Potentilla ambigens Greene (silkyleaf cinquefoil): A Technical Conservation Assessment

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COVER PHOTO CREDIT

Potentilla ambigens (silkyleaf cinquefoil). Photograph by Renée Rondeau, used with permission.

…an immense and comparatively smooth grassy prairie, in very strong contrast to the black masses of timber, and the glittering snow behind them. This is the picture which has been left on my mind…

— The first impression of the Black Forest on General John Charles Frémont in 1843, who also passed through Wagon Wheel Gap in his exploration of Colorado.

(From Von Ahlefeldt 1979)

SUMMARY OF KEY COMPONENTS FOR CONSERVATION OF *POTENTILLA AMBIGENS*

Status

Potentilla ambigens (silkyleaf cinquefoil) is distributed in 44 occurrences across 17 counties in Wyoming, Colorado, and New Mexico. Most of the population probably occurs in New Mexico, but the overall distribution of this species is poorly understood. Within USDA Forest Service Region 2, there is one reported occurrence in Wyoming and 25 in Colorado. Four or possibly five of the Colorado occurrences are located on the Roosevelt and Rio Grande national forests. The other occurrences are known from lands managed by the National Park Service, Department of Defense, State of Colorado, Jefferson County, Estes Park High School, private owners, and possibly the Bureau of Land Management. Ownership is unknown for of four Colorado occurrences and the one Wyoming occurrence due to imprecise location information.

The total population of *Potentilla ambigens* is unknown. Population size was not estimated at the Wyoming occurrence. Quantitative population estimates have been made at 16 occurrences in Colorado and total approximately 8,500 plants. Although it is likely that the total population of this species in Region 2 is larger than this figure, current knowledge of the distribution and abundance of this species indicates that concern for its viability in Region 2 is warranted.

Potentilla ambigens is ranked globally vulnerable (G3) by NatureServe, and it is considered imperiled (S2) in Colorado, historic (SH) in Wyoming, and reported (SR) in New Mexico. *Potentilla ambigens* is not considered sensitive by the USDA Forest Service Region 2 or by the Bureau of Land Management in Colorado and Wyoming, nor is it listed as threatened or endangered under the Federal Endangered Species Act.

Primary Threats

Observations and quantitative data indicate several threats to the persistence of *Potentilla ambigens*. In order of decreasing priority, these threats include off-road vehicle and other recreational use; residential and commercial development; the secondary impacts of grazing, roads, and water development; exotic species invasion; altered fire regime; global climate change; and pollution. Not every threat affects every site, and some threats are more immediate than others. Because most occurrences known in Region 2 are represented by few individuals, they may also be threatened by the effects of small population size and stochastic events.

Primary Conservation Elements, Management Implications and Considerations

Most occurrences of *Potentilla ambigens* in Region 2 are located on public land, where they are less likely to be impacted by residential development. However, *P. ambigens* has no special status designation with any public land agency, so it is generally given no consideration during management planning. Protective land status changes for occurrences on public lands (e.g., Special Interest Area, Research Natural Area, Area of Critical Environmental Concern) could help to protect *P. ambigens*. Pursuing conservation easements on private properties would help to ensure the viability of these occurrences. Additional inventory work for this species is a high priority and is likely to be successful. Research is needed to investigate the population biology and autecology of *P. ambigens* so that conservation efforts on its behalf can be most effective.

TABLE OF CONTENTS

ACKNOWLEDGMENTS 2
AUTHOR'S BIOGRAPHY 2
COVER PHOTO CREDIT 2
SUMMARY OF KEY COMPONENTS FOR CONSERVATION OF *POTENTILLA AMBIGENS* 3
Status 3
Primary Threats 3
Primary Conservation Elements, Management Implications and Considerations 3
LIST OF TABLES AND FIGURES 6
INTRODUCTION 7
Goal of Assessment 7
Scope of Assessment 7
Treatment of Uncertainty in Assessment 7
Treatment of This Document as a Web Publication 8
Peer Review of This Document 8
MANAGEMENT STATUS AND NATURAL HISTORY 8
Management Status 8
Existing Regulatory Mechanisms, Management Plans, and Conservation Strategies 8
Adequacy of current laws and regulations 8
Adequacy of current enforcement of laws and regulations 9
Biology and Ecology 10
Classification and description 10
History of knowledge 13
Non-technical description 14
Technical description (from Greene 1893) 15
Technical description (from Harrington 1954, p. 306) 16
Published descriptions, keys, checklists, and photographs 16
Distribution and abundance 16
Wyoming 16
Colorado 17
New Mexico 24
Southern extent of distribution 25
Abundance 25
Population trend 25
Habitat 26
General habitat description 26
Moisture availability 27
Fire 29
Slope, aspect, and elevation 31
Soil and geology 31
Precipitation 31
Reproductive biology and autecology 31
Reproduction 33
Pollinators and pollination ecology 34
Phenology 34
Fertility and propagule viability 34
Propagation and planting methods 34
Dispersal mechanisms 35
Cryptic phases 35
Phenotypic plasticity 35
Mycorrhizae 35
Hybridization 36
Demography 36

Community ecology 37
Coniferous forest communities 37
Grasslands 38
Vegetation change 39
Herbivores and relationship to habitat 39
Competitors and relationship to habitat 40
Parasites and disease 40
Associated species 40
CONSERVATION 40
Threats 40
Influence of management activities or natural disturbances on habitat quality and individuals 40
Recreation 40
Residential and commercial development 41
Secondary impacts of grazing 42
Road impacts 42
Water resource development 42
Exotic species 42
Small population size 44
Altered fire regime 44
Climate change 44
Pollution 44
Over-utilization 45
Conservation Status of *Potentilla ambigens* in Region 2 45
Is distribution or abundance declining in all or part of its range in Region 2? 45
Capacity of habitats to support this species 45
Vulnerability due to life history and ecology 46
Evidence of occurrences in Region 2 at risk 46
Management of *Potentilla ambigens* in Region 2 47
Implications and potential conservation elements 47
Tools and practices 47
Species and habitat inventory 47
Population monitoring 48
Habitat monitoring 49
Beneficial management actions 49
Seed banking 50
Information Needs 51
Distribution 51
Life cycle, habitat, and population trend 51
Response to change 51
Metapopulation dynamics 51
Demography 51
Population trend monitoring methods 52
Restoration methods 52
Research priorities (in order of priority) for Region 2 52
Additional research and data resources 53
DEFINITIONS 54
REFERENCES 56

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List of Tables and Figures

Tables:

Table 1. Land ownership status of the 26 occurrences of *Potentilla ambigens* in USDA Forest Service Region 2. 9

Table 2. Taxonomic placement of *Potentilla ambigens*. 12

Table 3. Summary of Colorado Natural Heritage Program surveys in which occurrences of *Potentilla ambigens* were found or revisited. 15

Table 4. Potential Conservation Areas defined by the Colorado Natural Heritage Program in which *Potentilla ambigens* occurs. 15

Table 5. Summary information for the known occurrences of *Potentilla ambigens*. 18

Table 6. Species reported to be associated with *Potentilla ambigens*. 41

Table 7. Summary of U.S. census data for the counties of USDA Forest Service Region 2 in which *Potentilla ambigens* occurs. 47

Figures:

Figure 1. Distribution of *Potentilla ambigens* in the states of USDA Forest Service Region 2. 10

Figure 2. Photograph of *Potentilla ambigens*. 11

Figure 3. *Potentilla ambigens* at Beaver Meadows, Rocky Mountain National Park. 11

Figure 4. *Potentilla ambigens* (yellow arrow) with *P. hippiana* (red arrows) at the Estes Park High School occurrence. 13

Figure 5. The known global range of *Potentilla ambigens* in Wyoming, Colorado, and New Mexico. 17

Figure 6. Distribution of *Potentilla ambigens* in USDA Forest Service Region 2 in relation to major physiographic landscape features. 24

Figure 7. *Potentilla ambigens* along a roadside at the U.S. Air Force Academy on July 10, 2002. 26

Figure 8. Pool Table Road near Wagon Wheel Gap on the La Garita Ranch. 27

Figure 9. The large occurrence of *Potentilla ambigens* at Rattlesnake Park, Larimer County, discovered in 2004. 28

Figure 10. Habitat of *Potentilla ambigens* at Goose Creek. 28

Figure 11. *Potentilla ambigens* habitat at the La Garita Ranch. 29

Figure 12. *Potentilla ambigens* habitat at Goose Creek. 30

Figure 13. *Potentilla ambigens (*foreground) at Estes Park High School. 30

Figure 14. Annual precipitation for Region 2 occurrences of *Potentilla ambigens*. 32

Figure 15. Hypothetical life cycle graph for *Potentilla ambigens*. 38

Figure 16. *Cynoglossum officinale* with *Potentilla ambigens* (foreground) at Estes Park High School. 43

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). *Potentilla ambigens* is the focus of an assessment because of concern for its viability and because little is known about it. It was considered for sensitive species status, but a lack of information precluded listing (Warren 2003). *Potentilla ambigens* remains a management concern for Region 2 because four or possibly five occurrences exist on lands administered by Region 2. It is also known from lands administered by USFS Region 3 in New Mexico.

This assessment addresses the biology of *Potentilla ambigens* throughout its range in Region 2. The broad nature of the assessment leads to some constraints on the specificity of information for particular locales. This introduction defines the goal of the assessment, outlines it scope, and describes the process used in its production.

Goal of Assessment

Species conservation assessments produced as part of the Species Conservation Project are designed to provide forest managers, research biologists, and the public with a thorough discussion of the biology, ecology, conservation status, and management of certain species based on scientific knowledge accumulated prior to initiating the assessment. The assessment goals limit the scope of the work to critical summaries of scientific knowledge, discussion of broad implications of that knowledge, and outlines of information needs. The assessment does not seek to develop specific management recommendations. Rather it provides the ecological background upon which management must be based and focuses on the consequences of changes in the environment that result from management (i.e., management implications). Furthermore, this assessment cites management recommendations proposed elsewhere and examines the success of those recommendations that have been implemented.

Scope of Assessment

This assessment examines the biology, ecology, conservation status, and management *Potentilla ambigens* with specific reference to the geographic and ecological characteristics of Region 2. Although some literature on the species originates from field investigations outside the region, this document places that literature in the ecological and social context of the central Rocky Mountains. Similarly, this assessment is concerned with reproductive behavior, population dynamics, and other characteristics of *P. ambigens* in the context of the current environment rather than under historical conditions. The evolutionary environment of the species is considered in conducting the synthesis, but placed in a current context.

In producing the assessment, refereed literature, non-refereed publications, research reports, and data accumulated by resource management agencies were reviewed. All known publications, reports, and element occurrence records for *Potentilla ambigens* in Region 2 are referenced in this assessment, and all of the available experts on this species were consulted during its synthesis. All available specimens of *P. ambigens* were viewed to verify occurrences and to incorporate specimen label data. Specimens were searched for at COLO (University of Colorado Herbarium), CS (CSU Herbarium), RM (Rocky Mountain Herbarium), SJNM (San Juan College Herbarium), CC (Carter Herbarium), Great Sand Dunes National Park Herbarium, GREE (University of Northern Colorado Herbarium), NMCR (New Mexico State University Range Science Herbarium), and UNM (University of New Mexico Herbarium). This assessment emphasizes refereed literature because this is the accepted standard in science. Non-refereed publications or reports were used when information was unavailable elsewhere, but these were regarded with greater skepticism. Unpublished data (e.g., Natural Heritage Program records) contain the vast majority of the useful information known for *P. ambigens* and were important in estimating its geographic distribution.

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 observations limited, science focuses on approaches for dealing with uncertainty. A commonly accepted approach to science is based on a progression of critical experiments to develop strong inference (Platt 1964). However, strong inference, as described by Platt, suggests that experiments will produce clean results (Hillborn and Mangel 1997), as may be observed in physics. In the ecological sciences, where experiments do not always produce clean results, observations, inference, and models must be relied on to guide understanding. Confronting uncertainty, then, 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 are being published on the Region 2 World Wide Web site. Placing the documents on the Web makes them available to agency biologists and the public more rapidly than publishing them as reports. More important, Web publication will facilitate the 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 before their release on the Web. This assessment was reviewed through a process administered by the Society for Conservation Biology, employing two experts on this or related taxa. Peer review was designed to improve the quality of communication and to increase the rigor of the assessment.

MANAGEMENT STATUS AND NATURAL HISTORY

Management Status

In Region 2, *Potentilla ambigens* is known from lands administered by the Roosevelt and Rio Grande national forests. The USFS does not list *P. ambigens* as a sensitive species (USDA Forest Service 2003). It was considered for sensitive species status (Handley and Heidel 2002), but it was left off the list during the latest revision due to insufficient information (Warren 2003). *Potentilla ambigens* is not included on the sensitive species lists maintained by the Bureau of Land Management for Colorado (Bureau of Land Management 2000) or Wyoming (Bureau of Land Management 2001a). NatureServe (2004) ranks this species as globally vulnerable (G3). In Wyoming, it is ranked historic (SH) based on a single occurrence that has not been seen since 1900 and may have been extirpated (Handley and Heidel 2002, Heidel 2003, Heidel personal communication 2004, NatureServe 2004). Prior to the research done for this species assessment, *P. ambigens* was ranked between critically imperiled and imperiled (S1S2) in Colorado because it was known from only nine occurrences (Colorado Natural Heritage Program 2004). This rank has been changed to S2 since it is now known from 25 occurrences in Colorado. The New Mexico Natural Heritage Program does not track *P. ambigens*, and it is ranked as reported (SR). For an explanation of NatureServe's ranking system, see the **Definitions** section. Of the states within its range, only New Mexico gives plants special state status, but *P. ambigens* is not included on this list. It is not listed as threatened or endangered under the Federal Endangered Species Act and has never been a candidate for listing.

Existing Regulatory Mechanisms, Management Plans, and Conservation Strategies

Adequacy of current laws and regulations

There are no known protective state or federal laws, designations, conservation agreements, or approved management plans that would prevent the destruction of *Potentilla ambigens* habitat or individuals. There is no known conservation or recovery planning for this species. Because there are no laws that protect this species on private or public lands, current laws and regulations protecting this species are inadequate to conserve the species throughout its native range.

Of the 26 occurrences of *Potentilla ambigens* in the states of Region 2, 18 (and possibly as many as 20) are on public land (**Table 1**, **Figure 1**). Four or possibly five occurrences are known from Region 2 National Forest System land in Colorado. These include three occurrences on the Rio Grande National Forest, one at Goose Creek Road that has not been seen since 1911, one at Wagon Wheel Gap, and one at East Bellows Creek, and two occurrences on the Roosevelt National Forest, one at Rustic Hill that has not been seen since 1896 and another possibly on the east side of State Highway 36 (**Figure 1**). Because *P. ambigens* currently has no special USFS status, it does not benefit from many of the considerations that are required for sensitive species under the National Environmental Policy Act. However, managers may still give *P. ambigens* consideration in project planning exercises if proposed activities threaten to compromise the viability of the species (Popovich personal communication 2004).

Seven Region 2 occurrences of *Potentilla ambigens* are within national parks; six are in Rocky Mountain National Park, and one is in Great Sand Dunes National Park. One occurrence is known from the Elk Meadow Open Space Park, which is managed for its natural values by Jefferson County. The State of Colorado manages lands that contain two occurrences, and lands managed by the City of Estes Park and

Table 1. Land ownership status of the 26 occurrences of *Potentilla ambigens* in USDA Forest Service Region 2. Because some occurrences are lands with multiple owners, the total is less than the sum of the rows in the table. See **Table 5** for ownership of specific occurrences.

Land Ownership Status	Number of Occurrences	Subtotals
USDA Forest Service Region 2	**4 +1?**	
Roosevelt National Forest		1+1?
Rio Grande National Forest		3
Bureau of Land Management	**1?**	
Rawlins Field Office		1?
National Park Service	**7**	
Rocky Mountain National Park		6
Great Sand Dunes National Park		1
U.S. Air Force Academy	**1**	
Colorado State Land Board	**2**	
Colorado State University	**1**	
Private	**6**	
Under Conservation Easement		1
Jefferson County	**1**	
Estes Park High School	**1**	
Town of Estes Park	**1**	
Unknown	**1**	
TOTAL	**26**	

Estes Park High School each contain one occurrence. Another occurrence is on land owned by Colorado State University. There is also an occurrence on U.S. Air Force Academy property that is somewhat protected since the Academy's natural resource staff is aware of the plant, and development of this location is unlikely. Six occurrences are known from private land in Jefferson and Larimer counties, and these are threatened by residential development. One occurrence from private land is protected by a conservation easement held by The Nature Conservancy, which includes *P. ambigens* as a target for conservation planning in the Southern Rocky Mountain Ecoregion (Neely et al. 2001). *Potentilla ambigens* occurs in the Upper Bioregion of the Rio Grande in Reach 1 (at Wagon Wheel Gap and other sites in Mineral County, Colorado) as described in a broad plan for the restoration of the Rio Grande Watershed (Fullerton and Batts 2003). While this species is noted in this plan, no specific restoration objectives are outlined for it.

The Colorado Natural Heritage Program has identified eight Potential Conservation Areas (PCAs) that contain *Potentilla ambigens* (Ellingson et al. 1995, Rondeau 1999, Doyle et al. 2001). PCAs delineate the primary area encompassing the biological processes supporting the long-term survival of a targeted species and generally include an assessment of the management needs of the species. The San Juan National Forest is using PCAs to determine suitable locations for Special Interest Area designation (Redders personal communication 2006).

The occurrence of *Potentilla ambigens* in Wyoming has not been seen in more than 100 years. It may have been on land managed by the Rawlins Field Office of the BLM. The Rawlins Field Office is in the process of writing a Resource Management Plan and Draft Environmental Impact Statement (Bureau of Land Management 2004), but this document will probably not have provisions for the protection of *P. ambigens* because the Wyoming Bureau of Land Management does not consider it a sensitive species (Bureau of Land Management 2001a).

Adequacy of current enforcement of laws and regulations

There are currently no laws or regulations that protect occurrences of *Potentilla ambigens* on private, state, or federal lands. There have been no known cases in which an occurrence of *P. ambigens* was extirpated due the failure to enforce any existing regulations. Human impacts such as residential development and grazing may have diminished the abundance of this species. Enforcement of existing restrictions on

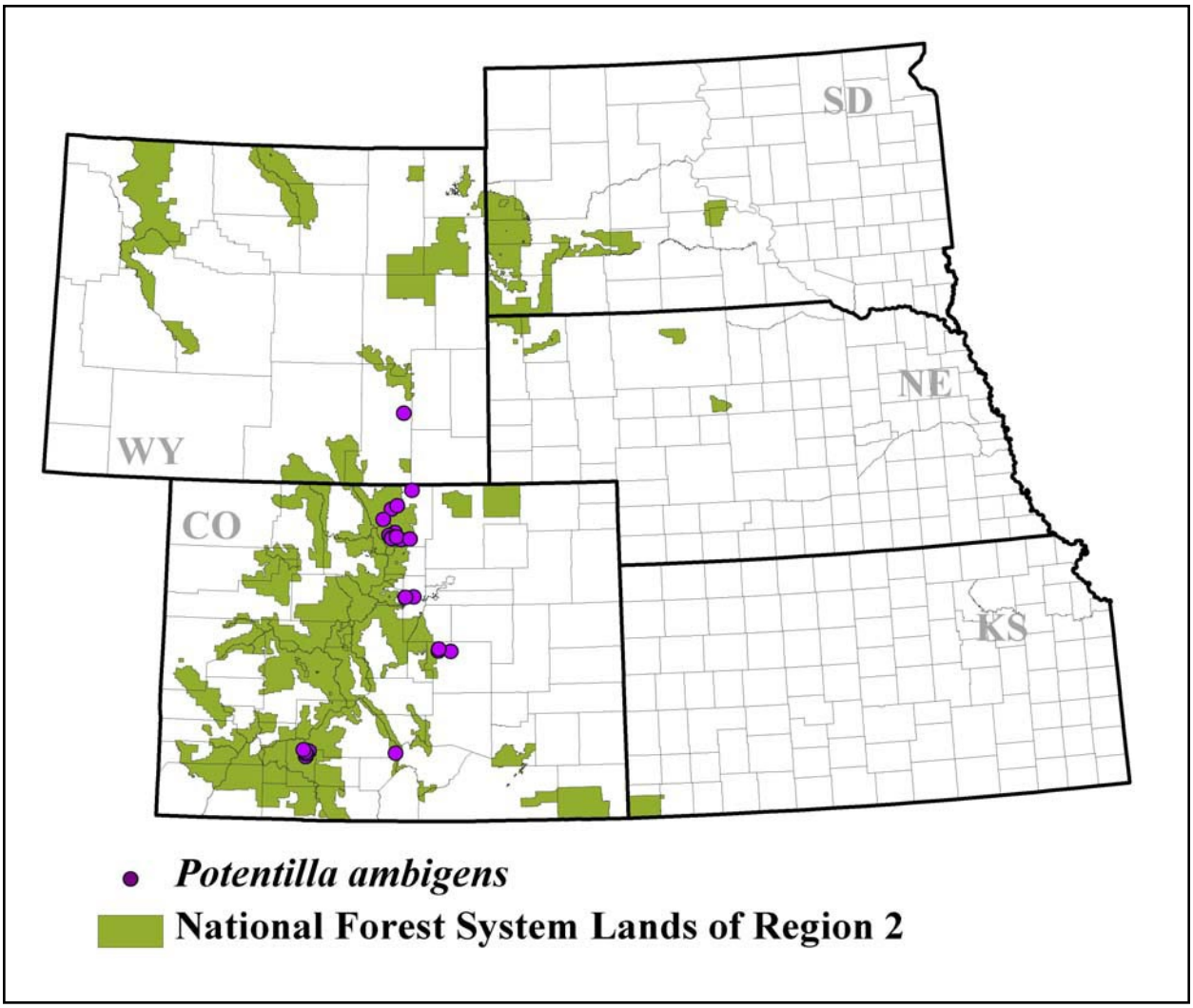

Figure 1. Distribution of *Potentilla ambigens* in the states of USDA Forest Service Region 2.

off-road vehicle use on public lands is very difficult. Users frequently pull down barriers and breach fences to gain access to off-limits areas (Brekke personal communication 2004). Federal agencies lack sufficient resources to patrol the vast areas they manage.

