COMPARATIVE ANALYSIS OF COMMUNITY AND POPULATION LEVELS OF ORGANIZATION IN THE RARE GRASS, *ACHNATHERUM HENDERSONII*

by

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ABSTRACT

Studies of rarity tend to focus on the population level of the species in question. A complete understanding of rarity however, requires understanding both population and community patterns and processes. To that end, population and community levels of organization were compared in the rare grass, *Achnatherum hendersonii*. *Achnatherum hendersonii* occurs in small, local populations in central Washington and north-central Oregon. I compared sympatric and disjunct populations of *A. hendersonii* from its northern and southern distribution limits. I also compared *A. hendersonii* with the closely related common grass, *A. lemmonii*. Plant species coverage in vegetation plots was used to estimate community level organization, and morphology of inflorescence and vegetative leaves was used to estimate population level organization. Principal components analysis (PCA) was used to make comparisons. Organization was assessed through the calculation of 95% confidence level bivariate ellipses about the first two PCA axis scores. The ellipse statistics theta, eccentricity, and area were used to quantify three components of organization for each group: theta reflects the covariance or organization *sensu stricto*; eccentricity reflects the strength of correlation or organization as order; area relates to the amount of variation. Community level organization differed throughout the distribution range of *A. hendersonii*. At the northern distribution limit, variation in the vegetation was less for the rare grass than the common grass, however, in the southern limit *A. hendersonii* vegetation had the greatest overall variation. In the southern end of the distribution range, variation in the vegetation was influenced by the coverage of cryptogamic crust. Population level organization was similar throughout the distribution range of *A. hendersonii*. *Achnatherum hendersonii* morphology was congruent within and among populations. There was less morphological variation in *Achnatherum hendersonii* than *A. lemmonii*. Overall, community and population levels of organization were dissimilar. Comparisons of community and population levels

organization of rare species increases our theoretical understanding of biological organization, by increasing our power of examination. In this case, they reveal different responses by the plant as compared with its vegetation. This different response argues for different causal agents affecting morphology and vegetation.

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INTRODUCTION

Rarity

Rarity in vascular plants as well as other organisms is largely an idiosyncratic phenomenon - no one theory, hypothesis, or description explains rarity - a taxon can be rare for any number of different reasons (Drury 1974 1980; Kruckeberg and Rabinowitz 1985; Fiedler 1986; Gaston 1994). Defining rarity can be as confounding (Drury 1974, 1980; Harper 1981; and Rabinowitz 1981; Kruckeberg and Rabinowitz 1985; Gaston 1994). Also recognized is that if organisms are rare for a variety of reasons then ecological and evolutionary consequences of rarity are equally diverse (Drury 1974, 1980; Rabinowitz 1981; Fiedler 1986; Gaston 1994).

Drury's (1974, 1980) operational definition of rarity included those species that occur in widely separated sub-populations where interbreeding between the subpopulations is reduced or eliminated, or in extreme cases, those species that are restricted to a single population. More recently Argus and Pryer (1990) characterized rarity as species occurrence in a limited area or in few numbers. McJannet et al. (1993) added to Argus and Pryer's (1990) definition the concepts of geographic distribution, such as peripheral (at the edge of the distribution range) and endemic (small global population restricted to a small area). Rabinowitz (1981) developed a theoretical framework to categorize different types of rarity. She categorized rarity based on geographic range, habitat specificity, and local population size, and described seven forms of rarity (Table 1). Essentially, as summarized by Fiedler (1995), "Rarity is really a statement about geographic distribution and abundance".

Rarity is generally studied on the autecological, or population level. Representative works include those of Gankin and Major (1964) on *Arctostaphylos myrtifolia*, Meagher et al. (1978) on *Plantago cordata*, Griggs and Jain (1983) on *Orcuttia*, and Waller et al. (1987) on *Pedicularis furbishae*. This level of investigation is important, and much valuable information about rarity has been learned through studies such as these.

Table 1. The typology of rare species proposed by Rabinowitz (1981) based on three characteristics: geographic range, habitat specificity, and local population size. All categories except the first in the table define a particular type of rarity.

Local population size	Geographic range and habitat specificty			
	Large and wide	Large and narrow	Small and wide	Small and narrow
Large, dominant in some places	Locally abundant over a large range in several habitats i.e. common	Locally abundant over a large range in a specific habitat	Locally abundant in several habitats but restricted geographically	Locally abundant in a specific habitat but restricted geographically
Small, nondominant	Constantly sparse over a large range and in several habitats	Constantly sparse in a specific habitat but over a large range	Constantly sparse and geographically restricted in several habitats	Constantly sparse and geographically restricted in a specific habitat

Despite the fact that both rare and common species occur in communities, studies of rarity at the community level have been largely ignored.

The notion that both population and community levels of study are important to understand rarity is not new. It has been recognized as early as Darwin (1859), and more recently by Stebbins (1980), that a synthesis of population-level and community-level processes is needed for a full understanding of the ecological and evolutionary causes of rarity. In the same vein, Levin (1988) recognized that a synthesis of population and community theory is needed to understand processes underlying the biological organization seen at different ecological levels.

Although Darwin (1859) primarily viewed rare species as being "old", and nearing extinction, he understood that the concept of rarity included inherited, evolutionary, geographic, geologic, and ecological factors.

Stebbins (1980) recognized that each rare species has unique features, and for theories to provide a complete explanation of rarity they must encompass three major variables: the intricate mosaic of the environment in which the rare species grows; the complex genetic structure of its populations; and the history of the populations. With this in mind he proposed the gene pool-niche interaction theory that attempts to integrate the interactions of the three parameters. This theory proposes that the primary cause of rarity is adaptation to a combination of ecological factors, such as edaphic factors, that are themselves rare. Factors inherent in the gene pool of the population, such as total amount of variability, the amount of variability that can be released at one time, and the amount of variation that can be generated with respect to those particular characteristics that strongly affect the establishment of new populations (e.g. seed production and dispersal), are also important.

Levin (1988) states that one of the fundamental challenges of ecological science is to blend population and community theory. He believes that reductionistic and holistic approaches must be synthesized to understand system structure and function, particularly in relation to the way higher levels of organization may influence lower levels.

Comparative studies of rare species with common congeners increase our understanding of rarity (Gaston 1994). They assist in revealing how rare species differ from common species, provide insight into causes of rarity, and provide a framework from which to contrast degrees of rarity. A number of studies have explored rare species within a comparative framework, contrasting a rare species with a closely related but more cosmopolitan species (e.g. Kruckeberg 1951; Babbel and Selander 1974; Rabinowitz et al. 1979; Primack 1980; Pigott 1981; Greig-Smith and Sagar 1981; Rabinowitz 1981; Mehrhoff 1983; Rabinowitz et al. 1984; Fiedler 1987, 1986; Linhart and Premoli 1993; Rapson and Maze 1994; Robson and Maze 1995). While these studies have expanded our understanding of rarity, they are, with the exception of Fiedler (1986, 1987), all solely concerned with the population level of organization and lack community level comparisons.

Fiedler (1986, 1987) attempted a synthetic approach to the study of rarity and commonness in the genus *Calochortus* by incorporating several relevant causes and consequences of rarity. She collected data from nine major factors of varying influence affecting rarity and commonness of a plant taxon (Table 2). Her results demonstrated inadequacies of earlier, more general hypotheses about rarity, the need for clarification of the causes and consequences of rarity, and the need for a frame of reference. Fiedler (1986) concluded that it was unproductive to develop general theories of rare taxa until the idiosyncratic nature of rare plant species was better understood. Her approach was commendable and enhanced our understanding of rarity beyond the isolated features of individual rare species. However, her synthesis was limited to population and community level factors that directly affect the species in question, and did not account for the full range of interactions that can occur in a natural community.

Table 2. Factors outlined by Fiedler (1986) as important in a synthesis for the determination of rarity in any plant taxon.

Age of taxon
Genotype of taxon
Evolutionary history
Taxonomic position
Ecology
Population biology
Reproductive biology
Land use history
Recent human use

One way to study the full range of interactions that can occur in a natural community is by evaluating the organization of that community. Ecological organization involves the structural relationships among the elements of a system (Brulisauer et al. 1996), and can be described as suites of interrelated variables (Robson et al. 1988). Organization at the population level is reflected in the amount of phenotypic variation of a plant species, and at the community level in the structure and composition of the vegetation-unit that the particular plant species grows in.

Concepts for quantifying organization have primarily been developed at the population level, in studies of the development of an organism (Scagel et al. 1985; Robson et al. 1987; Robson and Maze 1995). Scagel et al. (1985) used quantitative multivariate methods to describe ovule development in *Nothofagus antarctica*. They measured various features of the ovules over a two week period and used principal components analysis to quantify change in ovule organization over time. The quantitative changes they observed suggested that development should be viewed in relation to the generation of complexity and organization, and corresponded to evolutionary theory based on nonequilibrium thermodynamics. Robson et al. (1987) compared morphological variation and organization within and among populations of *Balsamorhiza sagittata*. Three groups of structures were measured: leaf length and width, shoot length, and inflorescence width. These structures represented different phases of growth, and the relationships among them were assessed using principal components analysis. Variation within a population was found to be greater than variation among populations, and different structures (e.g. vegetative and reproductive) showed different organization. In respect to rarity, Robson and Maze (1995) compared growth and variation in rare and common species of *Achnatherum*. They measured blade and sheath length on vegetative and inflorescence leaves, and internode and inflorescence length on inflorescence stems, weekly over two growing seasons. Principal components analysis revealed that in addition to disparity in organization between vegetative and inflorescence shoots, disparity in organization between rare and common species was also observed.

Brulisauer et al. (1995) applied concepts of ecological organization at the community level in a study of successional change after fire in a forest understorey. A logical subsequent step is to use these concepts to make comparisons of population and community organization, and to attempt a synthesis.

It has been argued that the concept of biological organization contains two logically independent components, order and organization *sensu stricto* (Banerjee et al. 1990). In an abstract sense, order refers to the tightness of the interrelationships among the parts of an organism (or some higher level entity), whereas organization *sensu stricto*, relates to the particular parts that show relationships, i.e. the relative relationship among parts regardless of the strength of that relationship. These concepts can be depicted using descriptive statistics for the 95% confidence ellipses of scatter plots generated through multivariate analysis, where the shape of the ellipses can be related to order, and orientation of the ellipses to organization *sensu stricto* (see Methods for more detail). The general term, organization, is used in the context of both order and organization *sensu stricto*; the distinction is evident from the statistics used. These concepts and associated methods have been used to describe organization in the development of an organism (Robson and Maze 1995), as well as the development in an ecosystem (i.e. succession, Brulisauer et al. 1996).

The Rare Grass, Achnatherum hendersonii

Achnatherum hendersonii (Vasey) Barkworth occurs in several isolated populations throughout its distribution range and is restricted to a specific habitat type. Thus, according to Rabinowitz (1981), it falls in the category of a small local population with narrow geographic distribution and restricted habitat type (see Table 1). *Achnatherum hendersonii* is edaphically restricted to shallow soils on rocky basaltic outcrops, or ridges, that commonly experience frost heave or other cryogenic processes. It is known to occur in several locations east of the Cascade Mountain range in central Washington and central Oregon (Figure 1; Hitchcock et al. 1969; Vrilakas 1990; Salstrom 1994).

Taxonomic studies of *A. hendersonii* were made by Spellenberg (1968), Spellenberg and Mehlenbacher (1971), Maze et al. (1972), and Barkworth (1993). Through these studies, *A. hendersonii* was moved from the genus *Oryzopsis* to the genus *Stipa* (Spellenberg and Mehlenbacher 1971; Maze et al. 1972), and more recently to the genus *Achnatherum* (Barkworth 1993).

Maze (1981) was the first to focus on the rarity and ecology of *A. hendersonii*, describing morphological adaptations of the root system that help to explain the local distribution of this species. Rapson and Maze (1994) and Robson and Maze (1995), studied *A. hendersonii* to examine a potential correlate of rarity, namely the collapse in genomic integration of growth processes. In that view, rarity of a species is related to a less precise genomic control over the integration of the various developmental phenomena compared with more common species. Phenotypic variation of different morphological structures, variation in relation to growth, and comparisons with the more common congeners, *A. lemmonii*, *A. occidentalis*, and *A. thurberiana*, have been studied. These studies were all done at the population level, and with populations of *A. hendersonii* from one site only. Comparisons have not been made among disjunct populations throughout the distribution range of *A. hendersonii*, nor have comparisons at the community level been made.

The nature of rarity in *A. hendersonii* appears similar to that in *Arctostaphylos myrtifolia*. *Arctostaphylos myrtifolia* is limited to certain outcrops of Eocene laterite, kaolin-altered rhyolite, and an acid sericitic schist in the foothills of the Sierra Nevada, California (Gankin and Major 1964). These soils are acidic and sufficiently low in nutrients to exclude dominance of the typical climax ("zonal") vegetation of the area. Gankin and Major (1964) found that the disjunct distribution of *Arctostaphylos*

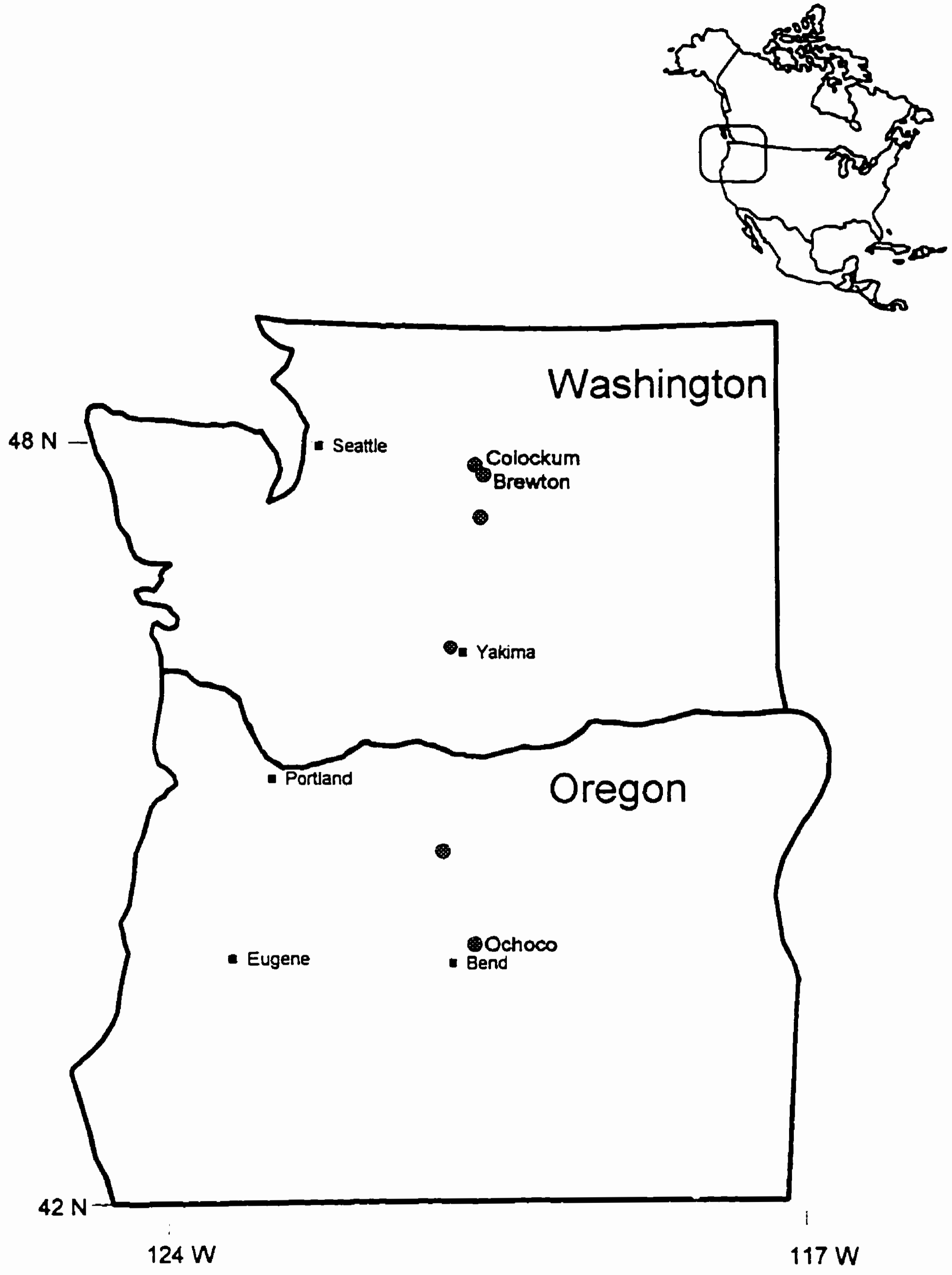

Figure 1. Distribution range of *Achnatherum hendersonii* and study site locations. Each symbol represents the general location where several to many populations of *A. hendersonii* occur. The study sites are labeled: Colockum; Brewton; Ochoco.

myrtifolia was related to specific edaphic conditions that weakened competition from the zonal vegetation.

Achnatherum hendersonii and *Poa secunda*, both perennial bunch grasses, often grow within the same clump (Maze 1981; pers. obs.). *Achnatherum hendersonii* is not found on deeper soils where vegetation cover is more dense, whereas *P. secunda* grows abundantly in those areas. *Achnatherum hendersonii* may have a competitive advantage over *P. secunda* in lithosolic habitat types that experience frost heave, because *A. hendersonii*, as observed by Maze (1981), has a deeper root system, with cortex independent of the stele, thereby allowing soil movement while the anchoring and absorbing stele remains. This appears to stabilize *A. hendersonii* during freeze and thaw because, unlike *P. secunda*, *A. hendersonii* does not have exposed roots and is not thrust from the ground through frost action. The long roots may also allow *A. hendersonii* access to soil water deep within the fractures of the basalt that *P. secunda* cannot reach because of its shallower root system.

Natural disturbances such as those caused by frost heave are common in the areas in which *A. hendersonii* grows. These particular disturbances as well as natural disturbances in general are an integral part of community level organization (Sousa 1984). The intermediate disturbance hypothesis (Connell 1978) addresses community level organization in relation to disturbance as a mechanism of species coexistence in plant communities.

Plant Community and Population Concepts

Banerjee et al. (1990) suggest that concepts of organization in biology are more appropriately applied to population levels (e.g. development of the individual) than to community levels. Each of these levels of biological organization, however, involves a complex of numerous causal variables, each affecting the other, and none can truly be observed autonomously. The basic principles of biological organization, i.e. the structural relationships between interrelated variables, can be quantified on both the population and community levels. Once quantified, these levels of organization can be compared and synthesized.

Community level organization can be estimated by analyzing the vegetation with which the plant in question is associated. The vegetation of an area is the result of the interaction of numerous abiotic and biotic factors of a given region. Vegetation, through the integrative ability of plant growth, represents an effective summary of those factors. Mueller-Dombois and Ellenberg (1974) expressed this relationship in the form of a function :

$$\text{plant community} = \int(f,\ a,\ e,\ h,\ t)$$

where flora (f) consists of all the plant species present in an area providing the basic raw material of the vegetation; accessibility factor (a) refers to the distributions of the species, including their dispersal ability and establishment potential; ecological plant properties (e) consists of species lifeforms, physiological requirements, and competitive abilities; habitat (h) is the total of environmental factors (e.g. macro- and microclimate, soil, topography, aspect, elevation, fire, predation, human intervention); and time (t) denotes a temporal complex of rate of change, community age, and historical disturbance. The last noted factor, time, is an overriding dimension according to Billings (1965). Moreover, plant community formation can be viewed on different temporal scales. For example, on a short-time scale, community formation can be viewed as succession, and on a long-time scale, as evolution (Mueller-Dombois and Ellenberg 1974).

A similar model was introduced by Major (1951) showing vegetation as a function of various determining factors by applying the five-factor approach of soil formation (Jenny 1941). The Mueller-Dombois and Ellenberg (1974) function is similar to Major's (1951) equation, but emphasizes properties of the organism and combines separate environmental factors into habitat.

As community level organization can be estimated through vegetation, organization at the population level can be estimated through the morphology of the species in question. The morphology or phenotype of a plant can be expressed as the sum of the genotype (g), prevailing environment (c), and past environment (p) (Barbour et al. 1987). As a functional relationship this can be expressed as:

$$\text{phenotype} = \int(g, c, p)$$

The effect of past environment on phenotype was illustrated by Billings et al. (1971) who reported that optimum temperature for photosynthesis in alpine specimens of *Oxyria digyna* shifted by as much as 11° C, whereas optimum temperature for photosynthesis in arctic specimens of the same species shifted by only 1° C.

It is interesting to note the similarities among the functional models of plant community and phenotype formation, and the factorial approach used by Fiedler (1986). For example, age of taxon, genotype of taxon, evolutionary history, taxonomic position, ecology, population biology, reproductive biology, land use history, and recent human use (Fiedler 1986) are all expressed in terms of flora, accessibility factor, ecological plant properties, habitat, and time (Mueller-Dombois and Ellenberg 1974), and in genotype, prevailing environment, and past environment (Barbour et al. 1987).

Thesis Objectives

The purpose of this dissertation is to compare the rare grass species, *Achnatherum hendersonii*, with the related common species *A. lemmonii*, on both population and community levels of organization. *Achnatherum lemmonii* was chosen for a frame of reference because it is closely related to *A. hendersonii*, and the two species have been reported to form a morphologically intermediate, sterile hybrid (Spellenberg and Mehlenbacher 1971). Moreover, *A. lemmonii* is found in the same locale within the northern distribution range of A. *hendersonii*, thereby removing the effect of prevailing and historical macroclimate variation on the comparisons made.

On the community level I examined the relationship of the organization in the vegetation in which A. *hendersonii* grows, comparing both sympatric and disjunct populations of the rare grass. The disjunct populations included both geographically near (Colockum and Brewton) and distant (Ochoco) sites, from the northern and southern distribution limits of A. *hendersonii*. For a frame of reference I also made comparisons with the organization in adjacent vegetation where A. *hendersonii* was absent, including areas where A. *lemmonii* grows, areas dominated by *Agropyron spicatum* in the northern distribution limit, and vegetation that appeared otherwise similar to that in which A. *hendersonii* grows but lacked A. *hendersonii* in the northern and southern distribution limits.

On the population level I examined the relationship of morphological organization in sympatric and disjunct populations of A. *hendersonii* as well as morphological comparisons with populations of the common grass, A. *lemmonii*. The morphological comparisons were made from the same locations as used for the vegetation comparisons.

To address an indirect result of the causal mechanism of rarity in A. *hendersonii* proposed by Maze (1981), I examined competitive interactions between A. *hendersonii* and *Poa secunda*. The thrusting of *Poa secunda* plants out of the soil column and the consequent exposure of roots through frost heave is related to Gankin and Major's (1964) contention that azonal soils (soils not typical of a given area) weaken competition from the zonal vegetation, i.e., the exposure of roots may compromise competitive ability. Although tangential to the thesis, this was done to indicate where future studies might focus.

The specific questions addressed in this thesis fall into four general areas:

A. Community-level:

1. How does the organization (order, organization *sensu stricto*, and variation) of the vegetation in which a rare species grows compare with the organization of the vegetation in which a common congener grows?

2. How does the organization of the vegetation compare among sympatric and disjunct populations of a rare species?

3. Are there observable trends in the organization of the vegetation; e.g. can this type of rarity (geographically narrow and restricted to a specific habitat type; Table 1; Rabinowitz 1981) be predicted through the vegetation in which a rare species occurs?

B. Population-level:

4. How does the morphological organization of a rare species compare with that of a common congener?

5. How does the morphological organization of a rare species compare at its distribution limits (sympatric and disjunct populations)?

C. Community-population synthesis:

6. How does community- and population-level organization compare in a rare species and in a common congener?

7. What is the relationship between community- and population-level organization in a rare species and a common congener?

D. Mechanism for rarity:

8. How does seasonal growth of an edaphically restricted rare species compare to an associated but more cosmopolitan species?

METHODS

Plants Studied

The endemic grass, *Achnatherum hendersonii* (Vasey) Barkworth (Barkworth 1993), is a rare perennial bunch grass (Figure 2) that occurs in a few isolated areas in central Washington, and northern and central Oregon (Figure 1) (Spellenberg 1968; Hitchcock et al. 1969; Vrilakas 1990; Salstrom 1994; Washington Natural Heritage Program 1994). It is locally abundant but restricted to sites with shallow soils (lithosols) on rocky basaltic outcrops where cryogenic processes such as frost heave are common (Maze 1981). The common grass, *Achnatherum lemmonii* (Piper) Barkworth (Barkworth 1993), is also a perennial bunch grass, but extends from the central Sierra Nevada of California, north to southern British Columbia and east to Idaho, Montana, and Utah (Spellenberg and Mehlenbacher 1971; Barkworth and Linman 1984). *Achnatherum lemmonii* also grows on basaltic soil but usually in sites where the soils are deeper and more mesic (Spellenberg and Mehlenbacher 1971). Both species are native to the Pacific Northwest.

Achnatherum hendersonii and *A. lemmonii* are closely related. In several sites in Washington, *A. hendersonii* and *A. lemmonii* are sympatric and form sterile, morphologically and anatomically intermediate hybrids (Spellenberg and Mehlenbacher 1971). The two species also share unique events in development of the callus, outer integument, and apex of the lemma (Mehlenbacher 1970).

Habitat Description

Achnatherum hendersonii and *A. lemmonii* grow in the ecotone between the shrub-steppe and the *Pinus ponderosa* Zone (Daubenmire 1969; Franklin and Dyrness 1973). These areas are often characterized by a mosaic of shrub-steppe on basaltic outcrops within the lower elevational limit of *P. ponderosa* stands in Washington (Daubenmire 1972) and in basaltic outcrops within *P. ponderosa* forests (also termed scabs) within Oregon (J. Maze, pers. comm.). These grasses grow within the *Artemisia rigida* - *Poa secunda* and

Figure 2. *Achnatherum hendersonii*.

Agropyron spicatum - Poa secunda lithosolic phase, habitat types as described by Daubenmire (1970). The habitat types are named for the dominant species. The vegetation in these areas is characterized by a low percent coverage of vascular plant species and a patchy to continuous cryptogamic crust layer.

The substratum in these habitat types generally consists of a thin layer of frost heaved basalt rocks on top of fractured basalt bedrock. The soils between the fractures in the basalt are a sandy loam to a loam; Lithic Haploxerolls (Beieler 1969; Daubenmire 1970; Lenfesty and Reedy 1985).

Lithosolic habitat types are found on slopes and on flat areas that have no apparent drainage. Both flat and sloped areas often have standing water during periods of thaw, leading to diurnal freeze and thaw cycles and to the lifting of some species out of the soil. One result of this freeze and thaw is that individual plants of *Poa secunda* are often lifted until they are perched on mounds (Figure 3; Daubenmire 1970). Frost boils also occur where interstitial loam is suddenly extruded through a weak area in the frozen soil crust (Figure 4). The sudden extrusion can turn *Poa secunda* plants on their sides with roots exposed. These lithosolic habitat types experience much perturbation from summer drought and heat alternating with winter wetness and frost action. Frost action occurs diurnally also, especially during late spring and early fall. Despite this, these areas often have species diversity as great as habitat types with deeper soils (Daubenmire 1970). Another form of disturbance on the lithosolic habitats is related to the digging and burrowing activities of rodents (Daubenmire 1970).

For this study, a set of reference plant communities within the *Artemisia rigida - Poa secunda* and *Agropyron spicatum - Poa secunda* lithosolic phase, habitat types were selected for study. Areas that contained *Achnatherum hendersonii* were identified as *A. hendersonii* communities (Ache). These areas were selected specifically in order to compare variation and organization of vegetation with areas that appeared identical but did not contain *A. hendersonii*, referred to as the minus *A. hendersonii* communities (-Ache). It was felt that comparisons on the

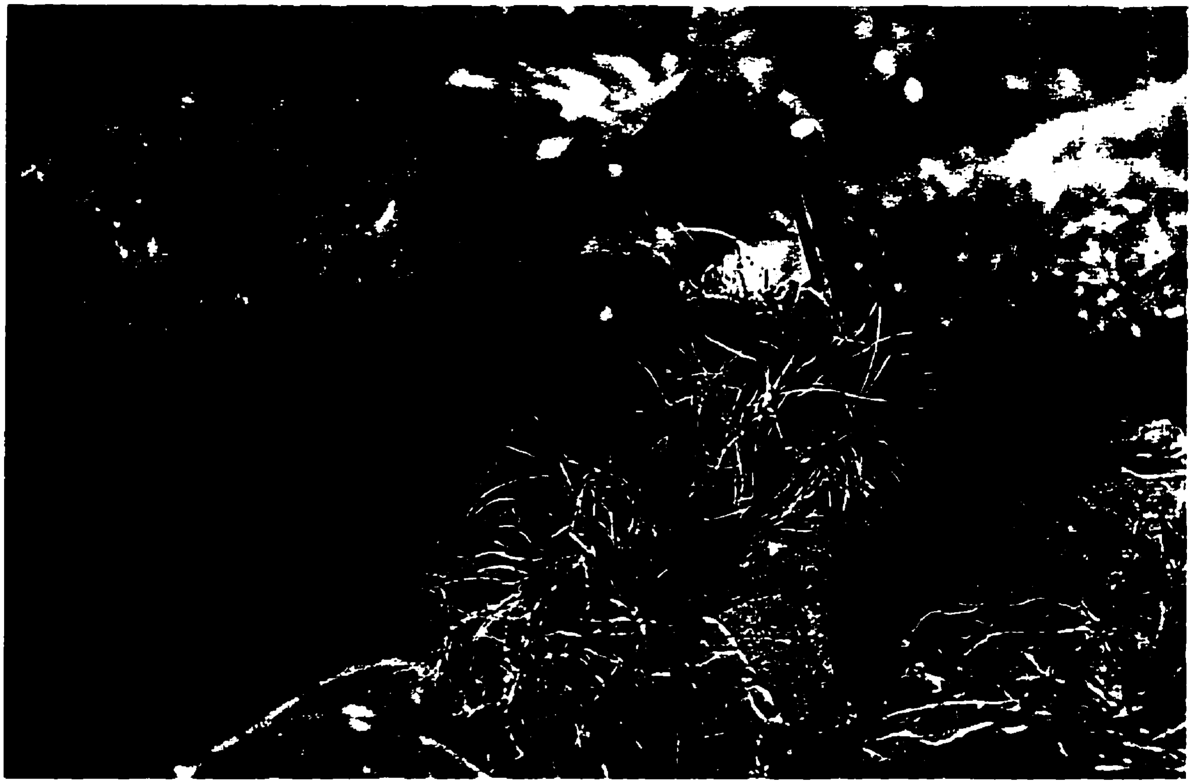

Figure 3. Frost heaved *Poa secunda* at the Colockum study site.

