecology of *Penstemon degeneri* are largely unknown; see the Pollinators and Pollination Ecology section for more details.

Other symbiotic interactions can occur between associated plant species. Woody perennials, such as shrubs, that grow with understory herbaceous species are sometimes called nurse plants (Callaway 1995). These nurse plants can alter the shared environment by modifying the microclimate (e.g., temperature, wind flow, light intensity, and soil moisture), trapping soil and organic debris, bringing water up to surface soils, providing protection from herbivores, and facilitating mycorrhizal growth. On the other hand, associated species can also compete for nutrients and water. The negative or positive interactions between associated species and *Penstemon degeneri* are unknown, as is the role of mycorrhizal associations.

Habitat influences

Penstemon degeneri appears to be geographically restricted, but the causes of endemism are unknown. It appears to be a habitat generalist with a tolerance for a wide range of environmental conditions. The availability and quality of suitable habitat most likely ranges from area to area, depending on heterogeneity in associated species, topography, substrate, disturbance factors, and competition with other species. The ability of this species to colonize disturbed areas is unknown.

CONSERVATION

Threats

Threats to the long-term persistence of *Penstemon degeneri* in USFS Region 2 are mostly unknown because of the lack of species understanding and research. The information presented in this section is primarily based on status reports of *P. degeneri* (Peterson and Harmon 1981, Anderson 1991), observations in occurrence records (Colorado Natural Heritage Program 2003), and personal communications with resource management specialists and botanists (Brekke personal communication 2002, Olson personal communication 2003, Spackman personal communication 2003). Refer to **Figure 5** for an envirogram outlining potential malentities to *P. degeneri*.

Of the 14 occurrences of *Penstemon degeneri* worldwide, five are on National Forest System lands in Colorado that are managed for multiple uses (**Table**

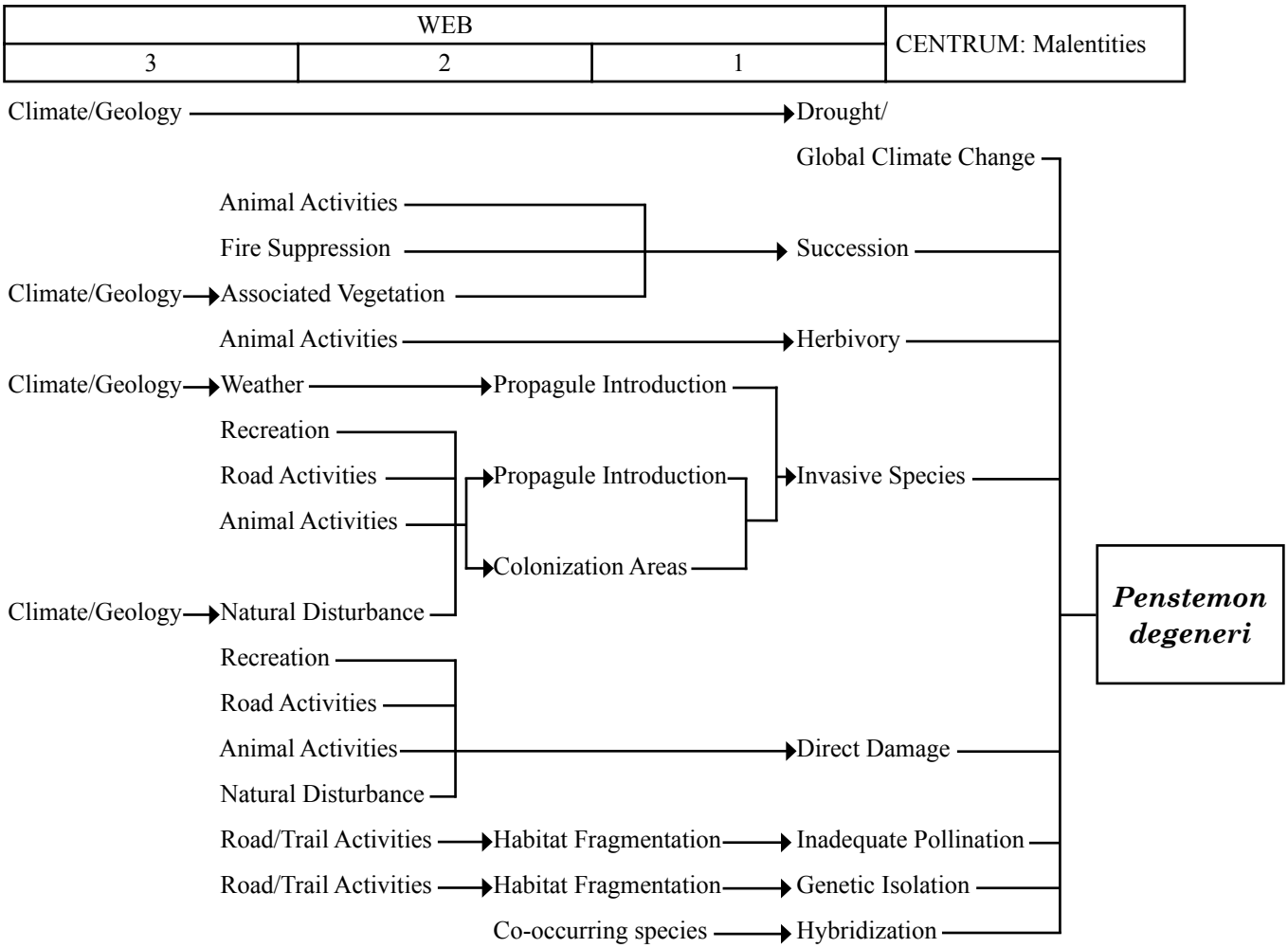

Figure 5. Envirogram outlining potential malentities to *Penstemon degeneri*.

1). The remaining populations occur on BLM lands, state lands, city lands, or private lands. As discussed earlier, populations of sensitive species on USFS and BLM lands obtain some protection from collection and from the impacts of federal projects. Any management or protection of the nine populations of *P. degeneri* on non-USFS lands is not known.