Biology and Ecology

Classification and description

Potentilla ambigens (**Figure 2**, **Figure 3**) is a member of the rose family (Rosaceae), a large, cosmopolitan family of approximately 100 genera and 2,000 species that are distributed from the high arctic and subantarctic zones to the tropics. This diverse family of herbs, shrubs, and trees includes many members that are of agricultural and economic significance (e.g., apples, pears, peaches; Heywood 1993). The Rosaceae is an ancient family and its members have many primitive (less specialized) characters such as actinomorphic flowers, large numbers of stamens and carpels, and variable numbers of floral parts (Heywood 1993 after Stebbins 1974).

The Rosaceae is in the Dicot group, subclass Rosidae, and order Rosales (Cronquist 1988, Heywood 1993, USDA Natural Resources Conservation Service 2003). Rosidae is the largest angiosperm subclass. The Rosales is ancestral to Salicales and Leguminales (Scagel et al. 1966), and it has many similarities to the Ranales from which it may have descended (Porter 1967).

Potentilla is in the subfamily Rosoideae (**Table 2**; Porter 1967, National Center for Biotechnology Information 2002) and tribe Potentilleae (Morgan et al. 1994). The genus *Potentilla* includes 300 to 350 species (Eriksen 2002). Weber and Wittmann (2000,

Figure 2. *Potentilla ambigens* taken on July 23, 1998 at Goose Creek. Photograph by Renée Rondeau, used with permission.

Figure 3. *Potentilla ambigens* at Beaver Meadows, Rocky Mountain National Park. Photograph by Leanne Benton, used with permission.

Table 2. Taxonomic placement of *Potentilla ambigens*.

Kingdom	Plantae
Subkingdom	Tracheobionta
Superdivision	Spermatophyta
Division	Magnoliophyta
Class	Magnoliopsida (Dicotyledons)
Subclass	Rosidae
Order	Rosales
Family	Rosaceae
Subfamily	Rosoideae
Tribe	Potentilleae
Genus	*Potentilla*
Species	*Potentilla ambigens* Greene

2001a, 2001b) recognize 27 species of *Potentilla* in Colorado, as well as many taxa in other genera that have been segregated from *Potentilla* such as *Drymocallis*, *Dasiphora*, *Acomastylis*, and *Argentina*. There is ample support for the recognition of these segregate genera based on morphology and breeding structure (Johnston personal communication 2004). For example, apomixis does not occur in *Dasiphora* (Innes and Lenz 1990), but *Potentilla* is replete with apomictic taxa. Recent taxonomic work suggests that the genus *Potentilla* is not monophyletic (Eriksson et al. 1998, Eriksson et al. 2003), so it may be split further. The Colorado Natural Heritage Program (2004) tracks three species of *Potentilla* (*P. ambigens*, *P. rupincola*, and *P. subviscosa*) as rare in Colorado.

Rydberg (1897) included *Potentilla ambigens* within section *Hippianae*. Rydberg distinguished members of section *Hippianae* from members of *Multijugae*, which he considered to be closely related to *Hippianae*, on the basis of vegetative characters. Members of section *Hippianae* are typically stouter than those of section *Multijugae*, and the leaves are "more or less white or grayish hairy, generally densely silky, villous or tomentose." Greene (1893) noted morphological affinities of *P. ambigens* with *P. arguta* and *P. pennsylvanica*. Wolf (1908) included *P. ambigens* in the group *Graciles* in the series *Eriotrichae*, in the subsection *Constylae*, and the section *Gymnocarpae*. Since Wolf's monograph and Rydberg's series of monographs on *Potentilla*, there has been considerable revision of the genus, which continues today. Eriksson et al. (1998) offer a very good overview of the history of taxonomic research in the Rosoideae. This paper presents the results of a phylogenetic analysis of *Potentilla* based on nuclear ribosomal internal transcribed spacer (ITS) DNA sequences, but *P. ambigens* was not included in this study.

Although there remains much taxonomic turmoil in the genus *Potentilla*, there have been no synonyms proposed for *P. ambigens* since it was described more than 100 years ago, and it is generally regarded as a good species. Rydberg (1897, p. 8) remarked, "It is strange that this very marked species should not have been described before 1893." However, Sivinski (personal communication 2004) opined that *P. ambigens* might merely be an especially vigorous expression of *P. hippiana*. This is also suggested in Neely et al. (2001), where it is noted that more recent collections from the Sacramento Mountains of New Mexico grade into *P. hippiana*. While these observations call into question to some degree the taxonomic validity of *P. ambigens*, Johnston (personal communication 2004) offered some thoughts on why *P. ambigens* should continue to be regarded as a valid taxon. Hybrid swarms are common in *Potentilla* and often form where ranges overlap. These swarms can sometimes persist indefinitely through apomixis (see the Reproductive biology and autecology and Hybridization sections for details). While it would not be surprising if there were some hybridization going on in parts of its range, *P. ambigens* is usually morphologically distinctive and readily identifiable. Rondeau (personal communication 2004) observed sympatric populations of *P. ambigens* and *P. hippiana* at Goose Creek in Mineral County, Colorado and found them to be readily distinguishable. *Potentilla ambigens* is also distinguishable from *P. hippiana* at Estes Park High School in Larimer County, Colorado (**Figure 4**). With respect to *P. hippiana*, *P. ambigens* has several diagnostic characteristics that are consistent in Region 2 (see the Non-technical description section for details). Many of these characteristics relate to the hairs on the leaves, which are variable in *P. ambigens*. Sivinski (personal communication 2004) questions the value of leaf hairs as a diagnostic character in

Figure 4. *Potentilla ambigens (*yellow arrow) with *P. hippiana* (red arrows) at the Estes Park High School occurrence. Hybridization between these species was not evident at this location. Photograph by the author.

this and other *Potentillas*. As noted by Neely et al. (2001), research is needed to clarify the taxonomic distinctness of *P. ambigens* with respect to *P. hippiana* and other members of *Potentilla*, and to determine the role of hybridization and introgression in its population biology.

History of knowledge

The earliest known collections of *Potentilla ambigens* were made by Hall and Harbour in 1862 (location not cited) and by William A. Bell in 1867 in the Raton Mountains of New Mexico (Rydberg 1897). The next known collection of *P. ambigens* was taken from an unknown location in New Mexico, probably in 1881, by George Richard Vasey. G.R. Vasey worked in the mountains west of Las Vegas, New Mexico where this specimen was probably collected. It is thought that his collections were sent to his father George Vasey (a renowned botanist) without labels or definite locality information (Ewan and Ewan 1984). Asa Gray included these plants within *P. hippiana* although their identification was contentious (Rydberg 1897).

Edward Lee Greene collected *Potentilla ambigens* in July 1889 "along Bear Creek, above Morrison." This collection became the type specimen for his description of *P. ambigens*, published in 1893 in *Erythea*, a botanical journal that he founded in that year. Kate Brandegee offered a scathing review of Greene's journal in 1893, citing his description of *P. ambigens* as an example of its shortcomings:

"*Potentilla ambigens* and *P. scopulorum* are perhaps of that genus [*Potentilla*], though experience has shown that it is not always safe to assume even that degree of accuracy on the author's part, and there is hardly anything in the descriptions to prove that he is not describing forms of *Barbarea vulgaris*, for instance. No information is 'vouchsafed' as to whether the plants are annual, biennial, or perennial; both species are said to have "about 5 pairs of leaflets," but whether scattered on long petioles or crowded near the top of them is left to the imagination along with such unconsidered trifles as stipules, bractlets, petals, stamens, styles, akenes, etc. Absolutely the only mention made of the floral organs is "flowers small, yellow," in one case, and corollas nearly an inch in diameter, pale yellow," in the other!"

Potentilla ambigens was collected several other times in the late 1800s and early 1900s in Colorado and New Mexico. Aven Nelson collected it at Halleck Canyon, Wyoming in 1900, but this occurrence has not been seen since. It was collected in 1896 by George E. Osterhout at Rustic Hill in Larimer County, where it also has not been relocated.

There are errors in the literature in how Greene's description and collection of *Potentilla ambigens* are cited. Most sources cite the description correctly as 1893, Volume 1, Number 5 of *Erythea*. However, Rydberg (1897) and Wolf (1908) cite it from Volume 1, Number 4, 1893. The W3 Tropicos Database cites the description from Volume 1, Number 1, Page 5 (Missouri Botanical Garden 2004). Coulter and Nelson (1909) and Harrington (1954) cite it from *Erythea* Volume 1, Number 4, 1903. Regarding the type specimen, Colorado Native Plant Society (1997) and Weber and Wittmann (2000) state that Greene collected it in 1899 (which would place the collection of the type after the publication of the description) and should read as 1889, as noted by Greene (1893) and Missouri Botanical Garden (2004).

After the early 1900, *Potentilla ambigens* was collected rarely in Colorado until the 1980s; collections from New Mexico were more consistent through the 20th century. In 1984, William Weber and Dan Randolph documented the first large *P. ambigens* occurrences in Region 2, at Goose Creek and Wagon Wheel Gap in Mineral County, Colorado. William Weber was also the first to recognize *P. ambigens* at Rocky Mountain National Park, where he found it in the maintenance area at Park Headquarters. A park ranger recognized this species as not previously recognized at Rocky Mountain National Park and showed it to Dr. Weber. Observations by Barry Bernier, Leanne Benton, and Lonnie Pilkington, and a collection from southeast of Estes Park in 1990 suggest that the area around Estes Park is another major population center for this species. *Potentilla ambigens* was discovered in El Paso County by Nancy Lederer at the U.S. Air Force Academy in 1993.

Most published accounts of *Potentilla ambigens* are found in floras. Thomas Wolf included *P. ambigens* in his monograph of the genus in 1908 (in German and Latin); this remains the most recent monograph of *Potentilla*.

In the 1970s, D. Acharya Goswami and B. Matfield studied the cytology and mating system of *Potentilla ambigens*, focusing on pseudogamy, but there have been no other academic studies involving *P. ambigens*. The source of the material used in their studies was the Chelsea Physic Garden in London, who provided material labeled "*Potentilla crinita*." However, the authors determined that the material they received was instead *P. ambigens*. No details are offered in their publications (Acharya Goswami and Matfield 1974, Acharya Goswami and Matfield 1975, Acharya Goswami and Matfield 1978) regarding the occurrence from which the material originated, or the location of any voucher specimens from their research. However, Acharya Goswami and Matfield (1975) note that records of the data and place of collection of some of the plants are available. Until the place of origin is determined, the correct identification of the material they used in this study must remain uncertain. An inquiry was sent to the Chelsea Physic Garden regarding *P. ambigens*, but no reply had been received by the time this assessment was completed. It is not known whether *P. ambigens* is still in cultivation at the Chelsea Physic Garden.

Knowledge of the distribution of *Potentilla ambigens* has been augmented by surveys, biological inventories, and weed mapping that the Colorado Natural Heritage Program conducted in the 1990s and 2000s. This fieldwork resulted in the discovery of several new occurrences (**Table 3**) and provided most of the detailed natural history information available for this species. This work also resulted in the development of PCAs containing occurrences of *P. ambigens*. The Mineral County occurrences fall into two PCAs, both of which include land managed by the Rio Grande National Forest. **Table 4** is a summary of all PCAs that include *P. ambigens*.

Non-technical description

Potentilla ambigens is known by at least three common names. The name recognized by the PLANTS database (and used in this assessment) is "silkyleaf cinquefoil" (USDA Natural Resources Conservation Service 2003). Other sources (e.g., NatureServe 2004) use "Southern Rocky Mountain cinquefoil" as the common name. However, this is confusing because another rare species in Colorado, *P. rupincola*, is known as "Rocky Mountain cinquefoil." *Potentilla ambigens* has also been referred to as "giant cinquefoil" (Handley and Heidel 2002). Its epithet, *ambigens*, means "to wander" (Griffith 2002).

Potentilla ambigens is a handsome plant. It is especially striking in the fall when the leaves turn bright red (Colorado Native Plant Society 1997). *Potentilla ambigens* is a taprooted perennial with

Table 3. Summary of Colorado Natural Heritage Program surveys in which occurrences of *Potentilla ambigens* were found or revisited.

Authors	Area Surveyed	Summary of Results
Ellingson et al. 1995	U.S. Air Force Academy	Searched but no new occurrences found
Kettler et al. 1996	Larimer County	One occurrence found
Rondeau 1999	Mineral County	Two occurrences found, one revisited
Doyle et al. 2001	El Paso County	One occurrence found
Anderson et al. 2003	U.S. Air Force Academy	Two new suboccurrences found
Doyle et al. 2005	Larimer County	Two new occurrences found
Anderson and Lavender 2006	U.S. Air Force Academy	Three new suboccurrences found

Table 4. Potential Conservation Areas defined by the Colorado Natural Heritage Program in which *Potentilla ambigens* occurs. See the **Definitions** section for an explanation of the B (Biodiversity Significance) rank.

PCA Name	County	EO #	B Rank
La Foret	El Paso	12	B4
Monument Creek	El Paso	7	B2
Wah Keeney Park	Jefferson	6	B4
Rattlesnake Park	Larimer	13	B3
Scout Camp Meadows	Larimer	14	B3
Sheep Mountain near Virginia Dale	Larimer	5	B3
East Bellows Creek	Mineral	1, 2, 8	B2
Goose Creek	Mineral	9	B3
Upper Medano Creek	Saguache	*Dixon s.n.*	B3

several stems emerging from a stout rootstock (**Figure 2**, **Figure 3**). *Potentilla ambigens* has large leaves that are borne basally and on the stems. The leaves are two or more decimeters in length and have nine to 15 leaflets. It has flowers (that are not numerous) with yellow petals that are slightly longer than the sepals, as is typical in *Potentilla* (Colorado Native Plant Society 1997, Johnston personal communication 2004). *Potentilla ambigens* is most commonly mistaken for *P. hippiana*, as shown by annotation labels on specimens at Rocky Mountain Herbarium, University of Colorado Herbarium, and others. The two species are found in similar habitats and have been documented together in Colorado.

Stature is an important diagnostic characteristic for *Potentilla ambigens*. Weber and Wittmann (2001a) describe it as "Tall and stout…a gigantic plant, the largest of all Colorado species." Its stems range from 40 to 70 cm in height (Harrington 1954), and it is a large plant when compared to most other *Potentilla* species. Adult plants at Rocky Mountain National Park are 45 to 60 cm in height (Benton personal communication 2004). *Potentilla ambigens* is distinguished from *P. rupincola*, *P. ovina*, and *P. plattensis* in Weber and Wittmann (2001a) based on size. *Potentilla recta*, a noxious weed with palmately compound leaves, can also become large but is easily distinguished from *P. ambigens*, which has pinnately compound leaves.

The hairiness of the leaves is another important diagnostic characteristic for identifying *Potentilla ambigens* (Johnston personal communication 2004). However, descriptions of the plant hairs of the leaves of *P. ambigens* are variable. Descriptions of the leaf hairs include "almost equally white-pubescent on both surfaces" (Wooton and Standley 1915), "covered in long, soft hairs" (Colorado Native Plant Society 1997), "densely pilose" (Weber and Wittmann 2001a), and "glabrate above on leaves, silky villous beneath, especially on the rachis and veins, slightly tomentulose when young" (Rydberg 1922). Leaf hairs on plants observed by the author appeared to best match the descriptions of Rydberg (1922) and Harrington (1954), but they were never the long, soft hairs as described by Colorado Native Plant Society (1997).

Technical description (from Greene 1893)

"Stout and tall, two feet high or more, the stem and petioles densely villous-hirsute; radical leaves firm, erect, a foot long, of about five pairs of

oblong or linear-oblong deeply and irregularly serrate leaflets, two inches long, or more; cauline similar, but smaller; flowers small, yellow, in a loose and ample cymose panicle."

Technical description (from Harrington 1954, p. 306)

"Perennial plants with thick, woody taproots; stems 40 to 70 cm tall, rather stout, silky-villous; basal leaves up to 20 cm long, irregularly pinnately compound; leaflets 9 to 15, 3 to 6 cm long, coarsely serrate, often decurrent on the rachis, especially the upper, silky-villous below especially on veins, tomentulose when young, more glabrous above but the color contrast not striking; stem leaves smaller with fewer leaflets; flowers in a narrow cyme; sepals about 6 to 7 mm long, lanceolate, strigose, bractlets as long or longer than sepals; petals about 8 mm long, yellow; style filiform, near apex; achenes glabrous."

Published descriptions, keys, checklists, and photographs

Several sources describe *Potentilla ambigens*. Greene's original (1893) description is included in this assessment as it is difficult to obtain, but later descriptions are more precise. Harrington (1954) includes a good description (see above) and is readily available. Rydberg (1922) also offers a very good description. Other descriptions appear in Wooton and Standley (1915), Tidestrom and Kittell (1941), and Martin and Hutchins (1980). Wolf (1908) includes a detailed description in Latin.

Dichotomous keys for the identification of *Potentilla ambigens* are available in many published sources. The best and most readily available is Weber and Wittmann (2001a). Other sources of keys include Rydberg (1906), Coulter and Nelson (1909), Wooton and Standley (1915), Rydberg (1922), Tidestrom and Kittell (1941), Harrington (1954), Martin and Hutchins (1980), Dorn (1992), and Komarek (1994). *Potentilla ambigens* is not included in *Plants of Rocky Mountain National Park* (Beidleman et al. 2000), which is in part why park staff did not recognize it earlier. *Potentilla ambigens* is included in several checklists, all of which are available online. These include Nelson and Hartman (1994), Weber and Wittmann (2000), Hartman and Nelson (2001), Allred (2003), and Snow and Brasher (2004).

Good photographs of *Potentilla ambigens* are available in Colorado Native Plant Society (1997) and older versions of *Colorado Flora: Eastern Slope* (e.g., Weber 1990, Weber and Wittmann 1996). The publisher required that the photographs be removed from the latest edition (Weber and Wittmann 2001a). Rondeau (1999) includes a photograph of *P. ambigens* that appears in this assessment (**Figure 2**). Acharya Goswami and Matfield (1978) include microphotographs of the chromosomes of *P. ambigens*. No illustrations exist for this species.

Distribution and abundance

The genus *Potentilla* is distributed from the subtropical to the arctic, but it is best represented in subalpine, alpine, and arctic mountain ranges throughout the Northern Hemisphere (Johnston 1980).

Potentilla ambigens is almost endemic to the Southern Rocky Mountain Ecoregion (Neely et al. 2001). This species is only known from one county in Wyoming, five counties in Colorado, and 11 counties in New Mexico (**Figure 5**; Coulter and Nelson 1909, Wooton and Standley 1915, Tidestrom and Kittell 1941). Summary information for occurrences of *P. ambigens* is presented in **Table 5**.

The distribution pattern within the range is curious. Weber and Wittmann (2001a) characterize it as "very sporadic." Its distribution is highly disjunct across the three states (Neely et al. 2001). The reason for this sporadic pattern remains unknown (Colorado Native Plant Society 1997). In Colorado, occurrences are clumped at four locations: Wagon Wheel Gap (Mineral County), Black Forest and U.S. Air Force Academy (El Paso County), Morrison (Jefferson County), and the Estes Park area (Larimer County) (**Figure 6**). There is some correspondence between the distribution of *P. ambigens* and Precambrian outcrops of granite, gneiss, and schist in Colorado, but this species is also found on sedimentary strata and Quaternary alluvium. See the Habitat section for details on associations with geologic strata.

Wyoming

Potentilla ambigens is known from one occurrence in Wyoming, in the Laramie Range in Albany County (#44 in **Table 5**; **Figure 6**). The collection was made in 1900 in Halleck Canyon, which includes private land and land managed by the BLM's Rawlins Field Office. This location is north of the Pole Mountain Unit of the Medicine Bow National Forest and south of the Laramie Mountains, which is also managed by the Medicine Bow National Forest (Handley and Heidel 2002). This occurrence has not been seen since 1900.