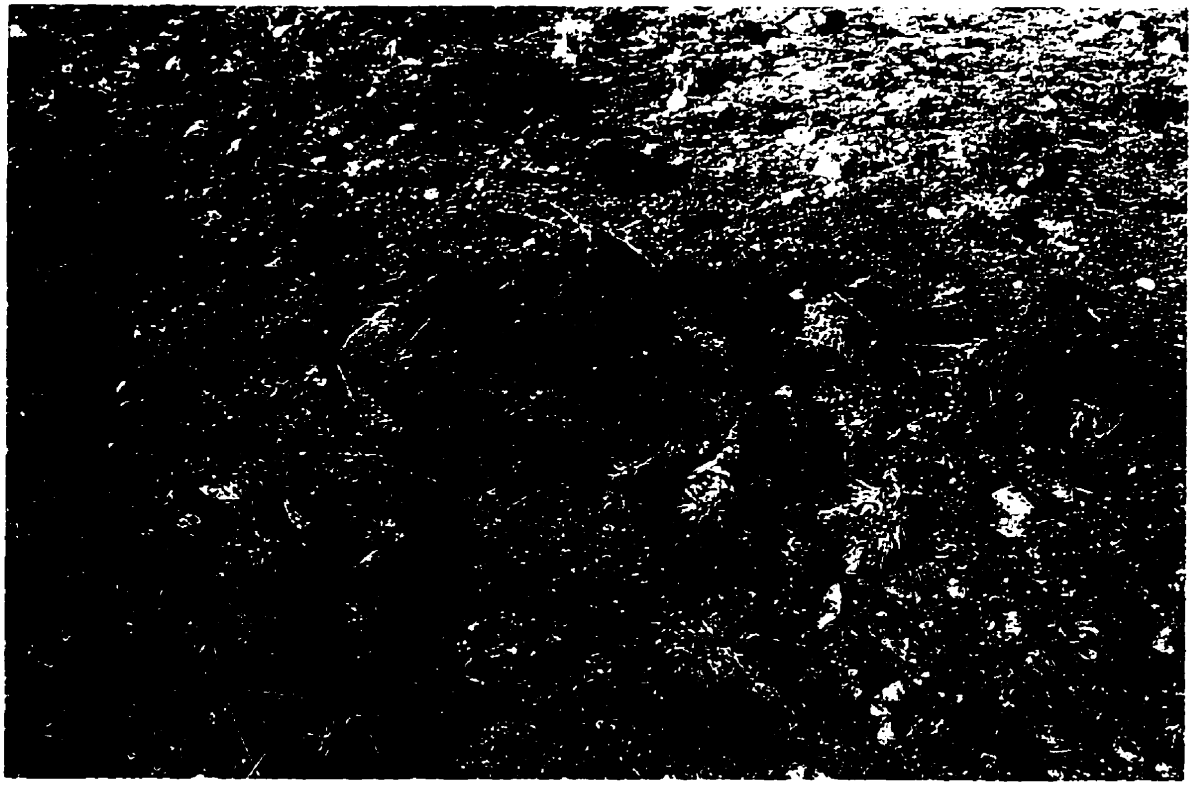

Figure 4. Frost boil at the Colockum study site (center of photo).

community level might show subtle differences that account for the lack of *A. hendersonii* in these areas. *Agropyron spicatum* communities (Agsp) were identified as areas dominated by *A. spicatum* but with no *Achnatherum hendersonii* present, although these areas are often adjacent to, or interspersed with the areas containing *A. hendersonii*. The *Agropyron spicatum* communities were selected for comparisons with the *Achnatherum hendersonii* and the minus *A. hendersonii* communities, and to contrast areas where there appeared to be obvious compositional differences between the communities. Finally, areas dominated by *A. lemmonii* (Acle) were selected for comparisons between a rare and a common grass species.

Study Sites

Three study sites were chosen to compare variation and organization on the population and community levels. The Colockum and Brewton study sites are in the Colockum Wildlife Area, Washington, U.S.A., at the northern distribution limit of *A. hendersonii*, and the Ochoco study site is in the Ochoco National Forest, Oregon, at the southern distribution limit of the rare species (Figure 1).

Colockum

The Colockum Wildlife Area is ca. 26 km SSE of Wenatchee, Washington. The Colockum study site (Sections 8 and 9, Township 20 North, Range 21 East; 47°15'0"N, 120°12'30"W) is at an elevation of 1060 to 1140 m, and consists of an exposed, southeast slope with a saddle in the middle, and rising to form a hill to the east (Figure 5). Precipitation is ca. 38 cm annually, with over 60 percent falling from November through April, and much of this as snow (NOAA et al. 1995; Franklin & Dyrness 1973). Mean January and July temperatures are -1.2° C and 22.8° C, respectively (NOAA et al. 1995; Franklin & Dyrness 1973).

The Colockum study site lies within the transition of shrub-steppe to closed coniferous forest (Daubenmire 1969; Franklin & Dyrness 1973). More

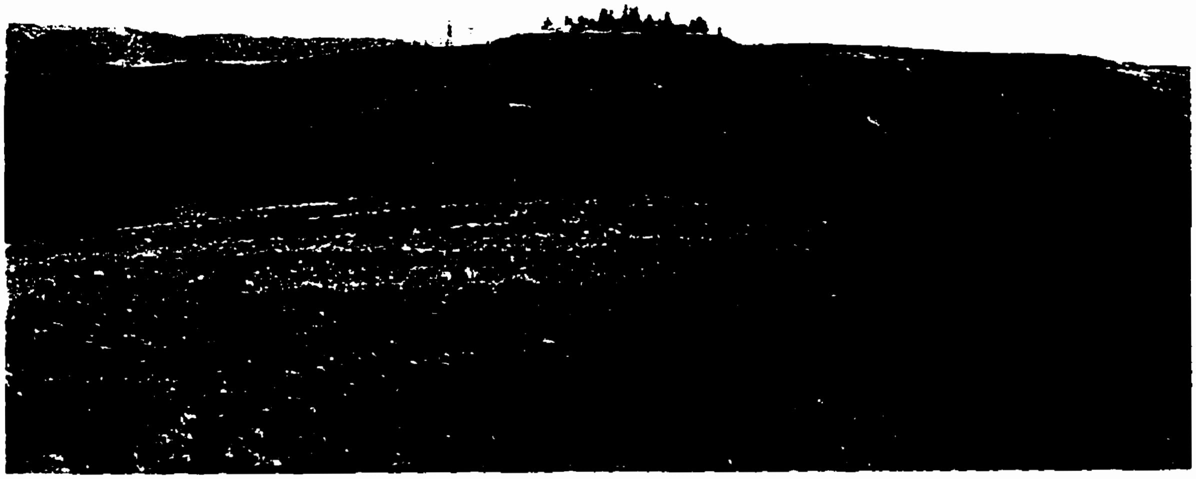

Figure 5. The Colockum study site looking east.

specifically, the study site consists of a mosaic of *Artemisia rigida* - *Poa secunda* and *Agropyron spicatum* - *Poa secunda* lithosolic phase, habitat types at the lower elevational limit of the *Pinus ponderosa* Zone (Daubenmire 1970). These areas have low percent coverage of vegetation, with bareground ranging from 30 to 85 percent. Dominant species include *Poa secunda*, *Lomatium* spp., *Balsamorhiza hookeri*, *Artemisia rigida*, and *Eriogonum* spp. Evidence of frost boils, frost heaving, and burrowing by rodents is common at this site.

The Colockum study site was the only site examined in this study where the rare (*Achnatherum hendersonii*) and the common (*A. lemmonii*) grew together in adjacent and similar habitats. *Achnatherum lemmonii* grew on the edge of the shrub-steppe zone adjacent to the *Pinus ponderosa* zone (Franklin and Dyrness 1973), in deeper soils than *A. hendersonii*. The *A. lemmonii* vegetation plots at the Colockum study site were on the west end of the same slope as the vegetation plots of *A. hendersonii* (Figure 5). Bareground is not a dominant feature in these areas, ranging from zero to 20 percent coverage. Dominant species include *Artemisia rigida*, *Poa secunda*, *Lomatium* spp., *Lithophragma* spp., and *Achillea millefolium*.

Brewton

The Brewton study site (southwest quarter of the southwest quarter of Section 20, Township 20 North, Range 22 East; 47°12'30"N, 120°7'30"W) is located ca. 8 km southeast of the Colockum study site within the Colockum Wildlife Area (Figure 6). This study site is within the shrub-steppe zone, in the same habitat types as the Colockum study site, namely *Artemisia rigida* - *Poa secunda* and *Agropyron spicatum* - *Poa secunda* lithosolic phase, habitat types (Daubenmire 1970). The site is on the saddle of a southeast to northwest oriented ridge at an elevation of 622 km. This area appears to be at the lower elevational limit of *Achnatherum hendersonii* in this location. Because of the lower elevation, the Brewton site is likely to be slightly drier and warmer than the Colockum site. *Achnatherum hendersonii* and associated species generally begin to grow, flower, and set seed earlier at

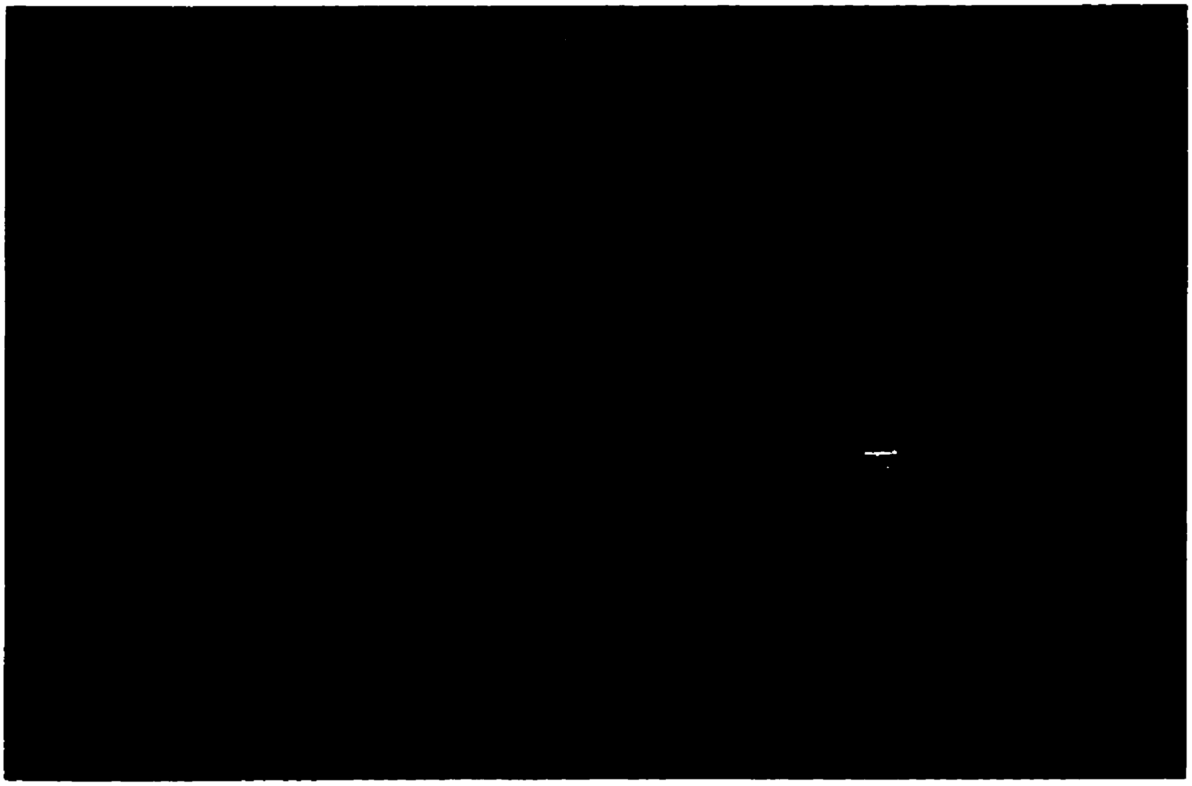

Figure 6. The Brewton study site.

Brewton than at Colockum; however, percent coverage of bare ground and dominant species is similar at both study sites. This site also shows evidence of frost action (e.g. frost heave and frost boils).

Ochoco

The third study site is in the Ochoco National Forest ca. 50 km east of Prineville, Oregon, (Northeast quarter of the Northeast quarter of Section 19, Township 15 South, Range 22 East; 44°15'30"N, 120°7'30"W), at an elevation of 1418 m (Figure 7). The Ochoco study site is in a shrub-steppe community that forms a mosaic with the *Pinus ponderosa* zone within the soil-plant defined North Central Area of central Oregon (Anderson 1956; Daubenmire 1969; Franklin and Dyrness 1973). As with the Colockum and Brewton study sites, a high percentage of bareground (20 to 85 percent) is a dominant feature of this site. Dominant species include *Poa secunda*, *Lomatium* spp., *Blepharipappus scaber*, and *Agoseris glauca*. The site consists of a shallow ridge that has an overall slope (ca. 5 percent) to the east, and slopes off gradually to the north and south.

January mean minimum temperature is -7.0° C, and July mean maximum temperature is 29.0° C (Franklin and Dyrness 1973). Mean annual precipitation is 40 cm, generally falling from October to April mainly as snow (Franklin and Dyrness 1973). This site generally has a deeper and longer lasting snowpack than the Colockum and Brewton study sites, and the growing season begins later in the year and is shorter (pers. obs.). The substratum is composed of basalt cobbles, gravel, and pebbles similar to the Colockum and Brewton study sites, although with a higher percentage of gravel (2 mm to 7.5 cm) than cobble (7.5 to 25 cm). The soils are a loam as compared to a sandy loam at the Colockum and Brewton study sites, and are formally classified as Lithic Haploxerolls (J. David, pers. comm.). This site also demonstrates distinct striping owing to alternating disturbances of the cryptogamic crust (Figure 8). The cause of disturbance appeared to be from frost action.

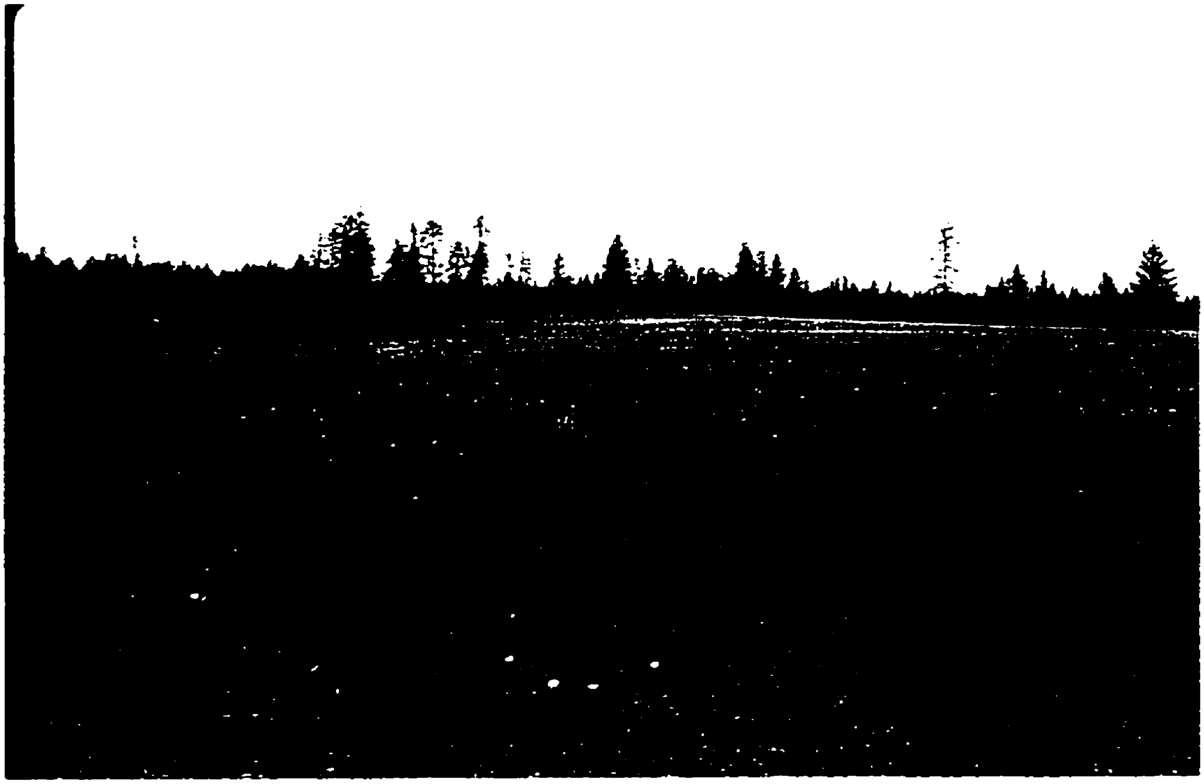

Figure 7. The Ochoco study site.

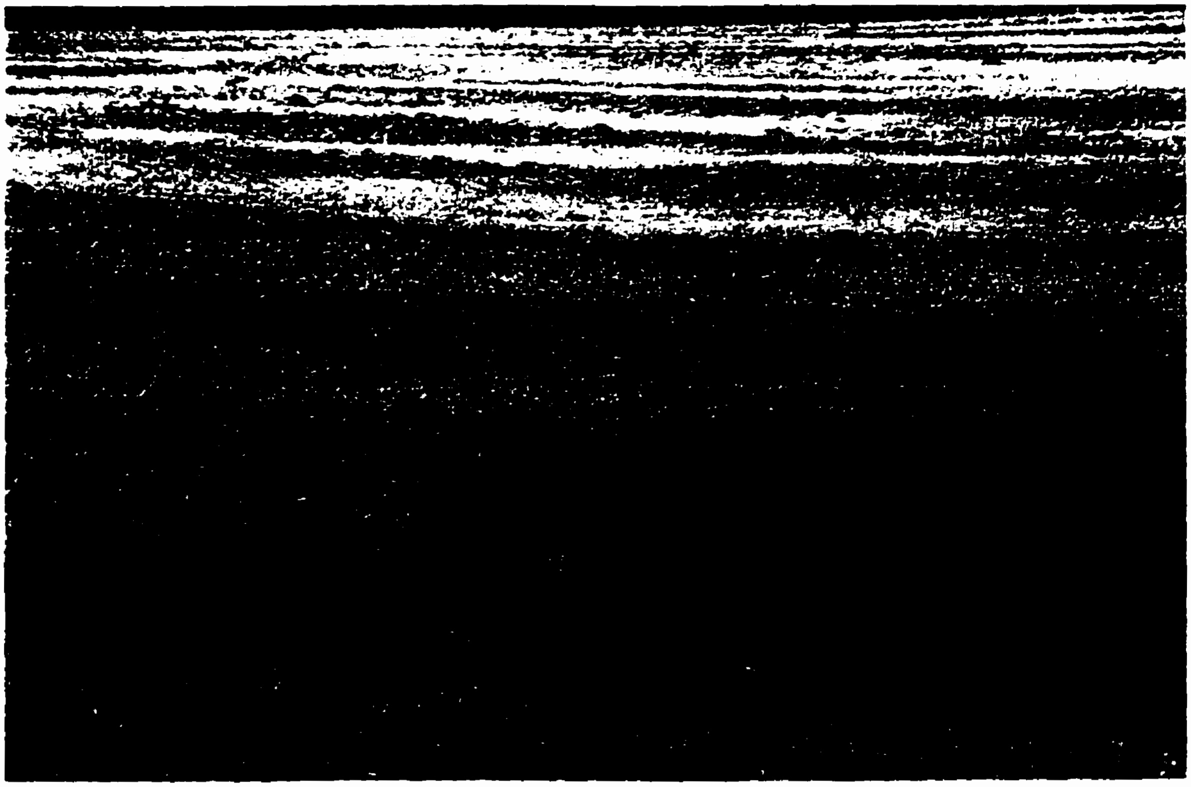

Figure 8. Striping of the vegetation, resulting from alternating bands of disturbed cryptogamic crust, at the Ochoco study site.

Sampling

Vegetation

Vegetation was sampled during the growing season from late-April to early-June of 1995 and 1996. Five by five meter plots were randomly selected within the desired communities at each of the three study sites. Vegetation was sampled systematically with a 20 X 50 cm plot-frame every meter starting at the southwest corner of each 5 X 5 m plot for a total of 25 plot-frames per plot. Areal percent ground coverage (percent cover) was estimated for every vascular plant species and bryophyte species within the 20 X 50 cm plot-frame (Daubenmire 1959). Vascular plant names followed Hitchcock and Cronquist (1973) except where noted, and bryophyte names followed W. B. Schofield (pers. comm.). Density was recorded for *Achnatherum hendersonii* and A. *lemmonii* by counting individuals in twenty-five - 1 m^2 quadrats within the 5 X 5 m plots used for vegetation sampling. Slope, aspect, and elevation were recorded for each vegetation plot. All vegetation plot corners were permanently marked with steel spikes.

Soil depth was measured with a metal probe (Collins et al. 1989) at the northwest corner, the center, and the southeast corner of every 20 X 50 plot-frame for a total of three depth measures per plot-frame, and 75 per 5 X 5 m vegetation plot.

Soil samples were collected within the top 10 cm of the soil profile, from soil pits dug adjacent to each vegetation plot. Soil samples representing vegetation plots of similar communities within each site were combined and analyzed for pH (saturated paste), P (μg/g), K (μg/g), NO_3-N (μg/g), NH_3-N (μg/g), texture (hydrometer method), percent carbon, percent hydrogen, and percent nitrogen, and percent organic matter (colorimetric). Soils were analyzed at the Analytical Sciences Laboratory, University of Idaho. The soil samples were collected at the Ochoco study site on 23 May 1996, at the Colockum study site on 25 May 1996, and at the Brewton study site on 14 June 1996.

The Colockum study site was selected for intensive vegetation study: *A. hendersonii* communities (Ache) were contrasted with *A. lemmonii* communities (Acle), with communities lacking *A. hendersonii* (-Ache), and with adjacent *Agropyron spicatum* communities (Agsp). The Brewton study site was selected as a nearby disjunct *Achnatherum hendersonii* population to compare with similar vegetation types at Colockum. The Ochoco study site was selected as a more distant disjunct *A. hendersonii* population to compare with the Colockum and Brewton study sites. The Colockum and Ochoco study sites represent the northern and southern distributional extremes, respectively, of *A. hendersonii.*

The Colockum study site consisted of ten plots labeled C1-C10. Plots C1, C3, and C5, represent *A. hendersonii* communities (Ache); C2, C4, and C6, represent *Agropyron spicatum* communities (Agsp); C7 and C9, represent minus *Achnatherum hendersonii* communities (-Ache); and C8 and C10 represent *A. lemmonii* communities (Acle).

The Brewton study site consisted of three plots: B1 (Ache), B2 (-Ache), and B3, (Acle).

The Ochoco study site consisted of four plots, two in areas where the cryptogamic crust was disturbed - O1 (Ache), and O3 (-Ache) - and two in areas where the cryptogamic crust was intact - O2 (-Ache) and O4 (Ache). *Agropyron spicatum* communities (Agsp) comparable to the Colockum and Brewton study sites were not available at the Ochoco study site.

Morphology

To test for within and between population variation and assess order and organization *sensu stricto*, morphological measurements were made on vegetative and inflorescence leaves. I measured both inflorescence and vegetative leaves because phenotypic variation differs between inflorescence and vegetative stems in *Achnatherum hendersonii* (Robson and Maze 1995). Morphology was measured after the plants had begun to flower, generally from mid- to late-May (1995 and 1996), and growth had ceased. Twenty-five plants from each A. *hendersonii* and each A. *lemmonii* vegetation plot were sampled randomly using random numbers to locate specific points (Rapson and Maze 1994). If the correct species was not within 20 cm of the sampling point, another point was taken. Morphology was sampled randomly instead of systematically because densities were low and individual plants were not always present in the 20 X 50 cm plot-frames used for sampling vegetation. Once selected, the inflorescence culm and vegetative tiller from each plant were removed. The variables measured for the inflorescence and vegetative leaves were the blade length, blade width, sheath length, and ligule length, because these structures are homologous in the inflorescence and vegetative stems (Figure 9). Measurements were made with a hand held ocular micrometer for blade width and ligule length, and a ruler for blade and sheath length. All measurements were recorded in the field.

Growth Experiment

To test a possible mechanism for the cause of rarity in A. *hendersonii* an experiment was designed to determine if *Poa secunda* has a competitive advantage over A. *hendersonii* in deeper soils. *Poa secunda* and A. *hendersonii* were planted in garden conditions and growth was measured over one growing season. Plants were collected from the Colockum study site on 30 March 1996, while the grasses were still dormant. The following day, tillers of each species were divided from the plants and planted into 15 X 30 cm pots with potting soil. The following planting combinations were used: A. *hendersonii* alone (A); A. *hendersonii* with A. *hendersonii* (AA); A. *hendersonii* with P. *secunda* (Ap); P. *secunda* with A. *hendersonii* (Pa); P. *secunda* alone (P); and P.*secunda* with P. *secunda* (PP). Ten of each combination were planted for a total of 50 pots. Capital letters denote plants that were measured; thus, Ap and Pa were the same species combination, except that the measurements were made on different species. The pots were arranged randomly, 35 cm apart on center, five across and ten deep. The soil was kept moist throughout the growing season. Growth measurements were

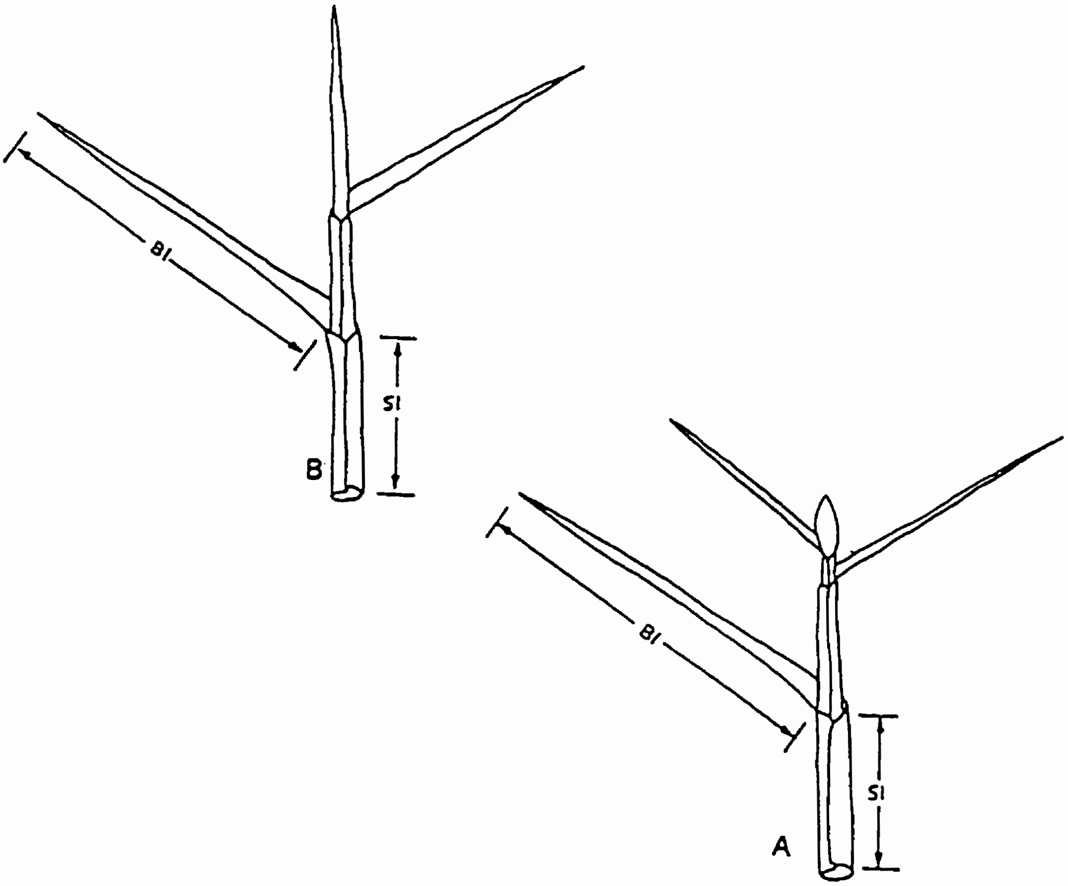

Figure 9. Inflorescence (A) and vegetative (B) leaf sheath length (Sl) and blade length (Bl) measures.

recorded every ten days beginning with the third day after planting and continued until plants completed flowering. Growth measurements consisted of the plant height (h) and diameter (d). Because many dead culms were present at the base of the plants, diameter was measured at half the height of the plant without compression of the stems. Growth was calculated as the difference in volume ($h\pi(d/2)^2$) between the final set of measurements and the second set of measurements during the 1996 growing season. Biomass was not used as a measure of seasonal growth for two reasons: the plants were small and contained dead culms from previous years that would distort biomass measurements, and measurements on the same plant were required throughout the experiment.

Data Analyses

Principal component analysis (PCA) was selected for the vegetation and morphological analyses. This method provides a quantitative assessment of community and population level variation within and between vegetation plots, study sites, and sympatric and disjunct populations. Moreover, the use of a common method allows vegetation and morphological variation to be compared directly. PCA reduces a large number of original correlated variables (i.e. plant species in plots and morphological traits on individuals) to a smaller number of summary variables. The transformation preserves the relationships in the original data as closely as possible, thereby achieving a more efficient description of the information (Gauch 1982; Manly 1986). The new, transformed variables are referred to as the principal components or PCA axes of the data.

