Great Basin Naturalist 57(1), © 1997, pp. 21–37

NATURAL VARIABILITY OF VEGETATION, SOILS, AND PHYSIOGRAPHY IN THE BRISTLECONE PINE FORESTS OF THE ROCKY MOUNTAINS

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ABSTRACT.—*Pinus aristata* Engelm. forest vegetation in Colorado was studied to determine vegetation composition and the relationship between vegetation and environment. Species percent cover, tree size class, and environmental variables were recorded for 49 plots. Previously collected data for 4 plots from New Mexico were included. Environmental variables included latitude, longitude, elevation, slope, aspect, topographic position, parent material, percent rock cover, mean rock size, litter depth, estimated plot age class, and evidence of anthropogenic disturbance. Soils were analyzed for texture, depth, and percent carbon and nitrogen. *Pinus aristata* foliage was analyzed for percent nitrogen and phosphorus. Direct and indirect gradient analyses (CANOCO) were used to determine environmental factors associated with community composition. Vegetation in *P. aristata* forests is influenced primarily by elevation and soil pH. Substrate, soil texture, topographic position, and geographic location are secondary factors. Six plant associations were identified using cluster analysis (listed in an elevational sequence from low to high): *Pinus aristata / Festuca arizonica* Vasey, *Pinus aristata / Festuca thurberi* Vasey, *Pinus aristata / Juniperus communis* L., *Pinus aristata / Vaccinium myrtilus* L., *Pinus aristata / Ribes montigenum* McClatchie, and *Pinus aristata / Trifolium dasyphyllum* Torr. & Gray.

Key words: bristlecone pine, Rocky Mountains, vegetation, Colorado, gradient analysis, classification.

Managing an ecosystem within its range of natural variability is the best way to maintain diverse, resilient, productive, and healthy ecosystems (Society of American Foresters Task Force 1993, Swanson et al. 1994). (The range of natural variability [RNV] of an ecosystem is the range of variation in composition, structure, and dynamics before the influence of European settlers [Swanson et al. 1994]). Insight into the RNV of forest composition, for example, can be gained by studying stands across a range of environmental variation.

The Rocky Mountain bristlecone pine (*Pinus aristata*) is the longest lived tree in the Rocky Mountains, reaching over 2400 years in age (Brunstein and Yamaguchi 1992), about half the age of the oldest specimen of *Pinus longaeva*, a related bristlecone pine most common in the Great Basin (Ferguson 1968). Studies in Rocky Mountain bristlecone pine forests have focused on dendrochronology and tree population structure (Krebs 1972, LaMarche and Stockton 1974, Baker 1991, 1992, Brunstein and Yamaguchi 1992), but little is known about the range of variability in understory species or how vegetation composition changes with environment. Also, the existing classification is based on relatively few data and little quantitative analysis (DeVelice et al. 1986, Hess and Alexander 1986, Komarkova et al. 1988).

Classification of compositional data can be useful for research, management, and conservation (Pfister and Arno 1980, Alexander 1987). Managers may assume that if a particular site belongs to a vegetation type, it will respond to management similarly to other sites of the same vegetation type. When the objective is to preserve representative sites that span the RNV, classification can help in selecting a reserve system. Gradient analysis is also useful for analyzing the relationship between vegetation and environment (Whittaker 1967).

There are several approaches to classifying mountain vegetation. Many researchers have classified mountain vegetation into elevation-based life zones (Ramaley 1907, Daubenmire 1943, Weber 1965). Another approach is the habitat-typing method, which is based on the assumption that potential climax vegetation is the best reflection of the overall environment. Potential climax vegetation is predicted from stand structure and relative shade tolerances of the trees (Pfister and Arno 1980). However, *P. aristata* does not appear to be a climax species, based on habitat type definitions, because it is not regenerating in forests it dominates (Baker

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1992). Baker (1984) proposed a "natural vegetation" classification of "plant associations" based on the composition and structure of mature examples of vegetation as free as possible from human alterations. This approach is more appropriate for *P. aristata* forests because it eliminates the need for inference about the climax vegetation. The climax vegetation paradigm has been challenged recently (Baker 1995, Cook 1996).

Elevation, soil moisture, soil nutrients, soil texture, topography, disturbance, and latitude influence the species composition and structure of forests in the Rocky Mountains (Peet 1978, 1981, Allen and Peet 1990, Allen et al. 1991, Baker 1992). Higher elevations are associated with decreases in temperature and increases in precipitation and snow depth (Barry 1973). In the Sangre de Cristo Mountains, higher elevations have lower soil pH and percent base saturation and higher total nitrogen than lower elevations (Allen and Peet 1990). Soil moisture, which is associated with topographic position, also significantly affects the vegetation composition, as do soil texture and chemistry (Daubenmire 1943, DeVelice et al. 1986, Peet 1988, Allen and Peet 1990).

In this paper we study the plant species composition of *P. aristata* forests across the range of environments they occupy, then classify these forests and analyze the associated environmental factors influencing their composition.

STUDY AREA

Pinus aristata forests are found in the Front, Mosquito, Sawatch, San Juan, and Sangre de Cristo ranges of Colorado (Fig. 1) and extend into New Mexico in the Sangre de Cristos. These forests grow primarily on dry, steep, south-facing slopes at elevations between 2750 and 3670 m (Baker 1992). Soils are shallow and often skeletal. Convective thunderstorms are the main source of summer precipitation, and cyclonic storms often cause heavy winter snows (Peet 1981). Due to their high elevations, *P. aristata* forests are cool even in summer. In the Front Range mean annual temperatures along a transect from 2195 m to 3750 m ranged from 8.3°C to 3.3°C (Barry 1973). Strong winds of 24–40 km per hour are common in the high-elevation forests of the Front Range (Peet 1981).

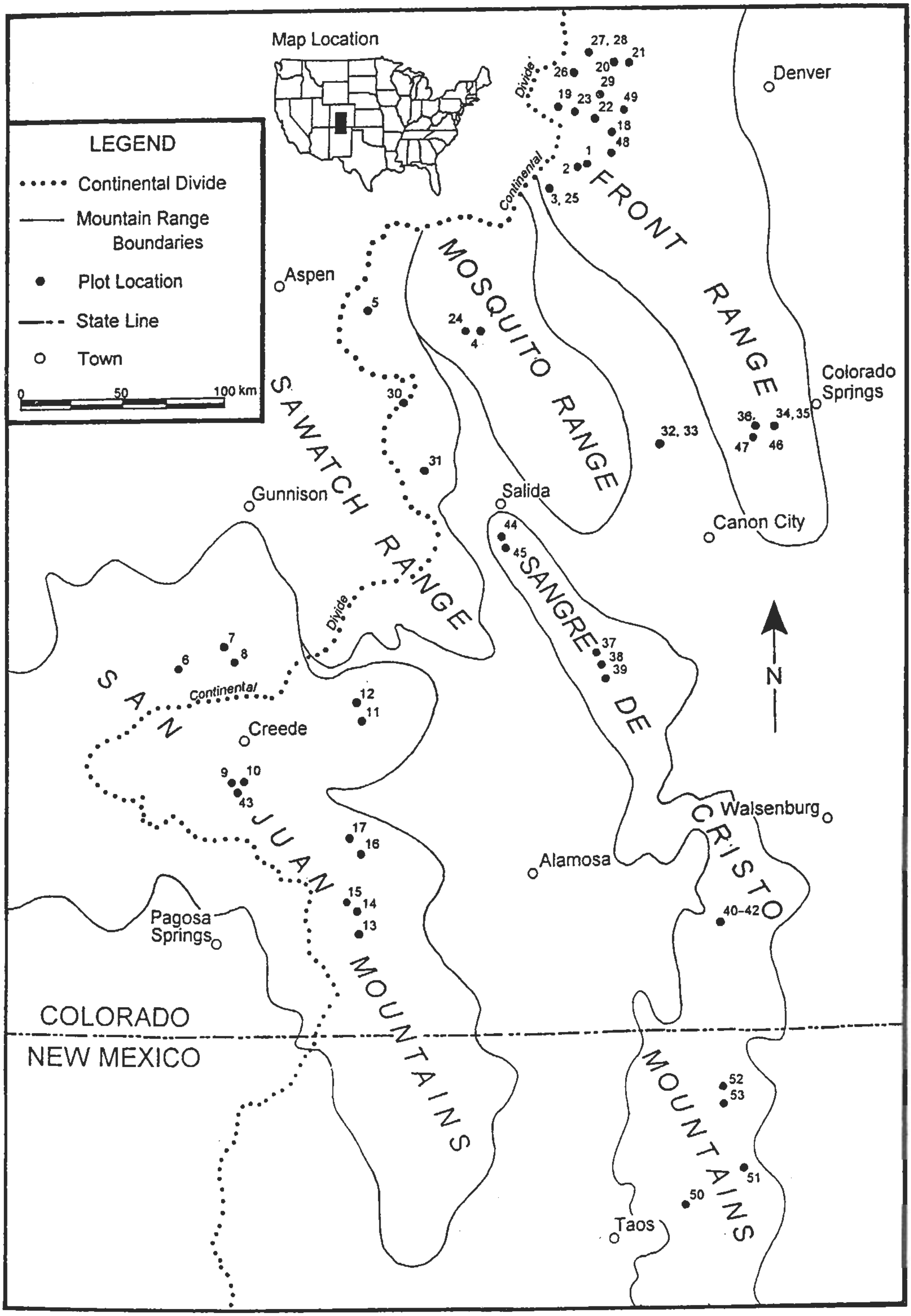
The geology of *P. aristata* forests, where they occur, varies greatly among mountain ranges. In the Front Range, *P. aristata* forests are found on Precambrian granites (Scott et al. 1984). Stands in the Mosquito Range may occur on Precambrian granites or Pennsylvanian sandstone (Tweto et al. 1978). Middle Tertiary intrusive rocks, Laramide intrusive rocks, Precambrian granite, or Felsic and Hornblendic gneisses underlie stands in the Sawatch Range (Tweto et al. 1978). In the San Juans, *P. aristata* forests grow on pre-ashflow andesitic lavas, breccias, tuffs, and conglomerates or ashflow tuff; in the Sangre de Cristos, stands are underlain by Pennsylvanian-Permian sandstones, siltstones, and conglomerates (Tweto et al. 1978, Tweto 1979).