All populations of *Penstemon degeneri* could potentially be threatened by a variety of human-related activities (e.g., recreation, livestock grazing) or environmental changes (e.g., global climate changes, invasive species introduction). The specific threats will vary from population to population. Estimating the numbers of populations potentially threatened by certain activities (e.g., road activity) is associated with considerable uncertainty because descriptions of the populations and their landscape context are sparse. For example, a population may be "near a road" and could subsequently suffer intense impacts from direct trampling, road dust, associated erosion and deposition, or alternatively it could suffer minimal effects if the road is not heavily traveled or if the population is some distance from the road. In addition, human-related activities and other disturbances can either create suitable habitat throughout a landscape or directly impact an existing population, depending on frequency, intensity, size, and location. Direct impacts could either damage the existing individuals or reduce reproductive success, available habitat, establishment of new populations, or other factors important for long-term persistence of the species.

Direct or indirect negative impacts to *Penstemon degeneri* populations or habitat by human-related activities could occur from motorized and non-motorized recreation, trail or road construction and maintenance, changes to natural disturbance regimes, domestic livestock activities, invasive species introduction, structure construction, or small-scale

mining. Those populations closest to roads, trails, campgrounds, picnic grounds, and quarries are likely at the most risk. Overutilization of *P. degeneri* for educational, horticultural, or scientific purposes is unknown, but any increased demand for this species could be a future threat. Horticultural collecting has been implicated as a threat to *P. lemhiensis* in Idaho (Mosely et al. 1990). In addition, the possibility for breeding or hybridization with any cultivated varieties of this species is unknown.

Existing *Penstemon degeneri* individuals near trails, roads, and campgrounds could potentially be damaged by trampling, maintenance activities, or erosion/deposition causing burial of existing individuals. Recreational activities (e.g., hiking, camping, rafting, fishing, hunting, OHV use, and rock climbing) are popular in areas with *P. degeneri* populations. Of the five occurrences within Pike-San Isabel National Forest, at least one occurrence is along a forest road to a campground, and three occurrences are bisected by a trail used by hikers, mountain bikes, and motorbikes (Colorado Natural Heritage Program 2003, Olson personal communication 2003). *Penstemon degeneri* populations that are located near campgrounds and bisected by trails on USFS lands are susceptible to off-trail trampling. Although travel on USFS lands is restricted to designated trails and roads only, there still might be prohibited off-road use by motorized or mechanized vehicles. Of the nine populations on non-USFS lands, at least three occurrences are in heavily-used recreation areas. The Arkansas River corridor experiences high levels of recreational activities and "development of facilities to support recreational use will very likely affect [this] species." (Arkansas Headwaters Recreation Area 2001). Off-highway vehicle use is popular in some areas, and users are required to stay on existing trails (Brekke personal communication 2003), but *P. degeneri* individuals could be in jeopardy if users do not abide by the rules. One *P. degeneri* metapopulation is located in the Royal Gorge Park managed by Canon City. Recreational use of this park is high, and there are trails, picnic areas, and campgrounds in proximity to existing populations. If there are increases in off-trail use (especially with increased park visitation), changes to current facilities, or new construction projects in this park, populations could be extirpated (Peterson and Harmon 1981). One of the authors traveled through the Royal Gorge Park in 1989 and noticed that tourists predominantly stayed close to roads and rarely strayed off-trail. Another occurrence is in the vicinity of a BLM campground, trail, and popular rock climbing area. The actual proximity of the *P. degeneri* individuals to heavily used areas is not known.

Surface-disturbing activities, such as mining or road maintenance, could damage known populations of *Penstemon degeneri*. At least three *P. degeneri* populations (including one on USFS lands) are along roads accessible to passenger vehicles, and significant road or road construction activities (e.g., digging pits for aggregate or fill material) could negatively impact populations. Historical mining probably occurred within *P. degeneri* habitats, but it is unlikely that extensive natural resource development is currently occurring near existing populations. For example, there is a quarry in the vicinity of one occurrence, but the current status of any activity at that quarry is not known (Olson personal communication 2003). Any *P. degeneri* occurrences on or near private lands could be affected by possible housing development.

Current land management activities may play a beneficial role in maintaining suitable habitat for *Penstemon degeneri*, but these same activities could also be detrimental at high intensities or unsuitable timing. Based on the available information, one *P. degeneri* population on USFS lands was located in a historically active, but currently vacant, USFS grazing allotment (Olson personal communication 2003); additional populations on non-USFS lands may also be in grazed areas. It is possible that grazing may play a role in creating or maintaining suitable habitat, but heavy grazing could also pose a considerable threat to *P. degeneri*. For example, the occurrence in the historically grazed allotment was located near stock ponds with the potential for direct damage through heavy trampling. Livestock activity also has the potential to disturb soils, alter moisture levels through soil compaction, import weed seeds, facilitate exotic species invasion, and destroy important pollinator habitat areas. Timber harvest may occur in some of these locations, but we were unable to obtain information on details of these activities in locations with *P. degeneri*. Populations in steep, rocky areas are less likely to be exposed to livestock grazing or timber harvest than populations in more accessible grasslands or woodlands. A prescribed burn is being considered within the next few years for one area near a *P. degeneri* occurrence (Olson personal communication 2003). In areas that have low fuel loads, resulting low temperature fires may not kill perennials, like *P. degeneri*. Fire suppression activities could potentially alter community dynamics and reduce potential habitat for this species.

Other environmental or biological threats to populations or habitats of *Penstemon degeneri* could include non-native species introductions, excessive herbivory, inadequate pollination, genetic isolation, hybridization, global climate change, or changes to the natural disturbance regime that would affect fire, succession, erosion, or precipitation patterns.

Non-native plant species (i.e., *Poa pratensis*, *Bromus japonicus*) were found at many of the sites with *Penstemon degeneri* and possess the potential to compete with this species for resources. Any increase in non-native species invasion is a future risk for competition with *P. degeneri*, especially for populations along trails, roads, and other disturbed areas. Other invasive species of potential concern for increased establishment in the Arkansas River corridor include *Linaria vulgaris*, *Acroptilon repens*, *Kochia scoparia*, *Salsola iberica*, *Ambrosia artemisiifolia*, and *Melilotus officinalis* (Arkansas Headwaters Recreation Area 2001).