In a graphical sense, PCA projects a multidimensional cloud of points into a space of fewer dimensions (Gauch 1982). This is achieved through the calculation of eigenvectors and eigenvalues. Eigenvectors, also termed loadings, contain the weights of each of the original variables on each component axis (Kent and Coker 1992). Eigenvector elements are scaled similar to correlation coefficients, such that the further from zero an element is, the more important the corresponding variable is in influencing the variation along a particular component axis (Kent and Coker 1992). Eigenvalues represent the relative contribution of each component axis, the size of which gives a direct indication of the importance of that component in explaining the total variation within the data set (Kent and Coker 1992). PCA axes are ranked by their eigenvalues, such that the first PCA axis explains the greatest amount of total variance. When the first few eigenvalues account for much of the total variance, PCA projection allows insight into the structure of the data (Gauch 1982).

Community

I used separate PCAs of correlation matrices to analyze community level variation and organization of the following vegetation data sets:

1. Colockum vegetation - for comparisons of sympatric populations of a rare grass, and for comparison of a rare grass and a closely related common grass.
2. Brewton vegetation - for comparisons between disjunct reproductively isolated populations of a rare grass that are geographically close (Colockum).
3. Ochoco vegetation - for comparison between disjunct reproductively isolated populations of a rare grass that are geographically distant.
4. Vegetation of plots from all study sites containing *A. hendersonii* and vegetation plots containing *A. lemmonii* - to compare a rare grass and a closely related common grass.
5. Vegetation of plots from all study sites that contained *Achnatherum hendersonii* - to focus

exclusively on community level variation and organization of a rare grass.

6. Vegetation of plots from all study sites - to analyze overall community level variation and organization at the distribution limits of a rare grass.

The data for the PCAs consisted of percent cover values recorded for species in the 20 X 50 cm plot-frames for each vegetation plot. The species were the variables and the plot-frames were the samples. To reduce the amount of noise in the data sets, a species had to have at least 0.5% mean areal coverage in the 5 X 5 m vegetation plots, to be included in the PCA analyses.

Population

Population level variation was analyzed using PCA on the morphological measures of the inflorescence and vegetative leaves. Separate PCAs of correlation matrices were run for *A. hendersonii* and *A. lemmonii* morphology at the Colockum, Brewton, and Ochoco study sites. The following data sets were analyzed: inflorescence morphology; vegetative morphology; and, inflorescence and vegetative morphology combined. Inflorescence and vegetative morphology data were analyzed separately and together because patterns of variation are reported to differ between inflorescence and vegetative shoots (Robson and Maze 1995). Inflorescence shoots of rare species display less variation than vegetative shoots. PCA of the combined inflorescence and vegetative data was performed to indicate the overall variation within and among populations of the whole plant. The data for the morphological PCAs consisted of the morphological measurements (inflorescence and/or vegetative blade and sheath length, blade width, and ligule length) recorded for individual plants for every vegetation plot that contained *A. hendersonii* or *A. lemmonii*. The measurements were the variables and the individual plants were the samples.

Organization

Bivariate 95% confidence limit ellipses, calculated and plotted on the first two PCA axes, were used to delineate the particular groups described above. These ellipses describe the position and spread of PCA scores along the first two axes. The descriptive statistics theta, eccentricity, and area were calculated from the ellipses (Robson et al. 1988; Scagel et al. 1985; Jolicoeur 1968; Jolicoeur and Mosimann 1960). Theta describes the orientation of the ellipse relative to the first PCA axis, eccentricity (ratio of minor and major axes) describes the shape of the ellipse, and area describes the size of the ellipse. These statistics give an indication of organization *sensu stricto* and order by estimating variable covariation (theta), and strength of correlation (eccentricity (0, no correlation; 1, perfect correlation)) respectively, as well as the relative amount of variation (area) (Robson et al. 1988).

The bivariate 95% confidence ellipses offer two major advantages for this study. First, they give a summary of the positions of communities or plants being compared without the clutter and confusion of ordinations in which every item analyzed is presented as a symbol. Second, the associated statistics can be used to estimate the variation and organization expressed in the communities and populations compared. Variation is related to the area of the 95% confidence ellipses. This relationship is a fairly obvious one through the univariate analogy between area and variance of the PCA axis scores from which the 95% confidence ellipses were derived. The two aspects of organization, order and organization *sensu stricto*, are depicted in the shape and orientation of the 95% confidence ellipses, order as eccentricity, and organization as theta. The relationship between eccentricity and correlation strength (see Banerjee et al. 1990) is like that between area and variation, fairly straightforward. The relevant univariate analogy is regression analysis; as eccentricity approaches 1.0, the ability of the scores on one axis to predict those on the other also approaches perfection (see Banerjee et al. 1990). In contrast, theta has a less obvious relationship to covariation structure (i.e. organization *sensu stricto*). Because of several computational steps between the covariation among specific variables and theta it is extremely difficult, if not impossible, to relate a specific theta to specific among-variable covariations; however, it can be said that a change in theta indicates an unspecified change in among-variable covariation.

There is another advantage to using bivariate ellipses from PCA in a study comparing population attributes, expressed as morphology, and features of communities, expressed as percent species cover. Such advantage is conveyed in a reduction of very different sources of data to common parameters. Thus, it is possible to compare the 95% confidence ellipse statistics among populations and communities as a way to compare, and ultimately integrate, different types of data, both of which seem to be relevant to understanding the concept of rarity.

Synthesis

A synthesis of the community and population levels of organization was achieved by plotting the first PCA axis scores from vegetation of plots from all study sites containing A. *hendersonii* and A. *lemmonii*, against first PCA axis scores of inflorescence and vegetative morphology combined. Bivariate ellipses were constructed and descriptive statistics were calculated. Because vegetation was sampled systematically and morphology was sampled randomly, morphology PCA axis one scores were randomized ten times, and the resulting ellipses constructed and statistics calculated. Mean ellipse statistics from the ten randomizations are reported.

Analytical Tools

The vegetation and morphological data were analyzed by principal components analysis (PCA) with the PC-ORD program (McCune and Mefford 1995). All other statistical analyses were run using SYSTAT (Wilkinson 1990b). The ellipse statistics were calculated using a SYSTAT command file developed by

R. K. Scagel. SYGRAPH (Wilkinson 1990a) was used to plot the bivariate 95% confidence limit ellipses of the PCA results. Morphology PCA axis one scores were randomized using the randomization program in PC-ORD (McCune and Mefford 1995). Soil depth, plant morphology, seasonal growth, plant density, and first PCA axis scores were analyzed with separate completely randomized design analysis of variance tests. Significant differences among means of the previously listed data sets were tested with the Tukey multiple comparison test. A 5% confidence level was selected before the data were analyzed.

RESULTS

Vegetation

Colockum

Species composition in the vegetation plots at Colockum are summarized in Table 3. Total percent vegetation coverage varied from 18% to 95%. The *Achnatherum hendersonii* vegetation plots had the lowest total percent cover while the *A. lemmonii* plots had the highest. Vegetation plots dominated by *Agropyron spicatum* had higher total percent coverage than the *Achnatherum hendersonii* vegetation plots. *Poa secunda* was common to all vegetation plots. The *A. hendersonii* southwest facing vegetation plot (C1; 210°) had the lowest total percent cover. Species composition was similar among the three *A. hendersonii* vegetation plots, however the south (C3; 150°) and northeast (C5; 50°) facing plots had the most species in common. Plot C3 had the highest cover of *A. hendersonii*. Soil depths in these three vegetation plots (C1, C3, and C5) were not significantly different (Table 4).

Total percent cover values for the three *Agropyron spicatum* vegetation plots (C2, C4, and C6) were similar. The southwest facing plot (C2; 210°) had the most different species. Soil depths for these plots were not significantly different; all were significantly deeper than the *Achnatherum hendersonii* vegetation plots, except for *Agropyron spicatum* vegetation plot C2, which was not significantly different from *Achnatherum hendersonii* vegetation plots C1 and C5 (Table 4).

Of the two minus *A. hendersonii* vegetation plots (-Ache; C7 and C9), plot C7 was almost identical in species composition and density (Table 5) to *A. hendersonii* vegetation plot C5, except that plot C5 had higher percent coverage of the moss, *Tortula intermedia*. Minus *A. hendersonii* vegetation plot C9 had a higher total percent cover than the *A. hendersonii* vegetation plots, C1, C3, and C5, but a similar percent cover of *Tortula intermedia* as *A. hendersonii* vegetation plot C5.

The two *A. lemmonii* vegetation plots (C8 and C10) had the highest total percent cover and were similar in overall species composition. *Lomatium*

Table 3. Mean percent cover (C) and frequency (F) and physical characteristics for plots at the Colockum study site grouped by vegetation type. -Ache, lacking *Achnatherum hendersonii*.

	Achnatherum hendersonii						-Ache			
Plot	C-1		C-3		C-5		C-7		C-9	
Aspect (degrees)	210		150		50		50		40	
Slope (%)	20		7		10		10		10	
Elevation (m)	1073		1061		1122		1122		1134	
	C	F	C	F	C	F	C	F	C	F
Bareground	86.2	100	48.2	100	45.4	100	54.2	100	32.6	100
SHRUB										
Artemisia rigida			0.4	4	0.2	4			3.4	8
GRASS										
Achnatherum hendersonii	4.2	72	10.1	80	3.6	44				
Poa secunda	2.5	76	5.7	80	11.5	96	16.0	100	18.8	96
Agropyron spicatum	0.3	4								
Sitanion hystrix			0.2	8			0.3	8	0.1	12
Festuca idahoensis										
Achnatherum lemmonii										
Bromus tectorum										
FORB										
Balsamorhiza hookeri	3.7	28								
Lomatium triternatum	1.5	44	7.4	84	15.7	96	17.4	88	9.5	76
Haploppapus stenophyllos	1.2	16	6.0	40					4.9	52
Microsteris gracilis	1.1	8							0.1	4
Lomatium macrocarpum	1.0	40	0.6	16					1.2	20
Collinsia parviflora	0.8	64	2.1	72	1.9	60	0.6	24	2.8	72
Eriogonum thymoides	0.6	16	2.2	20	0.8	4	2.8	16		
Lewisia rediviva	0.4	24	2.1	36	1.6	24	0.2	8	1.3	28
Lithophragma bulbifera	0.3	12			0.5	16			3.2	40
Cryptantha ambigua	0.1	4							0.2	8
Viola trinervata			7.0	76	5.1	68	6.1	60		
Trifolium macrocephalum			1.6	16	2.3	20	0.5	8	1.2	4
Antennaria flagellaris			0.5	8	1.2	24	1.8	56	3.6	56
Ranunculus glaberrimus			0.3	12					0.7	16
Microseris troximoides			0.1	4					1.1	12
Erigeron poliospermus			0.1	4	0.1	4				
Allium acuminatum			0.1	4	0.2	16	0.1	8		
Sedum lanceolatum					0.4	20	1.5	12	0.3	8
Fritillaria pudica							+	4	1.2	24
Achillea millefolium										
Castilleja thompsonii									1.4	12
Delphinium bicolor									3.4	44
Oenothera hilgardii									1.6	32
Montia siberica										
Geum triflorum										
Eriogonum sphaerocephalum										
Lithophragma parviflora										
Phacelia linearis										
Phlox hoodii										
Eriogonum compositum										
MOSS										
Tortula intermedia	0.4	32	8.2	72	16.6	84	8.2	56	16.1	72
Ceratodon purpureus	0.3	20	0.1	4			0.1	4	0.3	4
Total Cover	18.4		54.8		61.7		55.4		76.4	

Table 3 Continued.

	Agropyron spicatum						Achnatherum lemmonii			
Plot	C-2		C-4		C-6		C-8		C-10	
Aspect (degrees)	210		150		50		95		100	
Slope (%)	20		7		10		2		2	
Elevation (m)	1073		1061		1122		1146		1146	
	C	F	C	F	C	F	C	F	C	F
Bareground	34.4	88	41.8	92	38.6	92	17.4	84	9.3	84
SHRUB										
Artemisia rigida	19.5	52	14.1	36	23.2	64	18.4	44	1.4	8
GRASS										
Achnatherum hendersonii										
Poa secunda	2.9	44	4.4	44	9.4	88	16.6	72	17.4	76
Agropyron spicatum	29.8	84	29.1	76	31.2	76	0.5	16		
Sitanion hystrix							1.1	24	4.7	56
Bromus tectorum	0.9	32								
Festuca idahoensis	0.2	4					0.3	8		
Achnatherum lemmonii							4.7	44	11.6	72
FORB										
Balsamorhiza hookeri	5.5	48	3.9	28	2.9	16				
Lomatium triternatum			5.5	68	0.6	20	21.8	76	19.0	92
Haploppapus stenophyllos			0.1	4						
Microsteris gracilis	0.2	8	0.6	20	0.3	12	2.1	32	1.3	36
Lomatium macrocarpum	0.4	8	0.8	8			0.8	12		
Collinsia parviflora	0.9	32	1.9	52	0.8	28	3.3	48	9.5	100
Eriogonum thymoides	0.7	12	0.4	4	0.6	8				
Lewisia rediviva										
Lithophragma bulbifera					2.2	44	7.3	64	3.0	48
Cryptantha ambigua	0.5	24	0.4	20					6.0	72
Viola trinervata										
Trifolium macrocephalum					+	4				
Antennaria flagellaris			0.2	4						
Ranunculus glaberrimus			0.3	12	0.1	4				
Microseris troximoides	1.4	20					0.1	4		
Erigeron poliospermus										
Allium acuminatum										
Sedum lanceolatum										
Fritillaria pudica	0.1	8			0.1	4	1.2	24		
Achillea millefolium							3.9	36	6.0	40
Castilleja thompsonii	0.6	8								
Delphinium bicolor	0.1	4								
Oenothera hilgardii			0.3	12			3.6	36		
Montia siberica							3.3	40		
Geum triflorum							1.1	24	2.4	28
Eriogonum sphaerocephalum	2.0	4								
Lithophragma parviflora	1.0	16					5.3	32	3.8	44
Phacelia linearis	0.7	20								
Phlox hoodii	0.6	8								
Eriogonum compositum	0.4	4								
MOSS										
Tortula intermedia			1.6	4	0.2	4				
Ceratodon purpureus										
Total Cover	68.4		63.6		71.6		95.4		86.1	

Table 4. Mean soil depths for vegetation plots at all study sites. Values with the same letter are not significantly different. Ache, *Achnatherum hendersonii*; Agsp, *Agropyron spicatum*; -Ache, *Achnatherum hendersonii* absent; Acle, *Achnatherum lemmonii*; /c, cryptogamic crust intact; /dc, cryptogamic crust disturbed. N=75 for all plots.

Plot	Community	Depth (cm)	SD
C1	Ache	3.84*a*	4.78
C2	Agsp	6.17*abc*	5.74
C3	Ache	3.55*a*	4.45
C4	Agsp	8.07*bc*	5.05
C5	Ache	3.95*a*	4.92
C6	Agsp	9.41*c*	6.58
C7	-Ache	3.56*a*	4.44
C8	Acle	20.59*d*	8.60
C9	-Ache	4.96*ab*	5.91
C10	Acle	29.13*g*	9.20
B1	Ache	1.19*a*	1.59
B2	-Ache	3.92*a*	3.92
B3	Agsp	6.44*abc*	6.88
O1	Ache/dc	8.07*abc*	3.62
O2	-Ache/c	2.77*a*	3.13
O3	-Ache/dc	7.85*abc*	3.28
O4	Ache/c	6.07*abc*	4.79

Table 5. Mean density (plants/m²) of *Achnatherum hendersonii* and *A. lemmonii* for vegetation plots at each study site. Values with the same letter are not significantly different. N=25 all plots.

	A. hendersonii						*A. lemmonii*	
	C-1	C-3	C-5	B-1	O-1	O-4	C-8	C-10
Density	3.8*cd*	4.7*d*	2.9*bc*	0.5a	1.5*ab*	2.1*abc*	2.3*abc*	3.5*cd*
SD	2.7	3.3	2.5	0.8	1.3	1.6	1.3	2.4

triternatum and *Poa secunda* were the species with the highest percent cover in both plots. Vegetation plot C8 had higher cover of *Artemisia rigida*, but lower cover of *Achnatherum lemmonii* than plot C10. Vegetation plot C10 had significantly greater mean soil depth than plot C8; mean soil depths of both *A. lemmonii* plots were significantly greater than all the other plots at the Colockum study site (Table 4). In general, the range in mean plant densities were comparable between the *A. hendersonii* and *A. lemmonii* vegetation plots (Table 5).

Principal components analysis (PCA) of the Colockum vegetation resulted in 49% of the variance explained by the first ten PCA axes (Table 6). All ten axes had an eigenvalue greater than one. Given these results it is apparent that no one factor/axis strongly relates to the distribution of the vegetation, i.e. there are many trends in the data. Considering the complexity of interactions controlling vegetation this is not surprising. Despite the lack of a strong relation to any one axis, a Bartlett's and Anderson's test for sphericity indicate that the data are not spherical, i.e. the data have significant structure (Maze pers. comm.).

Eigenvectors for the first two axes are presented in Table 7. Although little of the variance was explained by the first few axes, strong loadings were observed for several eigenvectors. Bareground had the strongest negative loading on PCA axis one and largely explains the position of the *A. hendersonii*, -Ache, and *Agropyron spicatum* vegetation plots on the PCA ordination (Figure 10). *Collinsia parviflora*, *Lomatium triternatum*, and *A. lemmonii* had the strongest positive loadings on PCA axis one. The moss, *Tortula intermedia*, the forbs *Antennaria flagellaris* and *Lewisia rediviva*, and the grass, *Poa secunda*, had the strongest negative loadings on PCA axis two, while the grass, *Agropyron spicatum*, and the shrub, *Artemisia rigida*, had the strongest positive loadings.

Results for the analysis of variance of PCA axis one scores indicate that the *Achnatherum lemmonii* vegetation plots (C8 and C10) were significantly different from the other communities at Colockum (Table 8).

Table 6. Principal components analyses eigenvalues and percent of variance for the first ten axes of vegetation. Acle, *Achnatherum lemmonii*.

	Colockum		Colockum w/out Acle		Brewton		Ochoco		All plots	
Axis	Eigen-value	% of var.	Eigen-value	% of var.	Eigen-value	% of var.	Eigen-value	% of var.	Eigen-value	% of var
1	3.371	9.63	2.973	10.25	3.099	20.66	4.796	21.80	4.750	9.13
2	2.463	7.04	2.381	8.21	1.825	12.17	2.777	12.62	3.453	6.64
3	2.048	5.85	1.723	5.94	1.683	11.22	1.691	7.69	2.638	5.07
4	1.585	4.53	1.585	5.46	1.425	9.50	1.412	6.42	2.246	4.32
5	1.461	4.18	1.474	5.08	1.097	7.32	1.249	5.68	1.953	3.76
6	1.360	3.89	1.383	4.77	1.046	6.97	1.198	5.44	1.670	3.21
7	1.316	3.76	1.358	4.68	0.936	6.24	1.153	5.24	1.504	2.89
8	1.255	3.59	1.278	4.41	0.870	5.80	0.996	4.53	1.465	2.82
9	1.191	3.40	1.121	3.87	0.720	4.84	0.979	4.45	1.412	2.72
10	1.176	3.36	1.108	3.82	0.691	4.61	0.799	3.63	1.338	2.57
% of total variance		49.22		56.50		89.32		77.5		43.13

Table 7. Principal components analyses eigenvectors for the first two axes of vegetation at the study sites. Only eigenvector loadings >.2000 or <-.2000 for any one of the axes are presented; Acle, *Achnatherum lemmonii*; -, indicates not present.

	Colockum		Colockum w/out Acle		Brewton		Ochoco		All plots	
Species	1	2	1	2	1	2	1	2	1	2
Bareground	-.3248	-.0566	-.0961	.3959	-.1777	-.0496	-.3508	.2962	-.1045	.3025
Achillea millefolium	.2355	.0286	-	-	-	-	-	-	.1053	-.1719
Achnatherum hendersonii	-.1379	-.1546	.0432	.2599	-.3126	.3710	.1449	.1120	-.0146	.0282
Achnatherum lemmonii	.2900	.0596	-	-	-	-	-	-	.1360	-.2128
Agoseris glauca	-	-	-	-	-	-	.0979	.2637	-.1448	-.0682
Agropyron spicatum	-.1271	.3626	-.3144	-.2964	.3883	.2363	-	-	.0606	.1476
Allium acuminatum	-	-	-	-	-	-	-.1771	-.2553	-.1715	.0436
Antennaria flagellaris	-.0301	-.3120	.2950	-.0649	-	-	-	-	.0679	-.0407
Artemisia rigida	.0294	.2512	-.1475	-.2752	-.0810	-.3485	-.0559	.2336	.0859	-.0053
Balsamorhiza hookeri	-.1172	.2205	-.2129	-.1206	.1481	-.0570	-	-	.0353	.0975
Bletharipappus scaber	-	-	-	-	-	-	.0700	.2040	-.3297	-.0813
Bromus japonicus	-	-	-	-	-	-	.3371	-.0114	-.2600	-.2344
Bromus tectorum	-.0896	.1806	-.1597	-.0906	.4661	.1247	-	-	.0348	.2182
Ceratodon purpureus	-	-	-	-	-.3523	.3566	-	-	.0205	.0916
Collinsia parviflora	.3508	-.0187	.1734	.0309	-.0483	-.3288	.3653	-.0540	.1803	-.3056
Delphinium bicolor	.0178	-.2157	.2456	-.3187	-	-	-	-	.0464	-.0532
Eriogonum thymoides	-.0622	-.0786	.0398	.0214	-.0097	-.3753	-	-	.0285	.0648
Fritillaria pudica	.2065	.0258	-	-	-	-	-	-	.0883	-.1503
Geum triflorum	.2614	.0387	-	-	-	-	-	-	.1111	-.1916
Grimmia orbicularis	-	-	-	-	-	-	-.0496	-.3805	-.1833	-.0165
Haplopappus stenophyllos	-.0661	-.2006	.1421	-.0138	-	-	-	-	.0396	-.0053
Lewisia rediviva	-.0386	-.2365	.1951	.0890	-	-	-.0719	-.1847	.0257	-.0249
Lithophragma bulbifera	.2768	-.0045	.1900	-.3403	-	-	-	-	.1572	-.2182
Lomatium leptocarpum	-	-	-	-	-	-	.1902	.0151	-.2639	-.1427
Lomatium triternatum	.3036	-.1793	.2824	.2218	-	-	.0664	.2187	.2113	-.2558
Microseris troximoides	-.0443	.0103	-.0008	-.2332			-	-	.0309	.0107
Oenthera hilgardii	.1329	-.0016	-	-	.4062	.2455	-	-	.0208	.1557
Phlox hoodi	-.0361	.0806	-.0980	-.1496	-.0069	-.4301	-	-	.0216	.0870
Poa secunda	.2559	-.2514	.3826	-.1414	-.3903	.1012	.0148	-.2286	.1759	-.2138
Polygonum majus	-	-	-	-	-	-	-.2189	-.0847	-.3317	-.0155
Ranunculus glaberrimus	.0054	-.1813	.1893	-.2803	-	-	-	-	.0345	-.0362
Sedum stenopetalum	-	-	-	-	-	-	-.0686	-.3506	-.0946	.0100
Rigiopappus leptocladus	-	-	-	-	-	-	.3621	-.0415	-.2514	-.2441
Sitanion hystrix	.2675	.0741	-	-	-	-	-	-	.1191	-.1958
Tortula intermedia	-.0323	-.4007	.3829	-.0384	-	-	.3647	-.2566	-.2145	-.2398
Viola trinervata	-.0951	-.2155	.1298	.2464	-	-	-	-	.0463	.0113
Zygadenus venenosus	-	-	-	-	-	-	.2205	.0294	-.1772	-.1546

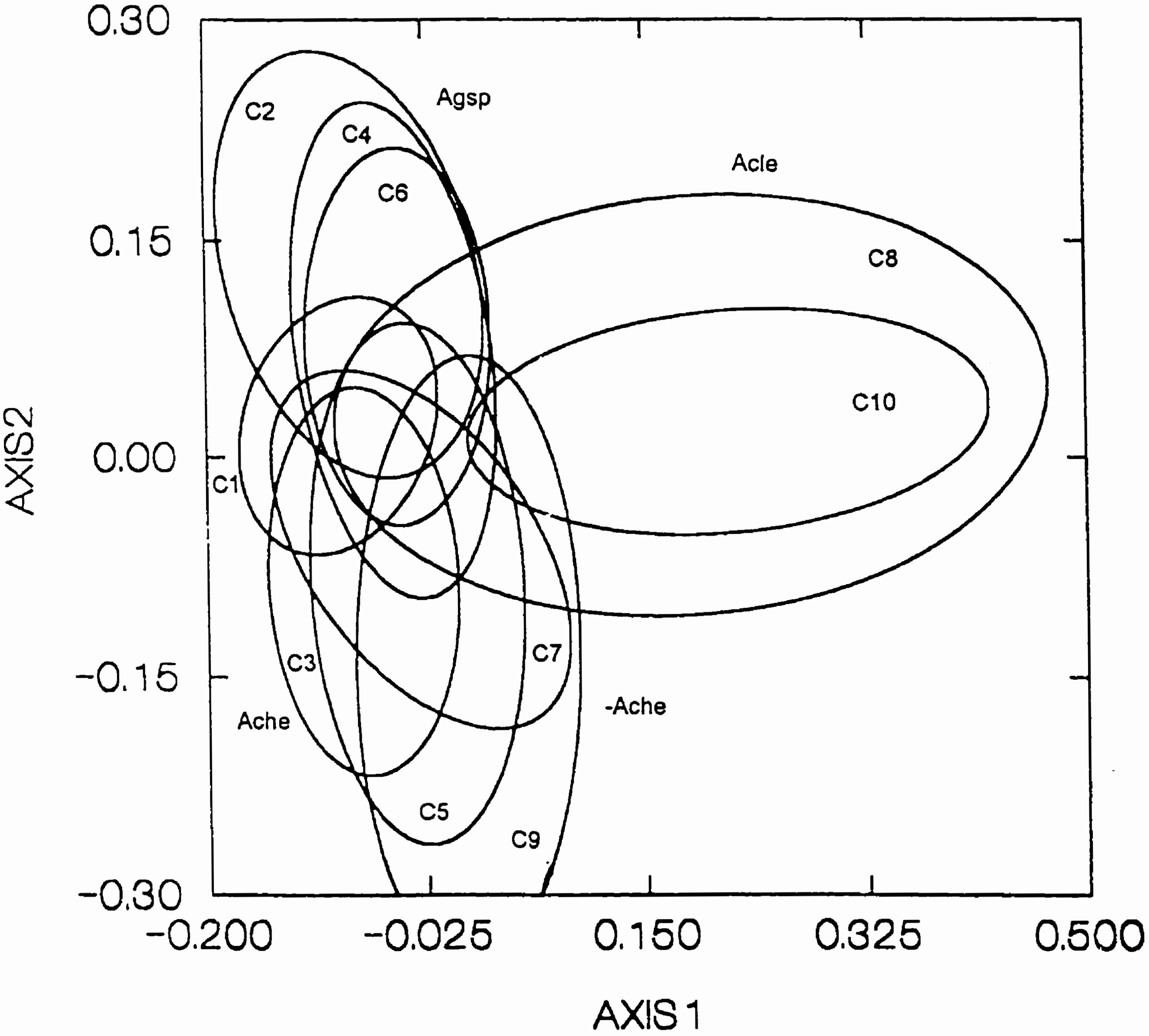

Figure 10. PCA ordination of the ten vegetation plots at the Colockum study site. 95% confidence limit ellipses denote the vegetation organization and variation in each plot. Ache, *Achnatherum hendersonii* (C1, C3, C5); -Ache, lacking *A. hendersonii* (C7, C9); Acle, *A. lemmonii* (C8, C10); Agsp, *Agropyron spicatum* (C2, C4, C5).

Table 8. Mean PCA axis 1 scores for vegetation. Values within the same column with matching letters are not significantly different. Ache, *Achnatherum hendersonii*; -Ache, Achnatherum hendersonii absent; Acle, *Achnatherum lemmonii*; Agsp, *Agropyron spicatum*; */c*, cryptogamic crust intact; */dc*, cryptogamic crust disturbed.

Plot	Veg. type	Colockum	Colockum w/out Acle	Brewton	Ochoco	Ache + Acle	Ache	All Plots
C1	Ache	-.094a	-.059a	-	-	.013a	.099a	.013a
C2	Agsp	-.085a	-.161c	-	-	-	-	.032a
C3	Ache	-.075ab	.049b	-	-	.033a	.120a	.029a
C4	Agsp	-.050ac	-.081a	-	-	-	-	.034a
C5	Ache	-.032bcd	.083b	-	-	.042a	.098a	.033a
C6	Agsp	-.046abc	-.082a	-	-	-	-	.036ab
C7	-Ache	-.029bcd	.066b	-	-	-	-	.042ab
C8	Acle	.186e	-	-	-	.176b	-	.139c
C9	-Ache	.008d	.189d	-	-	-	-	.067b
C10	Acle	.216e	-	-	-	.175b	-	.141c
B1	Ache	-	-	-.190a	-	.030a	.118a	.021a
B2	-Ache	-	-	-.041b	-	-	-	.025a
B3	Agsp	-	-	.231c	-	-	-	.024a
O1	Ache/dc	-	-	-	-.081a	-.141c	-.066b	-.112d
O2	-Ache/c	-	-	-	-.123ab	-	-	-.163e
O3	-Ache/dc	-	-	-	-.145b	-	-	-.095d
O4	Ache/c	-	-	-	.349c	-.328d	-.358c	-.266f

The *A. hendersonii* vegetation plots (C1, C3, and C5) were similar to each other, as were the minus *A. hendersonii* vegetation plots (C7 and C9), and the *Agropyron spicatum* vegetation plots (C2, C4, and C6). In general, these latter three groups of plots were similar along the first PCA axis.

The 95% confidence ellipse results of all vegetation plots at the Colockum study area are given in Figure 10 and Table 9. The main communities are well defined in the PCA ordination, which shows both the differences and overlap in species composition. The *Achnatherum lemmonii* vegetation plots (C8 and C10) had the greatest amount of variation along PCA axis one. Both *A. lemmonii* vegetation plots had similar eccentricity (order) and theta (organization *sensu stricto*) values; plot C8 had a larger area (greater variation) value than plot C10.