Fire, snow avalanches, livestock grazing, logging, mining, and tourism are important disturbance agents in *P. aristata* forests. Fire, often started by lightning strikes, appears to encourage *P. aristata* regeneration (Baker 1992). Snow avalanches have removed large patches of *P. aristata* forests, resulting in alternating strips with and without forest. Cattle grazing occurs in the more accessible stands, and sheep grazing occurs at high elevations, especially in the San Juans. Early miners valued the dense wood of the bristlecone pine for shoring up mine shafts.

METHODS

Site Selection

Sampling sites were selected mainly from those previously located by Baker (1992). A site is a location bounded by the limits of its contiguous *P. aristata* forests. Additional sites were chosen from stands sampled by Brunstein and Yamaguchi (1992) and from areas recommended by the USDA Forest Service. To ensure that a wide range of variation in *P. aristata* forest vegetation was sampled, sites were selected to fill "cells" defined by a stratification of elevation and geography (Table 1). Elevation was divided into three 300-m-wide categories, ranging from 2750 to 3650 m. The range of *P. aristata* in Colorado was divided into 4 geographical units based on mountain ranges: the Front, San Juan, Sangre de Cristo, and Sawatch-Mosquito ranges. Only sites with low cover by exotic plant species, no recent evidence of livestock grazing, and no other signs of significant human alteration were selected. Sampled sites



Donna Weatherman 1995

Fig. 1. Study area map. Numbers are plot numbers. The 4 plots in New Mexico were sampled by DeVelice et al. (1986).

were restricted to mature forests that originated prior to Euro-American settlement.

Vegetation Sampling

Forty-nine 0.1-ha (20 × 50-m) plots were sampled, with as many as 3 plots placed at different elevations in a single site. Each plot was placed in a representative location within the site. A visual estimation of percent canopy cover was made for every vascular plant species rooted in the plot after walking a transect completely traversing the plot. Estimates for plants with less than 10% cover were made in 1% increments, with 10–25% cover in 5% increments, and with greater than 25% cover in 10% increments. Plant nomenclature follows PLANTS, a standardized national list of plant names (USDA Natural Resource Conservation Service 1995). A voucher specimen of each species was deposited in the Rocky Mountain Herbarium in Laramie, Wyoming. Four plots from New Mexico, sampled by DeVelice et al. (1986), are also included in our analysis.

Tree age and size-class structure data were from Baker (1992) and Brunstein and Yamaguchi (1992). Where tree data were unavailable from a previous study, all living tree stems in a stand were tallied by species and size class. Woody stems <1 m tall were tallied as seedlings and small saplings. Stems >1 m tall with a diameter at breast height (dbh) of <2.5 cm were tallied as large saplings. The remaining tree size classes were in 5-cm-wide increments. Tree age was determined using cores extracted just above ground level from 5–15 of the largest trees. Due to imprecision in dating and the possibility of missing rings, tree ages were recorded in 25-yr classes.

Environmental and Geographic Data

Environmental and geographic variables recorded for each plot were chosen based on a literature review of the factors affecting vegetation structure and composition in Rocky Mountain forests. Latitude and longitude were obtained from topographic maps. Mountain range was recorded as Front Range, Sawatch-Mosquito Ranges, Sangre de Cristos, or San Juans. Elevation was measured with an altimeter, and slope and aspect were measured using a compass and clinometer. The topographic position of each plot was recorded as bottom (valley), lower 1/3 slope, middle 1/3 slope, top 1/3 slope, or ridgetop. Parent material was classified as intrusive igneous, extrusive igneous, sedimentary, or metamorphic. Within each plot percent rock cover was estimated as 0–25%, 26–50%, 51–75%, and 76–100%. Mean rock size at the soil surface was recorded as 0–1 m, 1–2 m, or >2 m. Litter depth was classified as <2 cm or >2 cm.

TABLE 1. Number of sites sampled in each cell. Cells are based on geographic and elevational divisions.

	2750 to 3050 m	3050 to 3350 m	3350 to 3670 m
Front Range	5	6	10
San Juans	3	9	1
Sangre de Cristos	2	6	4
Sawatch-Mosquitos	—	4	3

Soil was collected from the upper 15 cm of the profile every 5 m along the 50-m center line of the rectangular plot. Soil depth for the plot was an average based on the depth of soil above the C horizon at each of the 10 collection points. These 10 subsamples were mixed to form the plot sample, sieved to 2 mm, and dried at 100°C for 24 h prior to the analyses (pH, percent nitrogen, and percent organic carbon). Soil pH was measured on 7 g of soil 30 min after it had been mixed with 35 ml of 0.01 m $CaCl_2$. For the soil carbon and nitrogen analyses, the soil was ground to a fine powder in a ball mill, carbonates were liberated with acid, and 0.1-g samples were analyzed in a LECO CHN analyzer. Year-old foliage was collected from the south side of a *P. aristata* every 10 m along the 50-m plot center line. The foliage samples were air-dried for storage, then dried for 24 h at 70°C, ground to pass 40 mesh, and analyzed for nitrogen and phosphorus by autoanalysis of Kjeldahl digests (Anonymous 1992a, 1992b). Soil texture was determined by hand and recorded in general texture categories: loam, sandy loam, and loamy sand.

Gradient Analysis and Classification

The understory species composition data were ordinated with both indirect and direct gradient analysis using CANOCO (Canonical Community Ordination; ter Braak 1988). Ordination arranges species or plot samples along an axis based on their similarities. Soil chemical data were logarithmically transformed because with resource data, such as soil nutrients and rainfall, the difference between 1 and 10 is likely to be more significant to plants than the difference between 1000 and 1010 (Palmer 1993). Non-categorical environmental variables were checked for normality, and all were found, by visual inspection, to be approximately normally distributed.

Detrended correspondence analysis (DCA) is an indirect gradient analysis technique useful for revealing the major patterns of variation in plant community composition. In DCA, Pearson's correlation can be calculated between the axis scores and the environmental variables to assess how strongly the variable is related to the variation in community composition. Canonical correspondence analysis (CCA) is a direct ordination method to relate species composition data directly to environmental variables (Palmer 1993). Thus, CCA has the additional capacity to directly identify the important environmental gradients (ter Braak 1986). In CCA the correlation between an environmental variable and an ordination axis (intraset correlation) indicates the importance of that variable in defining the ordination axis (ter Braak 1986).

Comparison of DCA and CCA results reveals how much of the variation in the understory species data is explained by the measured environmental variables (ter Braak 1986). Eigenvalues measure the separation of species or plot distributions along the ordination axis (ter Braak 1988). An eigenvalue close to 1 indicates a high correspondence between plot scores and species scores, and eigenvalues near 0 represent low correspondence (Palmer 1993). If eigenvalues from DCA and CCA analyses are similar, one can assume that the measured environmental variables explain the main variation in species composition data (ter Braak 1986). Large differences between the 2 solutions suggest that an important environmental variable(s) was not measured. Species-environmental correlations are a measure of how well environmental variables explain the detected variation in community composition (ter Braak 1986).

Groups consisting of similar plots were identified using the SPSS/PC+ program for cluster analysis (Marija 1988). The cosine distance measure and the BAVERAGE method (average linkage between groups) were found to produce the most meaningful classification. Because cluster analysis of combined overstory and understory data often produces groups that reflect only the high cover values of the overstory species, understory and overstory data were clustered separately (Walford and Baker 1995). Results of the 2 analyses were then compared to determine if the overstory clusters correspond with the understory groups. Dendrograms from cluster analysis do not automatically produce a classification. To choose a single consistent level of similarity at which the groups are best defined, we worked down through the levels of the dendrogram until we found classification units that are internally homogenous (high constancy), compositionally distinct, and in a distinct environment.