Penstemon degeneri grows in areas that are susceptible to fire, but the characteristics of the natural fire regime and the response of this species to fire are not known. As discussed previously, *Penstemon degeneri* may possibly rely on fire to maintain suitable open habitat. If fire return intervals or natural successional patterns were altered, then appropriate habitat for this species might be threatened.

Changes to existing climatic and precipitation patterns, perhaps as a result of global environmental change, could also impact *Penstemon degeneri*. For example, average temperatures have increased 4.1 ºF, and precipitation has decreased up to 20 percent in some areas of Colorado (U.S. Environmental Protection Agency 1997). Climate change and changes to a suite of other environmental variables have the potential to affect plant community composition by altering establishment, growth, reproduction, and death of plants. It is possible that the apparent ability of *P. degeneri* to tolerate somewhat stressful environments, to exist at a range of elevations, and to grow in a variety of habitats may help it to persist. The extent and effects of atmospheric pollution (e.g., deposition of nitrogen oxides) in this region are unknown.

At several locations, nearly all of the *Penstemon degeneri* individuals showed evidence of herbivory, possibly by deer, bighorn sheep, elk, rabbits, and/or grasshoppers (Colorado Natural Heritage Program 2003). The extent and effects of this herbivory on the long-term persistence of those populations are unknown. Current levels may or may not be affecting the persistence of certain populations of *P. degeneri* depending on how the timing and intensity of the herbivory affects individual longevity, reproductive success, and development of seedlings. It is possible that if other *P. degeneri* populations are also affected by intense herbivore activity, perhaps as a result of an increase in the population of native herbivores, this could potentially affect the global persistence of this species.

If *Penstemon degeneri* is largely dependent on outcrossing for maximum seed set, then any reductions in pollinator efficiency could reduce the species' reproductive success. For example, environmental stochasticity could potentially cause fluctuations in pollinator activity and behavior. In addition, the amount of gene flow, genetic variability, and inbreeding depression is unknown for *P. degeneri*. The extent of landscape fragmentation in areas with this species has not been studied or quantified. Any increase in road and trail construction or other barriers to pollinators could potentially decrease gene flow. *Penstemon degeneri* appears to tolerate a wide range of environmental conditions; this may correlate with high genetic variability. These characteristics may help this species maintain viability in the face of environmental variability (Peterson and Harmon 1981). The possibility of hybridization with other co-occurring *Penstemon* species has not been assessed but is a possible threat, based on conservation issues raised for other rare *Penstemon* species (e.g., Glenne 2003).

Threats to the long-term persistence of *Penstemon degeneri* populations or habitats likely differ for each of the 14 occurrences. The most significant threats to the five occurrences of *P. degeneri* on USFS Region 2 lands probably include motorized and non-motorized recreation, non-native plant invasion, grazing and trampling, extensive herbivory, succession, and global environmental changes. Populations near roads, trails, or campgrounds are likely at higher risk for the detrimental effects of road or trail associated activities and non-native plant invasion.

Conservation Status of the Species in USFS Region 2

Penstemon degeneri is a species of special concern because of its endemic distribution, the small number of documented occurrences, and the possible human-related and environmental threats to its persistence. Much information is lacking concerning the full abundance, distribution, and biology of *P.*

degeneri. Five of the 14 known populations of *P. degeneri* occur on USFS lands (**Figure 1**, **Table 1**). The conservation of populations on National Forest System lands is important to the global conservation status of this species and is the main focus of the discussion presented in this document.

The viability of *Penstemon degeneri* within USFS Region 2 is difficult to ascertain because the full distribution and abundance is unknown, demographic parameters have not been studied, and the effects of management activities (i.e., livestock grazing, prescribed fires, recreation) have not been studied. Three of the 14 populations have not been observed within the last 10 years, but five new populations have been discovered since 1998. All five of the populations on USFS lands have been observed since 1989 (**Table 1**). Motorized and non-motorized recreation, non-native plant invasion, grazing and trampling, extensive herbivory, succession, and global environmental changes potentially threaten *P. degeneri* on USFS lands. Based on the available information, it is difficult to assess if this species is persisting under current natural disturbance regimes and with current levels of recreation and management activities. It is also difficult to predict this species' ability to tolerate environmental stochasticity in the future (e.g., global environmental changes, invasive species) and any future management changes (e.g., livestock grazing, natural resource development, prescribed burning). *Penstemon degeneri* appears to be adaptable to a wide range of environmental conditions; this may increase its long-term resiliency.

Population declines

Based on the existing estimates, we are unable to conclude that the distribution or abundance of *Penstemon degeneri* is declining or expanding throughout its range. Although several new populations have been found since 1989 and that has significantly increased the number and abundance of known occurrences, the current abundance is not known. The sizes of the populations range from 25 to greater than 1,000 individuals (Anderson 1991); one population is ranked as highly viable, three are ranked as moderately viable, and two are ranked with low viability (Colorado Natural Heritage Program 2003). Two populations re-surveyed in 1998 (including one occurrence on USFS lands) had experienced drastic population declines, perhaps as a result of severe grazing/browsing pressures (Colorado Natural Heritage Program 2003). Because of *P. degeneri*'s wide ecological amplitude, there may be more occurrences yet to be discovered, especially in infrequently surveyed areas away from trails and roads (Anderson 1991). However, there were also presumably suitable sites that were surveyed but lacked this species (Spackman personal communication 2003). The rate at which this species disperses and colonizes new locations is unknown because we know little of its dispersal and establishment capabilities. Not enough data are available to conclude if populations of this species are increasing, decreasing, or remaining stable.

Life history and ecology

The lack of information regarding the basic biology, colonizing ability, vegetative and sexual reproductive potential, or genetic variability of *Penstemon degeneri* makes it difficult to pinpoint the biological or ecological characteristics important for long-term persistence of this species.