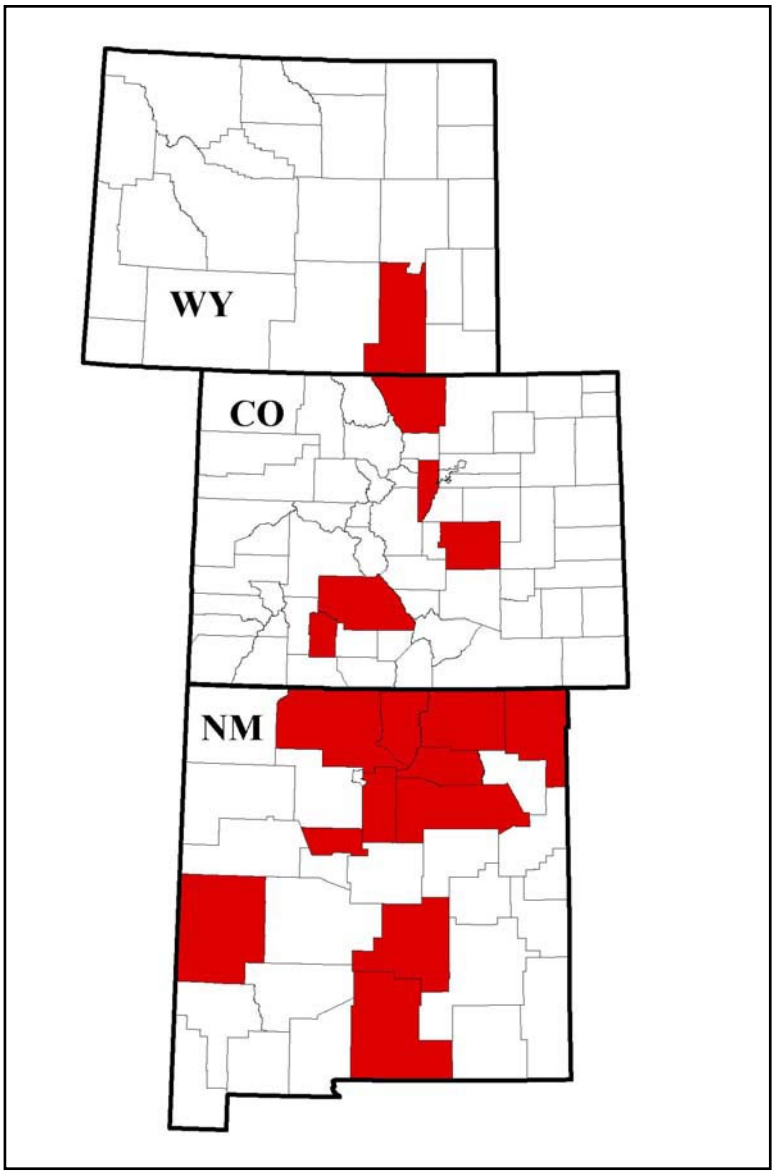

Figure 5. The known global range of *Potentilla ambigens* in Wyoming, Colorado, and New Mexico.

Colorado

In Colorado, *Potentilla ambigens* is known from 25 occurrences in five counties (**Figure 6**; El Paso, Jefferson, Larimer, Mineral, and Saguache). Four of these occurrences (#3, #11, #20, #25 in **Table 5**), however, have not been seen in more than 20 years. An occurrence at Great Sand Dunes National Park in 1984 (#25 in **Table 5**) is questionable because it was found in atypical habitat (on a steep rocky hillside in pinyon–juniper woodland). *Potentilla ambigens* is also reported from an uncertain location in the southern San Luis Valley where Barry Johnston noted it many years ago before it was recognized as rare (Johnston personal communication 2004).

Potentilla ambigens is not known to occur west of the Continental Divide in Colorado (Weber and Wittmann 2000). The type locality for *P. ambigens* (#3 in **Table 5**) is in Jefferson County where E.L. Greene collected it along Bear Creek above Morrison in 1889. It may be extirpated here and at Stonewall Creek in Larimer County (#12 in **Table 5**; see Population trend section for details). The largest known occurrences in Colorado are at Goose Creek (private; #24 in **Table 5**) in Mineral County and at Rattlesnake Park (Colorado State Land Board; #14 in **Table 5**) and Beaver Point (Rocky Mountain National Park; #16 in **Table 5**), both in Larimer County.

Table 5. Summary information for the known occurrences of *Potentilla ambigens*. Bold type indicates occurrences on National Forest System land.

Occ. #	State	County	Owner / Manager	Date last observed	Location	Population size	Elevation (ft.)	Habitat	Source
1	CO	El Paso	Department of Defense, U.S. Air Force Academy	7/7/2005	Air Force Academy	approx. 400	6,680 to 6,720	On alluvial plain in dry grassland; in gravelly/ sandy and sandy clay loam; numerous weeds; portions of the population are on a two track road (where 5-6 plants had been driven on); another portion adjacent to a 6 foot eroding gully; also adjacent to a natural wetland; in grassy area adjacent to a creek. In 2005 one plant was found in a monitoring plot for *Hypericum perforatum* in a seepy area. The population is vigorous but mostly confined to one dense stand with 360 plants, and another 25 plants in a patch approximately 10 meters across. Portions of the population are highly naturally or anthropogenically disturbed; other portions are undisturbed.	CNHP EO #7
2	CO	El Paso	State of Colorado, State Land Board	9/14/2000	Black Forest	20	7,580	Plants are growing approximately 10 feet upslope from a small creek. They may have received extra moisture from runoff, since the associated vegetation appeared relatively lush. Aspect: south-southwest. Slope: 10 degrees. Moisture: xeric. Light exposure: full sun. Soil: gravelly. Landform: creek bank. Occurrence is near a major intersection and is threatened by weeds.	CNHP EO #12
3	CO	Jefferson	Probably private	Jul 1889	Bear Creek, above Morrison	unknown	6,400	Moist meadows along creek.	E.L. Greene (coll. #unknown, NDG; type specimen)
4	CO	Jefferson	Jefferson County, Elk Meadow Open Space Park	8/24/1998	Bergen Creek	unknown	7,760	Level, open site on ridge crest. Moisture: dry. Total tree cover: 0 percent. Total shrub cover: ~1 percent. Total forb cover: 45 percent. Total graminoid cover: ~50 percent. Total moss/lichen cover: 0 percent. Total bare ground cover: 0 percent.	CNHP EO #6
5	CO	Larimer	National Park Service, Rocky Mountain National Park	2002	McGraw Ranch	unknown	8,200	In valley; grassy area downhill from a ditch where it is periodically flooded. Has been grazed.	L. Pilkington
6	CO	Larimer	Private	2001	McGregor Ranch	unknown	7,800	Grassy area downhill from a ditch where it is periodically flooded. Has been grazed.	L. Pilkington

Table 5 (cont.).

Occ. #	State	County	Owner / Manager	Date last observed	Location	Population size	Elevation (ft.)	Habitat	Source
7	CO	Larimer	National Park Service, Rocky Mountain National Park	2004	Rocky Mountain National Park Greenhouse Facility	hundreds	7,890	In waste places adjacent to Greenhouse; area has been heavily disturbed.	W.A. Weber, B. Bernier
8	CO	Larimer	National Park Service, Rocky Mountain National Park	7/30/2002	Maintenance Area, Park Headquarters	common	7,840	On neglected lawns, in ditches.	Weber and Wittmann (#19481 COLO); L. Benton
9	CO	Larimer	National Park Service, Rocky Mountain National Park	2004	Beaver Meadows Visitor Center	hundreds	8,200	Along trail and near a parking area in disturbed sites; in partial shade; another population established by Rocky Mountain National Park. Plants installed where landscaping is low.	L. Benton, B. Bernier
10	CO	Larimer	Estes Park High School	2003	Estes Park High School	~300	7,500	On dry, open, sloping disturbed areas; in sandy/ gravelly soil; adjacent to a bike path and school. The area where it occurs probably receives runoff from adjacent sprinklers used to water the school's lawn. Some plants appeared to have been mowed. Associated species: *Thlaspi arvense*, *Sisymbrium altissimum*, *Descurainia sophia*, *Agropyron cristatum*, *Cynoglossum officinale*, *Bromus tectorum*, *Penstemon virgatus*, *Potentilla hippiana*, *Linaria vulgaris*,and *Salsola tragus*.	L. Benton
11	**CO**	**Larimer**	**USDA Forest Service, Roosevelt National Forest**	**8/26/1896**	**Rustic Hill**	**unknown**	**7,470**	**None reported**	**CNHP EO #3**
12	CO	Larimer	Colorado State University	8/7/1996	Stonewall Creek	10	6,960	Plants are in a tight clump at the top of a sharply cut stream bank on the west side of the flat, dry, grassy bank of a small intermittent creek. In rolling shortgrass prairie; in full sun. Next to a downcut stream channel. Granitic gravel on nearby hillsides. Grazing is occurring at this site; downcutting of the stream may affect the population.	CNHP EO #5

Table 5 (cont.).

Occ. #	State	County	Owner / Manager	Date last observed	Location	Population size	Elevation (ft.)	Habitat	Source
13	**CO**	**Larimer**	**Private, possibly USDA Forest Service, Roosevelt National Forest**	**7/29/1990**	**East side of State Rt. 36, ca. 5 miles S. of Lake Estes**	**unknown**	**7,730**	**Mixed evergreen forest.**	**Unknown (collection #8856, Accession #737154 RM)**
14	CO	Larimer	State of Colorado, State Land Board	8/18/2004	Rattlesnake Park	Thousands	6,640 to 6,850	In a large, intermountain grassland ringed by mountains with *Pinus ponderosa* forest. *P. ponderosa* savanna occurs at the forest-grassland interface. The subpopulations occur along intermittent drainages below the *P. ponderosa* savanna at the forest-grassland interface. Aspect: east. Slope: 2-3 percent. Moisture: mesic. Light exposure: full sun. Parent material. Quartz or feldspathic mica schist and trandhyemite (porphyritic to medium-grained igneous rock). Soil: loam. Landform: intermittent streams. Dominant plant community: *Stipa comata - Bouteloua gracilis* herbaceous vegetation. Associated taxa: *Stipa comata*, *Elymus elymoides*, *Koeleria macrantha*, *Pseudoroegneria spicata*, *Monarda fistulosa*, *Symphoricarpos occidentalis*.	CNHP EO #13
15	CO	Larimer	Private	9/29/2004	Ben Delatour Scout Ranch	40	7,580	Mosaic of *Pinus ponderosa* forest patches on steeper, rockier terrain interspersed among montane meadows and traversed by riparian corridors. Aspect: south. Slope: 2 percent. Moisture; mesic. Light exposure: full sun. Parent material: granite. Soil: sandy loam (Breece series). Landform: valley floor. Dominant plant community: *Stipa comata-Bouteloua gracilis* herbaceous vegetation. Associated taxa: *Purshia tridentata*, *Ribes cereum*, *Stipa comata*, *Bouteloua gracilis*, *Muhlenbergia filiculmis*, *Elymus elymoides*, *Artemisia frigida*, *Achillea millefolium*, *Antennaria parvifolia*, *Allium* cf. *geyeri*, *Selaginella densa*, *Potentilla effusa*, and *Stellaria* sp. with *Danthonia parryii* and *Muhlenbergia montana* patches in the vicinity.	CNHP EO #14
16	CO	Larimer	National Park Service, Rocky Mountain National Park	11/3/2004	Beaver Point	2000+	7,680	In a meadow. Aspect: South. Slope: 2 percent. Slope shape: straight. Light exposure: open. Moisture: Dry. Soil texture: fine-medium. Associated species: *Bouteloua gracilis*, *Solidago* sp., *Chrysothamnus* sp., grasses. 100 percent fruiting to withering.	CNHP EO #15

Table 5 (cont.).

Occ. #	State	County	Owner / Manager	Date last observed	Location	Population size	Elevation (ft.)	Habitat	Source
17	CO	Larimer	National Park Service, Rocky Mountain National Park	11/3/2004	Moraine Park Museum	8	8,120	Near a path and other infrastructure in a disturbed dry meadow. Elk or deer predation of some fruits has occurred. Aspect: north-northeast. Slope: 5 percent. Slope shape: concave to straight. Light Exposure: open. Parent Material: granite. Soil texture: coarse, small rocks. Geomorphic land form: moraine. Associated species: *Achillea millefolium*, *Chrysothamnus* sp., *Antennaria* sp., and unknown grasses.	CNHP EO #16
18	CO	Larimer	Private	10/21/ 2004	Fish Creek Road	50+	7,520	In rolling uplands and on a disturbed roadside. 100 percent of plants in fruit or withering. Aspect: west. Slope: 5 percent. Slope shape: convex. Light exposure: open. Moisture: dry. Soil texture: coarse. Associated species: *Artemisia frigida* and unknown grasses.	CNHP EO #17
19	CO	Larimer	Town of Estes Park	11/03/ 2004	Lakeshore Drive	150+	7,680	Partially wooded to open areas in rolling uplands. Aspect: north. Slope: 20 percent. Slope shape: convex. Light exposure: partial shade. Moisture: dry. Parent material: granite. Soil texture: coarse. Associated species: *Ribes cereum*, *Pinus ponderosa*, *Verbascum thapsus*, *Penstemon virgatus*, *Artemisia frigida*, and unknown grasses.	CNHP EO #18
20	**CO**	**Mineral**	**USDA Forest Service, Rio Grande National Forest**	**7/30/1911**	**Goose Creek Road**	**unknown**	**8,500**	**On tuff.**	**J. Murdock Jr. (#4773 NY?)**
21	**CO**	**Mineral**	**USDA Forest Service, Rio Grande National Forest, Private (with conservation easement held by TNC)**	**7/9/1998**	**Wagon Wheel Gap, Spring Gulch**	**400**	**8,440 to 8,600**	**On grassy slopes in small drainages; seems to prefer sites at the base of slopes and between riparian areas, or small, usually dry gullies. Also observed to grow well along the roadside, possibly due to extra moisture from road runoff. Aspect: south; Soil: dry rocky clay colluvium; stony gravelly loam, probably with mollic epipedon (A horizon). Slope: 5-30 percent. Receives runoff from upslope. Parent Material: basalt; quartz latite porphyritic lava. Geomorphic landform: colluvial footslope and slope wash fan below steep talus and cliffs. One subpopulation has dirt two-tracks within it.**	**CNHP EO #1**

Table 5 (cont.).

Occ. #	State	County	Owner / Manager	Date last observed	Location	Population size	Elevation (ft.)	Habitat	Source
22	CO	Mineral	Unknown	7/9/1998	Farmers Creek	less than 100	8,560 to 8,720	West facing slope of fine scree and colluvium, on more or less level colluvium.	CNHP EO #2
23	**CO**	**Mineral**	**USDA Forest Service, Rio Grande National Forest**	**7/10/1998**	**East Bellows Creek**	**500**	**8,880**	**In a small rivulet on a south-facing slope; in grassland. Light exposure: full sun. Moisture: xeric. Parent material: gravelly clay. Landform: colluvial slope. Adjacent to a two-track road and a fishing trail.**	**CNHP EO #8**
24	CO	Mineral	Private	7/23/1998	Goose Creek	2000	8,480 to 8,880	Forb-dominated blue grama grassland on east facing colluvial slopes in montane valley running north to south. Dry sandy, clay loam soil. Two spots stand out along a creek, above and below a housing complex. Slightly wetter areas, such as small rivulets and along the roadside appear to be favorable sites. Most prevalent next to road and in or near gullies.	CNHP EO #9
25	CO	Saguache	National Park Service, Great Sand Dunes National Park	6/19/1984	Ridge between Little Medano and Medano Canyon	unknown	9,400	Piñon-juniper, steep rocky hillsides	H. Dixon (s.n. Great Sand Dunes National Park Herbarium)
26	NM	Bernalillo	Unknown	—	—	unknown	—	—	Martin and Hutchins (1980)
27	NM	Catron	Unknown	—	—	unknown	—	—	Martin and Hutchins (1980)
28	NM	Colfax	New Mexico State Parks	6/24/2001	Sugarite Canyon	unknown	—	—	Discovery Weekends (2001)
29	NM	Lincoln	Unknown	7/31/1897	White Mountains	unknown	6,800	—	Wooton (#468 NY)
30	NM	Lincoln	Unknown	8/18/1969	South fork of Eagle Creek	unknown	7,480	Gravel soils.	C.R. Hutchins (#2462 UNM)
31	NM	Lincoln?	Unknown	7/25/1970	Cedar Creek, White Mountains	unknown	7,000	Gravel loam.	C.R. Hutchins (#3133 UNM)
32	NM	Mora	USDA Forest Service, Santa Fe National Forest?	7/15/1908	Panchuela Creek	unknown	8,400	—	P. Standley (#4356 NY, RM)
33	NM	Otero	Unknown	9/7/1969	Silver Springs Canyon	unknown	—	—	J.D. Garcia (#1884 UNM)

Table 5 (concluded).

Occ. #	State	County	Owner / Manager	Date last observed	Location	Population size	Elevation (ft.)	Habitat	Source
34	NM	Otero	Unknown	7/29/1951	One mile northeast of Cloudcroft	unknown	c.a. 9,000	Open meadow and forest margin.	D.B. Dunn (#7556a NY)
35	NM	Otero	Unknown	7/28/1979	East side of Cloudcroft along U.S. Highway 82	unknown	8,500	Along highway (?)	R.D. Worthington (#4785 COLO)
36	NM	Otero	Unknown	6/29/1936	Top of divide on Whitetail Rd.	unknown	8,000	—	R.R. Humphrey (s.n. UNM)
37	NM	Otero?	Unknown	9/7/1969	5 mi. NW of Mescalero Sawmill, off Highway 24	unknown	—	Mountain meadow.	J.D. Garcia (#1883 UNM)
38	NM	Rio Arriba	USDA Forest Service, Santa Fe National Forest	8/1/1916	Rio Paloma Watershed	Frequent	10,000	North facing slope; damp soil.	E.W. Loveridge (#13 RM)
39	NM	San Miguel	Unknown	—	—	—	—	unknown	Martin and Hutchins (1980)
40	NM	Santa Fe	Unknown	7/29/1916	—	unknown	—	—	Bertaud (#89 NY)
41	NM	Taos	Unknown (Carson National Forest?)	8/24/1923	Webber's Cattle Camp, Rio Fernandes de Taos Canyon	unknown	8,860	—	Eggleston (#19275 NY)
42	NM	Union	Unknown	—	—	unknown	—	—	Martin and Hutchins (1980)
43	NM	—	Unknown	prob. 1881	—	unknown	—	—	G.R. Vasey (s.n. NY)
44	WY	Albana	Unknown (not USDA Forest Service), probably private or Bureau of Land Management, Rawlins Field Office	7/4/1900	Halleck Canyon	unknown	6,000	Wet sandy draw.	A. Nelson (#7438 COLO, NY)

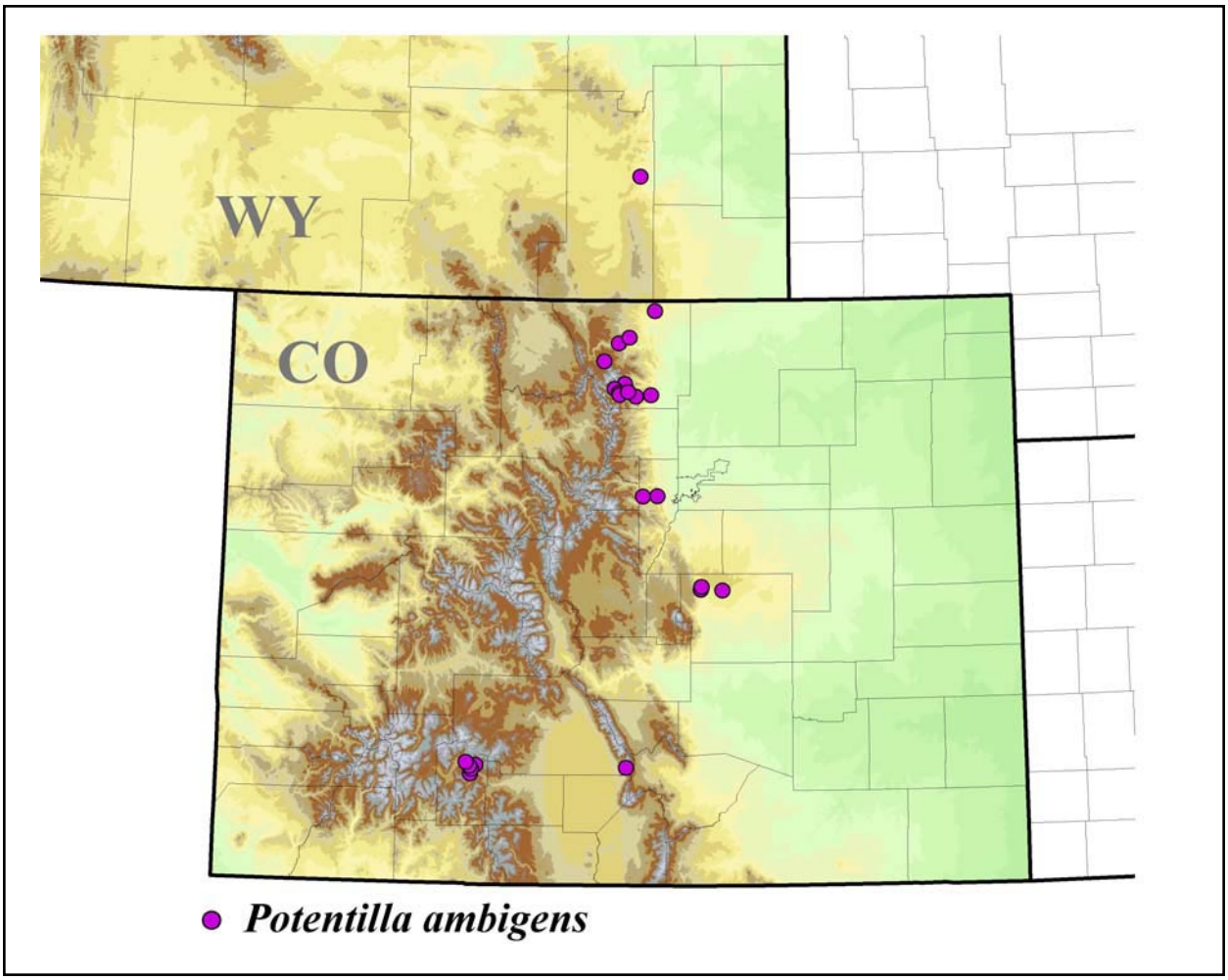

Figure 6. Distribution of *Potentilla ambigens* in USDA Forest Service Region 2 in relation to major physiographic landscape features.

