Primula egaliksensis Wormskjold ex Hornemann: (Greenland primrose): A Technical Conservation Assessment

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Cover Photo Credit

Primula egaliksensis (Greenland primrose). Photograph by David G. Anderson.

Summary of Key Components for Conservation of *Primula egaliksensis*

Status

Primula egaliksensis Wormskjold ex Hornemann (Greenland primrose) ranges across boreal and arctic North America from Alaska through Canada, with outlying populations in Chukotka, Russia and Greenland. It has apparently been extirpated in Iceland (Guggisberg personal communication 2005, Guggisberg et al. 2006). It is also known from two disjunct localities in Wyoming and from 20 occurrences in South Park, Colorado. One occurrence in Park County, Wyoming is in the Swamp Lake Special Botanical Area on the Shoshone National Forest within USDA Forest Service (USFS) Region 2. The other occurrence in Wyoming is in Sublette County on the Bridger-Teton National Forest (Region 4). In Colorado, one occurrence is known from the Pike National Forest (Region 2); the other Colorado occurrences are on private land or lands managed by the State of Colorado or possibly the Bureau of Land Management (BLM). Based on conservative estimates from element occurrence records, the total population of *P. egaliksensis* in Wyoming and Colorado is between 16,800 and 27,900, not including plants in occurrences where abundance was not estimated.

Primula egaliksensis is ranked globally apparently secure (G4) by NatureServe, but it is considered critically imperiled (S1) in Wyoming and imperiled (S2) in Colorado. Both Regions 2 and 4 of the USFS designate *P. egaliksensis* as a sensitive species. This species is also on the BLM Sensitive Species List for Colorado. It is not listed as threatened or endangered under the Federal Endangered Species Act, nor is it a candidate for listing.

Primary Threats

There are several threats to the persistence of *Primula egaliksensis* in Region 2. In approximate decreasing order of priority, threats include water development, peat mining, ditching, livestock grazing, road construction, right-of-way maintenance, global climate change, timber harvest, recreational activities, residential development, fire, exotic species, placer mining, pollution, and collection.

Primary Conservation Elements, Management Implications and Considerations

The distribution of *Primula egaliksensis* in Wyoming and Colorado suggests that the species is vulnerable due to its small number of disjunct occurrences, and because it is typically found in rare and highly specialized habitats that depend on specific moisture regimes. Occurrences of *P. egaliksensis* on federal land benefit to some extent from sensitive species status granted by the USFS and BLM . Hydrologic alteration, as a secondary effect of timber harvest, recreation, and weed management, is the primary threat to occurrences on National Forest System land. Most occurrences in Region 2 (12 or possibly 16 of 22) are found at least in part on private land where they are threatened by water resource development, ditching, and grazing. Occurrences on Colorado state trust lands are also threatened by water resource development and grazing.

Protecting the hydrology that supports *Primula egaliksensis* and its habitat is crucial to ensuring the long-term viability of this species in Wyoming and Colorado. Protective land status designations that also protect water resources are needed for the conservation of this species. Pursuing conservation easements on private properties where *P. egaliksensis* is found would help to ensure the viability of occurrences on private land. Bringing occurrences into federal ownership would also help to prevent the extirpation of occurrences of *P. egaliksensis*. Species inventory and monitoring are high priorities to determine population trends under different management prescriptions. Research is needed to investigate the population biology and autecology of *P. egaliksensis* so that conservation efforts on its behalf can be most effective.

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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). *Primula egaliksensis* is the focus of an assessment because it is a sensitive species in Region 2 (USDA 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 abundance or significant current or predicted downward trends in habitat capability that would reduce its distribution (FSM 2670.5(19)). A sensitive species may require special management, so knowledge of its biology and ecology is critical. This assessment addresses the biology of *P. egaliksensis* throughout its range in Region 2. This introduction defines the goal of the assessment, outlines its scope, and describes the process used in its production.

Goal of Assessment

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, conservation status, and management of certain species based on available scientific knowledge. The assessment goals limit the scope of 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 backgrounds upon which management must be based and focuses on the consequences of changes in the environment that result from management (i.e., management implications). Furthermore, it cites management recommendations proposed elsewhere and examines the success of those recommendations that have been implemented.

Scope of Assessment

The assessment examines the biology, ecology, conservation status, and management of *Primula egaliksensis* with specific reference to the geographic and ecological characteristics of Region 2. Although some of the literature on the species originates from field investigations outside the region, this document places that literature in the ecological and social contexts of the central and southern Rocky Mountains. Similarly, this assessment is concerned with the reproductive behavior, population dynamics, and other characteristics of *P. egaliksensis* 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.

This assessment incorporates peer-reviewed literature, non-refereed publications, research reports, and data accumulated by resource management agencies and other investigators. Because basic research has not been conducted on many facets of the biology of *Primula egaliksensis*, literature on its congeners was used to make inferences in many cases. The peer-reviewed and non-refereed literature on the genus *Primula* and its included species is more extensive and includes other endemic or rare species. All known publications on *P. egaliksensis* are referenced in this assessment, and many of the experts on this species were consulted during its synthesis. All available specimens of *P. egaliksensis* were viewed to verify occurrences and to incorporate specimen label data. Specimens were searched for at University of Colorado Herbarium (COLO), Colorado State University Herbarium (CS), Rocky Mountain Herbarium (RM), Kalmbach Herbarium, Denver Botanic Gardens (KHD), San Juan College Herbarium (SJNM), Carter Herbarium (COCO), University of Northern Colorado Herbarium (GREE), New Mexico State University Range Science Herbarium (NMCR), and University of New Mexico Herbarium (UNM).

The assessment emphasizes peer-reviewed literature because this is the accepted standard in science. While non-refereed publications or reports are often regarded with greater skepticism, they were used in the assessment because there is very little peer-reviewed literature that specifically treats *Primula egaliksensis*. Unpublished data (e.g., Natural Heritage Program records, reports to state and federal agencies, specimen labels) were important in estimating this species' geographic distribution. These data required special attention because of the diversity of persons and methods used in collection.

Treatment of Uncertainty in Assessment

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 perspective is limited, science includes 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 in the ecological sciences to conduct experiments that produce clean results. Observations, inference, models and good thinking must be relied on to guide our understanding of ecological relations. Confronting uncertainty is not prescriptive. In this assessment, the strength of evidence for particular ideas is noted, and alternative explanations are described when appropriate.

Treatment of This Document as a Web Publication

To facilitate the use of species assessments in the Species Conservation Project, they will be published on the 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. It also facilitates revision of the assessments, which will be accomplished based on guidelines established by Region 2.

Peer Review of This Document

Assessments developed for the Species Conservation Project have been peer reviewed prior to their 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 intended to improve the quality of writing and to increase the scientific rigor of the assessment.

MANAGEMENT STATUS AND NATURAL HISTORY

Management Status

Primula egaliksensis is included on the Regional Forester's sensitive species list in Region 2 (USDA Forest Service 2003) and in Region 4 (Joslin 1994, Fertig 1996); this designation affords the species some protection on National Forest System land. In Region 2, *P. egaliksensis* is known from the Pike-San Isabel National Forest in Colorado and the Shoshone National Forest in Wyoming. In Region 4, it is known from a single location on the Bridger-Teton National Forest in Wyoming. *Primula egaliksensis* is a sensitive species in Region 2 because it meets the second of the three formal criteria for inclusion on a USFS sensitive species list:

1. the species is declining in numbers or occurrences, and evidence indicates it could be proposed for listing as threatened or endangered under the federal Endangered Species Act if action is not taken to reverse or stop the downward trend

2. the species' habitat is declining, and continued loss could result in population declines that lead to federal listing if action is not taken to reverse or stop the decline

3. the species' population or habitat is stable but limited (USDA Forest Service 2003).

Because it is designated sensitive in Region 2, the USFS must consider this species during project planning in order to maintain habitat and plants (see Forest Service Manual 2670). The potential effects of projects and prescriptions on sensitive species must be evaluated for all projects that include suitable habitat for sensitive species, so that impacts can be mitigated. The USFS can modify allotment management plans, projects, or contracts to protect *Primula egaliksensis* on a discretionary basis. Sensitive species cannot be collected on National Forest System land without a permit (see Forest Service Manual 2670).

The U.S. Forest Service reviewed the status of *Primula egaliksensis* as a sensitive species during the revision of the Region 2 list in 2003. The USFS determined that *P. egaliksensis* should stay on the list because it occurs only in disjunct occurrences with no means of medium- and long-range dispersal, and because its habitat has declined in quantity and quality due to peat mining and heavy grazing (Warren 2003).

Primula egaliksensis is included on the BLM Sensitive Species List for the Royal Gorge Resource Area in Colorado (Bureau of Land Management 2000).

The NatureServe global rank for *Primula egaliksensis* is G4 (Colorado Natural Heritage Program 2005, NatureServe Explorer 2005). The global (G) rank is based on the status of a taxon throughout its range. A rank of G4 is ascribed to taxa that are apparently secure globally. These species may be uncommon, but they are not rare throughout their range. Typically, there is some cause for long-term concern due to declines in abundance or habitat, or other factors. In the case of *P. egaliksensis*, a rank of G4 is appropriate because the species, although widespread, is rarely abundant even where it is more common in the northern portion of its range, and occurrences are widely scattered.

The subnational (S) rank of a taxon is based on its status in a state or province, using the same criteria as

those used to determine the global (G) rank. In Colorado, *Primula egaliksensis* has a rank of S2 (imperiled) because of threats and observed declines in habitat quantity and quality, small population sizes, and small number of known occurrences (currently 20) (Colorado Natural Heritage Program 2005). In Wyoming, *P. egaliksensis* is ranked S1 (critically imperiled) due to its extreme rarity (Fertig 1996, Wyoming Natural Diversity Database 2004).

Primula egaliksensis is not listed as threatened or endangered under the federal Endangered Species Act of 1973 (U.S.C. 1531-1536, 1538-1540). Another species of *Primula*, *P. maguirei*, is listed as threatened (U.S. Fish and Wildlife Service 1990, U.S. Fish and Wildlife Service 2004). *Primula egaliksensis* is not listed as endangered or vulnerable by the International Union for Conservation of Nature and Natural Resources (Ayensu and DeFilipps 1978).

There are three occurrences of *Primula egaliksensis* on National Forest System land in Wyoming and Colorado; one occurrence is protected within the Swamp Lake Special Botanical Area designated in 1987 (Fertig and Jones 1992) on the Shoshone National Forest in Wyoming (Fertig 2000). The occurrence at Lower Green River Lake on the Bridger-Teton National Forest (Region 4) has no formal protection and is managed for multiple uses (Handley and Laursen 2002). The occurrence on the Pike National Forest in Colorado is also on land that is managed for multiple uses. *Primula egaliksensis* is not known from any proposed or potential Research Natural Areas (RNAs) in Wyoming (Fertig 1998) or Colorado. **Table 1** summarizes the land ownership status for all occurrences in Wyoming and Colorado.

Two occurrences of *Primula egaliksensis* on private lands in Colorado are protected. The occurrence at the Wahl Ranch is protected under a conservation easement held by Colorado Open Lands (Colorado Open Lands 2004). Another occurrence is within a preserve owned by The Nature Conservancy at High Creek Fen (Colorado Natural Heritage Program 2005, The Nature Conservancy 2005). The Colorado Natural Areas Program designated 1,147 acres of High Creek Fen as a State Natural Area in 1994 (Colorado Natural Areas Program 2004). High Creek Fen is a Wetlands Initiative Site, part of an endeavor to protect wetlands and wetland-dependent wildlife using voluntary, incentive-based mechanisms, involving numerous federal, state, local, and non-government partnerships (Colorado Division of Wildlife 2000).

Primula egaliksensis is present in 12 Potential Conservation Areas (PCAs), designated by the Colorado Natural Heritage Program as having natural heritage significance (Spackman et al. 2001, Colorado Natural Heritage Program 2005). PCA boundaries do not confer any regulatory protection, nor do they automatically exclude all activity. PCA boundaries represent the best professional estimate of the primary area supporting the long-term survival of the targeted species or plant associations, and they are often based on factors relating to ecological systems. The boundaries delineate ecologically sensitive areas where land-use practices should be carefully planned and managed to ensure that they are compatible with the natural heritage resources and sensitive species within them (Colorado Natural Heritage Program Site Committee 2002).

Existing Regulatory Mechanisms, Management Plans, and Conservation Strategies

Occurrences of *Primula egaliksensis* in peatlands in Park County, Colorado are currently protected by a moratorium on peat mining in the county (Spackman et al. 2001, Mayo 2005). However, Park County regulations allow peat mining to continue if it was permitted before the moratorium was instated. Park County records do not indicate any current activity (Mayo 2005), but peat mining is still occurring or has occurred within the last 10 years in South Park (Coles 2002).

Primula egaliksensis was included among the sensitive species analyzed for the Upper South Platte Watershed Protection and Restoration Project. The USFS determined this project will not affect *P. egaliksensis* because the proposed fuels reduction treatments will not occur in its habitat (USDA Forest Service 2004).

Primula egaliksensis is considered a facultative wetland indicator species in U.S. Fish and Wildlife Service Region 8 (Intermountain Region- includes Colorado but not Wyoming) and Region A (Alaska) by the Environmental Protection Agency (EPA). Facultative wetland indicator species usually occur in wetlands, but occasionally they are found in non-wetlands (USDA Natural Resources Conservation Service 2004).

Although there are no regulatory mechanisms, management plans, or conservation strategies explicitly concerned with *Primula egaliksensis*, a number or federal regulations, executive orders, and policies exist that could protect wetland habitats (as cited in Austin 2003):

Table 1. Land ownership status of the 22 occurrences of *Primula egaliksensis* in Colorado and Wyoming. Because some occurrences cross ownership boundaries, the total is less than the sum of the rows in the table. See **Table 4** for ownership of specific occurrences.

Owner	Total	Subtotal
USDA Forest Service	**3**	
Shoshone National Forest		1
Pike National Forest		1
Bridger-Teton National Forest (Region 4)		1
USDI Bureau of Land Management	**possibly 2**	
State of Colorado Land Board	**4**	
Colorado Division of Wildlife	**1**	
The Nature Conservancy	**1**	
Private	**12 (possibly up to 16)**	
TOTAL	**22**	

a. Federal Land Policy and Management Act of 1976 (FSM 2729.01) or individual Forest Management Plans. The Act was written to establish public land policy, guidelines for its administration, to provide for the management, protection, development, and enhancement of the public lands, and for other purposes.

b. Organic Administration Act of 1897 (16 U.S.C. 475) provides National Forests with goals for protecting watersheds and water flows in support of the timber program. It recognizes the need to protect stream and wetland habitat.

c. The forest supervisors of Region 2 have been urged to give careful consideration to avoiding impacts to fens, and to identify opportunities for their restoration (Hilliard 2002).

d. Multiple Use-Sustained Yield Act of 1960 (16 U.S.C. 528) defines sustained yield and multiple use emphasis that includes watersheds, fish and wildlife, range, recreation, and timber uses. The watersheds of some first order streams in Region 2 include peatland habitat for *P. egaliksensis*.

e. National Forest Management Act of 1976 (16 U.S.C. 1600-1602, 1604, 1606, 1608-1614) charges the USFS with protecting natural resources, especially wetlands, streams, lakes, and riparian areas, from damage. Management activities that could negatively affect wetland habitat should be avoided (36 CFR 219.27)

f. Clean Water Act as amended in 1977 (33 U.S.C. 1251, 1254, 1323, 1324, 1329, 1342, 1344) provides for restoring and maintaining the physical, biological, and chemical quality of water in the United States; section 404 requires a permit from the Corps of Engineers prior to filling a wetland.

g. National Environmental Policy Act of 1992 requires analysis of the effects of a project on the environment. Diversion of the source of water to a fen may cause an "irreversible or irretrievable commitment of resources" (40 CFR Part 1502.14).

h. Forest Service Manual (FSM) 2372.02 guides the management of special recreation areas with botanical, zoological, geological, scenic, paleontological, and archaeological, or other unique values.

i. Executive Order No. 11990, Protection of Wetlands, to support avoidance of new construction (i.e., dredging, draining, filling, diking, and channelizing) and minimizing damage to wetlands. Agencies are required to review project impacts on natural systems under this order (Carter 1977).

j. U.S. Fish and Wildlife, Region 6, Regional Policy on the Protection of Fens. No

mitigation granted for fens because of their extremely slow rates of peat accumulation and irreplaceability (Federal Register 1981).

The United States has a "national goal of no-net loss of wetland resources" (LaPeyre et al. 2001 as cited in Austin 2003). Region 2 considers fens valuable resources recommended for protection or special management (Austin 2003).

Adequacy of current laws and regulations

There are no federal or state laws that explicitly protect *Primula egaliksensis*. Laws and regulations that apply to wetlands (reviewed above) provide tools for the conservation of *P. egaliksensis* in peatland habitats, especially on National Forest System land. However, additional protection is needed for fens in Region 2. Regulations in the Department of Interior and the Department of the Agriculture still consider peat a renewable resource (USDI Bureau of Mines 1994) and saleable mineral (FSM 2822.1). On privately owned lands, current laws and regulations may be inadequate to prevent damage or destruction to occurrences and habitat.

Adequacy of current enforcement of laws and regulations

There are no documented cases in which an occurrence of *Primula egaliksensis* was extirpated due to human activities or the failure to enforce existing regulations. However, this does not necessarily indicate that current regulations or their enforcement are adequate for its protection. Human impacts, including peat mining, have probably diminished the distribution and abundance of this species in Park County, Colorado. In Canada, where peat mining is much more prevalent, it is likely that occurrences of *P. egaliksensis* have been extirpated. Our knowledge of the historical distribution and abundance of *P. egaliksensis* is insufficient to determine the degree to which its abundance has been diminished by human activities in any portion of its range. A gradual but steady loss of occurrences over time through a variety of causes could easily contribute to a contraction of the known range. Loss of peripheral and disjunct occurrences could reduce the genetic diversity of the species, as well as depress its resilience in the face of genetic, demographic, and environmental stochasticity.

Biology and Ecology

Classification and description

Primula egaliksensis is a member of the Primulaceae, or Primrose family. The Primulaceae consists of perennial and annual herbaceous and suffrutescent species, and its members are found on all continents except Antarctica (Heywood 1993). *Primula* is the largest genus in Primulaceae, containing approximately 425 species (Mast et al. 2001, Richards 2003). *Primula* is widely distributed throughout the northern latitudes of Eurasia and North America (Kelso 1991). Seventy-five percent of the species of *Primula* are concentrated in the Himalayan Mountains and western China (Richards 1993, Mast et al. 2001). About 25 species are known from North America (Kelso 1991).

Molecular phylogenetic analysis using sequences from the rbcL chloroplast gene has determined that the genus *Primula* is not monophyletic, because four other genera within the Primulaceae (*Dodecatheon*, *Cortusa*, *Sredinskya*, and *Dionysia*) have their closest relatives in the genus *Primula* (Trift et al. 2002). A phylogenetic analysis using ribosomal nuclear Internal Transcribed Spacer region (ITS) sequence data also supports the polyphyly of *Primula* (Martins et al. 2003).

There has been considerable effort over the last two centuries to resolve taxonomic relationships within *Primula*. Currently, the genus is divided into 38 sections (Richards 2003). *Primula egaliksensis* is a member of section *Armerina* (Kelso 1991), a predominantly Asian section whose members are distinguished by their non-farinose corollas with notched lobes, petiolate leaves, and non-farinose leaves (Kelso 1991, Fertig 1996, Richards 2003). Lindley (1846) described section *Armerina*, with *P. involucrata* as the type species of the section. Section *Armerina* is distinguished by its involucral leaves that extend downwards into a sheath (as in *Armeria*, from which the sectional name is derived). This section is represented in North America by two species, *P. egaliksensis* and *P. nutans* (Kelso 1991).

Kelso (1991), in her conspectus of these sections in North America, attributes taxonomic confusion over the circumscriptions of sections *Armerina* and *Aleuritia* to the morphological and ecological similarity of their

members, and to their distribution in remote northern areas where field studies have been limited. Many species in these sections superficially resemble each other, and some grow sympatrically. This has caused some monographers of the genus (Smith and Fletcher 1943, Wendelbo 1961) to lump these sections. Section *Armerina* and section *Aleuritia* were originally treated as subsections within the section *Farinosae* Pax (Kelso 1991). Kelso (1991) noted that Schwarz (1968) split section *Armerina* into two subsections, based on the persistence of rhizomes. Under this treatment, *Primula egaliksensis* was placed in subsection *Chamaecome*, which Schwarz noted to have persistent rhizomes, as opposed to taxa placed in subsection *Armerina* that have rhizomes lasting only a single growing season. However, Kelso (1991), Halda (1992), and Richards (2003) do not recognize these subsections in their treatments of this genus.

The rigorous application of modern techniques for phylogenetic inference during the last decade has begun to draw a clearer picture of the sectional classification of *Primula*. In a phylogenetic study of *Primula* that included one member of section *Armerina* (*P. involucrata*), Trift et al. (2002) did not suggest that *Armerina* should be lumped with section *Aleuritia* as did Smith and Fletcher (1943) and Wendelbo (1961). Section *Armerina* has been considered closely related to section *Aleuritia*, but this is not supported by a reconstruction of the phylogenetic history of members of *Primula* using DNA from the ribosomal nuclear Internal Transcribed Spacer region (ITS) (Conti et al. 2000). The results of this study suggest that section *Armerina* is most closely related to section *Crystallophlomis*. Mast et al. (2001) used trnL and rpl16 introns of the chloroplast DNA from 95 of the 425 species included in *Primula* by Richards (1993) to reconstruct their phylogenetic history. This study shows that a number of new alignments will be necessary in *Primula*, with the most dramatic changes expected in section *Aleuritia*.

Using cytological, phytogeographical, and morphological evidence, Kelso (1991) concluded that *Primula egaliksensis* is an allotetraploid resulting from hybridization between *P. mistassinica* (section *Aleuritia*, 2n = 2x = 18) and *P. nutans* (section *Armerina*, 2n = 2x = 22). The ranges of these three species overlap in Alaska, where it is likely that the ancestral hybridization event occurred (**Figure 1**). In this hybridization event, the offspring between *P. nutans* and *P. mistassinica* apparently doubled their chromosome complement and became homostylous, giving rise to *P. egaliksensis* (2n = 4x = 36,40). The pollen type, chromosome, number, and morphology of these species all support this hypothesis (Richards 2003). This hypothetical origin for *P. egaliksensis* has been supported by the phylogenetic trees of Mast et al. (2001) and Guggisberg et al. (2006). Chloroplast DNA, which is maternally inherited, places *P. egaliksensis* (best placed morphologically in *Armerina*) as a close sister to *P. mistassinica* in section *Aleuritia*, which must therefore have been the female parent in the original hybrid cross (Mast et al. 2001, Richards 2003). The polyphyly of *Armerina* noted by Mast et al. (2001) is probably due to the intersectional hybrid origin of *P. egaliksensis*.