The apparent physiological capabilities of *Penstemon degeneri* to exist at a range of elevations and in a variety of habitats may help it to buffer the possible effects of global environmental changes. The extent to which reproductive success of *P. degeneri* (i.e., persistence of populations and the species) depends on vegetative or sexual reproduction, pollinator dynamics, genetic variability, and gene flow is unknown. If *P. degeneri* is largely dependent on outcrossing for maximum seed set, like other *Penstemon* species, then the reductions in pollination efficiency could potentially reduce reproductive success. Successful germination and establishment of new seedlings could be affected by changes to moisture conditions, soil surface disruption to the topsoil horizons, lack of suitable germination sites, or competition with other plant species. In addition, factors related to metapopulation dynamics, such as the amount of gene flow, genetic variability, inbreeding depression, and minimum viable population size, are unknown for *P. degeneri*. It is possible that peripheral populations, such as the population identified in Custer County, may harbor rare alleles important to conserve for the long-term persistence of this species. The possibility of hybridization with other co-occurring *Penstemon* species has not been assessed but is a possible threat, based on conservation issues raised for other rare *Penstemon* species (e.g., Glenne 2003).

Habitat variation and risk

Penstemon degeneri inhabits a wide range of habitats from pinyon-juniper woodlands to montane meadows. It appears that this species is not significantly limited by habitat factors, is relatively adaptable, and may possess genetic potential for adaptation (Peterson

and Harmon 1981, Anderson 1991). Inhabiting different habitats over a range of elevations and within different landscape contexts somewhat insulates *P. degeneri* from complete extinction by one particular factor. Potential risks within the habitats could include competition from surrounding vegetation, lack of suitable germination sites, extensive herbivory, inadequate pollinator habitat, barriers to gene flow, conditions too harsh for adequate growth and development, or other fluctuations in disturbance processes that could affect existing populations or creation of habitat.

Natural disturbances (e.g., fire, erosion) and current land management activities (e.g., prescribed burning, grazing, timber harvest, thinning) likely play a beneficial role in creating suitable habitat for *Penstemon degeneri* but could also be detrimental to existing individuals. In addition, some occurrences of this species are found in popular recreational areas, susceptible to trampling and direct damage from mechanized or motorized use, hiking, and sightseeing. Of the five occurrences within the Pike-San Isabel National Forest, at least one is along a forest road, one is near a campground, and two are bisected by a trail used by hikers, mountain bikes, and motorbikes (Colorado Natural Heritage Program 2003, Olson personal communication 2003). This species exists in disturbed and gravelly areas, but it is difficult to determine how much disturbance is enough and how much disturbance is too much. Also, disturbance regimes most likely vary among the different habitat types. For example, *P. degeneri* populations in dense pinyon-juniper habitat may be less susceptible to intense grazing or OHV use than populations in more open areas (Spackman personal communication 2003). It is difficult to predict the spread of non-native invasive plants and potential risk of alteration to plant communities. Thus, the optimal type, size, frequency, and intensity of disturbances required to sustain populations of *P. degeneri*, especially in different habitats, is not known. Specific populations near roads and trails could be at a greater risk than other populations, depending on the landscape context and characteristics of the natural and human disturbance regimes.

Management of the Species in USFS Region 2

Quantitative demographic monitoring and detailed biological and ecological studies of *Penstemon degeneri* populations and its habitat have not occurred. While this species appears to be persisting under current natural disturbance regimes and with current levels of recreation and management activities, it is difficult to predict the ability of this species to tolerate any future management changes (e.g., livestock grazing, natural resource development, prescribed burning, mining, invasive species control). Based on the available information, we can only hypothesize how changes in the environment may affect the abundance, distribution, and long-term persistence of this species.

Management implications

Management activities such as prescribed fires, livestock grazing, and regulation of motorized and non-motorized recreation occur in USFS habitats with *Penstemon degeneri*. However, the specific beneficial or negative effects of these management activities on this species have not been studied or quantified. Prescribed fires and livestock grazing in habitats with *P. degeneri* could possibly have a beneficial effect if they maintain suitable open habitat. Prescribed fires are used for ecosystem management to help reduce understory brush and ground litter accumulation, and thus facilitate forage production, plant diversity and regeneration, and reduce the probability for catastrophic fires. The presence of *P. degeneri* in areas that have been prescribed burned or the effects of fire on this species are unknown. A prescribed burn is being considered within the next few years for one area near a *P. degeneri* occurrence (Olson personal communication 2003). Studies of *P. lemhiensis* have shown that fall prescribed burning is a useful technique to reduce litter and interspecific competition and to encourage germination (Heidel and Shelley 2001). In contrast, grazing of *P. lemhiensis* during the flowering season causes significant herbivory of flowers and reduces the reproductive success. *Penstemon degeneri* occurs at a variety of elevations and in a variety of habitat types, so the effects of fires or livestock activities in each of those areas could be different.

Other human-related threats to existing populations of *Penstemon degeneri* could include off-trail hiking or OHV use, highway construction, or introduction of non-native species. *Penstemon degeneri* is found near both USFS and BLM roads and trails, so understanding the effects of recreational activities may be important for conservation of this species. Motorized and mechanized recreation is regulated by USFS and BLM, but whether users follow the rules and what implications these types of recreation have on *Penstemon degeneri* are unknown. In addition, facility development within Royal Gorge Park or the Arkansas River canyon could be detrimental to this species. Currently, there is some protection of this species through travel management plans and

regulations requiring surveys before construction on USFS and BLM lands. Recreation development has served to minimize uncontrolled parking and foot traffic and encourage public awareness and the use of trails (Arkansas Headwaters Recreation Area 2001). Presumably, this species would benefit from some types of invasive species control if invaders encroach upon populations or potential habitat in the future.

The long-term persistence of *Penstemon degeneri* will rely on monitoring the effects of current management practices and reducing human-related threats to existing populations. Priority conservation tools for *P. degeneri* conservation may include assessing current distribution and abundance, identifying and protecting the highest quality occurrences, investigating the source of intense herbivory on some populations, documenting the effects of land-use practices and management activities, and monitoring population trends. Additional key conservation tools may include surveying high probability habitat for new populations, preventing non-native plant invasions, studying demographic parameters and reproductive ecology, and assessing the effects of environmental fluctuations, future management activities or changes in management direction. Some examples of management practices that would protect *P. degeneri* habitat and minimize possible plant destruction by human-related activities include re-routing trails away from existing populations, encouraging hikers to stay on trails, restricting off-road vehicle traffic, preventing the spread and establishment of non-native invasive species, and regulating livestock activities to avoid intense trampling at existing population sites. Habitat management could also consider issues related to the surrounding landscape, such as pollinator habitat needs, livestock movement patterns, trail/road proximity and position in relation to population locations, barriers to dispersal, and landscape fragmentation. Some populations are at greater risk than others; populations near roads, trails, and campgrounds are priorities for inventory.

