Machaeranthera coloradoensis (Gray) Osterhout (Colorado tansyaster): A Technical Conservation Assessment



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COVER PHOTO CREDIT

Machaeranthera coloradoensis (Colorado tansyaster). Photograph by William Jennings. Reprinted with permission of the photographer.

SUMMARY OF KEY COMPONENTS FOR CONSERVATION OF MACHAERANTHERA COLORADOENSIS

Status

Machaeranthera coloradoensis (Colorado tansyaster) is a regional endemic species with populations located in central, west-central, and southwestern Colorado and south-central Wyoming. Of the 33 occurrences of *M. coloradoensis* worldwide, 21 occurrences are on lands managed by the U.S. Forest Service in Colorado and Wyoming. One of these occurrences is within a recently designated Special Interest Area, and one may possibly be within a wilderness area.

The Global Heritage Status Rank for *Machaeranthera coloradoensis* is G2, or globally imperiled (NatureServe 2003). *Machaeranthera coloradoensis* has been ranked by the Colorado Natural Heritage Program as S2, or imperiled (vulnerable to extirpation; endangered or threatened in the state) and by the Wyoming Natural Diversity Database as S1, or critically imperiled (vulnerable to extirpation in state; critically endangered in state) (Colorado Natural Heritage Program 2003, Wyoming Natural Diversity Database 2003). *Machaeranthera coloradoensis* is currently designated a sensitive species by Region 2 of the U.S. Forest Service (U.S. Forest Service 2003). This tansyaster is not currently listed as a sensitive species by either the Colorado or Wyoming Bureau of Land Management (U.S. Bureau of Land Management 2000, 2001).

Recent taxonomic work based on molecular and morphological data has led researchers to propose placing *Machaeranthera coloradoensis* into the genus *Xanthisma* (Morgan and Hartman 2004). In addition, experts no longer recognize the two varieties of *Machaeranthera coloradoensis* (var. *brandegeei* and var. *coloradoensis*) as distinct since the recent discovery of new populations (R. Hartman personal communication 2003).

Primary Threats

Machaeranthera coloradoensis is vulnerable because of its restricted geographic range and small number of documented occurrences. Direct or indirect negative impacts to *M. coloradoensis* populations or habitats by human-related activities could occur from motorized and non-motorized recreation, trail or road construction and maintenance, reservoir expansion, housing development, changes to natural disturbance regimes, domestic livestock activities, invasive species introduction, or small-scale mining. Lower elevation populations and those populations closest to roads and trails are likely at the most risk. Other environmental or biological threats to populations or habitats of *M. coloradoensis* could include inadequate pollination, genetic isolation, herbivory, landscape fragmentation, hybridization, global climate changes, or changes to the natural disturbance regime that would affect natural succession, erosion, or precipitation patterns.

Primary Conservation Elements, Management Implications, and Considerations

Machaeranthera coloradoensis is a perennial forb species that occurs in a variety of habitats from montane to alpine areas. Little is known about the current abundance, basic biology, ecological requirements, or vulnerability to environmental stochasticity of this species. Based on the few available data on abundance and distribution, we can speculate that this species appears to be viable within U.S. Forest Service Region 2 under current natural disturbance regimes and current levels of recreation and management activities. Certain populations (e.g., populations on roadsides) may need immediate, active management to prevent extirpation. It is difficult to predict the ability of this species to tolerate environmental stochasticity in the future (e.g., global environmental changes, drought) and any future management changes (e.g., livestock grazing, natural resource development).

Features of *Machaeranthera coloradoensis* biology that may be important to consider when addressing conservation of this species (i.e., key conservation elements) include its apparent preference for exposed substrates of calcareous, sedimentary, and volcanic origin, its potential reliance on continuous natural disturbances to create/ maintain open habitat, its possible poor competitive abilities evidenced by its preference for sparsely-vegetated areas, its hybridization with closely-related species, and its possible outcrossing needs requiring efficient pollination. Priority conservation tools for *Machaeranthera coloradoensis* conservation may include assessing current distribution and

abundance, identifying and protecting the highest quality occurrences, and documenting and monitoring the effects of current land-use practices and management activities. Additional key conservation tools may include surveying high probability habitat for new populations, preventing non-native plant invasions, studying demographic parameters and reproductive ecology, and assessing the effects of environmental fluctuations, future management activities, or changes in management direction.

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INTRODUCTION

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

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

Goal

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

Scope and Information Sources

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

In producing the assessment, an extensive literature search was performed to obtain material focusing on Machaeranthera coloradoensis, as well as information on related species and on the geographical and environmental contexts of this species. Reviews were completed of refereed literature (e.g., published journal articles), non-refereed publications (e.g., unpublished status reports), theses and dissertations, data accumulated by resources management agencies (e.g., Natural Heritage Program [NHP] element occurrence records), and regulatory guidelines (e.g., USFS Forest Service Manual). Visits were not made to every herbarium with specimens of this species, but we did include specimen label information provided by herbarium staff and available in NHP element occurrence records. Because studies of rare plants are often ongoing processes, we attempted to include the most recent information available and to cite where work is currently in progress (e.g., R. Hartman personal communication 2003, Morgan and Hartman 2004). Additionally, we incorporated information from studies of closely-related Machaeranthera species or Machaeranthera species in USFS Region 2 or adjacent areas, and we avoided extrapolating from studies of unrelated Machaeranthera species or Machaeranthera species of drastically different environmental contexts. While the assessment emphasizes refereed literature because this is the accepted standard in science, nonrefereed publications and reports are used extensively in this assessment because they provided information unavailable elsewhere. These unpublished, non-refereed reports were regarded with greater skepticism, and all information was treated with appropriate uncertainty.

Treatment of Uncertainty

Science represents a rigorous, synthetic approach to obtaining knowledge. Competing ideas regarding how the world works are measured against observations. However, because our descriptions of the world are always incomplete and our observations are limited, science focuses on approaches for dealing with uncertainty. A commonly accepted approach to science is based on a progression of critical experiments to develop strong inference (Platt 1964). However, it is difficult to conduct critical experiments in the ecological sciences, and often observations, inference, good thinking, and models must be relied on to guide the understanding of ecological relations. In this assessment, the strength of evidence for particular ideas is noted, and alternative explanations are described when appropriate. While well-executed experiments represent the strongest approach to developing knowledge, alternative methods (modeling, critical assessment of observations, and inference) are accepted approaches to understanding features of biology. In this assessment, the strength of evidence for particular ideas is noted, and alternative explanations are described when appropriate.

Because of a lack of experimental research efforts concerning Machaeranthera coloradoensis, this assessment report relies heavily on the personal observations of botanists and land management specialists from throughout the species' range. Much of the knowledge about the biology and ecology of M. coloradoensis is based on the observations of USFS botanists (Gay Austin, Dean Erhard, Wendy Haas, Barry Johnston, Benjamin Madsen, John Proctor), Natural Heritage Program botanists (Walter Fertig, Bonnie Heidel, Susan Spackman Panjabi), herbarium botanists (Dr. Ronald L. Hartman, E. Nelson), and other botanists referenced in element occurrence records and herbarium records (Fertig 1984, Johnston 2001, G. Austin personal communication 2002, D. Erhard personal communication 2003, B. Johnston personal communication 2002, J. Proctor personal communication 2003, W. Fertig personal communication 2003, W. Haas personal communication 2003, R. Hartman personal communication 2003, B. Heidel personal communication 2003, Morgan and Hartman 2004). When information presented in this assessment is based on our personal communications with a specialist, we cite those sources as "personal communication". Unpublished data (e.g., NHP element occurrence records and herbarium records) were also important in estimating the geographic distribution and in describing habitats of this species. These data required special attention because of the diversity of persons and methods used to collect the data, and unverified historical information.

We also incorporated information, where available, from other *Machaeranthera* species endemic to USFS Region 2 or adjacent states to formulate this assessment. However, not only is there

is a paucity of knowledge specific to *M. coloradoensis*, but there is little published information available on the reproductive biology and ecology of other Machaeranthera species. The reproductive biology (e.g., hybridization) of other Machaeranthera species has been the subject of preliminary investigative study (e.g., Hartman 1976, Stucky 1978). Most other studies focus on taxonomic relationships rather than ecology, with a few exceptions (e.g., Anderson and Szarek 1981, Parker and Root 1981). Any comparisons are not meant to imply that *M. coloradoensis* is biologically identical to these other species, but they represent an effort to hypothesize about potential characteristics of this species. We avoided extrapolating from studies of unrelated Machaeranthera species or Machaeranthera of drastically different environmental species contexts. As a result of limited research specific to M. coloradoensis, the biology, ecology, conservation, and management issues presented for this species in USFS Region 2 are based on inference from these published and unpublished sources. We clearly noted when we were making inferences based on the available knowledge to augment or enhance our understanding of M. coloradoensis.

Publication of Assessment on the World Wide Web

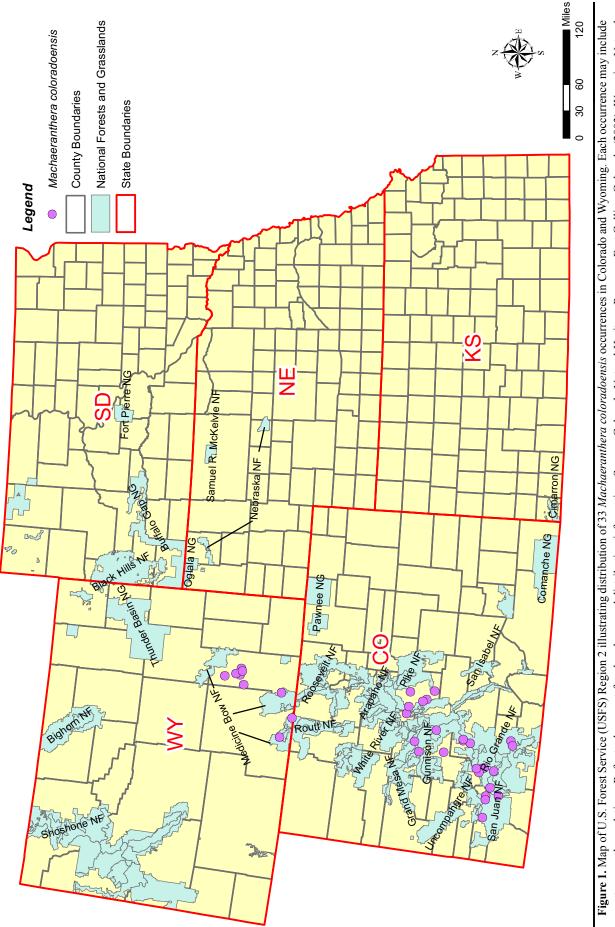
To facilitate use of species assessments in the Species Conservation Project, they will be published on the USFS Region 2 World Wide Web site. Placing documents on the Web makes them available to agency biologists and the public more rapidly than publishing them as reports. More importantly, it facilitates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

Peer Review

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

MANAGEMENT STATUS AND NATURAL HISTORY

Machaeranthera coloradoensis is a regional endemic species found within two states of USFS Region 2 (Figure 1). This section discusses the





management status, existing regulatory mechanisms, and biological characteristics of this species.

Management and Conservation Status

Federal status

The Endangered Species Act of 1973 was passed to protect plant and animal species placed on

the threatened or endangered species list. The listing process is based on population data (e.g., trends) and is maintained and enforced by the U.S. Fish and Wildlife Service. *Machaeranthera coloradoensis* is not currently listed under the Endangered Species Act, nor has it ever been considered for listing (**Table 1**; Spackman et al. 1997).

Table 1. Conservation and management status of *Machaeranthera coloradoensis* as ranked by the U.S. Fish and Wildlife Service, U.S. Forest Service, U.S. Bureau of Land Management, NatureServe, and Natural Heritage Programs in USFS Region 2 states.

Listing	Status
U.S. Fish and Wildlife Service Endangered Species Act	Not listed
U.S. Forest Service Region 2 Sensitive Species List ¹	Sensitive
U.S. Bureau of Land Management	Not listed
NatureServe Global Ranking ²	Imperiled (G2)
U.S. Forest Service Region 2 St	tate Natural Heritage Programs
Wyoming Natural Heritage Program	Critically imperiled (S1)
Colorado Natural Heritage Program	Imperiled (S2)
Kansas, Nebraska, South Dakota Natural Heritage Programs	Not listed; not known in states

¹As designated by a USFS Regional Forester; population viability is a concern due to downward trends in population numbers, density, or habitat capability.

²Key to rankings: G = Global rank based on rangewide status, S = State rank based on status of a species in an individual state.

- G1 <u>Critically imperiled</u> globally because of extreme rarity (five or fewer occurrences or very few remaining individuals) or because of some factor making it especially vulnerable to extinction.
- G2 Imperiled globally because of rarity (six to 20 occurrences) or because of factors demonstrably making a species vulnerable to extinction.
- G3 <u>Vulnerable</u> throughout its range or found locally in a restricted range (21 to 100 occurrences) or because of other factors making it vulnerable to extinction.
- G4 <u>Apparently secure</u>, though it may be quite rare in parts of its range, especially at the periphery.
- G5 <u>Demonstrably secure</u>, though it may be quite rare in parts of its range, especially at the periphery.
- S1 <u>Critically imperiled</u> in the state because of extreme rarity (five or fewer occurrences or very few remaining individuals) or because of some factor making it especially vulnerable to extinction.
- S2 <u>Imperiled</u> in the state because of rarity (six to 20 occurrences) or because of factors demonstrably making a species vulnerable to extinction.
- S3 <u>Vulnerable</u> throughout its statewide range or found locally in a restricted statewide range (21 to 100 occurrences) or because of other factors making it vulnerable to extinction.
- S4 Apparently secure, though it may be quite rare in parts of its statewide range, especially at the periphery.
- S5 <u>Demonstrably secure</u>, though it may be quite rare in parts of its range, especially at the periphery.

Machaeranthera coloradoensis is currently designated a sensitive species by USFS Region 2 (**Table 1**; U.S. Forest Service 2003). This tansyaster is not currently listed as a sensitive species by Bureau of Land Management in Colorado or Wyoming (**Table 1**; Bureau of Land Management 2000, 2001).