Alessia Guggisberg, a graduate student at the University of Zurich, is currently investigating the phylogeny of *Primula* sections *Aleuritia* and *Armerina*.

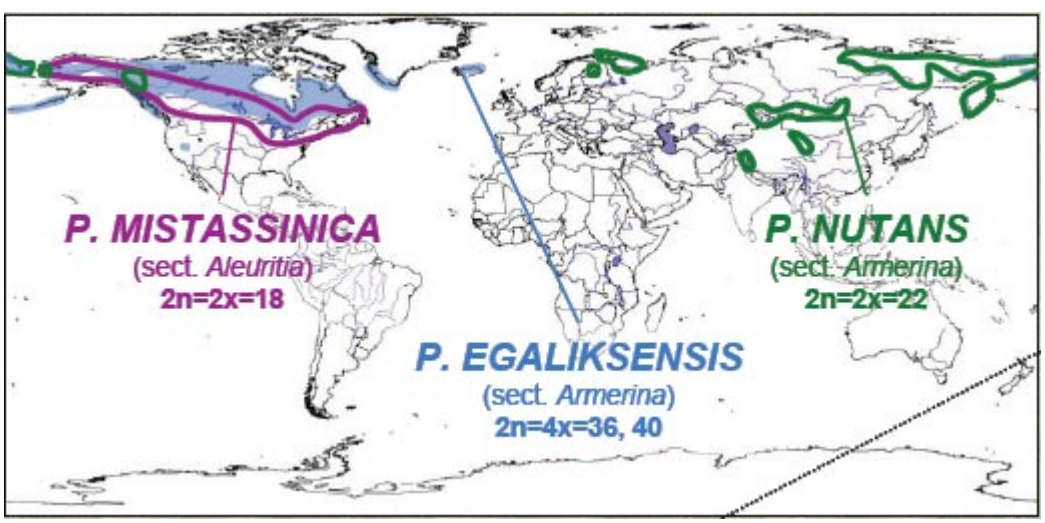

Figure 1. The global distribution of *Primula egaliksensis* relative to the distributions of its putative maternal (*P. mistassinica*) and paternal (*P. nutans*) parents. Map provided by A. Guggisberg, used with permission.

Using chloroplast markers and ribosomal nuclear Internal Transcribed Spacer region (ITS) data, her results to date are congruent with the hypothesis of an allopolyploid origin of *P. egaliksensis*, resulting from hybridization between the diploid heterostyles *P. mistassinica* and *P. nutans*. *Primula egaliksensis* groups with the North American *P. mistassinica* on the chloroplast phylogeny, whereas it forms a well-supported clade with the circumboreal *P. nutans* on the ITS tree. The fact that *P. egaliksensis* consists of several different haplotypes and ribotypes also suggests a recurrent origin of this taxon, a hypothesis that can be tested by a deeper study of this hybrid complex (Guggisberg personal communication 2005, Guggisberg et al. 2006).

History of knowledge

Morten Wormskjold (1783-1845) made the first major botanical collections in Greenland when he led a naval expedition there in 1813 (Reveal and Pringle 1993). It was on this expedition that he collected *Primula egaliksensis* at Igaliko in southern Greenland. Wormskjold described the species three years later in volume 9, issue 2 (fasc. 26) of Flora Danica (t. 1511) (Wormskjold 1816). Flora Danica was written and published between 1761 and 1883 to describe the entire flora of Denmark (including Greenland). The taxa included in these volumes are hand-illustrated with beautiful watercolors. Images from these volumes are available on the internet (Danish National Library of Science and Medicine 2005). The illustration of *P. egaliksensis* from Flora Danica (**Figure 2**) is the first depiction of this species, but artistic liberties were taken and better illustrations (e.g., **Figure 3**) are available to assist with species identification.

A holotype specimen of Wormskjold's collection of *Primula egaliksensis* is stored at the University of

Figure 2. The first illustration of *Primula egaliksensis*, included with the description of the species in Flora Danica (Wormskjold 1816). This illustration, although artistically pleasing, is misleading. The leaves of *P. egaliksensis* are not pointed as shown in this illustration, and the flowers are portrayed here as disproportionately large.

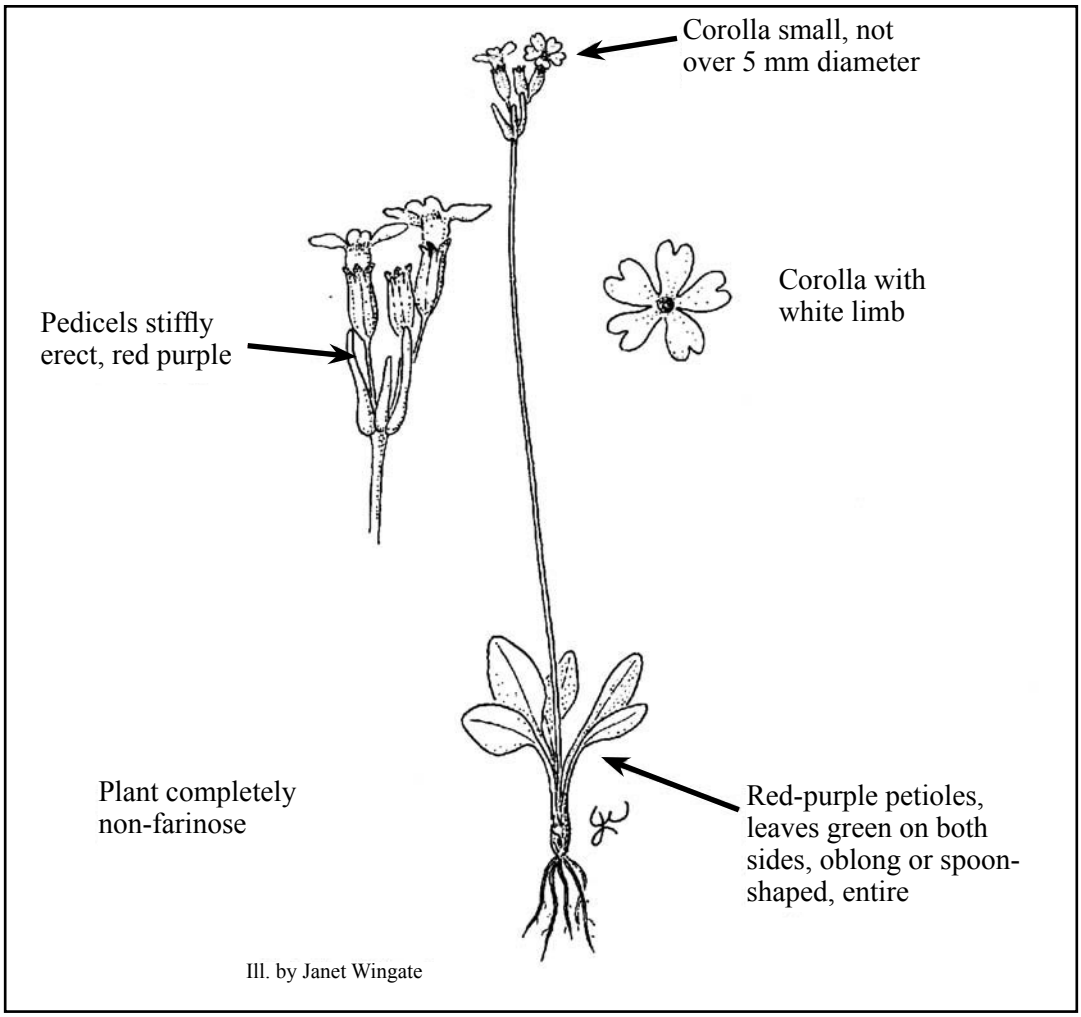

Figure 3. Illustration of *Primula egaliksensis* (from Spackman et al. 1997) by Janet Wingate, showing diagnostic characteristics.

Copenhagen Herbarium (C), and an isotype specimen is deposited at the Royal Botanic Garden in Edinburgh, Scotland (E) (Kelso 1991). There may also be an isotype specimen housed at the Conservatoire et Jardin Botaniques de la Ville de Genève (G) in Switzerland (Fenderson 1986).

Several taxa have been described over the years that were subsequently reduced to synonymy with *Primula egaliksensis* (**Table 2**). Based on his observations of specimens and plants in the field, Fernald (1928) recognized in Newfoundland that what Warming (1887, as cited in Kelso 1991) had called *P. stricta* var. *groenlandica* was merely a purple-flowered variant of the white-flowered plant described by Wormskjold.

Hultén (1970) reported that *Primula egaliksensis* was found in "a very isolated spot" in Colorado by William A. Weber, but no discovery date was provided. The discovery of *P. egaliksensis* in South Park is described by Weber (1955) as follows:

> "Mr. Hubert Vogelman, who is studying the cytotaxonomy of *Primula*, discovered *Primula egaliksensis* while making a routine check of specimens in the University of Colorado Herbarium. Several individuals of this Arctic species were mixed on a sheet of *P. incana* collected almost twenty years ago by Ramaley [collection number 16881 on July 13, 1939 with William Gambill at COLO, originally identified as *P. americana*]. The locality, other than "north end of South Park", was not given. By a coincidence, I had collected *P. incana* near Jefferson a few days before Vogelman arrived, and a quick examination showed that my collection also contained a mixture of the two species.

Table 2. Synonymy of *Primula egaliksensis*.

Synonym	Authority	Reference	Source of Reference
P. stricta Hornemann *var. groenlandica*	Warming	Warming 1887	Kelso 1991
P. farinosa var. *groenlandica*	(Warming) Pax	in Engler, pro parte	Kelso 1991
P. egaliksensis forma *violacea*	Fernald	Fernald 1928	Kelso 1991
P. sibirica	Hooker pro parte	Hooker 1838	Kelso 1991, Richards 2003
P. egalliccensis	Lehman	Mongr. Gen. Prim. 64. 1817	Fenderson 1986
P. groenlandica	(Warming) W.W. Sm. & G. Forrest (Richards 2003 cites (Warming)Balfour)	Balfour 1913	Kartesz 1999, Richards 2003
P. sibirica Jacq. var. *minor*	Duby	Duby 1944	Richards 2003
P. sibirica Jacq. var. *arctica*	Fernald non Pax	Fernald 1926	Richards 2003
P. borealis	Gray pro parte non Duby	Gray 1878, Duby 1843	Richards 2003

> "On July 11, we both returned to the South Park locality and found *Primula egaliksensis* to be abundant in the wet meadows of the north end of South Park for at least a mile on each side of the village of Jefferson" [collection number 8762 with Hubert Vogelman at COLO) on July 11, 1954 at the "north end of South Park, one mile east of Jefferson," on which "new to United States" was noted].

Since Weber and Vogelman's discovery, *Primula egaliksensis* has been documented in a number of sites in the northwestern portion of South Park, Colorado through collections and element occurrence records. Cooper (1990) identified many new occurrences in a study of South Park fens, in which he recognized the unique chemistry and flora of these wetlands. It was his work that identified High Creek Fen as the best example of an extreme rich fen wetland in Colorado, leading eventually to its purchase by The Nature Conservancy (The Nature Conservancy 2005). Sanderson and March (1996) conducted a survey of the extreme rich fens of South Park in which other occurrences of *P. egaliksensis* were found. Tass Kelso and Betsy Neely also discovered several occurrences of *P. egaliksensis*. *Primula egaliksensis* is well-documented in South Park through collections made by these experts and others, deposited at regional herbaria.

Primula egaliksensis was first found in Wyoming by Erwin Evert at Swamp Lake in 1984 (Fertig 1996), who collected it with Ron Hartman on August 12 of that year. Walt Fertig found a second occurrence in Wyoming on the east bank of the Green River in Sublette County in 1990 (Fertig et al. 1991, Fertig 1996).

Technical description (from Kelso 1991 and Kelso personal communication 2005)

Plants slender, completely efarinose. Scape 4 to 12.5 (up to 25) cm tall. Leaves distinctly pedicellate, including the petiole 1.5 to 5.5 cm long, blade elliptical, to 0.9 cm wide, 0.7 to 2.5 cm long, margins entire, obscurely undulate or slightly denticulate in age. Involucral bracts lanceolate, to 0.6 cm long, distinctly saccate but not auriculate at the base, somewhat involute above. Umbel 1 to 3 (6) flowered, pedicels pendant, 0.2 to 0.9 cm long. Flowers homostylous. Calyx cylindrical, obscurely ribbed, 0.4 to 0.6 cm long, green or with purple stripes, divided to 1/3 by teeth with glandular cilia on the margins. Corolla white or lavender, throat yellow; limb 0.6 to 0.8 cm wide, slightly emarginate, tube 0.6 to 0.8 cm long, equal to or slightly exserted from the calyx. Stamens ca. 0.75 mm long, anthers located adjacent to stigmas in upper one third of corolla tube. Pollen 5-syncolpate. Stigma cylindrical. Capsule narrowly cylindrical, up to 1.2 cm long, ca. 0.1 cm in diameter. Seeds green to light brown, obscurely reticulate, to 0.3 mm long.

Non-technical description

Primula egaliksensis has several distinguishing characteristics that are useful in field identification. It is a perennial herb of small stature, reaching 20 to 25 cm in very large plants, but typically much shorter. Its inflorescence usually consists of one to three (occasionally up to six) small flowers, borne on a leafless flowering stem in a small, umbel-like cluster. The flowers are white or lavender or sometimes pinkish

(**Figure 4**); the color morphs are about equally common, and adjacent occurrences are possible. The flowers are small (less than 8 mm across) with five wedge-shaped petals. *Primula egaliksensis* has a basal rosette of spoon-shaped, non-mealy leaves (Douglas et al. 1991, Kelso 1991, Fertig 1996). The flowers of *P. egaliksensis* are homostylous (Smith and Fletcher 1943, Kelso 1991, Fertig 1996, Mast et al. 2001, Richards 2003), meaning that anthers and stigmas are at the same level relative to each other. The leaves of *P. egaliksensis* may have their edges curled underneath (Mast et al. 2001), but this is not obvious on most specimens. The fruit of *P. egaliksensis* is a distinctive narrow capsule that opens at the top when ripe but is difficult to find among surrounding vegetation (Mills and Fertig 1996). This species is most easily identified in flower, when it best distinguishes itself from dense surrounding vegetation (Mills and Fertig 1996). Diagnostic characteristics of *P. egaliksensis* are portrayed in **Figure 3**.

Pollen

The most important diagnostic characteristics of section *Armerina* for taxonomic purposes are its pollen morphology and base chromosome numbers (typically 10 or 11) (Richards 2003). *Primula egaliksensis* has a unique pollen type best described as 5-stephanosyncolpate, which presumably has resulted from its hybrid origin between species in sections *Aleuritia* (3-syncolpate pollen) and *Armerina* (6-stephanocolpate pollen) (Richards 2003). The 5-stephanosyncolpate pollen of *P. egaliksensis* has five longitudinal grooves that may or may not fuse at the apex. Large exine reticulations in *P. egaliksensis* parallel those seen in *P. nutans*; reticulations in section *Aleuritia* are much smaller in diameter (Kelso personal communication 2005).

Figure 4. *Primula egaliksensis*. (A) photograph by Tass Kelso (used with permission). (B) photograph by David G. Anderson.

Chromosomes

Chromosome number is remarkably stable within groups of *Primula* and has been used as a diagnostic character in sectional classification (Richards 1993). *Armerina* members typically have a base chromosome number of 10 or 11 (Richards 2003). However, *P. egaliksensis* is unlike other members of section *Armerina* in this regard. *Primula egaliksensis* is a tetraploid whose populations have a base chromosome number of either 9 or 10 (Kelso 1991, Richards 2003). Plants in Colorado (Löve et al. 1971, Kelso 1991), Greenland (Jørgenson et al. 1958), and Alaska (Johnson and Packer 1968, Kelso 1991, Murray and Kelso 1997) are 2n = 4x = 36 with a base chromosome number of 9. However, a base chromosome number of 10 (2n = 4x = 40) was observed in northeast Siberia (Zhukova et al. 1973, Zhukova 1982) and Labrador (Hedburg 1967). Of these observations, Richards (2003, p. 254) wrote "Siberian plants have 2n = 40 as predicted, but plants from Alaska, Greenland, and Colorado have apparently lost two pairs of chromosomes, having 2n = 36. The isolated localities in the Rocky Mountains suggest that *P. egaliksensis* arose during an interglacial period and during glacial periods had a wider distribution from which the southern stations are now relictic (as is also the case for *P. incana*, which grows with it in Colorado)." It is important to note that the chromosomes of *Primula* species are tiny and difficult to count; the observed differences could easily be due to counting error (Kelso personal communication 2004). Aneuploidy is common in *Primula*, suggesting that chromosomes may have been lost in the 2n = 36 populations. The difference in number of chromosomes does not necessarily suggest that these races are different species (Kelso personal communication 2004).

Distinguishing Primula egaliksensis from P. incana

In Colorado, *Primula egaliksensis* can be difficult to distinguish from *P. incana*, and accurate identification takes practice (Kelso personal communication 2004). Viewing herbarium specimens prior to attempting field identification is helpful. The two species are often found growing next to each other in South Park, but *P. incana* has not been found with *P. egaliksensis* in Wyoming (Fertig 1996).

A key characteristic in distinguishing *Primula egaliksensis* from *P. incana* in the field is the complete lack of farina on most individuals of *P. egaliksensis*. On *P. incana*, farina is usually present on the undersides of the leaves, on the floral bracts, and on the upper flowering stem, where it forms a conspicuous yellowish-white coating. This is most evident on young plants; older plants are typically less farinose to almost glabrous. *Primula egaliksensis* is typically completely efarinose, with the upper scape appearing almost shiny (Fertig 1996, Sanderson and March 1996, Sanderson personal communication 2005). **Table 3** is a summary of all characteristics useful in the diagnosis of these species, and **Figure 3** illustrates diagnostic characteristics of *P. egaliksensis*.

Other look-alikes

Particularly when vegetative, *Primula egaliksensis* may be confused with *Parnassia parviflora*, which is very common throughout South Park. *Parnassia* is characterized by leafy stems, leaves that are less distinctly petiolate than those of *Primula egaliksensis*, white flowers, and broad, oval-shaped fruits (Sanderson and March 1996). *Parnassia parviflora* is found with *Primula egaliksensis* in Wyoming (Fertig 1996). *Dodecatheon* species in fruit differ from *P. egaliksensis* in having broader capsules. *Stellaria longipes* occurs with *P. egaliksensis* in Wyoming and has flowers with five deeply-lobed white petals (superficially appearing like 10 petals), opposite leaves, and weak stems with opposite leaves (Dorn 1992, Fertig et al. 1994, Mills and Fertig 1996).

Primula egaliksensis is distinguished from the other member of section *Armerina* in North America, *P. nutans*, by the involucral bracts (distinctly auriculate at the base in *P. nutans*, but merely saccate in *P. egaliksensis*) and the size of the flowers (8 mm or more in diameter in *P. nutans*, less than 8 mm in diameter in *P. egaliksensis*) (Kelso 1991). These species are not sympatric within Region 2. *Primula egaliksensis* also has morphological characteristics that are very similar to members of section *Aleuritia* (Kelso 1991). Unlike members of section *Aleuritia*, *P. egaliksensis* is efarinose, but it has glands that are similar to those in section *Aleuritia* in addition to the jointed hairs characteristic of section *Armerina* (Kelso personal communication 2005).

Given the popularity of *Primula* species among gardeners, it is not surprising that some authors have compared *P. egaliksensis* with other *Primula* species. There has been much critique of the value of *P. egaliksensis* as an ornamental. Nicholls (2002) wrote "This homostylous species is not attractive," and quoted Lunn (1990, reference not provided in Nicholls 2002) as saying "this plant will never be the belle of the garden." Richards (1993) similarly noted that "this little

Table 3. Diagnostic characteristics for distinguishing *Primula egaliksensis* from *P. incana*. From Douglas et al. (1991), Kelso (1991), Richards (2003), Kelso personal communication (2004), Kelso personal communication (2005), and Johnson personal communication (2005).

Characteristic	*Primula egaliksensis*	*Primula incana*
Leaf shape	rounded, not toothed	elliptic or oblanceolate, slightly toothed on margins or not
Leaf petiole	distinctly petiolate	blade gradually narrowing to a broadly winged petiole
Bracts	shortly saccate, not farinose	saccate to slightly gibbous, heavily farinose
Farina	farina completely absent; upper scape almost shiny and purplish	heavily farinose in young plants, becoming less so with age, rarely efarinose in some populations; undersides of leaves, bracts, and on upper scape particularly farinose on; traces of farina typically remain on the bracts and/or calyces of older plants
Glands	glandular articulated hairs and "light bulb shaped" glands	"light bulb shaped" glands but no glandular articulated hairs
Petals	slightly notched, white or lavender	notched, lavender
Capsule	narrowly cylindrical with parallel sides	broader at the base, more broadly cylindrical
Pollen	5-stephanosyncolpate	4-syncolpate
Ploidy	2n = 36,40	2n = 50,72

species has no garden merit." However, Polunin (1940), in comparing *P. egaliksensis* with *P. stricta*, regarded *P. egaliksensis* as "more slender but equally beautiful."

Descriptions, photographs, keys, and illustrations

There are numerous sources of descriptions, photographs, keys, and illustrations of *Primula egaliksensis*, which vary considerably in their thoroughness, emphasis, and availability.

Kelso (1991) includes a very good description and illustration. Fertig et al. (1994) and Spackman et al. (1997) are useful resources that offer descriptions, photographs of plant and habitat, illustrations, and other useful information, and both are available online. Weber and Wittmann (2001) and Dorn (1992) are both valuable keys for field identification in Colorado and Wyoming, respectively.