The ellipses for the *Agropyron spicatum* vegetation plots (C2, C4, and C6) were ordinated towards the positive end of PCA axis two (Figure 10). All had similar eccentricity (order), theta (organization *sensu stricto*), and area (variation) values, indicating strong similarities in overall organization.

The ellipses for the *Achnatherum hendersonii* vegetation plots exhibited differences in eccentricity, theta, and area. In particular, these values were substantially lower in plot C1 compared to plots C3 and C5.

The ellipses for the two minus *Achnatherum hendersonii* vegetation plots (-Ache; C7 and C9) occurred in the same general location of the PCA ordination as those for the *A. hendersonii* vegetation plot ellipses (C1, C3, and C5). Plot C7 had a substantially higher theta value than the others, hinting at a difference in vegetation organization (*sensu stricto*), whereas plot C9 had the highest eccentricity value. These differences stemmed partly from a higher percentage cover of *Poa secunda* in plot C7, and a slight shift in species composition and coverage in plot C9 (Table 3).

The results of the PCA for the Colockum vegetation plots with the *A. lemmonii* plots removed are shown in Figure 11 and Tables 7 and 10. As with the PCA for all the vegetation plots at the Colockum study site, the

Table 9. Descriptive statistics of the 95% confidence ellipses from PCA of vegetation at the Colockum study site. Ache, *Achnatherum hendersonii*; Agsp, *Agropyron spicatum*; -Ache, *Achnatherum hendersonii* absent; Acle, *Achnatherum lemmonii*. See text for explanation of descriptive statistics and plot descriptions.

Plot	Community	Theta	Eccen.	Area
C1	Ache	58.14	0.634	0.018
C3	Ache	93.36	0.825	0.027
C5	Ache	93.68	0.882	0.050
C2	Agsp	110.52	0.762	0.039
C4	Agsp	99.20	0.892	0.035
C6	Agsp	90.62	0.821	0.025
C7	-Ache	133.16	0.819	0.033
C9	-Ache	89.24	0.904	0.049
C8	Acle	3.88	0.862	0.107
C10	Acle	4.15	0.930	0.042

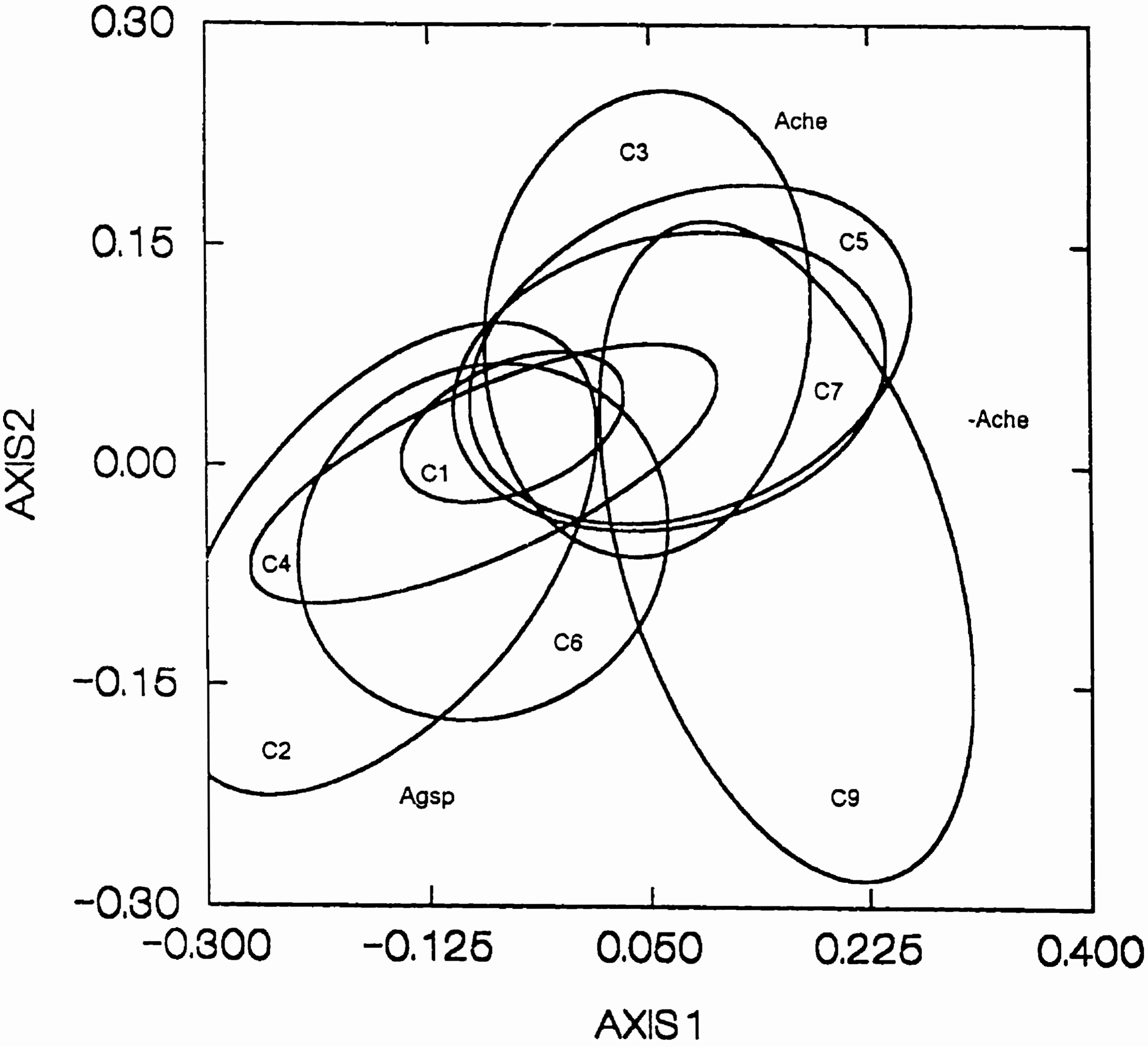

Figure 11. PCA ordination of the Colockum study site vegetation plots with the two *Achnatherum lemmonii* plots removed. 95% confidence limit ellipses denote the vegetation organization and variation in each plot. Ache, *A. hendersonii* (C1, C3, C5); -Ache, lacking *A. hendersonii* (C7, C9); Agsp, *Agropyron spicatum* (C2, C4, C6).

Table 10. Descriptive statistics of the 95% confidence ellipses from the PCA of vegetation without *Achnatherum lemmonii* vegetation plots at the Colockum study site. Ache, *Achnatherum hendersonii*; Agsp, *Agropyron spicatum*; -Ache, *Achnatherum hendersonii* absent. See text for explanation of descriptive statistics and plot descriptions.

Plot	Community	Theta	Eccen.	Area
C1	Ache	18.78	0.877	0.011
C3	Ache	76.97	0.595	0.054
C5	Ache	17.26	0.806	0.051
C2	Agsp	43.08	0.841	0.060
C4	Agsp	20.93	0.957	0.030
C6	Agsp	15.40	0.588	0.047
C7	-Ache	9.50	0.825	0.045
C9	-Ache	109.42	0.964	0.174

eigenvalues for first ten PCA axes were all greater than one, with 56% of the variance explained by the first ten axes (Table 5).

Analysis of variance of the PCA axis one scores indicated that differences among the remaining communities appeared to increase when the *A. lemmonii* community was removed from the analysis (Table 8). In particular, the minus *A. hendersonii* (-Ache) vegetation plot C9, and the *Agropyron spicatum* vegetation plot C2, were now significantly different from the other vegetation plots and from each other.

In general, the results for the PCA of the vegetation at the Colockum study site with the *A. lemmonii* vegetation plots removed, more clearly delineated the relationship between the different communities. Removal of the *A. lemmonii* vegetation resulted in large organizational shifts among the *A. hendersonii* plots (C1, C3, and C5), and the two -Ache plots (C7 and C9), compared to the three *Agropyron spicatum* plots (C2, C4, and C6), where the changes were less pronounced (cf. Tables 9 and 10).

Brewton

Table 11 summarizes the species composition and physical characteristics for the vegetation plots at the Brewton study site. The *A. hendersonii* vegetation plot (B1) and the -Ache plot (B2) had similar total percent cover. The *Agropyron spicatum* plot (B3) had the highest total percent cover of the three vegetation plots. Plot B1 had higher mean cover of the moss, *Ceratodon purpureus*, than plot B2, and *Ceratodon purpureus* was the only moss present in plot B3. Plots B1 and B2 had more species in common with each other than with plot B3. Mean density of *Achnatherum hendersonii* was significantly lower at Brewton than at Colockum, but not significantly different from mean densities at the Ochoco study site (Table 5).

Mean soil depth of the *A. hendersonii* vegetation plot (B1) was significantly shallower than at plots B2 and B3; mean soil depths at the latter two plots were not significantly different from each other (Table 4).

Table 11. Mean percent cover (C) and frequency (F) and physical characteristics for plots at the Brewton study site. -Ache, lacking *Achnatherum hendersonii*.

	Achnatherum hendersonii		-Ache		*Agropyron spicatum*	
Plot	B-1		B-2		B-3	
Aspect (degrees)	138		138		140	
Slope (%)	10		10		25	
Elevation (m)	610		610		610	
	C	F	C	F	C	F
Bareground	60.0	100	57.4	96	44.2	84
SHRUB						
Artemisia rigida	10.2	32	12.8	28		
GRASS						
Poa secunda	10.1	88	6.6	72	1.3	16
Achnatherum hendersonii	3.5	52				
Bromus tectorum	0.3	28	3.3	88	9.0	92
Agropyron spicatum			0.7	16	40.3	88
Stipa thurberiana			0.2	4	0.1	4
FORB						
Eriogonum thymoides	1.2	12	9.8	40		
Pediocactus simpsonii	0.7	12	0.6	8		
Lomatium macrocarpum	0.6	4	0.4	4		
Crepis modocensis	0.3	8				
Lewisia rediviva	0.2	8				
Penstemon gairdneri	0.2	4				
Balsamorhiza hookeri	0.1	4	1.2	12	1.1	8
Microsteris gracilis	0.1	4				
Phlox hoodii			1.9	44		
Eriogonum compositum			1.2	4		
Collinsia parviflora			0.6	20		
Oenothera hilgardii					5.9	64
Geum triflorum					0.4	24
MOSS						
Ceratodon purpureus	14.3	76	2.4	40	0.4	8
Tortula intermedia	0.2	4				
Total Cover	42.0		41.7		58.5	

The PCA indicated that more variance is explained along PCA axis one for the Brewton study site than for the Colockum study site (Table 6). This was possibly a result of fewer variables (species) at the Brewton study site. Only the first five axes had eigenvalues greater than one, and the first two axes accounted for 32% of the variance. The communities at the Brewton study site were more discrete than at the Colockum study site. Overall species coverage was lower, as was individual coverages of moss species (Tables 3 and 11).

Eigenvectors and mean PCA axis one scores are shown in Tables 7 and 8. *Bromus tectorum*, *Oenthera hilgardii*, and *Agropyron spicatum* had the strongest positive loadings, while *Poa secunda*, *Ceratodon purpureus*, and *Achnatherum hendersonii* had the strongest negative loadings on PCA axis one (Table 7). On PCA axis two, *A. hendersonii* and *Ceratodon purpureus*, had the strongest positive loadings, while *Phlox hoodii*, *Eriogonum thymoides*, *Artemisia rigida*, and *Collinsia parviflora* had the strongest negative loadings.

Analysis of variance of the PCA axis one scores, indicates all three communities, *A. hendersonii* (B1), -Ache (B2), and *Agropyron spicatum* (B3), were significantly different from each other (Table 8).

PCA 95% confidence interval bivariate ellipses indicate differences in organization (eccentricity and theta) between the three vegetation plots (Figure 12 and Table 12). The ellipses for the *Achnatherum hendersonii* vegetation plot (B1) and the -Ache vegetation plot (B2), indicate that these communities varied more along PCA axis two than along PCA axis one. These two communities also had similar eccentricities (order). The ellipse for the -Ache vegetation plot (B2) had greater variation as indicated by a larger area value. The ellipse for the *Agropyron spicatum* vegetation plot (B3) had smaller theta (organization *sensu stricto*) and area (less variation) values than the ellipses for the other two plots.

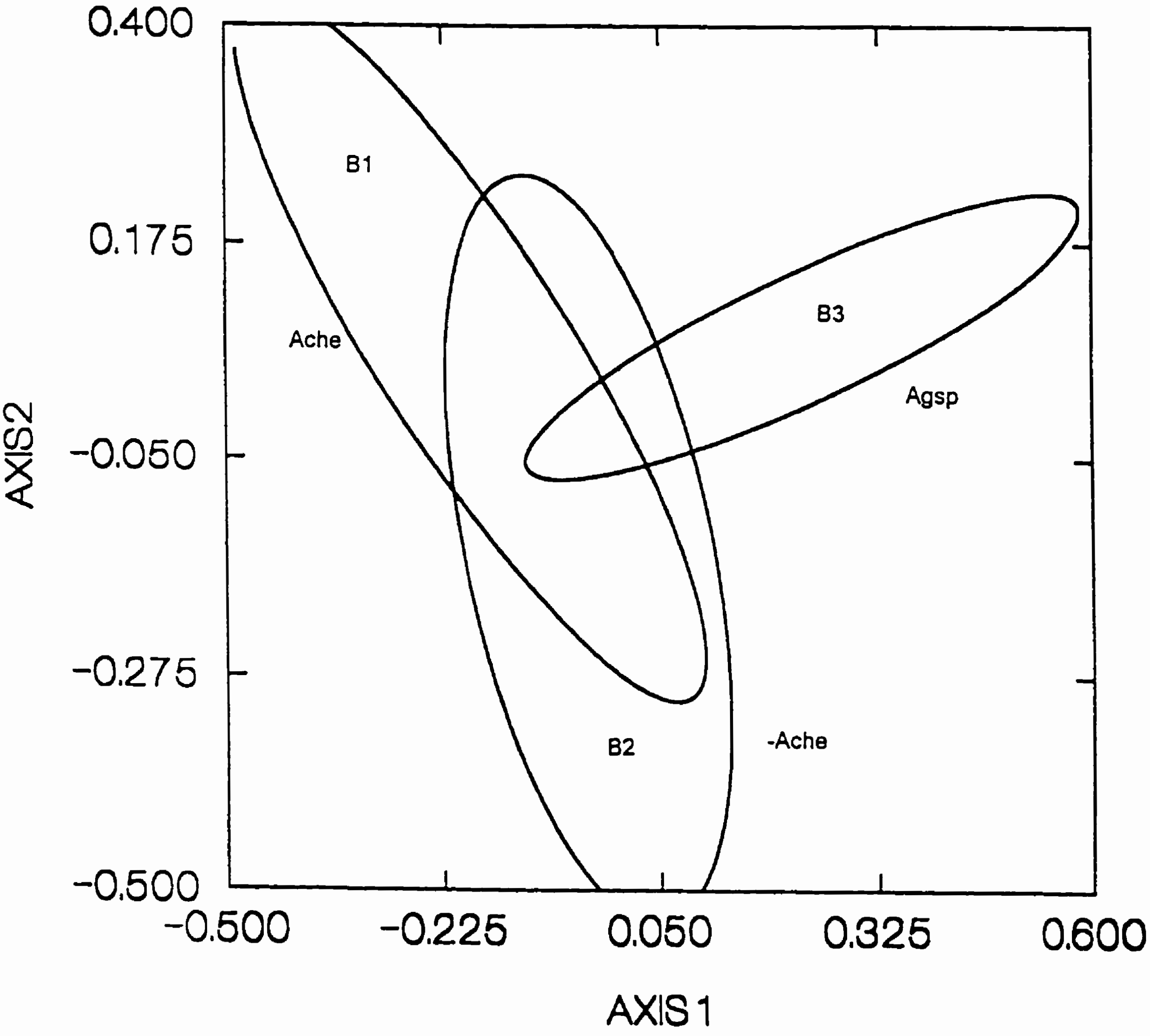

Figure 12. PCA ordination of the three vegetation plots at the Brewton study site. 95% confidence limit ellipses deonte the vegetation organization and variation in each plot. Ache, *Achnatherum hendersonii*; -Ache, lacking *A. hendersonii*; Agsp, *Agropyron spicatum*.

Table 12. Descriptive statistics of the 95% confidence ellipses from the PCA of vegetation at the Brewton study site. Ache, *Achnatherum hendersonii*; Agsp, *Agropyron spicatum*; -Ache, *Achnatherum hendersonii* absent. See text for explanation of descriptive statistics and plot descriptions.

Plot	Community	Theta	Eccen.	Area
B1	Ache	128.19	0.968	0.139
B2	-Ache	104.37	0.921	0.165
B3	Agsp	21.07	0.873	0.025

Ochoco

The Ochoco study site differs from the Colockum and Brewton study sites in that there were no *Agropyron spicatum* dominated vegetation plots. Species composition and plot physical characteristics for the Ochoco study site are summarized in Table 13. Total percent coverage of the communities at the Ochoco study site varied from 25 to 95 percent. Of the two vegetation plots with *Achnatherum hendersonii*, plot 04 had higher total percent cover than plot 01. The higher percent coverage was because mean cover of the moss, *Tortula intermedia*, was greater in plot 04 than in plot 01. Otherwise, species cover and composition were similar between the two plots. Of the vegetation plots without *A. hendersonii* (-Ache), plot 02 had higher total percent cover than plot 03; again, this was because of higher mean cover of moss (*T. intermedia*). Vegetation plots 02 (-Ache) and 04 (*A. hendersonii*) represented areas where the cryptogamic crust was intact as indicated by the relatively high mean coverage of moss species.

Vegetation plots 01 (*A. hendersonii*) and 03 (-Ache) had significantly deeper soils than vegetation plot 02 (-Ache) (Table 4). Mean soil depth at vegetation plot 02 (-Ache) was not significantly greater than plot 04 (*A. hendersonii*), and mean soil depths at vegetation plots 01, 03, and 04 were not significantly different. Mean densities of *A. hendersonii* at Ochoco were generally similar to those at the Brewton and Colockum study sites (Table 5).

PCA eigenvalues and percent of variance accounted for by the first ten axes are found in Table 6. The first seven eigenvalues were greater than one. The first axis accounts for 22% of the variance, and the first ten axes account for 79% of the total variance.

Eigenvectors are listed in Table 7. *Collinsia parviflora*, *Tortula intermedia*, *Rigiopappus leptocladus*, and *Bromus japonicus*, had the strongest positive loadings on PCA axis one, while bareground and *Polygonum majus* had the strongest negative loadings. On PCA axis two, bareground, *Agoseris glauca*, and *Artemisia rigida* had the strongest positive loadings, whereas *Grimmia orbicularis*, *Sedum stenopetalum*, *Tortula intermedia*, and *Allium*

Table 13. Mean percent cover (C) and frequency (F) and physical characteristics for plots grouped by vegetation type at the Ochoco study site. -Ache, *Achnatherum hendersonii*.

	Achnatherum hendersonii				-Ache			
Plot	O-1		O-4		O-2		O-3	
Aspect (degrees)	210		200		210		170	
Slope (%)	5		5		5		5	
Elevation (m)	1418		1418		1418		1418	
Cryptogamic crust	disturbed		intact		intact		disturbed	
	C	F	C	F	C	F	C	F
Bareground	79.2	100	20.6	100	48.6	100	85.8	100
GRASS								
Poa secunda	3.1	72	3.4	56	5.3	80	3.0	48
Achnatherum hendersonii	2.2	36	2.1	44				
Bromus japonicus	0.1	12	1.8	88	0.4	44		
Festuca octoflora			+	4	3.0	92		
Bromus tectorum					0.1	8		
Sitanion jubatum							0.1	4
FORB								
Blepharipappus scaber	3.0	100	2.4	96	1.6	88	1.9	96
Lomatium leptocarpum	2.7	64	8.4	84	1.0	32	4.2	60
Polygonum majus	2.4	100	1.7	92	2.9	100	2.9	100
Agoseris glauca	1.1	48	0.8	28	0.1	4	+	4
Lomatium triternatum	0.8	28	0.5	12				
Allium acuminatum	0.6	36			2.1	80	1.1	56
Trifolium macrocephalum	0.2	4	0.4	12				
Zygadenus venenosus	0.2	8	1.1	28				
Collinsia parviflora			1.4	84	+	4		
Rigiopappus leptocladus			0.8	68				
Fritillaria pudica			0.1	8				
Sedum stenopetalum					0.5	20		
Lewisia rediviva					0.5	16		
Erigeron chrysopsis							0.1	4
MOSS								
Tortula intermedia	8.9	92	70.8	100	37.3	100	2.9	60
Grimmia orbicularis			0.8	20	3.0	68	0.6	20
Total Cover	25.3		95.6		57.8		16.8	

acuminatum had the strongest negative loadings. PCA axis one appears to describe decreasing bareground coverage and increasing cover of *Collinsia parviflora*, *Tortula intermedia*, and *Rigiopappus leptocladus*. In contrast PCA axis two appears to describe decreasing coverage of *Grimmia orbicularis*, *Sedum stenopetalum*, *Tortula intermedia*, and *Allium acuminatum* and increasing coverage of bareground, *Agoseris glauca*, and *Artemisia rigida*. For the most part, areas within the study site that differed in whether *A. hendersonii* was present or absent, had subtle variations in plant community characteristics.

Analysis of variance of PCA axis one scores indicated that the *A. hendersonii* vegetation plot with intact cryptogamic crust (plot 04) was significantly different from any of the other vegetation plots (Table 8). The *A. hendersonii* vegetation plot with disturbed cryptogamic crust (plot 01) and the -Ache vegetation plot with intact cryptogamic crust (plot 02) were not significantly different, nor were the -Ache vegetation plots with intact and with disturbed cryptogamic crusts (plots 02 and 03 respectively).

Figure 13 illustrates the PCA 95% confidence interval bivariate ellipses for the Ochoco study site and Table 14 contains the descriptive statistics for the ellipses. Although eccentricity (order) was similar for all the plots, theta (organization *sensu stricto*) and area (variation) differed. Ellipses for *A. hendersonii* vegetation plots (01 and 04) had minimal overlap and different orientations (see theta values, Table 14) along PCA axis one. Vegetation plot 03 (-Ache, crust disturbed) appeared to be a subset of vegetation plot 02 (-Ache, crust intact). The two vegetation plots with intact cryptogamic crust, 02 (-Ache) and 04 (*A.hendersonii*), had higher area (greater variation) values than the vegetation plots where the crust was disturbed. Although eccentricity (order) was similar, vegetation plot 04 (*A. hendersonii*, crust intact), had larger theta (organization *sensu stricto*) and area (variation) values, compared with the remaining vegetation plots at this study site (Figure 13 and Table 14).

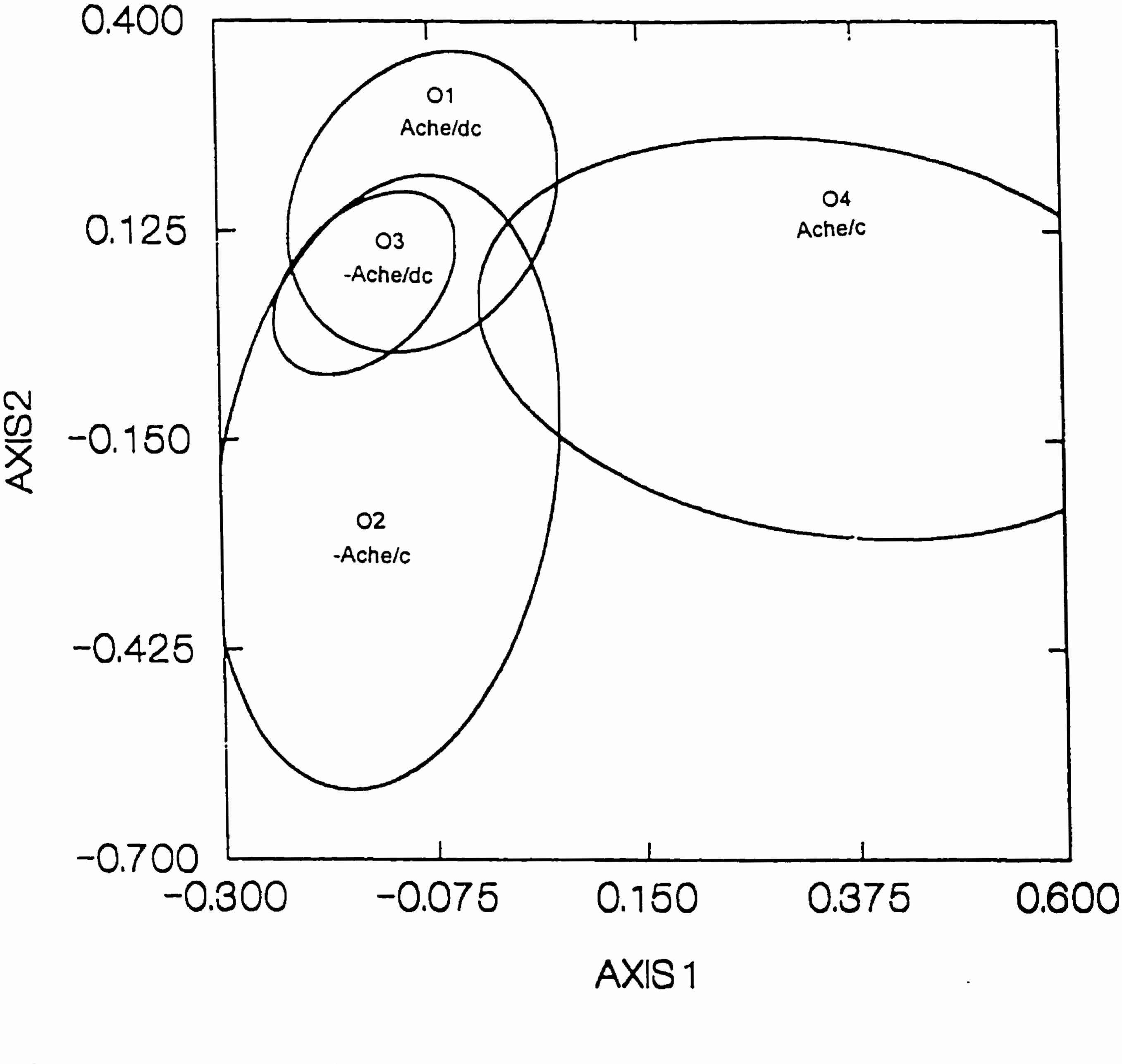

Figure 13. PCA ordination of the four vegetation plots at the Ochoco study site. 95% confidence limit ellipses denote the vegetation organization and variation in each plot. Ache, *Achnatherum hendersonii*; -Ache, lacking *A. hendersonii*; /c, cryptogamic crust intact; /dc, cryptogamic crust disturbed.

Table 14. Descriptive statistics of the 95% confidence ellipses from the PCA of vegetation at the Ochoco study site. Ache, *Achnatherum hendersonii*; -Ache, *A. hendersonii* absent; /c, cryptogamic crust intact; /dc, cryptogamic crust disturbed. See text for explanation of descriptive statistics and plot descriptions.

Plot	Community	Theta	Eccen.	Area
01	Ache/dc	71.84	0.739	0.073
04	Ache/c	166.24	0.736	0.256
02	-Ache/c	82.33	0.899	0.191
03	-Ache/dc	58.34	0.802	0.028

All Plots

To determine overall vegetation variation and to display relationships among all study sites, PCA was performed on the combined vegetation plots of all study sites. Tables 6 and 7 contain eigenvalues and eigenvectors, respectively. Figure 14 shows the PCA ordination of the 95% confidence limit bivariate ellipses for all vegetation plots. Table 15 contains the descriptive statistics for the ellipses.

Similar to the PCA results for the Colockum study site vegetation, the eigenvalues for the first ten axes were all greater than one for the PCA of all vegetation plots (Table 6). Only 9% of the variance was explained by the first PCA axis, with 6.6% by the second PCA axis, and 43% explained by the first ten axes (Table 6).

Polygonum majus, *Blepharipappus scaber*, *Lomatium leptocarpum*, *Bromus japonicus*, and *Rigiopappus leptocladus* had the strongest negative loadings on PCA axis one, whereas *Lomatium triternatum*, *Collinsia parviflora*, *Poa secunda*, *Lithophragma bulbifera*, and *Achnatherum lemmonii* had the strongest positive loadings on PCA axis one (Table 7). The species with the strongest negative loadings on PCA axis one were observed only at the Ochoco study site, while the first three species with the strongest positive loadings on PCA axis one were observed at the Colockum and Ochoco study sites, and the last two species were observed only at the Colockum study site. These results suggest that PCA axis one represents a latitudinal gradient, from south on the negative end to north on the positive end. On PCA axis two, *Collinsia parviflora*, *Lomatium triternatum*, *Rigiopappus leptocladus*, *Tortula intermedia*, and *Bromus japonicus* had the strongest negative loadings, and bareground, *Bromus tectorum*, *Oenthera hilgardii*, and *Agropyron spicatum* had the strongest positive loadings (Table 7).

