Leptodactylon watsonii (Gray) Rydberg (Watson's prickly phlox): A Technical Conservation Assessment

Prepared for the USDA Forest Service, Rocky Mountain Region, Species Conservation Project

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COVER PHOTO CREDIT

Leptodactylon watsonii growing on a limestone cliff in Five Springs Draw (north of the Yampa River) in Colorado. Photo taken June 1987 by Betsy Neely (used with permission).

SUMMARY OF KEY COMPONENTS FOR CONSERVATION OF *LEPTODACTYLON WATSONII*

Status

The global distribution of *Leptodactylon watsonii* (Watson's prickly phlox) is limited to the interior western states of Colorado, Wyoming, Utah, Idaho, and Nevada. Within USDA Forest Service (USFS) Region 2, *L. watsonii* exhibits a discontinuous distribution across Wyoming and Colorado. Habitat in Region 2 consists of ledges, rock crevices, or cliffs in the foothills or canyons, often on calcareous soils in vegetation zones ranging from sagebrush to spruce-fir from 1,402 to 2,682 m (4,600 to 8,799 ft.) in elevation. Of the 18 occurrences in Colorado and Wyoming, only three are located on National Forest System lands; two are on the White River National Forest in Colorado, and one is on the Bighorn National Forest in Wyoming.

Leptodactylon watsonii is neither federally listed nor a candidate for listing under the Endangered Species Act. Neither Region 2 nor Region 4 of the USFS have designated it a sensitive species. The final recommendation made during the 2003 revision of the Region 2 sensitive species list was that *L. watsonii* is "not a Region 2 Sensitive Species, but should be considered for other Emphasis Species lists." The Bureau of Land Management does not list this species as sensitive in any of the states in which it occurs. The Global Heritage status rank for the species is G3G5, between globally vulnerable and secure. In Colorado, *L. watsonii* is ranked S2, imperiled, and in Wyoming it is ranked S1, critically imperiled. Outside of Region 2, the conservation status of *L. watsonii* is S3, vulnerable, in Utah, and it is unranked in Idaho and Nevada.

Primary Threats

Leptodactylon watsonii is vulnerable because it occurs in small populations and has a limited global distribution. Insufficient information is available to determine if significant population or habitat loss has occurred because of human activities, but threats appear to be minimal at known sites due to the rugged nature of the plant's habitat. Populations of *L. watsonii* may be at risk from environmental or demographic stochasticity due to their small size. Environmental threats to *L. watsonii* include global warming and extreme weather events such as drought or unusually cold weather during the flowering and fruiting season. Air pollution, including acid rain, may also negatively affect *L. watsonii* habitat. Threats to reproductive processes such as inadequate pollinator activity, lack of safe sites for germination or seedling establishment, as well as undefined barriers to gene flow, may also threaten this species. The topographic setting of several occurrences of this species provides a degree of isolation from interactions with invasive species; however, recreation has the potential to introduce invasive species even in remote locations.

Primary Conservation Elements, Management Implications, and Considerations

Leptodactylon watsonii is vulnerable because of its limited global distribution in North America and small size of its populations. The species has a discontinuous distribution in Region 2. There is no information concerning reproductive success or range of genetic variability, nor is there information concerning the ability of the species to adapt to changing environmental conditions.

Features of *Leptodactylon watsonii* biology that may be important to consider when addressing conservation of this species include its preference for rock crevices and cliff face habitats on limestone substrates, relatively small population sizes, and apparently discontinuous distribution. Conservation of *L. watsonii* occurrences primarily involves safeguarding the microhabitats in which it occurs (namely ledges, rock crevices, or cliffs).

Priority conservation tools and future research studies for this species may include revisiting and mapping the extent of known occurrences, defining high-quality occurrences, identifying potential threats, and assessing population trends. Additional key conservation tools and research studies include surveying potential habitat for new occurrencess, preventing non-native plant invasions, studying demographic parameters and reproductive ecology, and assessing the effects of management actions or changes in management direction.

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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) of the USDA Forest Service (USFS). *Leptodactylon watsonii* (Watson's prickly phlox) is the focus of an assessment because of its small global population and its limited North American distribution. Populations on National Forest System lands in Region 2 are peripheral to the species' main range, which is centered in the Great Basin of Nevada. There is limited knowledge concerning its distribution, habitat, population trends, or threats. USFS Region 2 has not designated this species as sensitive.

This assessment addresses what is known about the biology, ecology, conservation status, and management of *Leptodactylon watsonii* throughout its range, which includes USFS Region 2 and Region 4. This introduction defines the goal of the assessment, outlines its scope, and describes the process used in its production.

Goal

Species 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, and conservation status 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. Rather, it provides the ecological background upon which management must be based and focuses on the consequences of changes in the environment that result from management (i.e., management implications).

Scope and Information Sources

This assessment examines the biology, ecology, conservation status, and management of *Leptodactylon watsonii* with specific reference to the geographic and ecological characteristics of Region 2. Similarly, this assessment is concerned with the reproductive biology, population dynamics, and other characteristics of *L. watsonii* 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, we reviewed refereed literature, non-refereed publications, personal communications, data managed by state natural heritage programs, and research reports. Very little information concerning *Leptodactylon watsonii* exists in the primary literature. Refereed literature was available for the discussion of systematics, breeding system, hybridization, and morphology, but no refereed literature concerning this species' population trends, autecology, or demography exists.

Unpublished data (e.g., Natural Heritage Program records) were important in estimating the geographic distribution and abundance of *Leptodactylon watsonii*). These data required special consideration because of the diversity of persons and methods used in collection. Data for this species assessment were obtained primarily by secondary sources through state natural heritage programs including the Wyoming Natural Diversity Database (WYNDD), herbarium specimen label data, scientific literature, and knowledgeable individuals. WYNDD currently has four element occurrence records (EOR) for this species in Wyoming. The Colorado Natural Heritage Program (CNHP) tracks this species but currently does not have any element occurrence records for it. Requests for herbarium label data were made to 53 herbaria throughout the region by mail and followed up by telephone and/or e-mail. All of the herbarium specimens of *L. watsonii* specific to Region 2 are housed at the Rocky Mountain Herbarium (RM) and the University of Colorado Museum (COLO). Several of the smaller regional herbaria did not respond to the query; it is possible that there are additional specimens representing locations not addressed in this assessment. Chadron State College Herbarium (CSCN) in Chadron, Nebraska responded with label data from a specimen from Idaho. The Stanley L. Welsh Herbarium (BRY) at Brigham Young University in Provo, UT provided label data from Utah specimens as did the Manti-LaSal National Forest Herbarium (MALS) in Price, Utah and the Intermountain Research Station Herbarium (SSLP) in Provo, Utah. All Utah herbaria that responded provided label data from collections from Utah; none were from Region 2. Distribution data for *L. watsonii* within Region 2 were obtained through WYNDD and herbarium specimen label data from the Rocky Mountain Herbarium (RM) and the University of Colorado Museum (COLO). Published papers concerned with closely related taxa were reviewed, and inferences were drawn when a basis could be established for application to *L. watsonii*. We present no empirical data in this assessment.

Treatment of Uncertainty

Science represents a rigorous, systematic 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, strong inference, as described by Platt, suggests that experiments will produce clean results (Hilborn and Mangel 1997) as may be observed in certain physical sciences. The geologist T.C. Chamberlain (1897) suggested an alternative approach to science where multiple competing hypotheses are confronted with observation and data. Sorting among alternatives may be accomplished using a variety of scientific tools (experiments, modeling, logical inference). Ecological science is, in some ways, more similar to geology than physics because of the difficulty in conducting critical experiments and the reliance on observation, inference, good thinking, and models to guide understanding of the world (Hilborn and Mangel 1997).

Publication of Assessment on the World Wide Web

To facilitate the use of species assessments in the Species Conservation Project, they are being published on the Region 2 World Wide Web site (see http://www.fs.fed.us/r2/projects/scp/assessments/index.shtml). Placing the documents on the Web makes them available to agency biologists and the public more rapidly than publishing them as books or reports. More importantly, Web-publication facilitates revision of the assessments, which will be accomplished based on guidelines established by 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 Society for Conservation Biology, employing 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

Management Status

Leptodactylon watsonii is not federally listed nor a candidate for listing under the Endangered Species Act (U.S. Fish and Wildlife Service 1990). Neither Region 2 nor Region 4 of the USFS designated this species as sensitive. The final recommendation from the Region 2 Sensitive Species revision in 2003 was that *L. watsonii* is “not a Region 2 Sensitive species, but should be considered for other Emphasis Species lists” (USDA Forest Service 2004). The Bureau of Land Management (BLM) does not list *L. watsonii* as a Species of Concern for any of the states in which it occurs.

NatureServe (2006) assigns *Leptodactylon watsonii* a global conservation rank of G3G5, indicating a degree of uncertainty as to whether the species is globally vulnerable (G3) or secure (G5). Within the states of Region 2, conservation status ranks assigned to this species by state natural heritage programs range from critically imperiled (S1) in Wyoming (Wyoming Natural Diversity Database 2006) to imperiled (S2) in Colorado (Colorado Natural Heritage Program 2006). Outside of Region 2, *L. watsonii* is ranked vulnerable (S3) in Utah, and it is unranked in Idaho and Nevada. Conservation status ranks are explained in the **Definitions** section.

Existing Regulatory Mechanisms, Management Plans, and Conservation Strategies

Both the CNHP and WYNDD track *Leptodactylon watsonii*, but no Element Occurrence Records (EORs) have been established for Colorado (Lyon personal communication 2004). In addition to the WYNDD data, requests for herbarium label data from the University of Colorado Museum and the Rocky Mountain Herbarium revealed 14 locations for this species in western Colorado and four in Wyoming, for a total of 18 occurrences in Region 2. Of these occurrences, only three are located on National Forest System lands; two are on the White River National Forest in Colorado, and one is on the Bighorn National Forest in Wyoming (**Figure 1**). The remaining 15 occurrences are mostly under the jurisdiction of other public land management agencies, including the BLM and the National Park Service (NPS).

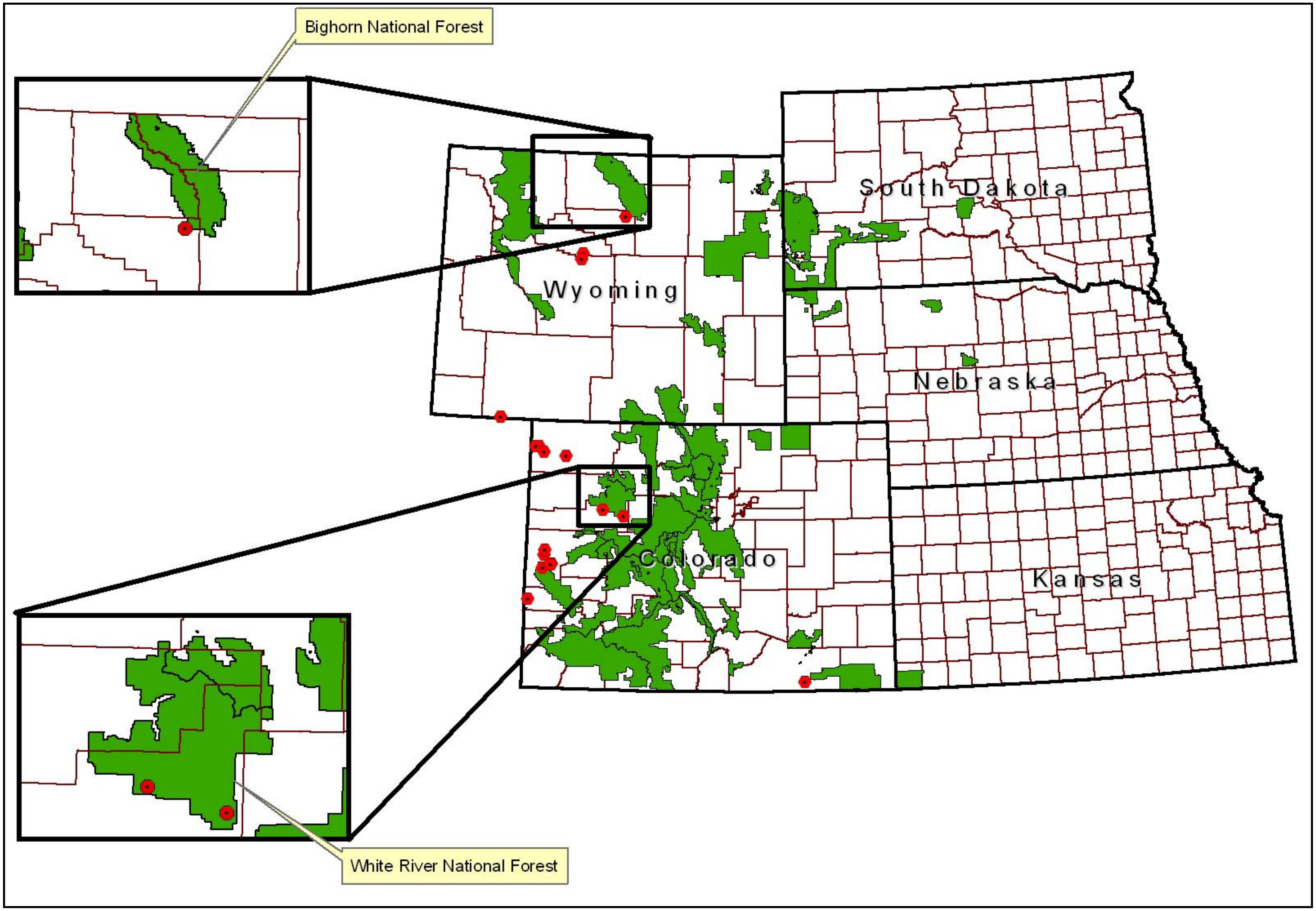

Figure 1. General location of *Leptodactylon watsonii* occurrences within USDA Forest Service Region 2.