Thorough descriptions of *Primula egaliksensis* are available in Polunin (1940), Smith and Fletcher (1943), Fernald (1950), Porsild (1951), Polunin (1959), Hultén (1968), Hultén (1971), Tutin et al. (1972), Welsh (1974), Porsild and Cody (1980), Fertig (1996), Mills and Fertig (1996), Cody (2000), Fertig (2000), and Richards (2003). *Primula egaliksensis* is also briefly described in Hughes and Blackwell (1987), Douglas et al. (1991), Dorn (1992), Hall (1995), Weber and Wittmann (2001), and Nicholls (2002). Keys for identifying *P. egaliksensis* outside of Region 2 are included in Polunin (1940), Polunin (1959), Welsh (1974), Porsild and Cody (1980), Douglas et al. (1991), Hall (1995), and Cody (2000). Richards (2003) includes a key to all members of *Primula*. Kelso (1991) includes a key to sections *Armerina* and *Aleuritia*. Distribution maps appear in Hultén (1968), Hultén (1971), Porsild and Cody (1980), Fertig et al. (1994), Spackman et al. (1997), and Cody (2000). Illustrations of *P. egaliksensis* are available in Britton and Brown (1913), Polunin (1959), Hultén (1968), Porsild and Cody (1980), Kelso (1991), Fertig et al. (1994), Hall (1995), Fertig (1996), Mills and Fertig (1996), Spackman et al. (1997) (**Figure 3**), Cody (2000), and Houston et al. (2001). The small illustration in Britton and Brown (1913) is available online at USDA Natural Resources Conservation Service (2004). The plate of *P. egaliksensis* accompanying its original description (Wormskjold 1816) portrays the plant and the homostylous flower of *P. egaliksensis*, and it is available online at Danish National Library of Science and Medicine (2005).

Distribution and abundance

Pleistocene distribution patterns and phytogeography

Many authors have speculated on the origins and historic distribution of members of *Primula*, including *P. egaliksensis*. Many *Primula* species have disjunct distributions in North America (Kelso 1992). These disjunctions are typically attributed to the phytogeographical effects of glaciation (Weber 2003).

Although the several episodes of glaciation that occurred during the Pleistocene certainly affected the distribution of plants, the last glacial maximum, the Wisconsin, is the episode that contributed most to defining the distribution of modern North American biotas (Brouillet and Whetstone 1993). The Wisconsin glacial maximum occurred about 18,000 years before the present. Two confluent ice sheets, the Cordilleran in the Canadian Rockies and the Laurentide covering the northern half of the continent east of the Rocky Mountains, constituted most of the continental ice cover. Discontinuous mountain glaciers were also present in high ranges of the western United States (Richmond 1965, Brouillet and Whetstone 1993, Delcourt and Delcourt 1993). In the Southern Rocky Mountains, during the maximum extent of Pleistocene glaciation, the highest elevations were nearly covered by glacial ice, and most major valleys were glaciated above about 8,000 ft. (Richmond 1965, Benedict 1991).

During the peak of the last continental glaciation, boreal forest communities dominated a belt south of the Laurentide ice to approximately 34° N latitude, and extended west across the Great Plains. Comparison of modern and fossil pollen assemblages indicates that these communities were similar in composition to modern boreal forest communities (Delcourt and Delcourt 1993). The southward retreat of boreal vegetation during the period of glacial expansion created patches of habitat suitable for colonization by arctic and boreal species, and some, possibly including *Primula egaliksensis*, remained in these refugia when the ice sheets retreated and species' ranges again moved north (Kelso 1992, Gates 1993).

Preliminary results by Conti (2004) suggest that the genetic profiles of populations of *Primula egaliksensis* from central Alaska differ from the genetic profiles of populations from other regions. If confirmed, this result supports the proposed refugial role of central and northeastern Alaska during Pleistocene glacial maxima (Conti 2004). *Primula egaliksensis* is now widespread across northern North America from Alaska to Newfoundland in areas that were covered by ice until the late Pleistocene (Kelso 1991).

Migration of *Primula egaliksensis* has been strongly to the east rather than to the west, probably from Alaska where its putative parents (*P. nutans* and *P. mistassinica*) are sympatric (**Figure 1**; Kelso 1992). The presence of *P. egaliksensis* in Greenland to the east and Colorado to the south can be traced to dispersal routes along coastlines and rivers, which may have followed different corridors as the Laurentide Ice Sheet melted than those of modern rivers (Kelso 1992). In contrast, *P. incana*, with which *P. egaliksensis* is sympatric in Colorado, has affinities with other members of section *Aleuritia* in eastern North American forests, from which it appears to have dispersed north to the Arctic.

Fernald (1925) included *Primula egaliksensis* among a group of species he considered "Cordilleran" that occur as disjuncts in eastern North America. However, Weber (2003) states that *P. egaliksensis* is better defined as part of a "remnant of the Tertiary alpine floras that must have been present in Greenland and northeastern North America as well as the western mountains."

As inferred from palynological evidence obtained from a sediment core at Lost Park, the late Pleistocene (approximately 12,000 YBP) environment in South Park was probably 3 to 3.5 ℃ cooler in winter than at present, with higher winter precipitation (Vierling 1997). This is suggested by the dominance of steppe vegetation in South Park (principally *Artemisia*). A shift to warmer, drier conditions dominated by a summer monsoon began approximately 9000 YBP, a trend that reversed approximately 1800 YBP (Vierling 1997).

Global distribution

Primula egaliksensis is found in widely disjunct occurrences across much of northern North America (**Figure 1**). It ranges as far west as the Chukotka Peninsula, Russia (Kelso 1991, Fertig et al. 1994, Guggisberg et al. 2003, Kelso personal communication 2004, Guggisberg personal communication 2005, Guggisberg et al. 2006). The easternmost records are from northern Iceland; it is not known from Scandinavia (Fenderson 1986, Kelso personal communication 2004). Outlying occurrences in southern Greenland (Wormskjold 1816, Polunin 1940, Fernald 1950, Polunin 1959, Hultén 1968, Feilberg et al. 1984, Fenderson 1986, Kelso 1991, Fertig et al. 1994, Richards 2003, and others) may currently represent the eastern limit of the range of *P. egaliksensis*, since it appears to have been extirpated in Iceland (Guggisberg personal communication 2005, Guggisberg et al. 2006). Although the range of *P. egaliksensis* extends beyond North America, Kelso (1992) describes *P. egaliksensis* as "almost entirely North American, at least in its distribution if not in its genetic heritage." Within North America it is known from Alaska (Fernald 1950, Wiggins and Thomas 1962, Hultén 1968, Douglas et al. 1991, Hall 1995), Yukon Territory (Hultén 1968, Welsh 1974, Douglas et al. 1991), the eastern Canadian Arctic (Polunin 1940, Polunin 1959, Douglas et al.

1991), British Columbia (Fernald 1950, Fenderson 1986, Douglas et al. 1991), Alberta (Fernald 1950), the northern third of Manitoba (Scoggan 1957), northern Ontario (Meades et al. 2004), Quebec, Labrador (Fenderson 1986), and northern Newfoundland (Fernald 1950, Fenderson 1986, Douglas et al. 1991). It ranges as far south as Wyoming (Fertig 1992, Fertig et al. 1994, Fertig 1996) and Colorado (Weber 1955, Hultén 1971, Douglas et al. 1991, Kelso 1991, Fertig et al. 1994, Spackman et al. 1997). *Primula egaliksensis* has not yet been found in Montana but more surveys are needed, as there is probably suitable habitat there (Kelso personal communication 2004).

Primula egaliksensis has a wide geographic range, but it is not abundant anywhere (Kelso 1991). Even in Alaska where it is relatively widespread, it is described as widely disjunct and locally rare. Hall (1995) reports it from scattered sites throughout Alaska. It is reportedly rare in the foothills of the Brooks Range and on the Coastal Plain (Wiggins and Thomas 1962). Welsh (1974) reports *P. egaliksensis* as "disjunct at widely separated locations almost throughout Alaska and the Yukon; eastward to Labrador and Greenland and south to BC." In the Northwest Territories, it is reported as "rare, but gregarious" (Polunin 1940). *Primula egaliksensis* is infrequent in northern and southeastern British Columbia and Vancouver Island (Douglas et al. 1991). It is also rare in Chukotka (Kelso personal communication 2004) and Greenland (Feilberg et al. 1984). *Primula egaliksensis* is considered vulnerable in British Columbia, imperiled in Newfoundland, Labrador, and Colorado, and critically imperiled in Wyoming (**Figure 5**; NatureServe Explorer 2005).

Distribution in and near Region 2

Primula egaliksensis is an arctic North American species with disjunct occurrences in the Southern Rockies (Hultén and Fries 1986, Weber 2003, Kelso personal communication 2004). In the contiguous United States, *P. egaliksensis* is restricted to three isolated areas (Fertig 1996). Two are in northwestern Wyoming in Park and Sublette counties (Fertig et al. 1994), and one is in South Park in central Colorado (Spackman et al. 1997, Colorado Natural Heritage Program 2005).

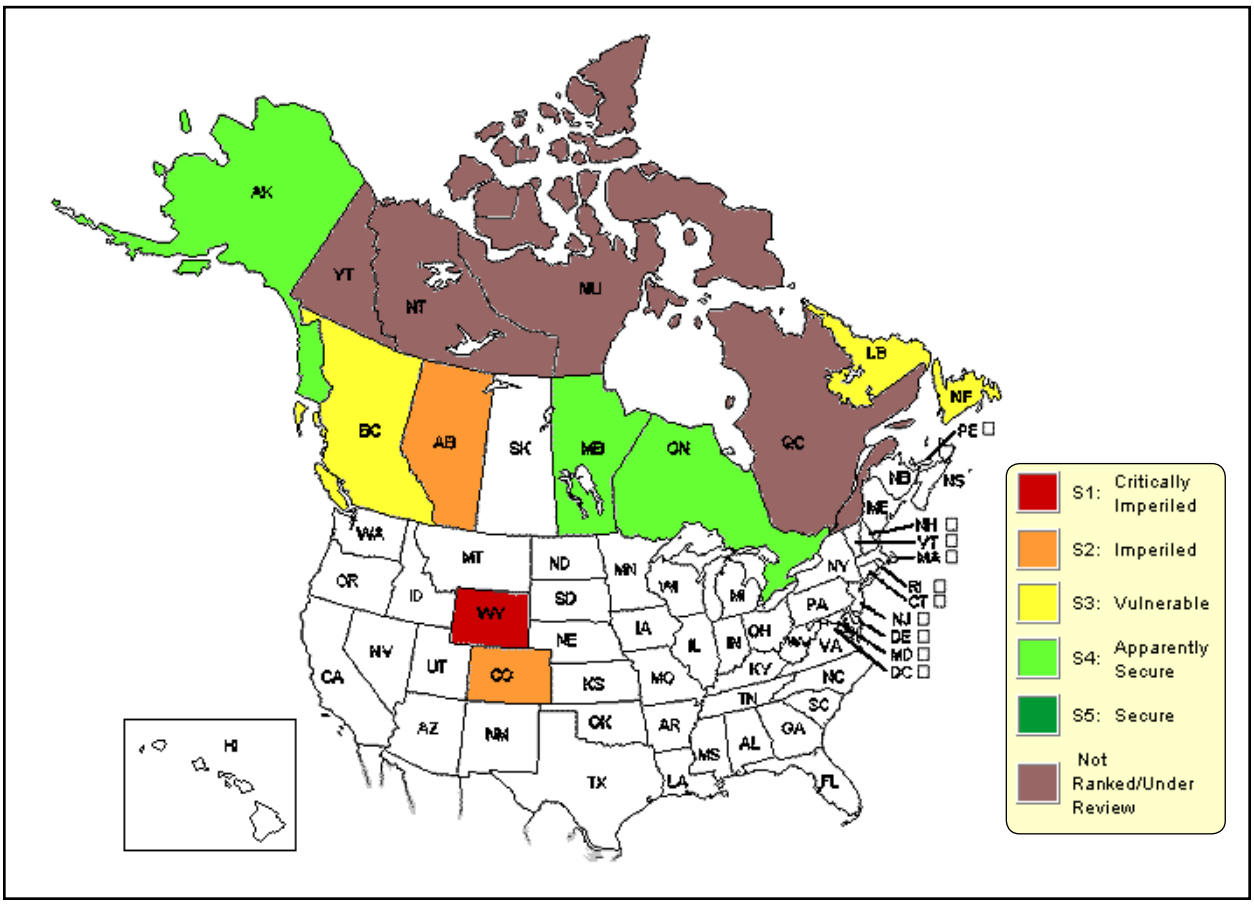

Figure 5. Conservation status ranks for *Primula egaliksensis* in the states and provinces in North America in which it occurs (NatureServe Explorer 2005).

Occurrences in South Park in Colorado and Swamp Lake in Wyoming fall within the administrative boundary of Region 2. The occurrence in Sublette County, Wyoming is on the Bridger-Teton National Forest in Region 4. **Figure 6** is a map of the distribution of *P. egaliksensis* in the states of Region 2. **Table 4** is a summary of the known occurrences of *P. egaliksensis* in Regions 2 and 4. The distribution of *P. egaliksensis* in the states of Region 2 is limited to calcareous wetlands, primarily extreme rich fens. It is unlikely that *P. egaliksensis* occurs in Colorado outside of South Park (Coles 2002). Swamp Lake, Wyoming is separated from High Creek Fen in Colorado by 650 kilometers (Cooper 1996).In Wyoming, *Primula egaliksensis* is known only from Swamp Lake in the Clarks Fork Valley in the northern Absaroka Mountains (Shoshone National Forest), and the Upper Green River Valley on the west slope of the Wind River Range (Bridger-Teton National Forest) (Fertig 1998, Fertig 2000, Welp et al. 2000, Wyoming Natural Diversity Database 2004). In Colorado, *P. egaliksensis* is known from 20 occurrences in the northwestern portion of South Park (Sanderson and March 1996, Spackman et al. 1997, Colorado Natural Heritage Program 2005). These occurrences grow along streams and in alkaline wet meadows and peatlands from the north end of South Park to Antero Reservoir (Cooper 1990). One occurrence is on the Pike National Forest. **Figure 7** illustrates the distribution of *P. egaliksensis* in South Park.

Abundance

In Wyoming, the total population of *Primula egaliksensis* is estimated at 10,000 to 14,000 individuals on 105 acres (**Table 4**; Fertig 1998, Fertig 2000, Welp et al. 2000, Wyoming Natural Diversity

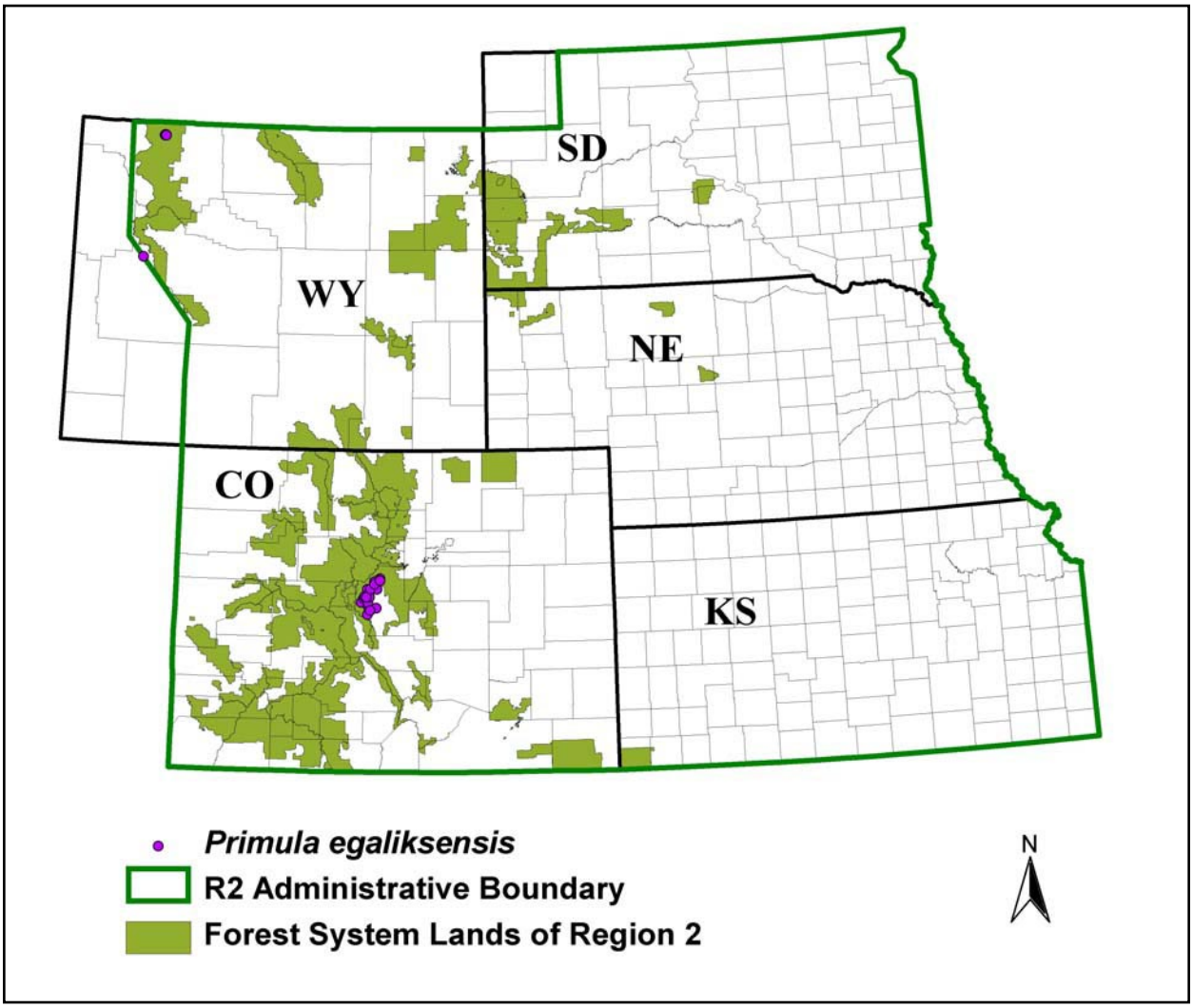

Figure 6. Distribution of *Primula egaliksensis* in the states of Region 2, relative to the administrative boundary and National Forest System land.

Table 4. Summary information for the known occurrences of *Primula egaliksensis*. Source I.D. is Colorado Natural Heritage Program and Wyoming Natural Diversity Database element occurrence number unless otherwise noted. Key to element occurrence (EO) ranks: A = excellent estimated viability, B = good estimated viability, C = fair estimated viability, E = not evaluated. Occurrences on National Forest System land are in bold type.

Source ID	County/ State	Location	Owner	Date last observed	EO rank	Abundance	Elevation (ft.)	Habitat and notes
1	Park/ CO	Wahl Ranch (under a conservation easement held by Colorado Open Lands)	Private	23-Jul-1995	A	~300-5,000 individuals	9,480-9,720	A large expanse of extreme rich fen emanating from at least two groundwater discharge areas. Soil: moist to wet black loam. Slope: 0-2%. Many state-rare plants are present here, as well as *Ptilagrostis porteri* and *Sisyrinchium pallidum*. Hummocks found across the area provide habitat for the *Kobresia simpliciuscula-Scirpus pumilus* community. Also with *Thalictrum alpinum*, *Salix candida*, *Primula incana*, *Dodecatheon pulchellum*, *Pedicularis*, *Polygonum*, and *Eleocharis*. Also in a roadside right-of-way with *Taraxacum officinale* and *Achillea lanulosa*, and in an irrigated hay meadow cut in the fall, dominated by sedges, rushes, and *Caltha leptosepala*. *Primula incana* was not observed at this site.
2	Park/ CO	Middle Fork South Platte River	Private	24-Jul-1995	C	~300 individuals	9,500	Growing on grass and sedge hummocks possibly created by cattle trampling. Associated taxa: *Carex*, *Poa*, *Primula incana*, *Salix*, *Pedicularis*, *Plantago*, *Gaura*, and *Ranunculus*. Area is fenced and disturbed; a new canal and bulldozer were observed nearby. Close to a highway.
3	Park/ CO	N Tarryall Creek	Private	21-Jun-1985	C	~1,000 individuals	9,645	Meadow and moist slope beside creek, moist soils with sedges, Poas, and scattered willows. Occurrence is grazed by cattle.
4	Park/ CO	Jefferson East	Private	07-Jul-1989	B	~1,000 individuals	9,500	In wet rich black loam in an irrigated hay meadow and adjacent to road right-of-way. Slope: 0%. Associated taxa: *Carex*, *Primula incana*, *Dodecatheon pulchellum*, *Poa*, *Juncus*, and *Sisyrinchium montanum*. Potential habitat extends beyond occurrence in wet hay meadows. Plants in the right-of-way are vulnerable to road maintenance. *Primula incana* is abundant at this site.
5	Park/ CO	Red Hill Ranch	Private/ possibly Bureau of Land Management Royal Gorge Field Office	29-Jun-1985	C	~200 individuals	9,590	Wet sedge meadow on both sides of creek. Grazed pasture dominated by sedges. Aspect: flat and south. Soil: wet black loam. Slope: 0-2 degrees. Associated taxa: *Carex*, *Juncus*, *Pedicularis*, *Poa*, *Primula incana*, and *Triglochin*. Population is grazed by cattle.
6	Park/ CO	Four Mile Creek	Private	15-Jun-1985	C	~50 individuals	9,700	With *Dodecatheon pulchellum*, *Dasiphora fruticosa*, *Salix*, *Poa*, and *Carex*. Slope: flat. Area is grazed; grazing and trampling is causing hummock formation.
7	Park/ CO	High Creek	Private: The Nature Conservancy	28-Jul-1992	A	3,000 or more individuals	9,290	On peat hummocks and flats in extreme rich fen, fed by calcareous seeps. Often on hummocks with sedges, rushes, and moss, with *Primula incana*, *Carex microglochin*, *Sisyrinchium pallidum*, and *Kobresia simpliciuscula*; high species diversity. Geology: Holocene alluvium in minerotrophic peatland. Plants scattered over a large area; locally common.

Table 4 (cont.).