RESULTS

Gradient analysis

Eigenvalues for the DCA and CCA analyses are similar (Table 2), suggesting that measured environmental variables explain most of the variation between plots (ter Braak 1986). Species-environment correlations are very high (Table 2), suggesting that the detected variation in species composition between plots is well explained by environmental variables. The strongest environmental and geographic correlates with plot composition are represented by arrows on the CCA ordination diagram (Fig. 2). The length of the arrow is a measure of the magnitude of differences in plot distribution along that environmental variable (ter Braak 1986).

Environmental and geographic variables with the highest Pearson (DCA) or intraset (CCA) correlation coefficients are those most strongly related to the variation in plot composition (Table 3). Elevation, soil pH, location in the San Juans, and extrusive igneous parent material correlate most strongly with the first DCA and CCA axis (Table 3). Values for pH were between 4.47 and 6.85. Weaker variables

TABLE 2. Eigenvalues and species-environment correlation coefficients for the detrended correspondence analysis (DCA) and canonical correspondence analysis (CCA).

	Axis 1	Axis 2	Axis 3	Axis 4
		Eigenvalues		
DCA	0.675	0.385	0.263	0.215
CCA	0.645	0.363	0.351	0.278
		Species-environment correlation coefficients		
DCA	0.972	0.896	0.862	0.858
CCA	0.981	0.921	0.950	0.956

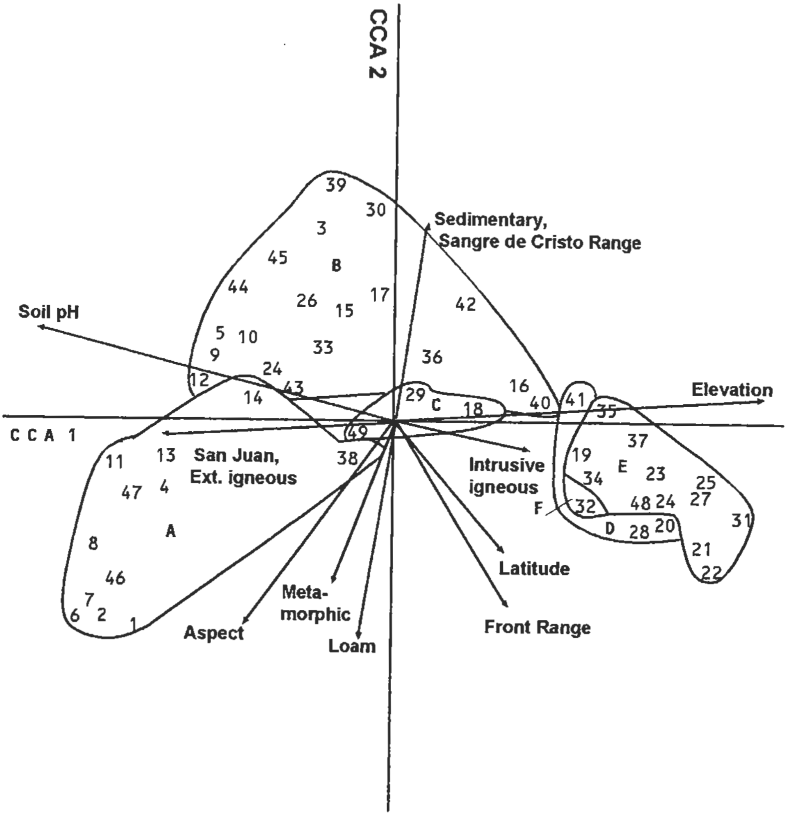


Fig. 2. Canonical correspondence analysis (CCA) ordination diagram. The most important environmental and geographic variables are illustrated by arrows. Letters represent plant associations identified in the classification: A = *Pinus aristata / Festuca arizonica*, B = *Pinus aristata / Festuca thurberi*, C = *Pinus aristata / Juniperus communis*, D = *Pinus aristata / Vaccinium myrtillus*, E = *Pinus aristata / Trifolium dasyphyllum*, F = *Pinus aristata / Ribes montigenum*. Numbers are plot numbers as illustrated in the study area map (Fig. 1).

on the first DCA and CCA axes include intrusive igneous parent material, location in the Front Range, longitude, latitude, plot age class, topographic position, and aspect (Table 3).

The second DCA axis scores are correlated with elevation and topographic position and weakly correlated with plot age, soil pH, and ratio of carbon to nitrogen (Table 3). The second CCA axis, however, had a moderate negative correlation with loamy soils, metamorphic parent material, aspect, and location in the Front Range, and a moderate positive correlation with sedimentary parent material and location in the Sangre de Cristos (Table 3).

As indicated by soil nitrogen and organic carbon and by foliar nitrogen, site fertility varied widely among bristlecone pine stands. For example, foliar nitrogen in 1-yr-old needles (an indicator of photosynthetic capacity) varied from 0.74% to 1.09%, and soil carbon-to-nitrogen ratio (an indicator of the availability of nitrogen for growth) varied from 10 to 33. Among sites, soil carbon-to-nitrogen ratio and foliar nitrogen were only weakly correlated (r = 0.41). Despite the wide variation in site fertility, soil and foliar nutrients were only weakly correlated with variation in plot composition.

Classification

The cluster analysis of the understory data suggested that the stands could be divided into 5 plant associations, 1 tentative plant association, and 3 outliers at the 20% similarity level. The 5 associations have distinct environmental settings, species composition, and species abundance. Group A, found in the lowest elevation *P. aristata* forests, is dominated by *Festuca arizonica*. *Festuca thurberi* dominates group B. Group C is characterized by an abundance of *Juniperus communis* and *Carex pityophila*

TABLE 3. Pearson's (DCA) and intraset (CCA) correlation coefficients of the first 2 axes with environmental and geographic variables. Coefficients ≥ 0.4 are in bold. Variables with all values <0.2 are not shown. Variables are listed in the order of their loadings.

	DCA		CCA	
Environmental variable	Axis 1	Axis 2	Axis 1	Axis 2
Elevation	**0.85**	**0.55**	**0.88**	0.07
Soil pH	**–0.72**	–0.33	**–0.75**	0.22
San Juan Range	**–0.46**	–0.15	**–0.47**	–0.00
Extrusive igneous	**–0.44**	–0.14	**–0.44**	–0.01
Intrusive igneous	0.39	0.21	**0.40**	–0.10
Longitude	–0.38	–0.12	–0.39	0.08
Latitude	0.36	0.12	0.37	–0.31
Topographic position	0.24	**0.47**	0.27	–0.27
Front Range	0.35	0.23	0.38	**–0.40**
Aspect	–0.27	0.04	–0.26	**–0.40**
Sedimentary	0.08	–0.10	0.07	**0.43**
Metamorphic	–0.12	–0.03	–0.11	**–0.41**
Loam	–0.08	–0.09	–0.08	**–0.43**
Sangre de Cristo Range	0.08	–0.10	0.07	**0.43**
Plot age class	0.29	0.38	0.31	–0.10
Soil carbon-to-nitrogen ratio	–0.05	–0.35	–0.08	–0.05
Percent rock cover	–0.04	0.28	–0.03	0.09
Mean rock size	0.15	0.22	0.16	0.07
Soil nitrogen	0.20	0.02	0.19	0.27
Foliar nitrogen	0.19	0.20	0.21	0.16
Soil organic carbon	0.16	–0.12	0.14	0.28
Foliar phosphorus	–0.04	–0.01	–0.04	–0.24

Mackenzie. *Vaccinium myrtilus* dominates group D, with *Juniperus communis* and *Carex foenea* Willd. present in all stands. The final group (E) is dominated by *Trifolium dasyphyllum.* A 6th plant association (F), dominated by *Ribes montigenum,* is tentatively identified based on plot 32 and previous research (DeVelice et al. 1986). A DCA ordination of the understory species data supports the 6 groups identified by cluster analysis (Fig. 3).

In addition, 2 phases were separated at a lower level of similarity. A *Ribes cereum* Dougl. phase (A1) of the *Pinus aristata / Festuca arizonica* association was identified, and a *Ribes cereum* phase (B1) can be separated from group B. Both phases, while sharing many common species with their respective associations, have a distinct set of species not common to the stands of the associations and occur in a slightly different environmental setting.

All associations are dominated by *P. aristata,* but the structure and composition of associated tree species vary (Fig. 4). A cluster analysis of the overstory data alone suggested that differences in overstory composition are insufficient to warrant splitting groups identified by clustering the understory data. The understory appears to be more sensitive than the overstory to environmental conditions.

Plant Associations

The environmental setting, tree species composition and structure, and understory species composition for each plant association and phase are described below. More detailed information for each association or phase is provided in the table of understory mean cover and constancy values (Table 4), and in the summary of tree species age-class data (Fig. 4). A complete list of species cover and constancy values, as well as summaries of the environmental variables determined to influence species composition, is given for each association and phase in Ranne (1995).