Heritage program ranks

Natural Heritage Programs store information about the biological diversity of their respective states and maintain databases of plant species of concern. These lists are not associated with specific legal constraints, such as limits to plant harvesting or damage to habitats supporting these plants. Machaeranthera coloradoensis is currently known from approximately 24 occurrences in Colorado and 9 occurrences in Wyoming (Colorado Natural Heritage Program 2003, Wyoming Natural Diversity Database 2003). The Global Heritage Status Rank for M. coloradoensis is G2, or globally imperiled, as a result of its limited abundance and distribution making it vulnerable to extinction throughout its range (Table 1; NatureServe 2003). Machaeranthera coloradoensis has been ranked by the Colorado NHP as S2, or imperiled (vulnerable to extirpation; endangered or threatened in the state) and by Wyoming Natural Diversity Database (WYNDD) as S1, or critically imperiled (vulnerable to extirpation in state; critically endangered in state) (Table 1; Colorado Natural Heritage Program 2003, Wyoming Natural Diversity Database 2003). Experts in the taxonomy of the Machaeranthera genus no longer recognize the two varieties of Machaeranthera coloradoensis (var. brandegeei and var. coloradoensis) as distinct (R. Hartman personal communication 2003). The global rank for each of the varieties was G2T2?, or critically imperiled with uncertainty (NatureServe 2003).

In Wyoming, plant species of special concern are also prioritized by WYNDD for conservation attention within the state on a three-part scale of priority (low, medium, and high), based on global rankings. *Machaeranthera coloradoensis* is ranked as a high priority for conservation attention in the state of Wyoming. A high priority species is primarily a state and/or regional endemic that is ranked G1 or G2, or that is an inadequately protected and highly threatened G3 species (Fertig and Heidel 2002).

Machaeranthera coloradoensis is not known to occur in the other three states of USFS Region 2 (i.e., Kansas, Nebraska, or South Dakota), and it is unlikely to be found there due to lack of suitable habitat. Therefore, this species is not currently listed or ranked

in those states (Kansas Natural Heritage Inventory 2000, Nebraska Natural Heritage Program 2001, C. Freeman personal communication 2002, R. Schneider personal communication 2002, South Dakota Natural Heritage Program 2002).

Existing Regulatory Mechanisms, Management Plans, and Conservation Practices

Known populations of Machaeranthera coloradoensis occur in a variety of land ownership and management contexts in Colorado and Wyoming. Of the 33 occurrences of M. coloradoensis throughout its range in USFS Region 2, 19 occurrences are on USFS lands in Colorado, five occurrences are on non-USFS lands in Colorado (i.e., private, Colorado BLM, or State of Colorado lands), two occurrences are on USFS lands in Wyoming, and seven occurrences are on non-USFS lands in Wyoming (i.e. Wyoming BLM, or State of Wyoming lands) (Figure 1, Table 2; Colorado Natural Heritage Program 2003, Wyoming Natural Diversity Database 2003). Of the 19 occurrences of M. coloradoensis on USFS lands in Colorado, five are within the San Juan National Forest, five are within the Rio Grande National Forest, six are in the Grand Mesa, Uncompanyer, and Gunnison National Forest, two are within the Pike-San Isabel National Forest, and one occurrence is in the White River National Forest. Within the San Juan National Forest, one population may occur within the Weminuche Wilderness Area, but there is some uncertainty concerning the precise location of this population (University of Colorado Herbarium 2003). In the White River National Forest, the one known occurrence is within a recently designated Special Interest Area (SIA) created to protect botanical resources, including populations of M. coloradoensis (U.S. Forest Service 2002, K. Giezentanner personal communication 2003). Within Wyoming, the two occurrences on USFS lands occur within the Medicine Bow National Forest (Table 2).

Although *Machaeranthera coloradoensis* has been identified as a species of special concern, there are few existing regulatory mechanisms at the federal or state level to regulate its conservation. *Machaeranthera coloradoensis* is not designated as a threatened or endangered species by USFWS and does not receive legal protection from the ESA. This species is currently designated as a USFS Region 2 sensitive species, and as such the USFS is directed to develop and implement management practices to ensure that it does not become threatened or endangered (U.S. Forest Service 1995).

Table 2. Information on 33 *Machaeranthera coloradoensis* occurrences in U.S. Forest Service Region 2. Includes state, county, occurrence identifier, date of recorded observations, estimated abundance and area, and land management context. ? - indicates uncertainty. Sources: Colorado Natural Heritage Program (2003); Rocky Mountain Herbarium (2003); University of Colorado Herbarium (2003), Wyoming Natural Diversity Database (2003).

		NHP Occurrence	Date of Recorded	Estimated	Estimated Area	Management Area/
State	County	Identifier	Observation	Abundance	(acres)	Ownership
Colorado (24 occurrences)	Dolores	Not included in NHP records	1995	Not Available (NA)	Not Available (NA)	San Juan National Forest
	Gunnison	005	1950	NA	NA	Grand Mesa, Uncompahgre, and Gunnison National Fores
		Not included in NHP records	1997	NA	NA	Grand Mesa, Uncompahgre, and Gunnison National Fores
		Not included in NHP records	1999	NA	NA	Unknown (Private or state lands)
	Hindsdale	014	1938	"common"	NA	Rio Grande National Forest
		015	1975, 1995	500+; possibly up to 1000	5 or less	Rio Grande National Forest
		016	1946	NA	NA	Rio Grande National Forest
		020	1998	500+	25	Grand Mesa, Uncompahgre, and Gunnison National Fores
	La Plata	008	1982	NA	NA	San Juan National Forest - Weminuche Wilderness?
	Lake	003	1985	NA	NA	Pike-San Isabel National Forest
	Park	009	1993, 2000	258; possibly up to 500	NA	Non-USFS lands
		010	1985, 1986	"rare or infrequent"	NA	Non-USFS lands
		021	2000	1000 +	NA	Non-USFS lands
		022	2000	1500 +	NA	Non-USFS lands
		023	2000	20	NA	Pike-San Isabel National Forest
	Pitkin/Gunnison	002	1984, 1998	100; 2 sub- populations	NA	White River National Forest
	Rio Grande	018	1997	700+	2	Rio Grande National Forest
		019	1997	1500+; 9 sub- populations	5	Rio Grande National Forest
	Saguache	012	1950	NA	NA	Grand Mesa, Uncompahgre, and Gunnison National Fores
		017	1955, 1999	100-200	3	Grand Mesa, Uncompahgre, and Gunnison National Fores
		024	2000	NA	NA	Grand Mesa, Uncompahgre, and Gunnison National Fores
	San Juan	001	1934	"frequent"	NA	San Juan National Forest
		006	1982	NA	NA	San Juan National Forest
		007	1972	NA	NA	San Juan National Forest

		NHP	Date of	Fatim at a d	Estimated	Manager
State	County	Occurrence Identifier	Recorded Observation	Estimated Abundance	Area (acres)	Management Area/ Ownership
Wyoming (9 occurrences)	Carbon	001	NA	No individuals found; occurrence has not been verified	NA	Medicine Bow National Forest
		002	1957, 1997	80; "locally common"; "frequent"; "scarce"	1-4	Medicine Bow National Forest
	Albany	003	1953, 1999	11; 3; "very small"; "common"	2	State of Wyoming
		004	1997	several hundred	NA	State of Wyoming
		005	1998	NA	NA	State of Wyoming
		006	1999	NA	NA	State of Wyoming
		007	1999	NA	NA	Wyoming Bureau of Land Management (BLM; Rawlins Field Office)
		008	1999	NA	NA	Wyoming BLM (Rawlins Field Office)
		009	1999	NA	NA	Wyoming BLM (Rawlins Field Office)

Table 2 (concluded).

For example, The National Environmental Policy Act requires an environmental impact assessment of impacts from a proposed federal project to the environment (U.S. Congress 1982), and USFS policies require Biological Evaluations to determine the impacts of USFS projects to sensitive species (U.S. Forest Service 1995). Machaeranthera coloradoensis was one of 12 species evaluated by the White River National Forest in Habitat Relationships and Management Direction Reports to ensure that the USFS is maintaining or enhancing the species' viability (B. Heidel personal communication 2003). Populations of M. coloradoensis within the recently established SIA near Taylor Pass in the White River National Forest will benefit from management designed to help protect botanical resources (U.S. Forest Service 2002, K. Giezentanner personal communication 2003). A detailed management plan for the area has not yet been created by the ranger district, but it will likely include prohibition of motorized or mechanized vehicles and livestock grazing (K. Giezentanner personal communication 2003).

In addition, the USFS prohibits the collection of any sensitive plants without a permit (U.S. Forest Service 1995). U.S. Forest Service travel management plans protect some rare species by restricting vehicle use to established roads only (U.S. Forest Service/U.S. Bureau of Land Management 2000, U.S. Forest Service 2002), and wilderness areas also have restrictions on motorized travel (Office of the Secretary of the Interior 1964). Occurrences of this species on private land are not protected, especially as landowners may not even know if the species occurs on their property.

Three examples provide evidence of measures taken by USFS staff to protect populations of Machaeranthera coloradoensis on USFS lands, even where there are no management plans aimed specifically at protecting populations of this species. Dean Erhard, ecologist with the Rio Grande National Forest, has developed biological evaluations of proposed trail projects leading to designs that minimize impact on existing M. coloradoensis populations (D. Erhard personal communication 2003). In addition, he suggested lining a footpath and tourist trailhead area near existing M. coloradoensis populations with landscape logs in order to encourage hikers to stay on the trail. Wendy Haas, rangeland management specialist with the Medicine Bow National Forest, considers the presence of *M. coloradoensis* populations when

annually reviewing the condition of grazing allotments. She personally inspects grazing use levels in the area and any possible impacts of grazing to *M. coloradoensis* individuals (W. Haas personal communication 2003). There are also plans to put large boulders in a road pullout in order to protect *M. coloradoensis* individuals from roadside parking and trampling (W. Haas personal communication 2002). Gay Austin, botanist with Grand Mesa, Uncompahgre, and Gunnison National Forest, will be establishing an exclosure in a grazing allotment with populations of *M. coloradoensis* (G. Austin personal communication 2003). There is no funding to monitor this species, but she hopes students from the local Mesa State College may be able to help document the effects of the exclosure on this species.

Although *Machaeranthera coloradoensis* has been identified as a species of special concern, the full abundance and distribution of this species is largely unknown and specific populations may possibly be threatened by human-related or environmental/ biological threats. The establishment of a Special Interest Area and efforts taken by USFS staff are positive steps to help conserve this species over the long term.

Biology and Ecology

Classification and description

Systematics and synonymy

Machaeranthera coloradoensis (Gray) Osterhout is a member of the Blepharodon section of the Machaeranthera genus within the Asteraceae (Compositae, aster) family of flowering plants (Anthophyta) (Hartman 1976, Morgan and Simpson 1992, Integrated Taxonomic Information System 2003, NatureServe 2003). There are 36 species of Machaeranthera, ranging from western United States to adjacent Canada and Mexico (Hartman 1976, Hartman 1990, Morgan and Simpson 1992). However, the taxonomic placement of M. coloradoensis, the composition of species within the genus Machaeranthera, and the relationships of this genus with other closely related genera have been the subject of debate for many years (Rydberg 1905, Osterhout 1927, Cronquist and Keck 1957, Hartman 1976, Watson 1977, Hartman 1990, Morgan and Simpson 1992, Morgan and Hartman 2004). Major changes to the Machaeranthera genus, including a reclassification of M. coloradoensis to Xanthisma coloradoense, are proposed in the newest work by Morgan and Hartman (2004).

Machaeranthera coloradoensis was first identified and described as Aster coloradoensis by Asa Gray (1876) from specimens collected near "San Juan Pass", Colorado. This pass may be the location called Spring Creek Pass (Johnston 2001) or Weminuche Pass (based on historical research by W. Jennings). Per Axel Rydberg (1905) reclassified Aster coloradoensis as part of an older genus (Xylorrhiza) and separated the specimens into two distinct species: Xylorrhiza coloradoensis and Xylorrhiza brandegeei. George Osterhout (1927) placed Xylorrhiza coloradoensis into the genus Machaeranthera, and this move was supported by Cronquist and Keck (1957). The Machaeranthera genus was re-configured in the 1970s to include similar species from the Haplopappus and Aster genera (Hartman 1976). Hartman (1990) and Morgan and Simpson (1992) used chemical and chromosomal analyses to further resolve systematics of the Machaeranthera genus. In addition, Hartman (1976, 1990) presented a morphological key to distinguish between the two varieties of M. coloradoensis var. coloradoensis (Gray) Osterhout and var. brandegeei (Rydberg) T.J. Watson ex R.L. Hartman. Although two distinct varieties of this species were recognized by Hartman (1976), the identification of the two varieties in the field was found to be difficult (Spackman et al. 1997, Johnston 2001). Johnston (2001, 2002) presented a tabular summary of morphological characters used to distinguish between the two varieties.

Although this species assessment treats this species as Machaeranthera coloradoensis as presented in the PLANTS database (USDA/Natural Resources Conservation Service [NRCS] 2002), ITIS database (ITIS 2003), and NatureServe database (NatureServe 2003), current taxonomic work by experts of the genus propose a new classification of this species to Xanthisma coloradoense. The most recent work by Morgan and Hartman (2004) will propose a significantly revised classification of Machaeranthera as a result of molecular, morphological, cytological, and chemical evidence. This newest treatment of Machaeranthera, among other changes, will result in the reclassification of several species into other genera. Under this proposed classification, M. coloradoensis and the other Machaeranthera species in section Blepharodon will be incorporated into the genus Xanthisma. In addition, the morphological differences between two distinct varieties of M. coloradoensis are no longer supported as a result of the discovery of new populations in recent years (R. Hartman personal communication 2003). Thus, the new classification of M. coloradoensis will be Xanthisma coloradoense (A. Gray) D.R. Morgan & R.L. Hartman, comb.nov., and no varieties will be recognized.

History of species

As described above, the taxonomic history related to the composition of the genus *Machaeranthera* and nomenclature of *Machaeranthera coloradoensis* has been complex, and Morgan and Simpson (1992) provide a historical synopsis. Morgan and Hartman (2004) present the most recent taxonomic treatment of *M. coloradoensis*. *Machaeranthera coloradoensis* populations in the White River National Forest were the subject of a status report in 2001 (Johnston 2001) and a Biological Evaluation in 2002 (U.S. Forest Service 2002) as a result of management plan revisions.

The type specimen of *Machaeranthera* coloradoensis is housed at the Gray Herbarium (Cambridge, MA). Additional *M. coloradoensis* specimens are housed at the Rocky Mountain Herbarium (Laramie, WY), University of Colorado Herbarium (Boulder, CO), Kathryn Kalmbach Herbarium (Denver, CO), Colorado State University Herbarium (Fort Collins, CO), and New York Botanical Garden Herbarium (New York, NY).

The common name for this species is Colorado tansyaster, Colorado tansy-aster, or Brandegee tansyaster, and synonyms include *Aster coloradoensis*, *Haplopappus coloradoensis*, *Xylorrhiza coloradoensis*, and *Xanthisma coloradoense* (Johnston 2001, Morgan and Hartman 2004).

Morphological characteristics

Members of the family Asteraceae are characterized by a head (capitulum inflorescence) with many tiny florets crowded onto the receptacle. In many cases, the inflorescence is a radiate head comprised of both "ray" florets (with strap-like corolla) arranged on the head margin and "disc" florets (with tubular corolla) in the center of the head. In addition, the heads are subtended by numerous phyllaries that protect the bud or close over the flower in cold weather (Zomlefer 1994).