Analysis of variance on PCA axis one scores indicated that the *Achnatherum hendersonii*, minus *A. hendersonii* (-Ache), and *Agropyron spicatum* vegetation plots at the Colockum and Brewton study sites were not significantly different (Table 8). The two *Achnatherum lemmonii* vegetation

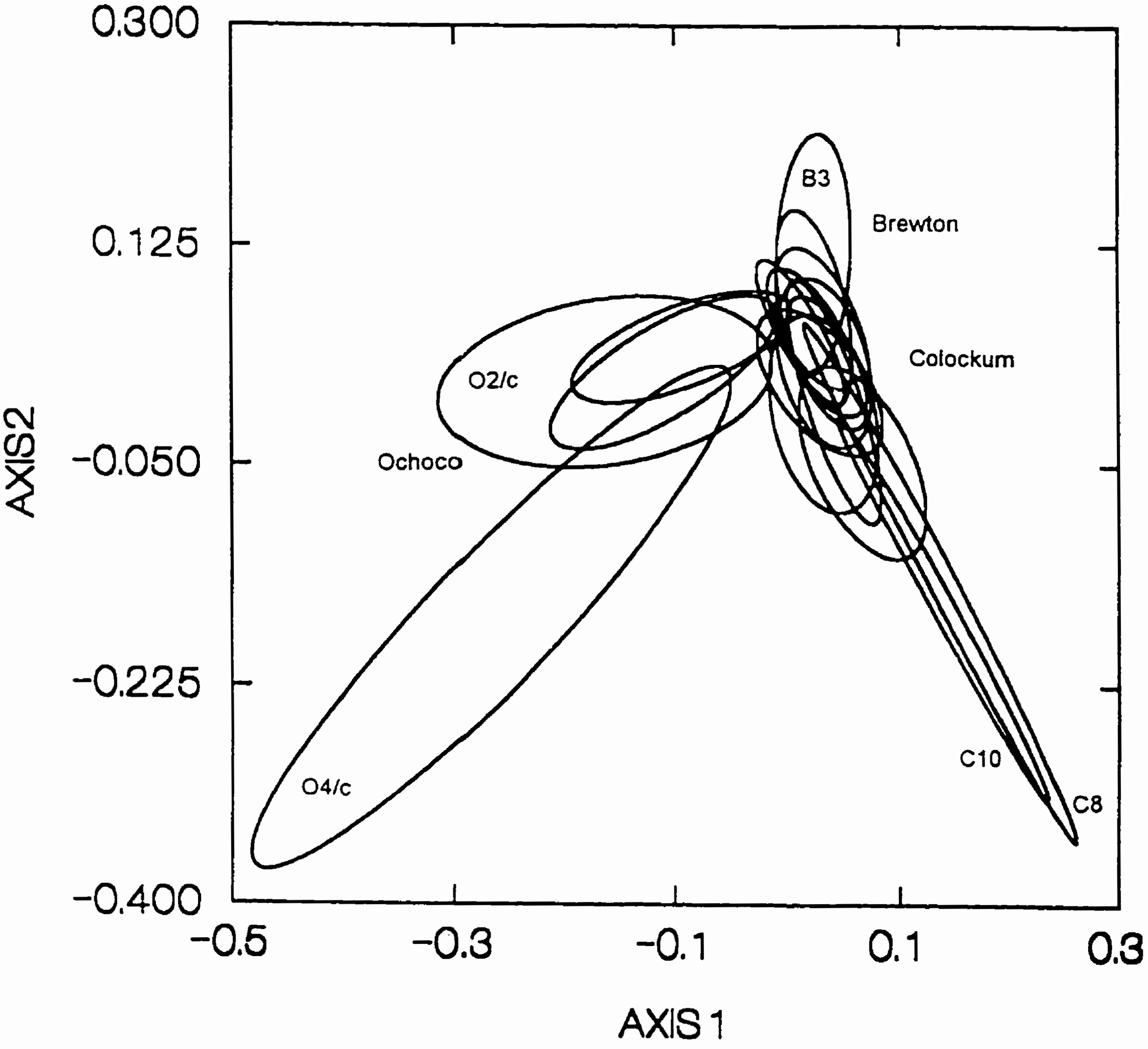

Figure 14. PCA ordination of vegetation of all study sites combined. 95% confidence limit ellipses denote the vegetation organization and variation in each plot. /c, cryptogamic crust intact.

Table 15. Descriptive statistics of the 95% confidence ellipses from the PCA of vegetation from all study sites. Ache, *Achnatherum hendersonii*; Agsp, *Agropyron spicatum*; -Ache, *Achnatherum hendersonii* absent; Acle, *Achnatherum lemmonii*; /c, cryptogamic crust intact; /dc, cryptogamic crust disturbed. See text for explanation of descriptive statistics and plot descriptions.

Plot	Community	Theta	Eccen.	Area
C1	Ache	122.21	0.960	0.003
C2	Agsp	114.44	0.893	0.006
C3	Ache	132.98	0.858	0.007
C4	Agsp	108.13	0.840	0.007
C5	Ache	105.20	0.830	0.010
C6	Agsp	118.54	0.909	0.004
C7	-Ache	109.92	0.974	0.006
C8	Acle	120.73	0.999	0.008
C9	-Ache	119.60	0.862	0.010
C10	Acle	121.94	0.999	0.005
B1	Ache	125.21	0.908	0.004
B2	-Ache	103.66	0.936	0.006
B3	Agsp	87.25	0.941	0.008
O1	Ache/dc	26.83	0.915	0.014
O2	-Ache/c	7.38	0.901	0.026
O3	-Ache/dc	17.80	0.951	0.009
O4	Ache/c	42.77	0.983	0.041

plots were not significantly different from each other, but were significantly different from the other vegetation plots at the Colockum, Brewton, and Ochoco study sites (Table 8). The vegetation plots at the Ochoco study site were significantly different from the vegetation plots at the northern two study sites (Colockum and Brewton). Within the Ochoco study site, the *A. hendersonii* vegetation plot with disturbed cryptogamic crust (O1) and the -Ache vegetation plot with disturbed cryptogamic crust (O3), were not significantly different from each other; the remaining vegetation plots were significantly different.

All ellipses, except for Ochoco vegetation plot O4, showed a slight degree of overlap (Figure 14). The ellipses for the vegetation plots at the Brewton and Colockum study sites had similar theta (organization *sensu stricto*), eccentricity (order), and areas (variation) values (Table 15). These results indicate that the two sites at the northern distribution of *A. hendersonii* have similar community level organization, distinct from that at the Ochoco study site. With this many plots and with the degree of overlap between the plots, the descriptive statistics (Table 15) give a clearer representation of the PCA results than the ordination. The ellipses for the vegetation plots of all the study sites had similar eccentricity (order) values. More notable were the differences observed in theta (organization *sensu stricto*) and area (variation) values. The ellipses for the vegetation plots in the northern distribution limit of *A. hendersonii* (Colockum and Brewton study sites) had theta values between 87 and 133, whereas theta values for ellipses in the southern distribution limit (Ochoco study site) were between 7 and 42. The Ochoco plots generally had greater area (variation) values, suggesting that there was more variation in the vegetation in the southern distribution limit of *A. hendersonii*. Overall, substantial differences in community level organization was evident between the northern and southern distributions of *A. hendersonii*.

The PCA ordination and, consequently, the theta values from the PCA of all vegetation plots combined, could be reflecting an "arch effect" (i.e.

horseshoe problem that occurs in PCA when beta diversity is high; Gauch, 1982). Detrended correspondence analysis (DCA) was developed to correct this fault inherent in PCA (Hill and Gauch, 1980). DCA was run on this data set to determine if an "arch effect" was present. The relative relationship of the ellipses from the DCA results were similar to those of the PCA; therefore, the PCA results were retained.

Achnatherum hendersonii and A. lemmonii Plots

The PCA results for *A. hendersonii* and *A. lemmonii* vegetation plots were similar to the results for all vegetation plots (Figures 15 and 14 respectively). All of the first ten eigenvalues were greater than one (Table 16). Fourteen percent of the variance was explained by axis one and 54% by the first ten axes (Table 16). *Tortula intermedia*, *Blepharipappus scaber*, *Polygonum majus*, *Bromus japonicus*, *Rigiopappus leptocladus*, and *Lomatium leptocarpum* had the strongest negative loadings on PCA axis one, whereas *Lomatium triternatum*, *Poa secunda*, and *Collinsia parviflora* had the strongest positive loadings (Table 17). For PCA axis two, bareground and *Achnatherum hendersonii* had the strongest negative loadings, and *Collinsia parviflora*, *Lithophragma bulbifera*, *Rigiopappus leptocladus*, *Lomatium triternatum*, *Bromus japonicus*, *Tortula intermedia*, and *Achnatherum lemmonii* had the strongest positive loadings. As with the results for the PCA of all vegetation plots, a latitudinal gradient was demonstrated along PCA axis one (Figure 15).

The results for the analysis of variance on PCA axis one scores were similar to those for all vegetation (Table 8). The *A. hendersonii* vegetation plots at the northern study sites (Colockum and Brewton) were not significantly different from each other, nor were the *A. lemmonii* vegetation plots, but the two communities were significantly different from each other. At the southern study site (Ochoco) the *A. hendersonii* vegetation plots with intact cryptogamic crust and with disturbed cryptogamic crust were significantly different from each other, as well as from the vegetation plots in northern study sites.

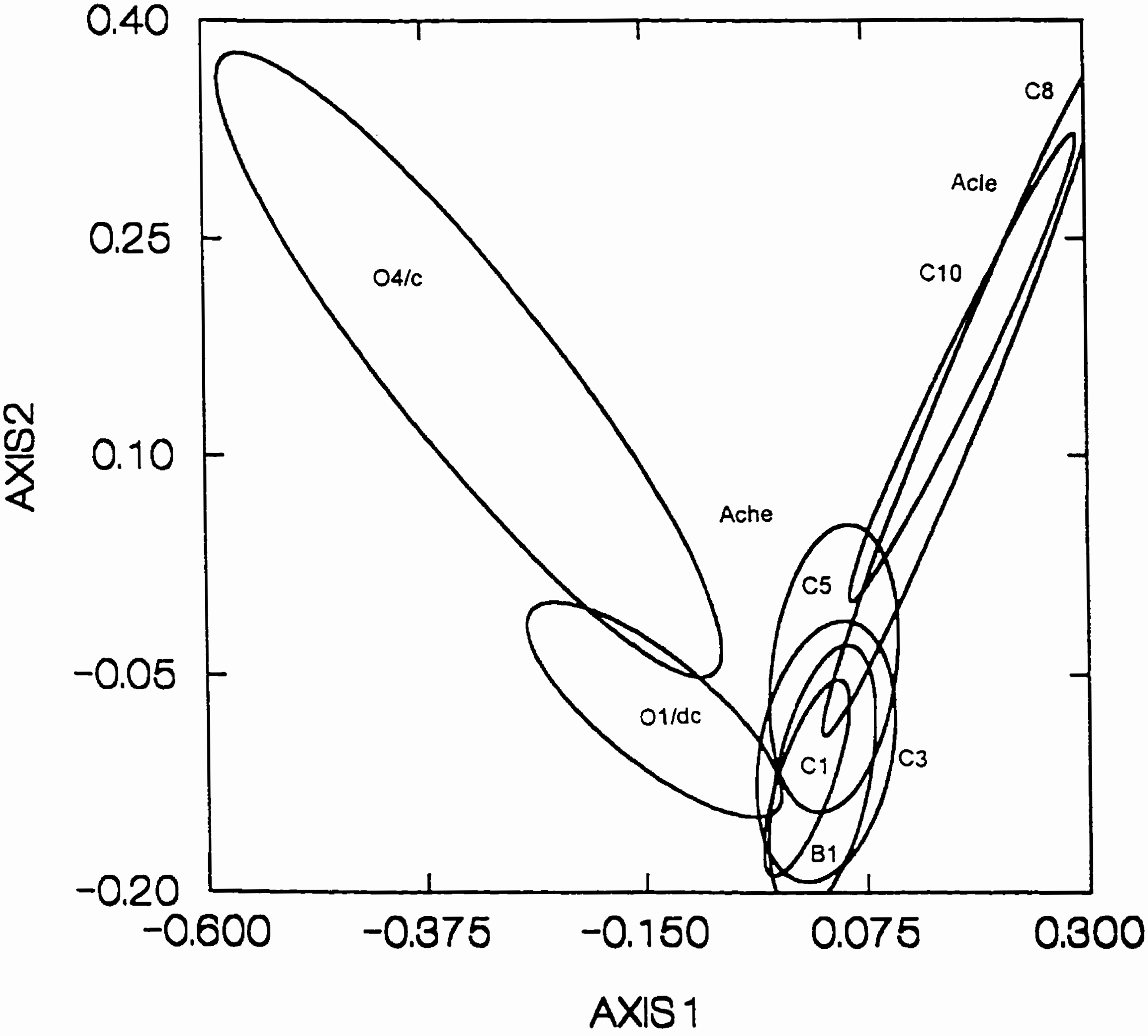

Figure 15. PCA ordination of *Achnatherum hendersonii* and *A. lemmonii* vegetation plots. 95% confidence limit ellipses denote the vegetation organization and variation in each plot. Ache, *A. hendersonii*; Acle, *A. lemmonii*; C1, C3, C5, C8, C10, Colockum; B1, Brewton; O1, O4, Ochoco; /c, cryptogamic crust intact; /dc, cryptogamic crust disturbed.

Table 16. Principal components analyses eigenvalues and percent of variance for the first ten axes of vegetation of all *Achnatherum hendersonii* and *A. lemmonii* plots, and of all *A. hendersonii* plots.

	A. hendersonii & *A. lemmonii*		*A. hendersonii*	
Axis	Eigen-value	% of var.	Eigen-value	% of var.
1	5.266	13.86	4.918	16.96
2	3.561	9.37	2.862	9.87
3	2.087	5.49	2.062	7.11
4	1.850	4.87	1.509	5.20
5	1.620	4.26	1.420	4.90
6	1.403	3.69	1.300	4.48
7	1.347	3.54	1.176	4.05
8	1.242	3.27	1.099	3.79
9	1.126	2.96	1.072	3.70
10	1.120	2.95	1.064	3.67
% of total variance		54.27		63.73

Table 17. Principal components analyses eigenvectors for the first two axes of vegetation of *Achnatherum hendersonii* and *A. lemmonii* plots, and of *A. hendersonii* plots. Only eigenvector loadings > 0.2000 or < -0.2000 for any one of the axes only are presented; -, indicates not present.

	A. hendersonii & *A. lemmonii*		*A. hendersonii*	
	Eigenvectors		Eigenvectors	
Species	1	2	1	2
Bareground	-0.0812	-0.4183	0.2070	0.4112
Achnatherum hendersonii	-0.0193	-0.1977	0.1048	-0.1517
Achnatherum lemmonii	0.1567	0.2071	-	-
Bletharipappus scaber	-0.3122	0.0697	-0.3098	0.2044
Bromus japonicus	-0.2926	0.2137	-0.3458	-0.0776
Collinsia parviflora	0.1888	0.2789	-0.0084	-0.3616
Lewisia rediviva	0.0313	-0.0654	0.0800	-0.2690
Lithophragma bulbifera	0.1716	0.2363	-	-
Lomatium leptocarpum	-0.2758	0.1630	-0.3136	0.0048
Lomatium triternatum	0.2453	0.2192	0.1396	-0.3289
Poa secunda	0.1897	0.1762	0.1171	-0.2344
Polygonum majus	-0.2951	0.0491	-0.2848	0.2414
Rigiopappus leptocladus	-0.2828	0.2317	-0.3410	-0.1371
Tortula intermedia	-0.3340	0.2095	-0.3838	-0.2035
Viola trinervata	0.0369	-0.1046	0.1067	-0.2577
Zygadenus venenosus	-0.1947	0.1324	-0.2261	-0.0259

The relationship between the *A. hendersonii* and *A. lemmonii* communities was clarified by excluding the additional vegetation plots (-Ache and *Agropyron spicatum*). The 95% confidence ellipses indicated a separation between the vegetation plots at the southern distribution limit (Ochoco) of *A. hendersonii* and the those at the northern distribution limit (Colockum and Brewton; Figure 15). The ellipse for the Ochoco vegetation plot with cryptogamic crust intact (O4) had the highest area (greatest variation) value, whereas the ellipse for Colockum *A. hendersonii* vegetation plot C1 had the lowest area (least variation) value (Table 18). Ellipse area values for the remaining vegetation plots were similar, an indication that they had similar amounts of variation. The ellipses for the Ochoco vegetation plots had high theta (organization *sensu stricto*) values compared with the other ellipses, suggesting that the communities in the southern distribution limit were organized *sensu stricto* differently than the communities in the northern distribution limit (Table 18). Theta values for the remaining vegetation plots were similar. Ellipse eccentricity values were similar for all vegetation plots, an indication that the vegetation at the northern and southern distribution ranges of *A. hendersonii* had similar organization in the sense of order.

Achnatherum hendersonii Plots

The results of the PCA for *A. hendersonii* vegetation plots only are similar to those for the combined *A. hendersonii* and *A. lemmonii* vegetation plots. As with the previous two PCAs, all of the eigenvalues for the first ten axes were greater than 1 (Table 16). The variance explained by the first axis was 17%, the first ten axes was 64%. *Tortula intermedia*, *Bromus japonicus*, *Rigiopappus leptocladus*, *Blepharipappus scaber*, and *Lomatium leptocarpum* had the strongest negative loadings on PCA axis one, whereas bareground, *Lomatium triternatum*, *Poa secunda*, *Viola trinervata*, and *A. hendersonii* had the strongest positive loadings (Table 17). These results were nearly identical to the previous PCA results (A.

Table 18. Descriptive statistics of the 95% confidence ellipses from the PCA of *Achnatherum hendersonii* and *A. lemmonii* vegetation. Ache, *A. hendersonii*; Acle, *A. lemmonii*; /c, cryptogamic crust intact; /dc, cryptogamic crust disturbed. See text for explanation of descriptive statistics and plot descriptions.

Plot	Community	Theta	Eccen.	Area
C1	Ache	60.40	0.942	0.005
C3	Ache	65.80	0.726	0.016
C5	Ache	74.70	0.791	0.016
B1	Ache	69.72	0.884	0.011
01	Ache/dc	153.70	0.958	0.016
04	Ache/c	140.51	0.978	0.059
C8	Acle	64.60	0.997	0.016
C10	Acle	54.15	0.996	0.011

hendersonii and *A. lemmonii* vegetation plots). Again, a latitudinal gradient was observed along PCA axis one. On PCA axis two, *Collinsia parviflora*, *Lomatium triternatum*, *Lewisia rediviva*, *Viola trinervata*, *Poa secunda*, and *Tortula intermedia* had the strongest negative loadings, and bareground, *Polygonum majus*, and *Blepharipappus scaber* had the strongest positive loadings. Results for the analysis of variance on PCA axis one scores were the same as the results for the *A. hendersonii* and *A. lemmonii* vegetation plots combined (Table 8).

The 95% confidence ellipses revealed a strong separation between the Ochoco study site and the Colockum and Brewton study sites (Figure 16). Table 19 lists the descriptive statistics for the ellipses. Again, the results are similar to the previous analysis, however the relationship between the *A. hendersonii* vegetation plots in the northern and southern distribution ranges of *A. hendersonii* was further refined by this analysis. The ellipses for the southern (Ochoco) vegetation plots had different theta values than the ellipses of the northern vegetation plots, an indication that they have different organization *sensu stricto*. The two southern vegetation plots had theta values quite different from each other, an indication that the organization *sensu stricto* within the southern study site (Ochoco) is also quite different. Ellipse eccentricity (order) values were similar for all vegetation plots, suggesting that the vegetation that *A. hendersonii* occurs in, regardless of geographic location, had similar organization in the sense of order. The ellipse for Ochoco vegetation plot with intact cryptogamic crust (O4) had the highest area (greatest variation) value of all vegetation plots, and Colockum vegetation plot C1 had the lowest area (least variation) value. The Brewton vegetation plot (B1) had the second lowest area value, while the remaining vegetation plots had similar area values, indicating similarities in variation among those vegetation plots.

The PCA on the *A. hendersonii* vegetation, without the affect of *A. lemmonii* vegetation, even further stresses the regional variation and

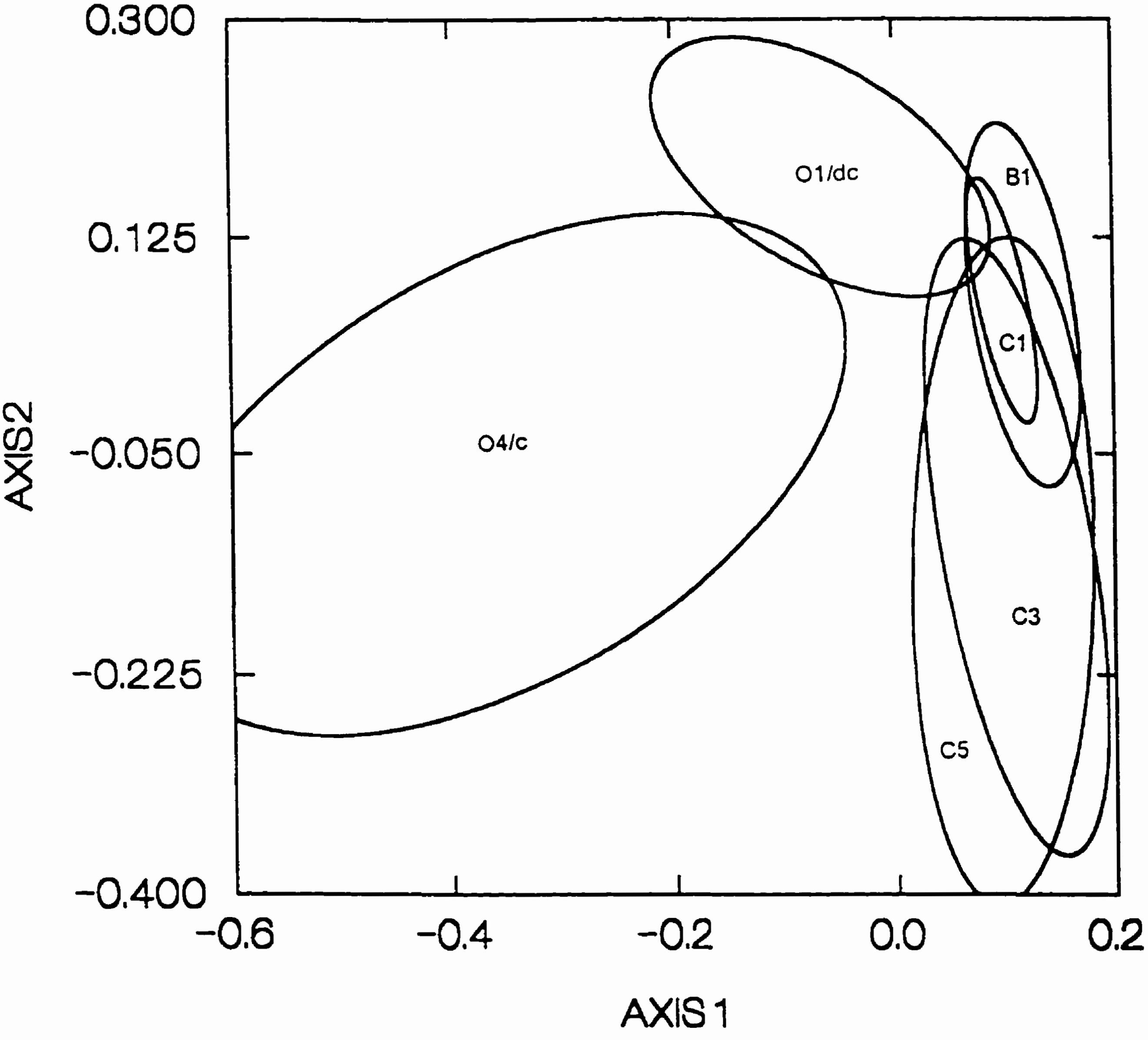

Figure 16. PCA ordination of *Achnatherum hendersonii* vegetation plots. 95% confidence limit ellipses denote the vegetation organization and variation in each plot. C1, C3, C5, Colockum; B1, Brewton; O1, O4, Ochoco; /c, cryptogamic crust intact; /dc, cryptogamic crust disturbed.

Table 19. Descriptive statistics of the 95% confidence ellipses from the PCA of *Achnatherum hendersonii* vegetation. /c, cryptogamic crust intact; /dc, cryptogamic crust disturbed. See text for explanation of descriptive statistics and plot descriptions.

Plot	Theta	Eccen.	Area
C1	103.21	0.972	0.006
C3	101.20	0.961	0.046
C5	88.67	0.950	0.059
B1	99.92	0.949	0.018
O1/dc	145.83	0.844	0.043
O4/c	25.06	0.867	0.150

organization of the communities, as well as within site variation and organization.

Soils

The soils were significantly deeper in the *Achnatherum lemmonii* vegetation plots than in any of the other vegetation plots (Table 4). Soil depths in the *Agropyron spicatum* vegetation plots were generally significantly greater than the remaining Colockum and Brewton plots, but were not significantly different from three of the Ochoco plots. Overall there was much overlap in the results of the multiple comparison test, creating ambiguity as to significant differences among means. This reflects the fact that the analysis of variance test is more powerful than the multiple comparison test (Zar 1984).

Table 20 summarizes the composition characteristics of the soils for each plant community for each study site. Nutrient levels were generally low for all communities. The highest nutrient values were observed in the *Achnatherum lemmonii* community. This community also had significantly deeper soils (Table 4) and higher percentage of vegetation coverage (Tables 3, 11, and 13), providing both a source of nutrients (plant matter) and nutrient retention (soil column).

Morphology

Achnatherum hendersonii plants were generally smaller than *A. lemmonii* plants (Tables 21 and 22), with sheaths, blades, and ligules longer in *A. lemmonii*. Blade width was similar in the two species.

Mean inflorescence blade length of *A. hendersonii* from Colockum study site plots C1 and C3 were not significantly different, but were significantly greater than mean inflorescence blade lengths of plot C5, the Brewton study site, and the Ochoco study site, all of which were not significantly different (Table 21). Inflorescence blade width was more variable. Mean inflorescence blade width of *A. lemmonii* plots C8 and C10 were not

Table 20. Soil characteristics. Samples were pooled by community type within the same study site. Ache, *Achnatherum hendersonii*; Agsp, *Agropyron spicatum*; -Ache, *Achnatherum hendersonii* absent; Acle, *Achnatherum lemmonii*.

	Veg. Type	pH	P (µg/g)	K (µg/g)	NO3-N (µg/g)	NH4-N (µg/g)	Organic Matter %	C %	H %	N %	Sand %	Clay %	Silt %
Colockum 1, 3, 5	Ache	6.6	2.8	77	4.8	2.6	1.36	0.84	0.43	0.11	71.6	6.4	22.0
Colockum 2, 4, 6	Agsp	6.3	3.4	134	3.6	2.2	1.73	1.2	0.55	0.14	67.6	6.4	26.0
Colockum 7	-Ache	6.7	2.1	32	1.8	2.5	0.94	0.47	0.63	0.12	-	-	-
Colockum 8, 10	Acle	6.3	6.6	318	8.7	4.1	2.67	1.6	0.66	0.16	43.6	16.4	40.0
Brewton 1	Ache	6.7	2.6	59	0.4	1.8	0.98	0.56	0.52	0.10	43.1	10.8	46.2
Brewton 2	-Ache	6.4	6.5	124	0.5	3.1	2.17	1.4	0.70	0.16	47.0	10.5	42.5
Brewton 3	Agsp	6.8	5.5	310	1.0	2.4	1.81	1.1	0.68	0.14	50.8	8.6	40.5
Ochoco 1, 4	Ache	6.3	1.8	58	0.7	2.9	0.97	0.66	0.81	0.11	33.6	16.4	50.0
Ochoco 2, 3	-Ache	6.5	2.4	67	2.2	2.2	1.17	0.70	0.85	0.08	39.6	20.4	40.0

Table 21. Mean inflorescence leaf variables (mm) and ANOVA results for leaf variables. Mean values with matching letters within each variable are not significantly different. N=25 for all plots.

	Plot	Mean	Max.	Min.	SD
Inflorescence					
Sheath length					
A. hendersonii	C-1	57.6*ab*	75	40	8.9
	C-3	63.6*bc*	76	50	7.7
	C-5	50.8a	64	39	7.3
	B-1	49.8a	67	33	9.4
	O-1	55.3a	86	37	12.0
	O-4	55.3a	70	40	6.8
A. lemmonii	C-8	95.3*d*	106	75	9.9
	C-10	71.3*bc*	94	55	11.0
Blade length					
A. hendersonii	C-1	37.5e	71	18	11.1
	C-3	38.1e	65	19	12.4
	C-5	27.7*f*	46	14	6.5
	B-1	29.6*f*	46	18	7.8
	O-1	25.0*f*	42	10	9.1
	O-4	26.2*f*	44	18	6.4
A. lemmonii	C-8	52.4*g*	88	26	14.2
	C-10	84.2*h*	143	54	21.6
Blade width					
A. hendersonii	C-1	1.32*ij*	1.8	1.1	0.15
	C-3	1.42*ij*	1.9	1.0	0.27
	C-5	1.25*i*	1.7	0.8	0.23
	B-1	1.23*i*	1.7	0.6	0.25
	O-1	1.35*ij*	1.8	0.8	0.29
	O-4	1.43*ij*	2.1	0.9	0.35
A. lemmonii	C-8	1.54*jk*	2.4	0.9	0.44
	C-10	1.70*k*	2.2	1.0	0.37
Ligule length					
A. hendersonii	C-1	0.56*l*	1.1	0.3	0.20
	C-3	0.43*l*	0.6	0.3	0.07
	C-5	0.43*l*	0.6	0.2	0.09
	B-1	0.44*l*	0.6	0.3	0.10
	O-1	0.63*l*	1.3	0.4	0.22
	O-4	0.56*l*	1.2	0.2	0.21
A. lemmonii	C-8	1.84*m*	3.0	1.1	0.47
	C-10	1.54*n*	2.4	1.0	0.41

Table 22. Mean vegetative leaf variables (mm) and ANOVA results for leaf variables. Mean values with matching letters within in each variable are not significantly different. N=25 for all plots.

	Plot	Mean	Max.	Min.	SD
Vegetative					
Sheath length					
A. hendersonii	C-1	36.4*c*	57	15	10.7
	C-3	34.6*bc*	47	22	7.2
	C-5	28.2*ab*	39	19	6.7
	B-1	26.2a	44	13	7.4
	O-1	23.9a	36	14	5.7
	O-4	24.3a	33	14	4.5
A. lemmonii	C-8	38.0*c*	56	25	7.7
	C-10	48.0*d*	76	33	9.9
Blade length					
A. hendersonii	C-1	71.7e	105	26	22.1
	C-3	70.1e	110	44	19.9
	C-5	49.2*f*	77	31	12.9
	B-1	46.6*f*	75	25	13.6
	O-1	42.4*f*	72	26	12.1
	O-4	42.1*f*	61	32	7.3
A. lemmonii	C-8	80.5e	138	30	25.9
	C-10	118.7*g*	178	57	29.0
Blade width					
A. hendersonii	C-1	1.16*h*	1.4	0.7	0.20
	C-3	1.30*hi*	1.9	0.8	0.28
	C-5	1.11*h*	1.4	0.8	0.21
	B-1	1.15*h*	1.5	0.7	0.23
	O-1	1.44*i*	2.0	1.0	0.26
	O-4	1.42*i*	1.9	1.0	0.28
A. lemmonii	C-8	1.25*h*	1.8	0.5	0.31
	C-10	1.43*i*	2.0	1.0	0.27
Ligule length					
A. hendersonii	C-1	0.43*jkl*	0.8	0.2	0.15
	C-3	0.35*jk*	0.5	0.1	0.10
	C-5	0.28*j*	0.5	0.1	0.10
	B-1	0.38*jk*	0.6	0.2	0.09
	O-1	0.54*l*	0.7	0.4	0.07
	O-4	0.49*kl*	0.9	0.3	0.13
A. lemmonii	C-8	1.17*m*	1.9	0.6	0.41
	C-10	1.32*m*	2.1	1.0	0.29

significantly different from each other. Mean inflorescence blade width of *A. lemmonii* from plot C8 was not significantly different than *A. hendersonii* from plots C1 and C3, nor from the Ochoco study site plots. *Achnatherum lemmonii* plot C8 mean inflorescence sheath length was significantly greater than mean inflorescence sheath length from all other plots, while *A. lemmonii* Colockum plot C10 was not significantly greater than *A. hendersonii* plot C3, although it was significantly greater than the remaining plots. *Achnatherum lemmonii* mean inflorescence ligule lengths were significantly different from each other, and both were significantly greater than all other plots.