Outside of the states of Region 2, there are more than 30 documented locations of this species across Utah. *Leptodactylon watsonii* has been reported from Arches National Park, Glen Canyon National Recreation Area, and Zion National Park in Utah. It is reported from the upper Snake River plains in Idaho (Bear Lake, Butte, and Bonneville counties, Idaho) and in the Toiyabe Mountains and Quinn Canyon Range in Nye County, Nevada (Cronquist et al. 1986).

In Colorado, three occurrences are reported from Dinosaur National Monument (NPS), two occurrences are located on Colorado National Monument (NPS), and six occurrences are located on public lands managed by the BLM (four occurrences by the Grand Junction Field Office, one by the Uncompahgre Field Office, and one by the Little Snake Field Office). One occurrence is located on private land. In Wyoming, one occurrence is located on the Wind River Indian Reservation, one is located in the Flaming Gorge National Recreation Area managed by the Ashley National Forest (Region 4), and one is located on public lands managed by the BLM Cody Field Office.

The Revised White River National Forest Land and Resource Management Plan (USFS 2002) and the Bighorn National Forest Land and Resource Management Plan (USFS 1985) provide direction for management of natural resources on National Forest System lands with occurrences of *Leptodactylon watsonii*. Although *L. watsonii* is not considered a sensitive species on the forests in which it occurs, the National Forest Management Act and its rules require the USFS to sustain habitats that support healthy populations of existing plant and animal species on the national forests and grasslands. However, since *L. watsonii* does not have sensitive species status, project-specific National Environmental Policy Act compliance is not required. During the 2003 revision of the Region 2 sensitive species list, staff stated that *L. watsonii* is "not a Region 2 Sensitive Species, but should be considered for other Emphasis Species lists" (USDA Forest Service 2004). One purpose of this assessment is to provide additional information to facilitate management decisions and to provide data that could be considered in re-evaluating the USFS status of this species.

National parks and monuments potentially provide some protection for the *Leptodactylon* occurrences at Colorado and Dinosaur national monuments although the monuments are generally not managed specifically for rare plant conservation. The General Management Plan, Development Concept Plans, and Land Protection Plan for Dinosaur National Monument provide direction for management of NPS lands within Dinosaur National Monument (U.S. National Park Service 1986). The Colorado National Monument Resources Management Plan provides direction for management of NPS lands within Colorado National Monument (U.S. National Park Service 1996). In addition, the NPS prohibits the collection of any native plants without permit (U.S. National Park Service 2002).

The Land Resource Management Plans for the Grand Junction Field Office, Little Snake River Field Office, Uncompahgre Field Office, and Cody Field Office provide direction for management on BLM public lands with occurrences of *Leptodactylon watsonii* (USDI Bureau of Land Management 1987, 1989a, 1989b, 1990). BLM Manual 6840 establishes Special Status Species policy for plant species and the habitat on which they depend, but the BLM does not list *L. watsonii* as a sensitive species in any of the states in which it occurs. No conservation strategies or management plans are in place for protection of this species on BLM public lands or NPS lands.

There are no other laws, regulations, management, or conservation plans specifically addressing the protection of *Leptodactylon watsonii*. However, existing laws and regulations appear to be adequate to protect the species, considering its inaccessible habitat and lack of apparent threats associated with this habitat.

Biology and Ecology

Classification and description

Systematics and morphology

Leptodactylon watsonii belongs to the Phlox family (Polemoniaceae), a relatively small family composed of 19 genera and approximately 349 species (Porter 1997, Grant 1998). The family is distributed primarily in the New World and is most diverse in western North America (Zomlefer 1994). The largest genera include *Gilia* (approximately 71 species), *Phlox* (approximately 63 species), and *Linanthus* (approximately 42 species).

The Polemoniaceae are readily identified by a three-carpellate ovary and apically trifid style, but they can have two to four carpels as seen in *Leptodactylon watsonii*. The corollas are united, and the inflorescence is typically determinate, most often cymose but can appear corymbose, capitate, or terminal. Occasionally the flowers can be solitary and axillary. Fruits generally consist of a three valve loculicidal capsule (Zomlefer 1994).

Some of our most showy cultivars are members of the Phlox family. The Polemoniaceae has been used as a model family to investigate everything from speciation to pollination. Several recent phylogenetic studies for this family have sought to resolve the placement of the Polemoniaceae in relation to other angiosperms (Johnson et al. 1996, Porter and Johnson 1998, Johnson et al. 1999, Prather et al. 2000).

Within the Polemoniaceae, genera have been assigned to five tribes whose circumscription has been in a state of flux. The controversy lies in the overlap of variation between genera and differences in approach (i.e., the evolutionary school versus the cladistic school) (Grant 1998, Prather et al. 2000). Several phylogenetic studies for tribal or generic relationships exist in the literature (Steele and Vilgalys 1994, Johnson et al. 1996, Porter 1997, Grant 1998, Porter 1998, Porter and Johnson 1998, Porter and Johnson 2000). Most of these studies are molecular in content and analyzed through cladistics, except for Grant (1998), who combined molecular and morphological data using an evolutionary approach.

All of the studies cited above placed *Leptodactylon* in a clade with *Linanthus*. Strict consensus trees in some of the studies also placed *Leptodactylon* with *Phlox* and *Microsteris* (Johnson et al. 1996, Porter 1997). The *Leptodactylon/Linanthus* group traditionally has been aligned with the Gilieae tribe, but flavonoid and pollen morphology show affinities with the Polemonieae tribe (Taylor and Levin 1975, Smith et al. 1977, Smith et al. 1982). Grant (1998) tackled the problem by creating another tribe, the Leptodactyloneae uniting *Leptodactylon* and *Linanthus*. Grant justified this circumscription based on the unique characters of palmately divided leaves and small chromosomes in a temperate group (Grant 1998). Other students of this tribe speculated that *Leptodactylon* and *Linanthus* are better combined into the genus *Linanthus*. This placement is supported by both molecular and morphological characters such as woody habit, palmately divided leaves, and white corollas (Patterson 1977, Patterson 2004 personal communication, Porter personal communication 2004). The principal difference between *Leptodactylon* and *Linanthus* is leaf insertion; *Linanthus* leaves are opposite, and most *Leptodactylon* species have alternate leaves. Past taxonomic keys split the two genera based upon whether or not the plant was woody only at the base (*Linanthus*) or woody throughout (*Leptodactylon*). A third character used to delineate the two groups is prickly leaves; *Leptodactylon* has prickly leaves, and *Linanthus* has soft leaves that are not especially prickly to the touch. *Leptodactylon watsonii* possesses opposite, prickly leaves and woody branches throughout. Additionally *L. watsonii* has stiff, prickly leaves. The latter two characters are the reason why *L. watsonii* has traditionally been placed in the genus *Leptodactylon*.

In 2000, Porter placed *Leptodactylon* into *Linanthus* and referred the combined entity to the Tribe Phlocideae (Porter and Johnson 2000). Based on the current literature and numerous phylogenetic studies accomplished for relationships within this family, the Flora of North America will follow this treatment, as will the second edition of the Jepson Manual of California Plants (Patterson 2004 personal communication). Thus, the accepted nomenclature for Watson's prickly phlox will likely change, and *Leptodactylon watsonii* will be reduced to a synonym of *Linanthus watsonii*. This nomenclatural change is already recognized in regional floras, such as the most recent edition of the Vascular Plants of Wyoming (Dorn 2001) and the upcoming Flora of the San Juan Basin (Heil personal communication 2006). According to the PLANTS National Database (USDA Natural Resources Conservation Service 2004), *Leptodactylon watsonii* is the current accepted name. Because this document is prepared for the USFS, convention dictates that this assessment use the PLANTS database name, *L. watsonii.* The name change will not change the conservation status of *L. watsonii*.

According to the PLANTS National Database, there are currently six species of *Leptodactylon* recognized in North America, *L. watsonii* (Gray) Rydb., *L. caespitosum* Nutt., *L. californicum* Hook. & Arn. (including five varieties), *L. glabrum* Patterson & Yoder-Williams, *L. jaegeri* (Munz) Wherry, and *L. pungens* (Torr.) Torr. Ex Nutt. (USDA Natural Resources Conservation Service 2004). **Table 1** summarizes the nomenclatural data for *L. watsonii*.

History of species

The earliest collection of *Leptodactylon watsonii* in North America was apparently made in the Bear River Canyon in Utah by Serano Watson in 1869 during the Kings survey of Utah and Nevada. Asa Gray originally described the Watson collection as *Gilia watsonii* in 1870. This species went through two

Table 1. Classification of *Leptodactylon watsonii*.

***Leptodactylon watsonii* (Gray) Rydberg**
Family: Polemoniaceae
Genus: *Leptodactylon*
Species: *Leptodactylon watsonii*
Citation: *Leptodactylon watsonii* (A. Gray) Rydb., Bulletin of the Torrey Botanical Club 33:3 1906. *Navarretia watsonii* (A. Gray) Kuntze, Revis. Gen. Pl. 1891. *Gilia watsonii* A. Gray, Proceedings of the American Academy of Arts and Sciences 8: 267. 1870.
Synonyms: *Navarretia watsonii* (A. Gray) Kuntze. *Gilia watsonii* A. Gray.
Vernacular Name: Watson's prickly phlox
Type: *Gilia watsonii* (Gray) Rydberg Proceedings of the American Academy of Arts and Sciences 8: 267. 1870. TYPE: USA. Utah. Cottonwood Canyon, Wasatch Mts.. 2591 m. Aug 1869. *Serano Watson* 908 (IT: US!, HT: GH!).

taxonomic changes from *Gilia* to *Navarretia* in 1891, and finally to *Leptodactylon* in 1906 (Wherry 1945, Cronquist et al. 1986, TROPICOS 2006).

In Region 2, the first documented herbarium specimen of *Leptodactylon watsonii* was collected by G. E. Osterhout in 1899 near Glenwood Springs, Colorado (*Osterhout #1814*). A series of collections in the early 1980's documented its distribution in western Colorado, and a 1985 collection by W.A. Weber and T. Hogan (*Weber #17525*) extended its range eastward into Las Animas County along the Front Range of Colorado. *Leptodactylon watsonii* was initially documented in Wyoming in July of 1950 by C. L. Porter (*Porter #5410*). Additional Wyoming occurrences were discovered during the early 1980's and 1990's.

Non-technical description

Leptodactylon watsonii is a loosely matted, perennial subshrub approximately 1 dm (3.9 inches) tall or less. The branchlets can have very small, coarse hairs or stipitate glands. The leaves are glabrous or glandular-hairy and nearly always opposite. The 6 to 20 mm (0.24 to 0.79 inches) long leaves are most often palmately cleft into three to nine linear-subulate divisions, where the central one is the largest, but can occasionally be entire. The flowers commonly have six calyx lobes, six corolla lobes, six stamens, and four carpels. The corollas are dull white or ochroleucous, 15 to 28 mm (0.59 to 1.10 inches) long, with the lobes 7 to 13 mm (0.28 to 0.51 inches) long. The fruit is a loculicidal capsule disarticulating into four valves at maturity. **Figure 2** is a line drawing of *L. watsonii* showing flowers, leaves, and habit. **Figure 3** is a photograph showing the opposite arrangement and palmate shape of the leaves.

Leptodactylon watsonii could be confused with *L. caespitosum*, but the two can be distinguished by *L. watsonii*'s widely spreading, loose clumped habit compared to *L. caespitosum*'s more or less crowded and tightly clumped habit, forming cushion-like mats. Additionally, the flowers of *L. caespitosum* are typically four-parted whereas *L. watsonii* is characterized by six-parted flowers (Cronquist et al. 1986).