The section *Blepharodon* of the genus *Machaeranthera* (proposed as genus *Xanthisma* in Morgan and Hartman 2004) includes perennial species with a taproot, entire or shallowly-toothed leaves with prominent spines, and pubescent obovate achenes (hairy, egg-shaped, one-seeded fruits) (Hartman 1976, 1990). *Machaeranthera coloradoensis* appears to be the most morphologically divergent member of the section *Blepharodon*. With solitary heads on short, hairy stems, this species may typify adaptations to subalpine or alpine environments (Hartman 1976).

Machaeranthera coloradoensis is a taprooted perennial herb with large, solitary, radiate heads on short stalks (Figure 2). The ray florets number from 20 to 35; are pink, rose, or purple in color; range from 9.3 to 15 millimeters (mm) long and 2.2 to 4.3 mm wide; and surround 50 to 150 yellow disc florets. The involucre bracts beneath the head have sharp tips and grow in two to three overlapping rows. The villous (hairy) achenes are 1.7 to 2.7 mm long, narrowly obovate to oblong, with a pappus 3.5 to 6.0 mm long comprised of 45 to 70 bristles. This tansyaster has gravish-white, pubescent, unbranching stems from 1 to 14 centimeters (cm) tall. The erect or ascending stems arise from a branching caudex (swollen base of stem). The leaves are spoonshaped to linear, coarsely-toothed with white bristles to 2 mm long, and densely hairy. The leaves range from 0.8 to 5 cm long and are mostly basal, or crowded in the lower third of the stem. This species is a low-growing, tufted, cushion plant (Hartman 1976, Fertig et al. 1994, Spackman et al. 1997).

Previous to the most recent taxonomic work by Morgan and Hartman (2004), two varieties of Machaeranthera coloradoensis (var. coloradoensis and var. brandegeei) were recognized by some authors (e.g., Hartman 1976). Using line drawings, photographs, and range maps, Hartman (1976) outlined differences between the two varieties of M. coloradoensis. In general, M. coloradoensis var. brandegeei was characterized by longer, broader leaves, and larger heads than var. coloradoensis (Hartman 1976). However, distinction between the two varieties in the field was difficult because one population could have individuals with a range of sizes (Johnston personal communication 2002). In addition, R. Hartman (personal communication 2003) clarified that the morphological differences and geographical separation between the two varieties of M. coloradoensis are no longer supported as a result of the discovery of new populations in recent years. Thus, no varieties are recognized in the newest treatment of M. coloradoensis (Xanthisma coloradoensis) by Morgan and Hartman (2004).

Machaeranthera coloradoensis can be distinguished from other closely related species by its deep, purple flowers, short stems, and toothed leaves (Spackman et al. 1997). A related species, *M. tanacetifolia*, has once or twice pinnately lobed leaves and taller, leafier stems than *M. coloradoensis* (Fertig and Heidel 2002). *Machaeranthera coloradoensis* is the only cushion-forming *Machaeranthera* (Colorado Natural Heritage Program 2003). The plants of a similar genus, *Townsendia*, have leaves with smooth margins. *Bolophyta* species tend to be stemless and have extremely (A)



Photograph by William Jennings. Reprinted with permission of the photographer.

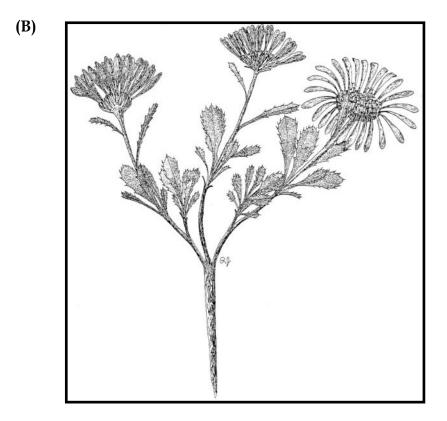


Illustration by Robin Jones. Reprinted with permission from: Fertig, W., C. Refsdal, and J. Whipple. 1994. Wyoming Rare Plant Field Guide. Wyoming Rare Plant Technical Committee, Cheyenne, WY.

Figure 2. *Machaeranthera coloradoensis* photograph in its natural habitat (A), and illustration of the vegetative and reproductive structures (B).

short-rayed heads (Weber and Wittmann 2001). Similar *Aster* species tend to lack a taproot and spiny-toothed leaves, and *Xylorrhiza* species have a massive taproot with extra periderm (bark) (Hartman 1990).

Technical descriptions of *Machaeranthera* coloradoensis (Xanthisma coloradoense) are presented in Morgan and Hartman (2004). Line drawings and photos are available in the Colorado Rare Plant Field Guide (Spackman et al. 1997) and Wyoming Rare Plant Field Guide (Fertig et al. 1994).

Distribution and abundance

Records of Machaeranthera coloradoensis population locations are based on the results of field surveys in some areas of its range and on historical records (i.e., herbarium specimens). Herbarium specimens often lack specific location descriptions and generally do not report counts of individuals. We have presented a distribution map and a table summarizing element occurrence records and herbarium records for this species (Figure 1, Table 2; University of Colorado Herbarium 2003, Colorado Natural Heritage Program 2003, Rocky Mountain Herbarium 2003, Wyoming Natural Diversity Database 2003). Each of the 33 occurrences of M. coloradoensis may include several populations. An element occurrence is defined as any naturally occurring population that is separated by at least 1 mile of unsuitable habitat or 2 miles of suitable habitat (Colorado Natural Heritage Program 2003). Based on the available information from element occurrence records, status reports, and mapping exercises, we hypothesized if these locations may possibly occur within National Forest System boundaries. Hypothesized land ownership is also presented on Table 2.

Regional distribution

Machaeranthera coloradoensis is known only from two western U.S. states, Colorado and Wyoming (**Figure 1**, **Table 2**; U.S. Department of Agriculture, Natural Resources Conservation Service 2001). Within USFS Region 2, this species has not been identified in Kansas, Nebraska, or South Dakota (Kansas Natural Heritage Inventory 2000, Nebraska Natural Heritage Program 2001, South Dakota Natural Heritage Program 2002), and it is unlikely to be found there due to lack of suitable habitat. **Figure 1** illustrates the distribution of *M. coloradoensis* based on reviewed literature, state NHP records, and herbarium specimens (Johnston 2001, Johnston 2002, University of Colorado Herbarium 2003, Colorado Natural Heritage Program 2003, Colorado State University Herbarium 2003, Wyoming Natural Diversity Database 2003). Because of its small distribution, *M. coloradoensis* is considered by the WYNDD to be a "regional endemic" (Fertig and Heidel 2002). The WYNDD defines a regional endemic species as a taxon with a global range restricted to a portion of Wyoming and one to two adjacent states. The entire range of the taxon is less than the total area of the state of Wyoming (Fertig and Heidel 2002).

addition, the known distribution In of Machaeranthera coloradoensis within its range appears to be clumped, with geographic isolation between Wyoming and Colorado populations and also among Colorado populations (Figure 1; Johnston 2001). This discontinuous distribution pattern could be the result of inadequate inventory, or it could be related to ecological differences among populations of this species. For instance, it is unknown to what extent botanists have searched for M. coloradoensis in areas between the known populations in southern Wyoming and the known populations in central Colorado. As will be discussed in subsequent sections, the habitats of M. coloradoensis range from alpine environments to lower elevation montane areas, and possible local adaptations to these different habitat types could help explain population clusters. As discussed previously, two varieties have historically been described for M. coloradoensis, and several researchers have suggested that habitat differences are possibly correlated with the ecological preferences of the two varieties (Fertig et al. 1994, Johnston 2001, Johnston 2002). However, recent taxonomic work indicates that the distinction of two varieties may not be warranted (R. Hartman personal communication 2003, Morgan and Hartman 2004).

Colorado distribution and abundance

In Colorado, *Machaeranthera coloradoensis* occurs in the central, west-central, and southwestern portions of the state. Specifically, Colorado NHP records (2003) indicate that this species has been recorded from 21 occurrences in Gunnison, Hinsdale, La Plata, Lake, Park, Pitkin, Rio Grande, Saguache, and San Juan counties (**Table 2**). There are also three herbarium specimens of this species collected from Dolores and Gunnison counties in 1998 and 1999 that are not included in the Colorado NHP records (University of Colorado Herbarium 2003, Rocky Mountain Herbarium 2003).

Of the 24 occurrences of *Machaeranthera coloradoensis* in Colorado, six occurrences are with the Grand Mesa, Uncompahgre, and Gunnison National Forest, five are within the San Juan National Forest, five are within the Rio Grande National Forest, two are within the Pike-San Isabel National Forest, and one is within the White River National Forest. In the San Juan National Forest, one population may occur within the Weminuche Wilderness Area, but there is some uncertainty concerning the precise location of this population (<u>Table 2</u>; University of Colorado Herbarium 2003). In the White River National Forest, one population occurs within the proposed Taylor Pass Special Interest Area. Five Colorado occurrences are not on National Forest System Lands and may occur on private land, state lands, or BLM lands.

The estimated abundance of Machaeranthera coloradoensis in Colorado ranges from 20 individuals to several hundred individuals to more than 1,500 individuals at different locations (Table 2; Johnston 2001, Colorado Natural Heritage Program 2003). It is difficult to ascertain total abundance or population trends from the occurrence records or herbarium specimens because (1) some researchers estimated population size (based on potential habitat) while others provided more conservative census information; and (2) some researchers neglected to present abundance data or only counted a small subset of the population. For example, observations of this species in Cochetopa Park in Gunnison County ranged from 2 to 35 individuals, but there were many uncounted individuals adjacent to these sightings (G. Austin personal communication 2002). Johnston (2002) noted that seven populations have been censused, ranging in population size from 100 to 1,500 individuals with an average of 550 individuals per population.

The total habitat occupied by *Machaeranthera coloradoensis* is also difficult to assess. Only five of the 24 Colorado occurrences include an estimate of occupied habitat. Based on that data, *M. coloradoensis* is known to occupy at least 40 acres.

Natural Heritage Programs assign element occurrence ranks to each occurrence in order to estimate long-term viability of each population. Based on element occurrence ranks, the occurrences of *Machaeranthera coloradoensis* ranged from good quality sites with 500 or more individuals (A rank) to less optimal or degraded sites with fewer (20 to 500) individuals (C rank) (Colorado Natural Heritage Program 2003). There is one A-ranked occurrence, eight B-ranked occurrences, and four C-ranked occurrences. In six cases there was insufficient information to assign a rank (E-rank), and five of the populations have not been visited in the last twenty years (H-rank).

Wyoming distribution and abundance

Within Wyoming, *Machaeranthera coloradoensis* is known from nine occurrences in Albany and Carbon counties (eastern foothills of Sierra Madre, foothills of Medicine Bow Range, northern Laramie Basin) (Welp et al. 2000, Wyoming Natural Diversity Database 2003). The occurrence of this species from Bridger Peak (occurrence #001 from Carbon County) has not been relocated or confirmed despite several searches by local experts, and it is probably incorrect (**Table 2**; Fertig 2000, Wyoming Natural Diversity Database 2003, W. Haas personal communication 2003).

Of the eight extant occurrences of *Machaeranthera* coloradoensis in Wyoming, one is on National Forest System lands, three are on Wyoming BLM lands, and four are on State of Wyoming lands (**Figure 1**, **Table 2**; Wyoming Natural Diversity Database 2003). The two occurrences (one extant and one unconfirmed) on USFS lands in Wyoming occur within the Medicine Bow National Forest (**Table 2**).

Several of the WYNDD (2003) occurrence records suggest that additional suitable habitat may exist adjacent to observed locations. For example, suitable habitat for this species exists in the Sheep Mountain Wildlife Refuge of the Medicine Bow National Forest, but occurrence of this species there has not been confirmed (Welp et al. 2000). The total habitat occupied by *Machaeranthera coloradoensis* is also difficult to assess. Only two of the nine Wyoming occurrences include an estimate of occupied habitat. Based on data for these two occurrences, *M. coloradoensis* is known to occupy at least six acres.

Machaeranthera coloradoensis populations in Wyoming range from very small to small in abundance. The most recent abundance information for three populations included 11 plants, about 80 plants, and several hundred plants (<u>Table 2</u>; Wyoming Natural Diversity Database 2003). Based on element occurrence ranks, the nine occurrences of *M. coloradoensis* include one B-ranked site, one C-ranked site, and seven sites with inadequate information for ranking (E-rank) (<u>Table 2</u>; Wyoming Natural Diversity Database 2003).

Population trends

There are no data on population trends for *Machaeranthera coloradoensis*. Although several populations have been counted, multi-year population or quantitative demographic monitoring has not been initiated for any occurrences of this species. State NHPs

keep occurrence records for this species, which often include repeated observations of individual populations but lack detailed demographic or abundance information. For example, a Wyoming population of M. coloradoensis has been observed intermittently from 1957 to 1979. In a series of observations of one population (Carbon County, WY) by a variety of observers, the population size ranged from "scarce" in 1957, to "common" in 1977, to "frequent" in 1979 (Wyoming Natural Diversity Database 2003). However, these reports may reflect inventory effort rather than actual population trends. Barry Johnston, ecologist with the Grand Mesa Uncompanyre Gunnison National Forest and author of status reports for this species, has not observed any noticeable, drastic declines in this species based on his personal observations during repeat visits (Johnston 2001, Johnston 2002, B. Johnston personal communication 2002).

Additional populations of *Machaeranthera coloradoensis* have been located in recent years, and several forest botanists believe that extensive surveys would discover more populations (G. Austin personal communication 2002, W. Haas personal communication 2002, Johnston 2002, J. Proctor personal communication 2002). Since 1997, 15 new locations have been discovered (Colorado Natural Heritage Program 2003, Rocky Mountain Herbarium 2003, Wyoming Natural Diversity Database 2003). Johnston (2002) estimated that potentially up to 90 populations of this species may be found, with up to 60,000 individuals.

Habitat characteristics

Machaeranthera coloradoensis is generally found in sparsely vegetated areas on rocky, exposed soils of sedimentary or volcanic origin (Hartman 1976, Johnston 2002, Colorado Natural Heritage Program 2003, Wyoming Natural Diversity Database 2003).

Colorado habitat

In Colorado, *Machaeranthera coloradoensis* is found from montane to alpine environments from 2,340 to 3,945 meters (m) (7,675 to 12,940 feet [ft]) in elevation (Hartman 1976, Johnston 2001, University of Colorado Herbarium 2003, Colorado Natural Heritage Program 2003, Rocky Mountain Herbarium 2003). Habitat descriptions for each of the *M. coloradoensis* occurrences summarized from Colorado NHP element occurrence records and herbarium records, including elevation, microhabitat, associated plant species, landscape context, substrate, slope, and aspect, are presented in **Table 3**.