[A] *Pinus aristata / Festuca arizonica*

The overstory of this association, represented in 6 stands, is dominated by *P. aristata. Pinus flexilis* and *Populus tremuloides* Michx. are often present, and *Pinus ponderosa* P. & C. Lawson and *Pseudotsuga menziesii* (Mirbel) Franco are occasional associates. The shrub layer is sparse, with less than 10% cover. *Juniperus communis* is the most abundant shrub, with

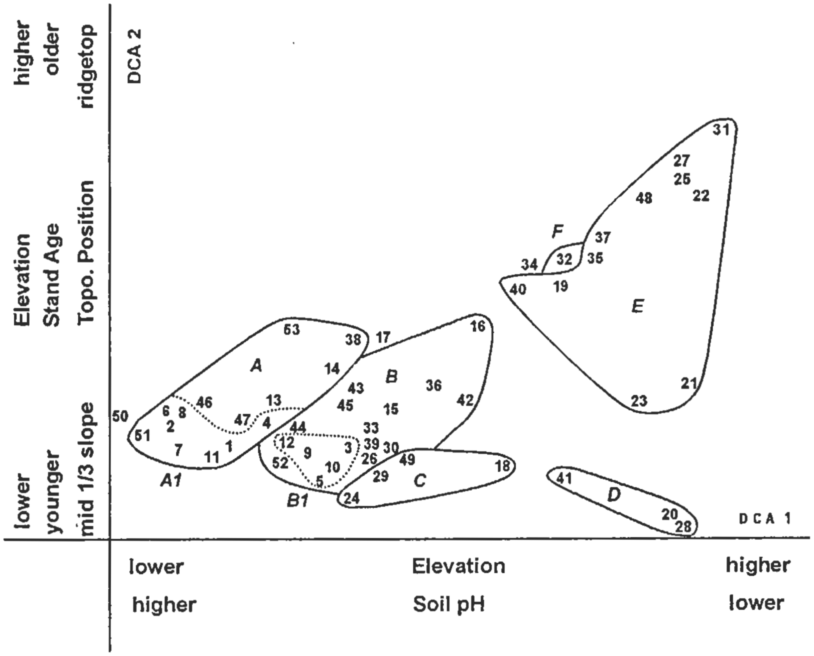


Fig. 3. Detrended correspondence analysis (DCA) ordination diagram. Environmental variables with the highest correlations with the axes are labeled along each axis. Letters represent plant associations identified in the classification: A = *Pinus aristata / Festuca arizonica*, B = *Pinus aristata / Festuca thurberi*, C = *Pinus aristata / Juniperus communis*, D = *Pinus aristata / Vaccinium myrtillus*, E = *Pinus aristata / Trifolium dasyphyllum*, F = *Pinus aristata / Ribes montigenum*. Dotted lines indicate phases: A1 = *Pinus aristata / Festuca arizonica : Ribes cereum* phase, B1 = *Pinus aristata / Festuca thurberi : Ribes cereum* phase. Numbers are plot numbers as illustrated in the study area map (Fig. 1).

Artemisia frigida Willd. and *Clematis columbiana* (Nutt.) Torr. & Gray occurring in small amounts. *Festuca arizonica* dominates the understory. Other common graminoids include *Koeleria macrantha* and *Carex foenea*. *Maianthemum stellatum* (L.) Link is the most common forb.

This association occurs in the lowest elevation *P. aristata* forests, between 2913 m and 3404 m. Stands were found in the Front, San Juan, Sangre de Cristo, and Mosquito ranges, on slopes ranging from 18% to 76%. A *Pinus aristata / Festuca arizonica* habitat type was described by Komarkova et al. (1988) in the San Juans and by DeVelice et al. (1986) in the Sangre de Cristos of New Mexico.

[A1] *Pinus aristata / Festuca arizonica : Ribes cereum* phase

The description of this phase is based on 8 stands. Composition of associated tree species is similar to that of group A. The understories of both the association and phase are dominated by *Festuca arizonica*. However, the phase is distinguished from association A by an abundance of *Ribes cereum*. Also distinctive is the abundance of *Carex pityophila*, high percent cover of *Muhlenbergia montana* (Nutt.) A.S. Hitchc. and *Koeleria macrantha*, and a set of forb species not present in association A. This phase occurs at similar elevations as the *Pinus aristata / Festuca arizonica* association, but on rockier slopes. It was identified in the Front, San Juan, and Mosquito ranges.

[B] *Pinus aristata / Festuca thurberi*

Pinus aristata is the dominant tree species. *Pinus flexilis*, when present, has a size-class structure similar to *Pinus aristata*, but it is much less abundant (Fig. 4). *Populus tremuloides* and/or *Picea engelmannii* Carr. is often present. The shrub layer is sparse, with *Juniperus communis* and *Rosa acicularis* Lindl. the most common species. The understory is dominated by *Festuca thurberi* in all 11 stands. *Koeleria macrantha*, *Carex foenea*, and *Achillea millefolium* DC. are usually present.

The elevation range for this association is between 3100 and 3600 m, usually above the *Pinus aristata / Festuca arizonica* association. The *P. aristata / Festuca thurberi* association

TABLE 4. Mean percent cover and constancy ( ) values for common (≥ 0.1% cover in at least 1 association) and constant (≥ 50% constancy in at least 1 association) species in the plant associations and phases, tr = <0.1%. A = *Pinus aristata / Festuca arizonica*, A1 = *Pinus aristata / Festuca arizonica : Ribes cereum* phase, B = *Pinus aristata / Festuca thurberi*, B1 = *Pinus aristata / Festuca thurberi : Ribes cereum* phase, C = *Pinus aristata / Juniperus communis*, D = *Pinus aristata / Vaccinium myrtilus*, E = *Pinus aristata / Trifolium dasyphyllum*, F = *Pinus aristata / Ribes montigenum*.

Association / Phase Number of Stands	A (6)	A1 (8)	B (11)	B1 (5)	C (4)	D (3)	E (12)	F (1)
SHRUBS								
Arctostaphylos uva-ursi (L.) Spreng.	.5 (33)	0 (0)	.5 (9)	2.4 (60)	1.8 (75)	.3 (13)	.2 (17)	0 (0)
Artemisia frigida Willd.	.7 (67)	1.7 (100)	.1 (18)	.2 (60)	0 (0)	0 (0)	0 (0)	0 (0)
Clematis columbiana (Nutt.) Torr. & Gray	.9 (67)	.1 (30)	tr (18)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Juniperus communis L.	1.7 (67)	2.3 (63)	3.6 (73)	6.4 (80)	9.0 (100)	6.0 (100)	.7 (45)	1.0 (100)
Pentaphylloides floribunda (Pursh) A. Love	.7 (67)	.4 (25)	.6 (27)	1.2 (60)	tr (25)	.3 (0)	.5 (43)	0 (0)
Ribes cereum Dougl.	0 (0)	7.4 (100)	.4 (27)	2.6 (100)	0 (0)	0 (0)	.4 (8)	0 (0)
Ribes montigenum McClatchie	.3 (17)	0 (0)	.2 (9)	0 (0)	tr (25)	.3 (33)	2.2 (57)	5.0 (100)
Rosa acicularis Lindl.	.7 (50)	.6 (50)	1.1 (67)	5.4 (60)	1.8 (75)	0 (0)	.3 (8)	0 (0)
Rubus idaeus L.	0 (0)	0 (0)	tr (9)	0 (0)	0 (0)	0 (0)	0 (0)	tr (100)
Vaccinium myrtillus L.	tr (17)	0 (0)	tr (9)	0 (0)	.8 (25)	25.0 (100)	1.0 (17)	0 (0)
GRASSES								
Bromus ciliatus L.	tr (33)	1.5 (25)	2.8 (73)	1.1 (80)	1.0 (25)	2.3 (33)	.5 (17)	0 (0)
Danthonia parryi Scribn.	1.0 (50)	tr (13)	.1 (9)	.4 (20)	0 (0)	0 (0)	0 (0)	0 (0)
Elymus elymoides (Raf.) Swezey	.2 (50)	tr (25)	tr (9)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Elymus trachycaulus ssp. *trachycaulus* (Link) Gould ex Shinners	0 (0)	tr (25)	.5 (36)	0 (0)	0 (0)	0 (0)	.2 (25)	0 (0)
Festuca arizonica Vasey	13.8 (100)	18.0 (100)	1.3 (18)	2.0 (67)	tr (25)	0 (0)	.3 (17)	tr (100)
Festuca ovina L.	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	3.0 (100)
Festuca thurberi Vasey	.7 (50)	tr (13)	13.1 (100)	18.0 (100)	0 (0)	2.7 (33)	.8 (25)	0 (0)
Koeleria macrantha (Ledeb.) J.A. Schultes	2.0 (83)	4.1 (88)	1.5 (73)	2.2 (80)	.5 (25)	0 (0)	.1 (25)	tr (100)
Muhlenbergia montana (Nutt.) A.S. Hitchc.	2.5 (50)	4.4 (75)	.4 (27)	2.6 (60)	0 (0)	0 (0)	0 (0)	0 (0)
Poa fendleriana (Steud.) Vasey	.1 (50)	1.5 (38)	.6 (18)	1.4 (80)	0 (0)	0 (0)	.4 (33)	0 (0)
Poa glauca ssp. *rupicola* (Nash ex Rydb.) W.A. Weber	0 (0)	.3 (13)	.2 (18)	0 (0)	0 (0)	0 (0)	.9 (50)	0 (0)
Poa interior Rydb.	.7 (33)	0 (0)	.4 (27)	0 (0)	0 (0)	0 (0)	.3 (17)	0 (0)
Poa leptocoma Trin.	0 (0)	0 (0)	.1 (18)	0 (0)	0 (0)	0 (0)	.7 (33)	2.0 (100)
Poa reflexa Vasey & Scribn. ex Vasey	.3 (17)	.3 (50)	.2 (27)	.6 (60)	1.0 (50)	0 (0)	.2 (17)	1.0 (100)
Trisetum spicatum (L.) Richter	.2 (17)	0 (0)	.7 (27)	.2 (20)	.5 (50)	.3 (33)	2.7 (83)	0 (0)

TABLE 4. Continued.