Distribution and abundance

The historic and current global distributions of *Leptodactylon watsonii* are in the Rocky Mountain Province as defined by Takhtajan (1986). Distribution of this species is limited to the central and southern Rocky Mountain region including Colorado, Wyoming, Utah, Nevada, and Idaho. (University of Colorado 1995, University of Colorado Museum 2004, USDA Natural Resources Conservation Service 2004, Idaho National Engineering and Environmental Laboratory 2006). The digital atlas of the vascular plants of Utah (Albee et al. 1988) reports 31 occurrences of *L. watsonii* in 15 Utah counties. It is reported from the upper Snake River plains in Idaho (Bear Lake, Butte, and Bonneville counties, Idaho) and in the Toiyabe Mountains and Quinn Canyon Range in Nye County, Nevada (Cronquist et al. 1986).

There are more than 30 documented locations of this species from Utah (**Figure 4**). In Idaho, *Leptodactylon watsonii* occurs in rocky areas located in the upper Snake River Plain, in north central Butte County, and in the southwestern part of the state. No distribution data were available for this species in Nevada.

In Region 2, *Leptodactylon watsonii* is known only from Colorado and Wyoming, where it exhibits a discontinuous distribution and occupies rocky habitats in foothills and canyons. The results of herbarium research yielded 14 locations of this species in Colorado

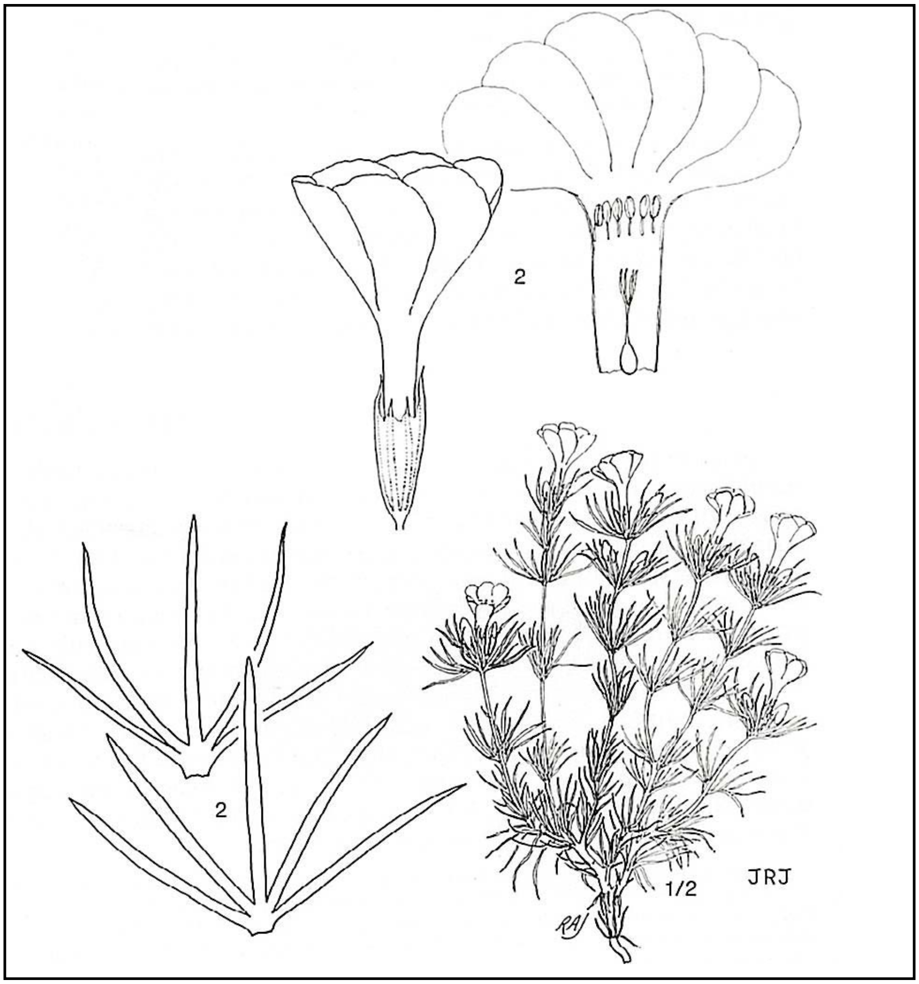

Figure 2. Line drawing of *Leptodactylon watsonii* showing growth habit, leaves, and flowers. The number next to each picture is a relative indication of scale. Drawing by Robin Jess. Used with permission of the artist and the New York Botanic Garden (Cronquist et al. 1986).

Figure 3. Photograph of *Leptodactylon watsonii* leaves showing palmate divisions and opposite arrangement. Photograph by Lynn Moore (September 2004).

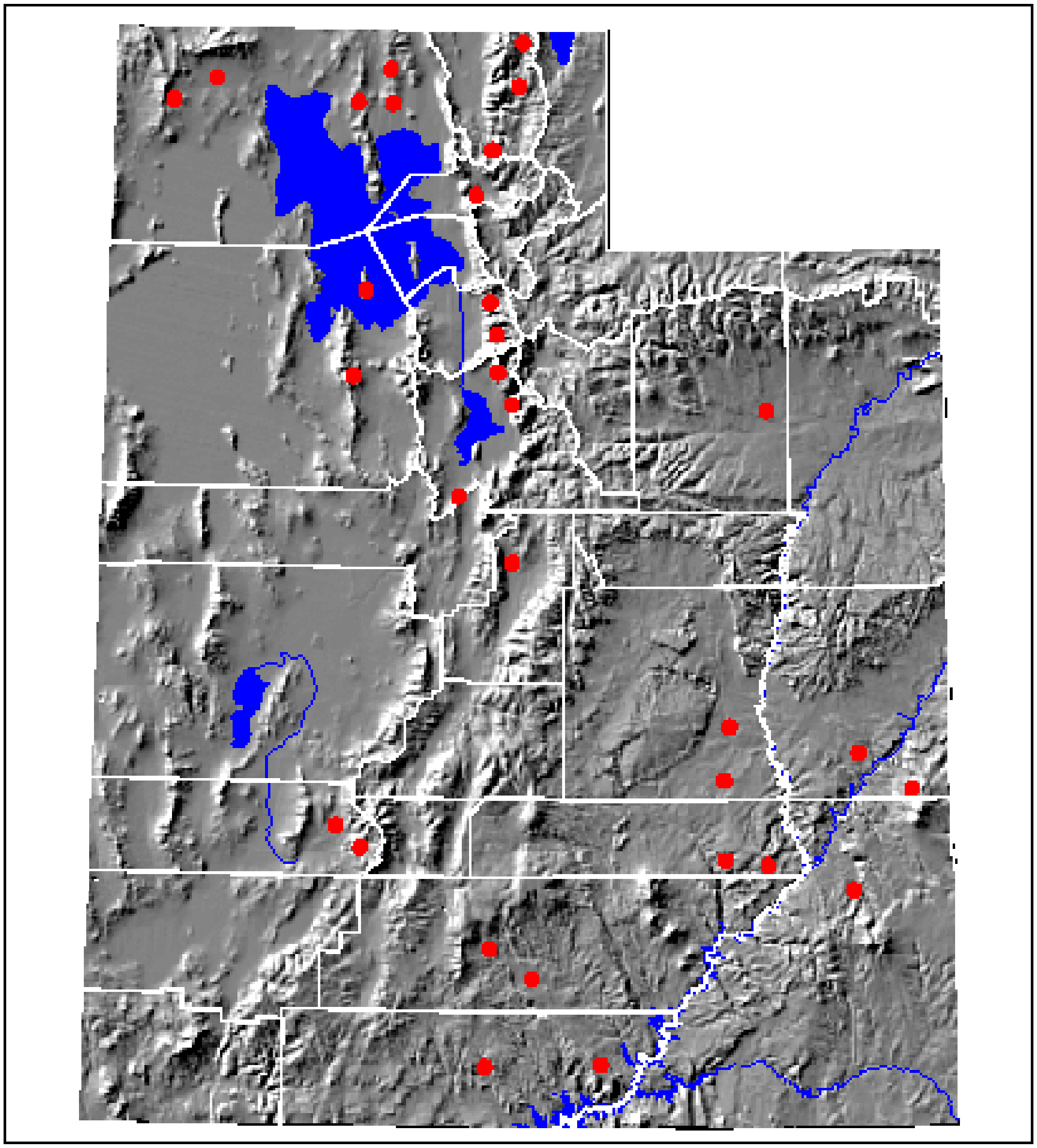

Figure 4. General location of *Leptodactylon watsonii* occurrences in Utah (Shultz et al. 2006). Used with permission.

and four in Wyoming, for a total of 18 occurrences in Region 2. *Leptodactylon watsonii* has been documented in Moffat, Garfield, Mesa, Montrose, and Las Animas counties, Colorado. In Moffat County, *L. watsonii* is apparently prolific in Dinosaur National Monument, which is managed by the NPS, and annual tracking has ceased due to the abundance of the taxon in the monument (Naumann personal communication 2006). There are unconfirmed reports of *L. watsonii* from the Piceance Basin area in Rio Blanco County, Colorado (Lyon personal communication 2004).There are two additional historical specimens from the vicinity of Glenwood Springs, Colorado collected by George E. Osterhout in 1899, but specific location or habitat data are not available, so these two records are not included in this assessment. In Wyoming, *L. watsonii* has been documented in Fremont, Hot Springs, Sweetwater, and Washakie counties. Of the 18 Region 2 occurrences, three are located on National Forest System lands, two on the White River National Forest in Colorado and one on the Bighorn National Forest in Wyoming.

Abundance information for *Leptodactylon watsonii* in Region 2 is essentially nonexistent. One WYNDD EOR noted four small plants in two groups. Occurrence *Moore #5567* in Colorado noted five plants within a 10 x 1 m (33 x 3 ft.) area. Experts who work on this group were contacted but were unable to recall patterns of plant density (Patterson personal communication 2004). An accurate estimate of abundance rangewide or in Region 2 is not possible given the available data. Distribution and abundance data are summarized in **Table 2**.

Population trend

No population trend studies have been completed for *Leptodactylon watsonii* in Region 2 or elsewhere. Because abundance data for this species are limited or nonexistent, it is impossible to make a rudimentary inference of population trend. It is that *L. watsonii* usually occurs in a clumped pattern, sometimes forming extensive mats. During surveys in the 1980s, thousands of plants were found in Dinosaur National Monument where suitable habitat is common (Naumann 2006 personal communication). No estimates of abundant have been made since at that time.

Habitat

Leptodactylon watsonii is a plant of the foothills, canyons, and mountains of the Rocky Mountain West. It is a loosely clumped, perennial subshrub species characteristically occurring on ledges, rock crevices, or cliffs, often on calcareous soils. It occurs in vegetation zones ranging from sagebrush to spruce-fir at elevations ranging from 1,402 to 2,682 m (4,600 to 8,799 ft.). **Table 2** presents the habitat data of known occurrences collected from EORs and herbarium label data; this includes vegetation, elevation, substrate, and aspect, if available. **Figure 5** is a photograph showing the habitat of *L. watsonii*. Geology information for Colorado occurrences was obtained from a digital geologic map of Colorado (Green 1992).

In Wyoming, *Leptodactylon watsonii* is a member of the Central Basin and Hills and Bighorn Mountains sections within the Intermountain Semi-Desert Province. It also occurs in the Uinta Mountains section of the Southern Rocky Mountain Steppe-Open Woodland-Coniferous Forest-Alpine Meadow Province (McNab and Avers 1994). In Colorado, *L. watsonii* is associated with the South Central Highlands, North Central Highlands, and Uinta Mountains sections located with in the Southern Rocky Mountain Steppe-Open Woodland-Coniferous Forest-Alpine Meadow Province. It also occurs in the North Canyon Lands Section of the Intermountain Semi-Desert and Desert Province and the Arkansas Tablelands Section of the Great Plains-Palouse Dry Steppe Province (McNab and Avers 1994).

There is very little information characterizing the associated plant community at any *Leptodactylon watsonii* location. However, some herbarium labels from Region 4 do mention associated vegetation. In Utah, the species has been documented as occurring in a *Pinus ponderosa/Arctostaphylos* sp. (ponderosa pine/manzanita) community (Washington County, Utah, *K. Thorne #6333*), in a *Pinus edulis-Juniperus* sp./*Coleogyne ramosissima* (piñon-juniper/blackbrush) community (Grand County, Utah, *B. Franklin #3091*), and in a *Fraxinus* sp./*Coleogyne ramosissima*/*Rhus trilobata* (singleleaf ash/blackbrush/fragrant sumac) community (Garfield County, Utah, *Welsh #21972*). Nearly all habitat descriptions for this species indicate a preference for rocky ledges, cliffs, or crevices. Some Utah herbarium labels indicate surrounding habitat consisting of wet meadows and hummocks (Box Elder County, Utah, *K. Thorne #2542*, Cache County, Utah, *Higgins #14839*), but they specifically describe the plants as occurring on rocky cliffs, ledges, or in crevices. Riparian areas often occur in the bottom of the canyons where *L. watsonii* individuals are located, but this species is consistently located on the cliffs and ledges above the riparian areas. It appears that while surrounding communities can vary greatly, specific microsites (i.e., cliff ledges, cracks, crevices) occupied by *L. watsonii* are consistent.