Machaeranthera coloradoensis macrohabitats range from plains/park grassland, to dry grassland communities within ponderosa pine (Pinus ponderosa) or bristlecone pine (Pinus aristata) areas, to pinyon/ juniper (Pinus/Juniperus) woodlands, to alpine fellfields and meadows (Chumley 1998, Johnston 2001, G. Austin personal communication 2002, University of Colorado Herbarium 2003, Colorado Natural Heritage Program 2003, Rocky Mountain Herbarium 2003). Within these areas, this species grows on slopes, bluffs, ridges, flats, or roadsides on sedimentary and calcareous substrates (e.g., limestone, dolomite, shale), volcanic substrates (e.g., volcanic ash), or granitic substrates (Table 3; Hartman 1976, Johnston 2001, Colorado Natural Heritage Program 2003, Rocky Mountain Herbarium 2003). This species is consistently found in areas with open exposure, but the slope, aspect, and moisture vary from site to site. Machaeranthera coloradoensis is found from flat areas up to 35 percent slopes, on slopes of all aspects, and in both dry and mesic areas (Table 3).

Based on qualitative estimates by botanists, many occurrences are in open settings with no or scattered trees, up to 5 percent cover by shrubs, 5 to 55 percent cover by grasses, 25 percent cover by forbs, 5 to 70 percent cover by bare ground, 0 to 1 percent cover by mosses/lichen, and 10 to 70 percent cover by gravel (G. Austin personal communication 2002, Colorado Natural Heritage Program 2003). Plant species associated with Machaeranthera coloradoensis include scattered trees (e.g., Pinus spp.), shrubs (e.g., Cercocarpus montanus, Chrysothamnus spp.), forbs (e.g., Astragalus spp., Erigeron spp., Potentilla spp.), graminoids (e.g., Festuca spp., Elymus spp.), and lichens (e.g., Xanthoparmelia spp.) (Table 3; Hartman 1976, Erhard 2001, Johnston 2001, University of Colorado Herbarium 2003, Colorado Natural Heritage Program 2003). Some of these associated species are also rare plants (e.g., Astragalus molybdenus), and many are indicators of limestone-based soils (Johnston 2001).

Wyoming habitat

In Wyoming, *Machaeranthera coloradoensis* is found mainly from foothills to subalpine environments on sparsely-vegetated slopes, rocky outcrops, roadsides, or subalpine meadows (**Table 3**). Reported elevations for this species range from 1,856 m to 2,590 m (6,090 ft to 8,500 ft) (Fertig 2000, Wyoming Natural Diversity Database 2003). The occurrence of this species from 3,292 m (10,800 ft) on Bridger Peak has not been relocated or confirmed despite several searches by local experts, and it is probably incorrect (Fertig 2000,

State	County	NHP Occurrence Identifier	Elevation Range (ft)	General Habitat Description	Associated Plant Species	Slope/Aspect	Substrate
Colorado (24 occurrences)	Dolores	Not included in NHP records	12940	Alpine tundra, talus slopes, meadow, and peak	Not available (NA)	North-facing	Not available (NA)
	Gunnison	Not included in NHP records	7675	NA	NA	NA	NA
		Not included in NHP records	10350-10800	Open forest along ridge top	Picea engelmannii, Juniperus spp.	NA	NA
		005	12080	Fellfield	NA	NA	NA
	Hinsdale	014	9000 -11040	Dry rocky slope; dry grassland, full sun, fine grained soil, among rocks	NA	NA	NA
		015	10040	Gravelly clearing, dry meadow; granitic gravelly soil; 70% bare ground cover; gravelly and sandy soil texture, tree cover 0%, shrub cover <5%, forb cover 25%, graminoid cover 5%, moss/lichen cover <1%, bare ground cover, 70%; dry meadow; <i>Festuca</i> <i>arizonica</i> cover 25%	Artemisia frigida, Eremogone fendleri, Festuca arizonica, Machaeranthera pattersonii, Penstemon caespitosus, Pentaphylloides floribunda, Potentilla pulcherrima	North- or east- facing: 0 to 5% convex slope; crest; open exposure	Granitic mountain slopes
		016	10200	Open grassy summit	NA	NA	NA
		020	10120-10250	<i>Festuca arizonica</i> habitat. Tree cover 0%, shrub cover trace, forb cover 25%, graminoid cover 40%, moss/lichen cover trace, bare ground cover 35%	Achillea lanulosa, Antennaria umbrinella, Bromopsis porteri, Carex obtusata, Chaenactis douglasii, Danthonia parryi, Elymus longifolius, Festuca arizonica, Festuca idahoensis, Koeleria macrantha, Potentilla hippiana, Pseudocymopterus montanus	South-facing; flat slope; lower slope; open exposure; dry	Glacial outwash terrace; fine sandy loam
	La Plata	008	11880	Alpine meadow with limestone outcrops	NA	NA	NA
	Lake	003	12250	Prospect piles	NA	NA	Leadville limestone
	Park	600	9122	On gravelly substrate off highway; plants localized to drainage of road	NA	NA	Gravelly roadside
		010	12000-12600	Cirque at head of creek	NA	NA	Alpine scree slopes in talus
		021		Gravelly outcrop between two forks of a river	Artemisia frigida, Astragalus kentrophyta ssp. implexus, Chrysothamnus nauseosus, Chrysothamnus viscidiflorus, Distichlis spicata spp. stricta, Elymus trachycaulus, Oreocarya thyrsiflora, Picradenia richardsonii	Flat slope; open exposure	Gravelly outcrop

State	County	NHP Occurrence Identifier	Elevation Range (ft)	General Habitat Description	Associated Plant Species	Slope/Aspect	Substrate
	Park	022	9100-9200	In Muhlenbergia filiculmis community	Artemisia frigida, Astragalus kentrophyta spp. implexus, Carex elocharis, Castilleja integra, Chondrosum gracile, Chrysothamnus nauseosus, Eriogonum flavum, Koeleria macrantha, Muhlenbergia filiculmis, Picradenia richardsonii, Xanthoparmelia chlorochroa	Flat slope; mesic; open exposure	Gravelly substrate
		023	9200	On gravelly substrate next to creek	NA	Flat slope; mesic; open exposure	Gravel alluvium
	Pitkin/ Gunnison	002	11960-12580	Sparsely vegetated tundra on ridge; alpine meadow; 50-80% vegetation cover	Achillea spp., Antennaria spp., Artemisia spp., Astragalus spp., Castilleja spp., Draba spp., Eriteron pinnatisectus, Erigeron spp., Eritrichum aretioides, Kobresia spp., Lupinus spp., Mertensia spp., Poa spp., Potentilla spp., Noccaea spp., Physaria spp., Smelowskia spp., Salix spp., Stellaria spp.,	Northeast facing; flat slope	Sandy soils
	Rio Grande	018	11100	Riparian and dry meadow; tree cover 0%, shrub cover 0%, forb cover 25%, graminoid cover 5%, moss/lichen cover 0%, bare ground cover 70%	NA	Southwest- facing; 0 to 35% straight to convex slope; lower slope to midslope; open exposure	Alluvial flood plain; dry, gravelly soil
		019	11800-12240	Dry meadow; tree cover 0%, shrub cover 0%, forb cover 30%, graminoid cover 5%, moss/lichen cover 5%, bare ground cover 60%	NA	Southwest- facing; 0 to 20% straight to convex slope; upper slope; open exposure	Dry, gravelly slope
	Saguache	012	9700-9760	NA	NA	NA	Volcanic ash deposits
		017	9260-9500	Arizona fescue-mountain mahogany-pingue; sagebrush- Arizona fescue communities; tree cover 0%, shrub cover 10%, forb cover 5%, graminoid cover 15%, moss/lichen cover 1%, bare ground cover 5-10%	Artemisia frigida, Artemisia spp., Cercocarpus montanus, Chrysothamnus spp., Elymus elymoides, Festuca arizonica, Geranium caespitosum, Hymenoxys newberryi, Koeleria macrantha	Northeast- to east-facing; 5% concave slope; upper slope to midslope	Volcanic ash; sandy soil; usually dry but can be very wet
		024	9820	Herbaceous dominated upland; tree cover 0%, shrub cover 0%, forb cover unknown, graminoid cover 55%, moss/lichen cover 0%, bare ground cover 15%	Festuca idahoensis, Festuca arizonica, Muhlenbergia filiculmis, Muhlenbergia montana, Poa fendleriana	North-east facing; 8% slope; open exposure	Dry

Table 3 (cont.).

StateCountyNIP OccurrenceElevationStateCountyIdentifierRange (ft)GeSan Juan00112400NA00611400-12160Alpwyoming (9Carbon00712600NAwyoming (9Carbon00110800NAwyoming (9Carbon00110800NAwyoming (9Carbon00110800NAwyoming (9Carbon00110800NAwyoming (9Carbon00110800NAwyoming (9Carbon00110800NAwyoming (9Carbon00110800NAwyoming (9Carbon00110800NAwyoming (9Carbon0037800Baroccurrences)0037800Par005006007170-7278Stoin00600769007170-7278Stoin0080086900-7050Stoin0080086900-7050Stoin008008008008008008008Stoin008008008Stoin007008008Stoin008008008Stoin008008008Stoin0080080080080080080080000080080080000080080080000080086	TADIC J (CONCINUCUJ).					
San Juan 001 12400 006 11400-12160 007 007 12600 Carbon 001 10800 Carbon 001 10800 Albany 003 7800 Albany 003 7800 005 6900 7170-7278 006 005 6900 007 006 7170-7278 008 006 7050 007 6900-7050 008 6850-7000			General Habitat Description	Associated Plant Species	Slope/Aspect	Substrate
006 11400-12160 01 007 12600 01 00800 002 8500 8500 7800 7800 01 7800		12400	NA	NA	Moderate slope	Rock
007 12600 Carbon 001 10800 002 8500 8500 Albany 003 7800 Albany 003 7800 004 003 7800 005 6900 7170-7278 007 008 6900-7050 008 006 7170-7278 007 6900-7050 6900-7050 008 6850-7000 6850-7000	900	11400-12160	Alpine meadow, growing above timberline on conglomerate boulders; around base of bluff overlooking lake	Arenaria rubellus, Erigeron compositus, Hymenoxys brandegeei, Poa glauca, Silene acaulis, Trifolium spp.	South-facing; 30% slope	Conglomerate boulders
Carbon 001 10800 002 8500 Albany 003 7800 Albany 003 7800 004 7050 6900 005 6900 7170-7278 007 6090-7050 6900-7050 008 008 6850-7000	007	12600	Alpine tundra meadow	NA	NA	NA
002 8500 003 7800 004 7050 005 6900 006 7170-7278 007 6090-7050 008 6850-7000		10800	NA	NA	NA	Quartz
003 7800 004 7050 005 6900 006 7170-7278 007 6090-7050 008 6850-7000	002	8500	Sandstone-limestone outcrops in sandy soil and roadside banks and borrow pits	Arenaria hookeri, Artemisia frigida, Astragalus kentrophyta, Elymus smithii, Erigeron nematophyllus, Eriogonum exilifolium, Lesquerella alpina, Penstemon saxosorum, Senecio canus	NA	NA
7050 6900 7170-7278 6090-7050 6850-7000		7800	Barren cushion plant-scattered shrub community on ridge	Atriplex spp., Chrysothamnus nauseosus, Eriogonum exilifolium, Oenothera cespitosa, Oryzopsis hymenoides, Stanleya pinnata	West-facing; toe of slope	Open white shaley gypsum ridge; soil dry, stony
6900 7170-7278 6090-7050 6850-7000	004	7050	On redbeds associated with calcareous slopes	Aster spp., Senecio spp.	NA	Redbeds; calcareous slopes
7170-7278 6090-7050 6850-7000	005	0069	Partly barren grassland	Lesquerella alpina, Paronychia sessiliflora	NA	NA
6090-7050 6850-7000	900	7170-7278	Stony, calcareous hill with limber pine woodland	Pinus flexilis	Hill	Stony, calcareous hill
6850-7000	007	6090-7050	Stony slopes on redbeds	NA	Slope	Stony slopes on redbeds
	008	6850-7000	Stony knolls and hilltops with mostly cushion plants	NA	Knolls and hilltops	NA
009 6980 Roc sage	600	6980	Rocky, red clay areas in sagebrush-rabbitbush grassland	Artemisia spp., Chrysothamnus spp.	NA	Rocky, red clay areas

Wyoming Natural Diversity Database 2003, W. Haas personal communication 2003). Thus, the elevational range occupied by *M. coloradoensis* in Wyoming is slightly lower and much narrower than the range of elevations occupied by this species in Colorado. The lowest elevation occurrence of *M. coloradoensis* in Colorado is at 2,340 m (7,675 ft), and the highest elevation is at 3,945 m (12,940 ft).

Machaeranthera The macrohabitat of coloradoensis occurrences in Medicine Bow National Forest are characterized by Artemesia tridentata/Chrysothamnus nauseosus/Elymus smithii communities within lodgepole pine/subalpine fir (Pinus contorta/Abies lasiocarpa) forests (Welp et al. 2000). Machaeranthera coloradoensis is found on sparsely-vegetated areas with other cushion-like plants within this context (W. Haas personal communication 2002). Occurrences of this species on non-USFS lands are also found in shrublands, partly barren grasslands, and woodlands.

Machaeranthera coloradoensis often occurs on slopes with exposed substrates such as rocky outcrops, gravelly and stony soils, roadsides, borrow pits, and other barren areas. Substrates include sandstonelimestone outcrops, redbeds, shaley-gypsum, and other calcareous or sedimentary parent material (Fertig 2000, Wyoming Natural Diversity Database 2003). Associated plant species with *M. coloradoensis* include scattered trees (e.g., *Pinus flexilis*), shrubs (e.g., *Chrysothamnus* spp.), forbs (e.g., *Lesquerella alpina*), and graminoids (e.g., *Oryzopsis hymenoides*) (**Table 3**; Fertig 2000, Wyoming Natural Diversity Database 2003).

Reproductive biology and autecology

Details concerning the reproductive biology and breeding system of *Machaeranthera coloradoensis* are largely unknown. In this section, we present information, when available, from other *Machaeranthera* species in an effort to elucidate potential reproductive mechanisms for *M. coloradoensis*. However, not only is there a paucity of knowledge specific to *M. coloradoensis*, but there is little published information available on the reproductive biology and ecology of other *Machaeranthera* species.

Reproduction

Machaeranthera coloradoensis produces an inflorescence with many florets. The inflorescence is a radiate head comprised of both "ray" florets and "disc"

florets. The ray florets are either pistillate or sterile, and the disc florets are staminate or perfect (Zomlefer 1994).