Potential conservation elements

Penstemon degeneri is a regional endemic with a small number of recorded populations and potentially high vulnerability to human-related activities and environmental changes. Features of *P. degeneri* biology that may be important to consider when addressing conservation of this species (i.e., key conservation elements) include its potential reliance on disturbances to create/maintain open habitat, its apparent susceptibility to herbivory, and possible outcrossing needs requiring efficient pollination. The full ecological amplitude of this species and intensity, frequency, size, and type of disturbance optimal for persistence of this species are unknown. Changes in the timing, intensity, or frequency of disturbances have the potential to damage existing populations and/or reduce habitat for future recruitment. For example, livestock grazing may create or maintain suitable habitat at low intensities, but could negatively impact existing plant populations at heavy intensities. The lack of information regarding the colonizing ability, adaptability to changing environmental conditions, sexual and vegetative reproductive potential, or genetic variability of this species makes it difficult to predict its long-term vulnerability. Management decisions could consider the effect of management activities on landscape fragmentation, erosion/deposition, pollinator habitat, and introduction of invasive species.

Tools and practices

There are no existing population monitoring protocols for *Penstemon degeneri*, and very little is known about its biology, ecology, and spatial distribution. Thus, additional habitat surveys, quantitative population inventories and monitoring, and ecological studies are priorities for constructing a conservation plan. Inventories are useful for re-locating historical populations, estimating current abundance, and identifying high-quality populations. Surveys will help locate any undiscovered populations. Quantitative monitoring will help obtain data for population trend and demographic modeling and assess the effects of management activities. Short-term research studies (e.g., genetic analyses, pollination studies) and long-term research studies (e.g., effects of environmental fluctuations) can supplement the current biological knowledge of this species and help estimate long-term persistence.

Species inventory and habitat surveys

Current reports of existing *Penstemon degeneri* populations provide a useful base of information, but the distribution and total abundance of this species are not sufficiently known to formulate regional conservation strategies. Abundance information is available for only seven of the 14 occurrences. Additional surveys of high probability habitat are needed to discover any additional populations and document the full spatial extent of this species. For example, Anderson (1991) suggested that additional populations of *P. degeneri* might exist, especially in less-traveled areas away from roads and trails. In general, Fremont County has not been intensively surveyed and is poorly represented in herbarium specimens. In addition, several populations of

P. degeneri appeared to be in decline as a result of intense herbivory (Colorado Natural Heritage Program 2003), and at least one population needs herbarium specimens to verify identification (Spackman personal communication 2003). Ascertaining the current abundance of this species would help to estimate the vulnerability of this species to environmental fluctuations.

The distribution of *Penstemon degeneri* is widely scattered, with populations or groups of populations spread over a range of elevations in a variety of habitat types. Most of the existing occurrences of this species, as defined by Colorado NHP (2000), are characterized by several suboccurrence population clusters over a large area with potential habitat between populations. Whether this distribution pattern is the result of genetic variation in ecological preferences, habitat heterogeneity (i.e., variability in the habitat suitability over space), or a reflection of inadequate surveying for undiscovered populations is not currently known. Anderson (1991) mapped existing populations on U.S. Geological Survey 7.5-minute topographic maps and found that some populations extended for several miles. New surveys could use these maps of existing populations as starting points, because similar habitats may extend along similar topographic lines. Researchers could also identify areas of potential habitat in a particular habitat type (e.g., montane meadows) using topographic maps, geologic maps, and aerial or satellite images. It is possible that additional populations exist along the length of Phantom Canyon, or in other side canyons of the Arkansas River corridor, or between the populations in Pike San-Isabel National Forest and Royal Gorge Park. These areas with similar habitats and topography could be surveyed.

Once located, the size and extent of *Penstemon degeneri* populations could be mapped and recorded using global positioning system (GPS) and geographic information systems (GIS) technology. Mapping the extent of each known population of this species will maintain consistency for future observations, facilitate information sharing between different management organizations, and help in making estimates of density and abundance. Mapping exercises will also elucidate the spatial distribution of populations at the local and regional levels and provide a framework for creating a metapopulation study. High-quality populations in pristine habitat could be identified. Populations in areas slated for various management, maintenance, or disturbance activities could be readily identified. A detailed assessment could be undertaken before activities such as road/trail reconfiguration or prescribed burn occur.

Population monitoring and demographic studies

Additional information is also needed to gain an understanding of the life cycle, demography, and population trends of *Penstemon degeneri*. Information is lacking on longevity, germination requirements, seed survival, extent of asexual reproduction, factors affecting flower development, pollination ecology, role of the seed bank, and gene flow between populations. This type of species-specific information would be useful in assessing threats to this species and estimating species viability. For example, seed bank studies could assess the abundance of seeds to reveal dispersal patterns in this species. Studies of germination needs in the field might elucidate potential limiting factors for the establishment of new individuals.

No data are available on population trends for *Penstemon degeneri* and no long-term demographic monitoring has been initiated. Long-term monitoring studies could yield helpful information, such as temporal and spatial patterns of abundance and dormancy; environmental factors that influence abundance (e.g., drought); whether populations are increasing, decreasing, or remaining stable; and the minimum number of plants necessary to perpetuate the species. Schemske et al. (1994) recommended that the most biologically relevant question in evaluating the status of rare plants is "given current conditions, is population size increasing, decreasing, or stable?" Even the collection of simple metrics would greatly augment the current understanding of distribution and basic biological information about this species. For example, researchers could record population size, area, and density, as well as the presence of different age classes at each population. Several populations from throughout the range and from different habitat types could be monitored every one to two years at first, and then every 5 to 10 years. Identifying life history stages and performing an annual census of each stage are the first steps in estimating the rate and direction of population growth (Schemske et al. 1994). Long-term population monitoring in conjunction with mapping may elucidate the temporary disappearance of aboveground individuals during unsuitable conditions, which would aid in understanding the effects of environmental fluctuations as well as provide better estimates of abundance. In addition, further studies on the morphological and genetic differences between and among *P. degeneri* populations will clarify metapopulation dynamics and ecological preferences.