Source ID	County/ State	Location	Owner	Date last observed	EO rank	Abundance	Elevation (ft.)	Habitat and notes
10	Park/ CO	Michigan Creek Drainage, Jefferson	Probably Private	24-Jun-1963	H	Not reported	9,600	Wet meadows.
11	Park/ CO	Upper Four Mile Creek	State of Colorado Land Board	09-Jul-1995	B	At least 200 individuals	9,780-9,850	Large willow carr with small patches of fen. Plants are on hummocks in wet fen areas. Population is concentrated in some areas south of a creek, with scattered individuals elsewhere. Geology: Pleistocene outwash. Soil: Peat. Associated taxa: *Salix*, *Deschampsia caespitosa*, *Carex*, and *Juncus*. The willow carr is heavily grazed in the summer. Willows and sedges are well-browsed except in wettest areas.
12	Park/ CO	Antero Reservoir NW	State of Colorado Land Board/ Private	04-Aug-1995	B	hundreds to ~1,500 individuals	8,940-8,960	This occurrence is part of an extreme rich fen complex on the northwest corner of the reservoir and on the outer river floodplain. In the peat area, hummocks are dominated by *Kobresia simpliciuscula*. Plants are evenly distributed throughout the wetland on hummocks. Swales are dominated by *Carex simulata* and others. Many state rare species occur here. *Carex scirpoidea* and *Senecio pauciflorus* occur mainly on the south edge of the peat on a light colored soil with a much lower organic content. Geology: Pleistocene alluvium overlaying Maroon fen. Slope: 0%. Soil: Peat. Associated taxa: C*arex*, *Juncus*, *Parnassia*, *Salix candida*, *Sisyrinchium pallidum*, and *Limnorchis hyperborea*. *Primula egaliksensis* is well developed here and there appears to be a relatively large population. However, an old railroad grade runs within 200 meters to the west of the population, and the area west of the railroad has been mined for peat. The railroad grade, peat mining, and ditching upstream have altered the hydrology of the area. Nonetheless, this occurrence is relatively large and appears robust. Denver Water is currently in the process of acquiring the lower portion of the PCA from the State Land Board for future expansion of Antero Reservoir.
13	Park/ CO	Crooked Creek	State of Colorado Land Board	27-Jul-1992	C	~40 individuals	9,745	Calcareous hummocks adjacent to *Carex nebraskensis/ Deschampsia caespitosa*. Mostly found on the sides of hummocks. Geology: Wisconsin outwash. Soil: Peat. Associated taxa: *Packera pauciflora*, *Carex scirpoidea*, and *Thalictrum alpinum*. Slope: 0%.
15	Park/ CO	Elkhorn Rd.	Probably Private/ Possibly Bureau of Land Management Royal Gorge Field Office	29-Jun-1985	E	Not reported	9,300	Dry hay meadow adjacent to rushes and sedges, disturbed.

Table 4 (cont.).

Source ID	County/ State	Location	Owner	Date last observed	EO rank	Abundance	Elevation (ft.)	Habitat and notes
17	Park/ CO	Fremont's Fen	Colorado Division of Wildlife/ Private	24-Aug-1995	C	~24 individuals	9,600	This site is an expansive occurrence of the *Kobresia myosuroides/ Thalictrum alpinum* plant association, estimated at nearly 1 mile in length and 1/5 mile in width. Most plants are growing on the sides of hummocks. The *Kobresia* has formed very large hummocks, sometimes approaching 50 cm in height. Considerable degradation to the area due to peat mining has occurred, although the area occupied by *Primula egaliksensis* and *Ptilagrostis porteri* appears hydrologically intact and viable. Light grazing is occurring at this location.
18	Park/ CO	Jefferson	Probably Private	11-Jul-1954	H	Not reported	9,500	In a wet sedge meadow with *Primula incana*. Discovered in Colorado at this site by Weber and Vogelman.
19	Park/ CO	Sweetwater Ranch	Private	23-Jul-995	C	~300 individuals	9,140-9,160	The north end of this site is a well-developed peatland with scattered blue spruce, with a deep ditch running down the middle of it. The state-rare plants *Salix candida*, *Scirpus pumilus*, and others) and plant communities (fen communities such as *Kobresia myosuroides-Thalictrum alpinum*) on this northern end appear robust despite the ditch, probably because they still receive sufficient groundwater. This area is not currently heavily grazed, if grazed at all. Immediately south of the spruce trees is a small reservoir and patches of sedge meadow with only a few signs of extreme rich fen plants. This area was likely an extension of the peatland to the north, but it has been significantly altered by hydrologic modifications and grazing. On the southern end of this site, there is a series of marly mires with small but well-developed examples of classic extreme rich fen plant communities. Several rare plant species occur in the southern end as well, but most show signs of heavy, deleterious impacts from cattle. Surrounding lands are all mesic to dry grasslands. Portions of the area are heavily grazed, and hydrologic modifications have occurred.
20	Park/ CO	High Creek at Warm Springs	Private	24-Aug-1995	C	20-30 individuals	9,830-9,970	In its entirety, this site stretches for about 1.5 miles. Much of the width of the riparian zone is peatland, and along almost the entire length, springs (groundwater discharge zones) replenish the surface and stream. Groundwater discharge is especially common along the west edge of the riparian area along the base of the hill. The extreme rich fen elements (both communities and plants) occur farther downstream at the base of a hill, sandwiched between the hill and the creek. Although this occurrence is relatively small, it is in very nice shape, having been protected from most grazing impacts by the hill on the west and by the creek and boggy ground to the east.
21	Park/ CO	High Creek - Four Mile Creek	Probably Private	11-Jul-1990	E	Not reported	8,970	Meadows and flats, and along creek. Water source: spring and high water. Associated taxa: *Juncus balticus* 30%, *Potentilla anserina* 15%, *Carex praegracilis* 25%, *Muhlenbergia filiformis* 10%, *Deschampsia caespitosa* 10%.

Table 4 (concluded).

Source ID	County/ State	Location	Owner	Date last observed	EO rank	Abundance	Elevation (ft.)	Habitat and notes
22	Park/ CO	Salt Creek	State of Colorado Land Board	05-Aug-1990	E	Not reported	9,100	Springs along creek west of highway, in a natural wetland. With *Carex utriculata* 60%, moss 60%, *Juncus balticus* 40%, *Muhlenbergia filiformis* 30%, *Potentilla anserina* 30%.
23	Park/ CO	Crooked Creek Spring	**USDA Forest Service Region 2 Pike San Isabel National Forest**	05-Aug-1995	C	"A few"	10,040	The spring appears to be the only one of several fens that occur in this area. Fed by a small creek. Tall willows (mostly Salix monticola) characterize the upper edge of the fen, but these grade quickly into the hummock/swale system that typifies south park's extreme rich fens. Many rare plants are present here, but in very small occurrences. The lower part of the fen dried up, and presumably, elements disappeared when a large ditch was dug across the bottom of the slope.
Kelso and Maentz 97-119 COCO	Park/ CO	12 Mile Creek	Private	12-Jul-1997	C	small area, 50+ individuals	9,900	A peaty sedge fen, open, scattered forb cover, 50% graminoid cover, 50% moss cover, flat, saturated. Moss understory with *Carex* spp., *Dodecatheon*, and *Triglochin maritima*. This fen has not been mined for peat.
1	Park/ WY	Swamp Lake	**USDA Forest Service Region 2 Shoshone National Forest, Clarks Fork Ranger District, Swamp Lake Special Botanical Area**	22-Jun-2004	A	100 acres/ 2,000-4,000 individuals	6,600-6,885	Semi-wet, marly hummocks dominated by *Eleocharis* and *Triglochin*, rarer on floating mats of *Carex simulata* (Swamp Lake). Also found in partially burned (1988 fire) white spruce swamp (Oliver Gulch).
2	Sublette/ WY	North of Lower Green River Lake	**USDA Forest Service Region 4 Bridger-Teton National Forest**	06-Jul-1995	AB	2.5 acres/ 8,000- 10,000 individuals	8,000	Quaking mats and hummocks of *Deschampsia caespitosa* and *Carex simulata* at the edge of open water or shallowly flooded pinkish marl deposits. Mostly found on drier microsites within hummocks. Absent from areas with tall graminoid cover or willows. Substrate apparently derived from calcareous material (probably eroded down slope from the calcareous ridge on the west side of Osborn Mountain).

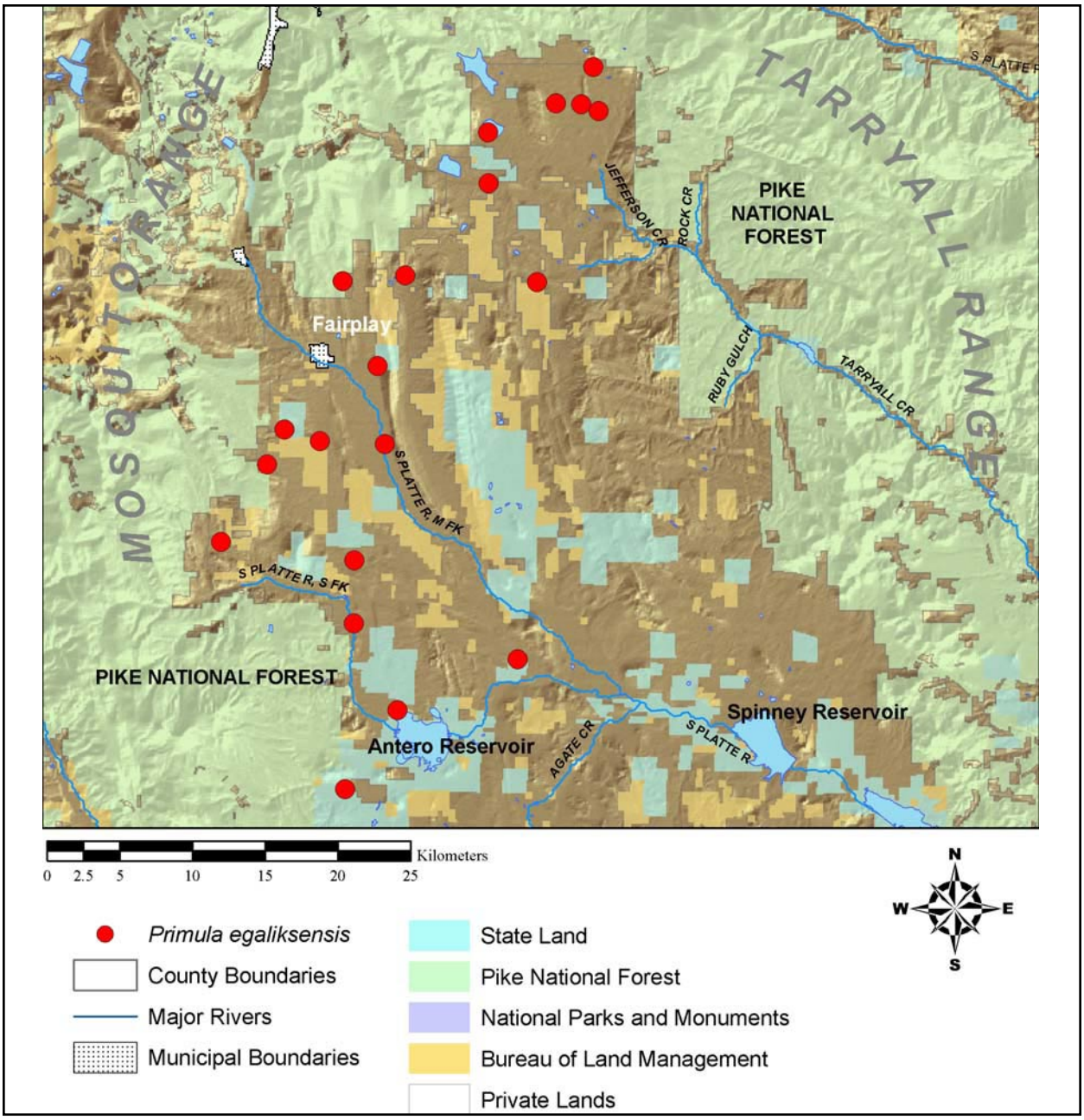

Figure 7. The distribution of *Primula egaliksensis* in South Park, Park County, Colorado, with respect to land ownership, physiographic features, major rivers, and municipal boundaries.

Database 2004). The occurrence at Swamp Lake occupies approximately 100 acres and consists of 14 sub-occurrences. Although a census has not been taken, this occurrence is conservatively estimated to contain at least 2,000 to 4,000 individuals (Fertig 1996). The Lower Green River Lake occurrence was reported to consist of only two individuals when it was first discovered in 1990 (Fertig et al. 1991). A more thorough survey in 1991 found 700 to 800 flowering plants in an area of about 5 acres (Fertig 1992). When this occurrence was revisited in 1995, 1,050 flowering, fruiting, and vegetative plants were observed in a walk-through survey. The total population size at this occurrence is estimated at 8,000 to 10,000 individuals in a 5-acre area (Fertig 1996). The Lower Green River Lake occurrence appears to be the largest population in Wyoming, but the plants occur in a very small area when compared with the Swamp Lake site.

The estimated total population of *Primula egaliksensis* in Colorado, based on element occurrence and specimen label data (**Table 4**), is between 6,800

and 13,900 individuals (Colorado Natural Heritage Program 2005). The estimates for Colorado provided by Coles (2002) and Warren (2003) are much lower ("almost certainly less than 5000 and may be less than 1000") but were based on a partial dataset. *Primula egaliksensis* may be more abundant in South Park (Kelso personal communication 2004). Because of the small flowers and generally short stature of this species, plants are inconspicuous even during the brief flowering period (Kelso 1991). **Table 5** includes a summary of population estimates for all occurrences in Wyoming and Colorado.

Population trend

The range of *Primula egaliksensis* probably changed considerably in response to climate change and glacial retreat at the end of the Pleistocene (Kelso 1992). Populations in the states of Region 2 may once have been more continuous with populations to the north. The range of *P. egaliksensis* in Region 2 probably contracted during the Holocene, leaving relict populations isolated from the main range of the species.

The Colorado population of *Primula egaliksensis* appears to be stable at present. However, occurrences are almost certainly fewer and smaller than they were historically due to the loss of habitat to peat mining (Coles 2002, Warren 2003). Other impacts, including ditching, road and railroad construction, and grazing, appear to have caused local declines in Colorado (Colorado Natural Heritage Program 2005).

Occurrences in Wyoming are also thought to be stable. Low population numbers may be due to the very limited area of suitable habitat, and not the result of a population decline (Fertig 1998, Fertig 2000, Welp et al. 2000, Handley and Laursen 2002). The occurrence at Swamp Lake, Wyoming appears stable at present, but long-term trends are unknown (Fertig 1996). The occurrence at Lower Green River Lake is probably also stable (Fertig 1996). The apparent population increase at this occurrence between 1991 (700 to 800 plants) and 1995 (8,000 to 10,000 plants) probably results from greater survey intensity rather than a true increase in the numbers of plants (Fertig 1996).

Some annual variation in populations of *Primula egaliksensis* can be expected in response to natural climatic variation. Kelso (personal communication 2004) noted that 2003 was a good year for *P. egaliksensis* in South Park, Colorado.

Habitat

General habitat description

Brief descriptions of the habitat of *Primula egaliksensis* outside Region 2 are available in numerous floras, monographs, and other sources (**Table 6**). The range-wide habitat of *P. egaliksensis* was best summarized by Smith and Fletcher (1943) as "wet meadows, edges of creeks, turfy shores, and peaty barrens." In Alaska, it is frequently reported from silty soils along creeks and braided rivers (Kelso personal communication 2004). It is reported to grow in peatlands throughout its range.

The habitats of *Primula egaliksensis* in Colorado and Wyoming are often similar to those in the boreal and arctic portions of its range. These are summarized by Richards (2003) as "flat open rather calcareous sedgy flushes in Colorado" and by Nicholls (2002) as "In wet meadows and along streams in the south central, interior, and arctic regions of Alaska. Also in Colorado and Wyoming in similar moist conditions."

Two habitat attributes are consistent throughout the global range of *Primula egaliksensis*. First, this species needs areas that remain wet all summer. Second, it requires moderately but not extremely alkaline conditions (Kelso personal communication 2004). Habitats are typically calcareous (Fernald 1950, Porsild 1951, Polunin 1959, Scoggan 1979, Fenderson 1986, Richards 2003, Guggisberg 2004). It is not found in acidic peatlands. Members of section *Aleuritia* (to which *P. mistassinica*, the maternal parent of *P. egaliksensis* belongs) are calciphilic, though not necessarily true calciphiles (Kelso personal communication 2004, Kelso personal communication 2005), and *P. egaliksensis* may also have basophilic tendencies in some portions of its range.

In Region 2, *Primula egaliksensis* is most often associated with the Montane Fen ecological system (Rondeau 2001), which corresponds to the Rocky Mountain Subalpine-Montane Fen ecological system of NatureServe (2005). Montane fens occur as a "small patch" type of system, characterized by distinct boundaries, specific environmental requirements, and strong links to the surrounding landscape (Anderson et al. 1999). Fens usually form where groundwater intercepts the soil surface, often at low points within the landscape or on slopes (Rondeau 2001). Groundwater discharge maintains the water level at near constant temperatures and levels, at or near the soil surface.

Table 5. Summary of population estimates for *Primula egaliksensis* occurrences in Colorado and Wyoming.

Source ID (CO)	Reported Population Size	Low Estimate	High Estimate
1	~300-5,000 individuals	300	5000
2	~300 individuals	300	300
3	~1,000 individuals	1000	1000
4	~1,000 individuals	1000	1000
5	~200 individuals	200	200
6	~50 individuals	50	50
7	3,000 or more individuals	3000	4000
10	Not reported	—	—
11	At least 200 individuals	200	400
12	hundreds to ~1,500 individuals	300	1500
13	~40 individuals	40	40
15	Not reported	—	—
17	~24 individuals	24	24
18	Not reported	—	—
19	~300 individuals	300	300
20	20-30 individuals	20	30
21	Not reported	—	—
22	Not reported	—	—
23	"A few"	—	—
Kelso and Maentz 97-119 COCO	small area, 50+ individuals	50	75
TOTAL (CO)		**6784**	**13919**
Source ID (WY)	**Reported Population Size**	**Low Estimate**	**High Estimate**
1	2,000-4,000 individuals	2000	4000
2	8,000- 10,000 individuals	8000	10000
TOTAL (WY)		**10000**	**14000**
GRAND TOTAL		**16784**	**27919**

Table 6. Summaries from published sources describing habitats for *Primula egaliksensis* outside of Wyoming and Colorado.

Author(s)	Region	Habitat Description
Hall 1995	Alaska	Moist soils, stream banks, marshes, and rock outcrops
Hultén 1968	Alaska	Wet meadows, along streams
Nicholls 2002	Alaska	In wet meadows and along streams in the south-central, interior, and arctic regions of Alaska (also in CO and WY in similar moist conditions)
Racine et al. 2001	Alaska	c.f. *egaliksensis* was found in wet sand on silty stream banks at Fort Greely, Alaska. Identification is uncertain due to nonreproductive status
Welsh 1974	Alaska	Moist soils, stream banks, marshes, and rock outcrops
Polunin 1959	Arctic	Calcareous shores and moist grassy areas especially near the sea
Richards 2003	Arctic	Soggy hollows above permafrost. Wet meadows, edges of creeks, wet peaty limestone barrens
Douglas et al. 1991	British Columbia	Wet meadows, streams, and marshes in the upper montane to alpine zones
Scoggan 1979	Canada	Meadows and wet calcareous shores
Fernald 1950	Eastern North America	Meadows and wet calcareous shores
Guggisberg 2004	Greenland	Damp silt along stream banks, wet meadows, edges of creeks, wet peaty limestone barrens; often found with *Primula stricta*
Tutin et al. 1972	Iceland	Moist pastures near the sea
Cody 2000	Yukon	Damp banks of streams and rivers, lakeshores, and meadows
Porsild 1951	Yukon	Alluvial meadows; in calcareous sand by river; in wet places in river meadow
Fenderson 1986	Range-wide	Wet meadows, edges of creeks, wet, peaty limestone barrens; sea level to 2400 m
Smith and Fletcher 1943	Range-wide	Wet meadows, edges of creeks, turfy shores, and peaty barrens

In Region 2, *Primula egaliksensis* is found in a particular type of wetland called an extreme rich fen (**Figure 8**). The intricate relationship of environmental conditions that maintain extreme rich fens in Region 2 includes landscape position, groundwater, geology, and climate. In Region 2, groundwater feeding extreme rich fens percolates through glacial outwash derived from dolomite and limestone high in magnesium bicarbonates, calcium, and sulfates (Cooper 1996, Heidel and Laursen 2003). The constant soil saturation provided by upwelling groundwater creates anaerobic conditions. The lack of oxygen combined with cold temperatures dramatically slows decomposition, leading to the accumulation of peat (Mitsch and Gosselink 1993). The high pH produced by the enriched groundwater limits plant growth (McBride 1994) and supports a highly specialized suite of calcium-tolerant plant species. Although occurrences of *P. egaliksensis* are at elevations with relatively low average annual temperatures, the climate of Region 2 is arid, and evaporation can concentrate minerals at the ground surface.

The extreme rich fens of *Primula egaliksensis* are restricted to Park County (Coles 2002) between 8,940 and 10,040 ft. in elevation (Colorado Natural Heritage Program 2005). Wyoming occurrences of *P. egaliksensis* are in montane fens and wet meadows, where the species grows on hummock with floating mats or in wetlands with moist, calcareous soils (Fertig and Jones 1992, Fertig et al. 1994, Fertig 1996, Mills and Fertig 1996, Fertig 2000, Welp et al. 2000, Handley and Laursen 2002). The elevation range of *P. egaliksensis* occurrences in Wyoming is 6,600 to 8,000 ft. (Fertig et al. 1994).

At Swamp Lake, *Primula egaliksensis* is found primarily on moist marl hummocks in montane fen communities dominated by patches of *Triglochin maritimum* and *Eleocharis pauciflora*. Small colonies may also occur on densely vegetated floating mats dominated by *Carex simulata* (Fertig and Jones 1992, Fertig 1996).

The Lower Green River Lake occurrence of *Primula egaliksensis* is on quaking mats and hummocks dominated by *Deschampsia caespitosa* and *Carex simulata* at the edge of open water or on shallowly flooded marl deposits. Shrubs such as *Salix brachycarpa* and *Dasiphora floribunda* may be present at low densities. Total vegetative cover is more than 100 percent, but it is relatively short in stature. Many of the

Figure 8. Habitat of *Primula egaliksensis* in High Creek Fen in South Park, Colorado. Photograph by David G. Anderson.

plants found with *P. egaliksensis* at this location are boreal species that are disjunct from the main portions of their range (Fertig 1996).

While *Primula egaliksensis* is found primarily in extreme rich fens in Wyoming and Colorado, it occurs in other habitats (including peaty areas along creeks and in hay meadows) where there is a strong influence from calcium-rich groundwater upwelling (Colorado Natural Heritage Program 2005). In South Park, Colorado, *P. egaliksensis* is found in peatlands and alkaline wet meadows, and along streams (Cooper 1990, Sanderson and March 1996).