In Region 2, *Leptodactylon watsonii* is consistently documented to occur in rocky habitats similar to that shown in **Figure 5**. Very few vegetation data from Region 2 occurrences appear on herbarium labels or in WYNDD EORs. In Wyoming, EOR WY 004 notes vegetation cover of less than 1 percent on a south-facing, sheer cliff face located above *Cercocarpus ledifolius* (curl-leaf mountain mahogany) dominated slopes. One occurrence (EOR WY 001) is noted as occupying dry, cliff slopes and rocky crevices within a piñon-juniper woodland. The remaining two Wyoming occurrence records have no associated vegetation data.

In Colorado, vegetation information is limited to herbarium label data since the CNHP does not currently track the species. Only two of the available herbarium specimens indicate associated vegetation. One location, *Hartman #25835*, notes a *Quercus gambellii/Juniperus* sp. (oak-juniper) scrub community and a *Picea* sp./*Pseudotsuga menziesii* (spruce-Douglas fir) community on the bottom and lower slopes of a canyon. The other Colorado collection with vegetation information (*Moore #5567*) records a riparian area dominated by *Acer negundo* (box elder), *Fraxinus anomala* (ash), *Pinus edulis-Juniperus* sp., and *Pinus ponderosa*. Associated

Table 2. Summary of abundance and habitat data for *Leptodactylon watsonii* taken from Wyoming Natural Diversity Database Element Occurrence Records (EORs), herbarium label data, and USGS 7.5 minute topographic maps.

EOR and Collection Number	Dates collected	County	Number of occurrences	Number of plants (Area covered)	Land ownership/ management	Elevation in meters (feet)/ Aspect	Substrate	Habitat characteristics and association	Herbarium location
Wyoming locations									
WY 001 *Porter #5410* *Evert #6474*	10-Jul-50 14-Jun-84	Hot Springs	1	Not recorded	Bureau of Land Management (BLM) Cody Field Office	1402 (4600)/ West	Madison Limestone	Open juniper woodland; dry cliff slopes and rock crevices	Rocky Mountain Herbarium
WY 002 *Fertig #13850* *Dorn #3458*	12-Jun-93 23-Jun-80	Fremont	1	Not recorded	Boysen State Park; Wind River Indian Reservation	1493 (4898)/ Not recorded	Madison Limestone	Vertical, gray limestone cliff face below summit ridge in cracks and crevices	Rocky Mountain Herbarium
WY 003 *Dorn #4827*	28-Aug-87	Sweetwater	1	Not recorded	USDA Forest Service (USFS) Region 4 Ashley National Forest Flaming Gorge National Recreation Area	1859 (6099)/ North	Wasatch Formation	Sandstone ledges	Rocky Mountain Herbarium
WY 004 *Fertig #17744*	23-Jul-97	Washakie	2	8	USFS Region 2 Bighorn National Forest Powder Ranger District	1706 to 1767 (5597 to 5797)/ South	Madison Limestone and Darby Formation	Sheer cliffs above *Cercocarpus ledifolius* slopes; vegetative cover <1 percent	Rocky Mountain Herbarium
Colorado locations									
R.L. Hartman #25835	24-Jun-90	Garfield	5	Not recorded	USFS Region 2 White River National Forest Rifle Ranger District	1706 to 1950 (5597 to 6398)/ Not recorded	Leadville Limestone	Oak-juniper scrub community below; spruce, spruce-Douglas-fir communities in canyon bottoms and sides above	Rocky Mountain Herbarium
Osterhout #1814 *Vanderhorst #2697*	18-Jun-1899 19-Jun-91	Garfield	1	Not recorded	USFS Region 2 White River National Forest Rifle Ranger District	1889 to 2255 (6198 to 7398)/ Not recorded	Leadville Limestone	On vertical cliffs	Rocky Mountain Herbarium

Table 2 (cont.).

EOR and Collection Number	Dates collected	County	Number of occurrences	Number of plants (Area covered)	Land ownership/ management	Elevation in meters (feet)/ Aspect	Substrate	Habitat characteristics and association	Herbarium location
Siplivinsky #4119	10-Jul-82	Mesa	1	Not recorded	National Park Service (NPS) Colorado National Monument	2011 (6598)/ Not recorded	Kayenta, Wingate Sandstone and Chinle Formations	Precambrian granite ledges in lower part of the canyon	University of Colorado Museum
Siplivinsky #4293	21-Jul-82	Mesa	1	Not recorded	NPS Colorado National Monument	1706 (5597)/ Not recorded	Biotitic gneiss, schist, and migmatite- -derived principally from sedimentary rocks	On cliffs of Precambrian granite	University of Colorado Museum
Siplivinsky #1549, #1540	11-Jul-81	Mesa	1	Not recorded	BLM Grand Junction Field Office	1981 (6499)/ Not recorded	Wingate sandstone and chinle formation	On massive outcrop of Precambrian granite	University of Colorado Museum
Siplivinsky #4182, #4176	17-18-Jul-82	Mesa	1	Not recorded	BLM Grand Junction Field Office	2145 (7037)/ Not recorded	Wingate sandstone and chinle formation	Crevices of pre-cambrian granite cliffs along canyon side	University of Colorado Museum
D.H. Wilken #13870	15-Jul-82	Moffat	1	Not recorded	BLM Little Snake River Field Office	1830 (6004)/ Not recorded	Madison limestone and lodore formation	Hanging from crevices in rock outcrops and cliffs	University of Colorado Museum
W.A. Weber #15925	11-May-81	Mesa	1	Not recorded	BLM Grand Junction Field Office	1950 (6398)/	Granitic rocks of 1,400-M.Y. age group	On massive outcrops of Precambrian granite; forming a solid dense mat 1m (3 ft.) in diameter in a vertical crevice	University of Colorado Museum
W.A. Weber #17525	23-Aug-85	Las Animas	1	Not recorded	Private	2170 (7119)/ North	Granitic rocks of 1,400-M.Y. age group	Scrub covering talus at the base of granite cliff	University of Colorado Museum
H. Beck #3685	06-Jun-82	Mesa	1	Not recorded	BLM Grand Junction Field Office	1935 (6348)/ North	Madison limestone formation	In cracks of rocks	University of Colorado Museum

Table 2 (concluded).

EOR and Collection Number	Dates collected	County	Number of occurrences	Number of plants (Area covered)	Land ownership/ management	Elevation in meters (feet)/ Aspect	Substrate	Habitat characteristics and association	Herbarium location
B.E. Neely #4435	27-Jun-87	Moffat	1	Not recorded	NPS Dinosaur National Monument	2407 (7897)/ South	Lodore Formation (cambrian)--sandstone, shale, and conglomerate	In shady cracks of limestone outcrops	University of Colorado Museum
B.E. Neely #4395	15-Jun-87	Moffat	1	Not recorded	NPS Dinosaur National Monument	2682 (8799)/ Not recorded	Lodore formation (cambrian)--sandstone, shale, and conglomerate	On rock ledges	University of Colorado Museum
B. Clarfield #s.n.	03-Jun-86	Moffat	1	Not recorded	NPS Dinosaur National Monument	2103 (6900)/ Not recorded	Ogallala formation	Around rocks at the very edge of the promontory, plants erect	University of Colorado Museum
L. Moore #5567	17-Jun-95	Montrose	1	5 (10 m^2)	BLM Uncompahgre Field Office	1706 (5597)/ North	Morrison formation, summerville formation (shale and siltstone), and entrada sandstone	Cracks of rock ledges above riparian zone along creek	Rocky Mountain Herbarium, University of Colorado Museum

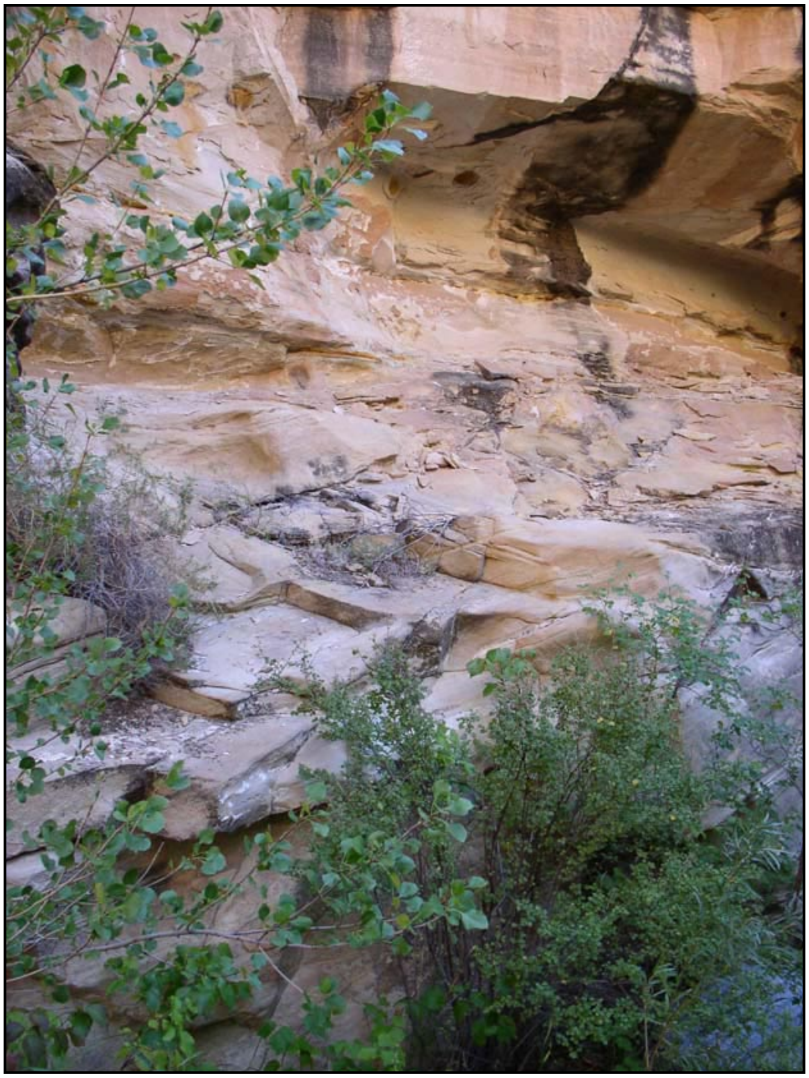

Figure 5. Photograph of habitat for *Leptodactylon watsonii* where *Moore #5567* was collected (**Table 2**). Photograph by Lynn Moore.

herbaceous species noted to occur with *Leptodactylon watsonii* appear in **Table 3**.

According to the available WYNDD EOR and herbarium label data, elevations in Region 2 range from 1,402 to 2,682 m (4,600 to 8,799 ft.) (**Table 2**, **Figure 6**). The majority of occurrences within Region 2 are located between 1,500 and 2,000 m (4,921 to 6,562 ft.) (**Figure 6**). In Region 2, slope aspect is variable and includes north, south, and west (**Table 2**).

Documented habitat descriptions consistently note that this species occurs on substrates derived from calcareous parent materials. In Wyoming, *Leptodactylon watsonii* occurs primarily on Madison Limestone, but it also occurs on exposures of the Wasatch and Darby formations. In Colorado, five occurrences were observed on limestone or dolomite (including Madison, Leadville, Williams Canyon, and Manitou formations). Several rare plants in Region 2 are restricted to limestone, but most are alpine species, including *Astragalus molybdenus* (Leadville milkvetch) Barneby, *Saussurea weberi* (Weber's saw-wort) Hultén, and *Braya glabella* (smooth northern-rockcress) Richardson.

Six occurrences of *Leptodactylon watsonii* were reported to occur in sandstones of Jurassic and Triassic age and two on Precambrian granite. One location in Logan Canyon, Utah reported limestone but did not indicate the specific formation. Calcium carbonate (the principal component of limestone) is often present

Table 3. Plant species noted to occur with *Leptodactylon watsonii*. List generated from herbarium label and Wyoming Natural Diversity Database Element Occurrence Records.