Machaeranthera coloradoensis flowers from the beginning of July until the middle of August, and it sets seed from August through September (Colorado Natural Heritage Program 2003). This tansyaster produces achenes with thick walls, a pubescent exterior, and a pappus 3.5 to 8.0 mm long (Hartman 1976, 1990).

Although many perennial species in alpine habitats reproduce vegetatively and sexually in order to take advantage of the resources and protection from the parent plant (Grime 1979, Zwinger and Willard 1996), there is no information concerning the extent of sexual or vegetative reproduction in *Machaeranthera coloradoensis*. *Machaeranthera* species tend to have several short rhizomes arising from the caudex (Hartman 1990), which may or may not function in vegetative reproduction.

Observations of *Machaeranthera coloradoensis* populations in both Wyoming and Colorado indicate that most populations had a mix of vegetative, flowering, or fruiting individuals (Colorado Natural Heritage Program 2003, Wyoming Natural Diversity Database 2003). The number of individuals in each reproductive stage depended on the date of the observation; the reported percentage of fruiting individuals ranged from 0 to 100 percent at different sites and dates.

There have also been no studies on vital aspects of *Machaeranthera coloradoensis* reproduction, such as breeding system, germination requirements and success, demographic parameters, genetic aspects of reproduction, or which insect species are effective pollinators. The extent to which this species is selfcompatible or requires outcrossing is not known.

Life history and strategy

There have not been any studies on the life history, demography, fecundity, or longevity of *Machaeranthera coloradoensis*. In addition, *M. coloradoensis* is found from foothills to alpine environments, and life history and demographic patterns may vary among habitats. In general, this species is a perennial forb growing close to the ground in dry, sparsely-vegetated, erodible environments. The hypothesized life history of this perennial plant is depicted in **Figure 3**. The rates of growth, survival, recruitment, dispersal, and longevity are unknown. The optimal habitat conditions or successional stage for *M. coloradoensis* or other issues

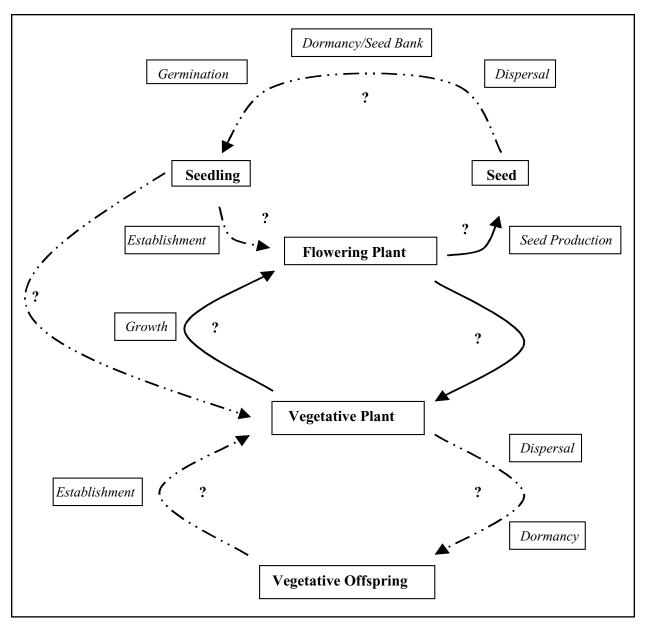


Figure 3. Schematic representation of the hypothesized life cycle of *Machaeranthera coloradoensis*. Dotted lines indicate juvenile phases of the life cycle and solid lines indicate mature phases of the life cycle. Extent of sexual and vegetative reproduction is unknown for this species. Rates of growth, dispersal, and seed production are also unknown (indicated by "?"). Figure adapted from Grime (1979).

related to competitive abilities and ecological tolerances have not been studied.

The competitive relationships, ecological limitations, and reproductive biology of *Machaeranthera coloradoensis* are really not adequately known to assess the life history and strategy of this species based on vegetation strategies described by Grime (1979). Stress-tolerant, or s-selected, species have a perennial life history, an ability to withstand harsh or unproductive environments, and a capability to access resources

with well-developed roots (Grime 1979, Barbour et al. 1987). Ruderal, or r-selected, species can exploit low stress, high disturbance environments by minimizing vegetative growth and maximizing reproductive output (Grime 1979, Barbour et al. 1987). Good competitors, or c-selected, species tend to be robust, perennial plants that can maximize resource capture in relatively undisturbed conditions and allocate resources to growth (Grime 1979, Barbour et al. 1987). *Machaeranthera coloradoensis* may be considered an s-selected species because of its perennial life history, its ability to

withstand harsh and unproductive conditions, and its capability to access resources with a taproot.

Machaeranthera coloradoensis can be found in alpine areas, among other habitats, and it may share similar strategies and adaptations to harsh environmental conditions as other alpine plants (Grime 1979, Zwinger and Willard 1996). Almost all alpine plants, including *M. coloradoensis*, have a perennial life history, because the short growing season precludes annual plants from producing stems, leaves, flowers, and fruit. Using food reserves stored in underground roots allows alpine perennials to flower early in the season and take advantage of the short summer heat to ripen seeds. In addition, many alpine plants have extended growth patterns where it may take many years for a plant to grow, produce buds, and eventually flower and set seed (Grime 1979, Zwinger and Willard 1996).

The morphology of Machaeranthera coloradoensis may include adaptations that may increase chances of survival in harsh conditions such as cold temperatures, dessicating winds, intense solar radiation, and low moisture (Grime 1979, Zwinger and Willard 1996). These conditions can be especially intense in M. coloradoensis habitat, which can include alpine fellfields with dry soils and sparse plant cover. The small size of M. coloradoensis may keep it out of harsh winds, reduce plant tissue growth needs, create less distance to transport water, allow interception of both solar radiation and ground-reflected radiation, and afford protection to the inner parts of the plant. The compact growth may also cause accumulation of organic matter to help in retaining moisture. Many alpine plants grow long taproots in order to exploit precious moisture and to anchor them in strong winds. The pubescent (hairy) stem and leaf tissue of M. coloradoensis may also help to prevent water loss, to protect against damaging solar radiation, and to trap heat radiation (Zwinger and Willard 1996).

The optimal habitat conditions or successional stage for *Machaeranthera coloradoensis* or other issues related to competitive abilities and ecological tolerances have not been studied.

Pollinators and pollination ecology

Pollination biology and specific pollination mechanisms for *Machaeranthera coloradoensis* have not been studied. Members of the Asteraceae family are well equipped to attract pollinators and to disperse pollen. The showy inflorescences attract pollinators and allow many flowers to be visited in a short time. In addition, unique flower adaptations cause nectar and pollen to be easily accessed and dispersed by pollinators (Zomlefer 1994). Bumblebees, butterflies, and other insects are common pollinators in montane ecosystems (Zwinger and Willard 1996), but the most effective pollinators for M. coloradoensis are not known. Effective pollination depends on the timing of reproductive maturity of anthers and stigmas, activity and behavior of pollinators, and flower and insect morphologies. Important issues related to the pollination of rare plants that need to be researched for M. coloradoensis include the identification and effectiveness of pollinators, the role of plant density on pollinator behavior, pollinator limitations to reproduction, annual fluctuations in pollinator activity and timing of flowering, and genetic implications of cross-pollination. For example, the abundance of different species of pollinators may fluctuate from year to year, and the timing of pollinator activity does not always match the reproductive timing of flowers. As a result, conservation of the full complement of pollinators is an important feature of a rare plant species conservation plan.

Dispersal mechanisms

Details of seed dispersal mechanisms in *Machaeranthera coloradoensis* are not known. This species has a bristly pappus on the fruits, which probably acts like a small parachute during wind dispersal (Zomlefer 1994, Handley and Laursen 2002). The seeds could also be dispersed downslope by soil or water movement (e.g., spring snowmelt, surface runoff). Where this species grows in fairly dry environments, water dispersal may not be a reliable means of dispersal. Presumably, dispersal success depends on wind patterns, topographic heterogeneity, precipitation amount and frequency, depth of eroded material, and availability of suitable "safe" sites for seed germination.

Fertility and seed viability

Minimal information is available concerning the fertility, seed viability, and germination requirements of *Machaeranthera coloradoensis*. Greenhouse studies of 28 species of subalpine and alpine plants from the Olympic Mountains in Washington discovered that their germination requirements ranged widely (Kaye 1997). Some species required after-ripening, cold stratification, scarification, darkness, or light, while the seeds of other species did not germinate under any experimental conditions. An online database on rock garden plants notes that *M. coloradoensis* has been cultivated in sunny, dry, rock crevices, and otherwise poor, drained

soils (Slaby 2001). This species can be seeded in the spring or propagated from cuttings taken in late summer. *Machaeranthera coloradoensis* is also listed in the Denver Botanic Gardens living collections database, although details of cultivation are not presented (Denver Botanic Gardens 2003).

Cryptic phases

No information regarding cryptic phases of *Machaeranthera coloradoensis* is available. Seed dormancy can be an important adaptation by which alpine plant populations exploit favorable conditions in a harsh environment (Kaye 1997). It is not known whether a persistent seed bank exists or what the extent of seed dormancy is for *M. coloradoensis*. Details of seed longevity, patterns of seed dormancy, and factors controlling seed germination for *M. coloradoensis* have not been studied.

Phenotypic plasticity

Phenotypic plasticity is demonstrated when members of a species vary in height, leaf size, flowering (or spore-producing) time, or other attributes, with changes in light intensity, latitude, elevation, or other site characteristics. Populations and individuals of Machaeranthera coloradoensis differ in morphological characteristics of the leaves, heads, and stems (Hartman 1976, B. Johnston personal communication 2002, R. Hartman personal communication 2003). These morphological differences between populations were the main reason that two varieties were identified for this species (Hartman 1976, Johnston 2001, Johnston 2002). As discussed earlier, recent taxonomic work indicates that distinction of two varieties may not be warranted (R. Hartman personal communication 2003, Morgan and Hartman 2004).

Several other examples demonstrate that phenotypic variability exists for this species. For example, one population exhibited 95 percent maroon flower heads and 5 percent white flower heads, and another population consisted of both rayed and rayless individuals (Wyoming Natural Diversity Database 2003). One observer found an individual greater than 30.5 cm in diameter, with over 30 flowers (Colorado Natural Heritage Program 2003). The possible role of age, genetic resources, or site conditions was not discussed. Overall, it is difficult to ascertain to what extent these phenotypic differences are caused by genetic or environmental influences (B. Johnston personal communication 2002).

Mycorrhizal relationships

The existence of mycorrhizal relationships with *Machaeranthera coloradoensis* or other *Machaeranthera* species was not discussed in the literature.

Hybridization

Some Machaeranthera species are known to hybridize with congeners, as well as with species from other genera (e.g., Aster, Haplopappus) (Hartman 1976, Stucky 1978). Machaeranthera coloradoensis hybridizes with M. grindelioides at two of the occurrences in Wyoming (R. Hartman personal communication 2003, Wyoming Natural Diversity Database 2003). The extent to which observers were looking for hybrids or the cooccurrence of *M. coloradoensis* with synchronously flowering related species at other locations is not known. In addition, it is difficult to determine what the possible implications of hybridization on the long-term persistence of *M. coloradoensis* may be. Hybridization can lead to rare species extinction in cases when a more abundant congener genetically swamps the rare species, when hybrid offspring outcompete the rare parent species, or when the production of hybrid seed reduces reproductive success of the rare species (Glenne 2003). The current levels of hybridization do not appear to be a risk for *M. coloradoensis* unless the extent of hybridization is underestimated or increases in the future (R. Hartman personal communication 2003). The existence of pre-zygotic or post-zygotic isolating mechanisms may be an important area of research for this species.

Demography

Life history characteristics

There is no information regarding population parameters or demographic features of *Machaeranthera coloradoensis*, such as metapopulation dynamics, life span, recruitment, and survival.

Life cycle diagram and demographic matrix. Demographic parameters, such as recruitment and survival rates, have not been investigated for *Machaeranthera coloradoensis*, and so there are no definitive data regarding the vital rates that contribute to species fitness. Although stage-based models based on population matrices and transition probabilities can be used to assess population viability (Caswell 2001), adequate quantitative demographic data are needed for input into the model. A corresponding life cycle diagram could also be constructed, if data were available. A life cycle diagram is a series of nodes that represent the different life stages connected by various arrows that represent the vital rates (i.e., survival rate, fecundity). The specific events in the life cycle or longevity of *M. coloradoensis* are unknown. For *M. coloradoensis*, the stages that could potentially be incorporated into a demographic matrix include seed, seedling, vegetative individuals, reproductive adults, and dormant individuals (Figure 3).

Presumably, there are seeds or propagules in the soil at existing population locations of Machaeranthera coloradoensis. The probability of germination and subsequent establishment depends on the longevity of these propagules and whether appropriate environmental conditions exist for germination and growth. Seeds that germinate may assimilate resources and become established plants. Growth rates may be influenced by the intensity and frequency of disturbance and by the availability of resources, such as space, light, moisture, and nutrients. If appropriate conditions exist, then individuals in the population may produce flowers. Successful seed set will depend on the rate of pollen and ovule formation, pollination, fertilization, and embryo development. If adequate conditions do not exist, then plants may exist as vegetative individuals until dormancy at the end of the season and senesce before flowering. Fecundity rates depend on the production of seeds and the percentage of those seeds that overwinter and survive to germination the next year.

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

Ecological influences on survival and reproduction

No information exists concerning the ecological factors affecting reproduction, growth, and establishment of Machaeranthera coloradoensis. The long-term persistence of this species at a location most likely depends on a range of ecological influences on reproduction and growth, including climatic fluctuations, microsite conditions (e.g., moisture), availability of suitable germination sites, pollinator activities, disturbance patterns, and interspecific competition. fluctuations, such as available Environmental moisture, length of growing season, and temperature fluctuations, could potentially affect vegetative growth as well as flowering times and seed production. At

one site in Colorado, one of the authors failed to find *M. coloradoensis* individuals during the drought year of 2002. These factors are likely different in foothills or montane habitats compared to subalpine or alpine environments. In addition, the age of the individuals in a population (and possibly plant size and root growth) and the time since establishment may mediate the effect of disturbances. The establishment of new populations most likely depends on barriers to dispersal and the availability of suitable germination sites.

Spatial characteristics

The factors affecting the spatial distribution of *Machaeranthera coloradoensis* have not been studied. The size and extent of populations have not been extensively described or mapped. B. Johnston (personal communication 2002) noted that the size and distribution of *M. coloradoensis* populations varied widely, ranging from a few to 1,500 individuals and from 2 to 25 acres. All of the populations within the White River National Forest occurred along the north slopes of a mountain ridge and pass. Several observations in Wyoming noted that the *M. coloradoensis* populations were restricted to roadsides and adjacent areas where suitable soil substrate was exposed.