Association / Phase Number of Stands	A (6)	A1 (8)	B (11)	B1 (5)	C (4)	D (3)	E (12)	F (1)
SEDGES								
Carex foenea Willd.	2.8 (83)	.4 (13)	2.9 (73)	1.2 (40)	.3 (25)	5.3 (100)	8.8 (83)	0 (0)
Carex pityophila Mackenzie	tr (17)	2.9 (75)	.3 (9)	4.8 (100)	3.3 (100)	1.7 (33)	1.0 (33)	4.0 (100)
FORBS								
Achillea millefolium var. *occidentalis* DC.	.5 (67)	tr (25)	1.3 (91)	.6 (60)	tr (25)	1.7 (100)	1.3 (75)	0 (0)
Allium cernuum Roth	.4 (50)	tr (25)	.3 (27)	.2 (40)	0 (0)	0 (0)	0 (0)	tr (100)
Androsace septentrionalis L.	tr (17)	.2 (75)	tr (18)	tr (40)	0 (0)	0 (0)	tr (8)	0 (0)
Antennaria parvifolia Nutt.	.5 (75)	tr (38)	tr (18)	tr (40)	0 (0)	0 (0)	0 (0)	0 (0)
Antennaria rosea Greene	tr (17)	0 (0)	.7 (54)	tr (40)	0 (0)	.1 (100)	.6 (75)	0 (0)
Arabis drummondii Gray	.2 (17)	0 (0)	.1 (55)	.1 (60)	tr (25)	tr (33)	.1 (50)	0 (0)
Arabis fendleri (S. Wats.) Greene	.1 (50)	.2 (75)	0 (0)	.4 (60)	tr (25)	tr (33)	tr (8)	tr (100)
Arenaria fendleri Gray	.4 (50)	tr (25)	.4 (18)	0 (0)	0 (0)	.4 (13)	1.3 (83)	0 (0)
Artemisia ludoviciana Nutt.	.4 (33)	.7 (50)	tr (18)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Artemisia scopulorum Gray	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	.4 (50)	0 (0)
Campanula rotundifolia L.	tr (33)	.1 (25)	.8 (45)	1.0 (80)	.3 (25)	1.3 (67)	.5 (67)	0 (0)
Castilleja integra Gray	.2 (33)	tr (13)	.2 (18)	0 (0)	0 (0)	.4 (67)	.2 (42)	0 (0)
Descurainia incana ssp. *incana* (Bernh. ex Fisch. & C.A. Mey.) Dorn	0 (0)	tr (13)	0 (0)	.1 (60)	0 (0)	0 (0)	0 (0)	1.0 (100)
Draba aurea Vahl ex Hornem.	.1 (50)	.1 (25)	.1 (36)	.4 (80)	.1 (50)	0 (0)	.1 (50)	0 (0)
Epilobium angustifolium L.	tr (33)	0 (0)	.5 (36)	.4 (60)	tr (25)	.1 (67)	.4 (58)	0 (0)
Erigeron compositus Pursh	0 (0)	0 (0)	tr (9)	0 (0)	0 (0)	0 (0)	.3 (8)	2.0 (100)
Erigeron speciosus (Lindl.) DC.	.2 (17)	0 (0)	.3 (9)	1.2 (80)	0 (0)	0 (0)	0 (0)	0 (0)
Erigeron subtrinervis Rydb. ex Porter & Britt.	1.3 (50)	.4 (63)	1.4 (45)	tr (40)	tr (25)	0 (0)	.1 (8)	0 (0)
Fragaria vesca L.	0 (0)	tr (13)	tr (9)	.4 (60)	.3 (8)	0 (0)	.1 (8)	0 (0)
Frasera speciosa Dougl. ex Griseb	.2 (17)	0 (0)	0 (0)	0 (0)	.3 (50)	tr (33)	tr (8)	0 (0)
Geranium viscosissimum Fisch. & C.A. Mey. ex C.A. Mey.	0 (0)	.9 (63)	.2 (18)	0 (0)	tr (25)	0 (0)	0 (0)	0 (0)
Geum rossii var. *turbinatum* (Rydb.) C.L. Hitchc.	0 (0)	0 (0)	.1 (18)	0 (0)	0 (0)	.3 (33)	1.3 (58)	0 (0)

TABLE 4. Continued.

Association / Phase Number of Stands	A (6)	A1 (8)	B (11)	B1 (5)	C (4)	D (3)	E (12)	F (1)
FORBS (continued)								
Heterotheca villosa (Pursh) Shinners	.3 (17)	tr (13)	.6 (27)	0 (0)	.1 (50)	tr (33)	.5 (50)	0 (0)
Heuchera bracteata (Torr.) Ser.	0 (0)	.1 (13)	.1 (18)	0 (0)	.1 (50)	tr (33)	.1 (50)	0 (0)
Maianthemum stellatum (L.) Link	.7 (83)	.3 (25)	.6 (54)	1.4 (100)	.5 (25)	0 (0)	0 (0)	0 (0)
Mertensia lanceolata (Pursh) DC.	0 (0)	.5 (75)	.2 (27)	.4 (60)	0 (0)	0 (0)	.4 (50)	0 (0)
Minuartia obtusiloba (Rydb.) House	.2 (17)	0 (0)	.5 (27)	0 (0)	.3 (25)	0 (0)	1.0 (83)	2.0 (100)
Penstemon whippleanus Gray	0 (0)	0 (0)	.1 (27)	0 (0)	5 (50)	.4 (100)	.4 (67)	0 (0)
Polemonium pulcherrimum ssp. *delicatum* (Rydb.) Brand	tr (17)	0 (0)	tr (9)	0 (0)	0 (0)	.1 (67)	.6 (58)	0 (0)
Potentilla fissa Nutt.	.7 (33)	.6 (25)	.3 (36)	0 (0)	.1 (50)	0 (0)	0 (0)	0 (0)
Potentilla pensylvanica L.	0 (0)	0 (0)	0 (0)	tr (20)	0 (0)	0 (0)	0 (0)	tr (100)
Potentilla rubricaulis Lehm.	.7 (33)	.1 (25)	.1 (9)	.6 (60)	0 (0)	0 (0)	.2 (25)	0 (0)
Pseudocymopterus montanus (Gray) Coult. & Rose	.1 (50)	tr (13)	.7 (54)	.7 (80)	tr (25)	0 (0)	0 (0)	0 (0)
Sedum stenopetalum Pursh	.7 (50)	.4 (38)	.1 (36)	.2 (20)	.1 (50)	.1 (67)	.7 (92)	0 (0)
Senecio fendleri Gray	.5 (50)	.2 (8)	.7 (45)	.6 (60)	.8 (50)	.7 (33)	.5 (33)	2.0 (100)
Senecio pudicus Greene	tr (17)	tr (13)	tr (9)	.8 (60)	0 (0)	0 (0)	0 (0)	0 (0)
Solidago simplex ssp. *simplex* var. *nana* (Gray) Ringius	.7 (50)	0 (0)	.6 (36)	0 (0)	.3 (25)	2.0 (100)	1.0 (75)	0 (0)
Thermopsis rhombifolia var. *divaricarpa* (A. Nels.) Isely	.5 (33)	0 (0)	2.7 (60)	tr (20)	0 (0)	0 (0)	0 (0)	0 (0)
Trifolium dasyphyllum Torr. & Gray	.5 (17)	0 (0)	1.4 (40)	0 (0)	1.5 (25)	6.3 (100)	10.1 (100)	0 (0)
Woodsia oregana D.C. Eat.	tr (33)	tr (13)	tr (20)	.1 (60)	0 (0)	tr (33)	0 (0)	0 (0)
Zigadenus elegans Pursh	0 (0)	0 (0)	.1 (60)	0 (0)	tr (25)	tr (33)	tr (8)	0 (0)