Understanding certain aspects of demography is a priority in order to provide basic population information. These aspects are indicated by the following questions:

- What are the rates of survival, longevity, and recruitment?
- What are the population fluctuations from year to year?
- What are the effects of disturbances on demographics?
- What are the role, status, and longevity of the seed bank?
- What is the age structure of the population?
- What is the age at which individuals become reproductive?
- What is the extent of vegetative and sexual reproduction?
- What is the gene flow between populations?

Several groups have developed protocols for monitoring population and demographic trends of rare plant species. These protocols can be easily accessed and used to develop specific monitoring plans for use in USFS Region 2. For example, *Measuring and Monitoring Plant Populations* (Elzinga et al. 1998) and *Monitoring for Conservation and Ecology* (Hutchings 1994) are general references that provide concrete guidance on designing and implementing quantitative monitoring plans for rare plant species. *USDA Forest Service Region 2 TES Plant Management Strategy* (Austin et al. 1999) and *Protocols and Models for Inventory, Monitoring, and Management of Threatened and Endangered Plants* (Bonham 2001) provide helpful protocols specifically designed for federal agencies monitoring plants on public lands. Lesica (1987) has developed a technique for monitoring perennial plants on permanent belt transects that has been used by other *Penstemon* studies in Montana and Wyoming to gauge population density and changes in age classes over time (Fertig and Welp 2001, Heidel and Shelley 2001). In addition, population matrix models that measure individual fitness and population growth provide flexible and powerful metrics for evaluating habitat quality and identifying the most critical feature of the species' life history (Schemske et al. 1994, Hayward and McDonald 1997). Deterministic demographic models of single populations are the simplest analyses and are powerful tools in making decisions for managing threatened and endangered species (Beissinger and Westphal 1998).

Habitat monitoring and management

The general habitat characteristics of *Penstemon degeneri* have been identified, but there are too many unknowns regarding microhabitat requirements and basic population dynamics to know which factors are critical in maintaining or restoring habitat for this species. For example, it is currently not known what types, intensities, or frequencies of disturbance create and maintain habitat and are tolerated by existing populations of this species. Land management techniques, such as livestock grazing, timber harvest, thinning, prescribed burns, and fire suppression, are probably used throughout these habitats and may influence the persistence of this species. The cumulative beneficial or detrimental effects of these activities on *P. degeneri* and its habitats have not been studied or monitored.

The types of monitoring studies required to understand how *Penstemon degeneri* responds to environmental fluctuations, changes in the disturbance regime, or natural succession would be complex and could take decades. For example, precipitation fluctuations have the potential to affect erosion rates, germination success, pollinator population trends, timing of flowering, and/or growth of surrounding vegetation. Populations of *P. degeneri* are found in a variety of habitats with different disturbances and characteristics, so research studies could initially focus on a few populations from each type of habitat (e.g., pinyon/juniper, alpine meadows). It will be difficult to determine to what extent disturbances are necessary to create habitat and/or maintain a population, what disturbance intensity and frequency may be most appropriate, and what factors would result in local extirpation of a population. Researchers could take advantage of current or future management activities to assess the effects of various types of disturbance on *P. degeneri* using techniques such as livestock exclosures and pre- and post-prescribed burn monitoring with control plots. Documenting land management and monitoring habitat could occur in conjunction with population monitoring efforts in order to associate population trends with environmental conditions. Habitat management could also consider issues related to the surrounding landscape, such as pollinator habitat needs, herbivore movement patterns, encroachment of non-native invasive plants, and trail proximity and position in relation to population locations.

Because the range of *Penstemon degeneri* occurs largely on USFS and BLM lands, some examples of management practices that would protect habitat and minimize possible plant destruction by human-related activities include re-routing trails away from existing populations, encouraging hikers to stay on trails, restricting off-road vehicle traffic, preventing the spread and establishment of non-native invasive species, and regulating livestock activities to avoid intense trampling at existing population sites. Peterson and Harmon (1981) suggested that public education about the *P. degeneri* populations in Royal Gorge Park would help to protect the existing populations, as well as increase public awareness about sensitive plants. Habitat management could also consider issues related to the surrounding landscape, such as pollinator habitat needs, herbivore movement patterns, and trail proximity and position in relation to population locations.

Biological and ecological studies

Much of the information regarding habitat requirements, establishment, reproduction, dispersal, relationship with herbivores, competition with other species, and overall persistence has not been studied for *Penstemon degeneri*. In particular, several populations of *P. degeneri* have experienced significant herbivory, and identifying the source of the browsing pressure is a research priority. In addition, the response of *P. degeneri* to habitat changes is not known in sufficient detail to evaluate the effects of changes in disturbance patterns. Research studies to evaluate the effects of drought, succession, and fire at several scales (local and regional) would provide valuable input to the development of conservation strategies and management programs. It will be difficult to determine to what extent disturbances are necessary to create habitat and/or maintain a population, what disturbance intensity and frequency may be most appropriate, and what factors would result in local extinction of a population.

This species assessment has referred to supporting literature on closely related *Penstemon* species or other *Penstemon* species in USFS Region 2 to provide possible insights on *P. degeneri* biology (e.g., Grey 1982, Flessner 1989, Flessner and Stubbendieck 1992a, Kitchen and Meyer 1992, Davis et al. 1997, Caha et al. 1998, Nielson 1998, McMullen 1998, Tepedino et al. 1999, Fertig 2000). This body of research on the biology of other *Penstemon* species could also provide useful information for designing future studies of *P. degeneri*, even though these species may not be closely related. For example, McMullen (1998) undertook studies to identify the causes of effects of physical and chemical edaphic characteristics on the survival of *P. debilis* (an unrelated penstemon endemic to oil shales in western Colorado). Although *P. degeneri* does not inhabit oil shales, microhabitat characteristics could be studied for *P. degeneri* using similar methodologies. Researching issues related to possible hybridization of *P. degeneri* with other more common, co-occurring *Penstemon* species may be important for the conservation of this rare species. Glenne (2003) and Chari and Wilson (2001) provide examples of research efforts to assess hybridization barriers between *Penstemon* species through crossing experiments, pollinator observations, and morphological measurements. Wolfe et al. (1998a, 1998b) used genetic markers to assess variability among natural populations of *Penstemon* species and to detect evidence of hybridization. Status reports and recovery plans for the conservation of other rare and endangered species in USFS Region 2 also discuss important issues to consider (e.g., Mosely et al. 1990, Fritz et al. 1992, McMullen 1998, Nielson 1998, Fertig 2001), that we have also incorporated into the Information Needs and Research Priorities section. For example, the recovery of *P. haydenii* depends on the protection of the known occurrences of the species, field surveys to discover new populations and habitat suitable for restoration, research, and long-term monitoring to understand its basic natural history, reintroduction of new populations, maintaining an artificial seed bank, and developing public awareness (Fritz et al. 1992).