Potentilla ambigens may be distributed more widely in Colorado than is currently known. Suitable habitat is widely distributed throughout the Front Range and elsewhere. *Potentilla ambigens* is known from Sugarite Canyon State Park, New Mexico, which is within 5 miles of the Colorado state line south of Trinidad. Similar sites in Las Animas County may support other occurrences of *P. ambigens*. The Species and habitat inventory section under Tools and practices describes areas that may support undiscovered occurrences.

New Mexico

It is likely that most of the global population of *Potentilla ambigens* resides in New Mexico; however, this is not well documented in collections at the University of New Mexico Herbarium (Neely et al. 2001). *Potentilla ambigens* has been reported from 11 counties in New Mexico (Bernalillo, Catron, Colfax, Lincoln, Mora, Otero, Rio Arriba, San Miguel, Santa Fe, Taos, and Union). The author did not locate specimens to verify the presence of *P. ambigens* in Bernalillo, Catron, San Miguel, and Union counties as reported in Martin and Hutchins (1980). Lowry (personal communication 2004) advised caution in the use of the range maps included in Martin and Hutchins (1980) since they contain many errors. However, there may be specimens from these counties in herbaria that were not searched. Wooton and Standley (1915) report *P. ambigens* from the Santa Fe and Las Vegas Mountains, Sierra Grande, and White and Sacramento Mountains. *Potentilla ambigens* is included on a checklist of the plants at Sugarite Canyon State Park in Colfax County (Discovery Weekends 2001).

Southern extent of distribution

The southernmost occurrences of *Potentilla ambigens* are in Otero County near the southern border of New Mexico. *Potentilla ambigens* has not been documented in Texas, which is adjacent to Otero County (Correll and Johnston 1970, USDA-Natural Resources Conservation Service 2003), and its presence there is unlikely. However, it is possible that *P. ambigens* occurs in the mountains of northern Mexico.

Abundance

In his description of *Potentilla ambigens*, Greene (1893) noted that it is "apparently rare; at all events, during my former years of residence in Colorado, I met with no such plant." Similarly, Colorado Native Plant Society (1997, p. 46) states "Some Colorado rare species may be considered rare only because they are poorly collected, but the rarity of this large and obvious species has gone unchallenged." Given the large stature and general conspicuousness of this plant, it is likely that it would have been noticed and collected far more often on the Colorado Front Range if it were not rare. On the other hand, *Potentilla* species are notoriously difficult to identify, so populations may have been observed but not identified to species.

Colorado element occurrence records, herbarium specimens, and personal accounts have documented approximately 8,500 individuals. However, abundance is unknown for eight of the 25 occurrences in Colorado. There has been no effort to assess the size of *Potentilla ambigens* populations using quantitative methods, and all known population data on *P. ambigens* were gathered from ocular estimates. There are no abundance data from Wyoming or New Mexico.

Approximately 2,500 plants were reported at Goose Creek and Bellows Creek in Mineral County (#24 and #23 in **Table 5**). Another 400 plants were reported from the Rio Grande National Forest and private land at Wagon Wheel Gap (#21 in **Table 5**). *Potentilla ambigens* is relatively abundant in the eastern portion of Rocky Mountain National Park and adjacent areas (Weber personal communication 2004). A large occurrence was documented at Beaver Point, Rocky Mountain National Park (#16 in **Table 5**) in 2004, where more than 2,000 individuals were counted. Another large occurrence (#14 in **Table 5**) consisting of thousands of individuals was found at Rattlesnake Park in 2004.

Population trend

There are no quantitative data that could be used to infer the population trend of *Potentilla ambigens*. There has been no population monitoring that could provide insight into population trend, and population size is not known for many occurrences in Region 2 and in New Mexico. As a long-lived, polycarpic perennial that does not exhibit prolonged dormancy, populations of *P. ambigens* are unlikely to fluctuate greatly from year to year.

Available information suggests that there have been downward population trends for some occurrences of *Potentilla ambigens*. This species has not been observed in Wyoming since 1900 and may be extirpated in Halleck Canyon (#44 in **Table 5**; Handley and Heidel 2002). It has probably also been extirpated at the type locality along Bear Creek above Morrison (#3 in **Table 5**; Weber personal communication 2004). The occurrence at Stonewall Creek (#12 in **Table 5**) in Larimer County is very small, and the plants observed were about to succumb to erosion by a severely downcut stream when they were discovered in 1995 (Kettler et al. 1996); thus it is possible that *P. ambigens* is also no longer extant at this site. The situation is similar for part of the occurrence at the U.S. Air Force Academy (#1 in **Table 5**), where *P. ambigens* is adjacent to a six-foot-deep eroding gully. Direct impacts to individuals from off-highway vehicle use at the U.S. Air Force Academy (in this case, military vehicles) was noted; five or six plants had been driven on (Colorado Natural Heritage Program 2004). Other threats may be causing local declines in other occurrences (see the Threats section for details).

Urban development of the Colorado Front Range has reduced the extent of habitat for *Potentilla ambigens*. While there is no direct evidence linking this to a downward population trend, it appears likely that development has extirpated or negatively affected sites that were undocumented. Reservoir creation has reduced the extent of suitable habitat for *P. ambigens*, and given the species' affinity for bottomlands, it is possible that reservoir creation has extirpated occurrences. There are no data from which inferences can be made regarding population trends of *P. ambigens* on National Forest System land in Region 2.

Human activities in Rocky Mountain National Park may be causing local population increases. *Potentilla ambigens* has become established where it

was used to revegetate a site within the park following developments, and it may be used in future revegetation projects, including the area around the road to Bear Lake (Bernier personal communication 2004).

Habitat

General habitat description

Potentilla ambigens occurs in the Temperate Steppe Division of the Dry Domain in Bailey's system of ecoregion classification (1995). Within the Temperate Steppe Division, it occurs in the Southern Rocky Mountain Steppe-Open Woodland-Coniferous Forest-Alpine Meadow Province. This province is referred to as the Southern Rocky Mountain Ecoregion by Neely et al. (2001).

Published descriptions of *Potentilla ambigens* habitat include "moist meadows along creek" (Greene 1893), "meadows in the Transition Zone" (Wooton and Standley 1915), "meadows of the yellow pine belt" (Tidestrom and Kittell 1941), and "woods, slopes, and meadows" (Dorn 1992). Neely et al. (2001) note that most Colorado occurrences are on grassy or colluvial slopes, but it may also occur in montane woods.

Some sites where *Potentilla ambigens* is found have been heavily altered by human activities. Around Estes Park and the east entrance to Rocky Mountain National Park, *P. ambigens* grows in waste places, neglected lawns, and in a weedy lot near the park herbarium (Benton personal communication 2004, Bernier personal communication 2004, Weber personal communication 2004). It also grows adjacent to Estes Park High School, a bike path, and local trails, where it is probably occasionally trampled.

Potentilla ambigens is documented along roads, where it is likely to be disturbed periodically and is ecologically influenced by the proximity of the road. It is found along gravel roads and two-track roads at the U.S. Air Force Academy (**Figure 7**), near Wagon Wheel Gap along Pool Table Road (**Figure 8**), Goose Creek

Figure 7. *Potentilla ambigens* along a roadside at the U.S. Air Force Academy on July 10, 2002. Thirty percent of plants observed flowered despite severe drought conditions. Photograph by Ron Abbott, used with permission.

Figure 8. Pool Table Road near Wagon Wheel Gap on the La Garita Ranch. *Potentilla ambigens* occurs along both sides of this road. Photograph by Renée Rondeau, used with permission.

(along Goose Creek Road), and East Bellows Creek. It is adjacent to an intersection of two paved county roads at Black Forest, along State Highway 36, and at the Beaver Meadows Visitors Center.

At many sites, there is evidence of substantial habitat degradation resulting from human activities and management. Only five occurrences in the states of Region 2 (#4, #11, #22, #25, #44 in **Table 5**) do not report human impacts to habitat. Two of these occurrences (#11 and #44 in **Table 5**) were documented more than 100 years ago and may now have noteworthy human impacts. Habitat degradation includes weeds, off-highway vehicle use, and trampling. Grazing may be accelerating the downcutting of Stonewall Creek (#12 in **Table 5**).

Potentilla ambigens is often reported from ecotonal sites at the edges of relatively discrete vegetation types. It is commonly near, but not in, forests dominated by *Pinus ponderosa* (ponderosa pine). These sites are typically open or in partial shade. At Beaver Meadows, *Potentilla ambigens* is in the shade of trees in the morning and in the late afternoon, but in open sun through the middle of the day (#9 in **Table 5**; Benton personal communication 2004). However, most reports are from sites where plants are in full sun such as meadows or grasslands. Vegetation and plant communities in which *P. ambigens* occurs are discussed in the Community ecology section.

Moisture availability

Potentilla ambigens is reported from both natural and anthropogenically-altered settings that are hydrologically influenced although dry through most of the growing season. Occurrences in natural settings include the banks of intermittent creeks, streams, rivulets, and gullies. At some sites, *P. ambigens* may be periodically inundated. Inundation is probably rare at some sites, but it may occur more than once per growing season at others. *Potentilla ambigens* has also been reported from swales, shallow drainages (**Figure 9**), moist meadows, and adjacent to wetlands. Where it is found on slopes, such as in the Black Forest (#2 in **Table 5**) and at Wagon Wheel Gap (#21 in **Table 5**), the soils are kept moist by runoff and may be naturally subirrigated at some times during the year. In the Wagon Wheel Gap area, *P. ambigens* grows adjacent to small gullies (**Figure 10**) and in sites where it may

Figure 9. The large occurrence of *Potentilla ambigens* at Rattlesnake Park, Larimer County, discovered in 2004. *Potentilla ambigens* is the dominant species in the foreground and left midground of this photo. Photograph by Stephanie Neid, used with permission.

Figure 10. Habitat of *Potentilla ambigens* at Goose Creek. This area is dominated by *Chrysothamnus*, *Gutierrezia*, and *Krascheninnikovia*. Note the shallow gully right of center. Photograph by Renée Rondeau, used with permission.

get extra runoff from adjacent cliffs and shallow slopes (Rondeau personal communication 2004). At these sites, inundation could result from extreme rain events ("gully washers"), but the associated erosion would have detrimental effects. Some sites are wetted in spring by snowmelt; others would tend to be wet during runoff from monsoonal thundershowers. Although it has been reported from dry sites (e.g., #1, #5, #7, and #9 in **Table 5**), it appears that most of these locations are still influenced by adjacent riparian areas or wetlands.

The habitat descriptions for occurrences at Great Sand Dunes National Park (#25 in **Table 5**) and Bergen Creek (#4 in **Table 5**) do not suggest augmented soil moisture. The occurrence at Great Sand Dunes National Park is in a pinyon-juniper woodland on a steep rocky slope, and the associated species indicate that this is a dry site. This is the only report of *Potentilla ambigens* from a pinyon-juniper woodland. At Bergen Creek, *P. ambigens* occurs on a ridge crest where soils are probably excessively well drained. More information about these sites is needed. In the Wagon Wheel Gap area, *P. ambigens* is found in shortgrass prairie where there is no obvious source of added moisture (**Figure 11**, **Figure 12**, #21 in **Table 5**; Rondeau personal communication 2004).

Many anthropogenically-modified sites where *Potentilla ambigens* has been documented are likely to receive additional moisture during the growing season. It has been observed on roadsides (**Figure 7**, **Figure 8**), in roadside ditches, next to two-track roads, and down slope of irrigation ditches. At Estes Park High School (#10 in **Table 5**), it is growing down slope of a lawn where it receives excess water from the school's sprinkler system (**Figure 13**).

Fire

Most occurrences of *Potentilla ambigens* fall within the montane zone where *Pinus ponderosa* is the dominant forest tree. *Potentilla ambigens* has been frequently reported in close proximity to this species, and their elevation limits correspond closely (between 6,000 and 9,000 ft.; Rondeau 2001). *Pinus ponderosa* forests below 8000 feet are highly susceptible to fire in the Southern Rocky Mountains and have a short fire return interval. Fires may have occurred every eight to

Figure 11. *Potentilla ambigens* habitat at the La Garita Ranch. Wagon Wheel Gap is visible at top center. Photograph by Renée Rondeau, used with permission.

Figure 12. *Potentilla ambigens* habitat at Goose Creek. Photograph by Renée Rondeau, used with permission.

Figure 13. *Potentilla ambigens* (foreground) at Estes Park High School. Photograph by the author.

15 years in the *P. ponderosa* woodlands and savannas of the Southern Rocky Mountains (Mehl 1992, Harrington and Sackett 1992 as cited in Rondeau 2001). Fire has probably played an important role in the maintenance of suitable habitat for *Potentilla ambigens*. See the Reproductive biology and autecology section for a discussion of the role of fire and other kinds of disturbance in habitat dynamics.

Slope, aspect, and elevation

Potentilla ambigens has been reported mainly from flat sites, but it may also grow on gentle hillsides and slopes with up to 30 percent gradient. If on a slope, the site usually has a source of water upslope that increases soil moisture. The "steep rocky hillside" at Great Sand Dunes National Park (#25 in **Table 5**) is the exception to the norm. Where aspect has been reported, *P. ambigens* occurs on south and south-southwest facing slopes, but aspect is unknown for most occurrences.

Elevations reported at *Potentilla ambigens* occurrences range from 6,000 to 10,000 ft. Occurrences in Region 2 are distributed along an elevational gradient from 6,000 to 9,400 ft. The median elevation for Region 2 occurrences is 7,760 ft., while the mean is 7,840 ft. In New Mexico, occurrence elevations range from 6,800 to 10,000 ft. The mean elevation of occurrences in New Mexico is slightly higher (8,227 ft.), suggesting that suitable elevation for *P. ambigens* decreases with increasing latitude.

Soil and geology

Potentilla ambigens is not endemic to a particular geologic stratum. Although there is much variation in the parent material underlying *P. ambigens* occurrences, many occurrences share geologic similarities. Most Colorado occurrences (44 percent) are underlain by Precambrian granite and metamorphic rocks such as gneiss or schist. Another 40 percent of the occurrences are on Quaternary surfaces composed of alluvium, gravels, or glacial drift. The remaining occurrences are on Tertiary strata. These data were generated by intersecting the locations of the known occurrences in Colorado with the Colorado state geological map (Tweto 1979). Tweto's is primarily of bedrock geology at a very coarse scale that may be spatially inaccurate. Surface geology may be quite different from the underlying bedrock geology.

At Wagon Wheel Gap, East Bellows Creek, and Goose Creek, *Potentilla ambigens* grows on either Ash Flow Tuff or Intra-Ash Flow Latitic Lavas that originated from the explosion of the nearby La Garita Caldera approximately 30 million years ago. It is found on strata of similar age in the Black Forest, which is underlain by Dawson Arkose, an alluvial deposit of reworked volcanic material that includes sandstone, conglomerate, and shale. At the U.S. Air Force Academy (#1 in **Table 5**), *P. ambigens* is found on alluvial soils near Monument Creek and its tributaries that are probably derived from Dawson Arkose.

Potentilla ambigens is typically found in soils that are either alluvial or colluvial (Colorado Natural Heritage Program 2004). All reports of soil texture where *P. ambigens* is found note the presence of coarse-textured, often gravelly soils. Gravelly soils are reported at six Colorado occurrences, and gravelly/sandy and sandy clay loam soils are also reported. Coarse-textured, gravelly soils are common in soils derived from granitic parent material throughout the Rocky Mountains (**Figure 3**). These soils are droughty because they drain quickly and do not retain moisture. However, occurrences in gravelly soils can receive additional moisture due to their topographic position or from seeps nearby. Coarse soil texture may be an important habitat attribute for *P. ambigens* since it may prevent the encroachment of forest into its open habitats.

Precipitation

Potentilla ambigens is found in areas where orographic lifting results in higher precipitation than in adjacent piedmont, plains, and mountain parks. In an intersection of the point locations of *P. ambigens* in Colorado with a map of precipitation isolines (Bureau of Land Management 1998), almost all the occurrences of *P. ambigens* in Colorado fall in areas receiving between 12 and 20 inches of rain per year (**Figure 14**).

Reproductive biology and autecology

In the Competitive/Stress-Tolerant/Ruderal (CSR) model of Grime (2001), the characteristics of *Potentilla ambigens* most closely approximate those of a competitive-ruderal species. In this model, competitive-ruderal species occur in habitats where productivity is high, but dominance by more strictly competitive species is precluded by disturbance. Features of *P. ambigens* that typify it as competitive include its affinity for habitats where moisture is relatively abundant, its potential for rapid growth, storage of photosynthate in its taproot, and its relatively large size that allows its canopy to overtop those of other species. It probably flowers every year and maintains nutrient reserves in its taproot, both of which also typify competitive

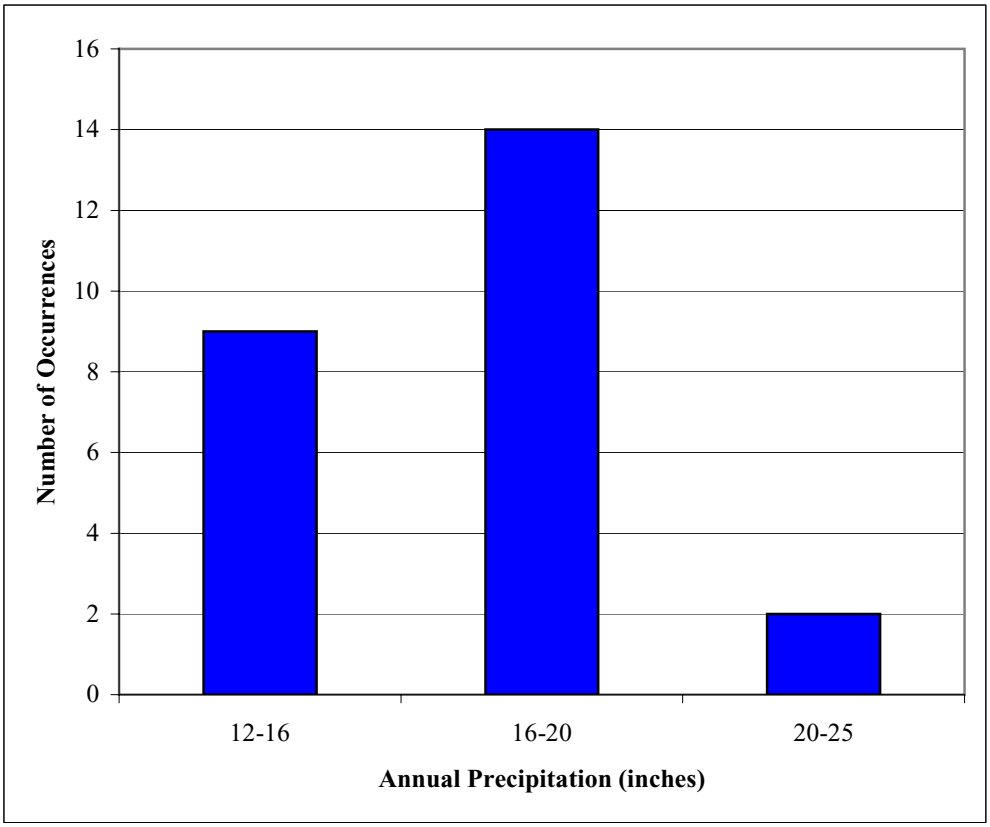

Figure 14. Annual precipitation for Region 2 occurrences of *Potentilla ambigens*.

species. Ruderal tendencies of *P. ambigens* include its ability to colonize disturbed sites (Weber personal communication 2004). In more mesic sites, *P. ambigens* is more aggressive (Rondeau personal communication 2004). Very little is known about the life history of *P. ambigens*, making it difficult to make inferences about its competitive strategies.