Machaeranthera coloradoensis tends to grow on calcareous, granitic, or volcanic soils in open plant communities with a high percentage of bare soil or rock (Johnston 2001). This may indicate an inability to survive in closed communities and a reliance on natural disturbances to reduce competition and to maintain open soil (Moseley 1996). Other characteristics that could influence the spatial distribution of rare species may include seed/ramet dispersal, presence of other vegetation, landscape and microsite heterogeneity, ecological fluctuations, and disturbance patterns. Individuals or populations may be dormant during unsuitable environmental conditions (e.g., drought), which would affect the spatial distribution and abundance of aboveground individuals from year to year.

Disturbances in mountainous environments can include water erosion, rockslide, fire, blowdowns, frost heaving, wind-scouring, small mammal activity, and human influences (Zwinger and Willard 1996). *Machaeranthera coloradoensis* populations in alpine areas with scattered tree cover and minimal fuels are less likely to be affected by blowdowns or fire than populations at lower elevation sites within forested areas. Several populations exist near trails and two-track roads, and they could be affected by any trail- or roadrelated damage, such as trampling or soil movement (e.g., erosion and deposition). Disturbances leading to exposure of substrate, such as historical mining activities and erosion on steep slopes, most likely play(ed) a role in creating suitable habitat throughout the landscape, as well as directly impacting existing populations. The type, size, frequency, and intensity of disturbances that define the natural disturbance regime are unknown. It is also unclear to what extent *M. coloradoensis* is capable of dispersing, colonizing, and establishing new populations around the landscape.

Genetic characteristics and concerns

In general, the genetic status of Machaeranthera coloradoensis, including issues related to hybridization, polyploidy, and genetic variability, is largely unknown. Understanding the genetic variability between populations or possible varieties of M. coloradoensis would have important implications for our understanding of this species. Chromosome studies by Hartman (1976) discovered that M. coloradoensis has a haploid number of four chromosomes. Species with a low chromosome number could potentially have lower offspring variability as a result of lower gamete variability and lower rates of recombination, but any genetic consequences of a low number of chromosomes for M. coloradoensis has not been determined. Issues related to gene flow, inbreeding, hybridization, and genetic isolation could affect the demography, ecology, and management considerations for this species.

Factors limiting population growth

Based on the information presented in the preceding sections, population growth or establishment of *Machaeranthera coloradoensis* could be limited by competition with other species, inadequate pollinators, lack of suitable habitat, or inappropriate environmental conditions for germination or growth.

Community ecology

Herbivores and relationship to habitat

The effects and extent of mammalian and insectivorous herbivory on the stems, leaves, or fruits of *Machaeranthera coloradoensis* are not fully known. One occurrence noted that there was some minor clipping of stems that was attributed to rodents or insects (Colorado Natural Heritage Program 2003). A study of *M. canescens* in arid grasslands of New Mexico found that grasshoppers significantly defoliated this species (Parker and Root 1981). Although this study involved a species from a different environment

than *M. coloradoensis*, it suggests that herbivory on *M. coloradoensis* is possible. The identification or presence of insect herbivores in different habitats of *M. coloradoensis* has not been studied. Researchers hypothesize that *M. coloradoensis* is unpalatable or at least unattractive to large mammals because it is found in dry, sparsely-vegetated environments, is low-growing, and has somewhat "spiky" leaves (W. Haas personal communication 2002). Sheep grazing could potentially have more impact than cattle grazing, because sheep tend to graze closer to the ground and eat more forbs than cattle. However, a population of *M. coloradoensis* found in a sheep pasture did not appear to be adversely affected (B. Johnston personal communication 2002).

Of the 21 occurrences of Machaeranthera coloradoensis on USFS lands, at least 14 of those locations are within active livestock grazing allotments (Johnston 2001, K. Giezentanner personal communication 2003, W. Haas personal communication 2003, S. Olson personal communication 2003, J. Redders personal communication 2003). Overall, cattle grazing appears to be more prevalent at the lower elevation sites, whereas higher elevation alpine sites have domestic sheep grazing or no grazing. The grazing regime on allotments in the San Juan National Forest generally consists of cattle or sheep on pastures in summer and fall in a rotational grazing system (J. Redders personal communication 2003). Several allotments in the Rio Grande National Forest have sheep grazing every year for a short period of time at different times during the growing season (G. Snell personal communication 2003), and other allotments in the forest have deferred-rotation cattle grazing for up to 35 days during the period from mid-June to mid-October (G. Becenti personal communication 2003). Although M. coloradoensis occurs in an allotment with livestock grazing in the Pike-San Isabel National Forest, the rocky and steep terrain would most likely minimize extensive livestock activity around microsites with this tansyaster (S. Olson personal communication 2003). Grazing at lower elevation sites in the Gunnison National Forest consists of a deferred-rotation grazing system where a series of pastures are lightly grazed annually during a period from June to September or August to October (Mauch 2002a, 2002b). In Wyoming, cattle grazing occurs in a pasture with M. coloradoensis for a two week period between July and mid-September (W. Haas personal communication 2002).

No declines of this species have been specifically attributed to livestock grazing or trampling. One occurrence record from a population in the Gunnison National Forest specifically noted that although the area was clearly grazed by livestock, no damage to Machaeranthera coloradoensis plants was recorded. W. Haas (personal communication 2003) also reported that cattle avoided the specific habitat with M. coloradoensis in the Medicine Bow National Forest pasture, because it is a cushion plant community with significant bare ground between plants. She also reported that no plants looked grazed. The only possible impact from cattle activities in that area would be from trampling as the animals moved to and from a creek (W. Haas personal communication 2003). Two other element occurrence records noted the presence of cattle trails passing through the population area (Colorado Natural Heritage Program 2003). Other indirect impacts of grazing activities, such as importation of invasive weed seeds, soil erosion or compaction, or destruction of pollinator habitat, have not been studied.

In addition, possible grazing impact from native herbivores has not been identified, although elk, bighorn sheep, mule deer, and pronghorn occur in habitats with *Machaeranthera coloradoensis* (Welp et al. 2000, Johnston 2001, Mauch 2002a).

Competitors and relationship to habitat

The interactions of Machaeranthera coloradoensis within the plant community are not well known. This tansyaster is commonly found in sparsely vegetated areas, suggesting that it is a poor competitor with meadow species and/or a superior competitor in somewhat stressful environments. Succession is a slow process in alpine environments, but historical evidence demonstrates that cushion plants of fellfields can be outcompeted by taller grasses and sedges over time to form alpine meadows (Zwinger and Willard 1996). Erosion by wind, water, or gravity may play a role in maintaining suitable open habitat for M. coloradoensis and in reducing competition with shrub, forb, and grass species. The presence of fire in foothills and montane environments may also play a role in maintaining open habitat for M. coloradoensis and in reducing competition with shrub and grass species (W. Haas personal communication 2002). Prescribed fires are used for ecosystem management in Gunnison National Forest pastures with ponderosa pine and other fire-dependent species (Mauch 2002a). The fires help to reduce understory brush and ground litter accumulation, thus facilitating forage production, plant diversity, and tree regeneration, and reducing the probability for catastrophic fires. The presence of M. coloradoensis in areas that have been prescribed burned and the effects of fire on this species are unknown.

There are no reports of non-native invasive plant species specifically affecting Machaeranthera coloradoensis. Many non-native, invasive species can invade disturbed (e.g., roads, trails) or undisturbed sites, form dense, monospecific stands, and outcompete native species by using space, nutrients, and water (Cronk and Fuller 1995, Luken and Thieret 1997, Mack et al. 2000). Mauch (2002a) reports that small infestations of Canada thistle (Cirsium arvense) and dalmation toadflax (Linaria genistifolia ssp. dalmatica) have been identified in Gunnison National Forest pastures, and they will be targeted for control. The proximity of these populations to M. coloradoensis or any possible effects of control efforts is not known. Botanists specifically noticed the absence of any invasive species at one location of M. coloradoensis occurring near an old road (Colorado Natural Heritage Program 2003). Sixteen invasive species have been identified throughout the White River National Forest, but the presence of invaders near M. coloradoensis was not identified (U.S. Forest Service 2002). An area with potential habitat for M. coloradoensis in Wyoming is invaded by Canada thistle and Kentucky bluegrass (Poa pratensis) in the riparian areas and by cheatgrass (Bromus tectorum) in the uplands. Especially dry and erodible habitats or high elevation alpine sites with M. coloradoensis may not be as readily colonized by invading species as other sites.

Parasites and disease

There is no information concerning the role of parasites or diseases in the life cycle of *Machaeranthera coloradoensis*. Several records in the Colorado NHP database (2002) reported that there was no evidence of disease, predation, or injury.

Symbiotic interactions

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

Habitat influences

Machaeranthera coloradoensis inhabits a wide variety of elevations and habitats generally characterized by sparse vegetation and exposed soils, ranging from ponderosa pine parks to alpine meadows

(Colorado Natural Heritage Program 2003, Wyoming Natural Diversity Database 2003). Microhabitats include montane parks, rocky outcrops, talus slopes, fellfields, and roadsides, among others. Populations have been found on sedimentary and calcareous substrates (e.g., limestone, dolomite, shale), volcanic substrates (e.g., volcanic ash), and granitic substrates (Johnston 2002). Thus, this species does not appear to be a strict habitat specialist.

The availability and quality of suitable habitat most likely ranges from area to area, depending on heterogeneity in topography, substrate, disturbance factors, and competition with other species. For example, the availability of *Machaeranthera coloradoensis* habitat in the White River National Forest may depend on the occurrence of alpine fellfields, whereas the availability of habitat in the Medicine Bow National Forest may be related to the creation of open foothills habitats by erosive forces or fire (Johnston 2001, J. Proctor personal communication 2002). This species' ability to colonize disturbed areas is unknown.

CONSERVATION

Threats

Threats to the long-term persistence of Machaeranthera coloradoensis in USFS Region 2 are mostly unknown because of the lack of species understanding and research. The information presented in this section is primarily based on status reports of M. coloradoensis in the White River National Forest (Johnston 2001, Johnston 2002, U.S. Forest Service 2002), observations in occurrence records (Colorado Natural Heritage Program 2003, Wyoming Natural Diversity Database 2003), and personal communications with rangeland management specialists and forest botanists (B. Johnston personal communication 2002, B. Madsen personal communication 2002, J. Proctor personal communication 2002, G. Austin personal communication 2003, G. Becenti personal communication 2003, D. Erhard personal communication 2003, W. Haas personal communication 2003, G. Snell personal communication 2003).

Of the 33 occurrences of *Machaeranthera* coloradoensis worldwide, 21 occurrences are on National Forest System lands in Colorado and Wyoming. Most of the occurrences on USFS lands are in areas managed for multiple uses, and two occurrences may be in special management areas (**Figure 1**, **Table 2**). The remaining populations occur on BLM lands,

state lands, or private lands. As discussed earlier, populations of sensitive species on USFS lands obtain some protection from collection and from the impacts of federal projects. Additionally, populations in special management areas are protected from motorized and mechanized travel. Any management or protection of the 12 *M. coloradoensis* populations on non-USFS lands is not known.

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

Direct or indirect negative impacts to *Machaeranthera coloradoensis* populations or habitats by human-related activities could occur from motorized and non-motorized recreation, trail or road construction and maintenance, changes to natural disturbance regimes, domestic livestock activities, invasive species introduction, small-scale mining, housing construction, or reservoir expansion. Lower elevation populations and those populations closest to roads and trails are likely at the most risk. Overutilization of *M. coloradoensis* for educational or scientific purposes is unknown but probably not a threat (Johnston 2001).

Existing *Machaeranthera coloradoensis* individuals near trails, roads, and trailheads could potentially be damaged by trampling, maintenance activities, or erosion/deposition causing burial of existing individuals. Recreational activities (e.g., hiking, backpacking, horseback riding, fishing, hunting, off-highway vehicle and snowmobile use) are popular on National Forest System lands with M. coloradoensis populations. Populations of this species in Wyoming are found near rivers and meadows used by hikers, bicyclists, horseback riders, fishermen, and hunters (Welp et al. 2000, W. Haas personal communication 2002). On the other hand, rugged alpine areas with M. coloradoensis may not experience heavy recreational use (K. Giezentanner personal communication 2003). Populations near highways are at the most risk to be damaged by right-of-way maintenance or activity at pullouts. Certain populations on roadsides may need immediate, active management to prevent extirpation. At least seven of the known occurrences are known to be located near a two-track road or highway; the distance of other populations to roads or trails is not known (Johnston 2001, Colorado Natural Heritage Program 2003, Wyoming Natural Diversity Database 2003). Some plants on USFS lands have been directly damaged by cars and foot traffic at highway pullouts and trailheads (W. Haas personal communication 2002, D. Erhard personal communication 2003, Wyoming Natural Diversity Database 2003). Another occurrence includes plants growing in the gravelly substrate of the drainage gully along a highway; the effects of highway maintenance or road-associated pollution on this occurrence are not known (Colorado Natural Heritage Program 2003). Although travel in most USFS lands is restricted to designated trails and roads only and at least one occurrence is likely to be protected from motorized travel under SIA restrictions, there still might be prohibited off-highway vehicle use (Johnston 2001). The effect of a major USFS road on a population located downslope is not known. In addition, some plants are located next to a two-track road on USFS lands that does not appear to have much, if any, use (Colorado Natural Heritage Program 2003). It is unknown what effect winter snowmobile use may have on this species (Johnston 2001). However, M. coloradoensis can occur in areas with late-lying snowfields, and intense snowmobile activity could affect snowmelt timing and patterns. It is also important to note that substrate exposed during historical highway or mine road construction activities may possibly have created favorable habitat for *M. coloradoensis* to establish.

Surface-disturbing activities, such as mining or housing construction, could damage known populations and potential habitat for *Machaeranthera coloradoensis*. Any mining activity, road construction, or housing development that causes soil disturbance in areas with established populations of *M. coloradoensis* could negatively impact existing populations of this species (Johnston 2001). These activities could also serve to create suitable habitat for this species. For example, at least four occurrences of M. coloradoensis on USFS lands occur in areas with historic mining activity, and one population was growing on prospect piles created during historical mining activities. Based on element occurrence records (Colorado Natural Heritage Program 2003, Wyoming Natural Diversity Database 2003), at least one occurrence on USFS lands is located in a context with the potential for surface-disturbing activities in the area (i.e., near a pipeline, road, and radio towers). Some M. coloradoensis locations or potential habitat for populations are on or near private lands that could be subdivided and developed for housing (Welp et al. 2000, Colorado Natural Heritage Program 2003). One site with M. coloradoensis in Colorado occurs on limey volcanic tuff soils currently being excavated for the pet industry (i.e., kitty litter) (B. Johnston personal communication 2002). Another location with this species occurs right next to a reservoir that may be expanded for increased water storage purposes. The M. coloradoensis population at this location would be extirpated if the water level rises (Colorado Natural Heritage Program 2003).