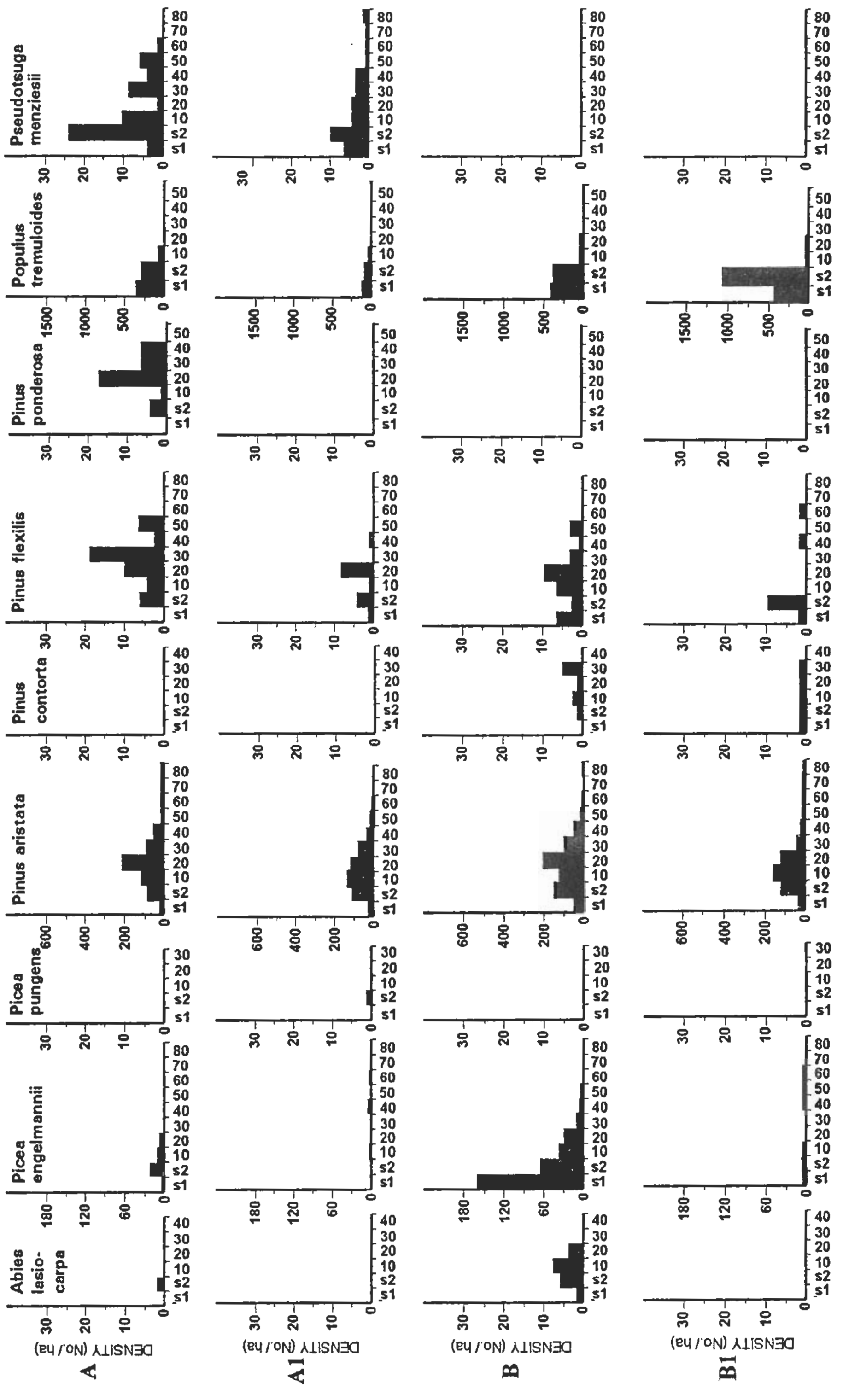
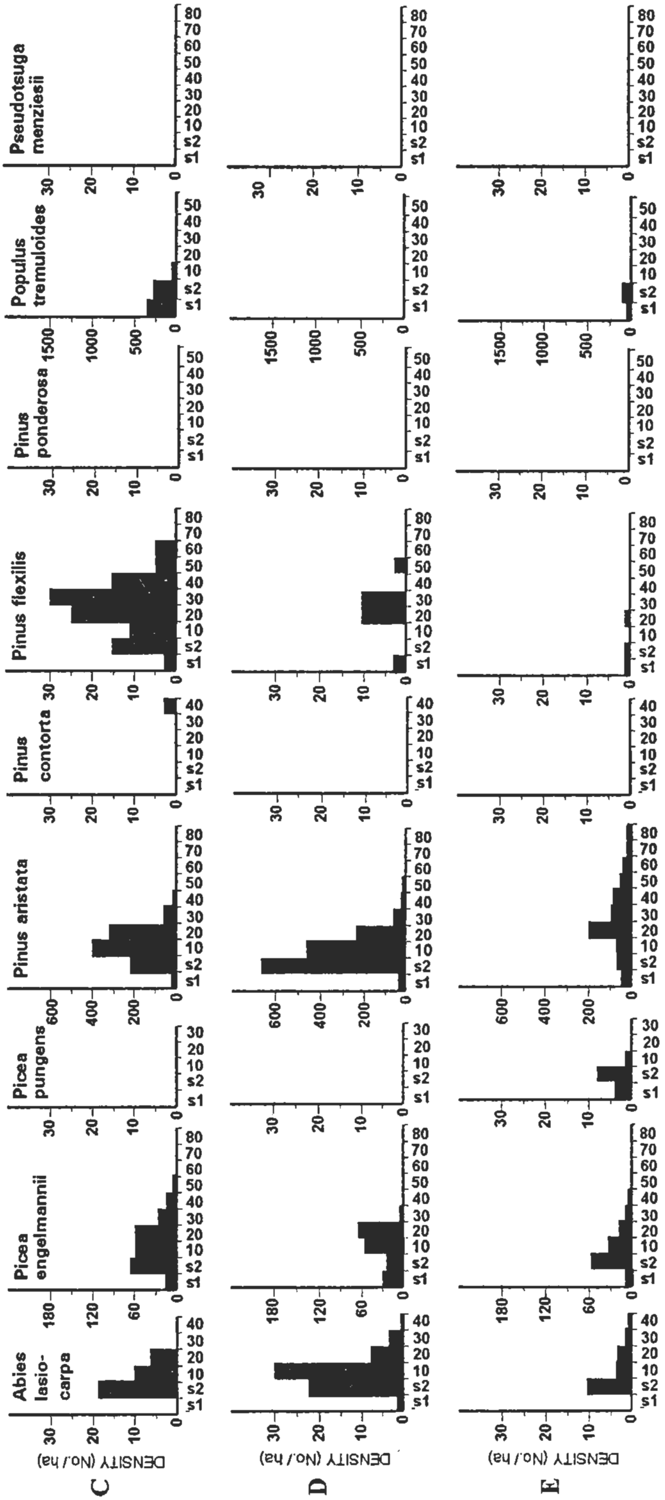


Fig. 4. Mean overstory stem density (number of stems per ha) by species, within plant associations and phases. Note that the vertical axes vary with the species. **A** = *Pinus aristata / Festuca arizonica*, **A1** = *Pinus aristata / Festuca arizonica : Ribes cereum* phase, **B** = *Pinus aristata / Festuca thurberi*, **B1** = *Pinus aristata / Festuca thurberi : Ribes cereum* phase,



C = *Pinus aristata / Juniperus communis*, D = *Pinus aristata / Vaccinium myrtillus*, E = *Pinus aristata / Trifolium dasyphyllum*, F = *Pinus aristata / Ribes montigenum*. Horizontal axes are tree size classes: s1 = seedlings and small saplings (stems <1 m tall), s2 = large saplings (stems >1 m tall, with a dbh <2.5 cm, remaining tree size classes are in 10-cm-wide increments (e.g., "10" means 10–20 cm) based on dbh.

was found in the Front Range, San Juans, and Sangre de Cristos. Komarkova et al. (1988) described a *Pinus aristata / Festuca thurberi* habitat type with similar species composition and environmental settings from 1 stand in the San Juans. DeVelice et al. (1986) also recognized a *Pinus aristata / Festuca thurberi* habitat type in the Sangre de Cristos and the San Juans.

[B1] *Pinus aristata / Festuca thurberi : Ribes cereum* phase

Overstory species composition is similar to group B. The shrub cover of this phase is much greater than in the previous association, with *Ribes cereum* present in all stands. *Juniperus communis* is usually present. *Festuca thurberi* dominates the understory, with *Bromus ciliatus* L., *Poa fendleriana,* and *Koeleria macrantha* occurring in most stands. *Carex pityophila* is present in all 5 stands. *Campanula rotundifolia* L., *Draba aurea* Vahl. ex Hornem., *Erigeron speciosus* (Lindl.) DC., and *Pseudocymopterus montanus* (Gray) Coult. & Rose are common forbs. This phase occurs at lower elevations than association B, between 2900 and 3100 m. It was found in the Front, San Juan, and Mosquito ranges.