Mean vegetative leaf morphology followed a similar pattern to mean inflorescence leaf morphology (Table 22). *Achnatherum lemmonii* plot C10 mean vegetative blade length was significantly greater than mean vegetative blade widths from all other plots. *Achnatherum lemmonii* vegetative mean blade length for plot C8 was not significantly different from Colockum study site *A. hendersonii* plots C1 and C3. Mean vegetative blade lengths for Colockum study site plot C5, the Brewton study site, and the Ochoco study site were not significantly different. Mean vegetative blade width was similar between all study sites and between *A. hendersonii* and *A. lemmonii*. Mean vegetative sheath length was not significantly different between the Ochoco study site, the Brewton study site, and plot C5 at the Colockum study site. Mean vegetative sheath lengths for the remaining *A. hendersonii* plots at the Colockum study site were similar. *Achnatherum lemmonii* plot C10 mean vegetative sheath length was significantly longer than in any other plot. Mean vegetative ligule length was similar for all *A. hendersonii* plots. *Achnatherum lemmonii* had significantly longer mean vegetative ligule lengths than *A. hendersonii*.

Inflorescence Leaf PCA

PCA inflorescence leaf data for *A. hendersonii* and *A. lemmonii* resulted in 67% of the total variance explained by the first axis (Table 23). All four leaf variables loaded negatively on the first axis indicating a size

Table 23. Principal components analysis of *Achnatherum hendersonii* and *A. lemmonii* inflorescence leaf morphology, eigenvalues and eigenvectors for axes 1 and 2.

	Axes	
	1	2
Eigenvalues	2.676	0.705
% of total variance	66.90	17.63
Eigenevectors		
Blade length	-0.5042	0.4611
Blade width	-0.5269	-0.1553
Sheath length	-0.4253	-0.7991
Ligule length	-0.5359	0.3531

gradient increasing from right to left among the plants analyzed. Of the PCA second axis eigenvectors, inflorescence blade length had the strongest positive loading and inflorescence sheath length had the strongest negative loading.

Analysis of variance of the PCA axis scores for inflorescence morphology revealed within species similarity and among species differences (Table 24). In other words, the amount of variation in inflorescence morphology along PCA axis one for *A. hendersonii* from all sites is the same, as is the amount of variation for *A. lemmonii*.

The 95% confidence ellipses for inflorescence leaf morphology indicated a separation between the *A. lemmonii* plots (C8 and C10) and the *A. hendersonii* plots (Figure 17 and Table 25). Although both species had similar eccentricity (order) and theta (organization *sensu stricto*) values, area (variation) values were greater for *A. lemmonii*. These results indicated that although organized similarly, *A. lemmonii* had greater inflorescence leaf variation than *A. hendersonii*. The ellipse for *A. hendersonii* plot C5 had the smallest area (variation), indicating that this population had the least variation. The *A. hendersonii* plots overlapped considerably and had similar eccentricity (order), theta (organization *sensu stricto*), and area (variation), values. The exception was the population at plot C1, which had a considerably smaller theta (organization *sensu stricto*) value, indicating that this population had a different organization *sensu stricto*.

Vegetative Leaf PCA

PCA of *A. hendersonii* and *A. lemmonii* vegetative leaves resulted in 63% of the total variance explained by PCA axis one (Table 26). All PCA axis one eigenvector loadings were negative with the strongest loading on vegetative blade width and the weakest on vegetative sheath length (Table 26). For PCA axis two, vegetative sheath length had the strongest negative loading and blade length had the strongest positive loading.

Table 24. Mean PCA first axis scores for morphology at each site. Mean scores in the same row with matching letters are not significantly different. N=25 for all plots.

	Achnatherum hendersonii						*A. lemmonii*	
	C1	C3	C5	B1	O1	O4	C8	C10
Inflor.	0.039*a*	0.024*a*	0.084*a*	0.084*a*	0.057*a*	0.051*a*	-0.171*b*	-0.168*b*
Veg.	0.001a	0.008a	0.077*b*	0.077*b*	0.060*ab*	0.064*ab*	-0.088*c*	-0.200*d*
Inflor. + veg.	0.029*ab*	0.025a	0.113*c*	0.112*c*	0.085*bc*	0.085*bc*	-0.187*d*	-0.262e

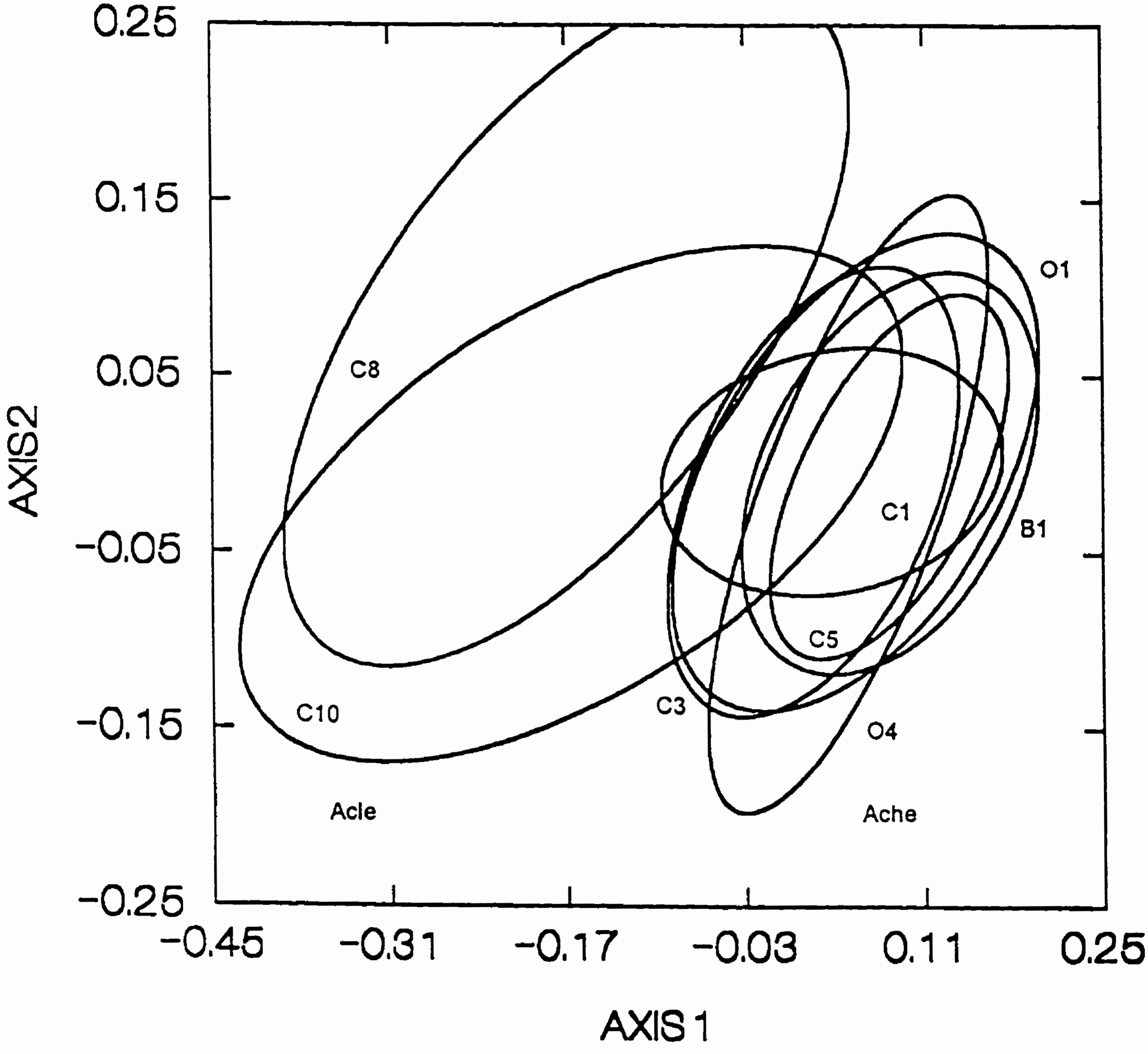

Figure 17. PCA ordination of inflorescence leaf morphology. 95% confidence limit ellipses denote the morphological organization and variation in each plot. C1, C3, C5, C8, C10, Colockum; B1, Brewton; O1, O4, Ochoco; Ache, *Achnatherum hendersonii*; Acle, *A. lemmonii*.

Table 25. Descriptive statistics of the 95% confidence ellipses from the PCA of inflorescence leaf morphology of *Achnatherum hendersonii* (Ache) and *A. lemmonii* (Acle) by plot. See text for explanation of descriptive statistics and plot descriptions.

Plot	Species	Theta	Eccen.	Area
C1	Ache	6.45	0.862	0.024
C3	Ache	51.05	0.814	0.034
C5	Ache	49.13	0.864	0.021
B1	Ache	43.02	0.758	0.032
O1	Ache	41.17	0.823	0.045
O4	Ache	61.30	0.940	0.035
C8	Acle	38.78	0.887	0.088
C10	Acle	21.47	0.779	0.127

Table 26. Principal components analysis of *Achnatherum hendersonii* and *A. lemmonii* vegetative leaf morphology, eigenvalues and eigenvectors for axes 1 and 2.

	Axes	
	1	2
Eigenvalues	2.515	0.921
% of total variance	62.86	23.02
Eigenevectors		
Blade length	-0.5684	0.2418
Blade width	-0.5863	0.1740
Sheath length	-0.2432	-0.9545
Ligule length	-0.5235	-0.0140

Analysis of variance of the PCA axis scores for vegetative morphology revealed that A. *hendersonii* from Colockum study site plots C1 and C3, and Ochoco study site plots O1 and O4 were not significantly different from each other (Table 24). Colockum study site plot C5, Brewton study site plot B1, and Ochoco study site plots O1 and O4 were also not significantly different from each other. However, Colockum study site plots C1 and C3 were significantly different from Colockum plot C5 and Brewton study site plot B1. Both A. *lemmonii* plots were significantly different from each other and were significantly different from the A. *hendersonii* plots. The amount of variation in vegetative leaf morphology observed along PCA axis one for A. *hendersonii* was similar among populations in its northern and southern distribution range, although there were some inconsistencies between sympatric populations.

The 95% confidence ellipse results for A. *hendersonii* and A. *lemmonii* vegetative morphology are given in Figure 18 and Table 27. Unlike the inflorescence leaf results (Figure 17 and Table 25), there was greater similarity between A. *hendersonii* and A. *lemmonii* as indicated by overlap of the ellipses. *Achnatherum lemmonii* had greater vegetative blade lengths and ligule lengths than A. *hendersonii*, resulting in the two populations (C8 and C10) being ordinated more negatively along PCA axis one (Table 26 and Figure 18). Ellipse eccentricity (order) values were fairly consistent throughout all populations of both species. Ellipse theta (organization *sensu stricto*) values were more variable in A. *hendersonii* vegetative leaves than were observed in inflorescence leaves (Tables 27 and 25), an indication that organization *sensu stricto* differs between these structures. *Achnatherum hendersonii* populations at the Colockum study site plot C1 and at the Brewton study site B1 had considerably higher theta (organization *sensu stricto*) values than the remaining populations. *Achnatherum lemmonii*, as in inflorescence leaf morphology, had greater area (variation) values than A. *hendersonii* and also had different theta (organization *sensu stricto*) values (Table 27). Thus, it appears that A. *lemmonii* has more variation in

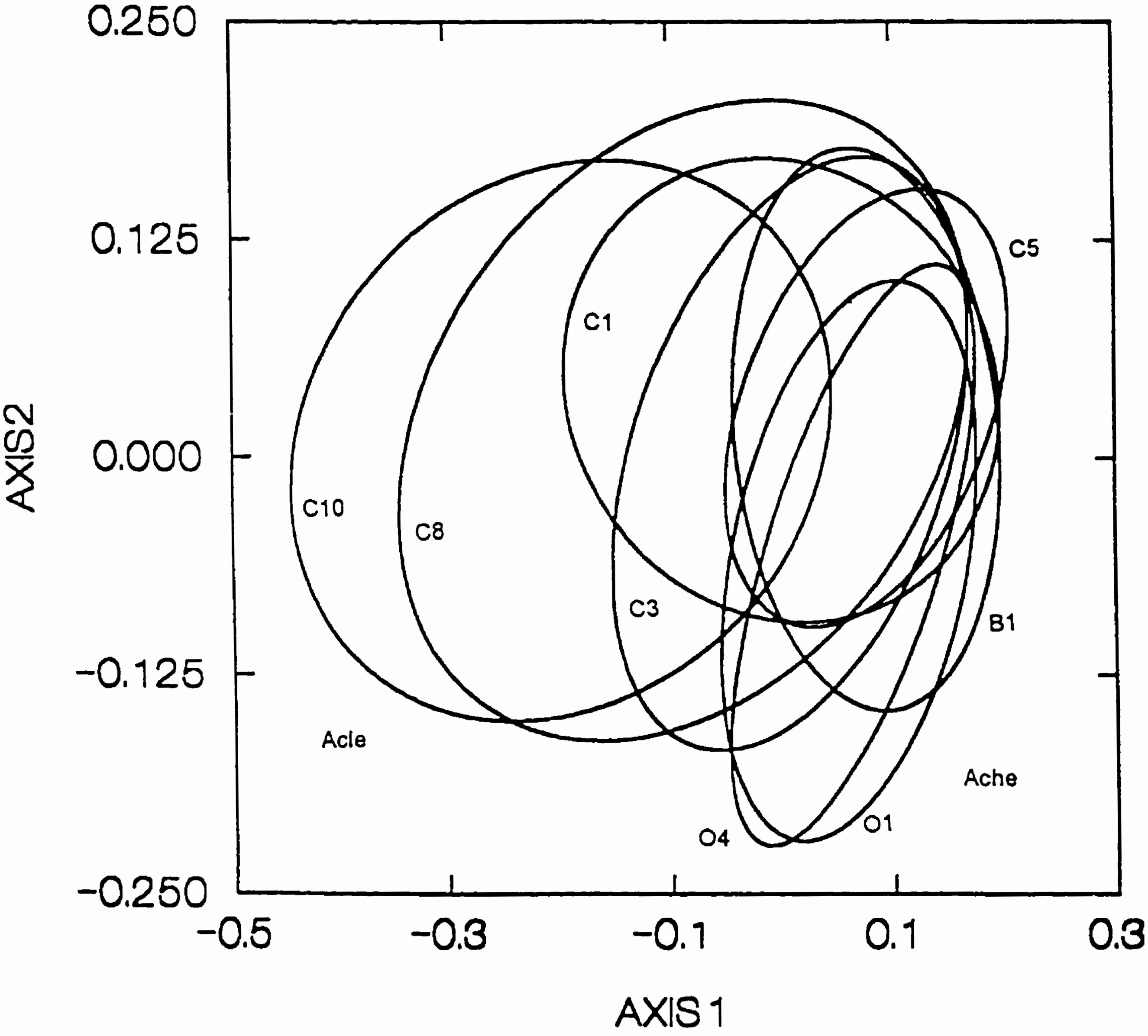

Figure 18. PCA ordination of vegetative leaf morphology. 95% confidence limit ellipses denote the morphological organization and variation in each plot. C1, C3, C5, C8, C10, Colockum; B1, Brewton; O1, O4, Ochoco; Ache, *Achnatherum hendersonii*; Acle, *A. lemmonii*.

Table 27. Descriptive statistics of the 95% confidence ellipses from the PCA of vegetative leaf morphology of *Achnatherum hendersonii* (Ache) and *A. lemmonii* (Acle) by plot. See text for explanation of descriptive statistics and plot descriptions.

Plot	Species	Theta	Eccen.	Area
C1	Ache	174.24	0.743	0.068
C3	Ache	48.84	0.764	0.066
C5	Ache	43.44	0.752	0.039
B1	Ache	101.17	0.684	0.051
O1	Ache	65.64	0.800	0.046
O4	Ache	60.43	0.921	0.036
C8	Acle	20.92	0.777	0.119
C10	Acle	11.15	0.775	0.102

vegetative leaf morphology than *A. hendersonii*, and that the two species have different vegetative leaf organization *sensu stricto*. Area (variation) values among the *A. hendersonii* populations differed slightly, with the population at Ochoco plot O4 displaying the least variation, and the population at Colockum plot C1 displaying the most variation. The sympatric populations of *A. hendersonii* at the Colockum site had dissimilar area (variation) values, with the population at plot C5 showing the least amount of variation. This population was the last to begin seasonal growth, and was several weeks behind the other two populations studied at Colockum. Although all populations were measured at the same stage of development, the compressed growing season may account for decreased variation at plot C5.

There appears to be more variation in vegetative leaf morphology, both within and among populations of *A. hendersonii*, than in inflorescence leaf morphology as indicated by ellipse area values (Tables 27 and 25). Similar area values indicate that variation in inflorescence and vegetative leaf morphology are similar within and between populations of *A. lemmonii* (Tables 27 and 25). Although both species tend to have similar inflorescence and vegetative leaf morphology organization in the sense of order (eccentricity), organization *sensu stricto* (theta) and variation differ between the species (Tables 27 and 25).

Inflorescence & Vegetative Leaf PCA

PCA of *Achnatherum hendersonii* and *A. lemmonii* inflorescence and vegetative leaf data combined, resulted in 56.7% of the total variance explained by the first axis (Table 28). All first axis eigenvector loadings were negative, with the strongest loading on inflorescence blade width and the weakest on vegetative sheath length (Table 28). On the second PCA axis, vegetative sheath length had, by far, the strongest positive loading and inflorescence ligule length had the strongest negative loading.

Analysis of variance of the PCA axis one scores for inflorescence and vegetative leaf morphology combined indicated that the two plots of A.

Table 28. Principal components analysis of *Achnatherum hendersonii* and *A. lemmonii* leaf morphology (inflorescence and vegetative), eigenvalues and eigenvectors for axes 1 and 2.

	Axes	
	1	2
Eigenvalues	4.538	1.025
% of total variance	56.73	12.81
Eigenevectors		
Inflorescence		
Blade length	-0.3686	-0.1630
Blade width	-0.4092	-0.0913
Sheath length	-0.2643	0.2852
Ligule length	-0.3852	-0.2051
Vegetative		
Blade length	-0.3791	-0.0410
Blade width	-0.3979	0.0060
Sheath length	-0.1203	0.9164
Ligule length	-0.4024	0.0100

lemmonii were significantly different from each other (Table 24). The *A. hendersonii* plots for the Ochoco study site, the Brewton study site, and Colockum plot C5 were generally not significantly different from each other. However, Colockum plots C1 and C3 were not significantly different, and Colockum plot C1 was not significantly different from the Ochoco plots. Essentially, there was little difference in the combined data set between *A. hendersonii* populations.

Figure 19 shows the 95% confidence limit ellipses calculated for *A. hendersonii* and *A. lemmonii* leaf morphology. Table 29 contains the descriptive statistics for these ellipses. *Achnatherum lemmonii* (plots C8 and C10) had greater area (variation) values than *A. hendersonii* (plots C1, C3, C5, B1, O1, and O4), an indication that *A. lemmonii* had greater leaf morphological variation than *A. hendersonii*. All variables contributed negatively to *A. lemmonii* variation along PCA axis one, suggesting that this was primarily an axis of increasing size from right to left (Table 28). The *A. lemmonii* population from plot C8 was influenced more by vegetative sheath length and inflorescence ligule length on PCA axis 2 than the population from plot C10 (Figure 19 and Table 28). With the exception of the *A. hendersonii* populations at Colockum plot C1 and Brewton plot B1, the remaining *A. hendersonii* populations have similar ellipse theta (organization *sensu stricto*) values, differing from the two *A. lemmonii* populations. Ellipse eccentricity (order) values (Table 29) were more varied among the populations of *A. hendersonii* than was observed in the separate inflorescence and vegetative leaf morphology analyses (Tables 25 and 27). The *A. hendersonii* plots overlapped considerably, and all had more variation along PCA axis two than along PCA axis one. There was a slight overlap between the two species along PCA axis one.

Comparison of Morphological PCAs

In all analyses at least 50% of the total variance was accounted for by PCA axis one (Tables 23, 26, and 28). Also in all analyses, *A. lemmonii*,

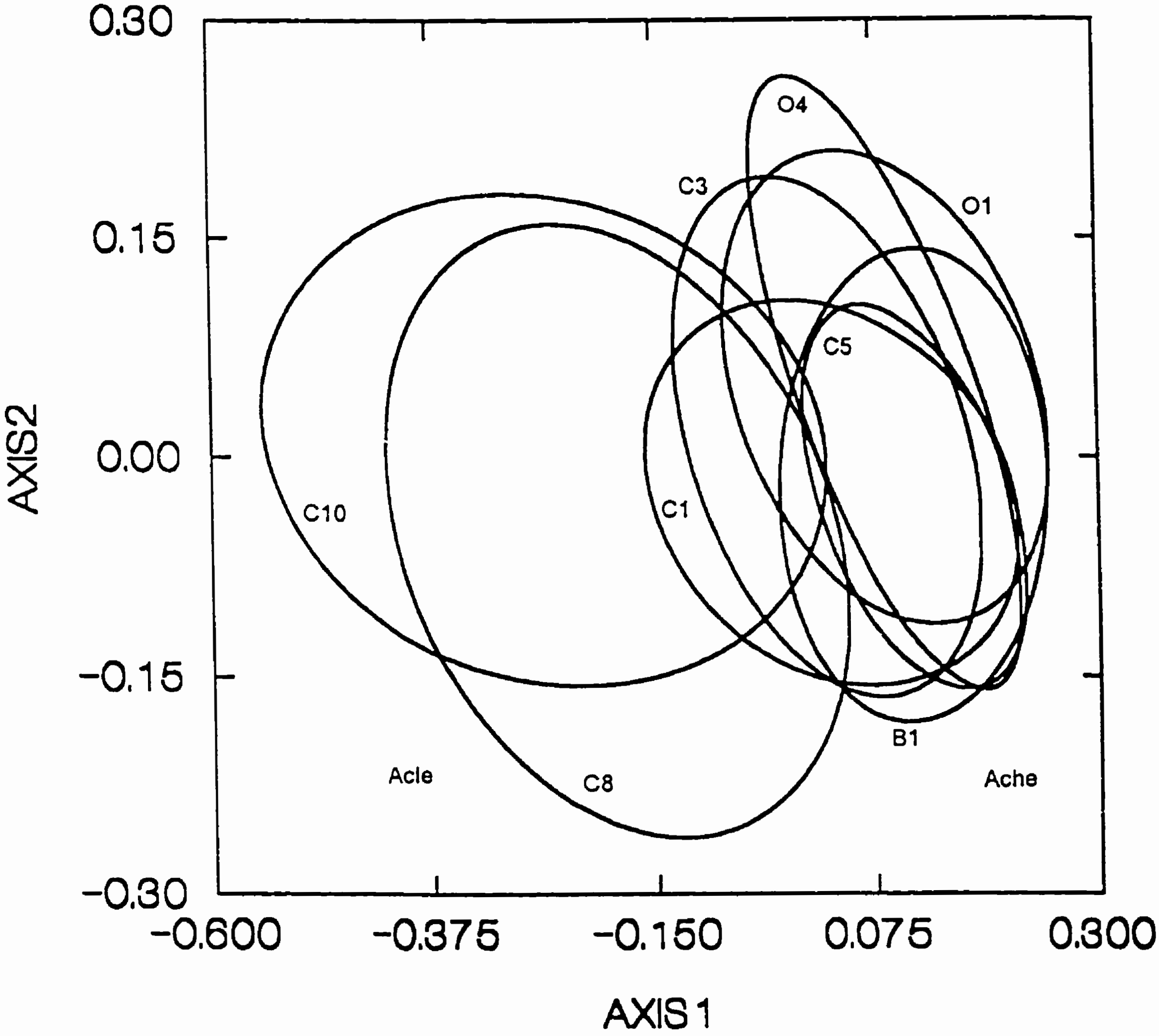

Figure 19. PCA ordination of leaf morphology (inflorescence and vegetative combined). 95% confidence limit ellipses denote the morphological organization and variation in each plot. C1, C3, C5, C8, C10, Colockum; B1, Brewton; O1, O4, Ochoco; Ache, *Achnatherum hendersonii*; Acle, *A. lemmonii*.

Table 29. Descriptive statistics of the 95% confidence ellipses from the PCA of leaf morphology (inflorescence and vegetative combined) of *Achnatherum hendersonii* (Ache) and *A. lemmonii* (Acle) by plot. See text for explanation of descriptive statistics and plot descriptions.

Plot	Species	Theta	Eccen.	Area
C1	Ache	164.53	0.755	0.064
C3	Ache	124.62	0.745	0.067
C5	Ache	125.11	0.809	0.034
B1	Ache	83.93	0.557	0.057
O1	Ache	136.54	0.675	0.066
O4	Ache	118.59	0.935	0.052
C8	Acle	146.17	0.672	0.124
C10	Acle	173.78	0.818	0.126

ordinated more towards the negative end of PCA axis one than *A. hendersonii* (Figures 17, 18, and 19). The variation (area) and organization (theta and eccentricity) of the inflorescence leaf morphology was similar to that of the respective whole plant (inflorescence and vegetative leaf morphology combined) for both the rare and the common species (Figures 17 and 19). *Achnatherum hendersonii* had the greatest amount of relative variation (area; Table 27) in the vegetative leaves (Figure 18), compared to the inflorescence leaf morphology (area, Table 26; Figure 17), and the leaf morphology of the whole plant (area, Table 29; Figure 19). *Achnatherum lemmonii* had similar amounts of variation (area) in inflorescence leaves, vegetative leaves, and whole plant leaves (Tables 25, 27, and 29).

In general, population level variation (area) and organization (theta and eccentricity) in *A. hendersonii* were similar within and among sympatric and disjunct populations, and were similar among sympatric populations of *A. lemmonii*. Although the two species have similar population level organization in the sense of order (eccentricity), organization *sensu stricto* (theta), and especially variation (area) differed.

Comparison of Vegetation and Morphology Organization

Direct comparisons between vegetation and morphology were made by contrasting results from the PCA of *A. hendersonii* and *A. lemmonii* vegetation with the PCA of *A. hendersonii* and *A. lemmonii* morphology (inflorescence and vegetative combined) for all study sites (Tables 18 and 29, and Figures 15 and 19). The results for combined inflorescence and vegetative leaf morphology were used because they more accurately portray the whole plant, and because of their similarity with the separate vegetative and inflorescence leaf results; further comparisons would have been redundant.

Only 13.9% of the variance was accounted for by the first PCA axis for vegetation, while 56.7% of the variance was accounted for by the first PCA axis for morphology (Tables 16 and 28). The unequal amounts of total variance explained by the first axes reflects the different degree of complexity in the community and population level data sets, and comparisons should be made with this in mind. Regardless, any meaningful synthesis requires this comparison.

Tables 8 and 24 show the results for analysis of variance on PCA axis one scores for vegetation and morphology respectively. Comparisons are made with *A. hendersonii* and *A. lemmonii* communities for vegetation (Table 8) and inflorescence + vegetative for morphology (Table 24). On the community level (vegetation; Table 8) the northern (Colockum and Brewton) and southern (Ochoco) study sites were significantly different from each other, whereas, on the population level (morphology; Table 24), the northern and southern populations of *A. hendersonii* showed instances where they were not significantly different. The range of differences for the *A. hendersonii* populations (Table 24; infl.+ veg., 0.113 - 0.025), is less than that for the *A. hendersonii* communities (Table 8; Ache + Acle, 0.013 - -0.328). On both the community and population levels, *A. lemmonii* was significantly different from *A. hendersonii*. *Achnatherum lemmonii* plots on the community level were not significantly different from each other, but were significantly different on the population level. Opposite results were observed for *A. hendersonii* at the Ochoco study site (i.e. different on the community level, but not different on the population level). Thus, patterns in mean PCA axis one scores observed in morphology were not necessarily observed in the corresponding vegetation.

A comparison of the PCA 95% confidence limit bivariate ellipses results for vegetation (Figure 15) and morphology (Figure 19) shows that vegetation is separated geographically and by species, whereas morphology is separated only by species. Ellipses for the vegetation (Table 18) indicated that the Ochoco study site vegetation plot with intact crust (04) had the greatest amount of variation (area), whereas for morphology (Table 29), greater variation was observed in *A. lemmonii*. Organization *sensu stricto* (theta) for vegetation (Table 18) changed with respect to geographical location, whereas for morphology (Table 29), organization was similar for both species

(*A. hendersonii* at Brewton, B1, deviates slightly). Organization in the sense of order (eccentricity) was more consistent for vegetation (Table 18) than for morphology (Table 29).