Disturbance plays an important role in the persistence of competitive-ruderal species. Where competitive-ruderal species are found, periodic disturbance maintains habitat conditions that render these sites unsuitable to more strictly competitive species. *Potentilla ambigens* may require disturbance that prevents the dominance of sites by trees or other competitive vegetation in order to persist. The most prevalent disturbances in occurrences that have this effect are floods and fire. Sheet erosion appears to cause soil disturbance at some sites, such as those around Wagon Wheel Gap, where *P. ambigens* occurs. However, neither disturbance is likely to occur often at many sites. Dominance by woody vegetation is probably precluded at these sites by droughty soils that desiccate readily, and possibly by wind, which facilitates soil desiccation and damages trees (Rondeau personal communication 2004). Fire as a habitat attribute of *P. ambigens* is discussed in the Habitat section. Because competitive-ruderals typically maintain active growth through the growing season (as do strictly competitive species), they are vulnerable to habitat disturbance that occurs during the growing season (Grime 2001).

Observations by Dr. William Weber and by Rocky Mountain National Park staff suggest that *Potentilla ambigens* is capable of thriving, at least for limited periods, in areas that have been moderately or heavily disturbed. The occurrence at Rocky Mountain National Park Greenhouse Facility (#7 in **Table 5**) was denuded of vegetation during construction of the greenhouse (Bernier personal communication 2004). *Potentilla ambigens* may also be capable of withstanding some level of trampling or mowing since it occurs adjacent to a bike path at Estes Park High School (#10 in **Table 5**; Benton personal communication 2004). The species appears to tolerate some disturbance and to be capable of colonizing disturbed sites. Many species of *Potentilla* that are adapted to highly disturbed habitats, such as *P. anserina*, use stolons to propagate clonally (Stuefer and Huber 1999). *Potentilla ambigens* does not produce stolons, suggesting that at least with

respect to this character, it is not completely adapted to disturbance. It is not known if its persistence in disturbed areas is due to tolerance of disturbance, or an ability to disperse to and colonize sites that are disturbed more infrequently. How well *P. ambigens* tolerates disturbance is a key question to answer for designing appropriate management and stewardship.

While *Potentilla ambigens* is typical in many ways of competitive-ruderal species, it also has some similarities to the "CSR strategists" described by Grime (2001). As would be expected, plants exploiting this strategy have characteristics that are intermediate between competitors, stress-tolerators, and ruderals. These species can tolerate mineral nutrient stress and moderate intensities of defoliation by grazing. Taprooted plants often fall into this category because they have perennating buds near the ground that allow the plant to regenerate rapidly after grazing. However, these species typically do not have tall aerial shoots like those of *P. ambigens*. The long taproot of *P. ambigens* is probably highly adaptive for persisting in droughty soils since it allows *P. ambigens* to capitalize on water resources deep in the soil and perhaps store them. *Potentilla ambigens* is also apparently tolerant of drought stress (characteristic of stress-tolerators) since many occurrences are dry for much of the growing season.

As a competitive-ruderal, *Potentilla ambigens* does not fit neatly into the classification scheme of MacArthur and Wilson (1967), in which plants are categorized as *r*- or *K*-selected. *Potentilla ambigens* allocates relatively little biomass to the production of propagules (as a large plant with a small number of flowers, relative to a more ruderal species that allocates more relative biomass to reproduction) and is probably long-lived, which typifies it as *K*-selected. However, as discussed above, it also has some ruderal tendencies that would typify it as *r*-selected under this classification scheme, including an apparent ability to colonize disturbed sites. Bernier (personal communication 2004) noted that it sometimes produces large amounts of seed.

Reproduction

Members of the genus *Potentilla* employ many different reproductive strategies and mating systems, which are described in general by Eriksen (1996). Many species of *Potentilla* are obligate outcrossers, including *P. anserina*, which occurs in Region 2 (Saikkonen et al. 1998). Other species are facultatively apomictic (Eriksen 1996, Hansen et al. 2000, Nylehn et al. 2003), as is probably the case for *P. ambigens*. Apomixis is a common phenomenon among members of the genus *Potentilla* (Acharya Goswami and Matfield 1974, Eriksen 1996, Holm and Ghatnekar 1996, Holm et al. 1997). Facultative apomicts are mainly clones of the mother plants, but some seeds may be produced sexually. Apomixis has not been observed in diploid species of *Potentilla*, but it is common among polyploid taxa (Holm et al. 1997), and it is strongly related to polyploidy in angiosperms (Asker and Jerling 1992), including the genus *Potentilla* (Holm and Ghatnekar 1996). The proportion of sexually produced offspring varies among species and populations of facultatively apomictic taxa (Eriksen 1996). In some species, more than 90 percent of the seed is of maternal origin (Johnston personal communication 2002). The particular type of apomixis employed by *Potentilla* species is pseudogamous agamospermy, in which pollen from a compatible species is needed to produce endosperm. This is a very interesting phenomenon in which a pollen nucleus fuses with the two polar nuclei of the embryo sac, as typically occurs during fertilization in angiosperms, to form the endosperm. However, the embryo develops without fertilization from an unreduced egg (Asker 1977, Eriksen 1996). Although pollination is required to form the seed, the offspring are clones of the maternal plant. It is not known whether pollen from other species is compatible with *P. ambigens* for pseudogamy; no compatible taxa were identified by Acharya Goswami and Matfield (1975).

Clonal growth is also common in many species in *Potentilla*, and it is best developed in stoloniferous species such as *P. anserina* (Stuefer and Huber 1999). In nature, *P. ambigens* probably reproduces only by seed although it can be propagated vegetatively in a greenhouse (Bernier personal communication 2004).

The base chromosome number for *Potentilla* is 7, and the chromosomes are small (Johnston 1980, Asker 1985, Delgado et al. 2000). Polyploidy and aneuploidy are common (Holm and Ghatnekar 1996, Johnston personal communication 2002). There are many polyploids in *Potentilla*, including *P. ambigens* with 82 chromosomes (Acharya Goswami and Matfield 1974, Acharya Goswami and Matfield 1975, Acharya Goswami and Matfield 1978). This chromosome number is described by Acharya Goswami and Matfield (1978) as "hypo 12x," meaning that it has almost 12 times the base number of chromosomes but is missing a portion of the chromosome complement it should have. In the case of *P. ambigens*, the chromosome number probably arose from the spontaneous doubling

of the chromosomes in a hypo 6x (hexaploid) ancestor (with 41 chromosomes instead of 42). The ancestral hexaploid probably became hypo through an error in the division of chromosomes during meiosis. Without this error in the division of chromosomes, *P. ambigens* would have been 2x = 84 like other polyploid *Potentilla* species including *P. atrisanguinea* (Acharya Goswami and Matfield 1975, Acharya Goswami and Matfield 1978).

Müntzing and Müntzing (1943) observed the spontaneous doubling of the chromosome number in *Potentilla collina* from 42 to 84. This phenomenon is known as autopolyploidy. They concluded that this duplication in chromosome number probably arose from the occasional formation of a tetraploid embryo sac. It is interesting that the autopolyploid *P. collina* plants observed by Müntzing and Müntzing (1943), like *P. ambigens*, tended toward gigantism. The autopolyploids of *P. collina* produce plants in each generation that have reverted to a lower ploidy level. Newly created autopolyploids are generally genetically isolated from their parents because of the different number of chromosomes, thus resulting in new species.

Pollinators and pollination ecology

There has been no research regarding the pollinators and pollination ecology of *Potentilla ambigens*. The floral biology of other *Potentilla* species has been investigated, revealing a number of strategies for pollen transfer. Smaller-flowered members of the Rosaceae, like *Potentilla*, are typically visited by flies and short-tongued bees (Zomlefer 1994). *Potentilla rivalis* is partially reliant on thrips, which mediate self-pollination by moving pollen from the stamens to the stigma of the same flower (Baker and Cruden 1991). *Amecocerus senilis* LeConte, a Dasytinid beetle, is common on flowers in *Pinus ponderosa* woodlands of Colorado, including those of *Potentilla gracilis* (Mawdsley 1999). This beetle feeds on both nectar and pollen and is thus a potential pollinator for *P. ambigens*. Flies, ants, and bumblebees have been observed visiting the flowers of *P. rupincola*, but never specialists such as wasps (Child personal communication 2002, Johnston personal communication 2002).

Acharya Goswami and Matfield (1974) performed artificial pollinations of *Potentilla argentea* and *P. recta* using pollen from *P. ambigens* (see the Hybridization section). No successful crosses resulted from this attempt. Poor pollen tube growth was observed on *P. argentea*, but long, well-developed pollen tubes were observed on *P. recta*, indicating the viability of the *P. ambigens* pollen they used. In later experiments, stunted pollen tube growth was observed when pollen of *P. ambigens* was placed on *P. atrisanguinea* (with which *P. ambigens* can hybridize when it is the maternal parent), *P. reptans*, *P. erecta*, and "c.f. *hirta*" (Acharya Goswami and Matfield 1975). Interestingly, pollen tubes of four other species (*P. reptans*, *P. erecta*, *P. anglica*, and *P. anserina*) grew normally on *P. ambigens* in this study. It is not known whether other species of *Potentilla* are compatible with *P. ambigens* for pseudogamous reproduction.

Phenology

Potentilla ambigens is one of the first plants to produce leaves in the spring (Benton personal communication 2004). Leaves emerge in mid-March, and plants are 3 inches tall by mid-April. Flowering begins in June and early July. Of the occurrences where a collection date was noted, most specimens were collected in July when the plants were fully elongated and in flower. By early August, *P. ambigens* is in fruit. By September 14, plants observed in the Black Forest had flowered, set fruit, dispersed seed, and were beginning to senesce (Colorado Natural Heritage Program 2004).

Fertility and propagule viability

Potentilla ambigens produces about 30 achenes (each containing one seed) per flower. Under greenhouse conditions, Bernier (personal communication 2004) noted very high seed viability in *P. ambigens* collected from MacGregor Ranch and McGraw Ranch, but this was not quantified. It is not known how long seeds remain viable. Seeds of *P. rupincola* are viable for at least 2 years (Child personal communication 2002). Three percent of unscarified seeds of *P. norvegica* were still viable after 9.7 years of burial in a study of seed viability and dormancy (Conn and Deck 1995). The seeds of *P. ambigens* germinate readily, and no stratification or scarification is needed to promote germination (Bernier personal communication 2004).

Propagation and planting methods

Bernier (personal communication 2004) summarized the methods used to propagate *Potentilla ambigens* as follows: Seeds are germinated in January in a greenhouse that is maintained at 72 ºF (although temperatures drop into the 60s at night). A heating mat underlain with polyfoam insulation is used to maintain temperatures in the germination beds. Seeds are sprinkled into flats, and germinating mix is sprinkled

on top of them. After an initial thorough saturation, the seeds are kept moist in a mister tent. The seeds are misted for 15 seconds every 20 minutes. The seeds typically germinate within 5 to 9 days (emergence is spotty at first) after which they are placed into pots. In 2004, seeds sown on January 14 emerged January 23. By April or May, they are ready to plant, and are typically in a 3-inch or 1-quart pot by that time. Growth is normally vigorous, and sometimes the roots grow through the bottom of the pot and into the ground when they are placed outside in the spring. Juvenile plants can be propagated by division. After planting, survival is typically good. Park staff water transplants through the summer once or twice a week for the first two years. Overall, *P. ambigens* is easily propagated and established in revegetated or landscaped areas.

Dispersal mechanisms

The seeds of *Potentilla ambigens* are likely to be dispersed by wind and water. However, they are relatively large and probably do not blow far in the wind. The achenes may adhere weakly to the fur of animals, but they do not have hooks adapted to this purpose. There have been no observations of herbivory that would suggest that seeds are eaten and dispersed in feces. There has been some speculation that ants are involved in the dispersal of the seeds of *P. rupincola*, but this has not been investigated (Child personal communication 2002).

Cryptic phases

The seed bank dynamics of *Potentilla ambigens* have not been investigated. Persistent seed banks are more likely to form from small, smooth seeds, but relatively large seeded species, including *P. erecta*, have also been observed to form seed banks (Baskin and Baskin 2001).

Bernier's observations (personal communication 2004) regarding the germination of *Potentilla ambigens* seed suggest that the seeds are nondormant. Nondormancy has been observed in *P. recta* (Baskin and Baskin 1990, Baskin and Baskin 2001). However, only 8 percent of polycarpic perennials studied exhibit nondormancy (Baskin and Baskin 2001). Shimono and Kudo (2003) observed intraspecific variation in seedling emergence between fell field and snowbed habitats in *P. matsumurae*, and they determined that the variation was due to differentiation between populations in these habitats. Given the variety of habitats and the barriers to geneflow found in *P. ambigens*, differentiation of this sort is a possibility in this species.

Phenotypic plasticity

There have been no morphometric analyses of diagnostic characters in *Potentilla ambigens* that define the limits of phenotypic plasticity in this taxon. Descriptions of *P. ambigens* reflect the variation in size of the whole plant and leaves that is readily observable in herbarium specimens and wild populations. The most variable character is leaf hair morphology. This is a key characteristic used in some keys to identify *P. ambigens*. Sivinski (personal communication 2004) doubts the diagnostic utility of leaf hairs in the identification of *Potentilla* species because of overlap among and inconsistency within some taxa. Specimens of *P. ambigens* from Region 2 are generally readily distinguishable from those of *P. hippiana* using the characteristics described in the Non-technical description section. However, genetic and morphometric studies are needed to investigate the hypothesis that *P. ambigens* is merely a vigorous ecophene of *P. hippiana*, especially where these species are reported to intergrade in the Sacramento Mountains of New Mexico (Neely et al. 2001).

Members of the genus *Potentilla* have been shown to respond morphologically to changes in light quantity and quality. In a study of the effects of shade (characterized by decreased light quantity and quality) on *P. anserina* and *P. reptans*, both species showed significant responses to both treatments in morphological and production parameters (Stuefer and Huber 1998).

Mycorrhizae

Virtually all members of the family Rosaceae have strong arbuscular mycorrhizal (AM) relationships (St. John 1996). AM fungi belong to a group of nondescript 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 some degree of specificity between some taxa (Rosendahl et al. 1992, Sanders et al. 1996). While this group has not previously been thought of as particularly diverse, recent studies are suggesting that there is unexpectedly high diversity at the genetic (Sanders et al. 1996, Varma 1999) and single plant root (Vandenkoornhuyse et al. 2002) levels. As root endophytes, the hyphae of these fungi enter the cells of the plant roots where water and nutrients are exchanged in specialized structures.

There has been no investigation of the mycorrhizal symbionts of *Potentilla ambigens*, but studies of other taxa suggest that it forms mycorrhizal relationships. Liu and Wang (2003) observed infection of the roots of *P. anserina* by 12 species of AM fungi in the genera *Acaulospora*, *Glomus*, and *Gigaspora*. Fertilization decreased the number of vesicles observed in the roots of *P. erecta* (Titus and Leps 2000). *Potentilla erecta* had significantly lower levels of vesicles in mowed plots at one sampling period in this study. Axenically reared *Dasiphora floribunda* seedlings grown in culture with *Phialocephala fortinii*, a common root endophyte, showed significant increases in shoot weight when compared with seedlings grown without (Fernando and Currah 1996).

Hybridization

There are many known and putative hybrids in the genus *Potentilla* (Eriksen 1997). Moore (1979, p. 134) aptly described the genus *Potentilla* as "a botanist's nightmare of crossbreeding." Hansen et al. (2000, p. 1466) noted that "extensive reticulate evolution via hybridization and polyploidy, combined with facultative, pseudogamous agamospermy, have probably caused many of the taxonomic problems in the genus." Although hybrids are often not highly fertile, apomixis allows them to persist indefinitely, during which they may backcross or hybridize again (Eriksen 1996). The patterns of morphological variation among related species of *Potentilla* are therefore very complex (Asker 1977). Other studies have addressed these issues for groups within *Potentilla* (e.g. Hansen et al. 2000, Child 2001).

Hybrids between *Potentilla ambigens* and *P. atrisanguinea* (with pollen from *P. ambigens*) were created under controlled conditions in a greenhouse (Acharya Goswami and Matfield 1975, Acharya Goswami and Matfield 1978). This hybrid is unlikely in nature because these species are not sympatric. *Potentilla atrisanguinea* is found only in New Brunswick, Canada (Kartesz 1999). The hybrids exhibited very irregular meiosis. Attempts to hybridize *P. ambigens* by placing its pollen on the stigmas of *P. argentea* and *P. recta* were unsuccessful (Acharya Goswami and Matfield 1974). In a more elaborate set of crosses, Acharya Goswami and Matfield (1975) tried to create hybrids between *P. ambigens* (as both a maternal and paternal parent) and numerous other species. Attempts to hybridize *P. ambigens* (with *P. ambigens* as the male parent) were unsuccessful with *P. nepalensis*, *P. argentea*, *P. recta*, *P. reptans*, *P. erecta*, and *P. anglica*. Attempts to hybridize *P. ambigens* (with *P. ambigens* as the female parent) were unsuccessful with *P. rupestris*, *P. nepalensis*, *P. atrisanguinea*, *P. argentea*, *P. recta*, *P. buccoana*, *P. reptans*, *P. erecta*, and *P. anglica*.

Hybrid swarms are common among *Potentilla* species (Johnston personal communication 2004). *Potentilla hippiana* is known to hybridize readily with other taxa. *Potentilla hippiana* and *P. pulcherrima* frequently hybridize (Weber and Wittmann 2001a). Hybrid swarms between *P. hippiana* and *P. effusa* have also been observed (Johnston personal communication 2002). Some intergradation has been observed between *P. ambigens* and *P. hippiana* in the Sacramento Mountains of New Mexico (Neely et al. 2001), where hybridization may be occurring. However, this has not been reported elsewhere. *Potentilla ambigens* and *P. hippiana* are known to co-occur at Goose Creek (Mineral County; #24 in **Table 5**) and at Estes Park High School (Larimer County; #10 in **Table 5**) in Colorado. No hybrids were observed at these locations, and the species were easily distinguished from each other at both locations (**Figure 4**).

Demography

There is no information on the longevity, mortality, seed biology, life history stages, or population structure of *Potentilla ambigens* (Handley and Heidel 2002). Maintaining genetic integrity and eliminating inbreeding and outbreeding depression are important management considerations for *P. ambigens*. The vulnerability of this species to inbreeding and outbreeding depression depends on whether maintenance of heterozygosity in populations requires some level of sexual reproduction. Small populations of *P. ambigens* may be more vulnerable to genetic concerns if sexual reproduction occurs often since it tends to maintain heterozygosity that suppresses recessive deleterious alleles. If *P. ambigens* is primarily apomictic, as suggested by the research of Acharya Goswami and Matfield (1978), then there is very little or no inter- and intra-population gene flow. Deleterious alleles are less likely to manifest themselves in populations since most individuals would tend to be homozygous at many loci. However, many *Potentilla* species are facultatively apomictic and retain the ability to reproduce sexually. Acharya Goswami and Matfield (1974) demonstrated the viability of the pollen of *P. ambigens*, suggesting that it may be capable of sexual reproduction. Reports of hybrid swarms involving *P. ambigens* and *P. hippiana* also suggest that sexual reproduction sometimes occurs. In either scenario, pollen vectors are important because pseudogamous

apomicts depend on compatible pollen for production of endosperm in the seed (see the Reproductive biology and autecology section for details).

Holm et al. (1997) observed that in hexaploid *Potentilla argentea*, an apomict, most variation is between and not within populations. Extensive variation was observed between populations. The low variability within populations is probably due to the lack of sexual recombination of genetic material in these populations, while genetic drift or genetic differences present in founder populations might explain the variability between populations. This may be the case in *P. ambigens* as well. Even if *P. ambigens* is capable of sexual reproduction, the disjunct nature of its distribution suggests that gene flow among populations is probably very low. In general, the density of seeds decreases rapidly with increasing distance from the source (Barbour et al. 1987), and long-distance dispersal events are rare. Pollinator-mediated pollen dispersal is largely limited to the foraging area of pollinators (Kearns and Inouye 1993).

Outbreeding depression is a possible concern if hybridization is occurring with *Potentilla hippiana*. If restoration of occurrences is needed, using on-site material for restoration will reduce the risk of negative effects of outbreeding depression.