Geology and soils

All occurrences of *Primula egaliksensis* in Region 2 are associated with groundwater that is enriched by flowing through calcium-rich rocks. Occurrences of *P. egaliksensis* in Wyoming occur on calcareous substrates derived from adjacent mountain slopes. Often these occurrences are associated with flooded deposits of marl, a fine-grained, pinkish soil type rich in calcium carbonate and organic matter (Fertig and Jones 1992, Fertig 1996). The Lower Green River Lake occurrence of *P. egaliksensis* occurs within a shallow, bowl-shaped depression in a broad valley at the edge of the Green River floodplain. Drainage patterns and the proximity of this wetland to the calcareous ridge on the west side of Osborn Mountain probably resulted in the accumulation of lime-rich runoff in the depression (Fertig 1996). Swamp Lake is also in a broad valley influenced by the outwash of calcareous material from surrounding uplands. The fen at Swamp Lake is rich in marl deposits originating in calcareous material from the adjacent Cathedral Cliffs. The Swamp Lake area is also underlain by non-porous granite that allows the accumulation of base-rich soils (Welp et al. 2000). The spring-fed fens and wet meadows of South Park seep through limestone-rich glacial outwash derived from the high elevations of the Mosquito Range to the west (Cooper 1990, Sanderson and March 1996, Colorado Natural Areas Program 2004).

Microtopography

Microtopography appears to be an important habitat variable for *Primula egaliksensis*. The microtopography of a fen includes of hummocks, hollows, strings, and other surface patterns. The microtopographic pattern derives from how water flows through a fen and from vegetation development. Hummocks are remnants of past plant growth; perennial species add layers of vegetation that build peat above the permanently saturated zone and allow a wider variety of species to persist. Fertig (1996) speculated that frost action may contribute to the hummocky terrain at Lower Green River Lake.

Topographic variations (hummocks) in *Primula egaliksensis* habitat are associated with a steep moisture gradient, causing considerable changes in vegetation composition at small scales. Kelso (personal communication 2004) noted that *P. egaliksensis* is always found in areas with a high water table that never dry out. However, within a peatland, *P. egaliksensis* tends to be found on hummocks that represent drier microhabitats (Fertig 2000, Welp et al. 2000, Handley and Laursen 2002). Suitable microhabitats for *P. egaliksensis* within a peatland tend to be isolated and patchy (Handley and Laursen 2002). Fertig (1996) reported *P. egaliksensis* on slightly drier hummock tops at Lower Green River Lake, while several observers noted a tendency to find *P. egaliksensis* on the sides of hummocks in South Park (Sanderson and March 1996, Colorado Natural Heritage Program 2005).

Climate

Fertig (1996) summarized climatic data for occurrences of *Primula egaliksensis* in Wyoming. Climate data for the Green River Valley occurrence of *P. egaliksensis* can be inferred from weather data collected at Kendall Guard Station approximately 9 air miles southwest (Martner 1986). Precipitation in the area averages 13.8 inches per year, with peaks in December, January, and June. Mean annual temperature is 32.7 °F (0.4 °C), with mean maximum and minimum temperatures in January of 27 °F and –2.1 °F (-2.7 °C and –18.9 °C), and mean maximum and minimum temperatures in July of 74.9 °F and 34.8 °F (23.8 °C and 1.5 °C). Climate data from the Crandall Creek weather station indicate that the mean annual temperature near Swamp Lake is approximately 6 °F higher and slightly wetter than the Green River site (Martner 1986).

Climate data for occurrences of *Primula egaliksensis* in South Park, Colorado is derived from data taken at Antero Reservoir between 1961 and 2004 (Western Regional Climate Center 2005). Antero Reservoir lies at the southernmost limit of the range of *P. egaliksensis*, at approximately 9,000 ft. elevation. These data portray a slightly different climatic profile than Wyoming. Average annual precipitation at Antero Reservoir is 10.1 inches, most of which falls as rain in May through August. The average annual temperature is 35.7 °F (2.1 °C), with mean maximum and minimum January temperatures of 32.7 °F and –3.3 °F (0.3 °C

and -19.6 °C), and mean maximum and minimum temperatures in July of 76.1 °F and 40.1 °F (24.5 °C and 4.5 °C).

In Colorado and Wyoming, the sites occupied by *Primula egaliksensis* are in depressions in montane valleys. These sites are probably influenced by cold air drainage and are cooler than regional climate data would suggest (Fertig 1996, Kelso personal communication 2004). These sites in some ways recreate arctic conditions (Kelso personal communication 2004).

Reproductive biology and autecology

Life history and strategy

In the Competitive/Stress-Tolerant/Ruderal (CSR) model of Grime (2001), some of the life history characteristics of *Primula egaliksensis* are typical of ruderal species, particularly when compared with other species in its habitat. However, *P. egaliksensis* is not exceptionally fecund when compared to typical ruderal species, which generally devote a large proportion of their reserves to reproduction. Fertig (1996) characterized *P. egaliksensis* as a seral species since it does not colonize newly exposed sites in Wyoming and does not persist in areas invaded by taller graminoids and willows. *Primula egaliksensis* is not usually seen in close association with highly competitive species such as *Carex nebrascensis*, suggesting that it is not a strong competitor. Kelso (personal communication 2004) notes that *P. egaliksensis* can colonize the bare sediment in muddy river channels in South Park, Colorado. It also grows in braided river channels and creek banks in Alaska. Guggisberg (personal communication 2005) typically observed *P. egaliksensis* in areas with sparse vegetation cover. Although the vegetative cover of many sites where it is found is high (Fertig 1995), it appears likely that seasonal flooding from snowmelt runoff (which typically peaks in May) is responsible for an element of disturbance that may reduce the negative effects of competitors (Kelso personal communication 2004). The presence of *P. egaliksensis* in hay meadows also suggests some degree of tolerance of disturbance.

Reproduction

The complex floral biology of *Primula* has been a topic of study for many years. Reproductive biology has played a critical role in the evolution and ecology of *Primula* species (Kelso 1991). Nine percent of *Primula* species, including *P. egaliksensis*, have homostylous flowers, in which the anthers and styles are borne at the same height within the corolla tube. This tends to promote self-fertilization. *Primula egaliksensis* reproduces sexually by seed (Kelso 1991, Fertig 1996). Using bags to exclude pollinators from flowers, Kelso (personal communication 2004) noted that *P. egaliksensis* still produced seed, confirming the homostyly and self-compatibility of this species. However, *P. egaliksensis* is capable of both self-fertilization and outcrossing (Fertig 1996). The importance of outcrossing in maintaining genetic diversity in populations of *P. egaliksensis* is unknown.

In *Primula*, homostyly is linked to polyploidy (Kelso 1991). Most homostylous *Primula* species are polyploid (Richards 2003). Tetraploids such as *P. egaliksensis* may be distylous or homostylous, but higher polyploids are typically homostylous. Of polyploids, Kelso (1991) wrote, "a change in the breeding system from distyly to homostyly brought self-fertility and the potential for colonizing recently deglaciated habitats." This is supported by the tendency for arctic species to be homostylous and polyploid. This is also true of alpine primroses, but the relationship is less clear.

Richards (2003) offers four possible explanations for the relationship between homostyly and polyploidy:

- the genetic control of the pin/thrum system does not usually work in polyploids
- most polypoloids, and most secondary homostyles, are found in the Arctic (this is an indirect relationship)
- polyploidy is more likely develop in a plant that can mate with itself
- polyploids are more likely to resist inbreeding effects resulting from selfing.

Ninety-one percent of *Primula* species are heterostylous, where individuals have at least two arrangements of the anthers and stigmas. There has been considerable interest in the evolutionary mechanisms that lead to and maintain this mating system since Darwin's (1877) treatment of the phenomenon. Heterostyly is an effective means of ensuring cross-pollination. Heterostylous members of *Primula* are distylous, in which all the flowers on an individual are one of two morphs, termed 'pin' and 'thrum'. Pin flowers have a long style positioned near the mouth of the corolla, while the anthers are deep within the corolla tube. Thrum flowers have a short style, but the anthers are attached near the mouth of the corolla. The pin

morph is effectively female while the thrum morph is effectively male, although the morphs are still bisexual. Richards (2003) provides a review of the biology of homostyly and heterostyly, with photographs showing heterostylous and homostylous flowers.

Kelso (1992) describes a hypothetical pathway for the development of polyploidy and homostyly from distylous ancestors. Both putative ancestors of *Primula egaliksensis* (*P. mistassinica* and *P. nutans*) are distylous (Kelso 1991, Larson and Barrett 1998), suggesting that this has occurred in *P. egaliksensis*.

Many *Primula* species promulgate themselves through cloning, in which "daughter bulbils" are produced (e.g., Hambler and Dixon 2003). However, this mode of reproduction has not been reported for *P. egaliksensis*. The sometimes tightly clumped distribution pattern that has been reported for *P. egaliksensis* is probably the result of poor seed dispersal and limited germination sites rather than clonal perennation.

Pollinators and pollination ecology

Primula egaliksensis is presumably pollinated occasionally by small insects, but the pollination ecology of *P. egaliksensis* has not been studied (Fertig 1996). Heterostylous members of *Primula* are typically visited by large specialist pollinators such as bees (Richards 2003). Research is needed to determine the role of outcrossing in the population biology of *P. egaliksensis* (Kelso personal communication 2004).

Phenology

The flowering period of *Primula egaliksensis* is very short. Much of the blooming in an occurrence may take place within about three days and individual flowers bloom only briefly (Kelso personal communication 2004). *Primula egaliksensis* typically flowers in South Park after the first week of July, and plants tend to be in peak anthesis between July 7 and 15 (Kelso personal communication 2004). However, the timing of flowering varies considerably from year to year. Specimens from South Park at COLO in flower were collected between June 22 and July 20. Fertig (1996) reports a somewhat broader flowering period, from late May to early July. Fruits are present from late June to August (Fertig et al. 1994, Handley and Laursen 2002). In the Yukon Territory, Porsild (1951) observed *P. egaliksensis* in flower on July 3.

Primula egaliksensis was observed in fruit in August 1984 and August 1992 at Swamp Lake (Fertig 1996). At Lower Green River Lake, flowering, fruiting, and vegetative individuals were observed in early July 1995, with 50 to 80 percent in flower and 20 percent with ripening fruit (Fertig 1996).

The environmental cues that prompt *Primula egaliksensis* to initiate flowering have not been determined. Fertig (1996) noted that spring moisture conditions affect the timing of flowering, but he does not specify the nature of this relationship. Under cultivation, *P. malcoides* flowered in response to temperature cues but not photoperiod (Karlsson and Werner 2002).

Fecundity and propagule viability

Primula egaliksensis reportedly produces copious seed (Kelso personal communication 2004) although annual seed production has not been quantified. Selfing species of *Primula* often set more capsules and seeds per capsule than outcrossing relatives (Tremayne and Richards 2000). In three homostylous *Primula* species, seedlings derived from heavy seeds germinated in greater numbers and more quickly, and they formed larger rosettes, than seedlings derived from lighter seeds (Tremayne and Richards 2000). In the distylous species *P. elatior*, seed germination percentage was correlated with population size and seed mass. Larger seeds showed larger germination percentages only in the smallest populations (Jacquemyn et al. 2001).

Dispersal

The presence of *Primula egaliksensis* across boreal North America in areas that were covered by continental ice sheets during the Pleistocene suggests that it is able to disperse to and colonize deglaciated sites (Kelso 1991, Kelso personal communication 2004). The seeds of *P. egaliksensis* are dispersed locally by water in Alaska, Wyoming, and Colorado (Kelso 1992). In Alaska, this species is commonly found along creeks and rivers (Kelso personal communication 2004). *Primula egaliksensis* has no mechanisms for medium- or long-range dispersal (Warren 2003), and most occurrences in Region 2 are probably isolated from one another (Coles 2002). However, the seeds are small and light enough to permit local dispersal by wind (Kelso personal communication 2005).

Cryptic phases

There has been no study of seed bank dynamics, seed longevity, or dormancy in *Primula egaliksensis*, and the longevity of its seeds is unknown. Chang et al. (2000) observed the seeds of *P. egaliksensis* to be

"locally abundant" in soil cores from La Pérouse Bay, Manitoba, suggesting the existence of a seed bank. However, the authors did not distinguish between the seeds of *P. egaliksensis* and *P. incana*, and the seeds are very similar in size and morphology.

Phenotypic plasticity

Members of genus *Primula* are often phenotypically plastic in their vegetative and reproductive responses to environmental conditions (Kelso 1991). Kelso (1991) wrote: "However, while it is necessary in northern species of *Primula* to allow for generous morphological amplitude according to the effects of phenology and environment, all taxa [in *Armerina* and *Aleuritia*] show a coherent and identifiable phenotype." Both white and colored flower morphs have been reported for *P. egaliksensis*.

Mycorrhizae

The roots of *Primula egaliksensis* have not been assayed for the presence of mycorrhizal symbionts, and its role as a mycorrhizal host has not been investigated. Arbuscular mycorrhizal (AM) fungi belong to a group of non-descript soil fungi (Glomales) that are difficult to identify because they seldom sporulate (Fernando and Currah 1996). They are the most abundant type of soil fungi (Harley 1991) and infect up to 90 percent of all angiosperms (Law 1985). AM fungi are generally thought to have low host specificity, but there is increasing evidence for a degree of specificity between some taxa (Rosendahl et al. 1992, Sanders et al. 1996). Recent studies suggest unexpectedly high diversity at the genetic (Sanders et al. 1996, Varma 1999) and single plant root levels (Vandenkoornhuyse et al. 2002). As root endophytes, the fungal hyphae enter the cells of the plant roots where water and nutrients are exchanged in specialized structures.

No evidence of mycorrhizal relationships has been observed in *Primula egaliksensis* (Kelso personal communication 2004). *Primula* species are included among the species recommended for the use of mycorrhizal inoculum products in gardens (East of Eden Plants 2004), but this may bear little relevance to the role of mycorrhizae in natural settings.

Hybridization

Primula egaliksensis is a putative allotetraploid hypothesized to result from hybridization between *P. nutans* (section *Armerina*) and *P. mistassinica* (section *Aleuritia*). This conclusion is based on cytology and the morphology of pollen, glands, and vegetative parts (Kelso 1991, Kelso 1992, Mast et al. 2001, Richards 2003, Kelso personal communication 2004, Guggisberg personal communication 2005). Molecular phylogenetic research strongly supports the maternal contribution of *P. mistassinica* in the origin of *P. egaliksensis* (Mast et al. 2001). Although *P. egaliksensis* appears to have originated as a hybrid, it is now stabilized and fully differentiated from its parental species (Kelso personal communication 2004).

There are no reports of hybridization between *Primula egaliksensis* and *P. incana* in Region 2 or Region 4. There is no evidence of hybridization at either Wyoming location (Fertig 1996), and there are no reports suggesting that hybridization is occurring in Colorado where *P. egaliksensis* and *P. incana* often grow side by side. Kelso (personal communication 2004) suggests that hybridization between *P. egaliksensis* and *P. incana* is not possible because of their different ploidy levels. Chang et al. (2000) report that *P. egaliksensis* and *P. incana* "hybridize regularly" at La Pérouse Bay, Manitoba, where the species are also sympatric. However, this is the only report of hybridization occurring between *P. egaliksensis* and another species. In boreal and arctic North America, *P. egaliksensis* is often found in close association with *P. stricta* (Polunin 1940), but there has been no hybridization reported between these species. Many hybrids between *Primula* species have been created for horticultural purposes (e.g., Mizuhiro et al. 2001).

Demography

Demographic information for *Primula egaliksensis* is very limited. Data on life history stages, population structure, longevity, mortality, and seed biology of *P. egaliksensis* are not available (Handley and Laursen 2002). Information on seeds and recruitment would be especially valuable. Seed production, seed longevity, seed dormancy, and variables controlling these parameters would help reveal potential bottlenecks in the life history of *P. egaliksensis*. Recruitment rates and longevity are also unknown. **Figure 9** is a life cycle graph (after Caswell 2001) of *P. egaliksensis* based on available information.

Primula egaliksensis is an iteroparous perennial, which means that it flowers two or more times throughout its life span (Richards 2003). Most reports mention the presence of flowering plants within an occurrence of *P. egaliksensis*. It is likely that the documentation of *P. egaliksensis* in element occurrence records is heavily biased towards this conspicuous life

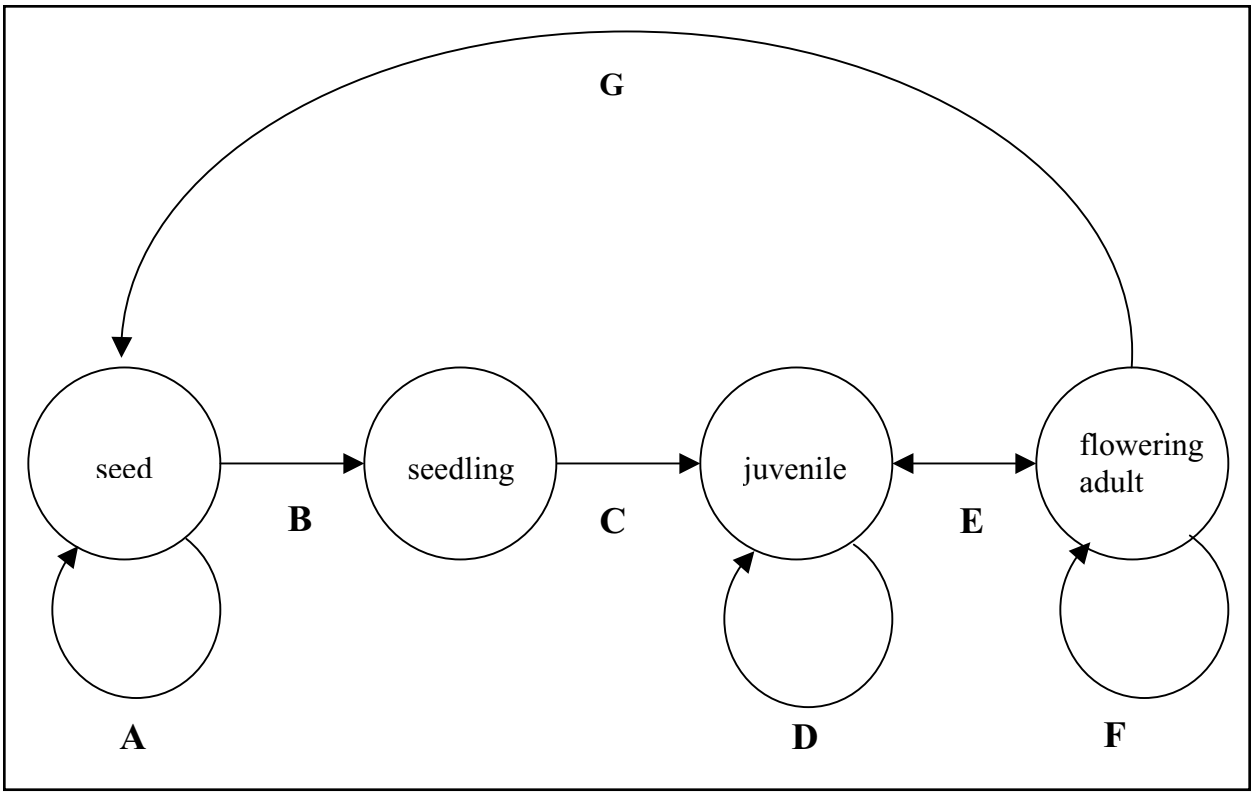

Figure 9. Hypothetical life cycle graph (after Caswell 2001) for *Primula egaliksensis*. Much of this diagram is speculative because there have been no studies where individuals were tracked through their life cycle. The value of A is not known, although the presence of seeds of *P. egaliksensis* is suspected in samples from Canada (Chang et. al. 2000). The duration of the juvenile stage is not known, but plants may be capable of remaining in the juvenile stage for multiple years (D). *Primula egaliksensis* is clearly a polycarpic perennial (F). The lifespan of *P. egaliksensis* is unknown. Fecundity has not been measured (G), but *P. egaliksensis* reportedly produces copious quantities of seed (Kelso personal communication 2004), as is typical of the homostylous members of *Primula*.

history stage because it is otherwise very difficult to find. There have been no reports of seedlings in Colorado and Wyoming. It is possible that the vegetative individuals that have been reported are juvenile (pre-reproductive) plants, but the time required to reach reproductive maturity is not known. Lower Green River Lake had flowering, fruiting, and vegetative individuals in 1995 (Fertig 1996).

As a homostyle, *Primula egaliksensis* is predisposed to selfing and high levels of inbreeding. The genetic diversity of *P. egaliksensis* has not been determined, but it is currently under investigation (Guggisberg personal communication 2005). A study of the population genetics of the rare endemic homostyle *P. scotica* showed no genetic diversity within or among four populations (Glover and Abbott 1995), and it is likely that other homostyles also have low genetic diversity. Although it is predominantly selfing, there is no evidence that *P. egaliksensis* suffers from the effects of inbreeding depression (Kelso personal communication 2004). Summarizing the demography of *P. egaliksensis*, Fertig (1996) wrote, "The predisposition of *P. egaliksensis* for self-fertilization, coupled with its clustered population structure and short dispersal distances probably result in limited outcrossing and a low degree of genetic variation within populations. The ability to self-pollinate, however, increases this species' ability to colonize new sites."

Negative alleles tend to be purged from populations of predominantly selfing species. There are probably some opportunities for outcrossing despite the species' homostyly, and these events may also contribute to the maintenance of heterozygosity and genetic diversity within populations of *P. egaliksensis*. Of the polyploid homostylous primroses, Kelso (1992) wrote, "Polyploidy can protect against the detrimental effects of inbreeding and enable homostyles to pass through the temporary bottleneck of inbreeding depression. Homostyly with or without other genetic change can be a successful mutation when coupled

with strong selective pressure for self-fertility and/or when the homostyle retains or develops the ability for facultative outcrossing."

The effects of habitat fragmentation on reproduction have been observed in distylous *Primula* species. Small populations of *P. sieboldii* set almost no seed consistently for three years, apparently due to pollinator limitation exacerbated by habitat fragmentation (Matsumura and Washitani 2000). Evidence of inbreeding depression was observed in small populations of *P. veris*, suggesting genetic deterioration resulting from habitat fragmentation (Kéry et al. 2000). Similar results were observed in fragmented populations of *P. vulgaris* (Van Rossum et al. 2004). Habitat fragmentation negatively affected populations of *P. farinosa* in Swiss fens; plants in larger fragments had greater rosette diameters and tended to have more flowers. Seed set was 11 percent lower at edges, suggesting that edge effects reduce reproduction in this species (Lienert and Fischer 2003). All of these effects probably resulted from the self-incompatibility of these species and reduced visitation by pollinators in fragmented habitats. The low reliance on pollinators for reproduction in *P. egaliksensis* may buffer populations of this species from similar effects. However, Lienert and Fischer (2003) observed other effects of fragmentation on populations of *P. farinosa*. Herbivory was 50 percent higher in habitat edges, but infection by smut fungus (which has not been documented in *P. egaliksensis*) was more likely in larger habitat fragments. In *P. egaliksensis*, the greatest impacts from fragmentation are likely to result from hydrological alteration (see the Threats section for a discussion of this topic).