Availability of reliable restoration methods

The successful germination and production of *Penstemon degeneri* seedlings in garden/greenhouse environments (Slaby 2001, Denver Botanic Gardens 2003, Grant personal communication 2003) introduces the possibility of restoration, if necessary. The collections of the Royal Botanic Gardens in Kew do not include *P. degeneri* material (Royal Botanic Gardens 2003), but the National Genetic Resources Program has over 3000 seeds of this species in long-term storage (Grotenhuis personal communication 2003). The seeds were collected from one occurrence (Royal Gorge Park) in 1990. Studies by the Denver Botanic Gardens in conjunction with the CPC found that there was 80 percent germination for those seeds after at least 10 years of storage (Grant personal communication 2003). Several plants are now growing in the Denver Botanic Gardens "Western Panorama" public garden, and they have flowered and persisted successfully for one year (DePrenger-Levin personal communication 2003, Grant personal communication 2003). It would be valuable to augment the number of collection sites for more adequate *ex situ* conservation of this species

(Center for Plant Conservation 2003, Dawson personal communication 2003, T. Grant personal communication 2003). Germination and transplantation studies in natural environments would be helpful if populations are at risk of habitat destruction.

There are still too many unknowns regarding habitat preferences and basic population dynamics to know what factors are critical in restoring habitat for *Penstemon degeneri*. For example, it is currently not known what types, intensities, or frequencies of disturbance are suitable for creating and maintaining habitat for this species. Management activities, such as livestock grazing and prescribed burns, in areas with occurrences of this species or similar habitats could be assessed for potential as habitat restoration techniques.

Information Needs and Research Priorities

Based on our current understanding of *Penstemon degeneri*, we can identify research priorities where additional information will help to develop management objectives, initiate monitoring and research programs, and inform a conservation plan. To address these data gaps, information can be obtained through surveys, long-term monitoring plans, and extended research programs. There is so little known about the biology and ecology of this species that there are a large number of research projects that could be implemented.

Identifying high-quality populations and populations that may be immediately threatened, monitoring population trends, studying herbivore dynamics, surveying for new populations, understanding the effects of management activities and disturbances, and studying basic biological traits are of primary importance to further the understanding of *Penstemon degeneri* in USFS Region 2. The following types of studies would supplement basic knowledge regarding this species:

- Re-visiting and detailed mapping and inventory of existing populations
- Population trend monitoring
- Identifying high-quality populations and habitat
- Surveying for new populations
- Identifying any imminent threats to known populations, especially as related to herbivory
- Identifying disturbance types, frequencies, and intensities; especially as related to management activities
- Defining and measuring microhabitat characteristics
- Studying reproductive biology, including pollinator surveys, germination trials, vegetative reproduction, mycorrhizal associations, and seedbank analyses
- Identifying possible causes of individual plant mortality (e.g., herbivory, parasites, diseases)
- Using genetic analyses to assess gene flow, variability, and possible hybridization throughout range.
- Increasing public awareness of this species to prevent inadvertent destruction in high-traffic areas

Additional research and data that may be useful but are not incorporated into this assessment include aspects related to managing data for efficient use. Data acquired during surveys, inventories, monitoring programs, and research projects are most easily accessible if they are entered into an automated relational database. Databases also facilitate the sharing of information to all interested parties. The Colorado NHP and NatureServe have developed databases and GIS components to assist in information storage and habitat modeling (Anderson personal communication 2003). Such a database should be integrated with GIS and allow activities such as the following:

- Efficient incorporation of data in the field
- Documentation and cataloging herbarium specimens
- Generation of location and habitat maps
- Characterization of associated habitat types
- Identification of population trends over time

- ❖ Identification of data gaps that require further information gathering
- ❖ Easy modification as additional information becomes available.

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DEFINITIONS

Amplitude – Breadth or range.

Annual – A plant that completes its entire life cycle (germinates, flowers, sets seed, and dies) in a single year.

Anther – Part of the flower reproductive structure (stamen) that bears pollen.

Asexual reproduction – Any form of reproduction not involving the union of gametes.

Bilabiate – Two-lipped; usually referring to a flower corolla.

Calyx – The collective name for sepals.

Category 1 (C1) ranking – Taxa for which substantial biological information exists to support proposing to list as threatened or endangered (USFWS).

Category 2 (C2) ranking – Taxa for which current information indicates that proposing to list as endangered or threatened is possible but there is insufficient information to support immediate rulemaking (USFWS).

Category 3C (3C) ranking – Taxa that have proven to be more abundant or widespread than was previously believed, and/or those that are not subject to any identifiable threat (USFWS).

Caudex – Short, swollen, often woody portion of a plant stem that is at or beneath ground level. This structure functions in new stem production, serves as a storage organ, and/or produces short rhizomes.

Cauline – On or pertaining to a stem.

Congener – A member of the same genus.

Corolla – Portion of flower comprised of petals.

Dehisce – To split or open, discharging seeds, pollen, or other contents, as the ripe capsules or pods of some plants.

Demographics – The study of fecundity and mortality parameters that are used to predict population changes.

Disjunct – A geographically isolated population or species outside of the range of other similar populations or species.

Dormancy – A period of growth inactivity in seeds, buds, bulbs, and other plant organs even when environmental conditions normally required for growth are met.