Scientific Name	Vernacular Name
Artemisia ludoviciana Nutt.	white sagebrush
Astragalus spp.	milkvetch
Chrysothamnus greenei (Gray) Greene	Greene's rabbitbrush
Clematis ligusticifolia Nutt.	western white clematis
Cryptantha celosioides (Eastw.) Payson	buttecandle
Cymopterus spp.	springparsley
Erigeron allocotus Blake	Big Horn fleabane
Fendlerella utahensis (S. Wats.) Heller	Utah fendlerbush
Haplopappus acaulis (Nutt.) Gray	stemless mock goldenweed
Holodiscus discolor (Pursh) Maxim.	oceanspray
Koeleria macrantha (Ledeb.) J.A. Schultes	prairie Junegrass
Lesquerella spp.	bladderpod
Paronychia spp.	nailwort
Petrophyton caespitosum (Nutt.) Rydb.	mat rockspirea
Polemonium brandegeei (Gray) Greene.	Brandegee's Jacob's-ladder
Rhus trilobata Nutt.	skunkbush
Toxicodendron rydbergii (Small ex Rydb.) Greene	western poison ivy

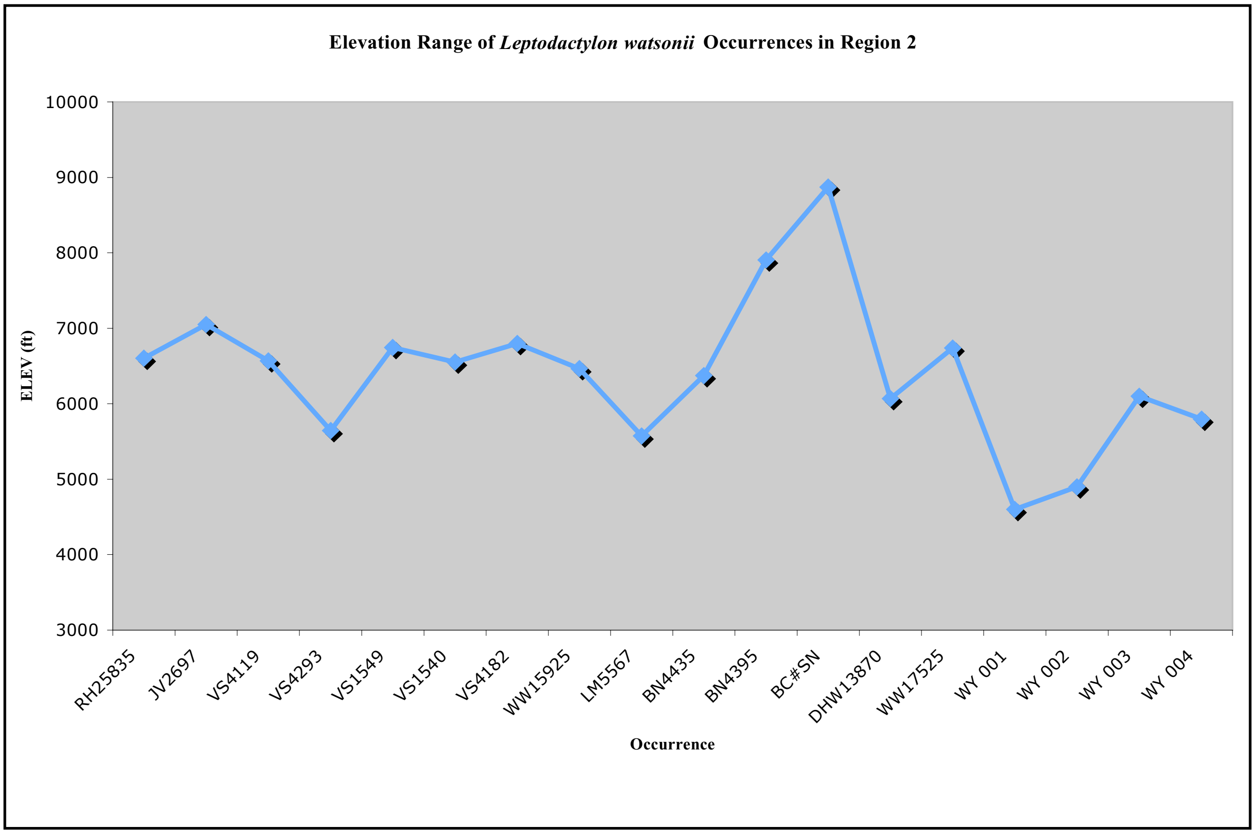

Figure 6. Elevation profile of *Leptodactylon watsonii* occurrences in USDA Forest Service Region 2. Data taken from herbarium specimens deposited at Rocky Mountain Herbarium, Laramie, WY.

as the cement in sandstones and other clastic rocks; therefore, it is possible that calcareous conditions may exist but are undetectable in the field.

Due to the lack of vegetation data, no inferences can be made concerning a characteristic community for this species. Information sources indicate that *Leptodactylon watsonii* can occur in a variety of vegetation zones. The key for locating habitat, then, is the presence of dry, rocky microhabitats. Nearly all available information describes the plants as located on some type of rock formation. Most are on cliffs, ledges, or canyon walls, generally with a steep slope. Other occurrences are located in bedrock crevices on canyon rims. Due to the steep topography and cliff-like landscape, shade is typically provided for at least part of the day and on some aspects for most of the day; one occurrence (*Neely #4395*) notes that the plants are located in the shady cracks of limestone outcrops. Occurrence *Moore #5567* records a north-facing ledge that is additionally protected by the shrubs and trees growing along an adjacent riparian area.

Salisbury (1920) pointed out that calcareous soils are often dry and porous. *Leptodactylon watsonii* shows a preference for rocky habitats including ledges, cliffs, and crevices. Soils that develop in rocky habitats are generally shallow and well drained.

Reproductive biology and autecology

Autecology

An extensive literature search resulted in no empirical data describing the ecological strategies that characterize *Leptodactylon watsonii*. Grime (1979) developed a conceptual model for classifying plant strategies based) on their basic response to stress. He termed the possible responses competitor, stress tolerant, and ruderal. Life history patterns have also been described as *r*- and *K*-selected, where the r-selected species typically allocate more resources to reproduction, and the *K*-selected species allocate more resources to survival (MacArthur and Wilson 1967). This system should be viewed as a continuum between the two resource allocation strategies.

The Grime (1979) and MacArthur and Wilson (1967) systems are functional for determining where in the broader picture of ecological strategy an individual species can be placed. Species can take on any combination of characteristics of ruderal, competitor, and stress tolerant responses. There are not enough data to classify *Leptodactylon watsonii* definitively. Because the species occupies a dry, resource-limited environment, this taxon is more likely to be stress tolerant than either a competitor or a ruderal, allocating its resources to survival rather than reproduction (K-selected). It may be that *L. watsonii* could survive in less severe habitats, but it is probably not a good competitor in mesic or resource-rich sites.

Reproduction

It is not known whether this species flowers consistently year after year, how long fruits remain on the plant, or how many seeds are produced each year. *Leptodactylon watsonii* is a loosely matted, perennial subshrub that reproduces sexually by seed. The inflorescence is typically a loose cymose cluster of dull white or ochroleucous salverform flowers with tubes approximately 15 to 28 mm (0.59 to 1.10 inches) long (Cronquist et al. 1986). Flowers are open at night (Porter personal communication 2004), and the peak blooming season extends between May and August. Undispersed fruits are present through August and occasionally September.

No formal investigations have been developed to identify the pollination mechanisms for this species. Effective pollination depends on timing of anthesis, reproductive maturity of the individual flowers, plant density, and fluctuations in pollinator activity (annually and seasonally). Entomophily, pollination or dispersal by insects, is common in the Polemoniaceae (Grant and Grant 1965). The flowers of *Leptodactylon watsonii* are presented in a loose cluster and are characterized by large, showy corollas, indicating that this species is most likely insect pollinated. A variety of insects are known to pollinate the Polemoniaceae, but specific pollinators of *L. watsonii* are not known. The flowers of this species have long corolla tubes with the nectaries located at the base of the pistil attached to the bottom of the corolla tube. The anthers are attached to the tube wall above the level of the stigma (**Figure 2**). In order to effect pollination, the pollinator would need to have a long enough tongue or proboscis to reach the nectaries and transfer pollen from the pollen donor to the stigmatic surface. It is possible that smaller insects may crawl in and effect pollination, but this observation has not been recorded for *L. watsonii* or any other species of *Leptodactylon* or *Linanthus*. Grant and Grant (1965) studied pollination in the Polemoniaceae, including one species in the genus *Leptodactylon*, *L. californicum*. This species has similar floral characteristics to *L. watsonii*, including length of the corolla tube and the position of the anthers in relation to the stigma. The two species differ in that *L. watsonii* blooms at night, and *L. californicum* blooms during the day.

Grant and Grant (1965) discovered that the most effective pollinators of *L. californicum* were butterflies, day-flying hawkmoths, and cyrtid flies. Because *L. watsonii* is a night-blooming species, it is possible that night-flying hawkmoths and/or other nocturnal insects with a long tongue or proboscis pollinate it (Grant and Grant 1965). Another significant difference between the two species is habitat preference and geographic location; *L. californicum* is a plant of the chaparral zone and sandy coastal plains of south-central California whereas *L. watsonii* is a plant of the Rocky Mountain foothills and Colorado Plateau. Any inference concerning specific pollinators for *L. watsonii* based upon pollinators of *L. californicum* has not been observed.

Leptodactylon watsonii has some characteristics that indicate that bats may pollinate this species; it is a night-blooming species of cliff habitats with dull colored, accessible inflorescences (Muchhala 2003). However, bat pollination is exceptional in the Polemoniaceae, occurring only in the genus *Cobaea* (Grant and Grant 1965). Flower morphology plays an important role in bat pollination; bat-pollinated flowers are typically wider, with copious amounts of nectar, and often with numerous protruding stamens (Gibson 2001). The salverform flowers of *L. watsonii* do not demonstrate this morphology; although bat pollination may occur, it is most likely not the primary pollination mechanism.

Grant and Grant (1965) observed pollination in *Linanthus dichotomus*, a white flowered night-blooming species of the southwestern deserts. This species opens it flowers at dusk, revealing a shiny, white inner surface and producing a strong fragrance. By sunrise the next day, the flowers are closed and odorless. The flowers of *L. dichotomus* appear to be rarely visited by insects, but at dusk a hawkmoth was observed with pollen adhering to its proboscis as it flew rapidly from plant to plant (Grant and Grant 1965).

Wind pollination has been shown to occur in *Linanthus parviflorus*. A study by Goodwillie (1999) suggests that wind pollination provides some reproductive assurance in an obligate outcrosser. Wind pollination is hypothesized to represent an alternative to selfing as an evolutionary solution to the problem of temporal or spatial variation in pollination visitation (Goodwillie 1999). There are no specific studies of *Leptodactylon watsonii* pollination mechanisms. Based upon the above-cited studies, it is likely that *L. watsonii* is pollinated by nocturnal moths and may occasionally be visited by other insects and rarely bats.

No information is available about the physiology of germination or establishment of seedlings for *Leptodactylon watsonii*. No experimental data exist concerning the fertility or viability of seeds. According to Grime (1979), a persistent seed bank is one in which at least some of the seeds are at least one year old. No seedlings or recruitment have been documented.

No investigations into seed dispersal have been undertaken for *Leptodactylon watsonii*. There are no observations describing seed predation. How long the seeds are viable is not known. Seed dispersal may occur through wind or water runoff after heavy rains or snow melt. It is unlikely that animal interactions affect dispersal because the capsules are devoid of any mechanism for grasping onto hair. Small mammals or birds may play a part in *L. watsonii* seed dispersal, but there have been no field observations to support this.

Members of the Polemoniaceae exhibit both autogamy (self-compatibility) and obligate xenogamy (self-incompatibility) as well as mixed breeding systems. Plitmann and Levin (1990) characterized the breeding systems of more than 163 taxa in the Polemoniaceae, including *Leptodactylon watsonii*. They looked at pollen to ovule ratios and percentages of stigmatic pollen germination. Based on their findings, *L. watsonii* is probably facultatively xenogamous (i.e., basically self-incompatible but capable of occasional self-fertilization). If *L. watsonii* were occasionally self-fertilizing, then a mechanism to overcome a lack of pollinators would exist, giving this species a reproductive advantage in the short term, when pollination vectors are absent. Over the long term, selfing may promote homozygosity and possibly reduce fitness and the species' ability to adapt to changing environmental conditions (inbreeding depression) (Menges 1991, Weller 1994). If *L. watsonii* is primarily an outcrosser, it would have a long-term reproductive advantage by maintaining higher heterozygosity. In the short term, any loss of pollination vectors could theoretically reduce seed set (Weller 1994).

The chromosome number of *Leptodactylon watsonii* is unknown. There is speculation that hybridization may have occurred between *L. watsonii* and *L. pungens*. *Leptodactylon pungens* is a common species in Region 2, and it can occur in similar habitats as *L. watsonii*. *Leptodactylon pungens* ssp. *hazeliae* is a Snake River Canyon endemic (Idaho and Oregon) that may represent the offspring of a cross between *L. watsonii* and *L. pungens* (Meinke 1988). *Leptodactylon pungens* ssp. *hazeliae* has five-parted flowers and at least some alternate leaves, as does *L. pungens*. *Leptodactylon pungens* ssp. *hazeliae* also possesses the sprawling habit, flowering stems, and few-flowered inflorescences of *L. watsonii*.