Potentilla ambigens is a long-lived, polycarpic perennial (Colorado Natural Heritage Program 2004), but its lifespan has not been determined. Based on other plant species with similar life history and morphological characteristics, Johnston (personal communication 2004) speculates the lifespan for *P. ambigens* to be approximately 40 years, perhaps reaching 50 to 70 years. This range is common among perennial forb species, but there has been almost no research on the age structure of herbaceous plant populations (Johnston personal communication 2004). It appears that most plants produce some flowers every year under normal conditions. However, at the U.S. Air Force Academy site (#1 in **Table 5**), only 30 percent of plants observed in 2002 flowered during a severe drought; the rest remained vegetative (Colorado Natural Heritage Program 2004). **Figure 15** is a diagrammatic representation of the life cycle of *P. ambigens*.

No Population Viability Analysis (PVA) has been performed for *Potentilla ambigens*. Apparently there has never been a PVA of any member of the genus *Potentilla* from which inferences could be drawn for this report, including two species of *Potentilla* (*P. hickmanii* and *P. robbinsiana*) that have been listed endangered (U.S. Fish and Wildlife Service 1999). Demographic monitoring data for *P. robbinsiana* were used to justify the delisting of this taxon (U.S. Fish and Wildlife Service 2002).

The reasons for the sporadic distribution of *Potentilla ambigens* are unknown (Colorado Native Plant Society 1997). There appears to be much suitable habitat for this species throughout its range that is unoccupied. *Potentilla ambigens*' habitat needs include a combination of gravelly or sandy soil, open canopy, and periodically elevated soil moisture levels. It is possible that the specific combination of these variables is rare, which would limit the species' habitat. However, its success in colonizing disturbed sites and its apparent ecological amplitude suggest otherwise.

It is not known if metapopulation structure is an important component of the population dynamics of *Potentilla ambigens*, which is found in both persistent and facile habitats. In the latter, the spatial and temporal distribution of suitable but unoccupied habitat is important for determining long-term viability.

Community ecology

There has been no formal study of the community ecology and interspecific relationships of *Potentilla ambigens*. Available information is limited to survey reports, herbarium specimens, observations, and inference from GIS data layers.

Potentilla ambigens is found across a range of elevations in the montane zone. Most occurrences are in areas dominated by coniferous forest matrix community types. It is typically found in patches of grassland in openings within forested areas. The relevant coniferous forest and grassland ecological systems where *P. ambigens* is found are discussed below.

Coniferous forest communities

Potentilla ambigens is associated with several coniferous forest types. These include ponderosa pine woodlands, ponderosa pine savannas, and mixed coniferous forests. In Mineral County, it is also found near spruce-fir forests, but *Pinus ponderosa* and *Pseudotsuga menziesii* (Douglas-fir) are also present (Rondeau 1999). Element occurrence, specimen label, and Colorado GAP vegetation data indicate that most Colorado occurrences of *Potentilla ambigens* are found in areas dominated by ponderosa pine forests (Colorado Division of Wildlife 1998, Colorado Natural Heritage Program 2004).

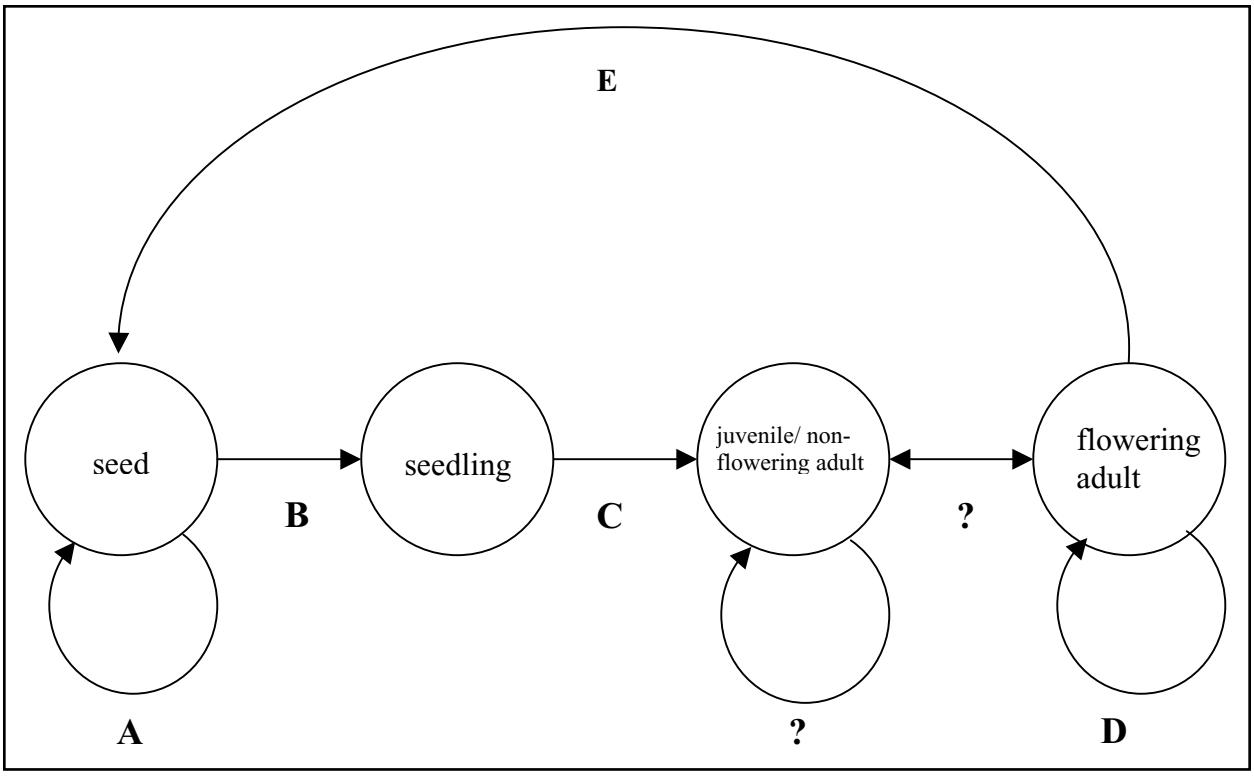

Figure 15. Hypothetical life cycle graph (after Caswell 2001) for *Potentilla ambigens*. There has been no formal investigation of the life history of this species. No transition probabilities are known for *P. ambigens*, and there has been no demographic monitoring of other species of *Potentilla* from which inferences can be drawn. The value of **A** probably varies from year to year depending on climatic variables. No seedlings have ever been observed, so there are no data from which to infer **B** and **C**. The duration of the juvenile stage is not known, and it is not known if plants are capable of flowering in the first year (hence the question marks for the juvenile stage). Plants probably survive for tens of years, perhaps 40 years or more (Johnston personal communication 2004) (**D**). Seed production per plant has not been quantified, but about 30 achenes are produced per flower (**E**).

Ponderosa pine forests fall into two ecological systems as defined by Rondeau (2001). These are ponderosa pine woodlands and ponderosa pine savannas. Fire plays an important role in the maintenance of both systems (see Fire section for details). Because they occur at lower elevations, contain valuable timber resources, are relatively accessible to livestock, and occur near the Colorado Front Range where they are attractive locations for low-density residential development, these systems have been heavily impacted and degraded by human use. In most areas of the Colorado Front Range, fire suppression has resulted canopy closure in ponderosa pine-dominated systems.

The distribution of montane coniferous forest in New Mexico delineated by Dick-Peddie (1993) closely matches the distribution of *Potentilla ambigens*. *Potentilla hippiana* is noted by Dick-Peddie (1993) as a characteristic species of the Douglas-fir-limber pine-bristlecone pine series of upper montane coniferous forests in New Mexico.

Grasslands

Potentilla species are characteristic of the montane grasslands of New Mexico (Dick-Peddie 1993) and a variety of other grassland communities. These may be extensive (Mineral County, and Stonewall Creek in Larimer County), or they may be small patches or meadows surrounded by forest (e.g., above Morrison in Jefferson County, Rocky Mountain National Park, and Rattlesnake Park). In Mineral County, sites are best characterized as shortgrass prairie dominated by *Bouteloua gracilis* (blue grama), but they also include shrubby species such as *Krascheninnikovia lanata* (winterfat) and *Chrysothamnus nauseosus* (rubber rabbitbrush) (Rondeau 1999, Colorado Natural Heritage Program 2004). At Stonewall Creek, *P. ambigens* was collected in shortgrass prairie. *Potentilla ambigens* was documented with *B. gracilis*, *Stipa comata* (needle-and-thread), *Elymus elymoides* (bottlebrush squirreltail), *Koeleria macrantha* (junegrass), and *Pseudoroegneria spicata* (bluebunch wheatgrass) at Rattlesnake Park.

Historically, portions of the occurrence at the U.S. Air Force Academy were probably dominated by shortgrass or midgrass prairie, but they are now dominated by smooth brome (*Bromus inermis*) (Anderson et al. 2003). The area around Rustic Hill is dominated by shrubland with interspersed grasslands (Kettler et al. 1996), but it is not known in what vegetation type *P. ambigens* grew when it was last seen at this site in 1896.

Vegetation change

Human activities have resulted in considerable change to the vegetation in most locations where *Potentilla ambigens* is found. Comparison of the current vegetation of the U.S. Air Force Academy with historic photographs and land survey notes made between 1864 and 1870 shows that there has been tremendous change in the vegetation (Armstrong and Stevens 2002). Grasslands were formerly much more extensive and were probably maintained by fire. When it was purchased by the Department of Defense in the 1950s, much of the U.S. Air Force Academy site was deforested and had been heavily grazed. Fire suppression since 1950 resulted in dense woody vegetation that has become a management concern. Because grasslands were apparently more common before post-settlement human land use in this area, it is possible that the historic extent of habitat for *P. ambigens* in this area was greater.

Development has altered the vegetation of other locations as well. Even within Rocky Mountain National Park, there has been considerable change (i.e., there was once a golf course in Moraine Park [#17 in **Table 5**]), and much effort has been put into restoration this site (Connor personal communication 2004). The area surrounding the occurrence in the Black Forest in El Paso County (#2 in **Table 5**) is forested by dense stands of *Pinus ponderosa*. The fire-maintained open savannas that historically dominated the area have succeeded to closed-canopy forest, reducing the quality and availability of habitat for many rare plants found in this area, including *Potentilla ambigens* (Doyle et al. 2001).

Herbivores and relationship to habitat

Potentilla ambigens is likely to have evolved with browsing by native ungulates. Bison (*Bison bison*) were present historically at some locations where *P. ambigens* is found in Colorado and Wyoming. Pronghorn (*Antilocapra americana*) probably still visit the Stonewall Creek occurrence in Larimer County (#12 in **Table 5**), but they may no longer have access to other occurrences. An area near Wagon Wheel Gap (#21 in **Table 5**) is called Antelope Park and once supported a population of pronghorn, but they have since been extirpated in this area of Mineral County (Rondeau personal communication 2004). Pronghorn forage preferentially on forbs and are thus more likely to have utilized *P. ambigens* for forage than bison, which prefer grasses (Rondeau personal communication 2004). Currently, the most abundant native ungulates in *P. ambigens* habitat are mule deer (*Odocoileus hemionus*) and elk (*Cervus elaphus*). Approximately 400 elk reportedly overwinter in the Goose Creek area (#24 in **Table 5**; Rondeau 1999). In Rocky Mountain National Park, deer and elk have done considerable damage to vegetation because their populations are too high (Soulé 2004). Elk are abundant throughout the town of Estes Park and its surroundings most of the year. However, Bernier (personal communication 2004) has observed that deer and elk do not eat *P. ambigens* and speculates that the plant may not be palatable.

There is only one record suggesting that herbivores consume *Potentilla ambigens*. This record, a specimen label by Earl Loveridge for a plant collected in 1916 from Rio Arriba County, New Mexico (#447 at RM; #38 in **Table 5**), specifies that it is grazed by sheep and goats but includes a note: "poisonous to sheep?"

Livestock grazing occurs at *Potentilla ambigens* occurrences in Larimer and Mineral counties in Colorado. In Larimer County, the McGregor Ranch (#6 in **Table 5**) and Stonewall Creek (#12 in **Table 5**) sites are grazed by cattle, and horses are pastured at Rattlesnake Park (#14 in **Table 5**). In Mineral County, cattle grazing occurs at the Goose Creek occurrence (#24 in **Table 5**) and probably others as well. At Goose Creek, pastures are summer-grazed because it is too cold in the winter (Rondeau personal communication 2004), and cattle appear to avoid *P. ambigens*. These observations and those of Bernier (personal communication 2004) support Loveridge's supposition that *P. ambigens* may harbor chemical defenses to deter grazing.

While direct impacts from grazing appear to be a minor concern for *Potentilla ambigens*, habitat damage from grazing may be a greater concern. Livestock can produce long-lasting detrimental impacts on riparian ecosystems (Briggs 1996). The impacts of grazing on channel morphology are well-studied. Downcutting commonly results from livestock grazing in riparian areas (Elmore and Kauffman 1994). Cattle trample banks, compact soils, and consume vegetation, which can lead to more erosion, greater runoff, faster stream downcutting, larger floods, and lower water tables (Fouty 2002). Overgrazing has apparently degraded

the habitat at Stonewall Creek to the point where extirpation of this occurrence (#12 in **Table 5**) by accelerated erosion is likely.

Livestock have not grazed at the U.S. Air Force Academy in El Paso County since the 1950s when the land was purchased by the Department of Defense. While grazing no longer occurs at this site, the legacy of past grazing persists. The introduction of pasture grasses such as *Bromus inermis* has altered grassland composition and function. While livestock grazing has damaged some sites, the occurrences in Mineral County and their habitat appeared to be suffering no ill effects from current land use practices.

Competitors and relationship to habitat

As described in the Reproductive biology and autecology section, *Potentilla ambigens* is often found with competitive species, suggesting that it is a strong competitor. Native and non-native grass species are among the strongest competitors with which *P. ambigens* occurs, including *Bouteloua gracilis* and *Bromus inermis*. *Potentilla ambigens* has been documented in weedy sites and with aggressive exotic plant species. The presence of competitive non-native species in *P. ambigens* occurrences is a concern because it is not known what long-term effects these species may have. *Phleum pratense* and *B. inermis* have the potential to form thick turfs and dense canopies that might enable them to outcompete *P. ambigens*, particularly in moister sites. Further investigation is needed into interspecific interactions involving *P. ambigens*.

Parasites and disease

There have been no reports in the literature or other sources of parasite or disease attack on *Potentilla ambigens*. Wild individuals and herbarium specimens generally appear robust and healthy. Plants observed in Mineral County in 1998, a relatively wet year, appeared healthy and vigorous with no apparent damage from parasites or disease.

Associated species

A list of species that have been documented with *Potentilla ambigens* in Region 2 is presented in **Table 6**. The areas supporting occurrences of *P. ambigens* also support other rare plants, animals, and natural communities. The Bellows Creek area of Mineral County supports three occurrences of *P. ambigens* (#1, #2, and #8 in **Table 5**) as well as the rare plants *Gilia penstemonoides* (Black Canyon gilia), *Draba smithii* (Smith's draba), and *Oreocarya weberi* (Weber's cats-eye) and animals Rio Grande cutthroat trout (*Oncorhynchus clarki virginalis*) and peregrine falcon (*Falco peregrinus*). This area is of very high value for biodiversity conservation (**Table 4**; Rondeau 1999).

CONSERVATION

Threats

Reports, observations, and opinions of experts suggest several threats to the persistence of *Potentilla ambigens*. In order of decreasing priority, these are off-road vehicle and other recreational use, residential and commercial development, secondary impacts of grazing, road impacts, water resource development, exotic species invasion, effects of small population size, altered fire regime, global climate change, and pollution. These threats and the hierarchy ascribed to them are speculative, and more complete information on the biology and ecology of this species may reveal other threats. Assessment of threats to this species will be an important component of future inventory and monitoring work.

In general, activities that concentrate disturbance in occurrences of *Potentilla ambigens* are likely to threaten it. It is possible that the observed response of *P. ambigens* to some types of human disturbance (reviewed in the Reproductive biology and autecology section) means that it is less vulnerable to anthropogenic disturbance than are most rare species of plants. The lack of information on *P. ambigens* and the lack of awareness by land owners or administrators are threats since land management decisions do not usually consider its needs.

Influence of management activities or natural disturbances on habitat quality and individuals

Recreation

Off-highway vehicle use is a common and growing threat to rare plants and to biodiversity in general. Off-highway vehicle use of public lands has burgeoned in recent years, and illegal off-road activity in closed areas has increased (Bureau of Land Management 2001b). The proximity of occurrences of *Potentilla ambigens* in Region 2 to large metropolitan areas and to popular tourist destinations leaves this species especially vulnerable to off-highway vehicle impacts, since some areas may be heavily used. See the Evidence of occurrences in Region 2 at risk section for details on this threat.

Table 6. Species reported to be associated with *Potentilla ambigens*.

Scientific Name	Exotic?	Scientific Name	Exotic?
Achillea millefolium		*Lepidium* sp.	
Agropyron cristatum	×	*Linaria vulgaris*	×
Agrostis sp.	×	*Lycopus americanus*	
Allium c.f. *geyeri*		*Monarda fistulosa*	
Antennaria parvifolia		*Muhlenbergia filiculmis*	
Antennaria sp.		*Oenothera* sp.	
Artemisia frigida		*Oxybaphus hirsutus*	
Artemisia ludoviciana		*Packera tridenticulata*	
Bouteloua gracilis		*Pediocactus simpsonii*	
Bromus inermis	×	*Penstemon virgatus*	
Bromus sp.		*Phleum pratense*	×
Bromus tectorum	×	*Pinus ponderosa*	
Castilleja sp.		*Poa compressa*	×
Chrysothamnus parryi		*Poa pratensis*	×
Chrysothamnus viscidiflorus		*Potentilla effusa*	
Cirsium arvense	×	*Potentilla hippiana*	
Cynoglossum officinale	×	*Potentilla* sp.	
Dasiphora floribunda		*Pseudoroegneria spicata*	
Descurainia sophia	×	*Pterogonum alatum*	
Elymus elymoides		*Purshia tridentata*	
Erigeron umbellatum		*Ribes cereum*	
Erysimum capitatum		*Rosa* sp.	
Festuca arizonica		*Rosa woodsii*	
Geranium richardsonii		*Salsola tragus*	×
Geranium sp.		*Selaginella densa*	
Geum macrophyllum		*Senecio spartioides*	
Glycyrrhiza lepidota		*Sisymbrium altissimum*	×
Gutierrezia sarothrae		*Solidago* sp.	
Helianthus nuttallii		*Stellaria* sp.	
Hymenoxys richardsonii		*Stipa comata*	
Hypericum perforatum	×	*Symphoricarpos* sp.	
Juncus sp.		*Symphoricarpos occidentalis*	
Koeleria macrantha		*Verbascum blattaria*	×
Krascheninnikovia lanata		*Verbascum thapsus*	×

Recreational use presents potential threats to *Potentilla ambigens*, but there is no evidence that significant impacts have occurred to date. Occurrences of *P. ambigens* in popular hiking areas are vulnerable to trampling. Trampling impacts were among the factors that contributed to the listing of both *P. robbinsii* (NatureServe 2004) and *P. hickmanii* (U.S. Fish and Wildlife Service 1998) as endangered species. Recreational uses can also disrupt the activities of pollinators. Recreational fishing is prevalent at the Goose Creek occurrence, but there is no evidence that this presents a direct threat to the occurrence (Colorado Natural Heritage Program 2004).

Residential and commercial development

Residential development poses a significant and increasing threat to the quality and availability of habitat for *Potentilla ambigens*. Urban growth is very rapid in all Colorado counties in which *P. ambigens* is

found (U.S. Census Bureau 2003). Development has encroached on Bergen Creek at the Elk Meadow Open Space Park in Jefferson County (Colorado Natural Heritage Program 2004) and is likely to have resulted in the extirpation of the type locality near Morrison (Weber personal communication 2004). Development near Estes Park may affect occurrences that have not yet been discovered. The occurrence adjacent to Estes Park High School is vulnerable to developments such as landscaping. Subdivision of property into ranchettes and dispersed development pose potential threats to occurrences on private land. Exurban development fragments natural habitats (Knight et al. 2002) and alters natural processes in ways that fall outside the range of normal variability (Theobald 2004).

Secondary impacts of grazing

While currently available information suggests that livestock grazing does not present a direct threat to *Potentilla ambigens*, the habitat degradation that can accompany livestock grazing, particularly at inappropriate stocking levels, probably represents a significant threat to some occurrences of *P. ambigens*. Severe downcutting exacerbated by grazing is threatening (and may have extirpated) the occurrence at Stonewall Creek. Rattlesnake Park (Colorado State Land Board) is currently used as horse pasture, but current grazing intensities do not appear to be diminishing the viability of the occurrence of *P. ambigens* (Doyle et al. 2005). On National Forest System lands in Region 2, *P. ambigens* is known to occur within an active grazing allotment only at East Bellows Creek. This occurrence is within the Halfmoon-Monument Allotment of the Rio Grande National Forest. See the Herbivores and relationship to habitat section for an overview of impacts to habitat from grazing.