[C] *Pinus aristata / Juniperus communis*

Pinus aristata dominates the overstory, and *Picea engelmannii* is an overstory associate. *Pinus flexilis* occurs in all but 1 stand. *Juniperus communis* has high cover values in all stands, and *Arctostaphylos uva-ursi* (L.) Spreng. and *Rosa acicularis* are often present. *Carex pityophila* is the only common, and the most abundant, graminoid. Grasses and herbaceous plants are sparse. This association was found only on intrusive igneous parent material (in the Front and Mosquito ranges) at elevations between 3233 and 3312 m. Komarkova et al. (1988) described a similar habitat type from a stand in the San Juans. Until now, this association was not described elsewhere in Colorado.

[D] *Pinus aristata / Vaccinium myrtilus*

Abies lasiocarpa (Hook.) Nutt., *Picea engelmannii,* and *Pinus flexilis* are associated tree species. *Vaccinum myrtilus* dominates the shrub layer in all 3 stands, and *Juniperus communis* is always present. *Carex foenea* is the only abundant and common graminoid. *Achillea millifollium, Antennaria rosea* Greene, *Penstemon whippleanus* Gray, *Solidago simplex* (Gray) Ringius, and *Trifolium dasyphyllum* occur in every stand. This association always occurs on the upper 1/3 of the slope, at elevations between 3343 and 3526 m, often near treeline. Stands of this association are underlain by intrusive igneous parent material and were found in both the Front and Sangre de Cristo ranges. Soil pH values (<5.1) are the lowest for any *P. aristata* association. This association has not been previously described.

[E] *Pinus aristata / Trifolium dasyphyllum*

Picea engelmannii is often present in the 12 stands of this association. The shrub layer is sparse, with the most common shrub, *Ribes montigenum,* occurring in only 57% of the stands. *Carex foenea* is the most prevalent and abundant graminoid. The understory is dominated by *Trifolium dasyphyllum. Sedum stenopetalum* Pursh and *Mertensia lanceolata* (Pursh) DC. are common forbs. This association occurs on the border of forest and alpine vegetation or on the ridgetops of lower peaks. Elevation range is between 3233 and 3633 m. It was located in the Front, Sawatch, Mosquito, and Sangre de Cristo ranges. A *Pinus aristata / Trifolium dasyphyllum* habitat type was reported by Hess and Alexander (1986) in the Front Range.

[F] *Pinus aristata / Ribes montigenum*

This plant association is tentatively described based on 1 stand (plot 32). The understory is dominated by *Ribes montigenum. Festuca ovina* L. and *Carex pityophila* are the most abundant graminoids. Abundant forbs include *Senecio fendleri* Gray, *Minuartia obtusiloba* (Rydb.) House, and *Erigeron compositus* Pursh. This association was found at an elevation of 3367 m on a scree slope. DeVelice et al. (1986) identified this habitat type also based on a single stand on a scree slope in the San Juans, but 5 of the most important species in the DeVelice et al. (1986) stand are missing from plot 32. Moreover, our single stand has many species in common with our *Pinus aristata / Trifolium dasyphyllum* association. Because of these discrepancies and the small number of known *Ribes montigenum*–dominated stands, this association is tentative.

DISCUSSION

Gradient Analysis

Elevation, which is a composite of environmental factors, was identified by both indirect and direct gradient analysis to be the most important variable influencing species composition. This is not surprising, as elevation has frequently been identified as the dominant variable influencing mountain vegetation (Ramaley 1907, Daubenmire 1943, Weber 1965, Whittaker 1967, Peet 1981, 1988, Allen and Peet 1990, Allen et al. 1991). With increasing elevation temperature decreases, and precipitation, snow depth, wind, and solar radiation increase (Peet 1988, Barry 1992). Allen and Peet (1990) found that increasing elevation was associated with decreasing pH, a relationship also identified in this study.

Soil pH values in *P. aristata* forests in this study (4.47–6.85) are slightly more acidic than previously reported pH values (5.6–7.7; Hess and Alexander 1986, Komarkova et al. 1988). Soil pH decreased with elevation, perhaps because high-elevation *P. aristata* forests are often underlain by granite, a parent material low in basic cations. Soil pH appears to directly influence community composition. For example, the 3 stands in the *Pinus aristata / Vaccinium myrtilus* association have low pH (<5.1); plants of the Ericaceae family, such as *Vaccinium myrtilus,* appear to grow better in highly acidic soils (Rendig and Taylor 1989).

Variation in geographic location and geologic substrate also influences composition in *P. aristata* forests. Geographic location involves a complex array of environmental factors, such as climate and isolation. Because geology varies with mountain ranges, these 2 variables are related. For example, the *P. aristata* stands in the Front Range grow primarily on intrusive igneous rock, while stands in the San Juans are found mainly on extrusive igneous rock. The type of parent material influences the chemistry and texture of the soil (Birkland 1984). Soils on extrusive igneous or sedimentary parent materials were, in general, finer textured than soils on intrusive igneous or metamorphic parent materials. Soils underlain by granite often had lower percent nitrogen and percent organic carbon than soils on other substrata. However, the relationship between parent material and nutrients was less distinct than the relationship between parent material and texture. The vegetation and distribution of Great Basin bristlecone pine (*Pinus longaeva*) forests in the White Mountains of California are also influenced by substrate (Mooney et al. 1962). *Pinus longaeva* are found at higher elevations on dolomite rather than on granite or sandstone, and granite supports a greater density of understory vegetation in these forests than does either dolomite or sandstone (Mooney et al 1962). Despain (1973) found that major forest vegetation types in the Big Horn Mountains are found on different geologic substrata.

Nutrient levels in the soils of *P. aristata* forests have not been studied prior to this research. Interestingly, we could not show soil fertility effects on plant species composition in *P. aristata* forests, even though many studies document the effect of fertility on productivity in forests in general.

Soil texture, which influences moisture availability, explained a moderate portion of the variation in community composition on CCA axis 2. More water is held in a form available to plants in finer soils than in coarser soils, but fine soils need more water to bring the water potential up to the range of availability of plants (Despain 1973). After a thunderstorm, coarse soils may therefore have more water available to plants (Despain 1973). Mooney et al. (1962) found that *Pinus longaeva* forests in the White Mountains vary along a soil moisture gradient related to substrate. The primary distinction in the *P. aristata* ordination is between loams and sandy loams. The finer, low-elevation loams may have less available water than the coarser, high-elevation soils.

The influence of aspect and topographic position on the ordination axes also suggests that soil moisture may be a factor influencing community composition. Calculations of soil moisture often incorporate indices of topographic position, potential solar radiation, and exposure (Birkland 1984, Allen and Peet 1990, Allen et al. 1991). Allen and Peet (1990) found that site moisture status was a major environmental factor controlling species composition in the Sangre de Cristos. Gradient analysis of 3 sites in the southern Rocky Mountains also revealed that soil moisture was related to a major compositional gradient (Allen et al. 1991).

Although not as influential as geographical location and substrate, variation in latitude and longitude did explain a small amount of the variation in plant community composition. Plots spanned a latitudinal range of approximately 3 degrees and a longitudinal range of approximately 2 degrees. Increases in latitude are associated with important climatic changes, such as larger annual temperature ranges

(Scott 1989). Peet (1978) found that composition of vegetation types changes with latitude in the southern Rocky Mountains. Yet, Allen et al. (1991) found that high-elevation *Picea engelmannii / Abies lasiocarpa* forests in the Rocky Mountains remained floristically similar over a smaller latitudinal range of 4 degrees. However, his plots were located at similar degrees of longitude in the easternmost ranges (Front and Sangre de Cristo) of the southern Rocky Mountains. Climatic differences between the eastern and western *P. aristata* stands may explain some of the variation. For example, maps of average annual precipitation indicate that some *P. aristata* stands near Pikes Peak may receive as little as 41 cm of precipitation per year, while other stands further west in the Sawatch and San Juan ranges receive between 102 and 152 cm (Krebs 1972, Brunstein and Yamaguchi 1992).

Classification

Prior to this research, knowledge of the distribution and composition of these associations was limited, due to small sample sizes and limited geographical sampling. A habitat type similar to the *Pinus aristata / Trifolium dasyphyllum* plant association had been recorded previously only in the Front Range (DeVelice et al. 1986). In this study we located this plant association in the Front, Sawatch, Mosquito, and Sangre de Cristo ranges. Similarly, Komarkova et al. (1988) described a *Pinus aristata / Juniperus communis* habitat from a single stand in the San Juans. Stands with the *Pinus aristata / Juniperus communis* plant association were described in this study in the Front and Mosquito ranges. Habitat types similar to the *Pinus aristata / Festuca arizonica* and *Pinus aristata / Festuca thurberi* plant associations had been described only in the San Juans and Sangre de Cristos (DeVelice et al. 1986, Komarkova et al. 1988). However, both were additionally located in the Front Range, and the *Pinus aristata / Festuca arizonica* association was also found in the Mosquito Range.