Ecotone – A transitional zone between two communities.

Endangered – Defined in the Endangered Species Act as a species, subspecies, or variety likely to become extinct in the foreseeable future throughout all of its range or extirpated in a significant portion of its range.

Endemic – A population or species with narrow physiological constraints or other restrictions, which limit it to a special habitat or a very restricted geographic range, or both.

Entire – Having a margin that lacks any toothing or division, as the leaves of some plants.

Fertility – Reproductive capacity of an organism.

Fitness – Success in producing viable and fertile offspring.

Forb – An herbaceous plant, other than grass.

Fruit – The ripened, seed-containing reproductive structure of a plant.

G2 ranking – Imperiled globally because of rarity (6 to 20 occurrences) or because of factors demonstrably making a species vulnerable to extinction (NHP).

Genotype – Genetic constitution of an organism.

Glabrous – Smooth, without hairs or glands.

Glands – Structures on the surface of a plant organ (i.e., leaf) that produce a sticky, greasy substance.

Glandular – With glands.

Guidelines – Streaks of color on flowers that may "lead" pollinators to the nectar.

Habitat fragmentation – The breakup of a continuous landscape containing large patches into smaller, usually more numerous, and less connected patches. Can result in genetic isolation.

Habitat isolation – When two or more habitats are separated (i.e., geographically) to an extent to prevent cross breeding, thereby genetically isolating two parts of a once continuous population.

Herbaceous – Adjectival form of herb (an annual or perennial plant that dies back to the ground at the end of the growing season because it lacks the firmness resulting from secondary, woody growth).

Hybridization – The result of a cross between two interspecific taxa.

Indeterminate – Not terminating growth with flowering; continuing to grow at apex.

Inflorescence – The flowering part of a plant, referring to a cluster of flowers on a single stem.

Interspecific competition – Competition for resources between individuals of different species.

Intraspecific competition – Competition for resources among individuals of one species.

Introgression – Transfer of genetic material from one taxonomic species to another, and its spread among individuals of the second species.

Iteroparous – Capable of reproducing several or many times over a lifetime (e.g., perennial plants.

Lanceolate – Lance-shaped; much longer than broad, widening above the base and then tapering to the tip.

Metapopulation – Group of populations that are linked through migration of individuals

Monocarpic – Flowering and bearing fruit only once.

Mycorrhiza – Symbiotic association between a fungus and the root of a higher plant.

Oligolege – Pollinator that visits one or a few related plant species for pollen.

Ovary – The enlarged portion of the female reproductive structure (pistil) that contains the ovules and develops into the fruit.

Ovate – Egg-shaped (two-dimensional), with the broadest end toward the base.

Ovoid – Egg-shaped (three-dimensional).

Ovule – Part of "female" plant reproductive system that becomes a seed after fertilization.

Palate – The raised part of the lower lip of a corolla, constricting or closing the throat.

Perennial – A plant that lives for 3 or more years and can grow, flower, and set seed for many years; underground parts may regrow new stems in the case of herbaceous plants.

Perfect flower – Flower with both "male" (stamens) and "female" (pistils) reproductive organs.

Petiole – Leaf stalk.

Phenotype – The external visible appearance of an organism.

Phenotypic plasticity – When members of a species vary in height, leaf size or shape, flowering (or spore-producing time), or other attributes, with changes in light intensity, latitude, elevation, or other site characteristics.

Pioneer species – Generally the first species to colonize an area during primary succession.

Pistil – The seed-producing organ of a flower, consisting of a stigma, style, and ovary.

Polycarpic – Flowering and bearing fruit multiple times.

Polyploidy – Having more than two complete sets of chromosomes per cell.

Population Viability Analysis – An evaluation to determine the minimum number of plants needed to perpetuate a species into the future, the factors that affect that number, and current population trends for the species being evaluated.

Propagule – A reproductive body, usually produced through asexual or vegetative reproduction.

Pubescent – Bearing hairs.

Ramet – An individual member of a clone.

Ramify – To send out branches or subordinate branchlike parts.

Recruitment – The addition of new individuals to a population by reproduction.

Reflexed – Bent backward.

Rhizomatous – Bearing rhizomes.

Rhizomes – Prostrate stem growing beneath the ground surface, usually rooting at the nodes.

Ruderal habitat – Temporary or frequently disturbed habitats.

Ruderal species – Species that can exploit low stress, high disturbance environments.

S2 ranking – Imperiled globally because of rarity (6 to 20 occurrences) or because of factors demonstrably making a species vulnerable to extinction (NHP).

Semelparous – Reproducing only once throughout a lifetime, usually followed by death (e.g., annual plants).

Senescence – Changes that occur in an organism (or part of an organism) between maturity and death (i.e., ageing).

Sensitive species – A species whose population viability is a concern due to downward trends in population numbers, density, or habitat capability, as identified by a regional forester (USFS).

Sepals – A segment of the calyx.

Sessile – Lacking a stalk.

Sexual reproduction – Reproduction involving the union of gametes.

Solitary – Single, sole.

Stamen – The pollen-producing structures of a flower; the "male" part of a flower.

Staminode – A sterile stamen or any structure lacking an anther but corresponding to a stamen.

Stigma – The surface of the plant reproductive structures (pistil) on which pollen grains land.

Succession – The orderly process of one plant community replacing another.

Suffrutescent – Dying back to a persistent base.

Symbiosis – An intimate association between two dissimilar organisms that benefits both of them.

Sympatric – Occupying the same geographic region.

Sympetalous – Having united petals, at least at the base.

Terminal – Occurring at the tip or end.

Threatened – Defined in the Endangered Species Act as a species, subspecies, or variety in danger of becoming endangered within the foreseeable future throughout all or a significant portion of its range.

Throat – The opening of a sympetalous corolla.

Vegetative reproduction – A form of asexual propagation whereby new individuals develop from specialized multicellular structures that often detach from the mother plant.

Viability – The capability of a species to persist over time. A viable species consists of self-sustaining and interacting populations that have sufficient abundance and diversity to persist and adapt over time.

Zygomorphic – Bilaterally symmetrical; displaying symmetry along one plane only.

Zygote – Cell formed from the union of two gametes.

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