The effects of livestock grazing on Machaeranthera coloradoensis are probably minimal, because this species is apparently unpalatable and prefers habitats that are sparsely vegetated and rocky (Fertig et al. 1994, Johnston 2001, W. Haas personal communication 2003). Populations in steep, rocky, alpine areas are less likely to be affected by livestock grazing than lower elevation populations in grasslands, woodland parks, and riparian areas. Based on the available information, at least 14 of the 19 M. coloradoensis occurrences on USFS lands are within areas with livestock grazing. Many of the populations on non-USFS lands are also likely to be in grazed areas. Several element occurrence records indicated that in the areas with grazing, there was evidence of slight disturbances from cattle, but the plants were not negatively affected. Machaeranthera coloradoensis could possibly be more susceptible to incidental trampling if grazing intensities increased. In the Medicine Bow National Forest, cattle have incidentally trampled or cascaded soil down upon M. coloradoensis plants as they traveled down the slope to the creek (W. Haas personal communication 2002). Two other element occurrence records noted the presence of cattle trails passing through the population area (Colorado Natural Heritage Program 2003). Sheep grazing could potentially be a threat, because sheep tend to graze closer to the ground and eat more forbs than cattle. However, a M. coloradoensis population found in a sheep pasture did not appear to be adversely affected (B. Johnston personal communication 2002). The possible indirect impacts of grazing activities on M. coloradoensis habitat, such as importation of invasive weed seeds, soil erosion or compaction, and destruction of pollinator habitat, have not been studied. The effects of native mammalian or insectivorous herbivores are not known.

Management activities such as timber harvest, thinning, fire suppression, or prescribed fires, are more likely to affect occurrences of Machaeranthera coloradoensis in lower elevation montane habitats than occurrences above timberline, which typically have low tree cover and low fuel loads (Johnston 2001). At lower elevations, Machaeranthera coloradoensis is typically found in open areas outside of tree stands, and fire may play a role in maintaining these open areas by reducing competition from tree seedlings and tall grasses. The effects of prescribed burns in areas of the Gunnison National Forest with occurrences of this tansyaster have notbeen studied. In a reasthat have low fuel loads, resulting low temperature fires may not kill deep-rooted perennials, like M. coloradoensis. Because this tansyaster is not usually found in dense stands of timber, it is possible that activities like timber felling, skidding, or loading might not be relevant for this species. However, the indirect effects of these activities, such as creation of roads and non-native plant invasion, may have implications for this species. If a population was located in an area with plans for timber harvest or if the areas adjacent to forest stands were used for staging areas or roads, then populations of *M. coloradoensis* could possibly be damaged by the activities of heavy equipment.

The threat of encroachment by non-native, invasive plant species into areas with Machaeranthera coloradoensis is unknown. Existing element occurrence records do not indicate a problem with invasive species at any of the M. coloradoensis locations. In addition, M. coloradoensis grows in rocky, alpine areas or other dry, erodible areas that may not be readily colonized by invading species. However, any increase in nonnative species invasion is a future risk for competition with M. coloradoensis, especially for lower elevation populations along trails, roads, and other disturbed areas. Invasive species of potential concern for increased establishment in central Colorado or southern Wyoming include cheatgrass, Kentucky bluegrass, Canada thistle, smooth bromegrass (Bromus inermis var. inermis) and meadow timothy grass (Phleum pratense) (Chumley 1998, Mauch 2002a, U.S. Forest Service 2002).

Other environmental or biological threats to populations or habitats of *Machaeranthera coloradoensis* could include inadequate pollination, genetic isolation, herbivory, landscape fragmentation, hybridization, global climate changes, or changes to the natural disturbance regime that would affect natural succession, erosion, or precipitation patterns. The extent and effects of atmospheric pollution (e.g., deposition of nitrogen oxides) in this region are unknown.

Machaeranthera coloradoensis is sometimes found in sparsely vegetated areas on highly erodible scree slopes. If natural erosion and successional patterns were altered, then appropriate open habitat for this species might not exist. Erosional events, caused by runoff or rockslides, can impact existing populations and/or create habitat suitable for the establishment of new populations. As discussed previously, *M.* coloradoensis may possibly rely on fire to maintain suitable open habitat. If fire return intervals or natural successional patterns were altered, then appropriate habitat for *M. coloradoensis* might be threatened. Livestock grazing may also play an important role in maintaining open habitat areas.

Changes to existing climatic and precipitation patterns, perhaps as a result of global environmental change, could also impact Machaeranthera coloradoensis. For example, average temperatures are projected to increase and precipitation is projected to decrease in some areas in the interior regions of North America (Watson et al. 2001). Climate change and other potential changes to a suite of environmental variables have the potential to affect plant community composition by altering establishment, growth, reproduction, and death of plants. It is possible that the apparent ability of M. coloradoensis to tolerate somewhat stressful environments, exist at a range of elevations, and grow in a variety of habitats may help it to persist.

If Machaeranthera coloradoensis is largely dependent on outcrossing for maximum seed set, then any reductions in pollinator efficiency could potentially reduce reproductive success. For example, environmental stochasticity could potentially cause fluctuations in pollinator activity and behavior. In addition, the amount of gene flow, genetic variability, and inbreeding depression is unknown for M. coloradoensis. The extent of landscape fragmentation in areas with this species has not been studied or quantified. Any increase in road and trail construction or other barriers to pollinators could potentially decrease geneflow. Machaeranthera coloradoensis has been reported to hybridize with M. grindelioides at two locations. It is difficult, however, to determine what the possible implications of hybridization on the long-term persistence of M. coloradoensis may be. The current levels of hybridization do not appear to be a risk for M. coloradoensis unless the extent of hybridization is underestimated or increases in the future (R. Hartman personal communication 2003).

Threats to the long-term persistence of coloradoensis Machaeranthera populations or habitats likely differ for each of the 33 occurrences. The most significant threats to the 21 occurrences on USFS Region 2 lands probably include motorized and non-motorized recreation, non-native plant invasion, grazing and trampling, succession, mining, and global environmental changes. Lower-elevation populations and populations near roads or trails are probably at higher risk for the detrimental effects of road or trail associated activities, non-native plant invasion, and livestock grazing. Imminent threats from reservoir expansion, housing construction, and highway maintenance exist for populations on non-USFS lands.

Conservation Status of the Species in USFS Region 2

Machaeranthera coloradoensis is a species of special concern because of its endemic distribution, small number of documented occurrences, and possible human-related and environmental threats to its persistence. Much information is lacking concerning the full abundance, distribution, and biology of *M. coloradoensis*. The majority of known populations of *M. coloradoensis* occur on National Forest System lands (Figure 1, Table 2). As a result, the conservation of those populations is especially important to the global conservation status of this species and is the focus of the discussion presented in this document.

The viability of Machaeranthera coloradoensis within USFS Region 2 is difficult to ascertain because the full distribution and abundance is unknown, demographic parameters have not been studied, and the effects of management activities (i.e., livestock grazing, prescribed fires) have not been studied. Many populations have not been observed within the last 20 years, and at least 20 occurrences lack enough information to estimate possible habitat quality and viability with element occurrence ranks. Livestock activities, motorized and non-motorized recreation, non-native plant invasion, mining, succession, and global environmental changes potentially threaten M. coloradoensis on USFS lands. Based on the few available data, it appears that population numbers are not declining, and new populations have been discovered in recent years. Johnston (2002) noted that habitats of this species appear to be stable in size and quality and to be fairly resilient to grazing and some trampling. While this species appears to be persisting

under current natural disturbance regimes and with current levels of recreation and management activities, it is difficult to predict its ability to tolerate environmental stochasticity in the future (e.g., global environmental changes, drought, invasive species) and any future management changes (e.g., livestock grazing, natural resource development, prescribed burning).

Population declines

Based on data collected, it would be difficult to conclude that the distribution or abundance of Machaeranthera coloradoensis is declining or expanding throughout its range. Although a few populations have been re-observed several times since their initial identification, the reports do not include detailed abundance or demographic information. There have been new discoveries of this species in recent years, and researchers believe that there are probably more occurrences yet to be found (G. Austin personal communication 2002, R. Hartman personal communication 2003, Johnston 2002, J. Proctor personal communication 2002). On the other hand, John Proctor, forest botanist with the Medicine Bow National Forest, found suitable habitat with similar associated species and soil structure that did not have any M. coloradoensis individuals (J. Proctor personal communication 2002). The rate at which this species disperses and colonizes new locations is unknown, and we know little of its dispersal and establishment capabilities. At best, we can conclude that there are several populations of varying sizes and occupied areas in existence, with potentially more populations to be discovered. Although there are a few *M. coloradoensis* populations in Colorado with over 1000 individuals, Wyoming populations appear to be smaller. Not enough data are available to conclude if populations of this species are increasing, decreasing, or remaining stable.

Life history and ecology

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

Persistence of *Machaeranthera coloradoensis* individuals most likely depends on the establishment of a well-developed root system to access moisture, store resources, and anchor it in unstable soils. An existing plant could be negatively impacted by disruption to the soil surface that jeopardizes its "hold" on the soil. The apparent stress-tolerating abilities of this species may possibly aid it to persist despite short-term environmental fluctuations, such as drought. In addition, the physiological capabilities of the species to exist at a range of elevations and in a range of habitats may also help to buffer the possible effects of global environmental changes. The extent to which reproductive success of M. coloradoensis (i.e., persistence of populations and the species) depends on vegetative or sexual reproduction, pollinator dynamics, genetic variability, and gene flow is unknown. If M. coloradoensis is largely dependent on outcrossing for maximum seed set, then the reductions in pollination efficiency could potentially reduce reproductive success. Successful germination and establishment of new seedlings could be affected by changes to moisture conditions, soil surface disruption to the topsoil horizons, lack of suitable germination sites, or competition with other plant species. In addition, factors related to metapopulation dynamics, such as the amount of gene flow, genetic variability, inbreeding depression, and minimum viable population size, are unknown for *M. coloradoensis*. It is possible that the separate clumps of populations, such as the Wyoming populations, may harbor rare alleles important to conserve for the long-term persistence of this species. Hybridization with other cooccurring Machaeranthera species has been documented, but the conservation implications have not been assessed.

Habitat variation and risk

Machaeranthera coloradoensis is not a habitat specialist restricted to only one specific soil type, vegetation association, or habitat context (slope, aspect, elevation) throughout its range. This species appears to require open, sparsely-vegetated areas often associated with exposed substrates of sedimentary, granitic, or volcanic origins. These areas are often dry and dynamic environments, susceptible to continual natural disturbance (Johnston 2002). In general, disturbances can either create suitable habitat throughout a landscape or directly impact an existing population, depending on frequency, intensity, size, and location.

As a whole, habitats of *Machaeranthera coloradoensis* do not appear to be at immediate risk or severely threatened by consequences of current land management. Johnston (2002) noted that habitats of this species appear to be stable in size and quality, and to be fairly resilient to grazing and some trampling. However, specific populations located near trails or roads, near a reservoir, on private lands that could be sold to development, in areas with extensive off-highway vehicle use, or in proximity to current mining activities could be at greater risk than other populations (Johnston

2001, Colorado Natural Heritage Program 2003, W. Haas personal communication 2002). Severe surfacedisturbing activities, such as off-highway vehicle use, intense grazing, use of heavy machinery, construction, or mining could endanger specific populations of M. coloradoensis and compromise the long-term persistence of this species. Certain populations on roadsides may need immediate, active management to prevent extirpation. Management activities such as prescribed fires do occur in habitats with M. coloradoensis, but the specific beneficial or negative effects of these activities on this species have not been studied or quantified. The effects of grazing have been qualitatively monitored by at least two USFS range management specialists, and a grazing exclosure will be set up in 2004 to further monitor and quantify the effects of this prevalent land use on *M. coloradoensis*.

Limiting factors or risks within the habitat could include competition from surrounding vegetation (including invasive species), lack of suitable germination sites, extensive herbivory, inadequate pollinator habitat, barriers to gene flow, extensive hybridization with other Machaeranthera species, other conditions too harsh for adequate growth and development (i.e., soil erosion and deposition, trampling), or other fluctuations in natural disturbance processes (e.g., precipitation, wind, fire). Fluctuations in natural disturbance processes could positively or negatively affect existing populations or creation of habitat. For example, erosional events could damage or bury existing individuals, or possibly aid in dispersal and creation of habitat for establishment of new populations. The colonizing ability of Machaeranthera coloradoensis has not been studied. The availability and quality of suitable habitat most likely ranges from area to area, depending on heterogeneity in topography, substrate, disturbance factors, and competition with other species. Marginal habitats for this species may include areas where competition from other species is intense. Invasive species have been identified on National Forest System lands with M. coloradoensis, but they have not been recorded in the direct vicinity of M. coloradoensis populations. The dry, erodible habitats of M. coloradoensis may not be suitable for the establishment and spread of any invasive plants, or it may just be a matter of time for an invasive species to exploit those habitats. Thus, competition from invasive species is not a current concern for M. coloradoensis or its habitats. However, invasive species are being introduced all the time, and it may be a future threat. Hybridization between M. coloradoensis and M. grindelioides has been documented at two locations, but the potential long-term effects of hybridization to M. coloradoensis are difficult to assess.

Management of the Species in USFS Region 2

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

Management implications

Management activities such as prescribed fires, livestock grazing, timber harvest, invasive weed control, and regulation of motorized and non-motorized recreation, do occur on National Forest lands with *Machaeranthera coloradoensis*. However, the specific beneficial or negative effects of these management activities on this species have not been studied or quantified. Prescribed fires in habitats with *M. coloradoensis* could possibly have a beneficial effect if they maintain suitable open habitat. *Machaeranthera coloradoensis* occurs at a variety of elevations and in a variety of habitat types, so the effects of fires in each of those areas could be different. Presumably, this species would benefit from invasive species control if invaders encroach upon populations or potential habitat in the future.

Most of the grazing scenarios consist of deferred rotation grazing by cattle or sheep for a few weeks during the summer. The effects of grazing have been qualitatively monitored by at least three USFS range management specialists, and a grazing exclosure will be set up in 2004 to further monitor and quantify the effects of this prevalent land use on *Machaeranthera coloradoensis*. Based on available observations, *M. coloradoensis* plants under these grazing regimes do not appear to be heavily impacted; they appear to be somewhat unpalatable to livestock, the sparsely vegetated areas in which they occur are not attractive to livestock, and livestock grazing intensities are not heavy enough to cause severe trampling.

Motorized and mechanized recreation is regulated in national forests, but whether users follow the rules and what implications these types of recreation have on *Machaeranthera coloradoensis* is unknown.