Leptodactylon glabrum is a species endemic to northwestern Nevada and southwestern Idaho that shares opposite leaves with *L. watsonii*. Meinke (1988) indicates that several of the characters that separate *L. pungens* ssp. *hazeliae* and *L. glabrum* are the same characters that separate *L. watsonii* from *L. pungens*. Additionally, he points out the narrow geographic distribution of the two endemics and suggests that these two taxa could be the vestiges of a past hybridization event between *L. pungens* and *L. watsonii* where their ranges once overlapped. It is not likely that another hybrid event between the two species would affect the viability of *L. watsonii*. More information should be compiled before any inferences can be made about the outcome of such an event. Necessary data may include collection of genetic information, careful comparisons of morphology between the species, and specific location information from occurrences within close proximity to each other. The relationship between rarity and genetic variation is a subject of increasing interest, and the past notion that rare species have a low level of genetic variation has been questioned (Linhart and Premoli 1993, Gitzendanner and Soltis 2000). There is no doubt that low genetic diversity does affect some rare plants' ability to reproduce and survive (Fenster and Dudash 1994, Weller 1994). Genetic factors such as inbreeding depression and outbreeding depression need to be considered in analyzing the genetic fitness of a species. *Leptodactylon watsonii* is an outcrossing species, which may increase the risk of outbreeding depression; however, the isolation of occurrences from one another means the possibility of gene exchange is remote. There is some speculation that *L. watsonii* may undergo natural hybridization. Given the lack of evidence and understanding, however, we can make no inferences regarding genetic issues associated with *L. watsonii*.

Phenotypic plasticity is defined as marked variation in the individual as a result of environmental influences on the genotype during development (Lincoln et al. 1982). There is no empirical evidence to suggest the presence of ecotypes in *Leptodactylon watsonii*. A study involving transplant experiments would address the question of phenotypic plasticity in *L. watsonii*.

Current literature indicates that relationships commonly exist between most higher plants and mycorrhizal fungi (Barbour et al. 1987). These relationships are poorly known; this is a growing area of scientific study. It is not surprising then, that there are no documented or observed mycorrhizal associations for *Leptodactylon watsonii*. Mycorrhizae have been documented to occur in alpine fellfield cushion plant communities in Wyoming and Montana, including some growing on Madison Limestone (Lesica and Antibus 1986). It is likely that vesicular-arbuscular mycorrhizal root infection occurs in *L. watsonii* populations. Conversely, there is literature indicating a detrimental effect of mycorrhizae on rare plants. Hartnett and Wilson (1999) conducted a study in which they reduced mycorrhizae with fungicides. The results included a consistent increase in the cover of the rarer forb species in fungicide-treated plots relative to controls. This study was done in a tall grass prairie community where bio-available soil nitrogen is more readily available through decomposition of organic matter. *Leptodactylon watsonii* occurs in rocky, often cliff forming habitats where soil development is poor and nutrient resources are limited. Regardless of the lack of information concerning any specific mycorrhizal association that *L. watsonii* may have, this species may ultimately benefit from the mycorrhizal relationships that other members of the habitat may contribute to the substrate (Bethlenfalvay and Dakessian 1984, Booth 1985, Wright and Upadhyaya 1998, Lutgen et al. 2003).

Demography

Because the life history of *Leptodactylon watsonii* has not been investigated, no information concerning its vital rates, recruitment, survival, or lifespan is available. No demographic studies have been completed to determine the generation time, net reproductive rate, or age distribution of *L. watsonii* populations. Estimates of the proportion of populations reproducing are not available. *Leptodactylon watsonii* is a mat-forming, perennial subshrub, suggesting that this species is at least a short-lived perennial and is probably a long-lived species. Observations by field botanists note that occurrences were flowering and fruiting, indicating the observed plants were reproducing (Wyoming Natural Diversity Database 2004). However, no observations were recorded concerning the presence of seedlings, and it is not possible to know whether effective reproduction was actually occurring.

A demographic projection matrix provides valuable information about a species' vital rates, and is determined by tracking the fate of individuals over time. There are no established demographic monitoring sites for *Leptodactylon watsonii*. No data exist for constructing a population projection matrix or a generalized life cycle diagram as per Caswell (2001). Nevertheless, a simple life cycle diagram is presented in **Figure 7**. Question marks reflect the lack of data regarding the mechanisms connecting stages. If there is a juvenile stage, it is unknown whether juveniles must attain a certain size or stage before becoming reproductive, nor is it known whether reproductive adults periodically revert to a vegetative state. Seed bank dynamics (e.g., recruitment rates, seed longevity, abundance) are unknown but are represented in the diagram by a question mark between seed bank and seed. No information is available on germination rate or seedling survival, depicted in the diagram by a question mark between seed and seedling. *Leptodactylon watsonii* is a sprawling, perennial subshrub and does not produce rhizomes. Therefore, vegetative reproduction is unlikely to occur.

A population viability analysis is a rigorous quantitative analysis using demographic data to predict the future status of a given species. No population viability analysis has been accomplished for *Leptodactylon watsonii*, nor has the Minimum Viable Population (MVP) size been determined. MVP (the minimum population necessary to have an acceptably low extinction probability) can provide useful information for management purposes. It has been suggested that demography is of more immediate importance than genetics in determining the MVP of a plant population (Landes 1988, Menges 1991).

Community ecology

Leptodactylon watsonii is generally located in isolated areas. The steep, cliffs and rocky environment that it inhabits may provide a degree of isolation from interactions with invasives as well as native species. No invasive species have been reported within the known occurrences of *L. watsonii*. It is unknown whether

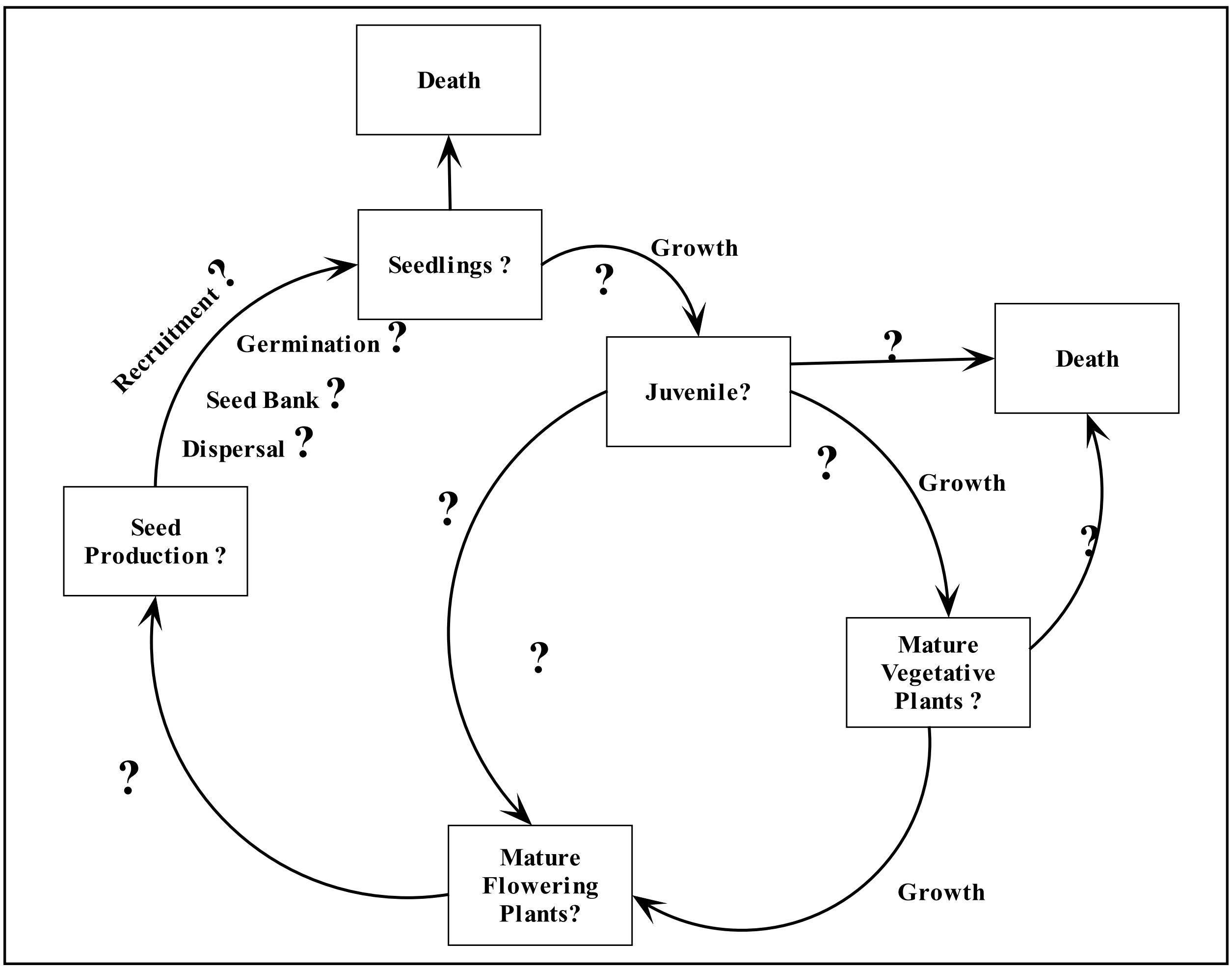

Figure 7. Generalized life cycle diagram of *Leptodactylon watsonii*. Question marks indicate uncertainty during a particular stage.

interactions with native or invasive species have any effect on its distribution or abundance. There have been no recorded observations of interactions between *L. watsonii* and herbivores.

In the absence of anthropogenic-related activities, habitats of *Leptodactylon watsonii* are relatively stable areas. Observations of habitat preferences and the autecology of *L. watsonii* lead us to conclude that this species is stress-tolerant and, as such, would likely not successfully establish in microhabitats where a competitive ability is essential to survival.

There are no studies investigating parasites or diseases that may affect *Leptodactylon watsonii*, nor have there been any investigations of symbiotic or mutualistic interactions. Entomophily is an important symbiotic relationship for most flowering plants. *Leptodactylon watsonii* most likely depends upon insects to effect pollination. Specific data concerning the interaction between *L. watsonii* and insects are not known. Refer to the discussion on reproduction for what is known about entomophily and the Polemoniaceae.

An envirogram is a useful tool for evaluating the relationship between the environment and a single species. It traces the environmental factors that affect a species from the most indirect (distal) interactions to factors that have a direct (proximal) effect (Andrewartha and Birch 1984). Traditionally, it is most often applied to animal/environment interactions. An example of an envirogram constructed for *Pinus lambertiana* (sugar pine) showed that the same principles used to construct one for animals could be applied to plants (Schlesinger and Holst 2000). The envirogram is a series of webs that converge upon a centrum. The centrum consists of the basic components of environment that cause an increase, decrease, or no change in the expectation of fecundity and survivorship of a species. It is the most proximal level of the envirogram and directly affects the target species (Andrewartha and Birch 1984). For plants, the centra consist of resources (i.e., light, soil moisture, nutrients), reproduction (i.e., flowering/fruiting, growth and development, seedling establishment), and malentities (i.e., human interactions, extreme weather).

The envirogram is constructed as a modified dendrogram, with the centrum placed at the most proximal level to the species. From each of the centrum components, a web is constructed distally, illustrating factors that affect the centrum component and being termed Web 1. Web 2 consists of factors that affect Web 1, Web 3 consists of factors that affect Web 2, and so on. Web 4 levels and above (Web *n*) generally identify areas beyond the ecological and biological scope of the species. One of the primary functions of an envirogram is to identify areas of research and to propose hypotheses (Andrewartha and Birch 1984). As with all analytical tools, the best envirogram is based upon a complete data set. An envirogram was constructed for *Leptodactylon watsonii*, despite the lack of ecological and environmental data. Entries with a question mark denote areas in need of further research, such as pollination mechanisms, flowering/fruiting, the effect of disturbance, and dispersal vectors. **Figure 8**, **Figure 9**, and **Figure 10** demonstrate a preliminary envirogram for *L. watsonii*. To aid in viewing, each centrum is color-coded. The resources centrum (**Figure 8**) is green; the reproduction centrum (**Figure 9**) is yellow; and the malentities centrum (**Figure 10**) is blue.

The resources centrum for *Leptodactylon watsonii* is made up three proximal factors: soil moisture, light, and nutrients. Soil moisture is affected by precipitation, soil porosity (permeability), soil water retention, and runoff. Light can be affected by community structure, rocks, or geology, and the nutrient centrum is affected by such things as substrate parent material and the addition of organic materials through decomposition of detritus. The reproduction centrum consists of factors affecting flowering and fruiting (i.e., pollination, weather, dispersal), seedling establishment (i.e., possible safe sites, substrate, protection from sun), and growth and development (i.e., weather, light, substrate). The malentities centrum identifies factors that may negatively affect *L. watsonii*. These include such things as extreme weather conditions like drought or unusually cold weather during the flowering and fruiting season. Competition from invasives, possibly introduced through recreational hikers or climbers, may have a negative effect upon the ability of *L. watsonii* to occupy available habitat. Air pollution, including particulates and the development of greenhouse gases, may also negatively affect *L. watsonii* habitat.