No population viability analysis (PVA) has been performed for *Primula egaliksensis*. One species of *Primula*, *P. maguirei*, is listed as threatened (U.S. Fish and Wildlife Service 1990, U.S. Fish and Wildlife Service 1999), but there has been no PVA performed on this species. The U.S. Fish and Wildlife Service (1990) notes that minimum viable population studies are needed for *P. maguirei*, which has been deemed unrecoverable. Demographic analyses have been conducted for many other *Primula* species. Based on observations made from 1986 to 1999, Endels et al. (2002) determined a minimum viable population size of 95 individuals for *P. vulgaris*. This number reflected the population size at which there was a 90 percent probability of survival from 1986 to 1999. The viability of small populations (fewer than 95 individuals) of *P. vulgaris* was observed to be lower than that of larger populations. Populations of *P. vulgaris* near agricultural lands are particularly susceptible to decline, largely as a result of herbicide overspray (Valverde and Silvertown 1997, Valverde and Silvertown 1998, Endels et al. 2002).

There are no data suggesting that metapopulations exist in *Primula egaliksensis*. Where *P. egaliksensis* occurs in chronically naturally disturbed habitats (e.g., adjacent to creeks and rivers), metapopulations of *P. egaliksensis* may occur. At least one *Primula* species, *P. vulgaris*, appears to form metapopulations in successional environments. This species is found in woodlands where it colonizes canopy gaps, but it cannot persist as the canopy closes (Valverde and Silvertown 1997). Identifying critical life history stages for population or metapopulation dynamics is crucial to developing recovery strategies for rare plants (Schemske et al. 1994).

The probability of seed dispersal and other propagules decreases rapidly with increasing distance from the source (Barbour et al. 1987). Long-distance dispersal events are rare. Pollinator-mediated pollen dispersal (if it occurs) is largely limited to the flight distances of pollinators (Kearns and Inouye 1993). Due to the physical limitations to seed dispersal (primarily by water in *Primula egaliksensis*, possibly by wind) and pollen drift among populations, gene flow between most populations of *P. egaliksensis* is probably restricted.

Community ecology

Vegetation and associated species

In extreme rich fen habitats in South Park, *Primula egaliksensis* has been reported in two plant associations, both of which are considered rare in Colorado (Colorado Natural Heritage Program 2005). These are the *Kobresia myosuroides-Thalictrum alpinum* plant association and the *K. simpliciuscula-Scirpus rollandii* plant association (Cooper 1990, Sanderson and March 1996, Colorado Natural Heritage Program 2005). Both of these plant associations are characterized by hummocky fen microtopography (Sanderson and March 1996).

Primula egaliksensis was sampled in a hierarchical vegetation classification of High Creek Fen by Cooper (1996). It was observed in hummocks within the fen's "peatland expanse." In this study, constancy of *P. egaliksensis* was highest where *Trichophorum pumilum* and *Kobresia simpliciuscula* formed hummock complexes in relatively wet portions of the peatland. Where *Thalictrum alpinum* forms a groundcover associated with patches of *Trichophorum pumilum*, the constancy of *P. egaliksensis* and *Carex microglochin* is also high, along with *Salix candida*, *S. brachycarpa*,

and *Dasiphora floribunda*. Mean percent cover of *P. egaliksensis* in areas dominated by *T. pumilum* and *K. simpliciuscula* was 0.3 percent in plots sampled by Cooper (1996), indicating that even within habitats where it is most abundant, it is not a dominant species.

Johnson and Steingraeber (2003) used classification and ordination to investigate community types adjacent to groundwater wells at three fens in South Park. In this study, *Primula egaliksensis* was observed in a somewhat wider range of habitat types. *Primula egaliksensis* formed a minor component of the tall-hummock fen, hummocky fen lawn, fen lawn, water track, and quagmire vegetation associations as typified by these authors. Cover was greatest in the quagmire vegetation association where *P. egaliksensis* fell into the 1 to 5 percent cover class. In all other vegetation associations, cover of *P. egaliksensis* was less than 1 percent. *Primula egaliksensis* is described as being diagnostic of the fen lawn subclass, where it occurs with *Thalictrum alpinum*, *Triglochin maritimum*, and *T. palustris*. The fen lawns described by Johnson and Steingraeber (2003) are found in open areas in the interior of fens where groundwater upwelling is occurring.

In Wyoming, *Primula egaliksensis* is found in different plant associations within fens than in Colorado. Fertig and Jones (1992) described eight vegetation types at Swamp Lake Special Botanical Area. *Primula egaliksensis* occurs in the *Carex simulata* type and the *Triglochin-Eleocharis* type. Although the *Triglochin-Eleocharis* vegetation type of Fertig and Jones (1992) is equivalent to the *Eleocharis quinqueflora-Triglochin* spp. plant association defined by Cooper (1990) and Sanderson and March (1996) in South Park, *P. egaliksensis* appears to be less common in this community in Colorado.

The *Triglochin-Eleocharis* vegetation type described by Fertig and Jones (1992) occurs on marl deposits along the southern side of the Swamp Lake wetland. Smaller patches also occur in the northern half of this wetland. Most of the marl deposits lie atop mineral soil, but some occur on floating organic mats (Fertig and Jones 1992). The *Carex simulata* vegetation type occurs on floating vegetation mats in the northwestern part of the wetland where the vegetation includes *C. simulata*, *C. limosa*, *Triglochin maritimum*, *Calamagrostis inexpansa*, and *Sphagnum* spp. Stands of this type merge into the *Triglochin-Eleocharis* type. *Carex simulata* stands form sharp boundaries with stands of the *C. rostrata* type, where the latter occupies open water around the margin of the wetland (Fertig and Jones 1992).

There are no community descriptions available for streamside and wet meadow habitats in Region 2, in which *Primula egaliksensis* is less well known. However, available data (**Table 4**), indicate that in all cases, the hydrology of stream sides and wet meadows where *P. egaliksensis* occurs is heavily influenced by adjacent extreme rich fens.

In Colorado, *Primula egaliksensis* may co-occur with *P. incana*, but *P. egaliksensis* appears to favor more continuously wet microsites (Kettler et al. 1993, Fertig 1996). *Primula incana* appears to tolerate dry periods better than *P. egaliksensis* (Kelso personal communication 2005). The two species have not been found together in Wyoming. **Table 7** is a complete list of associated species that have been documented with *P. egaliksensis* in Regions 2 and 4.

Species-environment relationships

Peatlands are unbalanced ecosystems where plant production exceeds decomposition of organic material, resulting in the accumulation of peat (Vitt 2000). Extreme rich fens are at one end of a continuum, where content of base cations, alkalinity, and water flow are high, while water level fluctuation, nitrogen and phosphorus levels and are low (Vitt 2000). Extreme rich fens are rich in calcium carbonate (Ca_2CO_3) (Cooper 1996). The pH in extreme rich fens can range from 7.0 to 8.5 or higher. Ca_2CO_3 may be deposited as marl under these conditions (Vitt 2000). Many species in extreme rich fens are calciphiles (Colorado Natural Areas Program 2004). It is likely that water chemistry, particularly the concentration of calcium carbonate and pH, is a critical habitat variable for *Primula egaliksensis*.

Water availability is also a critical habitat variable for *Primula egaliksensis*; it is found exclusively in sites that remain moist throughout the summer (Kelso personal communication 2004). Johnson and Steingraeber (2003) used canonical correspondence analysis to investigate species-environment relationships in three South Park fens, in which they observed correlations between community types and hydrology based on environmental data from groundwater sampling wells. In the fen lawn vegetation type (where *P. egaliksensis* was most often observed), the water table is typically just below ground level but may sometimes be above the ground surface (mean water table height was 0.0 ± 2.5 cm).

Table 7. Species that have been documented with *Primula egaliksensis* in Colorado and Wyoming.

Scientific Name	CO	WY	Life Form	Rare/ Exotic	Common associate	Scientific Name	CO	WY	Life Form	Rare/ Exotic	Common associate
Achillea lanulosa	X		F			*Parnassia parviflora*	X	X	F		
Betula glandulosa		X	S			*Pedicularis groenlandica*		X	F		
Caltha leptosepala	X		F			*Pedicularis* sp.	X		F		
Carex aquatilis		X	G			*Picea pungens*	X		T		
Carex aurea		X	G			*Plantago* sp.	X		F		
Carex capillaris		X	G			*Poa* sp.	X		G		
Carex limosa		X	G	R	X	*Polemonium occidentale*		X	F		
Carex microglochin	X	X	G		X	*Polygonum* sp.	X		F		
Carex praegracilis	X		G			*Polygonum viviparum*		X	F		
Carex scirpoidea	X		G	R		*Potentilla anserina*	X		F		
Carex simulata	X	X	G			*Primula incana*	X		F		X
Carex sp.	X		G			*Ptilagrostis porteri*	X		G		
Carex utriculata	X		G			*Ranunculus cymbalaria*		X	F		
Dasiphora floribunda	X	X	S			*Ranunculus* sp.	X		F		
Deschampsia caespitosa	X	X	G		X	*Salix brachycarpa*		X	S		
Dodecatheon pulchellum	X		F			*Salix candida*	X		S	R	
Eleocharis acicularis		X	G			*Salix monticola*	X		S		
Eleocharis pauciflora		X	G			*Scirpus pumilus*	X		G	R	
Eleocharis sp.	X		G			*Senecio pauciflorus*	X		F	R	
Gaura sp.	X		F			*Sisyrinchium montanum*	X		F		
Juncus balticus	X		G			*Sisyrinchium pallidum*	X		F	R	
Juncus sp.	X		G			*Stellaria longipes*		X	F		
Kobresia myosuroides	X		G		X	*Swertia perennis*		X	F		
Kobresia simpliciuscula	X		G	R	X	*Taraxacum officinale*	X		F	E	
Limnorchis hyperborea	X		F			*Thalictrum alpinum*	X	X	F		X
Muhlenbergia filiculmis	X	X	G			*Triglochin maritima*	X	X	F		
Muhlenbergia glomerata		X	G		X	*Triglochin palustre*		X	F		

Despite its preference for high water tables, *Primula egaliksensis* tends to be found on hummocky microsites that are locally drier than surrounding habitat (Fertig 1996, Fertig 2000, Welp et al. 2000, Handley and Laursen 2002). See the Microtopography section for more information on the role of moisture and microtopography in defining the habitat of *P. egaliksensis*.

Salinity and wetness are inversely related at High Creek Fen in South Park, Colorado. Soluble salts (Na_2+, Mg_2+, and K+) accumulate in drier portions of the fen, where they form salt flats. In the hummocky portion of the fen where *Primula egaliksensis* is found, these salts typically remain in solution (Cooper 1996).

Floristics

Many authors have recognized the relationships of Region 2's extreme rich fen species with boreal regions. The extreme rich fens of Region 2 are relicts of much colder and wetter conditions that prevailed during the Pleistocene. High Creek Fen has attracted much interest due to the richness of its flora; it contains more rare plant species than any other wetland in Colorado (The Nature Conservancy 2004). High Creek Fen supports occurrences of 14 species considered rare in Colorado, many of which are arctic disjuncts (Colorado Natural Areas Program 2004, Colorado Natural Heritage Program 2005). High Creek Fen is floristically similar to other calcareous fens in distant locales. Of the 118 vascular plant taxa known from High Creek Fen, 37 are also found at Swamp Lake, Wyoming (Cooper 1996).

Swamp Lake in Wyoming has also attracted much interest due to its uniqueness and species diversity. This wetland complex contains Wyoming's densest concentration of unusual plants, with more than 25 rare species documented. As at High Creek Fen, many of these are boreal disjunct species more typical of wetlands in taiga forest. One species, *Arctostaphylos rubra*, is known from nowhere else in the lower 48 United States (Welp et al. 2000).

Herbivory

There is very little information regarding the relationship of *Primula egaliksensis* with native herbivores or livestock. Livestock grazing by cattle or horses is reported at eight locations of *P. egaliksensis* in Colorado (CO EO #2, 3, 5, 6, 11, 17, 19, and 20), and it is probably occurring at many others in Colorado as well. It has been reported at both occurrences of *P. egaliksensis* in Wyoming also. One occurrence of *P. egaliksensis* (CO EO #23) is in an inactive grazing allotment (Olson personal communication 2004).

There was little direct evidence of herbivory observed at the Lower Green River Lake site in 1995, but several plants were found with damaged flower heads (Fertig 1996). This herbivory may have been caused by snails or insects. Some grazing at this location may also be the result of moose or occasional stray cattle. It is likely that primary negative effects of livestock on *Primula egaliksensis* are the result of hydrologic alteration. These are discussed in the Threats section.

Kühn and Kiehl (2004) studied the effects of livestock grazing on calcareous fens in Europe. In this study, the authors conducted an experiment to test whether grazing was analogous to late-season mowing. Traditionally, the fens studied had been mowed for straw in the fall; this apparently maintained diverse assemblage of rare plants. The target study species (among them *Primula farinosa*) did best in fens that were mowed in the traditional manner. Grazed fens were analogous to abandoned fens with respect to density of *Primula*, but frequency of *Primula* was greater in abandoned fens than in grazed fens. Grazing created habitat heterogeneity and uneven distributions of the target species. Removal of vegetation by grazing or mowing appeared to be necessary for the germination of the seeds of target species in this study. The relevance of this study to fens where *P. egaliksensis* occurs is uncertain. Unlike fens in Region 2, European fens have a long history of intensive use. Less than 15 percent of the peatlands of several western European countries remain unaltered (Mazerolle 2003).

Primula egaliksensis was formerly known from Iceland, but is believed to be extirpated there (Guggisberg personal communication 2005, Guggisberg et al. 2006). Its decline during the 20th century may have been the result of reduced grazing in its meadow habitats that allowed competitive grass species to increase. This is congruent with observations that *P. egaliksensis* tends to occur in areas where pressure from highly competitive species is minimal (Guggisberg personal communication 2005).

The palatability and the effects of grazing on occurrences of *Primula egaliksensis* are not known, but horses and cattle are known to consume congeners (Fertig 1996). Herbivory has negative effects on the reproductive performance of *P. veris* (García and Ehrlén 2002). Flower removal and leaf removal both reduced the population growth rate in this species.

Studies in Idaho found that grazing may be injurious to populations of *P. alcalina* when it occurs after the onset of flowering and before seed dispersal (Muir and Moseley 1994, Fertig 1996). However, the negative effects of grazing may be balanced somewhat by improved plant vigor following the removal of competing vegetation (Muir and Moseley 1994, Fertig 1995, Mills and Fertig 1996).

Competition

There is some evidence to suggest that *Primula egaliksensis* is a poor competitor that is excluded from productive sites by species that are more competitive. It is absent from wet meadows with tall graminoid vegetation or dense cover of shrubby willows (Fertig 1996). *Primula egaliksensis* is never a dominant species in South Park (Cooper 1990) or anywhere within its range. See the Life history and strategy section for further discussion of this topic.

Parasites and disease

Fungal pathogens have been documented on various species of *Primula*. Some *Primula* species are subject to infections of the smut fungus *Urocystis primulicola* (Nagler 1987 as cited in Lienert and Fischer 2003). Infections of *U. primulicola* have not been documented on *P. egaliksensis*, but they have been documented in northeastern Switzerland and in Poland on *P. farinosa*, a widespread fen species (Kucmierz 1971, Lienert and Fischer 2003). The fungal seed pathogen *Alternaria* c.f. *tenuis* was abundant in seed capsules of *P. farinosa* in Britain (Hambler and Dixon 2003). This fungus destroys the placenta and immature seeds. *Botrytis cinerea*, a common fungal pathogen of greenhouses, attacks *Primula* x *polyantha* under cultivation. The severity of symptoms is exacerbated by bacteria associated with *B. cinerea* (Barnes and Shaw 2002).

Insect seed predation has also been documented in several species of *Primula*, but not *P. egaliksensis*. Seed predation by *Pterostichus madidus*, a carabid beetle, was observed on *Primula veris* in Britain (Hurst and Doberski 2003). Pre-dispersal seed predation of *P. veris* by a plume moth, *Amblyptilia punctidactyla*, was observed in Finland (Leimu et al. 2002).

CONSERVATION

Threats

In approximate decreasing order of priority, threats to *Primula egaliksensis* in Region 2 include water resource development, peat mining, ditching, livestock grazing, road construction, right-of-way maintenance, global climate change, timber harvest, recreational activities, residential development, fire, exotic species, placer mining, pollution, and collection. These threats are speculative, and more complete information on the biology and ecology of this species may reveal other threats. These threats can interact with one another and exacerbate their overall negative effects, and the magnitude of each threat varies greatly across the range of *P. egaliksensis*. Assessment of threats to this species will be an important component of inventories and monitoring.

Threats to occurrences in Wyoming are addressed by Fertig (1996) and are included in this assessment where relevant. Fertig (1996) also offered management recommendations that are discussed in the Beneficial management actions section.

The extreme rich fen habitats occupied by *Primula egaliksensis* in Region 2 are unique and restricted in distribution and abundance. Fens are delicate, groundwater-fed systems that form under stable hydrological conditions over thousands of years. Extreme rich fens are specialized by being fed by groundwater that becomes enriched after percolating through limestone and dolomite. Constant saturation by cold, enriched groundwater over thousands of years produced the organic peat substrate of these fens. Peat soils act like sponges, holding water *in situ* longer than mineral soils and slowing water movement through these unique wetlands. Once damaged, recovery of this habitat is slow, if it is possible at all (Johnson 2000, Sanderson et al. in prep.).

Hydrologic alteration

Because water chemistry and availability are key habitat variables for *Primula egaliksensis*, any activity that alters the local hydrologic regime threatens habitat and occurrences of this species. Hydrologic alteration

encompasses any change in how water flows through fen systems or in the ratio of surface to groundwater. Alterations can result from either anthropogenic or natural causes. Straightening or diverting streams, digging ditches, building stock ponds and reservoirs, and road building alter water movement and the balance of groundwater and surface flow. Alteration of vegetative cover within a watershed can increase the amount of surface flow into a fen, also shifting the balance between hydrologic sources. Pumping groundwater for municipal use may alter the hydrology of fen systems significantly by depressing the water table and draining aquifers. Inundation resulting from road, reservoir, or livestock pond construction is likely to eliminate individuals and occurrences of *P. egaliksensis*. The vegetation patterns at Swamp Lake appear to be controlled to a large extent by water depth, suggesting that changes in hydrology represent the greatest threats to the rare plant species in this wetland (Fertig and Jones 1992, Handley and Heidel 2005).

In some situations, *Primula egaliksensis* may benefit from hydrologic alteration. Flood irrigation may enhance habitat. This is apparently occurring at occurrences on private land in South Park and may help to maintain the viability of this species, at least in the short term (Kelso personal communication 2005).

Small population size and fragmentation

Landscape fragmentation may have demographic implications for *Primula egaliksensis*. However, demographic stochasticity that results from distyly (as reported by Kéry et al. 2003 in *P. veris*, and by Jacquemyn et al. 2002 and Van Rossum et al. 2002 in *P. elatior*) is a relatively minor concern for *P. egaliksensis*. In obligate outcrossers, populations may be sensitive to fragmentation that results in pollen limitation; in distylous populations, reduced reproduction results from an imbalance in the proportion of pin and thrum flowers. Although it is probably primarily selfing, *P. egaliksensis* shows no evidence of inbreeding depression (Kelso personal communication 2004) and may be less susceptible to inbreeding depression as a homostyle. Genetic connectivity may still be important for *P. egaliksensis*, and this has not yet been studied. The observations made by Lienert and Fischer (2003) of edge effects on *P. farinosa* showing that herbivory is higher in the edges of habitat units also suggest that habitat fragmentation remains a concern for *P. egaliksensis*.

Threats to habitat and individuals

Water resource development

Water resource development is the greatest threat to *Primula egaliksensis* in Colorado (Kelso personal communication 2004) and in Wyoming. Development of water resources, either through diversion or dam construction, is likely to destroy *P. egaliksensis* habitat (Fertig 1996). Creation of reservoirs inundates vegetation and dramatically changes the hydrology, destroying the intricate balance that maintains these fens. Filling Antero Reservoir in Park County, Colorado destroyed an unknown amount of extreme rich fen habitat that may have supported *P. egaliksensis* (Sanderson and March 1996). *Primula egaliksensis* occurs in a portion of a fen that remains just above the inlet (CO EO #12). Antero Reservoir provides drinking water to the Denver metropolitan area. The Denver Water Board is in the process of acquiring land surrounding the reservoir to allow for reservoir expansion. Any expansion of this reservoir will likely drown the remainder of the fen.

An eight-fold increase in population between 1970 and 2000 has dramatically increased development pressure in South Park, Colorado. Residential development is the greatest projected source of future growth (Pikes Peak Area Council of Governors 2004). The demand for water will only increase. Surface waters diminished in the drought period between 2001 and 2004, and Antero Reservoir was dry in the summer of 2004. The loss of surface water leads to a greater reliance on groundwater resources, which themselves are reduced due to drought. Groundwater pumping has not yet significantly affected the water sources that feed fens in South Park, but it remains an important long-term threat that will require monitoring (Sanderson and March 1996).

A reduction in groundwater discharge in extreme rich fens during dry climate periods could reduce available habitat for taxa that require constantly-saturated soils, and it could result in increased salinity in portions of the fen (Cooper 1996).

Straightening or diverting streams and digging ditches moves water through these systems more quickly and can lead to drying out of adjacent wetlands. Ditches and diversions can lower the water table, which allows shrubs to colonize areas previously occupied by hydrophytic herbs (Glaser et al. 1981). These types of

alterations also remove vegetation, directly affecting occurrences and individuals. High Creek Fen was ditched to lower the water table and facilitate peat mining (De Prenger-Levin 2004).

Peat mining

Peat mining has significantly affected the habitat of *Primula egaliksensis* in Region 2 (Warren 2003). Within Region 2, commercial peat mining is permitted and is ongoing only in Colorado (USDI Bureau of Mines 1994) where peat is mined for horticultural use (Sanderson et al. in prep.). Peat mining is not a concern at present in Wyoming (Fertig 1996). Peat mining reduces vegetation cover and species richness, alters species composition and edaphic properties, and eliminates the hummocks that form the primary microhabitat of *P. egaliksensis* within fens. These effects alter soil and groundwater chemistry and impair wetland function (Johnson 2000). Mazerolle (2003) reviewed the detrimental effects of peat mining on species richness of bogs. Peat mining also modifies the structure of plant, bird, and small-mammal assemblages in remaining peatland fragments. Due to accumulation rates of 20 to 28 cm per 1,000 years (Cooper 1996), peat in Region 2 is not a renewable resource (Colorado Federation of Garden Clubs 1995).