Machaeranthera coloradoensis is found near twotrack roads and trails, so understanding the effects of recreational activities may be important for conservation of this species. USFS botanists have plans to set up protective measures (e.g., landscape logs, natural barriers) for M. coloradoensis plants at road pullouts and busy trailheads, but the implications of those measures have not yet been recorded. A Special Interest Area has been created in the White River National Forest to protect botanical resources, including populations of M. coloradoensis, but biologists have not yet created a detailed management plan for that area. Livestock grazing and motorized recreation at this site will most likely be prohibited in the management plan (K. Giezentanner personal communication 2003). Johnston (2001) identified motorized recreation as the most significant potential threat to populations on the White River National Forest, so these regulations will most likely have a beneficial effect on this species.

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

In a report prepared for the White River National Forest, B. Johnston (2001) suggested four recommendations for management direction pertaining to *Machaeranthera coloradoensis*: 1) more effectively protect the *M. coloradoensis* population near Taylor Pass, 2) improve overall management of alpine ecosystems, 3) conduct intensive searches for *M. coloradoensis* in potential habitat areas of other national forests, and 4) consider *M. coloradoensis* for the USFS Region 2 sensitive species list. As of 2003, *M. coloradoensis* populations on Taylor Pass were protected within a recently established SIA, and this species had been placed on the sensitive species list.

Potential conservation elements

Machaeranthera coloradoensis is a regional endemic species with a small number of recorded populations and with little known about its distribution, biology, or ecology. Features of M. coloradoensis biology that may be important to consider when addressing conservation of this species (i.e., key conservation elements) include its apparent preference for exposed substrates of calcareous, sedimentary, and volcanic origin, potential reliance on continuous natural disturbances to create/maintain open habitat, possible poor competitive abilities evidenced by its preference for sparsely-vegetated areas, hybridization with closelyrelated species, and possible outcrossing needs requiring efficient pollination. Changes in the timing, intensity, or frequency of natural disturbances have the potential to damage existing populations and/or reduce habitats for future recruitment. For example, increasing soil erosion on slopes through recreation, construction, or trampling may negatively impact existing plant populations, but it may create future suitable habitat. Invasive plant introduction could encroach on the "open" habitats that this plant prefers. The lack of information regarding the colonizing ability, vegetative and sexual reproductive potential, and genetic variability of this species makes it difficult to predict its vulnerability. Management decisions could consider the effect of management activities on landscape fragmentation, erosion/deposition, pollinator habitat, and introduction of invasive species.

Tools and practices

There are no existing population monitoring protocols for *Machaeranthera coloradoensis*, and very little is known about the distribution, biology, and ecology of this tansyaster. Therefore, additional habitat surveys, quantitative population inventories and monitoring, and ecological studies are priorities for constructing a conservation plan. Inventories are useful for re-locating historical populations, estimating current abundance, and identifying high-quality populations. Surveys will help to locate any undiscovered populations. Quantitative monitoring will help obtain data for demographic modeling and assess the effects of management activities. Short-term research studies (e.g., genetic analyses, pollination studies) and long-term research studies (e.g., effects of environmental fluctuations) can supplement the current biological knowledge of this species and help estimate long-term persistence. J. Proctor (personal communication 2002) suggested that *M. coloradoensis* would be relatively easy to monitor and study because it is a perennial species, is easy to see last year's growth, has flowers present for a long time, and is highly visible within its habitat.

Species inventory and habitat surveys

Current reports of existing Machaeranthera coloradoensis populations provide a useful base of information, but the distribution and total abundance of this species is not sufficiently known to formulate regional conservation strategies. For example, abundance information is available for only 13 of the 33 occurrences. Additional surveys of potential habitat are needed to discover any other populations and to document the full spatial extent of this species. For example, several botanists noted that additional populations of M. coloradoensis may exist in areas nearby existing populations as well as areas within its range that have not been intensively surveyed (G. Austin personal communication 2002, W. Haas personal communication 2002, Johnston 2002, J. Proctor personal communication 2002). J. Proctor, forest botanist with the Medicine Bow National Forest, informally surveyed habitat adjacent to existing populations and found more occurrences of M. coloradoensis (J. Proctor personal communication 2002). As a result, the actual distribution and abundance of the species may be underestimated. In addition, several of the sites (e.g., sites from Rio Grande County) do not have associated herbarium voucher specimens, and species identification at these sites should be verified.

The distribution of *Machaeranthera coloradoensis* is characterized by populations or groups of populations spread over its range from southcentral Colorado to southern Wyoming (**Figure 1**). Whether this distribution pattern is the result of genetic variation in ecological preferences, habitat heterogeneity (i.e., variability in the habitat suitability over space), or a reflection of inadequate surveying for undiscovered populations is not currently known. There are no populations of *M. coloradoensis* identified in the area between the northernmost Colorado populations in Park County and the southernmost Wyoming populations in Carbon County. It is likely that populations have yet to be discovered in Routt National Forest (Johnston 2002).

Because *Machaeranthera coloradoensis* appears to grow on specific substrates and topographies within different areas of its range, researchers could identify areas of potential habitat using topographic maps, geologic maps, aerial or satellite images, and existing Geographic Information System databases (i.e., Colorado NHP database). One botanist mapped existing populations on U.S. Geological Survey 7.5minute topographic maps while surveying Gunnison National Forest for vegetation communities. New surveys could use existing populations as a starting point because habitat zones may extend along the length of a ridge or slope. For example, two occurrences have been found in the Mosquito Range of Colorado, and the ridges in this area may contain additional populations of M. coloradoensis. In addition, locations downslope, downwind, or downstream from existing populations should be surveyed because M. coloradoensis seeds are most likely wind, water, and gravity dispersed. The Colorado NHP and NatureServe have developed databases and GIS components to assist in habitat modeling (D. Anderson personal communication 2003).

Once located, the size and extent of *Machaeranthera coloradoensis* populations could be mapped, labeled and, recorded using global positioning system and GIS technology. Mapping the extent of and providing a unique label for each known population of *M. coloradoensis* will maintain consistency for future observations and clarify the spatial distribution of populations at local and regional levels. In addition, high-quality populations in pristine habitat could be identified. Populations in areas slated for various management, maintenance, or disturbance activities could be readily identified. A detailed assessment could be undertaken before activities, such as road/trail reconfiguration or prescribed burning, occur.

Population monitoring and demographic studies

Additional information is needed to gain an understanding of the life cycle, demography, and population trends of *Machaeranthera coloradoensis*. The life cycle of *M. coloradoensis* is understood to be that of a taprooted perennial forb species. However, most aspects of the life cycle are not known. Information is lacking on longevity, germination requirements, seed survival, extent of asexual reproduction, factors affecting flower development, pollination ecology, role of the seed bank, and gene flow between populations. This type of species-specific information would be useful in assessing threats to this species and in developing mitigation and restoration strategies, if necessary. For example, seed bank studies could assess the abundance and spatial distribution of seeds to reveal dispersal patterns in this species. Studies of germination needs in the field might elucidate potential limiting factors for the establishment of new individuals and populations.

Minimal data are available on population trends for Machaeranthera coloradoensis. The existence of several populations has been noted over time, but no long-term demographic monitoring has been initiated. Long-term monitoring studies could yield helpful information, such as temporal and spatial patterns of abundance and dormancy, environmental factors that influence abundance (e.g., precipitation fluctuations), and whether populations are increasing, decreasing, or remaining stable. For example, long-term monitoring in conjunction with mapping may elucidate the temporary disappearance of aboveground individuals during unsuitable conditions. Such studies would aid in understanding the effects of environmental fluctuations as well as provide better estimates of abundance. Even the collection of simple metrics would greatly augment the current understanding of distribution and basic biological information about this species. For example, researchers could record population size, area, and density, as well as the presence of different age classes at each population. Several populations from throughout the range and from different habitat types could be monitored every one to two years at first, and then every 5 to 10 years after that.

In addition, further studies on the morphological and genetic differences between and among *Machaeranthera coloradoensis* populations will clarify metapopulation dynamics and ecological preferences.

Understanding certain aspects of demography are a priority in order to provide basic population information, and are indicated by these questions:

- What are the rates of survival, longevity, and recruitment?
- What is the extent of vegetative and sexual reproduction?
- What are the role, status, and longevity of the seed bank?
- What are the population fluctuations from year to year?
- What is the age at which individuals become reproductive?

- What is the age structure of the population?
- ✤ What is the gene flow between populations?

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

Habitat monitoring and management

of The general habitat characteristics Machaeranthera coloradoensis have been identified, but there are too many unknowns regarding microhabitat requirements and basic population dynamics to determine which factors are critical in maintaining or restoring habitat for these species. For example, it is currently not known what types, intensities, or frequencies of disturbance create and maintain habitat and are tolerated by existing populations of this species. It is likely that this species responds favorably to light disturbances (e.g., light grazing, erosion, low-temperature fire), but it may not tolerate intense disturbances (e.g., housing construction, mining). The response of M. coloradoensis to habitat changes is not known in sufficient detail to evaluate the effects of management or changes in natural disturbance patterns. As discussed above, much of the information regarding establishment, reproduction, dispersal, relationship with herbivores, and competition with introduced species has not been studied for this species. Research studies to evaluate these phenomena would provide valuable input to the development of conservation strategies and management programs.

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

Biological and ecological studies

Much of the information regarding habitat requirements, establishment, reproduction, dispersal, hybridization with co-occurring species, relationship with herbivores, competition with other species, and overall persistence has not been studied for *Machaeranthera coloradoensis*. The response of *M. coloradoensis* to habitat changes is not known in sufficient detail to evaluate the effects of changes in natural disturbance patterns. Research studies to evaluate the effects of drought, succession, and fires at several scales (local and regional) would provide valuable input to the development of conservation strategies and management programs.

Availability of reliable restoration methods

The successful production and germination of *Machaeranthera coloradoensis* seedlings in garden/

greenhouse environments (Slaby 2001, Denver Botanic Gardens 2003) introduces the possibility of restoration efforts if necessary. Germination and transplantation studies in natural environments would be helpful if populations are at risk of habitat destruction. There has been no research to date involving the harvest or storage needs of *M. coloradoensis* seed for use in a restoration projects. The collections of the National Genetic Resources Program (2003) or Royal Botanic Gardens in Kew (2003) do not include *M. coloradoensis* material.

There are still too many unknowns regarding habitat preferences and basic population dynamics to know what factors are critical in restoring habitat for Machaeranthera coloradoensis. For example, it is currently not known what types, intensities, or frequencies of disturbance are suitable for creating and maintaining habitat for this species. W. Haas (personal communication 2002) has avoided re-seeding or otherwise restoring an eroded slope where a population of *M. coloradoensis* exists. If a slope revegetation project is implemented, the revegetation may be successful, but the necessary open habitat of M. coloradoensis may be bypassed. Management activities, such as livestock grazing and prescribed burns, in areas with occurrences of this species or similar habitats could be assessed for potential as habitat restoration techniques.

Information Needs and Research Priorities

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

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

- Re-location and detailed mapping and inventory of existing populations
- Identification of high-quality populations and habitats
- Surveys for new populations
- Identification of any imminent threats to known populations
- Identification of disturbance types, frequencies, and intensities; especially as related to management activities
- Microhabitat characterizations and measurements
- Studies related to reproductive biology, including pollinator surveys, germination trials, vegetative reproduction, mycorrhizal associations, and seedbank analyses
- Identification of possible causes of individual plant mortality (e.g., herbivory, parasites, diseases)
- Genetic analyses to assess gene flow, variability, and possible hybridization throughout range.

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

- Efficient incorporation of data in the field
- Documentation and cataloging of herbarium specimens
- Generation of location and habitat maps

- Characterization of associated habitat types
- ✤ Identification of population trends over time
- Identification of data gaps that require further information gathering
- Easy modification of the database as additional information becomes available.

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DEFINITIONS

Achene – Small, dry fruit with a close-fitting wall surrounding a single seed.

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

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

Bracts - Reduced, modified leaf associated with flowers.

Calcareous - Composed of, containing, or characteristic of calcium carbonate, calcium, or limestone; chalky.

Capitulum – Inflorescence with many small flowers clustered on the receptacle.

Carpel – The plant organ that bears the ovules.

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

Corolla – Portion of flower comprised of petals.

Cushion plant – A plant found in alpine environments that grows low to the ground, with short, dense branching stems and a central taproot.

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

Disc floret – A flower with a tubular corolla (petals), present in Asteraceae. (Tubular floret)

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

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

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

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

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

Fellfield – Alpine community characterized by rocky ground, dry soils, and cushion plants.

Fertility – Reproductive capacity of an organism.

Fitness – Success in producing viable and fertile offspring.

Floret – Small, individual flowers.

Forb – A herbaceous plant, other than grass.

Fruit – A mature ovary; contains seeds.

Genotype – Genetic constitution of an organism.

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

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

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

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

Inflorescence – A group of flowers attached to a common axis in a specific arrangement.

Involucre – Series of bracts (phyllaries) surrounding or subtending a flower or inflorescence.

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

Obovate – Egg-shaped, with the narrower end near the point of attachment.

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

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

Pappus - The crown of hairs, bristles, awns, or scales on the ovary (and achene) of Asteraceae.

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

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

Periderm – Protective tissue around stem or roots, bark.

Petiole – Leaf stalk.

Phenotype – The external visible appearance of an organism.

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

Phyllaries – Bracts associated with the involucre of Asteraceae.

Pinnately-lobed – Consisting of projecting appendages arranged in two rows along an axis, like barbs along a feather.

Pistillate flower – A flower with "female" reproductive organs (pistils), and lacking "male" reproductive organs (stamens).

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

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

Prostrate – Flat on the ground.

Pubescent - Bearing hairs of any sort.

Raceme – An elongate inflorescence with pedicellate flowers arising from a central, unbranched axis.

Radiate head – Inflorescence of Asteraceae with "ray" florets arranged on the head margin and "disc" florets in the center of the head.

Ray floret – Flower with a strap-like corolla (petals), present in Asteraceae. (Ligulate floret)

Receptacle – Enlarged portion of the flower axis, which bears some or all of the flower parts.

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

Ruderal habitat – Temporary or frequently disturbed habitats.

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

Sexual reproduction – Reproduction involving the union of gametes.

Staminate flower – A flower with "male" reproductive organs (stamens) and lacking "female" reproductive organs (pistils).

Subtend – To underlie, so as to enclose, or surround.

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

Sympatric – Occupying the same geographic region.

Taproot – Main, central root growing straight down, often stouter than other roots.

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

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

Villous – Densely covered in long, soft hairs; shaggy.

Zygote – Cell formed from the union of two gametes.

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LIST OF ERRATA

09/22/05 Changed peer review organization from <u>Center for Plant Conservation</u> to <u>Society for Conservation</u> <u>Biology</u> on the cover and under "Peer Review" heading.

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