Conservation

Threats

Leptodactylon watsonii is vulnerable within Region 2 because of small population size and its limited global distribution. Insufficient information is available to determine whether significant population or habitat loss has occurred in the past because of human activities. The information presented in this section is primarily based on observations in occurrence records (Wyoming Natural Diversity Database 2006) and/or personal communications with resource management specialists

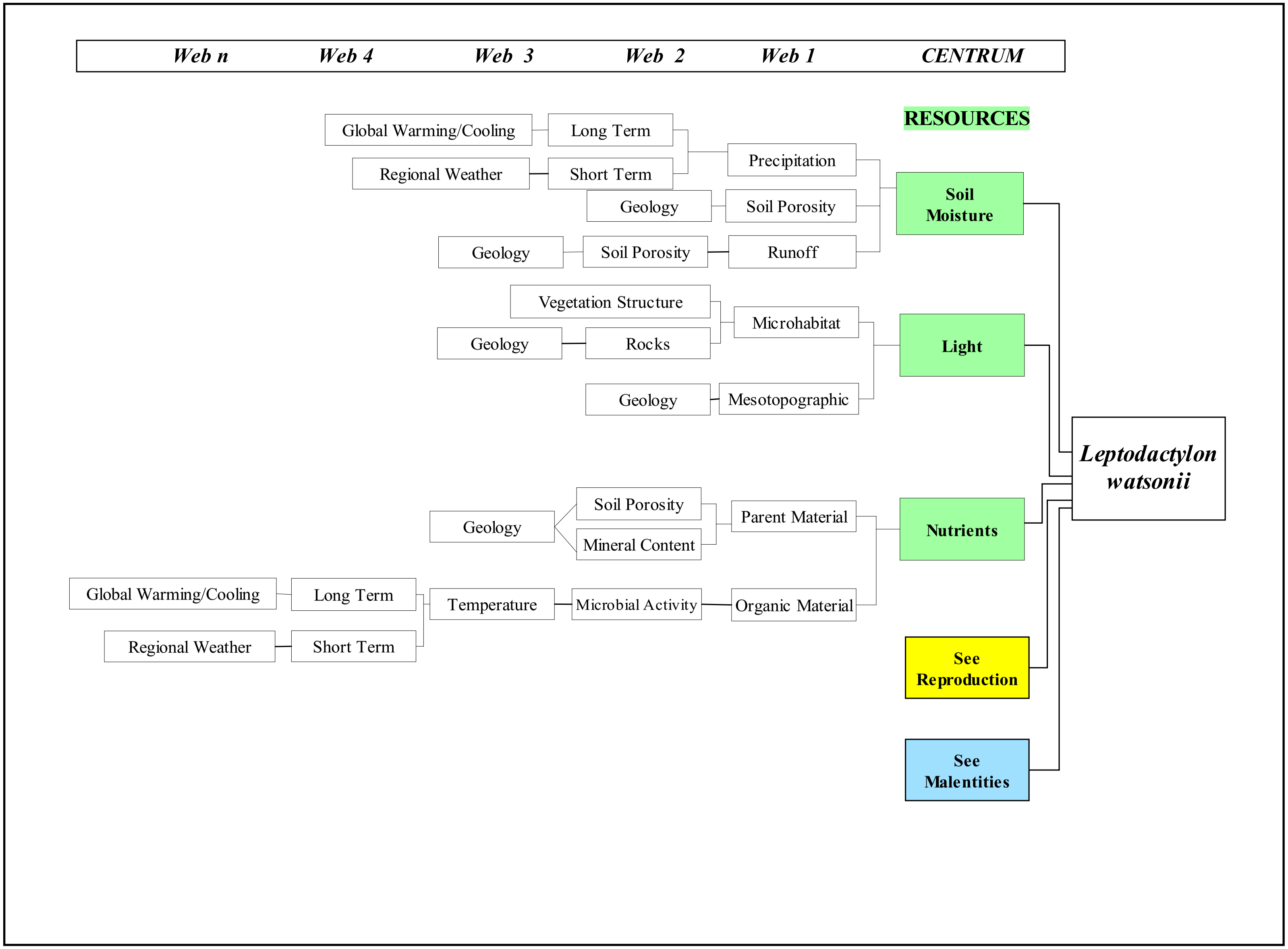

Figure 8. Resources centrum for *Leptodactylon watsonii* envirogram.

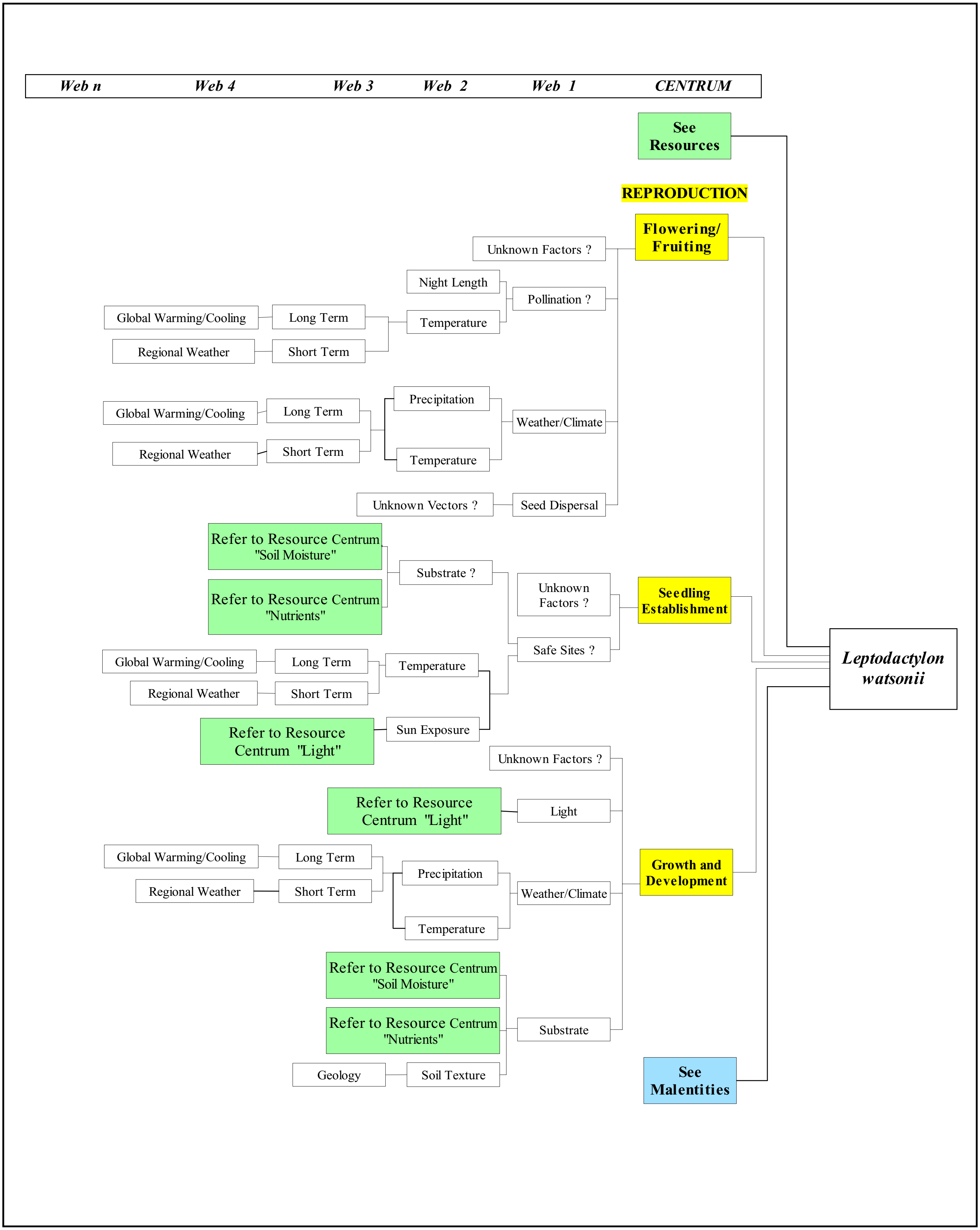

Figure 9. Reproduction centrum for *Leptodactylon watsonii* envirogram.

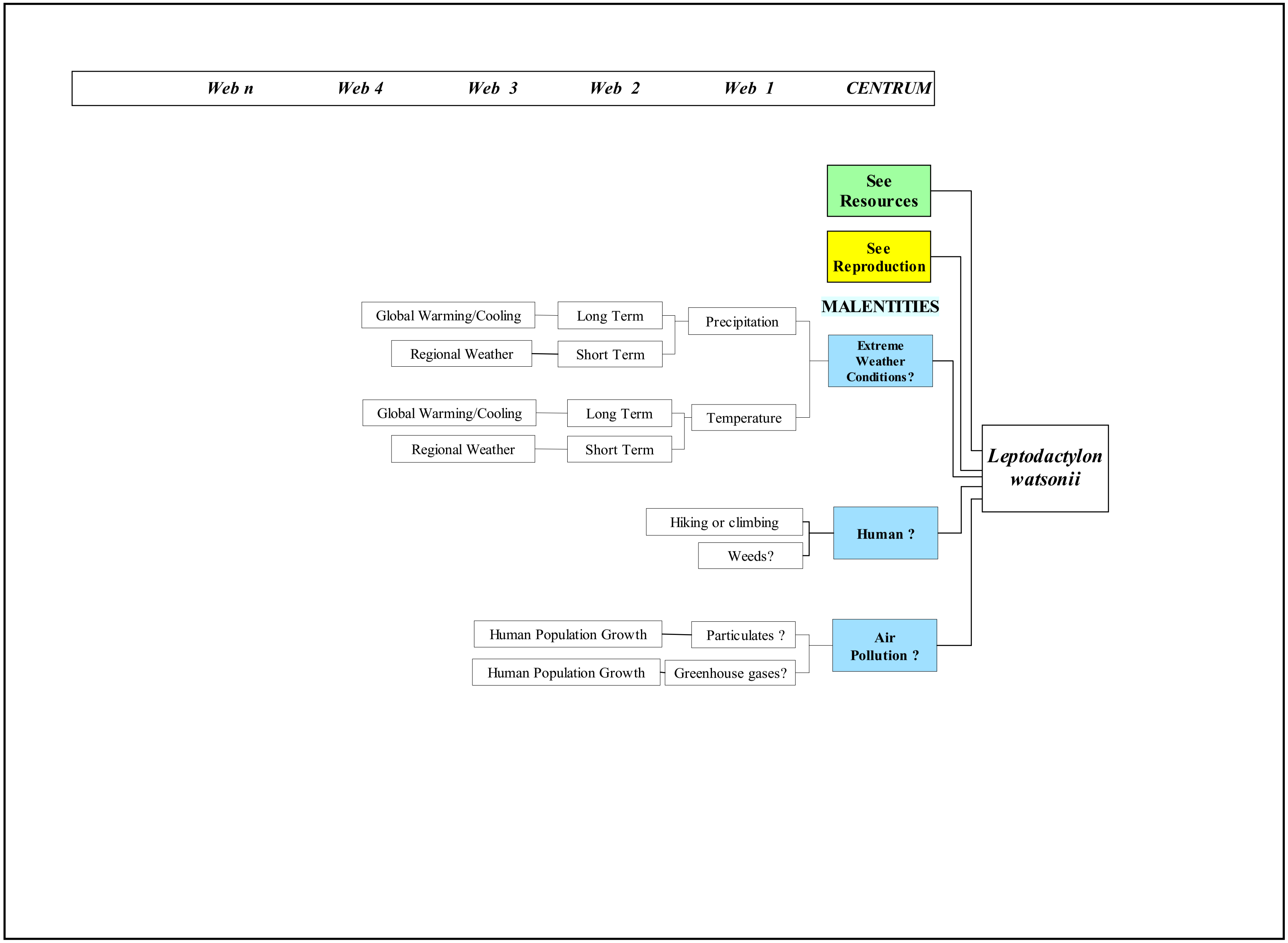

Figure 10. Malentities centrum for *Leptodactylon watsonii* envirogram.

and botanists (Johnston personal communication 2006, Naumann personal communication 2006).

Threats appear to be minimal at known sites in Wyoming and Colorado due to the rugged nature of the plant's habitat (Fertig 2000a, 2000b, Fertig personal communication 2004, Naumann personal communication 2006, Johnston personal communication 2006). Populations located in remote, rocky cliff sites are unlikely to be directly impacted by prescribed or natural fire, grazing, road construction, or recreation. However, any activities that directly affect the species' habitat or individuals could result in a population decline. The rugged habitat of *Leptodactylon watsonii* has also potentially prevented the discovery of additional occurrences, and land managers may be unaware of all occurrences within the species' range, which would limit their ability to make informed decisions concerning management objectives for the protection of individuals and their habitat.

The unstable nature of the cliff habitats where *Leptodactylon watsonii* occurs provides little opportunity for recreational activities, including hiking or rock climbing. The topographic location of several occurrences also provides a degree of isolation from interactions with invasive species; however, recreation has the potential to introduce invasive species even in remote locations. Invasive species may occur in the valley bottoms and along cliff bases where there is adequate soil development; however, there have been no reports of invasive species growing in the microhabitat of any of the known occurrences.