An ordination of the first PCA axis scores for *A. hendersonii* and *A. lemmonii* vegetation plotted against the mean of the randomized first PCA axis scores for morphology (inflorescence + vegetative) graphically synthesizes community and population organization (organization *sensu stricto* and order) and variation (Figure 20). The descriptive statistics for these ellipses mathematically synthesize the degree of community and population levels of organization and variation (Table 30). Theta (organization *sensu stricto*) values were similar for all ellipses, with the exception of the ellipse for the Ochoco study site with intact cryptogamic crust (O4). Therefore, organization *sensu stricto* was similar for synthesized community and population levels of both species, excepting the previously noted Ochoco study site plot. Eccentricity (order) values were also similar for all ellipses, although the Ochoco study site with disturbed cryptogamic crust (O1) differed slightly. Again, this indicates that both species had similar synthesized community and population organization in the sense of order. Area (variation) values exhibited the strongest pattern for both geographic and species separation. The northern (Colockum and Brewton) sites had the lowest *A. hendersonii* variation, with similar among site variation. The southern (Ochoco) sites had the highest *A. hendersonii* variation, and variation between the sites also differed, the site with intact crust (O4) had the greatest amount of variation. Overall, however, synthesized community and population variation was the greatest for *A. lemmonii*.

In summary, synthesized community and population organization (organization *sensu stricto* and order) was similar for both species in the northern distribution range of *A. hendersonii*. In the southern range dissimilarities in both organization *sensu stricto* and in the sense of order were observed. In contrast, synthesized community and population variation differed in respect to geographic location and species.

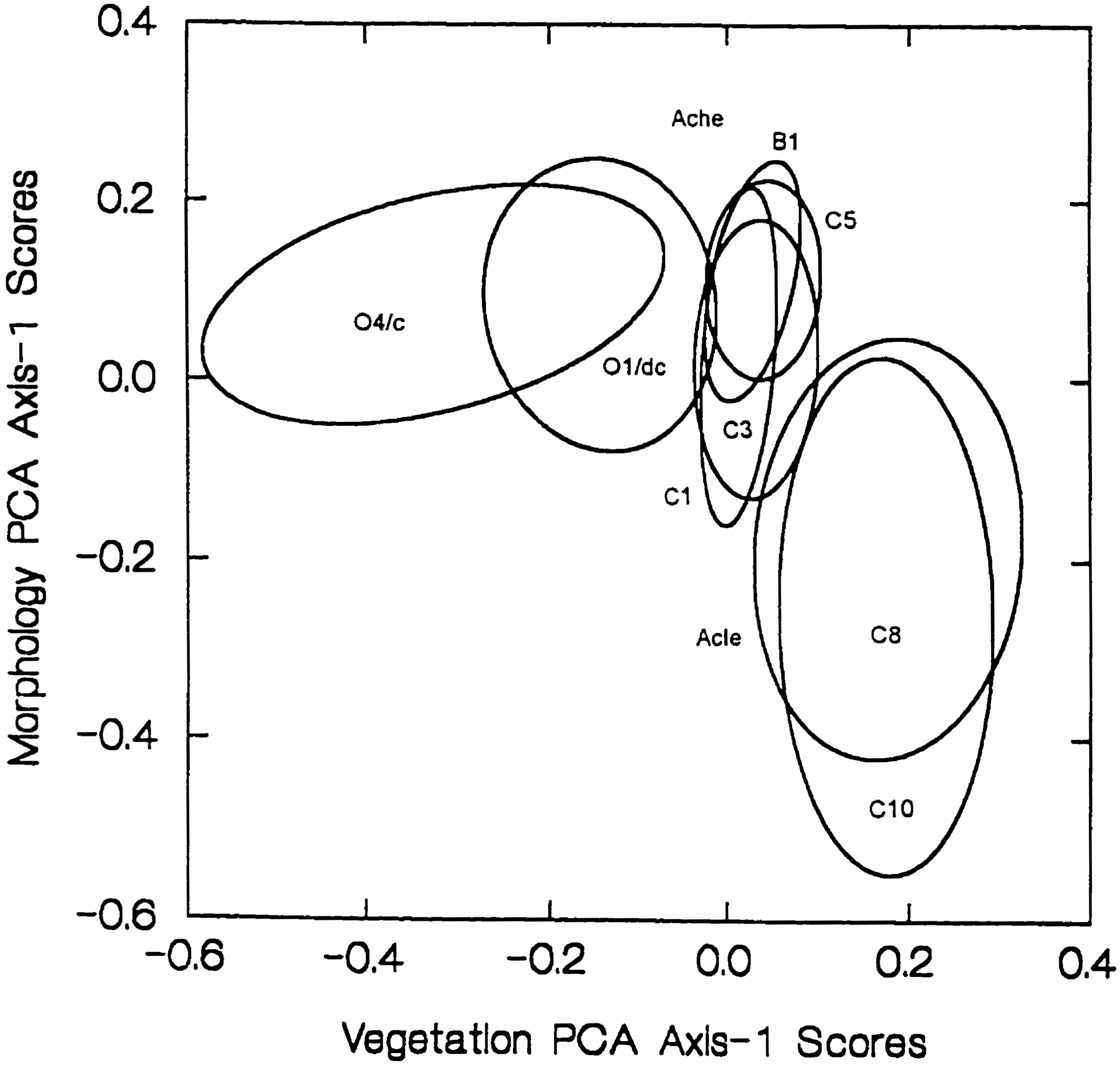

Figure 20. Representive ordination of *Achnatherum hendersonii* and *A. lemmonii* vegetation PCA axis 1 scores versus morphology (inflorescence and vegetative combined) PCA axis 1 scores. 95% confidence limit ellipses denote synthesized community and population level organization and variation. C1, C3, C5, C8, C10, Colockum; B1, Brewton; O1, O4, Ochoco; Ache, *A. hendersonii*; Acle, *A. lemmonii*; /c, intact cryptogamic crust; /dc, disturbed cryptogamic crust.

Table 30. Mean descriptive statistics of the 95% confidence ellipses of *A. hendersonii* and *A. lemmonii* vegetation first PCA axis scores and morphology (inflorescence and vegetative combined) first PCA axis scores. Ache, *A. hendersonii*; Acle, *Achnatherum lemmonii*; /c, cryptogamic crust intact; /dc, cryptogamic crust disturbed. See text for explanation of descriptive statistics and plot descriptions.

Plot	Community/ species	Theta	SD	Eccen.	SD	Area	SD
C1	Ache	87.99	2.30	0.974	0.0016	0.021	0.0006
C3	Ache	90.76	7.02	0.898	0.0080	0.028	0.0007
C5	Ache	88.02	9.04	0.827	0.0182	0.019	0.0005
B1	Ache	82.46	4.87	0.928	0.0121	0.018	0.0012
O1	Ache/dc	98.17	15.70	0.657	0.0503	0.055	0.0011
O4	Ache/c	6.21	4.38	0.861	0.0113	0.089	0.0022
C8	Acle	87.70	11.52	0.803	0.0208	0.088	0.0021
C10	Acle	87.62	5.21	0.918	0.0067	0.087	0.0027

Growth Experiment

Height for all plants increased for the first half of the growing season and remained stable for the last half (Figure 21). In general, *Poa secunda* was taller than *A. hendersonii* by the end of the growing season, and reached its maximum height earlier than *A. hendersonii*. Diameter was more variable than height over the growing season (Figure 22). *Poa secunda* diameters demonstrated a slight increase by the end of the growing season, whereas, *A. hendersonii* demonstrated a decrease.

Achnatherum hendersonii growing with *P. secunda* (Ap) and *A. hendersonii* growing with itself (AA) had significantly less growth over the 1996 growing season than *P. secunda* growing alone. The 1996 growth for all other combinations were not significantly different from one another (Table 31). Despite no significant difference between seasonal growth for most combinations it is interesting to note the ranked order of means:

P > Pa > PP > A > AA > Ap

These results give the impression that *P. secunda* grows best overall, under cultivated conditions, and even appears to suppress growth in *A. hendersonii*; however, *A. hendersonii* growing with itself also appears to have suppressed growth. *Achnatherum hendersonii* appears to grow best without neighboring plants, regardless of species. These results could also indicate that *A. hendersonii* has a slower growth rate than *P. secunda*.

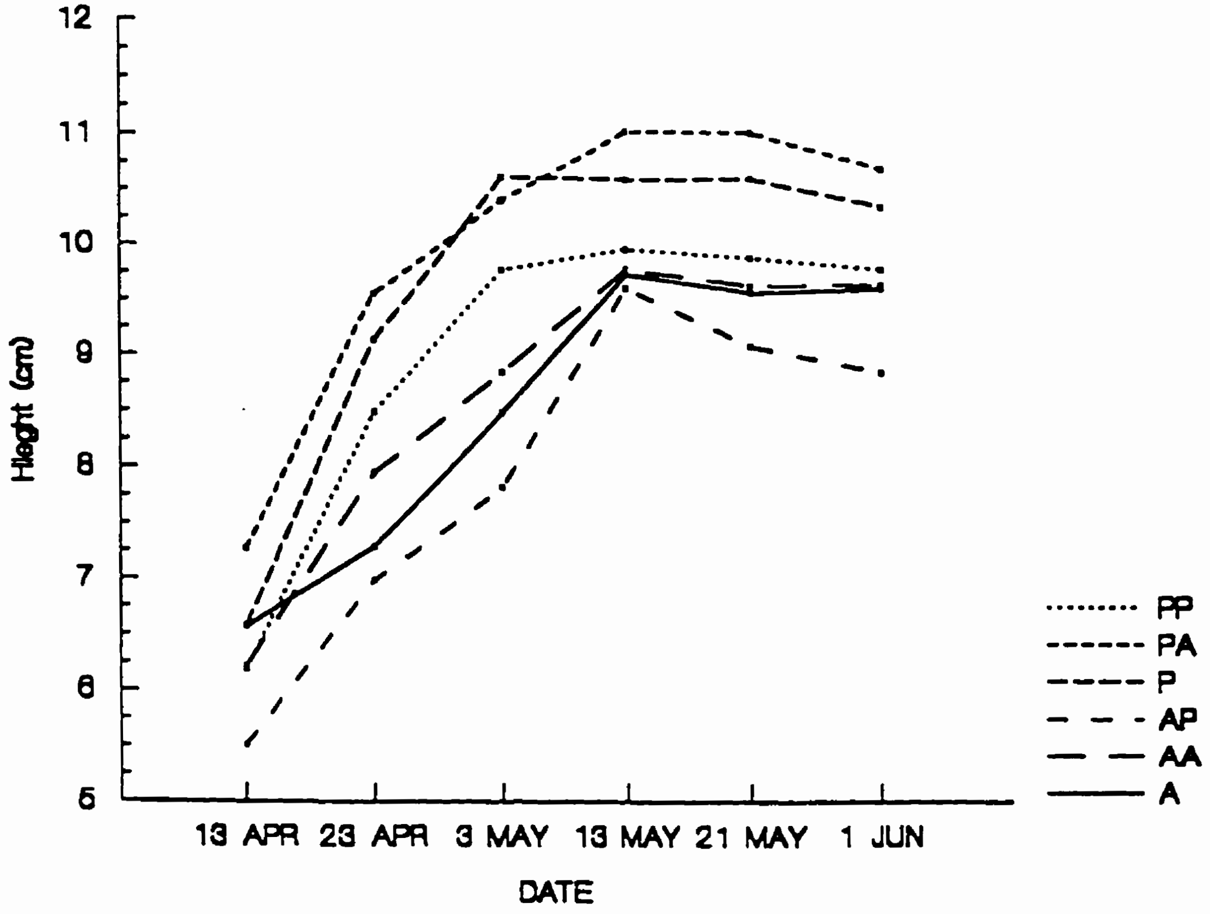

Figure 21. Mean heights for growth experiment combinations over the 1996 growing season.

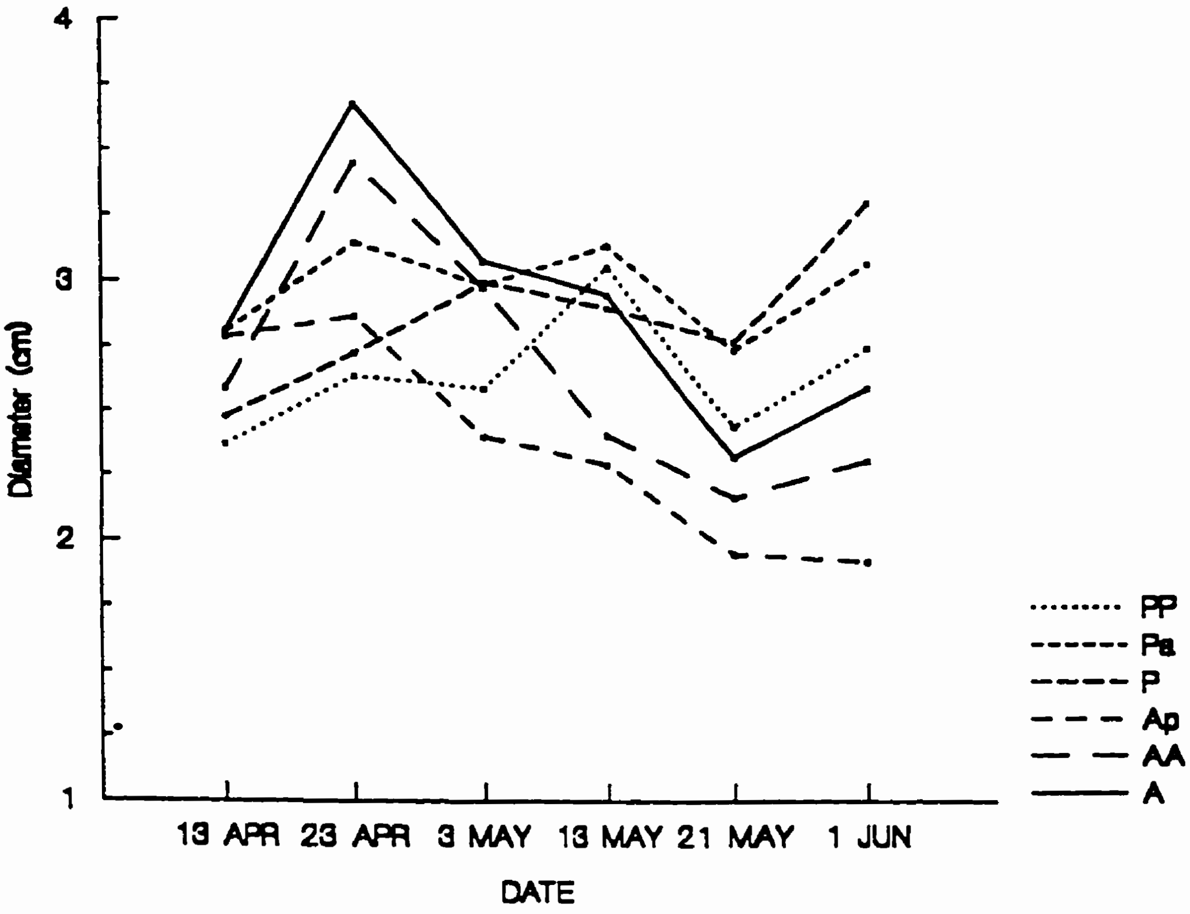

Figure 22. Mean diameters for growth experiment combinations over the 1996 growing season.

Table 31. Mean seasonal growth for the *Achnatherum hendersonii* and *Poa secunda* growth experiment. Combinations are: A, *A. hendersonii* growing alone; AA, *A. hendersonii* growing with *A. hendersonii*; Ap, *A. hendersonii* growing with *P. secunda*; P, *P. secunda* growing alone; PP, *P. secunda* growing with *P. secunda*; and Pa, *P. secunda* growing with *A. hendersonii*. Uppercase letter denotes plant measured. Growth values with the same letter are not significantly different.

	Combination					
	Ap	AA	A	PP	Pa	P
Growth (cm^3)	-4.3*a*	16.8*a*	22.1*ab*	30.3*ab*	47.7*ab*	64.0*b*
SD	15.6	36.9	23.9	37.0	66.1	54.0
N	10	20	10	20	10	10

DISCUSSION

Community

The plant communities I have described for the vegetation at the Colockum and Brewton study sites correspond to Daubenmire's (1970) lithosolic habitat types. Although they share common species, the communities at the Colockum study site are distinct from each other, as evidenced from the PCA ordination (Figure 10). For example the community that the rare grass, *Achnatherum hendersonii*, occupies is a different plant community from *Agropyron spicatum* dominated areas. These two communities share many species in common, yet occupy different areas of the PCA ordination. They are described by 95% confidence ellipses of different orientation, size, and shape (Figure 10 and Table 9). The differences in shape and orientation indicate that the two communities are organized in different ways. This is probably a result of different relationships among the species in common as well as those unique to each community. A detailed exploration of organizational differences may offer more insights as to why *Achnatherum hendersonii* grows where it does. These differences need to be assessed through much more intensive sampling of both vegetation and abiotic factors.

The sympatric populations of *A. hendersonii* occur within the same plant community and have minimal variation between them. The 95% confidence bivariate ellipses plot in the same area of the ordination and have similar shape and orientation. This indicates that they are organized similarly. Plot C1 appears intermediate between the *Agropyron spicatum* communities and the *Achnatherum hendersonii* communities. Plot C1 was located on an exposed south-facing portion of the slope and had the lowest total percent plant coverage of any vegetation plot at the Colockum study site.

The minus *A. hendersonii* (-Ache) vegetation plots (C7 and C9) are not a separate plant community from the *A. hendersonii* communities (Figure 10). The 95% confidence ellipses are plotted in the same location as the *A. hendersonii* ellipses and have either similar organization (plot C9) or similar variation (plot C7). Some subtle differences do occur in the -Ache communities. The ellipse of vegetation plot C7 has a different organization. This may reflect the lack of *A. hendersonii*. The ellipse for plot C9 is larger, indicating that it has more variation than plot C7, possibly reflecting a greater species richness.

The community in which the common grass, *Achnatherum lemmonii*, occurs is, as expected, a distinct plant community and differs from plant communities containing *A. hendersonii*, *Agropyron spicatum*, and from the -Ache community. *Achnatherum hendersonii* communities vary along PCA axis two. These communities are therefore more influenced by *Tortula intermedia*, *Antennaria flagellaris*, *Lewisia rediviva*, *Poa secunda*, and *Artemisia rigida*, whereas *A. lemmonii* communities vary along PCA axis one, and are more heavily influenced by *Collinsia parviflora*, *Lomatium triternatum*, and *A. lemmonii*. Although the 95% confidence ellipses have similar eccentricities, indicating a common order, they are plotted in a different portion of the ordination, have different organization *sensu stricto*, and have significantly greater variation (Figure 10). The larger size of the ellipses indicates that the plant community in which *A. lemmonii* occurs has greater overall variation than the other vegetation types at the Colockum study site (Figure 10 and Table 9). This is a possible indication of greater species diversity, because despite the fact that they have similar numbers of species, the community in which *A. lemmonii* occurs has greater total percent coverage of species (Table 3).

The PCA of the Colockum vegetation without the *A. lemmonii* vegetation plots clarifies the relationship among the *A. hendersonii*, -Ache, and *Agropyron spicatum* vegetation types, and allows for comparisons with the vegetation at the Brewton study site. The results are similar to the PCA of all communities at Colockum (Figures 11 and 10). The biggest differences are in the -Ache vegetation plots. Plot C7 (-Ache) appears nearly identical to plot C5 (*A. hendersonii* community). On the other hand, plot C9 (-Ache) is significantly different from plot C5, has greater variation as indicated by ellipse area, and different organization *sensu stricto*, as indicated by ellipse theta (Table 10). Plot C7 is adjacent to plot C5 in the field. This partly explains the similarity between these communities. By contrast plot C9 is approximately 10 m away from the nearest area where *A. hendersonii* is present. The differences in size and shape of the 95% confidence ellipses for the vegetation types reflects subtle differences in organization among the communities along the study slope.

The PCA results from the Brewton study site demonstrate a distinction between the *A. hendersonii* and the *Agropyron spicatum* communities that is similar to the results at Colockum (Figure 12). As with the Colockum study site, all communities at the Brewton study site have species in common. However, unlike Colockum, the 95% confidence ellipses plot in different locations of the PCA ordination and have different orientations. The eccentricities of all the ellipses are similar but areas are different, indicating that there is similar organization in the sense of order, but a difference in the amount of variation (Table 12). The *Agropyron spicatum* dominated community has the least amount of variation, and the -Ache vegetation plot has the most. The plant community in which *Achnatherum hendersonii* occurs and the -Ache vegetation plot have the most species in common. They also have similar total coverage of vegetation and bare ground (Table 11). Although they have slightly different organization *sensu stricto*, they have similar order and variation. This indicates that these two communities are closely related to each other (Table 12). The difference in organization appears to be because the -Ache community has a higher coverage of *Eriogonum thymoides* and lower coverage of cryptogamic crust, in particular the moss, *Ceratodon purpureus*. Frost action could account for the differences in cryptogamic crust coverage, but such processes were not evident during my field visits.

The vegetation at the Ochoco study site corresponds somewhat to the *Artemisia rigida/Poa secunda* association described by Hall (1967), although the *A. rigida* component is not as strong. The Ochoco vegetation differs considerably from the Colockum and Brewton vegetation. Considering the geographic separation, it is not too surprising that the plant communities are dissimilar; however, what was unexpected is the substantial amount of variation within the vegetation at the Ochoco study site (Tables 8 and 14). The vegetation plots of the two sympatric populations of A. *hendersonii* are less similar to each other than to the vegetation plots without A. *hendersonii*. Furthermore, the vegetation of one A. *hendersonii* plot (01) is a subset of the vegetation without A. *hendersonii* (Figure 13).

The 95% confidence ellipses of vegetation plots 01 (A. *hendersonii*), 02 and 03 (-Ache) all occur in the same portion of the PCA ordination and have similar orientations (Figure 13). Vegetation plot 04 (Ache), however, is in a different location and has a different orientation from the other plots. What is striking at this site is that the vegetation within areas where the cryptogamic crust is intact has more variation and higher species percent coverage than do the areas where the cryptogamic crust is not intact (Tables 14 and 13). *Achnatherum hendersonii* percent coverage and density are similar whether or not the cryptogamic crust is intact (Tables 13 and 5). Even though the two plots have A. *hendersonii* in common, other species within the plots appear to control the character of the plant community.

Comparisons of vegetation from all three study sites combined, from A. *hendersonii* and A. *lemmonii* vegetation combined, and from A. *hendersonii* vegetation alone, substantiate the patterns of organization observed for the individual study sites (Figures 14, 15, 16, and Tables 15, 18, and 19). The 95% confidence ellipses between the northern and southern study sites are plotted in different locations of the PCA ordination. The ellipses of the Colockum and Brewton study sites are all in the same location on the PCA ordination. This indicates that communities at the northern distribution limit of A. *hendersonii* are similarly organized, and the communities southern distribution limit are similarly organized, but the northern and southern communities are organized differently from each other.

The pattern of community organization differs between the northern and southern distribution limits of A. *hendersonii*. The community that contains

A.lemmonii, although similarly organized to the *A. hendersonii* communities in the northern distribution limit, has greater variation than the communities that contain *A. hendersonii* at Colockum and Brewton. On the other hand, communities containing *A. lemmonii* have less variation than the communities containing *A. hendersonii* at the Ochoco study site. The vegetation at the southern distribution limit of the rare grass has more variation than that for either the rare or common grass in the northern distribution range. Therefore, vegetation of the rare grass does not necessarily have less variation than the vegetation of a common congener. Moreover, species composition and community properties are not consistent over the distribution range of *A. hendersonii*. It follows that this type of rarity is not associated with a particular plant community type.

Predicting the locations where rare plants occur has been, for the most part, a concern of conservation biology (Miller 1986; Miller and Bratton 1987; White and Miller 1988; Nilsson et al. 1988). The literature demonstrates mixed results of predicting rarity. Miller (1986) found that species-area relations for rare plants were stronger within the Great Smokey Mountain National Park than in the southern Appalachian region overall. Elevational and slope diversity were found to be important predictors of rare plant species richness in these areas (Miller 1986; Miller and Bratton 1987). The practical applicability of these results, however, was inconclusive.

Nilsson et al. (1988) concluded that the only predictable feature found in their study of rarity along river banks was that species richness was higher on sites with rare species than on sites without rare species. Their results suggest that every river has largely unique vegetation features. This means that extensive field surveys are the only guarantee of success in selecting conservation sites.

In my study soil depth does not appear to control the distribution of the plant communities on the lithosols. However, soil depth was found to be an important factor in controlling species distribution in granite rock outcrop communities in Southern Oklahoma (Collins et al. 1989). Soil depth differences did not accurately delineate the various communities except in the extreme cases between the *A. hendersonii* communities and the *A. lemmonii* communities, where soil depths were significantly different (Table 4). Daubenmire (1970) speculated that in lithosols any controlling factors related to soil depth are associated with the fracture patterns of the basalt bedrock.

The basalt outcrop habitats where *A. hendersonii* is found have physiognomy and physical structure similar to alpine and subalpine habitats. Both also have similar microclimate influences; cold winters, short growing seasons, precipitation predominantly in the winter usually in the form of snow. Soil moisture is an important factor in controlling the distribution of plants in alpine and subalpine habitats (Billings and Bliss 1959; Billings and Mooney 1959; Klikoff 1965; Bliss 1969; Brooke et al. 1970; Billings 1973; Canaday and Fonda 1974; Douglas and Bliss 1977; Bell and Bliss 1979; Isard 1986; Evans and Fonda 1990), and in salt-desert shrub vegetation in Utah (West and Caldwell 1983). Depth and duration of the snowpack in these habitats influences the microclimate and soil moisture release. Considering the similarities between these habitats, it is possible that, as in alpine and subalpine habitats, snowpack also affects vegetation pattern in the basalt outcrops of my study areas. This may explain the difference in community level organization between the northern and southern distribution limits of *A. hendersonii*. The locations where this species occurs in its southern distribution limit have deeper and longer persisting snowpacks than in its northern distribution limit.

I observed no striking differences or patterns in the nutrient and texture analysis of the soils from the three study sites. I was mainly interested in detecting coarse scale differences in soils among the different communities. Hence, I pooled individual soil samples. Since the initial soils analysis indicated similar soil nutrient levels, I did not perform further analysis.

Other studies have examined soil variation at finer scales. For example, Schlesinger et al. (1996) found that the spatial distribution of essential and limiting plant nutrients in desert soils of the southwestern United States was autocorrealted to the area of biogeochemical cycling under the shrub canopy. It is possible that a similar fine-scale pattern exists in the basalt outcrop habitats of my study. However, no such patterns were indicated in the preliminary soil nutrient analyses.

Kruckeberg (1969) predicted that speciation within a contiguous genus is a response to sharp discontinuities in soil chemistry, where the difference in soil chemistry can serve as an isolating mechanism to bring about speciation. The soils in which *A. lemmonii* and *A. hendersonii* grow did not exhibit a sharp discontinuity in chemistry, indicating that this was probably not a factor in explaining the existence of the rare species or the differentiation of the vegetation types.

Rare species in the Sheffield region of central England are concentrated within less fertile sites (Hodgson 1986). Many of these rare species have a narrow ecological range. Hodgson (1986) states that, in this region, no single ecological characteristic is totally diagnostic of either common or rare species. Rather, most differences between common and rare species in the Sheffield region may be interpreted in terms of the availability of suitable habitats within the region, with common species occupying common habitats and rare species occupying less common habitats. *Achnatherum hendersonii* appears to follow this pattern. It is restricted to a specific habitat (basalt outcrops with shallow soils), and this habitat is not common. The implication that no single factor is totally diagnostic is confirmed by how little of the variance is explained in the first few axes of the PCA analyses (Tables 6 and 16). All in all, it appears that the interaction of the factors involved in forming vegetation are too complex to reliably use vegetation to predict forms of rarity. The large amount of variation observed in the *A. hendersonii* communities throughout its distribution range illustrates this point.

Variation in the vegetation in which A. *hendersonii* occurs within the southern distribution limit is considerable. Here, sympatric populations of A. *hendersonii* do not appear to grow in the same community. The vegetation of basaltic outcrops in this region appears to be influenced by the coverage of cryptogamic crust. There is more variation in the vegetation located in areas where the cryptogamic crust is intact than in areas where the cryptogamic crust is disturbed.

Cryptogamic crust appears to be an important factor in species richness and, possibly, in species diversity. The literature lacks studies on the importance of cryptogamic crust in relation to species composition and richness. Further research of this interaction is necessary to understand the processes involved and clarify the relationship. Such research would involve comparing species richness and diversity among a number of different sites that have intact and disturbed cryptogamic crusts. Determining the sources of the disturbance, such as natural or anthropogenic, would also assist in clarifying the relationships. A comparison of cryptogamic crusts from different biomes, such as shrub-steppe, arctic, alpine, and desert, would determine patterns associated with this relationship in regard to macroclimate influences.

The cryptogamic crust at the Ochoco study site appears to be disturbed by natural cryogenic processes such as frost boils, frost heave, and downslope soil frost creep. I observed cryogenic processes at the Colockum and Brewton study sites, but I did not observe the difference in variation and organization with respect to the cryptogamic crust at these sites as I did at the Ochoco study site.

Sorting of the substrate by cryogenic processes was observed in the alpine regions of Wyoming (Bliss 1956; Billings and Mooney 1959) and near timberline in the Sierra Nevada (Klikoff 1965). Benedict (1970) observed downslope soil movement in the Colorado alpine region, and Smith (1987) observed frost heave and soil frost creep activity in the Canadian Rocky Mountains. All of these regions have deeper soils than the basalt outcrops of my study. However, the same principles apply. Frost boils are the result of freezing soil water pushing rock and silt to the soil surface. Frost heave involves the upward pushing of plants and soil to form a mound, or the action of pushing individual rocks and plants out of the soil during freeze/thaw cycles. It occurs in saturated conditions that freeze slowly and deeply (Bliss 1956; Benedict 1970; Brady 1984). Frost creep is the net downslope displacement that occurs when the soil, during a freeze/thaw cycle, expands parallel to its subsurface and settles perpendicular to it (Benedict 1970).

Downslope movement (frost creep) of soils in the alpine regions of Colorado is influenced by differences in moisture availability and slope gradient, but is unaffected by soil texture and temperature (Benedict 1970). The action of frost creep results in larger materials being sorted from smaller materials, with the larger materials moving downslope at a faster rate, forming treads and risers. In cases where the substrate consists of rock and sand, this sorting results in areas termed stone-banked, or sorted terraces (Benedict 1970). This result corresponds to the perpendicular striping observed at the Ochoco study site. Stone-banked terraces were reported to be characterized by an absence of vegetation (Benedict 1970). However, whether the absence of vegetation was a result of frost creep or some other factor, was not examined.