Road impacts

New road construction threatens occurrences if it involves occupied habitat. As exurban expansion proceeds, the proliferation of roads and construction disturbance are likely to encourage the spread of weeds throughout *Potentilla ambigens*' habitat. The barrier effect of roads is known to have broad demographic and genetic consequences, which are reviewed in Forman and Alexander (1998).

Roads could potentially affect all occurrences on National Forest System land in Region 2. Roads pass through or next to at least 12 occurrences of *Potentilla ambigens*. Although some individuals may benefit from added runoff from road surfaces, roads also threaten occurrences through indirect effects such as weed invasion and as sources of erosion. Roads and trails can act as barriers to pollinators and prevent effective gene flow by disrupting pollinator traplines. Road widening or modification is a threat to roadside occurrences at many locations, including Wagon Wheel Gap (along Pool Table Road, Rio Grande National Forest), East Bellows Creek (Rio Grande National Forest), Goose Creek (along Goose Creek Road), U.S. Air Force Academy, Black Forest (adjacent to the intersection of two county roads), along State Route 36, and at the Beaver Meadows Visitor's Center. Right-of-way maintenance and other projects that affect right-of-ways, such as work on utilities, could affect roadside occurrences.

Water resource development

Potentilla ambigens' affinity for bottomlands makes it vulnerable to hydrologic alterations resulting from water resource development. The occurrence at Rattlesnake Park, Larimer County, Colorado, is adjacent to Pinewood Reservoir, which is a part of the Colorado-Big Thompson Project that provides water for Front Range agriculture and cities. Water diverted from west of the Continental Divide passes through Pinewood Reservoir as a part of this complicated water project (Bureau of Reclamation 2006). It is likely that *P. ambigens* habitat was inundated to create this reservoir. Expansion of the reservoir could threaten the occurrence of *P. ambigens* in Rattlesnake Park; however, the occurrence is situated in a drainage well above the current level of the reservoir. Creation of other reservoirs, which is ongoing on the Colorado Front Range, may imperil other occurrences of *P. ambigens* that are undiscovered, but no known occurrences fall within areas proposed for inundation by new reservoirs. Ditching or ditch maintenance could threaten occurrences of *P. ambigens*, but there is no evidence that this threatens any known occurrences. Water resource development is not known to be currently affecting any occurrences on National Forest System land in Region 2.

Exotic species

Exotic species have been reported at many *Potentilla ambigens* occurrences, but there are no reports of exotic species in occurrences on National Forest System land in Region 2. Exotic species were noted as problematic and requiring management at Stonewall Creek (Kettler et al. 1996). Exotic species were noted at both occurrences in El Paso County, Colorado.

Exotic grasses represent a particular threat to *Potentilla ambigens* because they are aggressive competitors for nutrients and water. These species are particularly invasive in moister sites, such as swales, riparian areas, and roadsides, where *P. ambigens* is usually found. Timothy (*Phleum pratense*), crested wheatgrass (*Agropyron cristatum*) and smooth brome (*Bromus inermis*) have been documented at multiple occurrences of *P. ambigens* including Stonewall Creek, U.S. Air Force Academy, Estes Park High School and Black Forest. Kentucky bluegrass (*Poa pratensis*) and Canada bluegrass (*P. compressa*) have also been observed at Rattlesnake Park.

Exotic forbs represent a two-fold threat to *Potentilla ambigens*. First, they compete well with native species for water, light and nutrients, and some species exude allelopathic compounds to reduce competition from other plants. Second, any means used to control exotic forbs, other than hand-pulling, is likely to affect *P. ambigens* equally. Impacts from weeds contributed to the listing of *P. hickmannii* as an endangered species (U.S. Fish and Wildlife Service 1998). **Table 6** is a complete list of exotic plant species that have been documented with *P. ambigens*.

At the U.S. Air Force Academy, St. John's-worth (*Hypericum perforatum*), yellow toadflax (*Linaria vulgaris*), Canada thistle (*Cirsium arvense*), diffuse knapweed (*Centaurea diffusa*), spotted knapweed (*C. biebersteinii*), Scotch thistle (*Onopordum acanthium*), and musk thistle (*Carduus nutans*) (Anderson et al. 2003, Anderson and Lavender 2006) are present. Yellow toadflax also threatens the occurrence in the Black Forest (Doyle et al. 2001). At Estes Park High School, *P. ambigens* occurs with hounds-tongue (*Cynoglossum officinale*; **Figure 16**), field pennycress (*Thlaspi arvense*), tumblemustard (*Sisymbrium altissimum*),

Figure 16. *Cynoglossum officinale* with *Potentilla ambigens* (foreground) at Estes Park High School. Other weeds found with *P. ambigens* at this location include *Linaria vulgaris*, *Agropyron cristatum*, *Thlaspi arvense*, *Salsola tragus*, *Sisymbrium altissimum*, and *Bromus tectorum*. Photograph by the author.

herb sophia (*Descurainia sophia*), cheatgrass (*Bromus tectorum*), yellow toadflax, and tumbleweed (*Salsola tragus*). At Rattlesnake Park, *P. ambigens* was reported with Canada thistle, tumblemustard, and mullein (*Verbascum blattaria*) (Doyle et al. 2005).

Yellow toadflax is particularly invasive in ponderosa pine woodlands and savannas (Doyle et al. 2001). This species has spread rapidly near the occurrences at Black Forest and the Air Force Academy, and it has the potential to infest most sites occupied by *Potentilla ambigens*. It has become the most widespread weed species at the U.S. Air Force Academy, with approximately 2.7 million ramets infesting 102 acres (Anderson et al. 2003).

Yellow starthistle (*Centaurea solstitialis*) is present in at least one site on the Colorado Front Range, at Carter Lake in Larimer County (Lane personal communication 2004). It poses a very real threat to *Potentilla ambigens* and many other native plant species if ongoing efforts to contain it fail. It has a wide ecological amplitude and the potential to spread widely in Colorado. It currently infests 10 million acres in California (Colorado Weed Management Association 2002).

Use of herbicides for right-of-way weed management and for range management threatens *Potentilla ambigens* where it occurs on road cuts or roadsides. Care must be taken with the application of herbicides in habitat for *P. ambigens*, and use of herbicides within known occurrences should be limited to hand application to the target species.

Small population size

Some occurrences of *Potentilla ambigens* in Region 2 are susceptible to stochastic processes because of their small size. However, the species' putative apomictic reproduction through pseudogamy leaves it less susceptible to inbreeding depression and other forms of demographic stochasticity (see the Demography section for details). Small occurrences are also vulnerable to environmental stochasticity (temporal variation in reproduction and survival as a consequence of changing environmental conditions such as weather, herbivory, pollinator availability, and other biotic or abiotic factors), which may lead to local extinction (Lande 1998, Oostermeijer et al. 2003).

Altered fire regime

The lack of a natural fire regime may represent a threat to *Potentilla ambigens*. However, the role of fire in the autecology of this species is unknown. Encroachment of forest into grass-dominated vegetation where *P. ambigens* is typically found could reduce available habitat and possibly result in extirpation at some sites. However, at other sites soil characteristics and water availability may prevent this. Ponderosa pine forests are highly susceptible to fire and ground fire have a short return interval. Thus, it is likely that periodic fire is not detrimental to *P. ambigens*, and it may depend to some extent on fire to prevent woody plant invasion of its habitat.

Climate change

Global climate change is likely to have wide-ranging effects in the near future. However, the direction of projected trends is yet to be determined, and predictions vary based on the environmental parameters used in predictive models. For example, Manabe and Wetherald (1986) suggest that, based on current atmospheric CO_2 trends, average temperatures will increase while precipitation will decrease in the West. However, Giorgi et al. (1998) showed that temperature and precipitation increased under simulated doubling of atmospheric CO_2 levels. Either scenario could significantly affect the distribution of *Potentilla ambigens* habitat in Region 2.

Effects of climate change on *Potentilla ambigens* and its montane habitats are difficult to project. *Potentilla gracilis* exhibited a high tolerance of elevated leaf temperatures in an experimental manipulation to investigate the possible effects of global warming (Loik and Harte 1996). In the same study, *P. gracilis* responded well to drought stress induced by infrared heating of plots. Like *P. ambigens*, *P. gracilis* often occurs in sites that are usually dry but sometimes wet, with a fluctuating but often low water table (Allen-Diaz 1991), so there may be valid inferences to be drawn from these studies.

Pollution

Atmospheric nitrogen deposition has become one of the most important agents of vegetation change in densely populated regions (Köchy and Wilson 2001).

Nitrogen loading and vegetation change have been observed to be greatest near large metropolitan areas (Schwartz and Brigham 2003). Thus, measurable impacts from nitrogen pollution might be expected in all locations where *Potentilla ambigens* has been documented in Region 2. Nitrogen enrichment experiments show universally that nitrogen is naturally limited (Gross et al. 2000). An increase in available soil nitrogen is likely to cause a few species to increase in abundance while many others decline (Schwartz and Brigham 2003). The degree to which nitrogen pollution has resulted in the encroachment of woody species into the habitats of *P. ambigens* in Region 2 is unknown. Acid deposition, which has increased markedly in Colorado through the 20th century, may have already caused changes to the soil chemistry that threaten the viability of *P. ambigens*. High elevation watersheds of the Front Range have reached an advanced stage of nitrogen saturation (Burns 2002).

The tolerance of *Potentilla ambigens* to heavy metals and other pollutants has not been investigated. Plant growth was limited and resource allocation was altered in *P. anserina* grown in high concentrations of copper and nickel (Saikkonen et al. 1998).

Over-utilization

There are no known commercial uses for *Potentilla ambigens*. Other species of *Potentilla* are widely used for medicinal purposes, and members of this genus have a long history of human use as remedies for various maladies. Gerard (1633, pp. 991-992) lists numerous ailments cured by cinquefoil ('Cinkfoile') including excessive bleeding, diseases of the liver and lungs, poisoning, and hernias ('guts falling into the cods'). Modern medicinal uses are principally as an astringent and for reducing inflammations (Moore 1979). Anti-tumor activity has been observed in root extract of *P. fulgens* (Syiem et al. 2003). *Potentilla* species are also an ingredient in anti-wrinkle cream (Shelton 2002), and many species are sought for use in the herb trade. Many members of the family Rosaceae are highly toxic, and many produce cyanogenic compounds, but no members of the subfamily Rosoideae (which includes the genus *Potentilla*) are cited for any particular toxicity issues (Burrows and Tyrl 2001). Moore (1979) notes that generally the whole plant is consumable, but there is evidence to suggest that *P. ambigens* may not be palatable to ungulates (see the Herbivores and relationship to habitat section). Due to its small population size, *P. ambigens* is vulnerable to the effects of harvesting wild populations if for some reason it became sought after as a medicinal herb.

Over-collection for scientific purposes, particularly in small occurrences, is a potential threat. Heavy collection of herbarium specimens of the federally endangered *Potentilla robbinsiana* contributed greatly to its imperilment (NatureServe 2004). Collection of plants from occurrences of fewer than 50 plants is not recommended.

Conservation Status of Potentilla ambigens in Region 2

Is distribution or abundance declining in all or part of its range in Region 2?

Because the pre-settlement population size and range of *Potentilla ambigens* is not known, and because significant gaps remain in our understanding of the distribution and abundance of this species, it is difficult to assess the effects of recreation, infrastructure, extractive use, and management regimes. Conducting additional surveys and establishing long-term monitoring plots will help to determine population trend in this species. As noted in the Population trend, Threats, and Evidence of occurrences in Region 2 at risk sections, evidence suggests that *P. ambigens* has declined in Region 2; two or three occurrences (#2, #12 and #44 in **Table 5**) may have been extirpated. Four occurrences (#2, #11, #25 and #44 in **Table 5**) have not been visited in more than 20 years and need to be relocated. *Potentilla ambigens* may be increasing in other parts of its range, especially at Rocky Mountain National Park, due to its use in restoration projects. Current management practices at occurrences in Mineral County appear suitable for maintaining their long-term viability, but they may need to be adjusted if new threats become apparent. See the Population trend section for other relevant details.

Capacity of habitats to support this species

It is likely that habitats vary in their capacity to support *Potentilla ambigens*, but critical habitat variables are not known. The large range of occurrence sizes observed in Region 2 suggests that sites vary considerably in their ability to support *P. ambigens*. This variability is probably due primarily to soil texture, water availability, disturbance regime, elevation, pollinator availability, and associated species. These variables are not independent of one another. The identification of the most important variables would be a good graduate research topic, using plots and canonical analyses such as those described in the Tools and practices section. There is some understanding of *P. ambigens* gleaned through scant observations of its natural history, but its physiological ecology and

tolerance limits with respect to habitat variables have not been measured, and its ecological amplitude is not known. Refinements of our understanding of the relationships between *P. ambigens* and its habitat will be possible only with more research.

Vulnerability due to life history and ecology

The intrinsic vulnerability of *Potentilla ambigens* has been rated as "moderate" by the Wyoming Natural Diversity Database (2004). The habitat specificity and sporadic distribution of *P. ambigens* leaves occurrences extremely vulnerable to extirpation. *Potentilla ambigens* habitats are amenable to human uses including development, grazing, and recreation. Much of the habitat for *P. ambigens* is found at low elevations in proximity to major metropolitan centers. Human activities are intense in bottomlands of the montane zone, resulting in considerable alteration of vegetation, hydrology, and ecosystem processes. Development is rampant in the ponderosa pine woodlands and savannas of the Colorado Front Range, and the pace of water resource development is rapid. *Potentilla ambigens* occurs very sporadically, and clusters of occurrences are isolated from each other. The species is vulnerable to impacts to its pollinators because it depends on outcrossing for successful seed set (see the Reproductive biology and autecology section for details).

Most occurrences of *Potentilla ambigens* for which abundance has been estimated are small by conventional measures of long-term population viability. Three of the occurrences in which abundance was documented had between 10 and 20 individuals; others may also be very small. Occurrences this small may lack the genetic diversity needed to ensure their long-term viability. They are also vulnerable to small-scale events and disturbances since they occupy very small areas.

The minimum viable population size is not known for *Potentilla ambigens*, but even small populations by the standards of the 50/500 rule of Soulé (1980) may still be viable and of conservation importance. The Colorado Natural Heritage Program considers occurrences of *P. ambigens* containing 10 or more plants as viable, but this threshold will be revised when a minimum viable population size is determined (Colorado Natural Heritage Program 2004). An 11-year demographic study of *P. robbinsiana* determined that the minimum viable population size of this species is 50 plants (U.S. Fish and Wildlife Service 2002).

Like all rare plants, *Potentilla ambigens* is vulnerable to impacts from noxious weeds. New exotic species are arriving constantly, and it may be only a matter of luck that the habitat for *P. ambigens* has not already been taken over by exotic species.

Activities that decrease the size or change the composition of pollinator populations will affect *Potentilla ambigens* if they result in a decrease of pollen exchange. Surface disturbance or compaction is a potential threat to ground nesting-pollinators, many of which are generalists that may visit *P. ambigens*. Studies are needed to determine whether sufficient pollinator resources are available for *P. ambigens* and whether disturbances in *P. ambigens* occurrences affect its pollinators.

Evidence of occurrences in Region 2 at risk

There is evidence to suggest that occurrences of *Potentilla ambigens* are at risk in Region 2. The small number of isolated occurrences, low numbers of individuals, and imminent threats all suggest that *P. ambigens* is imperiled. *Potentilla ambigens* habitat tends to be subjected to intensive land uses, including development, recreation, reservoir construction, and livestock grazing. Gene flow among populations (if *P. ambigens* is capable of some sexual reproduction) is probably extremely low. However, recent discoveries of large occurrences in Mineral and Larimer counties suggest that our knowledge of the distribution and abundance of this species is incomplete.

Human population growth is placing some occurrences of *Potentilla ambigens* at risk due to development pressures and increased use of habitat for recreation. All counties in the states of Region 2 where *P. ambigens* occurs realized significant population increases between 1990 and 2000 (U.S. Census Bureau 2003; **Table 7**). However, 18 (or possibly 20) of the 26 occurrences known from Region 2 are located on public land where they may be protected from development (**Table 1**). Nonetheless, some of these occurrences remain vulnerable to degradation from habitat fragmentation, illegal off-road vehicle use, hydrologic alteration, and secondary impacts of livestock grazing. Occurrences near Estes Park and the type locality in Jefferson County (if it is extant) are probably most at risk of extirpation from development. More than 90 percent of the potential habitat for *P. ambigens* at Goose Creek and Bellows Creek is privately owned (Rondeau 1999). Current management of the largest

Table 7. Summary of U.S. census data for the counties of USDA Forest Service Region 2 in which *Potentilla ambigens* occurs.

		Census Population		Change, 1990 to 2000	
County Name	**State**	**April 1, 1990**	**April 1, 2000**	**Number**	**Percent**
El Paso	CO	397,014	516,929	119,915	30.2
Jefferson	CO	438,430	527,056	88,626	20.2
Larimer	CO	186,136	251,494	65,358	35.1
Mineral	CO	558	831	273	48.9
Saguache	CO	4,619	5,917	1,298	28.1
Albany	WY	30,797	32,014	1,217	4.0

known occurrences (Goose Creek, Beaver Point, and Rattlesnake Park) appears to be compatible with the long-term persistence of *P. ambigens* at these locations.

Land management practices may be negatively affecting the occurrence at Stonewall Creek, where habitat degradation (possibly the result of overgrazing) has compromised the viability of the occurrence. This occurrence may no longer be extant.

Some occurrences of *Potentilla ambigens* are close to major roads where off-road vehicle use is likely to be greatest. Damage to roadside plants has been documented at the U.S. Air Force Academy (Colorado Natural Heritage Program 2004). Occurrences adjacent to Pool Table Road in Mineral County, and those within the town of Estes Park in Larimer County, are probably at greatest risk from these impacts.

Management of Potentilla ambigens in Region 2

Implications and potential conservation elements

Existing data suggest that *Potentilla ambigens* is imperiled due to a limited global range, a small number of occurrences, small population sizes, and threats to its habitat. The loss of an occurrence or a portion thereof is significant and may result in the loss of important components of the genetic diversity of the species. However, limited information is available for *P. ambigens*. Restoration policies will need to address appropriate restoration of native plant communities, grazing regimes, disturbance regimes, and pollinator resources. Given (1994) offers practical advice regarding restoration that can assist with the development of effective management and restoration policies. See the Beneficial management actions section for information on mitigating threats resulting from management.

Desired environmental conditions for *Potentilla ambigens* include sufficiently large areas where the natural ecosystem processes on which the species depends can occur, permitting it to persist unimpeded by human activities and their secondary effects, such as weeds. This includes a satisfactory degree of ecological connectivity among clusters of occurrences to provide corridors and other nectar resources for its generalist pollinators. It is possible that most or all of the ecosystem processes on which *P. ambigens* depends are functioning properly at many or most of the occurrences of this species. Further research on the ecology and distribution of *P. ambigens* will help to develop effective approaches to management and conservation.

Within the last 15,000 years, the climate in the southern Rocky Mountains has been both warmer and colder than it is at present. There is evidence to suggest that the elevational and latitudinal distributions of many plant species were different in these periods than they are today. Given the changes predicted in the global climate for the next 100 years, incorporation of higher elevation refugia for *Potentilla ambigens* into preserve designs and conservation plans will help to ensure its long-term viability.

A thoughtful assessment of current management practices on lands occupied by *Potentilla ambigens* will identify opportunities for change that would be inexpensive and have minimal impacts on the livelihood and routines of local residents, permittees, managers, stewards, and recreationists while conserving this species. Potential management actions to benefit *P. ambigens* are discussed in the next section.

Tools and practices

Species and habitat inventory

Available information on *Potentilla ambigens* is limited to herbarium specimen labels, Colorado Natural

Heritage Program element occurrence records, and personal observations. There has been no systematic effort to map the distribution of this species or to quantify the total population. Species inventories are needed to obtain baseline information from which conservation priorities can be determined. Inventories should include New Mexico because the species is poorly documented there as well.

It is likely that new occurrences of *Potentilla ambigens* remain to be discovered. Because of the broad distribution and variety of habitats in which *P. ambigens* is found, it is difficult to restrict the survey area. It could potentially be found across a range of montane habitats in Region 2. Because it has thus far only been found east of the Continental Divide, montane areas of the eastern slope are the highest priority for inventory. However, montane habitats on the western slope as well cannot be ruled out.

Visits to known occurrences are needed to document their spatial extent, numbers of plants, habitat, and threats. Sites in the San Luis Valley in particular need better documentation, including verification of *Potentilla ambigens* in the southern San Luis Valley (Johnston personal communication 2004). The occurrence observed on Rustic Hill in 1896 by George Osterhout (#3 in **Table 5**) is a high priority for the Roosevelt National Forest since this occurrence is probably located on National Forest System land. From descriptions of this site (Kettler et al. 1996, Colorado Division of Wildlife 1998), there is much suitable habitat in this area. The road through the canyon in this area was moved, so a search of the area adjacent to the old roadbed may be fruitful in finding this occurrence (Scully personal communication 2004).