Livestock grazing

Primula egaliksensis is threatened by loss or alteration of its wetland habitats by livestock (Fertig 1998, Fertig 2000, Welp et al. 2000, Handley and Laursen 2002). Livestock grazing has demonstrably affected some peatlands in Colorado (Warren 2003). Livestock grazing has been reported at seven occurrences in Colorado (CO EO #2, 3, 5, 6, 11, 17, 19) (Colorado Natural Heritage Program 2005) and at both Wyoming occurrences (Fertig 1996). Although cattle tend to avoid the softest, wettest parts of fens, vegetation is still damaged or diminished by trampling and consumption. Overgrazing degrades surface water quality through the sheet, rill, and bank erosion that it causes (Pikes Peak Area Council of Governors 2004). Grazers, both domestic and wild, are known to cause or accelerate the development of hummock-hollow topography, which in turn affects species composition (Johnson and Steingraeber 2003). Greater impacts were noted in smaller fens with limited groundwater resources. Larger fens generally are used lightly by livestock if sufficient pasture is available (Sanderson and March 1996).

Improper levels of grazing can cause a shift in species composition as a secondary effect; cattle prefer grasses, sedges, and willows, reducing the abundance and vigor of these taxa. Disturbance to peat soils by trampling also creates opportunities for invasive plants like Canada thistle (*Cirsium arvense*). Because *Primula egaliksensis* occupies hummocks in wet portions of its fen habitats, it is probably somewhat protected from the direct effects of grazing.

The palatability of *Primula egaliksensis* to livestock is not known (Fertig 1995). Other species of *Primula*, however, are known to be edible to cattle and horses (Muir and Moseley 1994). See the Herbivory section for further discussion of this topic. Individuals near trails may be threatened by trampling by livestock (Mills and Fertig 1996, Fertig 2000, Welp et al. 2000).

At present, grazing intensity is relatively low at the Swamp Lake site, with most activity coming from cattle and horses straying into the wetland from adjacent upland pastures (Fertig 1995). Grazing and trampling by livestock is a potential threat at the Lower Green River Lake site, but overall use appears low (Fertig 1992).

While there is evidence that fen habitats of *Primula egaliksensis* are threatened by grazing, there is little to suggest that individuals are threatened by this practice. There is anecdotal evidence from observations in Alaska (Kelso personal communication 2004) and in Iceland (Guggisberg personal communication 2005) that the reduced dominance of competitive species caused by grazing might benefit *P. egaliksensis*. More research is needed to study the effects of livestock grazing on the viability of *P. egaliksensis*.

Road construction and right-of-way maintenance

Roads near wetlands can increase and intensify surface runoff, thereby reducing percolation and aquifer recharge, and increasing erosion as well as pollutant inputs (Forman and Alexander 1998). Roads can also impede subsurface drainage by intercepting groundwater. Changes in ground and surface hydrology from road construction are potential threats at Swamp Lake (Fertig and Jones 1992). A paved highway crosses the north end of the site and the wetland outlet, apparently raising the water level in the wetland (Welp et al. 2000). A culvert was placed above local water levels during highway reconstruction and has potentially

increased water retention in the Swamp Lake basin (Heidel and Laursen 2003, Handley and Heidel 2005). Commercial truck traffic occurs on the highway, raising the potential for accidental spills that could contaminate the wetland (Welp et al. 2000). A gravel pit covering less than one acre has been excavated on the north side of the Swamp Lake wetland for road maintenance, but it does not appear to have affected occupied habitat for *Primula egaliksensis* (Welp et al. 2000). Right-of-way maintenance threatens four occurrences of *P. egaliksensis* in Colorado (CO EO #1, 2, 4, and 22; **Figure 10**) and Swamp Lake in Wyoming (Wyoming Natural Diversity Database 2004, Colorado Natural Heritage Program 2005).

Global climate change

Global climate change is possibly the most serious threat to the persistence of *Primula egaliksensis* in Region 2, but it has a lower priority because of uncertainty about its regional effects and severity. The constant supply of groundwater and the relatively high elevations of Wyoming and Colorado maintain boreal conditions, allowing isolated, relictual occurrences of *P. egaliksensis* to persist. The habitat occupied by *P. egaliksensis* in Colorado and Wyoming is isolated from the main part of the species' range as well as being very restricted in distribution and abundance. Without other suitable habitat nearby or the means of reaching it, global climate change is a major threat to occurrences of *P. egaliksensis* in Wyoming and Colorado.

Global climate change is likely to have wide-ranging effects in the near future for all habitats, but the direction of trends is yet to be determined and predictions vary based on environmental parameters used in predictive models. The prevailing scientific opinion based on numerous studies is that global temperatures are increasing and will continue to increase through the next century, due in part to anthropogenically increased levels of atmospheric CO_2 (Reiners 2003). The upper limit of global temperature increase over the next century is estimated to be 42.8 °F (6 °C) (Reiners 2003).

Climate change scenarios for the Rocky Mountains offer different predictions of precipitation quantity and pattern. Some scenarios indicate that annual precipitation will increase over the next 100 years, but growing season precipitation will decrease. Other scenarios indicate that parts of the Rocky Mountains will get drier. Any scenario could

Figure 10. Highway 285 and the town of Fairplay, Colorado. The construction of Highway 285 and other roads and railways resulted in hydrologic alterations of many fens in South Park. Right-of-way maintenance also threatens parts of five occurrences of *Primula egaliksensis* in Region 2. Photograph by Susan Spackman Panjabi, used with permission.

significantly affect the hydrology of extreme rich fens in Region 2. Temperature increase could cause vegetation zones to climb 350 ft. in elevation for every degree F of warming (U.S. Environmental Protection Agency 1997), and is likely to result in net drying due to increased evapotranspiration (Reiners 2003). This type of change is likely to degrade habitat quality or availability and may result in local extirpation of *Primula egaliksensis* as increased evaporation concentrates salts at the fen surface. Preliminary studies of the effects of temperature on reproduction of five *Primula* species (not *P. egaliksensis*) suggest that global temperature increase will adversely affect the quantity and quality of seed set in some species (McKee and Richards 1998). Decreased precipitation will dry out water sources, making the fens susceptible to invasion by shrubs, trees, and upland forbs. Increased precipitation will lessen the aridity that maintains high concentrations of minerals in extreme rich fens through evaporation (Cooper 1990 as cited in Sanderson and March 1996). Adjustment in element concentrations can alter substrate pH, making fens more available to competitive species.

Timber harvest

Timber harvest near habitats supporting *Primula egaliksensis* has the potential to disturb their hydrology. Deforestation in the immediate vicinity of wetlands can increase surface runoff and cause erosion, which affects the nutrient cycles within the fen. Past logging practices caused significant erosion implicated in major stream degradation in the South Platte River drainage, causing downcutting and sedimentation (Pikes Peak Area Council of Governors 2004).

Although logging on the slopes below the Cathedral Cliffs has been cited as a threat due to the potential for increased erosion, observations of the site since the 1988 fire suggest that erosion is a minor threat at Swamp Lake in Wyoming (Welp et al. 2000). Portions of Swamp Lake are managed under prescription 10G, which prevents logging, grazing, and other harmful activities within the wetland. Welp et al. (2000) wrote, "White spruce seedlings and saplings have been cut from the muskeg on the south side of the wetland, apparently to improve waterfowl nesting habitat, although this practice is forbidden by the current management prescription. The limestone and shale slopes south of the wetland have been logged in the past, both with small clearcuts and with selective logging, and some salvage logging has been done since the 1988 fires."

An environmental impact statement for fuels reduction within wildland-urban interface areas of Sublette County, Wyoming determined that the proposed action would have no effect on *Primula egaliksensis* and that *P. egaliksensis* was not likely to occur within the project area (USDA Forest Service 2004).

Recreational activities

Recreation threatens occurrences of *Primula egaliksensis* in both Colorado and Wyoming (Fertig 1998, Fertig 2000, Welp et al. 2000, Handley and Laursen 2002). Portions of occurrences near trails in Wyoming may be threatened by hikers trampling them (Mills and Fertig 1996, Fertig 2000, Welp et al. 2000). Fertig (1996) noted that "the Lower Green River Lake occurrence is in close proximity to the popular Green River Lakes campground, several wilderness trailheads, a large parking area, and an archaeological site (Fertig 1992). Impacts from trampling are low; however, due to the abundance of mosquitoes and the lack of trails directly through the plant's habitat. The Swamp Lake wetland is adjacent to the Chief Joseph Scenic Highway, but appears to receive little recreational use." At Swamp Lake, a guest ranch uses the dirt road south of the wetland and a two-track road along the north side of the wetland for horseback trail riding (Welp et al. 2000). Horses graze the uplands around the wetland but apparently do not enter the wetland. A boat ramp was built recently at the east end of the Swamp Lake wetland (Welp et al. 2000).

Fire

Forest fires have similar effects as timber harvest on surface water quality. A forest fire in the Clarks Fork Ranger District on the Shoshone National Forest burned much of the Swamp Lake watershed in 1988, including the cliffs above Swamp Lake (Wyoming Natural Diversity Database 2004). Debris flows from fire-denuded slopes have had notable impacts on the wetland below (Heidel and Laursen 2003). Likewise, the Hayman Fire increased sediment loads reaching the South Platte River in the southeastern portion of Park County, Colorado, downstream of extreme rich fens in South Park (Pikes Peak Area Council of Governors 2004). Fire frequency and severity are likely to be different for the disjunct occurrences of *Primula egaliksensis* in Colorado and Wyoming relative to occurrences in the boreal regions that comprise the majority its range. The fens of South Park occasionally burn on the surface, but the frequency, severity, and

effects of these fires are virtually unknown (Johnson and Steingraeber 2003).

Exotic species

Primula egaliksensis occurrences in Colorado (Kelso personal communication 2004) and Wyoming (Welp et al. 2000) are largely free of invasive, non-native plant species. Dandelion (*Taraxacum officinale*) and Kentucky bluegrass (*Poa pratensis*) have been reported from the Sweetwater Ranch on the South Fork of the South Platte River in Colorado, where heavy grazing is occurring. However, it does not appear that these species pose a threat to *P. egaliksensis* at this time (Colorado Natural Heritage Program 2005). It is likely that the high pH precludes establishment of many exotic species. However, hydrologic alterations or increased grazing may create favorable conditions for exotic plant invasion. It is likely that if weeds become problematic at an occurrence, other factors, such as drying of the substrate due to water table decline, are responsible. Nutrient loading from fertilizer or pollutant run-off can alter the pH of a fen, making the wetland more vulnerable to exotic plant invasion.

Populations of noxious weeds adjacent to occurrences of *Primula egaliksensis* may represent a threat. Numerous exotic forbs and grasses grow along the dirt road on the south side of Swamp Lake and on the logged area slopes above the wetland. These include the state-listed noxious weed Canada thistle (Welp et al. 2000), which has also been observed near High Creek Fen (Spackman et al. 2001). South Park in general is invaded by Canada thistle (Kelso personal communication 2005). Management of weeds along right-of-ways (e.g., overspray and herbicide runoff) could also affect nearby occurrences. Habitat monitoring is needed ensure that wetlands occupied by *P. egaliksensis* are not degraded by noxious weed invasion or weed management.

Placer mining

Placer mining destroyed much of the riparian zone of the Middle Fork of the South Platte River in South Park, Colorado. This practice began in 1859 with the discovery of gold in South Park. Placer mining peaked between 1860 and 1863, when small-scale operations were the favored method for extracting gold. The use of massive dredges began in the 1920s and continued until World War II (Pike National Forest 2004). The legacy of placer mining is obvious today near Fairplay, Colorado (**Figure 11**). The impact that placer mining had on *Primula egaliksensis* is not known.

Placer mining continues today at one location under a USFS permit issued in 1993. A draft Biological Evaluation by the USFS in 2000 (Howard 2000 as cited by Mayo 2005) found no effect on sensitive plant species resulting from this project. The current threat

Figure 11. Placer mine tailings along the South Platte River near Fairplay, Colorado. Although large-scale placer mining is no longer taking place in South Park, it may have diminished the range and abundance of *Primula egaliksensis* there. Photograph by Susan Spackman Panjabi, used with permission.

of placer mining to *Primula egaliksensis* is very low unless gold prices rise enough to revive placer mining on a broader scale.

Pollution

Increased nitrogen loading has been observed in plant communities worldwide. Nitrogen loading and vegetation change have been observed to be greatest near large metropolitan areas (Schwartz and Brigham 2003). Measurable impacts from nitrogen pollution might be expected in South Park, which lies approximately 50 miles southwest of Denver. Nitrogen enrichment experiments show that nitrogen is universally limited (Gross et al. 2000). Enrichment is therefore likely to cause a few species to increase in abundance while many others decline (Schwartz and Brigham 2003). Relatively low levels of nitrogen enrichment are advantageous to some species but deleterious to others, making it difficult to predict species- and community-level responses.

Collection

In collecting *Primula egaliksensis* for scientific purposes, care should be taken not to remove more than 5% of the plants present (Wagner 1991, Pavlovic et al. 1992). No collecting should be done in occurrences of fewer than 50 plants. Guggisberg (2004) provides guidance for collecting seed capsules, material for use in molecular research, and voucher specimens. Handlers of *Primula* species commonly contract contact dermatitis (Bhushan and Beck 1999, Aplin and Lovell 2001). Primin is the main allergen in *Primula* dermatitis (Aplin and Lovell 2001). The incidence of contact dermatitis is limited to horticultural species (notably *P. malacoides* and *P. obconica*) and is not known from *P. egaliksensis* and its relatives (Kelso personal communication 2005).

The genus *Primula* has a long history of medicinal and horticultural use (e.g., Gerard 1633, Richards 2003). *Primula* saponin exhibits antiexudative and expectorant effects and is useful in the treatment of coughs and other ailments (Hostettmann and Marston 1995). Commercial saponin extracts are obtained from the underground parts of *P. veris* and *P. officinalis*. Collection of *P. egaliksensis* for commercial purposes has not been documented, and it apparently is not sought after for medicinal or horticultural purposes. The lack of showiness and horticultural difficulties make it unlikely for *P. egaliksensis* to become popular among collectors.

Conservation Status of Primula egaliksensis in Region 2

Although occurrences are believed to be stable, there are no data from which population trends can be inferred for *Primula egaliksensis* in Wyoming and Colorado. The current perception of the insecure status of the species in Region 2 arises from demonstrable threats and the low number of occurrences, small or unknown population sizes, and the disjunct nature of Region 2 occurrences.

Primula egaliksensis is tied to a small-patch type of habitat that is found only in a narrow range of environmental conditions, often isolated from similar habitats. The current distribution of *P. egaliksensis* in Colorado and Wyoming is believed to be relictual. As the last ice age ended, *P. egaliksensis*, along with many other boreal plant species, migrated north behind the retreating ice. In a few isolated locations, local conditions allowed occurrences to persist. Although these isolated occurrences may have shifted somewhat as habitat shifted during Holocene climate changes, these glacial disjuncts are now isolated from other disjunct occurrences and from the central range of the species. Ultimately, the survival of these species in Region 2 habitats depends on climatic trends as well as the conservation efforts of land managers and owners.

There is evidence that at least some occurrences of *Primula egaliksensis* are at risk of extirpation in Region 2. The restricted and highly specialized habitat of *P. egaliksensis* leaves it vulnerable to habitat degradation and loss (Fertig 1996). The imperilment of the extreme rich fen habitats used by *P. egaliksensis* is best summarized by Sanderson and March (1996):

> "Extreme rich fens historically covered approximately 1.4% of the land area in South Park (this is an inclusive estimate that possibly exaggerates their extent. The actual area of extreme fens may be less). It appears that nearly 20% of the total extreme rich fen area in South Park has been permanently lost as a result of peat mining. The extreme rich fens lost include two sites that probably were once among the best representatives of these wetland ecosystems. Alterations of hydrology, especially the building of large and small reservoirs has also adversely affected these wetlands. Water ditching and water diversions appear at this point to have had only a small deleterious effect on extreme rich fens, but long-term effects are uncertain. As water becomes a more expensive commodity in Colorado,

more water diversions and removal of groundwater could become serious threats to the natural integrity of these wetlands. Heavy grazing has negatively affected extreme rich fens only very locally and mostly at small sites. In almost all cases noted, grazing effects could be reversed by altering grazing levels and timing."

Most occurrences in Colorado are on state or private lands where peat mining has degraded habitat (Coles 2002). One of the mined areas has been reclaimed to a peat surface, but in ten years, no *Primula egaliksensis* individuals have re-occupied the reclaimed area (Warren 2003).

Management activities that could occur on National Forest System land near *Primula egaliksensis* occurrences include timber sales, management-ignited (prescribed) burns, and the construction and maintenance of pipelines, ditches, power lines, and roads. These activities may affect occurrences of *P. egaliksensis* directly or indirectly. Despite its status as a special management area, Swamp Lake has sustained numerous impacts and alterations resulting from human activities, including road construction and hydrologic alteration (Welp et al. 2000).

Other *Primula* species linked to fens are in decline or have been extirpated from parts of their range in Europe because of habitat modification or destruction by humans (Hambler and Dixon 2003, Lienert and Fischer 2003). Dispersal of *P. egaliksensis* to new locations and recolonization of areas from which it has been extirpated are highly unlikely events (Cooper 1996).

Very little is known about the impacts of human activities on occurrences of *Primula egaliksensis*. Although the total population appears to be stable at present, the long-term impacts of human activities such as livestock grazing, mowing of hay meadows, and past hydrologic modifications on the population size of *P. egaliksensis* are not known. It stands to reason that the destruction of 20 percent of South Park's extreme rich fens over the last 150 years also reduced the population of *P. egaliksensis* by that amount, but the lack of historical distribution and abundance data makes this impossible to confirm. Conversely, the degree to which irrigation of hay meadows has increased potential habitat for *P. egaliksensis* is unknown, as is whether the increase resulting from this practice outweighs the loss of natural fen habitat for *P. egaliksensis*.

All occurrences of *Primula egaliksensis* in Colorado and Wyoming are at risk of water resource development. Pressure to develop the water resources on which *P. egaliksensis* depends is likely to escalate as human populations grow. Occurrences in Wyoming are at somewhat lower risk of water resource development than those of South Park. The occurrence of *P. egaliksensis* at Antero Reservoir Northwest (CO EO #12) is likely to be extirpated if plans to expand the reservoir are carried out.

Management of Primula egaliksensis in Region 2

Implications and potential conservation elements

In Region 2, occurrences of *Primula egaliksensis* are most vulnerable to changes in the environment that affect their habitat. Any management activities that maintain the correct hydrologic regime for these habitats will contribute to the persistence of *P. egaliksensis*. This includes the regulation and monitoring of hydrological modifications, livestock grazing, mowing, logging, mining, and road construction. Hydrological modifications are pervasive throughout the range of *P. egaliksensis*. Water that supplies occurrences in South Park originates in the Mosquito Range on the Pike National Forest. In Wyoming, watersheds supplying water to both occurrences of *P. egaliksensis* are also largely managed by Region 2 and Region 4. Activities on National Forest System land have the potential to affect all occurrences of *P. egaliksensis* in Colorado and Wyoming.

Natural environmental changes may also affect habitats favored by *Primula egaliksensis*. Changes in precipitation patterns and effects of natural disturbances elsewhere in the watershed may also lead to altered hydrology that is detrimental to *P. egaliksensis*. In these instances, management policy could focus on mitigating these effects where possible.

Peat mining in extreme rich fens where *Primula egaliksensis* is found results in permanent destruction of these habitats. On a reclaimed mined area in South Park, *P. egaliksensis* has not reoccupied the site in 10 years since the reclamation (Warren 2003). Continuing the peat mining moratorium in Park County, Colorado will benefit *P. egaliksensis*.

Desired environmental conditions for *Primula egaliksensis* include an intact natural hydrological regime with little or no evidence of wetland alteration due to anthropogenic disturbance. Conservation management for *P. egaliksensis* may require restoration

of water tables and drainages and changing livestock management. Exotic species should be absent, and roads or other anthropogenically induced fragmentation should be limited to less than 1 percent of the occurrence. Uplands surrounding the occurrence should be largely unaltered (>95 percent natural) by development, mining, or agricultural uses such as clearcuts, crop cultivation, or heavy grazing. Management prescriptions may need to focus on adjacent land use. Unnatural barriers that would inhibit movement of organisms and materials across system boundaries should be absent. Connectivity of habitats should be sufficient to allow natural processes and species migration to occur (Rondeau 2001).

A thoughtful assessment of current management of lands occupied by *Primula egaliksensis* would identify opportunities for change that would be inexpensive and have minimal impacts on the livelihood and routines of local residents, ranchers, managers, permittees, and recreationists while conferring substantial benefits to *P. egaliksensis*. See the Tools and practices section for potential beneficial management actions for *P. egaliksensis*.

Tools and practices

Species and habitat inventory

Species inventory remains a high priority for *Primula egaliksensis* conservation. Although considerable attention has been devoted to searching for this species, additional effort is likely to yield new occurrences. Many areas within the known range of *P. egaliksensis* remain to be searched because of the difficulties in obtaining permission to visit private land. When willing landowners are identified, the opportunity should be taken to search for the species on their property.

Primula egaliksensis may be found anywhere in South Park where the right combination of habitat conditions exists. More occurrences may be found around Jefferson. *Primula egaliksensis* may also be found anywhere in South Park where *P. incana* grows, as they require similar habitat conditions. However, *P. incana* tolerates higher summer temperatures and thus ranges far outside South Park (Kelso personal communication 2004). South Park is the only part of Colorado where the proper combination of climate and habitat required by *P. egaliksensis* is likely to occur (Coles 2002, Kelso personal communication 2004). *Primula incana* was found in an extreme rich fen in Grand County in 2005, but not *P. egaliksensis* (Culver and Jones 2006).

Kelso (personal communication 2004) searched two promising areas on the Pike National Forest in South Park. The area on the east side of Weston Pass was searched, but suitable habitat does not appear to be present in this area. The area around Guffy in South Park has some wet meadows that appear promising, but these lie beyond the extent of glacial outwash deposits containing limestone or dolomite and are thus unlikely to have the water chemistry appropriate for *Primula egaliksensis*.