I observed frost heave, frost boils, and frost creep at the Colockum and Brewton study sites, but saw no differential pattern of vegetation variation in relation to the cryptogamic crust. Such an unstable soil surface would result in the displacement of cryptogamic crust and inhibit initial vascular plant establishment. This process could explain the vegetation striping phenomenon at the Ochoco study site. Areas in which the cryptogamic crust was not disturbed possibly received less frost action. Thus, more plants would be able to persist. This could explain the differences in community level organization observed at the Ochoco study site.

An alternative explanation of processes determining spatial heterogeneity in vegetation was arrived at in a study on talus slopes of the Niagara Escarpment, Ontario (Cox and Larson 1992). In that study, local heterogeneity was controlled by nutrient inputs from slowly decaying woody material arriving from up-gradient locations on the slope. This nutrient input was followed by accelerated vegetation development on the more fertile patches of soil.

The rare grass, *A. hendersonii*, is limited to a restricted habitat, characterized by low plant cover, and exposed basaltic bedrock with shallow soils. The common grass, *A. lemmonii*, has a much wider distribution, occurring in similar areas as *A. hendersonii*, but also found on deeper soils and in areas with higher plant coverage. Given the restricted habitat of *A. hendersonii*, it would seem that the rare grass should grow in a similar plant community type throughout its distribution range. Although community structure is similar throughout the distribution range of *A. hendersonii*, composition and patterns of organization are not. In contrast, the common grass, given its potential for growing in more diverse habitats, would be expected to grow in a variety of plant community types. Further study of the vegetation throughout the distribution range of the common grass would reveal whether there is, overall, more community level variation for the common grass than for the rare grass.

Population

The morphological patterns of sympatric and disjunct populations of the rare grass, *A. hendersonii*, are congruent (Figures 17, 18, 19). The PCA ordinations of the 95% confidence ellipses for *A. hendersonii* are all superimposed, regardless of the data set analyzed (separate inflorescence leaf and vegetative leaf data sets, as well as the combined inflorescence and vegetative leaf data set). All but one of the populations have similar orientation, size, and shape, an indication that they are similarly organized and have similar amounts of variation (Figures 17, 18, and 19).

Population C1, although superimposed with the other populations, has inflorescence and vegetative ellipses of different shape (eccentricity) and orientation (theta), from the others. This indicates that this population has some organizational differences (Tables 25 and 27). These differences are lost when a PCA of the whole plant (inflorescence and vegetative leaves combined) is performed (Table 29). The differences may reflect the location of population C1 on an exposed south-facing slope, where the plants begin growth earlier than the other populations at the Colockum study site. As a result of its location, this population appears to have a shorter growing season, than the other populations at this site. This potentially decreases phenotypic variation. In general, the amount of phenotypic variation observed among sympatric and between disjunct populations of *A. hendersonii* is insignificant. Morphologically, *A. hendersonii* is nearly identical at its northern and southern distribution limits.

The morphology of the common grass, *A. lemmonii*, is more variable than that of the rare grass. The 95% confidence ellipses for inflorescence, vegetative, and combined morphology are plotted in a different location in the PCA ordination, and are larger than the ellipses for *A. hendersonii* (Figures 17, 18, and 19). For the most part, the 95% confidence ellipses for both species have similar shape and orientation, an indication that these two species have similar organization. This probably reflects the fact that these are closely related congeners. As indicated by greater ellipse areas (Tables 25, 27, and 29), there is more phenotypic variation in sympatric populations of *A. lemmonii* than in sympatric or disjunct populations of *A. hendersonii*. Rapson and Maze (1994), and Robson and Maze (1995) made similar observations between *A. hendersonii* and several common congeners, but only with local populations of the species.

In comparing variation in leaf types of *A. hendersonii*, phenotypic variation in inflorescence leaves is less than in vegetative leaves (Figures 17 and 18 and Tables 25 and 27). *Achnatherum lemmonii* has more phenotypic variation in its inflorescence leaves than *A. hendersonii*. The 95%

confidence ellipses for the two species lie in separate areas of the PCA ordination, although they overlap slightly. Those for *A. lemmonii* are larger and have different orientations between the populations, an indication of some organizational diversity within this species (C8 and C10; Figure 17 and Table 25). Again, *A. hendersonii* has less variation among sympatric and between disjunct populations than *A. lemmonii* has among sympatric populations.

The amount of variation in the morphology of vegetative leaves is similar in both *A. hendersonii* and *A. lemmonii*. The 95% confidence ellipses overlap the most in this PCA ordination (Figure 18). The amount of variation in the vegetative morphology of *A. hendersonii* approximates the amount of variation observed in the vegetative morphology of the common grass *A. lemmonii*. As a result, the vegetative leaves of these two species are similarly organized (Table 27).

In previous studies of variation in *A. hendersonii* and common congeners (Rapson and Maze 1994; Robson and Maze 1995), vegetative shoots tended to be more variable than reproductive shoots. Although I found this to be true for *A. hendersonii*, vegetative and inflorescence leaf variation within *A. lemmonii* appeared to be similar (Figures 17, 18, and 19, and Tables 25, 27, and 29).

Overall, the morphology of the rare grass, *Achnatherum hendersonii*, has less variation than the closely related common grass, *A. lemmonii*. These observations coincide with those made by Rapson and Maze (1994) and Robson and Maze (1995). Rapson and Maze (1994) found that phenotypic variation among populations of *A. hendersonii* was lower than that of parapatric populations of *A. lemmonii* and *A. thurberiana*. In addition to lower levels of phenotypic variation, Robson and Maze (1995) also observed lower growth rates in *A. hendersonii* as compared to its common congeners, *A . lemmonii*, *A. occidentale*, and *A. thurberiana*. Plants that grow faster are inferred to be better competitors. Therefore, it was implied that the slower growth rate of *A. hendersonii* precludes its survival away from its typical habitat (Robson and Maze 1995). This concurs with observations on *Arctostaphylos myrtifolia* (Gankin and Major 1964).

Less phenotypic variation in the rare grass, *A. hendersonii*, than in the closely related common grass, *A. lemmonii*, is consistent with other works comparing rare and related common species (e.g. Babbel and Selander 1974; Hamrick and Godt 1990; Rapson and Maze 1994; Robson and Maze 1995;). However, Fiedler (1987) found no differences in leaf morphology variation in rare and closely related common species of *Calochortus*.

Primack (1980) compared phenotypic variation between rare and widespread species of *Plantago*. Based on reproductive structures (inflorescence number per plant, capsule number per inflorescence, seed number per capsule, and weight per seed), no obvious pattern of increasing variation with increasing distribution was found. In other words, rare species of *Plantago* had neither more nor less phenotypic variation as compared to common species. From these results, Primack (1980) concluded that rare species do not necessarily have less phenotypic variation than closely related common species. This would indicate that we cannot assume that rare species are prone to extinction because they have insufficient genetic variation to respond to environmental changes.

Because Primack (1980) examined only reproductive structures, his results are not completely comparable with mine; nevertheless, I did find that *Achnatherum hendersonii* had more phenotypic variation in its vegetative leaves than in its reproductive leaves. These results indicate that the amount of phenotypic variation can be incongruent among different structures within a taxon. Since the amount of phenotypic variation in the vegetative leaves of *A. hendersonii* is similar to that of the more widespread grass, *A. lemmonii* (Figure 18), it appears that *A. hendersonii* is not necessarily genetically impoverished. The longer lifespan of vegetative leaves possibly explains their greater phenotypic variation, because they are exposed to a greater diversity of abiotic and biotic selective pressures. An indication that *A. hendersonii* may not necessarily be genetically impoverished is the existence of a recently described closely related rare species, *Achnatherum wallowaensis* Maze and K.A. Robson (Maze and Robson 1996). This species has been observed only in Oregon. Its distribution overlaps with that of *A. hendersonii* in north-central Oregon, but there are also disjunct populations in northeast Oregon. Genetic variability, however, does not guarantee that the population will persist if environmental changes are outside the physical tolerances of the species (Meagher et al. 1978).

Competition

The results from the plants grown in pots for the 1996 growing season indicate that *Poa secunda* has more overall seasonal growth and appears to have a faster growth rate than *A. hendersonii.* Therefore, *P. secunda* may have an overall advantage in the field. *Poa secunda* is a widespread species (Hitchcock et al. 1969) that has the ability to grow in a variety of substrates (Daubenmire 1970). Even though both *A. hendersonii* and *P. secunda* often grow within the same clump in rocky basaltic substrates, their differential growth habits and morphology allow them to occupy the same site without necessarily competing for resources. *Achnatherum hendersonii* has fewer but longer roots than *P. secunda* (Maze 1981). This enables it to take advantage of resources deep in the cracks of the basalt bedrock.

The longer roots of *A. hendersonii* also aid in anchoring the plant in the soil during frost heave events. I frequently observed *P. secunda* plants thrust out of the ground (Figure 3) in the same locations where adjacent plants of *A. hendersonii* remained anchored in the soil. I also observed *A. hendersonii* and *P. secunda* plants growing in the same clump (Figure 23). This raises the intriguing possibility that *A. hendersonii* may actually provide a stable location where *P. secunda* is able to persist, while individual *P. secunda* plants growing in isolation face a greater risk of being thrust from the soil by frost heave. Thus, rather than competition, the interaction between *A. hendersonii* and *P. secunda* may be one of facilitation.

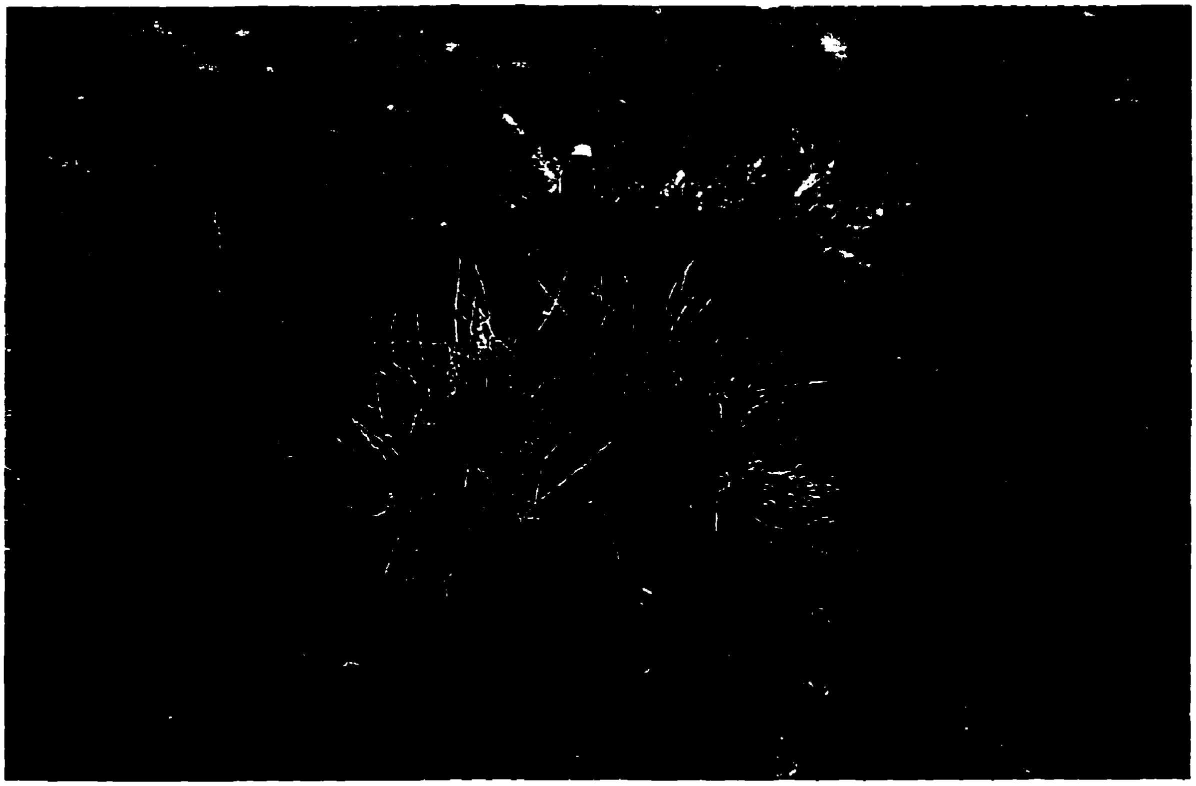

Figure 23. *Achnatherum hendersonii* (left of pencil) and *Poa secunda* (right of pencil) growing in the same clump.

As a logical extension of the speculations of Gankin and Major (1964), Robson and Maze (1995) tested the hypothesis that widespread species should grow at a faster rate than rare species. They found that common species of *Achnatherum* indeed grew at a faster rate than the rare *A. hendersonii*, indicating differential competitive ability between the common and rare species. However, the populations of the rare and common species occurred in different soil types (Robson and Maze 1995). Although slower growing, *A. hendersonii* is able to persist in the shallow soils of rocky basaltic outcrops from which common congeners are excluded. Following Gankin and Major's (1964) argument, the persistence of *A. hendersonii* in these areas may be more strongly related to the environment limiting the growth rate of other species or excluding them altogether. Similar observations were also made in several species of *Talinum* (Reinhard and Ware 1989), and in *Sedum pulchellum* (Ware 1990), all of which grow on rock outcrops.

Resource partitioning is often proposed for species that appear to occupy the same trophic and physical niche (Begon et al. 1990). Accordingly, it appears that niche differentiation/resource partitioning is a possible mechanism for the coexistence of *A. hendersonii* and *Poa secunda*. The two species may not be using different resources, but instead are obtaining similar resources (in form) from a different space; hence, the competition is apparent but not real.

Studies on competitive relationships between native and introduced grasses of the shrub-steppe regions of western North America indicate that the rate of root elongation is pertinent to seedling survival (Harris 1967; Harris and Wilson 1970). Species that had rapid root elongation were more successful competitors. Following this reasoning, *A. hendersonii*, with longer roots than *P. secunda* (Maze 1981), presumably has a competitive advantage. I observed that both *P. secunda* (Daubenmire 1972) and *A. hendersonii* have two seasons of vegetative growth, one in midfall and another in May. This further emphasizes the importance of differential root growth.

In response to predominant views in the literature that interspecific competitive abilities are an explanation for local abundances, and that the rarity or commonness of a species depends on its ability to compete with neighbors for limited resources, Rabinowitz et al. (1984) tested the competitive ability of rare and common perennial grasses of mixed genera common to tallgrass prairies. Results from a greenhouse de Wit replacement series indicated that rare species were not disadvantaged by interactions with their common neighbors. It was concluded that the competitive abilities of the rare species were not a cause of their rarity. Rather, their good competitive abilities appeared to be a mechanism that offset the hazards of low density and made local persistence more probable. Although *A. hendersonii* has lower growth rates than its common congeners and persists in restricted habitats, its unique root morphology may give it a competitive advantage in those habitats.

Synthesis

Comparisons between community and population levels of organization can be made using the *A. hendersonii* and *A. lemmonii* vegetation and morphology results (Figures 15 and 19; Tables 18 and 29).

Although the first PCA axis describes the highest amount of variation in the data set, 56.7% of the total variance is explained by the first PCA axis for population level variation (Table 28), while only 13.9% of the total variance is explained by the first PCA axis for community level variation (Table 16). In fact, it takes ten axes to explain 54.3% of the total variance at the community level, almost as much as is explained in the first axis at the population level. Because the amounts of total variance explained by the first axes for community and population levels of variation are not equal, comparisons should be made with prudence. The community is complex. This complexity is reflected by the number of axes it takes to explain 50% of the total variance. Considering the number of factors and the complexity of interactions controlling vegetation, this is not surprising.

Although a low percentage of the variation is accounted for by the first two PCA axes, it is greater than any other combination. Relying on other combinations of axes, e.g. those with eigenvalues greater than one, would generate a large number of comparisons, thereby rendering meaningful comparisons difficult, if not impossible to interpret. It would also be subject to criticism associated with selecting specific combinations that coincide with preconceived hypotheses.

Despite the discrepancy in the amount of variance explained by the first PCA axes of the vegetation and morphology data sets, PCA is an effective technique for comparing and synthesizing community and population levels of organization. Because this technique is flexible, it allows more potential for comparison of disparate entities at different levels of biological organization. Other techniques specifically designed to assess relationships between two sets of variables, such as canonical correlation analysis, are not, strictly speaking, appropriate, as they rely on the units of study being the same (Gauch 1982). In my study the units were not the same: quadrats as "community-units", and individual plants as "population-units".

The plots in the northern distribution limit of *A. hendersonii* have more morphological variation than vegetation variation. This is true for the common grass as well. In the southern distribution limit of *A. hendersonii*, the results are inconsistent. Plot 04 has greater vegetation variation than morphological whereas Plot 01 has slightly more morphological variation than vegetation. Over its distribution range, *A. hendersonii*, has greater vegetation variation than morphological.

Achnatherum lemmonii, the common grass, appears to have more population level variation than community level variation. Within the northern distribution range of the rare grass, more variation in vegetation and morphology is observed in the common grass than the rare grass. However, this does not hold true when comparisons are made with the southern distribution limit of *A. hendersonii*. When the entire distribution of the rare grass is incorporated, there is more community level variation for the rare grass compared with the common grass, although the common grass retains more population level variation. A common species does not necessarily have more community level variation than a closely related rare species. The amount of community level variation can vary throughout the distribution range of a rare species. The factors affecting community level variation are more numerous than those affecting population level variation, thereby increasing the potential of relative variation at the community level of observation. More specifically the sources of variation at the population level are found in the plants themselves, and is expressed in their phenotype, which results from the interaction between the plant and the environment in which it resides. The sources of variation at the community level comes from all the plants that make up the community, which includes the interactions between all the plants with the environment, thereby increasing community level variation.

There is a consistent pattern to the analyses reported here. The various communities in which *A. hendersonii* occurs are more different from one another than are the populations that occupy the various sites. This is true whether one is considering the relationship as determined by the variation among the entities being compared (communities or populations), i.e. how different they are from each other, or the organizational properties (order and organization *sensu stricto*) within each of the entities compared.

On the assumption that patterns perceived reflect some underlying causal agent, different patterns could be interpreted as the result of different causal agents. These different causal agents might be sought in the differences that exist among populations and communities. Populations consist of fairly tightly integrated components (individual plants) that have a certain history that can be followed back through intergenerational reproduction to an ancestral/descendent relationship. Or, the populations can be related to an evolutionary lineage. In this lineage the changes that occur are strongly determined by the lineage itself because of the simple expedient that offspring that are too extreme are unable to survive.

Communities are less tightly integrated because there are many different components that can contribute to a community that persists. As well, there are many more environmental factors which affect a community than affect individual plants. Furthermore, a part of a plant that happens to be non-functional may be lethal to the plant, whereas several different plants can fulfil a certain "functional role" in a community. Also, discordant distribution patterns mean that the same species will not be available to form communities in places as distant as the three study sites of this study.

The previous points argue that there are different phenomena that determine the nature of rare plants and the communities in which these plants occur. Rare plants are the result of a unique evolutionary history that is manifested over a broad geographic range, regardless of the driving force of evolution. The uniqueness of that evolutionary history is assured by the organizational properties (historical constraint) of the organisms in that lineage. The communities are also the result of unique events, but these events are more local in character. Thus, when we seek to account for taxonomic rarity, it is the evolutionary history and the attributes of the plant itself that should be the focus of study. On the contrary, when we seek an account of the communities in which the rare species occur, it is the local conditions (ecology) that should be the focus of study.

Despite the argument that different phenomenon determine the nature of a rare species and the communities in which these plants occur, ultimately, populations and communities cannot be separated. The rare species is a part of the community, and the community is in part made up of populations of the rare species. The factors that control and influence the character of the community also control and influence the rare species (e.g. phenotypic expression). Therefore, a synthesis of population and community organization and variation should increase our understanding of the phenomenon of rarity.

Fiedler's (1986, 1987) attempt of a synthesis consisted of a compilation of numerous comparisons between rare and closely related widespread species of *Calochortus*. The differences she observed between the rare and common species were not always consistent. Some of the characteristics initially thought to be unique to the rare species were also observed in some of the common species. Fiedler's (198, 1987) approach to synthesis did not actually synthesize community and population levels of biological organization.

In my study, a synthesis of these levels of organization was achieved by the ordination of the vegetation first PCA axis scores and the morphology first PCA axis scores. The 95% confidence bivariate ellipses and descriptive statistics quantify this synthesis (Figure 20 and Table 30). If population level and community level organization were coincident, the 95% confidence bivariate ellipses would plot as perfect circles. Coincident organization would indicate that the underlying processes of organization were the same. Not surprisingly, community and population levels of organization were not coincident, arguing that the underlying processes of organization differ.

The amount of variation at each level is an indication of biological organization, where increased variation indicates increased organizational complexity (Brooks and Wiley 1986). If the amounts of variation are equal at each level, then the biological organization of each level is the same. Greater variation at the community level implies that the community level is more complex. Greater variation at the population level implies that the population level is more complex. The community is a function of the interaction of the populations of plants present, the remainder of the biotic factors, and the abiotic factors. Therefore, community level variation and, consequently, organization is expected to be greater than population level variation. This relationship should be even more pronounced between a community and a population of a rare species that displays less phenotypic variation than a closely related common congener. The community reflects the variation of the populations of species as well as the interaction of the species and abiotic environment. By contrast, the population reflects only the variation observed in the single species.

Variation is greater in *A. lemmonii* than in *A. hendersonii* (area; Table 30). On the abstract synthesized level of organization, the common species has more variation than the rare species. Variation in *A. hendersonii* is greater in the southern distribution than in the northern distribution range, suggesting that this form of organization changes with respect to latitudinal position. Variation is congruent in *A. hendersonii* at the northern distribution limit. This congruency of variation within a geographic range does not hold in the southern distribution limit of *A. hendersonii*. It is possible that rare species in northern regions have less variation than rare species in southern regions. This raises a question: Does variation in rare species increase as latitude decreases?

Achnatherum hendersonii and *A. lemmonii* generally have similar strengths of correlation or order (eccentricity; Table 30). There appear to be more differences in order between sympatric populations of *A. lemmonii* than between sympatric populations of *A. hendersonii*, although *A. hendersonii* population 01 is different from all other populations of this species. Common species do not necessarily have greater diversity in organization, in the sense of order, than rare species.

Except for population 04 (Ache), covariance or organization *sensu stricto* is essentially the same between *A. hendersonii* and *A. lemmonii* (theta; Table 30). This suggests that these species have similar organization. The extremely different theta value for population 04 indicates that despite similarity, there is a certain amount of divergence in organization. This result is interesting and warrants further research to determine if this is a genuine phenomenon or a sampling artifact, and if indeed genuine, to determine the underlying mechanism of this divergence.

According to the information presented in Figure 20, it appears that in the northern distribution range there is more variation at the population level for the rare grass and the common grass than at the community level.

This goes against the expectation that the community is more complex, and therefore, should have more variation. In the southern distribution range the amount of community level variation is greater than population level variation for one population of the rare grass and nearly equal for a sympatric population. The population that has greater community level variation is the population that occurs in an area where cryptogamic crust is intact, whereas the population with nearly equal variation is in an area where cryptogamic crust is disturbed. This is interesting in that it seems contradictory to the intermediate disturbance hypothesis, which predicts greater species diversity in areas of moderate disturbance (Connell 1978).

The areas lacking cryptogamic crust appear to be affected by soil disturbances created by frost action. Natural disturbances play an important role in the organization of communities (Sousa 1984). Once an area is disturbed, a gap is formed and, according to the intermediate disturbance hypothesis, higher species diversity occurs during successional stages. Species diversity declines once the gap is filled. This hypothesis was supported by observations on intertidal algal communities (Sousa 1979a,b) and on the filling-in of gaps in intertidal beds of mussels (Paine and Levin 1981). In old-field plant communities, this hypothesis is supported depending upon the age of the community (Armesto and Pickett 1985). Fields that were 7 years old supported the hypothesis, whereas fields that were 2 years old did not. In tallgrass prairies the hypothesis was not supported with respect to intermediate levels of disturbance, but was supported in relation to an intermediate time span following disturbance (Collins et al. 1995).

At the Ochoco study site, I found that areas where the cryptogamic crust was disturbed had significantly lower variation than areas where the cryptogamic crust was intact. According to the hypothesis, if the frequency of disturbance is high or low then species richness will be lower than at intermediate levels of disturbance. In shortgrass prairies, the impact of disturbance on *Bouteloua gracilis* depends upon frequency and size, frequency tending to be inversely related to size (Coffin and Lauenroth 1988). Size and frequency together determine the total area affected by disturbances. If this hypothesis is supported in areas where frost action disturbances occur, then the frequency of frost action needs to determined. If the frequency is high or low relative to mean frequencies of frost action disturbance, then the hypothesis would be supported.

Although the variation between community and population level organization is not coincident, comparing these two levels of organization and synthesizing or integrating them increases our overall understanding of rarity. Population level observations increase our understanding of the individual species and the factors that affect it. Community level observations increase the overall understanding of the position of a rare species in relation to the larger community and provides a broad spectrum analysis in which plausible causal mechanisms are revealed. Understanding that the population is an integral part of the community and that species rarity is as much a process of community level organization as it is of population level organization, is important to the understanding of the processes of rarity as a whole.

A synthesis of community and population levels of organization does not answer why *Achnatherum hendersonii* is rare. Neither does it develop a general theory about rarity. It does, however, acknowledge that a rare species is not isolated from its community and that an understanding of the causes and consequences of rarity requires understanding community as well as population levels of organization. A synthesis forces one to analyze a rare species at several biological levels, thereby increasing the potential of reaching conclusions about the cause of rarity.

Whether looking at peculiarities of common species or at the idiosyncracies of rare species, comparative studies of community and population levels of organization and variation and a synthesis of these levels facilitate comprehension of underlying order and leads to otherwise unconsidered causal factors. A synthesis of synecological and autecological studies, in turn, enhances our understanding of ecological and evolutionary processes.

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IMAGE EVALUATION
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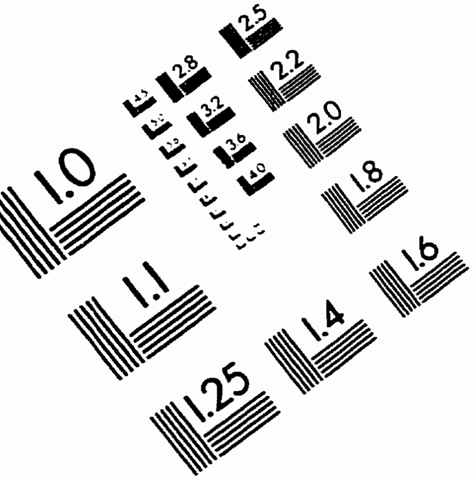

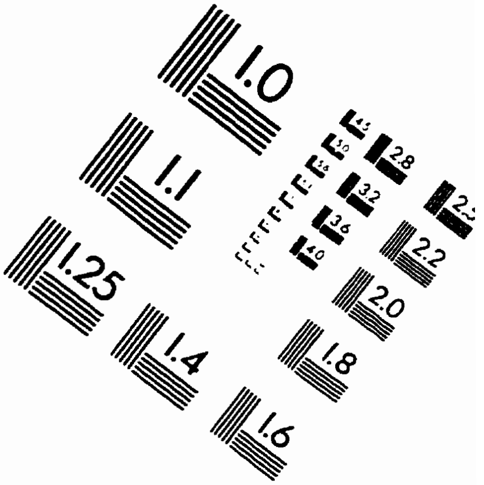

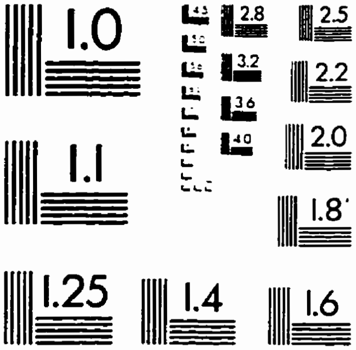

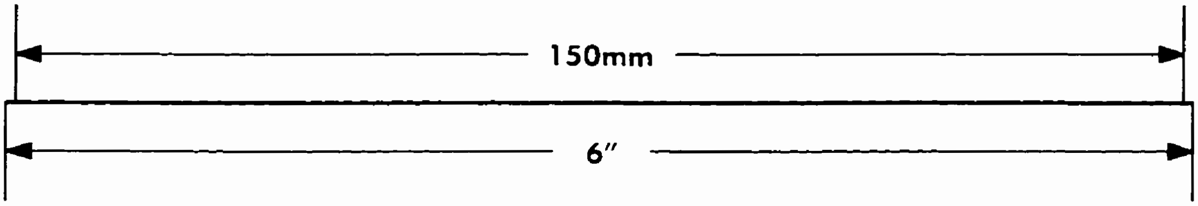

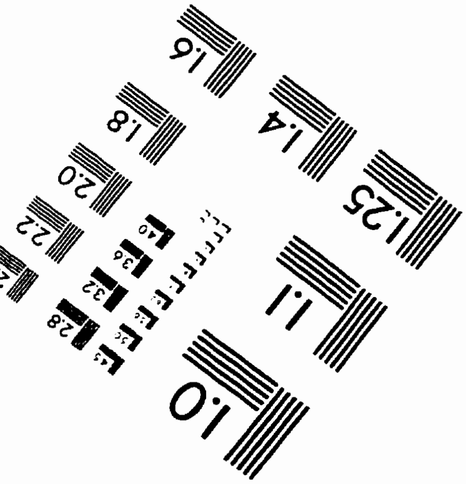

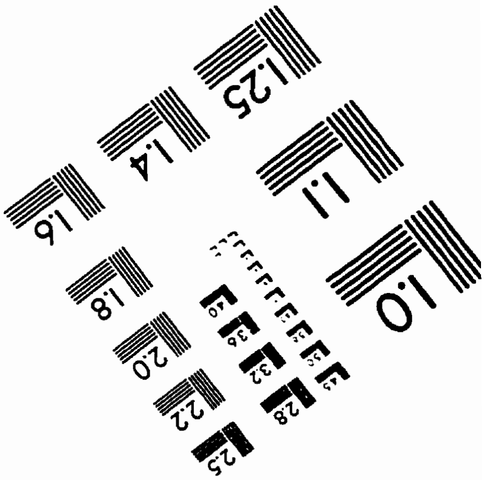

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