Occurrences of *Leptodactylon watsonii* may be at risk from environmental or demographic stochasticity due to the small size of populations. Inadequate pollinator activity, lack of safe sites for germination or seedling establishment, as well as unknown barriers to gene flow may pose possible threats to this species. Environmental threats include global warming and extreme weather conditions, such as drought or unusually cold weather during the flowering and fruiting season. Air pollution, including acid rain and the excessive development of greenhouse gases, may also negatively affect *L. watsonii* individuals and habitat. Menges (1991) suggested that if a plant population is able to buffer environmental stochasticity, then the population will be sufficient to protect the genetic integrity of plant populations.

Global warming has been identified as a potential threat to all plant communities (EPA 1997 and 1998). Warmer climates and less moisture caused by climate change could affect the rugged habitats where *Leptodactylon watsonii* occurs. A change in climate may also have affect pollinator activity and optimal conditions for flowering, such as water supply and temperature. Extreme drought may affect flowering, seed set, germination, seedling establishment, and dispersal (Barbour et al. 1987).

Leptodactylon watsonii is probably an outcrossing species. While outcrossing may buffer against a loss of heterozygosity, this may be affected in the short term by dependence upon pollination mechanisms or other mutualisms that have not been identified at this time (Menges 1991). Any event that causes habitat fragmentation such as road or trail building may impede pollinator activity and consequently reduce gene flow (Bowles 1983, Heywood 1993, Kearns et al. 1998, Moody-Weis and Heywood 2001).

Acid rain is formed when compounds, including NO_x and SO_2, are dissolved in atmospheric water, decreasing the pH of rain from normal levels of 5.6 to between 3.0 and 4.0. Acid rain can negatively affect vegetation by removing mineral nutrients from leaves and by degrading the waxy cuticle that protects the leaf from desiccation and absorption of additional pollutants. Likewise, the addition of acids to soils can result in the release of aluminum ions from soil minerals, causing aluminum toxicity in plants. The severity of acid rain is greatly influenced by the abundance of free calcium carbonate in soils, which acts as a buffering agent. Thus, in areas rich in calcium carbonate, including much of the interior the western United States, the impacts of acid raid can be negligible, whereas in areas where soils have low buffering capacity, the impacts of acid rain can be widespread and long lasting (ACE 2006).

Conservation Status of Leptodactylon watsonii in Region 2

Leptodactylon watsonii is vulnerable because of small populations and a limited global distribution in North America. The species also has a limited distribution in Region 2, and although it is not a sensitive species in Region 2 (see Management Status section), it was chosen for an assessment because of the limited knowledge concerning its distribution, habitat, population trends, and threats.

Leptodactylon watsonii is poorly understood both regionally and globally. The known distribution may be limited by a lack of inventory. Other than a few casual estimates, abundance data do not exist from Region 2 or from anywhere within the range of

L. watsonii. Given the lack of information concerning plant abundance at known occurrences, it is difficult to determine the viability of this taxon. Demographic parameters, population structure, and ecological strategies are all biological aspects of *L. watsonii* that remain uninvestigated at this time. Lack of information also prevents any conclusions about determining habitat quality, estimating population trends, and pinpointing risks associated with reproductive mechanisms for this species in Region 2 and throughout its range.

Because information in Region 2 is lacking, it is impossible to evaluate the effects of current management activities upon *Leptodactylon watsonii*. No immediate threats have been identified. No information concerning the viability of populations at any occurrences exists. No predictions about this species' ability to buffer against environmental or demographic stochasticity can be made until more data are accumulated. Since Dinosaur National Monument is one of the few known locations in Colorado with large expanses of suitable habitat for *L. watsonii* and large numbers of individual plants of the species, it may provide opportunities for research into the biology and ecology of the species.

Management of Leptodactylon watsonii in Region 2

Implications and potential conservation elements

As stated above in the Threats section, the concern for the viability of *Leptodactylon watsonii* reflects its small population size and limited global distribution. Protection of population numbers and the habitat in which they occur are elements necessary for maintaining the viability of this species on USFS lands in Region 2. No current threats have been identified at the remote, rocky cliff faces where occurrences have been observed.

No federally protected areas have been designated that include the conservation of this species or its habitat as an explicit goal. *Leptodactylon watsonii* does occur on NPS lands in Utah and Colorado. National parks and other conservation areas provide a conservation reserve for species (Falkner and Stohlgren 1997). *Leptodactylon watsonii* has been documented from three occurrences on USFS lands managed by the White River and Bighorn national forests within Region 2. This is approximately 17 percent of the total number of known occurrences of the species within Region 2. Although no threats to the species have been identified on USFS lands, management is needed to determine population viability and trend. Conservation of the species on USFS lands will protect populations on the periphery of their range where genetic and evolutionary changes are likely to occur. Since only a small proportion of the total population of the species occurs on USFS lands, much of the responsibility for conservation of the species rests with other agencies and private landowners. If threats are identified or declining trends are observed, coordinated efforts of landowners and managers of the lands where the species occurs may be needed to ensure its survival.

As a relatively rare species, *Leptodactylon watsonii* would be impacted by disturbance to individuals or their habitat. However, nothing is known about this species' response to disturbance (environmental or anthropogenic). Priorities for determining conservation elements include:

- ❖ inventory for additional occurrences
- ❖ identify any potential threats
- ❖ develop and implement a monitoring program to identify population trend.

Tools and practices

Continued efforts in the location of other occurrences of *Leptodactylon watsonii* by use of presence/absence surveys may provide additional information concerning its distribution. Potential habitat may exist in undiscovered calcareous and rocky microhabitats in Wyoming and Colorado. Steep cliffs and canyon walls are difficult to survey, and other occurrences may yet be found in the Wind River Canyon, Flaming Gorge Natural Recreation Area, suitable habitats along the west slope of the Bighorn Mountains of Wyoming, and in Colorado in any of the numerous canyons that drain into the Colorado River system. While much of the known extent of limestone and dolomite in Wyoming has been surveyed, some remains unsearched.

The *Leptodactylon watsonii* occurrences that have been documented are, for the most part, located in areas that are relatively easy to access. Given the fact that this species' distribution extends outside of Wyoming and Colorado into Utah, and to a lesser extent Idaho and Nevada, surveys centered on the canyon country in adjacent Utah would likely find more *L. watsonii* occurrences. Lands with potential *L. watsonii* habitat in Utah are managed by the BLM, the NPS, or are privately owned; the potential for numerous new occurrences on USFS lands is low.

Few current or historical abundance data are available. The lack of any abundance information for known occurrences makes it impossible to determine whether numbers are increasing, decreasing, or stable. Periodic revisits to known occurrences would alert land managers to any potential decline or threats that are not apparent at this time. The use of permanent photo plots could provide valuable information to evaluate change over time of a small population segment and to identify new plants. Elzinga et al. (1998) and Hall (2001) describe techniques for photo monitoring. Should data from periodic monitoring and photo point observations indicate any threats or obvious decline in numbers of individuals, then the species' status as a sensitive species on National Forest System lands could be reconsidered.

Leptodactylon watsonii is a night-blooming, persistent subshrub; therefore census surveys can be conducted throughout the growing season. However, if reproductive information is required, then surveys should be timed to coincide with flowering and fruiting so that reproductive output can be assessed. Characteristics required for field identification include the opposite dissected leaf arrangement (versus alternate), prickly cushions or mats, and limestone cliffs.

Habitat monitoring describes how well an activity meets the objectives or management standards for a habitat (Elzinga et al. 1998). Habitat monitoring is most effective when research has shown a clear link between a habitat parameter and the condition of a species (Elzinga et al. 1998). Without additional knowledge of specific factors controlling the growth and distribution of *Leptodactylon watsonii* and the inaccessible nature of the species habitat, it would be difficult to establish a habitat-monitoring program at this time.

The mission of the Center for Plant Conservation is to conserve and restore the rare native plants of the United States. No plant material for *Leptodactylon watsonii* has been stored with the Center for Plant Conservation. No seed is available through the North American Rock Garden Society (2006).

Information Needs

The primary information need for *Leptodactylon watsonii* is to obtain additional distribution information to assist in the formulation of conservation strategies for Region 2.

Actions that will provide needed information, listed in decreasing priority order, include:

- ❖ Initiate field surveys to relocate known locations and to determine abundance

- ❖ Search for potential habitat and new occurrences by use of presence/absence surveys

- ❖ Determine population trends by establishing permanent, long-term monitoring plots in known locations

- ❖ Establish permanent photo points to monitor any changes in individual plants.

Additional research topics that may provide useful data in case threats are identified include:

- ❖ Evaluate the reproductive and ecological characteristics of the species, including pollination mechanisms, seed germination, seedling establishment, flowering/fruiting, and dispersal vectors, to provide a basis for assessing the factors controlling the growth of *L. watsonii*

- ❖ Gather basic demographic data (i.e., vital rates, recruitment, survival, reproductive age, lifespan or proportion of populations reproducing, seed viability, seed bank dynamics, longevity)

- ❖ Evaluate impacts of management on the species.

Definitions

Calcareous: Limy, or rich in calcium carbonate (Cronquist et al. 1986).

Conservation Status Rank: The Global (G) Conservation Status (Rank) of a species or ecological community is based on the range-wide status of that species or community. The rank is regularly reviewed and updated by experts, and takes into account such factors as number and quality/condition of occurrences, population size, range of distribution, population trends, protection status, and fragility. A subnational (S) rank is determined based on the same criteria applied within a subnation (state or province). The definitions of these ranks, which are not to be interpreted as legal designations, are as follows:

- GX Presumed Extinct: Not located despite intensive searches and virtually no likelihood of rediscovery
- GH Possibly Extinct: Missing, known only from historical occurrences but still some hope of rediscovery
- G1 Critically Imperiled: At high risk of extinction due to extreme rarity (often five or fewer occurrences), very steep declines, or other factors.
- G2 Imperiled: At high risk of extinction due to very restricted range, very few populations (often 20 or fewer), steep declines, or other factors.
- G3 Vulnerable: At moderate risk of extinction due to a restricted range, relatively few populations (often 80 or fewer), recent and widespread declines, or other factors.
- G4 Apparently Secure: Uncommon but not rare, some cause for long-term concern due to declines or other factors.
- G5 Secure: Common, widespread and abundant.

Corymbose: Having flowers in corymbs; a corymb is a flat-topped or round inflorescence, racemose, but with the lower pedicels longer than the upper (Harris and Harris 1994).

Cymose: Infloresence composed of a cyme; a flat-topped or round-topped determinate inflorescence, paniculate, in which the terminal flower blooms first (Harris and Harris 1994).

Entomophily: Pollination by or dispersed by the agent of insects (Lincoln et al. 1982).

Environmental stochasticity: Variation over time in the population's operational environment (Menges 1991).

Generation time: The mean period of time between reproduction of the parent generation and reproduction of the first filial generation (Lincoln et al. 1982).

Genotype: The genetic makeup of an individual (Cronquist et al. 1986).

Glabrous: Smooth; without hairs (trichomes) or glands (Cronquist et al. 1986).

Glandular: Provided with glands, or functioning as a gland (Cronquist et al. 1986).

Heterozygosity: Having two different alleles at a given locus of a chromosome pair (Lincoln et al. 1982).

Hirsute: Pubescent with rather coarse or stiff, but not pungent, often bent or curved hairs; coarser than villous, but less firm and sharp than hispid (Cronquist et al. 1986).

Homozygosity: Having identical alleles at a given locus of a chromosome pair (Lincoln et al. 1982).

Inbreeding: Mating or crossing of individuals more closely related than average pairs in the population (Lincoln et al. 1982).

Inbreeding depression: Reduction of fitness and vigor by increased homozygosity as a result of inbreeding in a normally outbreeding population (Lincoln et al. 1982).

Loculicidal: Dehiscing along the midrib or outer median line of each locule, i.e., "through" the locules (Cronquist et al. 1986).

Longevity: The average life span of the individuals of a population under a given set of conditions (Lincoln et al. 1982).

Ochroleucous: Yellowish white (Cronquist et al. 1986).

Outcrossing: Mating or crossing of individuals that are less closely related than average pairs in the population, or from different populations (Lincoln et al. 1982).

Phenotype: The actual character of an individual, as expressed in its form, structure, or physiology (Cronquist et al. 1986).

Salverform: With a slender tube and an abruptly spreading, flattened limb (Harris and Harris 1994).

Selfing: Self-fertilizing or self-pollinating (Lincoln et al. 1982).

Stipe: The stalk of a structure, without regard to its morphological nature; the term is usually applied only where more precise terms such as petiole, pedicel, or peduncle cannot be used, as the stipe of an ovary (Cronquist et al. 1986).

Stipitate: Borne on a stipe (Cronquist et al. 1986).

Vesicular-arbuscular mychorrizal: The term applied to the combination between a plant and its symbiont.

Vital rates: The class-specific annual rates of survival, growth, and fecundity (Morris et al. 1999).

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