Considerable effort has been expended to find additional occurrences of *Primula egaliksensis* in Wyoming. Parts of the Shoshone National Forest in the northern Absaroka Range were surveyed in 1995, but no new occurrences were found (Fertig 1996). Surveys on the Bridger-Teton National Forest in 1995 in calcareous quaking mat-*Deschampsia caespitosa* hummock meadow habitat were also unsuccessful. The surveys were done in the Upper Green River Valley and Gros Ventre River-Fish Creek drainage, and near Mosquito Lake and other glacial ponds near Union Pass Road (Fertig 1996). Precise locations of the 1995 surveys are described in Fertig (1996). No peatlands or other wetlands with calcareous conditions suitable for *P. egaliksensis* were identified on the Medicine Bow National Forest in Colorado and Wyoming (Heidel and Laursen 2003).

Aerial photography and topographic, soil, and geology maps can be used to refine searches covering large areas, and they could be effective for designing surveys for *Primula egaliksensis*. These tools are most effective for species for which we understand the habitat variables, and from which distribution patterns and potential search areas can be deduced. Sanderson and March (1996) offer insights into the identification of extreme rich fens from their spectral signature on infrared aerial photos.

Searches for *Primula egaliksensis* could be aided by the use of deductive and inductive species distribution modeling techniques. Classification and Regression Tree (CART) modeling (Breiman et al. 1984) is an inductive technique suited to modeling the potential distribution of *P. egaliksensis*, using available data for geology, vegetation, and other habitat variables. Combining this technique with other inductive techniques such as envelope models (e.g., DOMAIN, BIOCLIM, MaxEnt) could refine a potential distribution map by predicting the likelihood that *P. egaliksensis* is present (Thuiller et al. 2003, Beauvais et al. 2004). CART has been used to model the distribution of sensitive plant species in Wyoming (e.g., Fertig and

Thurston 2003) and in Colorado (Decker et al. 2005, Decker et al. 2006). Species distribution modeling is an effective means of determining the extent of suitable habitat on National Forest System land. Techniques for predicting species distributions are reviewed extensively by Scott et al. (2002).

Population monitoring

Demographic monitoring could provide information to assist with the management and conservation of *Primula egaliksensis* in Colorado and Wyoming. Lesica (1987) described a technique for monitoring populations of non-rhizomatous perennial plant species that may be applicable to *P. egaliksensis*. Standard demographic monitoring methods generally employ the use of randomly arrayed systematic sampling units (quadrats). Within each quadrat, plants are counted or marked and tracked using an aluminum tag or other field marker. During annual visits, data are gathered for each marked plant. Ideally, this would include a measure of size. For *P. egaliksensis*, two perpendicular measurements can be taken across the basal portion of the plant and the formula for an ellipse used as a measure of size. Life history stage, fecundity (the number of fruits or some other measure of reproductive output), and mortality are also important demographic parameters to track. Recruitment within each quadrat is measured by counting seedlings. New recruits are also tagged and tracked. Finding seedlings of *P. egaliksensis* will be extremely difficult in dense fen vegetation. Elzinga et al. (1998) offer additional guidance for demographic monitoring.

Seed viability and longevity can be estimated using small, buried bags containing known numbers of live seeds that are collected and tested periodically using tetrazolium chloride and germination trials on subsets of each bag. Suitable methods for monitoring pollinators, which are a critical autecological factor for *Primula egaliksensis*, are discussed in Kearns and Inouye (1993).

Data from these studies could be used to calculate rates of change among different life history stages and to determine transition probabilities. They would also yield insight into the longevity, fecundity, seed bank dynamics, annual growth rate, and recruitment rate of *Primula egaliksensis*, and they would permit the use of modeling techniques to determine critical life history stages, minimum viable population size, and probability of long-term persistence.

Simpler, less labor-intensive approaches to monitoring can still yield valuable data. These involve the resampling of permanent plots; within each plot, an annual census is taken of the total number of plants and how many are in each life stage (e.g., seedling, nonreproductive, reproductive, dead). These data cannot be used to determine the life span of *Primula egaliksensis*, but they would provide information on recruitment, recruitment success, and population structure. This method is suitable for monitoring population trend because individual plots can be read rapidly, permitting a more extensive monitoring program. Ideally, each occurrence of *P. egaliksensis* would be monitored if the goal is to observe overall population trend.

If a complete census is not possible, site selection is an important consideration in developing a monitoring program. Including locations that are managed under different prescriptions will provide information useful to the conservation of *Primula egaliksensis*. It will be important to define *a priori* the changes that the sampling regime intends to detect, and the management actions that will follow from the results (Schemske et al. 1994, Elzinga et al. 1998).

Elzinga et al. (1998) recommend several methods of permanently marking plots, depending on site physiography and frequency of human visitation to the site. This is an important consideration that will reap long-term benefits if done properly at the outset of the monitoring program. In the wet habitats of *Primula egaliksensis*, site markers will need to be resistant at least to flooding, frost heave, and inundation, and possibly to grazing and mowing.

Estimating cover and/or abundance of associated species within the monitoring plots described above could permit the investigation of interspecific relationships through ordination or other classification techniques. In very sparsely vegetated plots, this can be done accurately using appropriate cover classes or subdivided quadrat frames.

Understanding environmental constraints on *Primula egaliksensis* will facilitate the management of this species. Gathering data on edaphic characteristics (e.g., moisture, texture and soil chemistry, particularly pH, if possible) from the monitoring plots described above would permit the canonical analysis of species-environment relationships. These data would facilitate hypothesis generation for further studies of the ecology

of this species. Johnson and Steingraeber (2003) have already applied these approaches at three occurrences of *P. egaliksensis* (see the Community ecology section for a discussion of the results of this study). Gathering data from unoccupied but hypothetically suitable sites is also very useful in establishing the autecological requirements of a species.

Adding a photo point component following recommendations offered in Elzinga et al. (1998) could facilitate the tracking of individuals and add valuable qualitative information. A handbook on photo monitoring (Hall 2002) offers detailed instructions on establishing photo point monitoring plots. Monitoring sites should be selected carefully, and a sufficient number of sites need to be selected if the data are intended to detect population trends.

Gathering abundance data through plot sampling methods can be done rapidly with only a small amount of additional time and effort (Elzinga et al. 1998). Bullock (1996) discusses approaches and challenges in applying counting and estimation techniques in the quantification of plant population sizes.

To address the metapopulation structure of *Primula egaliksensis*, one approach might be to select suitable but unoccupied sites adjacent to extant occurrences and attempt to observe colonization events. Observations of local extinctions would also add to our understanding of the metapopulation dynamics of this species. Establishing artificial populations in carefully studied suitable sites is one approach to testing metapopulation theory as it applies to *P. egaliksensis*. Even for species in which metapopulation dynamics can be inferred from regional extinction and colonization data, focusing efforts on monitoring of individual occurrences is more likely to provide an accurate assessment of population trend (Harrison and Ray 2002).

Habitat monitoring

Habitat monitoring is most efficient when conducted concurrently with population monitoring. Documenting habitat attributes, disturbance regime, and associated species during population monitoring will augment our understanding of the species' habitat requirements and guide appropriate management. These data could be incorporated into the field forms used for one of the quantitative sampling protocols described above. Habitat monitoring of known occurrences will alert managers of new impacts such as weed infestations and damage from human disturbance and grazing. It is important to document evidence of current land use practices and management while monitoring occurrences. Making special note of signs of degradation from overgrazing will alert managers to the need to change grazing prescriptions in order to prevent serious damage to the habitat. Changes in environmental variables might not cause observable demographic repercussions for several years, so resampling the chosen variables may help to identify underlying causes of population trends.

Elzinga et al. (1998) describe the use of photopoints for habitat monitoring. This powerful technique can be done quickly in the field. Although it does not provide cover or abundance data, it can help to explain patterns observed in quantitative data.

Beneficial management actions

Management actions that protect the hydrologic regime supporting occurrences of *Primula egaliksensis* are probably the most important steps needed to ensure the viability of this species in Colorado and Wyoming. Maintaining appropriate water levels will be an important component of long-term management plans for *P. egaliksensis* (Mills and Fertig 1996, Fertig 2000). Land trusts, including Colorado Open Lands and the Trust for Public Land, are working to link water resources to land via conservation easements to protect the hydrology of South Park (Kelso personal communication 2004).

Diverse land protection strategies are needed to ensure the protection of *Primula egaliksensis* in Colorado and Wyoming (Kelso personal communication 2004). The three occurrences known from National Forest System land in Wyoming and Colorado (two of which are within Region 2) benefit from protection due to sensitive species status. However, the occurrences on the Pike National Forest in South Park, Colorado and at Lower Green River Lake in Wyoming (Bridger-Teton National Forest Region 4) are managed for multiple uses. Swamp Lake benefits from the designation of this area as a Special Botanical Area, but additional protective measures are recommended for this site to ensure the protection of its botanical resources (Chadde et al. 1998). These include mitigation of human disturbance at this site. Fertig (1996) recommended designating a 5 to 15 acre area encompassing the Lower Green River Lake location as a Special Botanical Area or other designation recognizing it as an area of high biological value to protect *P. egaliksensis* and other biota at this location.

Of equal importance to land protection is the protection of water resources for conserving *Primula egaliksensis*. Any efforts to conserve the land occupied by *P. egaliksensis* are unlikely to enhance the long-term viability of this species if the hydrologic regime is not also preserved. Efforts to conserve occurrences of *P. egaliksensis* on National Forest System land in Region 2 will need to include actions that maintain natural surface and subsurface hydrology. The headwaters of the South Platte watershed upstream of occurrences of *P. egaliksensis* in Colorado are within the Pike National Forest. This means that water resources that feed these fens and provide suitable habitat for *P. egaliksensis* are affected by management actions on this forest.

Private land owners can take the initiative to manage their lands in a manner that ensures the viability of *Primula egaliksensis* occurrences. At one occurrence of *P. egaliksensis* in South Park (not disclosed due to data sensitivity), a consortium of co-owners manages a large tract for its biological resources. Grazing does not occur at this location, and the occurrence here appears to be thriving with minimal management (Kelso personal communication 2004). Continuing irrigation within occurrences of *P. egaliksensis* may be required to ensure their continued viability.

In designating protected areas for *Primula egaliksensis*, edge effects and management of adjacent lands must be considered. To mitigate the effects of herbicide drift, Endels et al. (2002) recommend buffers between populations of *P. vulgaris* and agricultural fields of 8 to 20 meters, although buffers of only 3 meters may reduce 95 percent of drift of herbicides into its habitat.

Fertig (1996) recommended closing areas of Lower Green River Lake containing occurrences of *Primula egaliksensis* (including an appropriate buffer) to trails or other enhancements for recreation, wildlife, or grazing. Fertig (1992) recommended construction of a buck-and-pole fence around the wetland complex occupied by *P. egaliksensis* in order to minimize trampling by hikers and to prevent livestock entry. Detrimental effects from livestock grazing in fens can be mitigated by reducing animal numbers during early and mid-summer when soils are wettest and most vulnerable to compaction and disruption (Sanderson and March 1996) Providing alternative water sources would also be beneficial (Pikes Peak Area Council of Governors 2004).

Fertig (1996) recommended continued sensitive species status for *Primula egaliksensis* in Regions 2 and 4. To prevent inadvertent impacts to known occurrences, all USFS personnel involved in planning and on-the-ground land management activities should be provided with location data for *P. egaliksensis* (Fertig 1996).

No data exist describing the response of this species to most types of management (Fertig 1996). A monitoring program is needed to address the management needs, trend, and habitat condition of *Primula egaliksensis* (Fertig 1996). Fertig (1996) recommends visits every two to three years to ensure that habitat quality remains high.

While control of weeds is important to prevent impacts to *Primula egaliksensis* and its habitat, the use of herbicides in and near occurrences is probably a greater threat. Use of herbicides to control arrowgrass (*Triglochin* spp.) should not be allowed in and near occurrences of *P. egaliksensis* due to possible negative effects on individuals and habitat. Weed control planners must consider the threats of herbicides to wetland vegetation (Welp et al. 2000).

Seed banking

No seeds or genetic material are currently in storage for *Primula egaliksensis* at the National Center for Genetic Resource Preservation (Miller personal communication 2004). It is not among the National Collection of Endangered Plants maintained by the Center for Plant Conservation (Center for Plant Conservation 2004). Collection of seeds for long-term storage will be useful if restoration of occurrences is necessary. Seeds of *P. farinosa* are in long-term storage at the Royal Botanic Gardens at Kew (Royal Botanic Gardens, Kew 2004). Specifications for storage conditions that may be relevant to *P. egaliksensis* are provided on their website as well. *Primula egaliksensis* is also grown in a greenhouse at Kew (Richards 2003).

Information Needs

Distribution

Despite efforts to document the distribution of *Primula egaliksensis* in Wyoming and Colorado, there remains a strong need for species inventory. Peatland inventories such as those of Heidel and Laursen (2003) in the Medicine Bow National Forest, and Chadde et al. (1998) in the northern Rocky Mountains are needed throughout more poorly surveyed areas of Region 2. Even without a complete inventory of occurrences, current knowledge of the distribution of *P. egaliksensis* is sufficient to formulate and implement conservation

strategies for this species. Assessing the number of plants in each occurrence of *P. egaliksensis*, along with documentation of land use and threats, will be important for assessing the conservation needs and priorities for this species. The best places to focus searches are described in the Species and habitat inventory section.

Life cycle, habitat, and population trend

The life cycle of *Primula egaliksensis* has not been investigated; its longevity and the transition probabilities between life history stages are not known. A demographic monitoring program in which individuals were tracked (as described in the Population monitoring section) would help to quantify these variables.

More information is needed before population trend in *Primula egaliksensis* can be understood. There has been no monitoring of occurrences that would permit a quantitative assessment of trend. Known occurrences should be revisited periodically to determine population size and condition (Welp et al. 2000).

A number of studies detail the ecology of the extreme rich fens that support *Primula egaliksensis* in South Park. However, more information is needed to identify the critical habitat variables of *P. egaliksensis* and the effects of management practices employed within its habitat. Welp et al. (2000) recommend a monitoring program to track water level, inflow, and outflow at Swamp Lake to gather more information on the hydrologic relationships within the wetland and inform management of this area. This type of information would be valuable anywhere *P. egaliksensis* occurs and would provide a better understanding of the ecological needs of this species.

Response to change

Understanding the specific responses of *Primula egaliksensis* to disturbance is important for determining compatible land management practices, but its resilience to human and natural disturbance has not been studied. The response of *P. egaliksensis* to grazing is unknown. Studies that measure responses to grazing using trend studies would be useful, as would demographic studies that succeed in identifying the most sensitive life history stage(s) of this species (e.g., García and Ehrlén 2002). Grazing is known to affect the extreme rich fen habitats of *P. egaliksensis* by causing or exacerbating the development of hummock-hollow topography, which in turn strongly affects species composition and distribution, but there has been no study of the effects of grazing on habitats inhabited by *P. egaliksensis* (Johnson and Steingraeber 2003).

Metapopulation dynamics

There is no information available to determine the importance of metapopulation structure and dynamics to the persistence of *Primula egaliksensis* at local or regional scales, but some observations do suggest that *P. egaliksensis* may have metapopulations. Emigration, immigration, and extinction rates are unknown for *P. egaliksensis*. Baseline population dynamics and viability must first be assessed. These analyses must rely on observable trends in individual occurrences. Observing population trends at the population level can provide reliable assessments of species status in the absence of metapopulation structure information (Harrison and Ray 2002).

Demography

Only the broadest generalizations can be made at present regarding the demography of *Primula egaliksensis*. Information on transition probabilities, population structure, longevity, mortality, and seed biology is not available (Coles 2002, Handley and Laursen 2002). Although *P. egaliksensis* probably reproduces primarily through selfing, outcrossing is possible and plays an unknown role in the maintenance of fitness and population viability (Kelso personal communication 2004). Pollinators of *P. egaliksensis* have not been documented in Region 2 or elsewhere. Factors necessary for seed germination and seedling survival are unknown. Some occurrences appear to be very small and may lack the genetic variability and adaptive capacity to ensure their long-term survival. However, there is no information on the genetic status of any population of *P. egaliksensis*. Critical life history stages of *P. egaliksensis* need to be identified before agencies can address potential bottlenecks through management.

The value of demographic data for conservation purposes cannot be overstated. However, short-term demographic studies often provide misleading guidance for conservation purposes. Lindborg and Ehrlén (2002) compared matrix models based on four years of demographic monitoring of *Primula farinosa* to the actual changes observed over a 70-year period. Due to inconsistencies between matrix model results and actual demographic change, the authors determined that complementary information, such as historical data and experimental manipulations should be included whenever possible (Lindborg and Ehrlén 2002).

Population trend monitoring methods

Methods are available to develop a monitoring protocol that would track population trends efficiently. The Population monitoring section contains details on monitoring methodology and considerations for establishing monitoring sites based on the literature. Selecting a variety of physiognomic and geological settings and land use scenarios will be necessary to monitor trend at the population level. Monitoring population trend will require plant counts (a census or sample) at many dispersed plots. Ideally, these plots will be established in each occurrence in Region 2.

Restoration methods

The applicability of existing methods to the restoration of *Primula egaliksensis* occurrences is unknown. The nature of its habitat and its apparent habitat specificity suggest that reintroduction to reclaimed or restored habitat may present many challenges. Attempts have been made to restore extreme rich fen habitats of *P. egaliksensis* in South Park (Coles 2002, Sanderson et al. in prep.). Restoration efforts at High Creek Fen have included pushing peat into the holes left by peat mining operations (De Prenger-Levin 2004). In 10 years since these efforts, *P. egaliksensis* has failed to recolonize restored portions of these fens (Coles 2002). This suggests that the restorability of these habitats may be low within a reasonable management timeframe; however, recolonization may also be inhibited by limited seed mobility.

There have been no attempts to restore occurrences of *Primula egaliksensis* through propagation and reintroduction. *Primula* species have long been cultivated, and there is a body of literature regarding floriculture and production for medicinal and horticultural purposes (reviewed by Karlsson 2001) that may be useful in the cultivation of *P. egaliksensis*. Richards (2003) grew *P. egaliksensis* in a partially shaded frame with regular misting from an automatic watering system while growing, but kept plants nearly dry and unprotected from frost when dormant. Methods have been developed for the *in vitro* micropropagation of the rare endemic homostyle *P. scotica* (Benson et al. 2000); these may be applicable for *P. egaliksensis* as well. The results of Tremayne and Richards (2000) suggest that reintroduction efforts may be more successful if relatively large, heavy seeds are selected. Developing techniques necessary to re-establish populations of *P. maguirei* is among the actions required for recovery by U.S. Fish and Wildlife Service (1990).

Research priorities for Region 2

The two highest research priorities for *Primula egaliksensis* are inventory and monitoring. Inventory is needed to locate all occurrences of *P. egaliksensis* in Region 2 so that conservation efforts can be made on their behalf. A complete inventory of private lands in South Park is needed to fill this data gap. Censusing occurrences as they are found will help to clarify the conservation priority of this species.

Population monitoring is needed to understand the effects of land uses, especially grazing, mowing, and any activities that result in hydrologic modification. Demographic monitoring data (e.g., lifespan, life stage transition probabilities) are needed to guide the appropriate management of this species. The importance of outcrossing and the role of pollinators in maintaining population fitness are also important to understand, due to the potential implications for management.

While much has been inferred from the habitats in which *Primula egaliksensis* is found, the autecology of this species remains poorly understood. A clearer understanding of habitat variables that control the density and distribution of *P. egaliksensis* is needed.

Additional research and data resources

Primula egaliksensis will be included in Volume 8 of the Flora of North America series. This volume is scheduled to be published in 2007 (FNA online 2006).

Definitions

Aneuploid – an organism with a chromosome number that is greater by a small number than the normal chromosome number for that species (Allaby 1998).

Auriculate – having small, ear-shaped appendages (Harris and Harris 1999).

Calciphile – a plant that grows best on limestone, or soils with a high percentage of free calcium carbonate (Art 1993).

Cladistics – a classification system that expresses the branching relationships between species through a phylogenetic tree with ancestral forms at the bottom and recently diverged ones at the top (Art 1993).

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 5 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.

Competitive/Stress-tolerant/Ruderal (CSR) model – a model developed by J.P. Grime in 1977 in which plants are characterized as Competitive, Stress-tolerant, or Ruderal, based on their allocation of resources; Competitive species allocate resources primarily to growth; Stress-tolerant species allocate resources primarily to maintenance; Ruderal species allocate resources primarily to reproduction; a suite of other adaptive patterns also characterize species under this model; some species show characteristics of more than one strategy (Barbour et al. 1987).

Distyly – a type of heterostyly in which there are two morphs, called 'pin' and 'thrum' morphs (Silverside 2002).

Efarinose – lacking farina (Harbourne 1968).

Extreme Rich Fen – (aka "extremely rich fen") - A type of fen with a very high pH (>7) and calcium concentration (>20 to 30 mg/l) and a characteristic assemblage of plant species (Chadde et al. 1998).

Farina – a powdery exudate composed primarily of flavones (Harbourne 1968).

Fen – a type of peatland that receives significant inputs of water and dissolved solids from a mineral source, such as runoff from mineral soil or ground water discharge (Chadde et al. 1998).

Gibbous – swollen or enlarged on one side (Harris and Harris 1999).

Heterostyly – a situation in which a plant species has two or more positional arrangements of its anthers and stigma(s) (Silverside 2002).

Homostyly – plants have only one flower type in which anthers and stigma are at the same level (Richards 2003).

Iteroparous – producing offspring more than once during the lifespan of an organism (Art 1993).

Marl – sediments rich in calcium carbonate and organic matter (Fertig and Jones 1992).

Monophyletic – a group of species that share a common ancestry (Allaby 1998).

Oblanceolate – inversely lanceolate, with the attachment at the narrower end (Harris and Harris 1999).

Pin – in heterostylous species, a flower in which the style is long enough that it is exposed at the mouth of the tube, and in which the anthers are fused to the walls of the corolla-tube, about halfway down (Richards 2003).

Polyphyletic Group – a group with two or more ancestors, but not including the true common ancestor of its members (Judd et al. 2002).

Potential Conservation Area – a best estimate of the primary area needed for the long-term survival of targeted species or natural communities; these areas are delineated for planning purposes only (Colorado Natural Heritage Program Site Committee 2002).

Saccate – with a sac, or in the shape of a sac; bag-shaped (Harris and Harris 1999).

Stephanocolpate – pollen with more than four (commonly six) longitudinal grooves that do not meet (Richards 2003).

Sympatric – species whose habitats (ranges) overlap (Allaby 1998).

Syncolpate – pollen with longitudinal grooves fused at the apex (pole) (Richards 2003).

Thrum – in heterostylous species, a flower in which the anthers are positioned at the mouth of the corolla-tube and in which the style is only half the length of the tube.

Valvate – opening by valves, as in many dehiscent fruits (Harris and Harris 1999).

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