A concerted effort is needed to determine if *Potentilla ambigens* remains extant in Wyoming. Ponderosa pine forests are widespread in the Laramie Mountains of northern Albany County (University of Wyoming 1996), where other occurrences may await discovery. Searching of this area and other portions of the Medicine Bow National Forest in Wyoming may be successful. Halleck Canyon has not yet been intensively searched for the occurrence reported by Aven Nelson in 1900.

There is a great deal of potential habitat in Colorado for *Potentilla ambigens* that should be considered for inventory. Searching suitable habitat near clusters of known occurrences may be most fruitful. Other areas with abundant potential habitat include Fremont County (Colorado Natural Heritage Program 2004), Douglas County (near the Black Forest or the Rampart Range), along the base of the Sangre de Cristo range and other portions of the Pike-San Isabel National Forest, and around edges of the mountain parks. An occurrence in Sugarite Canyon in Colfax County, New Mexico is within 5 miles of the Colorado border; searches in Las Animas County adjacent to this location may be successful if suitable habitat is present. Many areas within the known range of *P. ambigens* have not been 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.

A targeted inventory for *Potentilla ambigens* will be difficult because it is distributed so broadly. One step towards obtaining better information in the distribution of this species could be to raise the awareness of agency personnel in Wyoming and Colorado who might encounter it in the field. *Potentilla ambigens* is easily identified in July and early August when plants are in flower. It becomes more difficult to find after flowering until leaves turn bright red in the fall (Colorado Native Plant Society 1997). Either period would be a good time for surveys since the flowers are of little diagnostic value.

Potentilla ambigens could benefit from inventory and mapping using Global Positioning System (GPS) equipment to mark precise occurrence boundaries. This would provide land managers with data for use in land use planning and permitting processes. The value of GPS mapping would be increased by collecting plant census data and ecological data. Aerial photography, topographic maps, and vegetation maps could be effective for refining survey areas for *P. ambigens*.

Population monitoring

A monitoring program that tracks recruitment, seed production, seed and plant longevity, population variability, and pollinators would generate data useful to managers and the scientific community. Monitoring would also help to detect population trends under different management and human use regimes. A monitoring program for *Potentilla ambigens* targeting robust occurrences in both natural and artificial settings could incorporate an investigation of human impacts such as recreation and grazing. Monitoring sites under a variety of land use regimes will help to identify appropriate management practices for *P. ambigens*. It will be important to define *a priori* the changes the

sampling regime intends to detect, and the management actions that will follow from the results (Schemske et al. 1994, Elzinga et al. 1998).

Sampling monitoring plots every year will be necessary at first to gain insight into the population dynamics of *Potentilla ambigens*. To document important demographic parameters (e.g., seedling establishment and seed set), two trips per year may be required; one trip in early spring to record seedlings and another in mid August to record seed set.

A commonly used monitoring method involves tracking marked individuals over several years. One possible approach that is suitable for non-rhizomatous perennials such as *Potentilla ambigens* is described in Lesica (1987). Ideally, a subset of the occurrence is selected randomly, and individuals within quadrats or transects are marked using aluminum tags or other field markers. It is important that plots contain a reasonable sample size (perhaps 100 to 200 individuals). This will help to ensure that changes within plots resulting from death and recruitment do not eventually result in the obsolescence of the plot. Elzinga et al. (1998) offers additional suggestions regarding sampling design and protocol. Suitable methods for monitoring pollinators are discussed in Kearns and Inouye (1993). Several methods of monumentation are recommended in Elzinga et al. (1998) depending on the site physiography and how exposed the site is to casual human visitation. This is an important consideration that will reap long-term benefits if done properly at the outset of the monitoring program.

Adding a photo point component to monitoring following recommendations offered in Elzinga et al. (1998) and Hall (2002) could facilitate the tracking of individuals and add valuable qualitative information. Monitoring sites must be selected carefully, and a sufficient number of sites need to be selected if the photographs are intended to detect population trends.

Habitat monitoring

Habitat monitoring can be conducted concurrently with population monitoring. Estimating the cover and/or abundance of associated species within the plots described above could permit the investigation of interspecific relationships through ordination or other statistical techniques. Understanding environmental constraints on *Potentilla ambigens* would facilitate the development of beneficial management practices for this species. Gathering data on slope, aspect, and soil characteristics (particularly moisture and texture) in the permanent plots described above would permit the canonical analysis of species-environment relationships. These data would facilitate hypothesis generation for studies of the ecology of this species, and will help to explain observations of population change. Monitoring of known occurrences will alert managers to new threats such as weed infestations and damage from human disturbance and grazing. Changes in environmental variables might not cause observable demographic repercussions for several years; repeated sampling of key variables may help to identify underlying causes of population trends. Evidence of current land use practices and management is important to document while monitoring.

Habitat monitoring is usually better at identifying new impacts than at tracking change in existing impacts. Observer bias is a problem with habitat monitoring (Elzinga et al. 1998). For estimating weed infestation sizes, using broad size classes and training field crews carefully in accurate and consistent estimation of plant cover helps reduce the effects of observer bias. To assess trampling impacts, using photographs of impacts to train field crews will help them to rate consistently the severity of the impact.

Beneficial management actions

New inventory and monitoring projects would benefit *Potentilla ambigens*. Assessing all occurrences with respect to population size, condition, and landscape context will help managers to prioritize conservation efforts and to determine where management changes are most urgent. Developing a better understanding of the species' distribution will assist with the development of regional management protocols that favor the persistence of *P. ambigens*. Because there is much suitable habitat on National Forest System lands in Region 2, this is a high priority for the USFS, particularly on the Roosevelt and Rio Grande national forests.

Surveying potential habitat for *Potentilla ambigens* before carrying out management activities would help alleviate threats to this species from human impacts. Surveys will locate new occurrences and avert impacts from incompatible management. Considering the needs of *P. ambigens* in the management planning process and land use decisions will benefit the species.

Due to the accessibility and proximity of its habitat to human developments and tourist attractions, *Potentilla ambigens* is highly vulnerable to recreational uses. Management actions that limit recreational

impacts will confer significant benefits to this species. Routing new trails and rerouting existing trails around known occurrences may reduce direct human impacts to occurrences and may improve the security of occurrences in Rocky Mountain National Park, where trailside barriers have been installed to protect other rare plants, including *P. rupincola* (Anderson 2002). Barriers have also been installed to protect occurrences of *P. robbinsiana* from trampling; however, the stone wall protecting the *P. robbinsiana* occurrence may also be acting as a barrier to the natural spread of the population (NatureServe 2004).

Assessment of the susceptibility and impacts to all occurrences from off-road vehicle use is needed, and road closures, gates, and fences may warrant consideration. However, as noted previously in this assessment, the enforcement of off-road vehicle regulations and exclosures is challenging (Brekke personal communication 2004).

Given the demonstrated threats to *Potentilla ambigens* and its habitat from exotic species (Kettler et al. 1996, Doyle et al. 2001, Anderson et al. 2003), aggressive management of weeds in and near *P. ambigens* occurrences is a high conservation priority. Any management strategies that prevent the infestation of *P. ambigens* occurrences will confer the greatest benefits. The weed-free hay policies enforced by the USFS (e.g., Medicine Bow National Forest 2003) and other federal agencies are steps towards this goal. However, species such as smooth brome and timothy, which may present a threat to *P. ambigens*, are not covered under these policies, which generally only deal with state-designated noxious weed species (USDA Forest Service 2004).

Although mowing and other forms of weed control can affect portions of *Potentilla ambigens* occurrences, right-of-way management practices can be modified to mitigate these impacts. Hand-pulling weeds where possible and appropriate has the least impact on occurrences of *P. ambigens*. Limiting the use of herbicides within occurrences of *P. ambigens* to direct application to target species will mitigate the loss of plants due to overspray and indiscriminate application. Avoiding right-of-way mowing in *P. ambigens* occurrences from May until late August or September (after fruit has dried and seeds are released) might also be beneficial. Having someone who is familiar with *P. ambigens* search an area will help to prevent or mitigate impacts to occurrences during road projects such as utility line installation and road improvement.

Management practices that reduce the secondary impacts of grazing will benefit *Potentilla ambigens*. Research is needed to identify grazing regimes that are compatible with *P. ambigens*, and monitoring of grazed versus ungrazed occurrences can help determine the effects of grazing. Allotment management plans that give consideration to the viability of *P. ambigens* occurrences will have positive impacts. Plans may include recommendations to adjust stocking rates to reduce impacts to *P. ambigens* habitat if monitoring shows it to be warranted. Special attention to maintaining proper functioning condition in riparian areas will benefit occurrences near streams.

Most occurrences of *Potentilla ambigens* in Region 2 are found on federal, state, and county public lands (**Table 1**). However, some significant occurrences are on private lands where they are at risk from development. Conservation easements and other land trust conservation tools can help to protect occurrences on private land. Purchasing conservation easements even on small properties may assist the conservation of *P. ambigens* since its populations tend to be isolated and limited in size. Bringing sites on private land into public ownership through land exchange or purchase could also protect occurrences from residential development. Similarly, land exchanges involving sites that are currently on public land would not be beneficial to *P. ambigens*. The conservation of *P. ambigens* would be an appropriate goal to include in county and city planning efforts, particularly for the cities of Morrison, Colorado Springs, Black Forest, and Creede. Purchase of land or conservation easements by municipal open space programs is also an effective conservation tool.

Seed banking

No seeds or genetic material are currently in storage for *Potentilla ambigens* 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 2003). Collection of seeds for long-term storage will be useful if restoration work is ever needed.

Seeds are stored at the Rocky Mountain National Park Greenhouse and used to grow *Potentilla ambigens* for restoration and landscaping. Seeds were collected from occurrences at McGraw Ranch and McGregor Ranch. The seed from McGregor Ranch will be used to grow plants that will be planted on areas disturbed when

developing and modifying the access road and parking lot to Bear Lake. Use of seed from a local source reduces the threat of outbreeding depression that would result from the introduction of exogenous genestock.

Information Needs

Distribution

The distribution and abundance of *Potentilla ambigens* in Regions 2 and 3 are only broadly understood, and additional inventory is needed to fill out the picture. Recent discoveries of new occurrences suggest that others are likely to be found. While conservation can begin at known occurrences, it is difficult to formulate conservation strategies for this species in Region 2 based on current knowledge. Assessing the abundance and size of each occurrence of *P. ambigens* will be important for accurately assessing conservation needs and priorities for this species. Places to focus future searches are included in the Species and habitat inventory section.

Life cycle, habitat, and population trend

The life cycle of *Potentilla ambigens* is poorly understood. Plant longevity and transition probabilities between life stages are not known. A demographic monitoring program in which individuals are tracked (as described in the Population monitoring section) would help to quantify these variables. Developing an elasticity analysis could identify critical life history stages, which would help assess threats to the persistence of *P. ambigens*. Population trends could be assessed through multi-year monitoring of multiple, well-distributed occurrences.

Autecological research is needed to help refine our definition of appropriate habitat and facilitate effective habitat monitoring and conservation stewardship of this species. Information on the ecological amplitude of *Potentilla ambigens* with respect to soil texture, soil moisture, nutrient concentrations, and disturbance would be useful to scientists and land managers, and it is needed to understand species-environment relationships. Investigating spatial autocorrelation with other species may help to determine underlying ecosystem processes.

Response to change

How *Potentilla ambigens* responds to habitat change resulting from natural process and human land uses is unknown. Understanding the specific responses of this species to disturbance is important for determining compatible land management practices. The response of *P. ambigens* to grazing is unknown although observations suggest livestock and other herbivores avoid it (Rondeau 1999). See the Reproductive biology and autecology section for a discussion of the role of disturbance, and the Herbivores in relation to habitat section for a discussion of grazing and *P. ambigens*.

Although *Potentilla ambigens* has been determined to be a pseudogamous apomict (see the Reproduction and **Definitions** sections for details), its reproduction is not well studied. *Potentilla ambigens* relies on the services of pollinators even though its reproduction is functionally asexual. The possible role of sexual reproduction in the population biology of *P. ambigens* is in need of investigation. The importance of pollinators in the reproductive biology of *P. ambigens* indicates that information is needed on its pollination ecology and the efficacy of various pollinators. Dispersal mechanisms employed by *P. ambigens* have not been determined, and seedling establishment has not been observed.

Metapopulation dynamics

There is no information available to determine the role, if any, of metapopulation structure and dynamics to the long-term persistence of *Potentilla ambigens* at local or regional scales. Emigration, immigration, and extinction rates are unknown for *P. ambigens*. Baseline population dynamics and viability must first be assessed. These analyses must rely on observable trends in individual occurrences. Observing population trends at the occurrence 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 regarding the demography of *Potentilla ambigens*. Abundance has not been rigorously determined at any occurrence, and reproductive output, recruitment, longevity, and other demographic parameters are not known. Studies in which individual plants are tracked through time are needed before local and range-wide persistence can be assessed with demographic modeling techniques. Short-term demographic studies often provide misleading guidance for conservation purposes, so complementary information, such as historical data and experimental manipulations, should be included whenever possible (Lindborg and Ehrlén 2002). However, the value of detailed demographic data for

conservation planning and species management cannot be overstated.

Population trend monitoring methods

There has been no population monitoring of *Potentilla ambigens*, but methods are available that could easily be adapted for this species. See the Population monitoring section for details on monitoring protocols. Selection of monitoring sites from a variety of physiognomic and geological settings and land use scenarios will be necessary to monitor population trends.

Restoration methods

The methods currently being used by Rocky Mountain National Park to propagate and establish *Potentilla ambigens* are effective. Although restoration methods are available, it is not known whether these methods are widely applicable for *P. ambigens* or if restored or established occurrences remain viable over the long-term. See the Propagation and planting methods section for details.

Research priorities (in order of priority) for Region 2

The highest research priority in Region 2 is inventories to improve our understanding of the distribution and abundance of *Potentilla ambigens*. It is likely that at least a few occurrences remain to be discovered in Region 2. Inventories are also needed in New Mexico to determine the global status of this species. Determining abundance and distribution is a fundamental step towards understanding *P. ambigens*' conservation status and prioritizing its conservation needs. Identifying the site from which the Chelsea Physic Garden obtained the material used by Acharya Goswami and Matfield (1974, 1975, 1978) in their study of the reproductive biology of *P. ambigens* is needed.

Periodic monitoring is needed to document threats to *Potentilla ambigens*. Monitoring the impacts of exotic species, off-highway vehicle use, grazing, and other disturbance at known occurrences will enable managers to take steps when impacts to occurrences from human activities become evident. Monitoring the impact of non-native species on *P. ambigens* will help to ensure that occurrences are not invaded and degraded by weeds, and it will help to assess the importance of weed management for the conservation for this species.

Reaching a better understanding of the influence of human-mediated activities on individuals and habitat of *Potentilla ambigens* will assist land managers and planners in making good decisions. Identifying life history and phenological stages when *P. ambigens* is less sensitive to the effects of grazing would help to develop practices that are compatible with *P. ambigens*. Exploring the effects of exclosures, different stocking rates, timing of grazing, and resting pastures will yield valuable information. This and other research needs could be addressed through the population monitoring described in this assessment (see the Population monitoring section for details).

Further investigation of the reproductive biology of *Potentilla ambigens* is needed. Study of the role of pollinators in the population biology of *P. ambigens* will clarify the relative importance of floral visitors in pollen transfer. Studies should include bagging experiments to investigate the role of sexual reproduction in the population biology of *P. ambigens*. These experiments could include controls, emasculated flowers, and various crosses, followed by cytological or genetic analysis of the offspring to determine the relative contributions of maternal and outcrossed alleles. Nyléhn et al. (2003) describe methods used to test for pseudogamous apomixis in *Potentilla* section *Niveae* that could applicable to *P. ambigens*.

Investigation is needed to determine whether hybridization is occurring in *Potentilla ambigens*. This should include genetic analyses of the hybrid swarms reported from Sacramento Mountains of New Mexico. The possibility of hybridization with species other than *P. hippiana* also needs to be explored.

Studies of the habitat requirements and autecology of *Potentilla ambigens* are needed. Understanding the plant-environment relationship for this species will be helpful in defining its coping strategies, in modeling its potential distribution, and in clarifying why it is rare. Information from physiological and community ecology studies of *P. ambigens* will be valuable in the event that an occurrence needs to be restored, and it will help to determine biotic and abiotic factors that contribute to its survival. A better understanding of the species' floral biology, seed dispersal mechanisms, predators, seed germination, and longevity is needed. Testing hypotheses regarding the causes of rarity in *P. ambigens* will illuminate best management practices, target survey locations, and identify reintroduction sites. The role of disturbance in the autecology of *P.*

ambigens remains poorly understood. An understanding of the specific tolerances of *P. ambigens* to human and natural disturbance regimes will assist with developing conservation strategies and management plans by determining the types of disturbance most likely to have negative impacts.

Demographic studies are needed for *Potentilla ambigens*. Demographic data are more useful than genetic information for assessing status and for developing recovery plans (Schemske et al. 1994). Determining the critical life history stages of *P. ambigens* will allow managers to design management protocols that benefit those stages. A monitoring program that determines effective population size and investigates the growth, survival, and reproduction of individuals within occurrences will help to determine the conservation status of *P. ambigens*.

Additional research and data resources

Volume 9 of the Flora of North America (Magnoliophyta: Rosidae, Part 2) will include a treatment of *Potentilla* by Barbara Ertter that was not available for inclusion in this report. The Rawlins Field Office of BLM is currently drafting a Revised Resource Management Plan (Bureau of Land Management 2004) that will have implications for the management and viability of *P. ambigens* if it is still extant in Albany County, Wyoming. Attempts to verify the place of origin of material that was obtained from the Chelsea Physic Garden in London by Acharya Goswami and Matfield (1974) were not successful. This information would place the results of their research in a geographic context and would verify the relevance of the results.

DEFINITIONS

Agamospermy – apomictic reproduction involving seed production without fusion of gametes (Gould and Shaw 1983).

Apomixis – reproduction that involves structures commonly concerned in sexual reproduction but in which there is no actual fusion of male and female gametes (Gould and Shaw 1983).

Autopolyploid – an organism with three or more sets of chromosomes that come from the same species (Art 1993); may arise through the spontaneous doubling of the chromosomal complement as observed by Müntzing and Müntzing (1943) in *Potentilla*.

Axenic – not contaminated by or associated with any other living organisms.

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, and 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).

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

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

Ecophene – the morphological response of a phenotypically plastic species to environmental variation (after Cole 1967).

Monumentation – the process of marking permanent sampling units by installing rebar, stakes, or other markers, or by using landmark references; anything that is used to relocate a plot is called a monument (Elzinga et al. 1998).

Pilose – bearing long, soft, straight hairs (Harris and Harris 1999).

Polyploid – a condition in which an individual possesses one or more sets of chromosomes in excess of the normal two sets occurring in diploid organisms (after Allaby 1998).

Potential Conservation Area (PCA) – a best estimate of the primary area supporting the long-term survival of targeted species or natural communities; PCAs are circumscribed for planning purposes only (Colorado Natural Heritage Program Site Committee 2001) and are ranked based on their biodiversity significance:

- B1 **Outstanding Significance** - only location known for an element or an excellent occurrence of a G1 species.
- B2 **Very High Significance** - one of the best examples of a community type, good occurrence of a G1 species, or excellent occurrence of a G2 or G3 species.
- B3 **High Significance** - excellent example of any community type, good occurrence of a G3 species, fair occurrence of a G2 species, or a large concentration of good occurrences of state-rare species.

B4 **Moderate or Regional Significance** - good example of a community type, fair occurrences of a G3 species, excellent or good occurrence of state-rare species.

B5 **General or State-wide Biodiversity Significance** - good or marginal occurrence of a community type, S1, or S2 species.

Pseudogamous agamospermy – apomixis in which pollen from a compatible species is needed to produce endosperm. A pollen nucleus fuses with the two polar nuclei of the embryo sac, as typically occurs during fertilization in Angiosperms, to form the endosperm (which forms the nutritive tissue in the seed). However, the embryo develops without fertilization from an unreduced egg (Asker 1977, Eriksen 1996). Thus, although pollination is required to form the seed, the offspring are clones of the maternal plant as in other forms of apomixis.

Pseudogamy – a type of agamospermy where pollination takes place and a pollen nucleus fuses with the polar nuclei of the embryo sac to form endosperm, while the embryo develops without fertilization from an unreduced egg. Thus, pseudogamous plants require the pollen from another individual even though fertilization does not occur. This is common in members of the genus *Potentilla* (Eriksen 1996).

Pubescent – covered with short, soft hairs (Harris and Harris 1999).

Rachis – the main axis of a compound leaf (Harris and Harris 1999).

Strigose – bearing straight, stiff, sharp, appressed hairs (Harris and Harris 1999).

Tomentose – with a covering of short, matted or tangled, soft, wooly hairs (Harris and Harris 1999).

Villous – bearing long, soft, shaggy, but unmatted, hairs (Harris and Harris 1999).

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