Previous researchers did not identify the phases of the *Pinus aristata / Festuca arizonica* and *Pinus aristata / Festuca thurberi* plant associations. It is important that these phases be recognized because of the differences between the shrub layers of the phases and their related plant associations. *Ribes cereum* is a dominant plant in the phases but is absent from the main plant associations. Differences in environmental settings and species composition between the phases and associations further illustrate the need to recognize these variations within the plant associations.

Of the 4 plots from New Mexico (DeVelice et al. 1986), 2 were included in the *Pinus aristata / Festuca arizonica* plant association, and 1 was included in the *Pinus aristata / Festuca thurberi* association. *Pinus aristata* stands in New Mexico are, in general, floristically similar to those in Colorado. However, an outlier, plot 50, may be representative of an association unique to New Mexico. Because only 4 plots from New Mexico were included in this analysis, a more thorough study of *P. aristata* stands in New Mexico is needed.

Classification provides a means of dividing the natural continuum of vegetation into distinct units useful for research, management, and conservation. The 6 plant associations identified in this study can be used as the foundation for selecting future Research Natural Area (RNA) sites. To insure that the range of natural variability of *P. aristata* forests is represented in the RNA system, sites should be selected to represent each plant association.

LITERATURE CITED

ALEXANDER, R. R. 1987. Classification of the forest vegetation of Colorado by habitat type and community type. USDA Forest Service Research Note RM-478. Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO.

ALLEN, R. B., AND R. K. PEET. 1990. Gradient analysis of forests of the Sangre de Cristo Range, Colorado. Canadian Journal of Botany 68: 193–201.

ALLEN, R. B., R. K. PEET, AND W. L. BAKER. 1991. Gradient analysis of latitudinal variation in southern Rocky Mountain forests. Journal of Biogeography 18: 123–129.

ANONYMOUS. 1992a. Total Kjeldahl nitrogen in soil/plant. Lachat Instruments, Milwaukee, WI. 12 pp.

ANONYMOUS. 1992b. Total phosphorus in Kjeldahl digests. Lachat Instruments, Milwaukee, WI. 10 pp.

BAKER, W. L. 1984. A preliminary classification of the natural vegetation of Colorado. Great Basin Naturalist 44: 647–676.

______. 1991. Livestock grazing alters succession after fire in a Colorado subalpine forest. Pages 84–90 *in* S. C. Nodvin and T. A. Waldrop, editors, Fire and environment: ecological perspectives. Proceedings of an international symposium. USDA Forest Service General Technical Report SE-69. Southeastern Forest Experiment Station, Asheville, NC.

______. 1992. Structure, disturbance, and change in the bristlecone pine forests of Colorado. Arctic and Alpine Research 24: 17–26.

______. 1995. Multiple stable states and models of riparian vegetation succession on the Animas River, Colorado. Annals of the Association of American Geographers 85: 320–338.

BARRY, R. G. 1973. A climatological transect on the east slope of the Front Range, Colorado. Arctic and Alpine Research 5: 89–113.

______. 1992. Mountain weather and climate. Routledge, London. 402 pp.

BIRKLAND, P. W. 1984. Soils and geomorphology. Oxford University Press, Inc., New York. 372 pp.

BRUNSTEIN, F. C., AND D. K. YAMAGUCHI. 1992. The oldest known Rocky Mountain bristlecone pines (*Pinus aristata* Engelm.). Arctic and Alpine Research 24: 253–256.

COOK, J. E. 1996. Implications of modern successional theory for habitat typing: a review. Forest Science 42: 67–75.

DAUBENMIRE, R. L. 1943. Vegetation zonation in the Rocky Mountains. Botanical Review 9: 325–393.

DESPAIN, D. G. 1973. Vegetation of the Big Horn Mountains, Wyoming, in relation to substrate and climate. Ecological Monograph 45: 329–355.

DEVELICE, R. L., J. A. LUDWIG, W. H. MOIR, AND F. RONCO, JR. 1986. Classification of forest habitat types of northern New Mexico and southern Colorado. USDA Forest Service General Technical Report RM-131. Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO. 59 pp.

FERGUSON, C. W. 1968. Bristlecone pine: science and esthetics. Science 159: 839–846.

HESS, K., AND R. R. ALEXANDER. 1986. Forest vegetation of the Arapaho and Roosevelt national forests in central Colorado: a habitat type classification. USDA Forest Service Research Paper RM-266. Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO. 48 pp.

KOMARKOVA, V., R. R. ALEXANDER, AND B. C. JOHNSTON. 1988. Forest vegetation of the Gunnison and parts of the Uncompahgre national forests: a preliminary habitat type classification. USDA Forest Service General Technical Report RM-163. Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO. 65 pp.

KREBS, P. V. H. 1972. Dendrochronology and distribution of bristlecone pine (*Pinus aristata* Engelm.) in Colorado. Unpublished doctoral dissertation, University of Colorado, Boulder. 211 pp.

LAMARCHE, V. C., JR., AND C. W. STOCKTON. 1974. Chronologies from temperature-sensitive bristlecone pines at upper treeline in western United States. Tree-Ring Bulletin 34: 21–45.

MARIJA, M. J. 1988. SPSS/PC+ Advanced Statistics V2.0. SPSS, Inc., Chicago. 224 pp.

MOONEY, H. A., G. ST. ANDRE, AND R. D. WRIGHT. 1962. Alpine and subalpine vegetation patterns in the White Mountains of California. American Midland Naturalist 68: 257–273.

PALMER, M. W. 1993. Putting things in even better order: the advantages of canonical correspondence analysis. Ecology 74: 2215–2230.

PEET, R. K. 1978. Latitudinal variation in southern Rocky Mountain forests. Journal of Biogeography 5: 275–289.

______. 1981. Forest vegetation of the Rocky Mountains. Vegetatio 45: 3–75.

______. 1988. Forests of the Rocky Mountains. Pages 63–101 *in* M. G. Barbour and W. D. Billings, editors, North American terrestrial vegetation. Cambridge University Press, New York. 434 pp.

PFISTER, R. D., AND S. F. ARNO. 1980. Classifying forest habitat types based on potential climax vegetation. Forest Science 26: 52–70.

RAMALEY, F. 1907. Plant zones in the Rocky Mountains of Colorado. Science 26: 642–643.

RANNE, B. M. 1995. Natural variability of vegetation, soils, and physiography in the bristlecone pine forests of the Rocky Mountains. Unpublished master's thesis, University of Wyoming, Laramie. 68 pp.

RENDIG, V. V., AND H. M. TAYLOR. 1989. Principles of soil-plant interrelationships. McGraw-Hill, New York. 275 pp.

SCOTT, G. R., R. B. TAYLOR, R. C. EPIS, AND R. A. WOBUS. 1984. Geologic map of the Pueblo Quadrangle, south-central Colorado. U.S. Geological Survey Miscellaneous Investigations Series Map I-1022. Washington, DC.

SCOTT, R. C. 1989. Physical geography. West Publishing Company, St. Paul, MN. 541 pp.

SOCIETY OF AMERICAN FORESTERS TASK FORCE. 1993. Task force report on sustaining long-term forest health and productivity. Society of American Foresters, Bethesda, MD. 83 pp.

SWANSON, F. J., J. A. JONES, D. O. WALLIN, AND J. H. CISSEL. 1994. Natural variability—implications for ecosystem management. Pages 80–94 *in* M. E. Jensen and P. S. Bourgeron, editors, Eastside forest ecosystem health assessment. Volume II: Ecosystem management principles and applications. USDA Forest Service General Technical Report PNW-GTR-318. Pacific Northwest Research Station, Portland, OR.

TER BRAAK, C. J. F. 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. Ecology 67: 1167–1179.

______. 1988. CANOCO—a Fortran program for canonical community ordination by [partial] [detrended] [canonical] correspondence analysis. Technical report LWA-88-02. Agricultural Mathematics Group, Wageningen, The Netherlands; Microcomputer Power, Ithaca, NY.

TWETO, O., COMPILER. 1979. Geologic map of Colorado. U.S. Geological Survey, Denver, CO.

TWETO, O., R. H. MOENCH, AND J. C. REED, JR. 1978. Geologic map of the Leadville Quadrangle, northwestern Colorado. U.S. Geological Survey Miscellaneous Investigations Series Map I-999. Washington, DC.

USDA NATURAL RESOURCE CONSERVATION SERVICE. 1995. PLANTS database. U.S. Department of Agriculture, Natural Resource Conservation Service, Washington DC.

WALFORD, G. M., AND W. L. BAKER. 1995. Classification of the riparian vegetation along a 6-km reach of the Animas River, southwestern Colorado. Great Basin Naturalist 55: 287–303.

WEBER, W. A. 1965. Plant geography in the southern Rocky Mountains. Pages 453–468 *in* H. E. Wright and D. G. Frey, editors, The Quaternary of the United States. Princeton University Press, Princeton, NJ.

WHITTAKER, R. H. 1967. Gradient analysis of vegetation. Biological Review 42: 207–264.

Received 3 May 1996
Accepted 18 December 1996